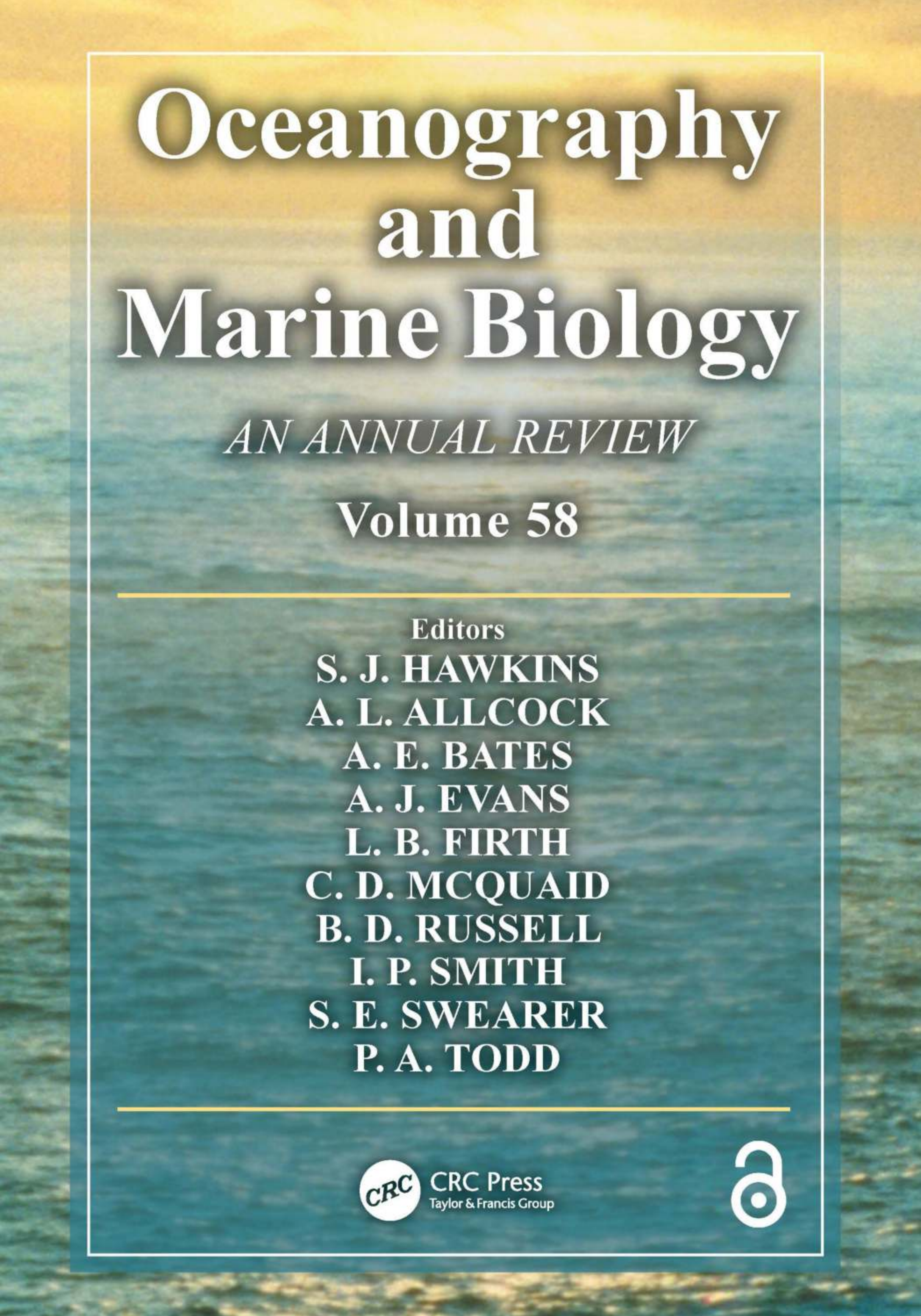

Oceanography and Marine Biology

AN ANNUAL REVIEW

Volume 58

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An Annual Review

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Preface

Oceanography and Marine Biology: *An Annual Review* remains one of the most cited sources in marine sciences. The ever-increasing interest in oceanography and marine biology and its relevance to global environmental issues, especially climate change and its interaction with regional and local scale impacts, creates a demand for authoritative peer-refereed reviews summarizing and synthesizing the results of recent research. This volume covers topics that include the effects of microplastics on zooplankton, the biology and biogeography of non-indigenous species, ecosystem functioning and services, novel ecosystems, tidal energy across a range of environments and scales, and the design of ecosystem-level observatories. For nearly 60 years, OMBAR has been an essential reference for research workers and students in all fields of marine science. Volume 58 ensures global relevance with an international Editorial Board from Australia, Canada, Hong Kong, Ireland, South Africa, Singapore and the UK. The series finds a place in the libraries of not only marine laboratories and institutes, but also universities. The editors thank the hard work of the referees in improving these reviews. We also wish to acknowledge the help and support of the team at Taylor & Francis (Alice Oven, Damanpreet Kaur and Marsha Hecht) and Nova Techset (Victoria Balque-Burns). In particular we wish to thank Kathryn Pack of the Marine Biological Association and University of Southampton for her much valued work as an Editorial Associate in seeing this volume to press.

Prof Stephen J. Hawkins
(Editor in Chief) on behalf of the Editorial Board.

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THE BIOLOGY OF *AUSTROMINIUS MODESTUS* (DARWIN) IN ITS NATIVE AND INVASIVE RANGE

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Abstract *Austrominius modestus,* formerly *Elminius modestus*, is a relatively small species of four-plated acorn barnacle, which is native to the subtropical and temperate zones of Australasia. It was introduced into Europe in the 1940s, where its current range includes England, Scotland, Wales, Ireland and continental Europe from Denmark to southern Portugal, as well as two reported locations in the Mediterranean Sea. This species occurs intertidally and subtidally on a very wide range of substrata in both its native and introduced range and is found on sheltered to intermediate exposed shores, but is absent from wave-exposed shores, probably due to the relative fragility of its shell. *A. modestus* is known to be both euryhaline and eurythermal, but its physiology (and that of other cirripedes) has been relatively little studied in comparison with other invertebrate species. Cold temperatures and competition from arctic-boreal barnacle species currently control its northern limit. At the southern limit, desiccation stress, or some other stress(es), may be limiting the abundance of *Austrominius modestus* by affecting cyprids and/or metamorphs at the settlement and recruitment stages. Abundance may also be limited by factors occurring at the reproductive stage. Since *Austrominius modestus* is an obligatory cross-fertiliser, the need for a critical breeding density is one of the factors that appears to have slowed the speed of its spread in Europe. Although this species can commence reproducing at a very young age and under optimal conditions produces multiple broods per year, its fecundity has not yet been studied. An examination of the age of first brooding, the timing and size and number of broods per year at sites at the northern (Scotland) and southern (Portugal) limits of the current invasive range of *Austrominius modestus* may provide a better understanding of the factors controlling its geographic distribution, abundance and speed of spread in its non-native range. For instance, warming waters could result in increased reproduction and recruitment of *Austrominius modestus*, leading to a reduced density of the native *Semibalanus balanoides* Linnaeus which may drive *Semibalanus balanoides* to extinction in certain parts of its range. Further research is necessary to determine the functional role of *Austrominius modestus* in relation to native species in order to understand the implications that changes in abundance and distribution of *A. modestus* may have for ecosystems.

Introduction

Austrominius modestus (Darwin 1854), formerly *Elminius modestus* Darwin (1854), is a species of barnacle, native to the subtropical and temperate zones of Australasia, that was introduced into Europe in the 1940s. While the spread of this species in its invasive range is well documented (e.g. Barnes & Barnes 1965b and subsequently), there has been little research regarding the ecology of this species. Research on the ecology of *Austrominius modestus* is timely because it may be an 'ecological sleeper' (Witte et al. 2010), with the potential for further increases in abundance accompanying predicted climate change, especially warmer air and seawater temperatures. A detailed understanding of the biology and ecology of *Austrominius modestus*, both in its native and introduced range, is necessary if we are to understand the causative factors controlling abundance changes in this species in the future and what implications these changes may have for ecosystems. Here we review what is known about the biology of *Austrominius modestus* in its native and invasive range and suggest key areas for future research. Each section of the review begins with a summary of the key findings before then describing them in detail.

Systematics

Subclass	Cirripedia Burmeister (1834)
Superorder	Thoracica Darwin (1854)
Order	Sessilia Lamarck (1818)
Superfamily	Tetraclitoidea Gruvel (1903)
Family	Austrobalanidae Newman & Ross (1976)
Subfamily	Elminiinae Foster (1982) (*nom correctum*, Buckeridge 1983)

Austrominius modestus (Darwin 1854).

Please see Buckeridge & Newman (2010) (Table 2 therein) for details of synonyms.

Description: Four symmetric wall plates usually tinged with slaty grey lines; plates thin but often with rounded ridges, giving the shell a sinuously octoradiate outline; basis membranous; tergo-scutal flaps of live specimens held flat, basically white, with brown marks at the pylorus and two blackish bands in the rostral half (Southward 2008) (see Plate 1).

Remarks: In young and uneroded specimens, each scutum carries a slaty grey line (Southward 2008). It is a small conical barnacle, measuring up to 10 mm in rostro-carinal diameter (RCD) when

Plate 1 Adult *Austrominius modestus* photographed at the new slipway in Bantry Harbour, south-west Ireland, by M.C. Gallagher.

fully grown, but specimens measuring up to 17 mm have been found under certain habitat conditions (Bishop 1954). *Austrominius modestus* does not possess pectinate setae on intermediate segments of cirrus III; the lack of this feeding development distinguishes it from other species of *Austrominius* (Buckeridge & Newman, 2010).

Knight-Jones & Waugh (1949) noted that Darwin (1854) suggested a close affinity between *Elminius*, *Tetraclita* and *Balanus*. *Elminius* is only distinguished from *Tetraclita* by the four compartments not being porose and by the basis being always membranous. Darwin considered *Tetraclita* closely allied to *Balanus* and could observe no difference in the animal's body, nor any constant difference in the opercular valves. According to Knight-Jones & Waugh (1949), the larval development of *Austrominius* confirmed that it was closely related to *Balanus*. However, when Pérez-Losada et al. (2014) undertook an extensive phylogenetic analysis of the familial relationships within the Balanomorpha, they found that neither *Austrominius modestus* nor *Elminius covertus* (*Austrominius covertus*) or *Elminius kingii* are closely related to *Balanus* species or *Semibalanus balanoides*.

There are five genera in the subfamily Elminiinae.

With four plates:

Austrominius Buckeridge (1983)	6 species
Elminius Leach (1825)	1 species
Matellionius Buckeridge (1983)	1 species
Protelminius Buckeridge & Newman (2010)	1 species

With six plates:

Hexaminius Foster (1982)	2 species

Distribution and zonation

Geographic distribution

Native range

Austrominius modestus is native to the subtropical and temperate zones of Australasia (see Figure 1), where it occurs in southern Australia and New Zealand (Buckeridge & Newman 2010). However, Flowerdew (1984), Foster (1982) and Foster & Anderson (1986) suggested the possibility that *Austrominius modestus* may have been introduced to southern Australian ports from New Zealand by shipping, pre-1836, when Darwin recorded it on oysters in Sydney Harbour (Darwin 1854). However, *Austrominius modestus* is not listed by Jones (2012) as one of the 16 barnacle species introduced into Australia. Moore (1944) and Foster (1978) showed maps of its distribution around New Zealand, relative to three and six other species of acorn barnacle species, respectively. While Bishop (1951) described *Austrominius modestus* as one of the most geographically confined of all barnacles (i.e. this species is only found in New Zealand and arguably in Australia), it is abundant. For instance, Hutton (1879) recorded *Austrominius modestus* as abundant on rocks in New Zealand, and this barnacle species is the most common fouling barnacle in New Zealand harbours (Foster 1982). In suitable habitats within New Zealand (see 'Horizontal and vertical zonation' subsequently), this barnacle species occurs in the North and South Islands, as well as Stewart Island. *Austrominius modestus* has not been recorded or collected from the Kermadec Islands or from the islands to the south of Stewart Island, New Zealand (Foster 1967a, 1978). Foster (1978) questioned whether *Austrominius modestus* occurs in Chatham Island, New Zealand, as Young (1929) recorded it

Figure 1 The current known distribution of *Austrominius modestus* in Australasia (green) and where introduced into Europe (red). (Drawn by M.C. Gallagher.)

there, but Knox (1963) stated that it was absent. In its proposed introduced range within Australia, *Austrominius modestus* occurs in South Australia, New South Wales, Tasmania and Victoria (e.g. Darwin 1854, Hutton 1879, Hoek 1883, Gruvel 1905, Jennings 1918, Nilsson-Cantell 1926, Moore 1944, Womersley & Edmonds 1958, Foster 1967a, 1978, 1982, Leslie 1968, Thomas & Edmonds 1979, Hutchings & Recher 1982, Keough 1983, Bayliss 1988, Jones 1990, Jones et al. 1990) but is apparently not present much north of Port Jackson (Pope 1945). *Austrominius modestus* is one of 279 barnacle species recorded in Australian waters but one of only six that have an Australasian distribution (Jones 2012).

Current invaded distribution

Austrominius modestus was introduced into Europe in the 1940s. Outside Australasia, Buckeridge & Newman (2010) described the distribution of *Austrominius modestus* as introduced and naturalised in Great Britain (including the Shetland Islands) [Ireland] and Western Europe and arguably naturalised in the Mediterranean (Bassin de Thau, near Marseilles). On the European continent, its current (2018) range is believed to be as described by Southward (2008), that is, from Denmark to southern Portugal (see Figure 1), but please see details of historical records in 'Changes in its distribution in its non-native range'. The first published record of *Austrominius modestus* in Europe was from Chichester Harbour in 1945 (Bishop 1947), but it is now known to have been present before 1945. This species was possibly transported to Britain via ship or flying boat (Bishop 1947, Crisp 1958). Since its introduction to Europe in the 1940s, *Austrominius modestus* has become widespread on European Atlantic shorelines (Harms 1999, Tøttrup et al. 2010) (see details in 'Changes in its distribution in its non-native range'). In Europe, *Austrominius modestus* was thought to be the only species within the Subfamily Elminiinae that successfully colonized outside its native range. Egan & Anderson (1985) cast doubt on this due to some anomalies (please see 'Larval Stages' subsequently regarding a possible explanation for these) when they compared larvae of the Australasian species with larval descriptions of European species. However, Foster & Anderson (1986) suggested subsequently that all European studies on the biology and ecology of *Elminius* refer to *Austrominius modestus*. Furthermore, Buckeridge & Newman (2010) do not list any other species of the Subfamily Elminiinae being introduced into Europe, although *Elminius kingii* has been introduced from South America to eastern Canada (Gollasch 2002). Following Barnes (1989), we have used *Austrominius modestus* for all of the European publications, except in direct quotes. Buckeridge & Newman (2010) mentioned a record of *Austrominius modestus* from the Azores but noted that it is of "questionable identification". Southward (1998) indicated that this record was more likely to be a juvenile of *Chthamalus stellatus* with plate abnormalities (Southward pers. comm. to R. O'Riordan). Torres et al. (2012) also suggested that this specimen was probably misclassified. The only known published record of *Austrominius modestus* in South Africa is of a single individual in 1949 (Sandison 1950), and it has not been recorded there subsequently and is assumed to have failed to colonize there (Barnes 1989, Buckeridge & Newman 2010). Kerckhof (2002) suggested that *Austrominius modestus* had spread to Japan but provided no reference to this record.

Several publications, such as, for Australasia, Foster (1982), Bayliss (1988, 1994), Jones (1990) and Buckeridge & Newman (2010) and Southward (2008) for its introduced range, provide details on how to distinguish *Austrominius modestus* from other species of adult barnacles.

Horizontal and vertical zonation

In both its native and introduced range, *Austrominius modestus* attaches to a wide range of substrata and occurs intertidally and subtidally. Although *Austrominius modestus* can be found at higher shore levels, greater densities occupy middle and lower levels. *Austrominius modestus* is found on sheltered to intermediate exposed shores in habitats including rocky shores, estuaries, mangroves, harbours and ports but is absent from the most wave-exposed shores, probably due to the relative fragility of its shell.

Australasia In New Zealand, *Austrominius modestus* is the species of barnacle that penetrates furthest into harbours and estuaries and is common in mangrove forest and eelgrass beds (i.e. *Zostera*), occurring more often in sheltered locations on open coasts with clean water. However, *Austrominius modestus* withstands only moderate wave action and is absent from the most exposed stretches of rocky coasts (Moore 1944). Foster (1978) commented that it was not surprising that *Austrominius modestus* occupies habitats that are not prone to severe wave action. This is due to certain features of its shell, which is weakly constructed but solidly calcareous, with narrow radii that abut onto the adjacent parietes only basally (Foster 1978). Although *Austrominius modestus* cannot tolerate wave-exposed shores, it can grow well in strong currents in more sheltered habitats, for example, in its native range at the edge of channels in mangrove forests, where the current is fast (Moore 1944). An ability to thrive in very fast currents has also been seen in its introduced range in drowned river valleys in northern France, where they can reach larger sizes than reported elsewhere (see details in 'Size, growth rate and age' subsequently).

Austrominius modestus is fairly versatile with respect to tidal level (Moore 1944), and it has been recorded on a wide range of substrata in the midlittoral and shallow sublittoral zones (Moore 1944, Morton & Miller 1968, Foster 1978, Jones 1990). Gruvel (1905) noted that it occurred attached to rocks in the littoral as well as attached to shellfish and was often associated with *Balanus trigonus* and *Balanus vestitus*. In Australasia, the main level that it occurs at intertidally is the middle shore, reaching high abundances. Similar abundances can be found in slight shade on wharf piles or under mangroves (Moore 1944). However, it can be found higher up the shore, above other species, where fresh or brackish water seeps over a rock or where there is a damp shaded ledge (Moore 1944). Foster (1978) noted that on sheltered shores in its native range, it can reach as far up as the high water of neap tides. According to Davey (last accessed, 2018), on southern Australian shores, it shows a preference for higher shore levels, where it might be only covered for a few hours each month. Unlike other belt-forming intertidal barnacles, *Austrominius modestus* grows not only on the upper rock and other surfaces but also on the underside of stable boulders (Moore 1944), which, as Foster (1978) had noted, is a desiccation-protected habitat. Where *Austrominius modestus* occurs on horizontal surfaces, this species may be protected from desiccation by a layer of silt, sometimes with small algae. Clean vertical rock, facing the sun, is unfavourable due to the lack of protection from desiccation (Foster 1978). With respect to its lower limit, *Austrominius modestus* has been collected on mussels from a depth of 3.7 m and on test panels down to about 5 m (Jones 1990). *Austrominius modestus* survives well on sublittoral surfaces, including ships' hulls (Foster 1967a). This fouling proclivity enabled *Austrominius modestus* to overcome oceanic barriers and become sympatric with related species in Australia and Europe (Foster 1978). Along with *Austrominius modestus*, *Amphitrite amphitrite* and *Balanus trigonus* are frequent fouling species on boats in the north of New Zealand (Foster 1967a), and all three species are now known in European waters (Southward 2008). In 1946, all three species were found together in Liverpool on the hull of a ship that had been in southern Australia and New Zealand, which had journeyed for 30 days through the freshwater conditions of the Panama Canal (Bishop 1947) (see 'Salinity tolerances' subsequently).

Europe In Europe, *Austrominius modestus* is typically found in sheltered waters, including estuaries, harbours, bays and sea lochs, rather than on wave-exposed coastlines (e.g. Southward 1955b, Crisp 1958, Crisp & Fischer-Piette 1959, Barnes & Barnes 1961, Foster 1971b, Gomes-Filho et al. 2010, Gallagher et al. 2017). *Austrominius modestus* was not found in quadrats at the most wave-exposed sites studied in Plymouth, England (Burrows 1988), and Lough Hyne, west Cork, Ireland (O'Riordan 1992). *Austrominius modestus* in its native waters appears to occupy the position held by *Amphibalanus improvisus* in British waters (Bishop 1947). In their 1954–1956 survey, Crisp & Southward (1958) noted that *Austrominius modestus* had already replaced *Amphibalanus improvisus* in many of its habitats in England. By 2003, estuaries in south-west England were dominated by *Austrominius modestus*, accompanied by *Amphibalanus improvisus* and *Balanus crenatus* at low tide levels, with all three occurring intertidally (Ross et al. 2003). The latter authors also reported *Austrominius modestus* at low densities on shores of moderate wave exposure, with normal salinities, but it was outnumbered by three native species of barnacles at all shore heights in the intertidal. Southward (1958) had described the normal zonation of *Austrominius modestus* in Great Britain as midlittoral and infralittoral, mean high water neap (MHWN) to shallow water. At Warwick Bay, Dale, Pembrokeshire, adults were found as high ~5.4 m above chart datum (CD) there, but maximum densities (of adults and spat) were seen at ~2.7 m above CD (Moyse & Knight-Jones 1967). Foster (1971b) commented that on shores where these barnacles co-occurred, without the modifying effect of wave action, *Austrominius modestus* could survive 30–60 cm higher than *Semibalanus balanoides*. Foster (1987) described *Austrominius modestus* as biologically competent in shallow seas, and it was recorded sublittorally in Great Britain down to a depth of about 5 m below low water spring (Crisp 1958), which is similar to its depth in Australasia, as well as occurring on sublittoral panels (e.g. Crisp & Davies 1955). In the early years of its spread to continental Europe, Hartog (1953) said it behaved as an intertidal species, with only a few specimens below water mark on Dutch shores, which was the same situation recorded by Wolf (1973) in the Dutch Wadden Sea. At Cuxhaven, in the Elbe estuary, Kühl (1954, Figure 2, p. 55) showed *Austrominius modestus* occurring from about 3 m (co-occurring there with *Amphibalanus improvisus* and *Mytilus* mussels) to 6 m (just below MHW), where it was the only barnacle species, having co-occurred with *Semibalanus balanoides* (and *Mytilus*) from about 3.3–4.3 m above CD. However, *Austrominius modestus* was subsequently recorded sublittorally in a number of areas in the North Sea (e.g. Anger 1978, Harms & Anger 1983). It has been reported to have been found in the Northern Adriatic Sea, Italy, at a depth of 22–24 m (Casellato et al. 2007), but this record does not appear in national reports of the International Council for the Exploration of the Sea Working Group on Introductions and

Tranfers of Marine Organisms (ICES WGITMO), and this is much deeper than it has been found elsewhere. Kerckhof (2002) said that *Austrominius modestus* was the most common barnacle of Belgian fauna, including dominating most of the offshore buoys (Kerckhof & Cattrijsse 2002), but sublittoral offshore substrata were not colonized by *A. modestus*, remaining the exclusive habitat of *Balanus crenatus*. In the sublittoral zone in Ireland, *Austrominius modestus* has been recorded occurring with *Balanus crenatus* (O'Riordan 1967), as well as with other sublittoral species on plates down to a depth of 12 m (Watson et al. 2005). Southward (2008) noted that, in the sublittoral, specimens of *Austrominius modestus* and *Balanus crenatus* may be found co-occurring. He warned that sometimes *A. modestus* resembles *B. crenatus* and needs to be cleaned of any epizoic growth to confirm identity. Barnes et al. (1972) also pointed out that, where there is sand scour (e.g. Hossegor, France), erosion can cause the specimens to be mistaken as *Amphibalanus improvisus* or *Amphibalanus eburneus*.

Physiology and function

Over 20 years ago, Anderson (1994) pointed out that surprisingly little research had been carried out on the physiology of cirripedes, despite their diversity, widespread availability and ecological importance, although there has been some research undertaken more recently on a few species of barnacle (e.g. Wrange et al. 2014). With respect to *Austrominius modestus*, research has focussed on this species's tolerances to temperatures and salinities and the effects of these environmental parameters on cirral activity and metabolism during various stages in its life cycle. The small amount of research to date on its endocrinology looked at the processes and substances controlling hatching, larval metamorphosis and moulting, while its shell structure and growth under different conditions have also been examined. Subsequently we summarise what is known about *Austrominius modestus*, most of which is based on the species in its introduced range in Great Britain (England, Scotland and Wales).

Cirral activity and metabolism

Austrominius modestus has a faster cirral beating rate than most other species in British waters (Crisp & Davies 1955), including *Semibalanus balanoides* (Southward 1955a). This cirral activity can occur over a wider range of temperatures, affecting both its feeding and respiration, when immersed. Adult thoracican barnacles use their cirri to filter food from the water and gather oxygen, so the rate of beating of these cirri reflects the general metabolic rate of a barnacle (Southward 1955a, Crisp & Southward 1961). For maximum growth, *Austrominius modestus* needs a high concentration of suspended material (Crisp & Davies 1955), which is characteristic of rich inshore waters (Crisp 1964a). *Austrominius modestus* is one of the barnacle species that can show both normal and fast (accelerated) beating of the cirri, but fast beat planktivory is the most usual/dominant feeding mode of this species (Crisp & Southward 1961, Anderson & Southward 1987). This mode of feeding is also seen in at least two other members of the Subfamily Elminiinae (Anderson unpublished, cited in Anderson & Southward 1987). Anderson & Southward (1987) mentioned further unpublished research by Alan Southward on the cirral activity of *Austrominius modestus*. Using milk trails and carmine suspensions, he showed that this fast beat can generate a water flow that is at least twice as wide as the spread cirral net and extends at least three shell diameters each way along the rostro-carinal axis. Fast beating therefore greatly increases the flow of particles nearby, which benefits species such as *Austrominius modestus* when it occurs in sheltered waters. The fast beat is best seen in medium and small *Austrominius modestus* and in laboratory temperatures is extremely fast (Anderson & Southward 1987). Southward (1955b) reported a significantly higher mean frequency of cirral beating in less than one-year-old *Austrominius modestus* collected from the mean low water neap (MLWN) than MHWN in Plymouth. According to Crisp & Patel (1961), the usual activity in *Semibalanus balanoides,* a species with which it may compete, at least at the northern limits of its introduced range (see subsequently), is the normal beat. In comparison to *Semibalanus balanoides*, *Austrominius modestus* has relatively longer cirri, with a few more segments (Crisp & Maclean 1990). However, Crisp & Maclean (1990) warned that the number of segments in each cirrus cannot be used as a taxonomic character because the number of segments increases with animal size, but the equation describing the relation between segment number and animal size may well be diagnostic. Southward (1965) had mentioned that certain physiological data, such as cirral activity rather than cirral size, can be of use in the taxonomy of barnacles but emphasised the need for systematic exactness in physiological work. Moore (1944) described the cirral structure of *Austrominius modestus* in detail, and Jones (1990) provided cirral counts.

Southward (1955a) examined how cirral activity, which may affect both feeding and respiration, varied with temperature in the laboratory. He found that *A. modestus* was active at lower and higher temperatures than native southern and northern species, respectively, while it was active at a wider range of temperatures than *Balanus crenatus*, which occurs, like *A. modestus*, in sheltered conditions. *A. modestus* showed a much greater frequency of cirral beating (17–18 beats/10 seconds at 20°C) than the five native species tested (Southward 1957). Feeding of *Austrominius modestus* ceased at temperatures below 2.5°C and above 32.5°C. A maximum of 22 beats/10 seconds occurred at 24°C.

Southward (1955a) pointed out that it would be interesting to know the range of cirral activity of *Austrominius modestus* in Australasia, since the lower temperatures tolerated by the British-bred specimens are lower than the lowest (7°C) monthly mean seawater temperatures there, suggesting that *A. modestus* has acclimatised to European conditions (see also Southward 1964). However, Ritz & Foster (1968) noted that air and seawater temperatures in its native range may be as low as 0°C and 4°C, respectively. Patel & Crisp (1960b) reported that the rate of cirral beating of *Austrominius modestus* prior to collection was much faster than that of the other three barnacle species tested. The ambient mean seawater temperature in the relatively cool waters of North Wales in the four weeks prior to collection was 12°C. In the laboratory, Crisp & Ritz (1967) acclimated *Austrominius modestus* for five months at 4, 15 and 25°C and then examined the activity patterns (cirral beating) over five hours in either 3–4, 14–15, 21–22 or 30–31°C. They found that below the temperature of maximum frequency of beating, the animals that had been acclimated at the lowest temperature showed the highest rate of cirral beat. The temperature of the maximum rate of beating and the upper limit of activity increased as the acclimation temperature increased. They noted that the acclimation half-time was found to be on the order of 5–10 days in *Austrominius modestus*. They also examined the influence of temperature on the rate of normal and fast beating in fed *Austrominius modestus* before and after seven months acclimation to three temperatures, as well as the effect of starving. They reported that prolonged starvation at the higher temperatures eventually resulted in a lowered rate of cirral beating.

Anderson (1994) described barnacle digestion, while a number of authors have calculated the ingestion rate of *Austrominius modestus*. Crisp (1964a) gave a value of 0.6 mg tissue dry wt d^{-1}, for a barnacle with a RCD of 10 mm (at 13–17°C). According to Rainbow & Wang (2001), the dry weight of this sized barnacle would be 1.37 mg, giving a value of 0.44 g $g^{-1}d^{-1}$. Using the filtration rate of 11.4 ml hr^{-1} per individual, suggested by Crisp & Southward (1961), and assuming a typical seston concentration of 2 mg l^{-1} in the sea, Rainbow & Wang (2001) calculated an ingestion rate of 0.55 mg d^{-1} or 0.40 g $g^{-1}d^{-1}$ for a barnacle of 1.37 mg tissue dry weight.

Emersion, oxygen uptake, anaerobic metabolism and lactic-acid production

Similar to other intertidal barnacle species, adult *Austrominius modestus* utilize the pneumostome to use atmospheric oxygen for respiration during emersion, forming lactic acid under anoxic conditions and in emersion. The use of a pneumostome subjects the mantle cavity minimally to the atmosphere (Barnes & Barnes 1957, Barnes et al. 1963, Grainger & Newell 1965, Crisp & Ritz 1968, Foster 1970). However, the oxygen consumption when emersed is much lower than when immmersed (Grainger & Newell 1965). Since the water that is lost from the mantle cavity is replaced by air bubbles, the mantle cavity can fill with air (Davenport & Irwin 2003). *Austrominius modestus* and *Semibalanus balanoides* usually use up the oxygen in these bubbles within two–three hours and do not regain oxic conditions until re-immersed in seawater, but in *Chthamalus stellatus*, the air bubble is repeatedly refreshed for many hours by pneumostome formation. However, in response to low environmental salinity, all three barnacle species close their opercular plates firmly and rapidly use up oxygen within the mantle fluid. A similar valve closure occurs during extensive desiccation, when they use energy derived from anaerobic metabolism (Barnes & Barnes 1964, Hammen 1972). Barnes et al. (1963) found that three species of European barnacles formed lactic acid under anoxic conditions and in emersion. Boulton et al. (1967), who were studying the metabolic pathways in *Austrominius modestus* in order to understand the biochemical mechanisms by which toxic compounds in antifouling substances could affect this species (see 'Pollution' subsequently), found only very minor incorporation of labelled substrates into lactic acid of *A. modestus*. They mention previous research by Munday & Walker (unpublished), demonstrating the operation of several enzymes of the glycolytic and tricarboxylic acid cycle pathways in adult *Austrominius modestus*.

Little has been reported about the respiration rates of adult *Austrominius modestus*, but CO_2 fluxes due to respiration (and calcification; see subsequently) ranged from 3.6 ± 0.84 to 14.1 ± 3.63 $\text{mol}_{CO2}\ \text{m}^{-2}\ \text{year}^{-1}$ in intertidal specimens at two sites in France (Golléty et al. 2008). Bhatnagar & Crisp (1965) examined the oxygen consumption, as measured by respirometry, of stage II nauplii of *Austrominius modestus*. With a dry organic weight of 0.38×10^{-6} g, the actual oxygen uptake was 2.2×10^{-6} ml O_2 per hour, giving a weight-specific oxygen uptake of 5.8 (ml O_2 hr^{-1} g [dry weight]). Similar levels of oxygen uptake occur in *Austrominius modestus* nauplii as in other invertebrate planktotrophic larvae (Crisp 1976).

Temperature

Austrominius modestus is eurythermal (Barnes & Barnes 1966), tolerating temperatures ranging from approximately −5°C up to 48°C in experimental conditions. The distribution of *Austrominius modestus* in its native New Zealand suggested that it is a temperate to warm-water species (Foster 1969), since the water temperature range in the subtropical and temperate parts of New Zealand varies between 4 and 21°C (Ritz & Foster 1968) but can reach 24°C (Harms & Anger 1989), and air temperatures may reach 40°C (Foster 1969) (compared to >30°C in Plymouth, Great Britain [Southward 1958]), while air temperatures in the south of New Zealand seldom go below 0°C (see Figure 8 and references cited by Harms & Anger 1989). In its invasive range, *Austrominius modestus* tolerates higher temperatures than the arctic-boreal *Semibalanus balanoides* (Southward 1958). However, it is not as tolerant as warm-water species, such as '*Chthamalus stellatus*', which has a very high upper temperature limit, which is in line with the latter's tropic-Mediterranean centre of distribution (Foster 1969). Please note that '*Chthamalus stellatus*' is used for research predating Southward's (1976) separation of '*Chthamalus stellatus*' into *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. In Europe, *Austrominius modestus* cannot tolerate as low temperatures as arctic-boreal species, for example, *Semibalanus balanoides*. Hence, cold temperatures and competition from arctic-boreal barnacle species are believed to affect its current northern limit as well as historic invasive range in Europe. Unusually cold winters in Europe are believed to have delayed extensions northwards (in 1946 and 1947) and resulted in greater mortality in Ireland of *Austrominius modestus* than native barnacle species (in late 2009 and 2010). In contrast, mild winters and warmer-than-normal summers allow increases in its abundance there.

Effect of high temperatures and variation with season and life stage

Although thoracican barnacles can tolerate high temperatures, this varies among species and intraspecifically with age, season and habitat. Southward (1955a) reported that heat coma in adult *Austrominius modestus* (loss of irritability – when normal reaction to touch, namely a closing of the terga and scuta, failed to occur) occurred at 36–38°C. However, subsequent research established that the upper lethal temperature (ULT) of adult *A. modestus* from British waters was between 48.0–48.3°C and 44.2–44.8°C (for 50% mortality with a heating rate of 1°C min^{-1} and 2°C min^{-1}, respectively) (Southward 1958, Crisp 1968, Foster 1969). Southward (1965) reported that *Austrominius modestus* collected from English shores showed 50% mortality after 7 h 30 min at 37°C, but only 5 h 15 min at 40°C. In comparison, '*Chthamalus stellatus*' could survive for 29–30 hours at 40°C and 30 minutes at 50°C. Southward (1958) found that *Austrominius modestus* was more resistant to high temperatures than *Semibalanus balanoides* and *Perforatus perforatus*. This allows it to occur at higher levels on the shore than the two latter species. Foster (1969) suggested that 50% mortality would occur in *Semibalanus balanoides* and *Austrominius modestus* at temperatures of 36°C and 38°C, respectively, at mid-tide levels on shores with semi-diurnal tides, if maintained for a full 6 hours. Foster (1971b) reported on the water loss and mortality of *Austrominius modestus* on pier piles at Menai Bridge. After two weeks of unusually fine weather in June 1969, coincident with neap tides and above-normal temperatures, he found that some of those occurring highest on the pier piles were quite dry and shrivelled and it was not possible to extract blood from the organisms. Younger (spat) and smaller (up to 4 mm) *Austrominius modestus* were particularly affected.

High temperature tolerances may not vary seasonally for subtidally occurring barnacles, but species which live in the intertidal may show variation with season. For example, when Foster (1969) tested barnacle species collected in Great Britain in summer (July) and winter (February) for high temperature tolerance, continuously submerged adults of *Austrominius modestus* (and *Balanus crenatus*) showed no seasonal change in high temperature tolerance. However, intertidal arctic-boreal *Semibalanus balanoides* were more susceptible to prolonged high temperatures in the winter.

At the southern invasive limit of *Austrominius modestus* in Europe, desiccation stress, or some other stress(es), may be limiting the abundance of *A. modestus* by affecting cyprids and/or metamorphs at the settlement and recruitment stages. When emersed, barnacles in the intertidal may have to survive both high temperatures and resist desiccation (Foster 1969). Although temperature tolerance is independent of size (Foster 1971b), the length of time that barnacles survive under desiccation stress is dependent on the size of the individual. Desiccation results from the combined effect of temperature, humidity and wind speed (Foster 1971a). When Foster (1971a) examined the median lethal time (h) for barnacles, measuring a range of rostro-carinal diameters at different temperatures and humidity, he found that smaller *Austrominius modestus* (and *Balanus crenatus* and *Semibalanus balanoides*) were more susceptible to desiccation at normal temperatures and low humidities than larger barnacles. When individuals of about the same size were compared, the lower shore *Balanus crenatus* was much more susceptible to desiccation and lost water more quickly than the other two species, which lost water at similar rates, but *Semibalanus balanoides* survived slightly longer than the same-sized specimens of *Austrominius modestus*. Foster (1971a) noted that high intertidal '*Chthamalus stellatus*', which survived longest in emersion, appeared to be relatively impermeable. For barnacles of the same volume and at 0% relative humidity, the mean lethal time for spat (at 18°C) and adults (at 19°C) was much shorter in *Austrominius modestus* (spat = 7 h, adults = 46 h) than in '*Chthamalus stellatus*' (spat = 48 h, adults = 165 h). Although *Austrominius modestus* is slightly more tolerant of high temperatures and *Semibalanus balanoides* appears to tolerate slightly greater tissue dehydration (which may be linked with to greater tolerance of cold), Foster (1971b) wrote that it is unsurprising that these two species occupy similar intertidal stations. Foster's (1971b) research on salinity and desiccation is discussed subsequently. Cawthorne (1979) investigated the high temperature tolerances of newly released nauplii of *Austrominius* *modestus* and *Semibalanus balanoides* to sinusoidal, abrupt or steady-state changes. For both species, the sinusoidal regime was tolerated best and allowed survival to maximum temperatures, but *Austrominius modestus* nauplii were significantly more tolerant of cyclic exposure to high temperatures (Cawthorne 1980).

When discussing the spread of *Austrominius modestus* to more southerly shores on European coasts, Foster (1971a) noted that *A. modestus* may survive better under warmer and, presumably, drier environments, in comparison to *Semibalanus balanoides*. Foster (1969) and Southward (1958) concluded that the temperature tolerances were linked to the temperatures in the geographical distribution and vertical zonation of these barnacle species (see 'Horizontal and vertical zonation' previously). In its native range, *Austrominius modestus* shows considerable resistance to desiccation, with some specimens attached to a mangrove leaf showing active feeding when placed in fresh water. This is despite having been left on a sunny laboratory bench for ten days without water (Moore 1944). However, *Austrominius modestus* does not tolerate too much direct sunlight (Moore 1944, Knight-Jones & Stevenson 1950), with, as mentioned previously, vertical rock facing the sun being unfavourable (Moore 1944). Similarly, Foster (1987) pointed out that the densest populations of *Austrominius modestus*, along with another member of the Subfamily Elminiinae, *Austrominius covertus*, occurred where there was some protection from direct insolation.

Effect of low temperatures

Thoracican barnacles can survive temperatures below 0°C, but this varies with species, season and whether the species is living in the intertidal or subtidal. Southward (1955a) had reported that chill coma occurred at 0°C in *Austrominius modestus*, but Crisp & Davies (1955) noted that at Burnham-on-Crouch, south-east England, *A. modestus* could survive at temperatures well below 0°C, but they may have been referring to subtidal, rather than intertidal, specimens. At −5.0°C (but not at −10.0°C), *Austrominius modestus* was less tolerant than the native *Semibalanus balanoides* and '*Chthamalus stellatus*' (Southward 1958). After 18 h, 50% mortality of *Austrominius modestus* occurred at −4.3°C in the summer and −6.0°C in the winter, while for *Semibalanus balanoides*, the respective temperatures were −6.0°C and −16.0°C (Crisp & Ritz 1967, Ritz 1967). Ritz (1967) and Tooke & Holland (1985) commented that *S. balanoides* had greatly enhanced cold tolerance in the winter (lower mean lethal temperature range of −17.3 to −19.2°C in winter vs −7.0 to −8.2°C in summer), but *Austrominius modestus* showed little seasonal variation (mean lethal temperature range of −4.9 to −6.7°C in winter vs −5.1 to −6.3°C in summer). Southward (1958) commented that the relatively low resistance of *Austrominius modestus* to cold temperatures was surprising considering its abundance at that time on the cold east coast of England. However, after the unusually cold winter of 1962/63, only 50%–80% mortality of *Austrominius modestus* occurred, in comparison to 100% mortality in some molluscan species, in the intertidal zone in south and south-east England (Crisp 1964a). It was thus suggested that *Austrominius modestus*, along with *Semibalanus balanoides* and '*Chthamalus stellatus*', which are subjected to desiccation by evaporation in summer, may be pre-adapted to withstand the effects of dehydration of the tissue fluids by freezing in winter (Crisp 1946). In the laboratory, Tooke & Holland (1985) found very similar phospholipid fatty acid composition in samples from Great Britain, which they thought might reflect the similarity of their physical environment and diet. However they did find changes in sphingomyelin (essentially confined to the plasma membrane) between winter (January) and summer (August). In *Austrominius modestus*, there was an increase and decrease in levels of monounsaturated fatty acids and saturated fatty acids, respectively, going from winter to summer. The differences in the ability of *Austrominius modestus* and *Semibalanus balanoides* to acquire freezing tolerance may be related to seasonal changes in total phospholipid fatty acid of the plasma membrane (Tooke et al. 1985). At Lough Hyne Marine Nature Reserve (LHMNR), southwest Ireland, *Austrominius modestus* was found to experience higher levels of mortality than native barnacle species during the cold winters of 2009/2010 and 2010/2011 (Gallagher et al. 2017). In The Netherlands, although *Austrominius modestus* survived the cold and protracted winter of 1946–1947, this abnormally cold winter delayed its spread. Based on laboratory and field research at Helgoland, Germany, it was suggested that extreme winters may act as a strong factor in genetic selection towards cold temperature adaptation in these populations of *Austrominius modestus*, which are towards their current northerly continental European invasive limits (Harms 1986, Harms & Anger 1989). Temperatures during such extreme winters may drop to less than −20°C on single days and caused mortality there of most of the adult intertidal *Austrominius modestus* and ca. 70% of subtidal *A. modestus* (Harms & Anger 1989). Kühl (1963) suggested that *Austrominius modestus* was more sensitive to low winter temperatures than some of the native species in the Elbe estuary, resulting in high winter mortality of the former species. However, when air temperatures drop below normal winter ones, they survive in the tidal zone of Helgoland or Borkum. Theisen (1980) attributed the disappearance over winter of *A. modestus* from an intertidal area in Danish waters to a severe winter. In December 1978, over 70% of the intertidal barnacle population at their site consisted of *Austrominius modestus*, but no living specimens could be found intertidally the following March or October (although they noted that they may have survived subtidally). Jensen & Knudsen (2005) had suggested that they were not able to establish themselves in the Danish Wadden Sea because of the borderline low temperatures. This results in them dying during cold winters, due to ice formation, but repopulating during milder ones. However, Witte et al. (2010) has described, towards its northern introduced range, the impact of a series of mild winters and warm summers. Barnes & Barnes (1966) noted that it only started to increase in abundance in the Clyde estuary in Scotland after a warmer summer than normal, in 1959.

Salinity

Austrominius modestus has been described as extremely euryhaline (e.g. Southward 1955a, Barnes & Barnes 1974) and hardy (Knight-Jones 1948). This tolerance to a wide range of salinity allows *Austrominius modestus* to occupy fully marine habitats, but also those that are characterised by lower and higher salinities. In its native range, in Australasia, this species is able to penetrate deep into estuaries and harbours, since it can tolerate brackish and muddy waters, including mangroves. Darwin (1854) recorded *Austrominius modestus* on oysters in Sydney Harbour, in a lagoon, which was almost separated from the sea. Jones (1990) noted its tolerance to reduced salinities, although Foster (1987) suggested that these conditions were rather unfavourable to barnacles. In Europe, salinity fluctuations have been found to affect its distribution within estuaries (see e.g. Wolf 1983, Attrill & Thomas 1996, Gomes-Filho et al. 2010), but it is able to extend further into estuaries than the native *Semibalanus balanoides* (Foster 1970, 1971b).

The embryos of *Austrominius modestus* can develop at salinities between 15–20 and 40, which is similar to other thoracican barnacle species tested (Barnes & Barnes 1974), but the nauplii of *A. modestus* can be slightly more tolerant to lower salinities than the other species (Bhatnagar & Crisp 1965). Crisp & Costlow (1963) pointed out, that by living in estuaries, the adults of *Austrominius modestus* experience very low salinities periodically. Since egg masses are permeable to salts, they may be subjected to the same salinities as the adults. Barnes & Barnes (1974) subsequently examined the responses of the embryos of six species of thoracican barnacles, including *Austrominius modestus*, to hypo- and hypersaline media in the laboratory. Regardless of what stage of development the cultures were started, the range of salinity over which the embryos would develop, to give free-swimming stage I naupliar larvae, was similar in all species, irrespective of their known habitat preferences. Each species was investigated at a single temperature only, which was 20°C for *Austrominius modestus* and at a salinity of 16. Embryos which had already developed segments and appendages continued to develop and were successfully reared to hatching, however this did not occur in embryos that were at earlier stages of development. At salinities ranging from 21 up to 42.8, viable nauplii hatched (please see p. 200 of Barnes & Barnes 1974, for full details). Cawthorne (1978) investigated the tolerances of newly released nauplii of *Austrominius modestus* to sinusoidal, abrupt and steady changes in salinity, while Bhatnagar & Crisp (1965) investigated the time-temperature-salinity relationships for survival of the first-stage nauplii of *Austrominius modestus* (as well as *Semibalanus balanoides* and '*Chthamalus stellatus*'). At normal temperatures, salinities below 12 or above 50 caused complete immobility (Bhatnagar & Crisp 1965).

Salinity tolerance of barnacles is independent of size (Foster 1971b), and those of the adults of *Austrominius modestus* (Foster 1970) are similar to their early nauplii (Bhatnagar & Crisp 1965). The adults of *Austrominius modestus*, along with other species of acorn barnacle tested, have been found to be osmoconformers (Foster 1971b, Davenport 1976). Although adult *Austrominius modestus* are able to tolerate brackish waters, they are not as tolerant to low salinities as the estuarine barnacle *Amphibalanus improvisus* (see details subsequently). Barnacles can adjust to small changes of environmental salinity by tissue acclimation, allowing free exchange between the external medium and the mantle cavity. However, if the salinity change is too great, they can withdraw into the shell and close the mantle cavity (Foster 1971b, Davenport 1976). In aquaria, when salinity repeatedly fell to 20% seawater, Davenport (1976) found that they could survive indefinitely, and he noted that they often encounter virtually freshwater in the field. Prasada Rao (1999) pointed out that in tropical barnacles, the closure of the opercular valves at critical salinities, with the formation of a pneumostome, is a similar response to that of *Austrominius modestus* and *Balanus crenatus* from other regions. Foster (1971b) followed up his laboratory observations with field observations on the effects of salinity and desiccation on the determinants of the upper limit of the intertidal distribution of *Austrominius modestus* and *Semibalanus balanoides*. The blood concentration of both species, naturally subjected to temporary freshwater influences during tidal emersion, confirmed that the adverse effects of salinity and desiccation are avoided by closure of the opercular valves before the blood reaches intolerable dilutions. On a sheltered shore, desiccation death of both species was observed at levels in the range between spring tides (Foster 1971b).

After experimental or natural acclimation, *Austrominius modestus*, *Semibalanus balanoides* and *Balanus crenatus* are tolerant to salinities down to 14 to 17 (Foster 1970, Davenport 1976). Although intertidal *Austrominius modestus* and *Semibalanus balanoides* from the same habitat (e.g. from a shore experiencing full salinity seawater) showed similar responses to osmotic stress because of acclimation, *Austrominius modestus* may, with acclimation, be slightly more tolerant of low salinity (Foster 1970, 1971b). However, the estuarine *Amphibalanus improvisus* can, with gradual acclimation, be induced to be active at much lower salinities (~2 or even as low as 1.1) than the other three species of barnacle. This has been attributed to a wider tissue resistance by *Amphibalanus improvisus*, tolerating considerable dilution of its blood and not to any ability to regulate. This enables *Amphibalanus improvisus* to dominate where other barnacle species are excluded by prolonged periods of low salinity (Foster 1970). Davenport and other authors (1995) reported that another member of the Subfamily Elminiinae, *Elminius kingii*, is one of the few benthic invertebrate faunal species present in the Laguna San Rafael (Southern Chile). They noted that its presence there suggests that it is as tolerant to low salinity as the cosmopolitan low salinity specialist *Amphibalanus improvisus*.

Salinity affects cirral activity of barnacles, with cirral beating of *Austrominius modestus* limited to salinities above 17, while two tropical barnacle species tested continued to be active at lower salinities (Foster 1970). However, this result may have been due to the narrow annual range of salinities (32–34) experienced by *Austrominius modestus* at the site where it was collected in the Menai Straits (Foster 1970), since samples from a site where the salinity varied from ~0 at low tide to 20 at slack high water showed acclimation, with *Austrominius modestus* being active in seawater dilutions down to about 14, compared to about 21 for the Menai Straits samples. Optimum cirral beating was at a salinity of 30, while there was no activity above 53 (Foster 1970).

Shell structure

Crisp (1958) reported that the shells of *Austrominius modestus* are less resistant to mechanical damage than more open water species of barnacle. The absence of *Austrominius modestus* from wave-exposed shores has been attributed to the relative fragility of the shell (Foster 1971b, 1982), since when there was no wave action, *A. modestus* survived ~30–60 cm higher that *Semibalanus balanoides*. When the composition of barnacle shells (calcium carbonate and organic matter are the main components) was examined, organic matter constitutes <1% of the weight of the shell in *Austrominius modestus*, *Semibalanus balanoides* and various *Balanus* species, but >2% in some *Chthamalus* species (Bourget 1974, 1977, 1992). Although the two members of the Subfamily Elminiinae, *Austrominius modestus* and *Elminius kingii*, contain the same three types of shell microstructure types (granular, orientated prisms and radiating prisms), there are differences in the number of layers and also in the way that the organic matter is organised. *Austrominius modestus* has a two-layered shell, with the wall plates consisting of a simple granular arrangement of small crystals, unlike that of other Elminiinae (see details of other differences in Bourget 1977). For example, *Elminius kingii* has thick organic sheets and pillars of orientated crystals. In contrast to *Austrominius modestus*, the type of shell structure and organisation seen in *Elminius kingii* and chthamalids is believed to be very resistant to wave action (Bourget 1992).

Levels of trace elements in the shell vary with environmental factors, with an increase in Manganese in *Austrominius modestus* and *Semibalanus balanoides* being related to salinity. For both species, Manganese:Calcium and Magnesium:Calcium decreased with decreasing shore levels, while the Strontium:Calcium levels varied in the opposite direction (Bourget 1974). Bocquet-Védrine (1964, 1965) explored the relationship between the production of the epicuticle and cuticle layers, as well as that of the opercular membrane, and moulting in *Austrominius modestus* and how it differed from '*Chthamalus stellatus*'. In *Austrominius modestus*, the activity of the epidermis at the basal growth zone is discontinuous and synchronised with the moulting cycle (Bocquet-Védrine 1965). Bubel (1975) subsequently carried out an ultrastructural study of the mantle, its membrane-secreting cells and membranes in relation to shell formation. The number of calcareous growth bands laid down by *Austrominius modestus* has been seen to coincide with the number of tidal immersions (Crisp & Richardson 1975). Golléty et al. (2008) reported that the organic and $CaCO_3$ production was much higher in *Austrominius modestus* than *Chthamalus montagui*, particularly at a site which was dominated by *A. modestus*, where CO_2 fluxes were actually higher than those estimated for coral reefs, which highlights the importance of calcification in temperate marine invertebrates, such as *A. modestus*. Furthermore, at their sites at Roscoff, France, much higher $CaCO_3$ production values were obtained for the *Austrominius modestus* populations (1803.9 g_{CaCO_3} m^{-2} $year^{-1}$ and 481.0 g_{CaCO_3} m^{-2} $year^{-1}$) than those from further south in the Arcachon Basin, where the annual rate was estimated to be 1.02 g_{CaCO_3} m^{-2} $year^{-1}$ (Barnes 1971).

Size, growth rate and age

Subsequently is summarised what is known about the size, growth rate and age of *Austrominius modestus* and how they vary with latitude and various environmental parameters, including whether the individuals are intertidal or subtidal. Similar to other barnacle species, *Austrominius modestus* shows faster growth rates in early life, growing more slowly later, as it increases in size (Barnes & Barnes 1962, Anderson 1994). As an *Austrominius modestus* individual grows, it orientates itself to the water current, so that the cirral net faces the current. Growth rate varies with food availability and speed of water flow, with faster growth rates occurring subtidally and lower on the shore than higher up, and non-breeding *Austrominius modestus* grow faster than those with egg masses. Crisp & Patel (1961) noted that the growth of the opercular valves appears to be less dependent on environmental factors than other shell parts, but usually the rostro-carinal diameter (RCD) is measured. Most studies on growth rates give linear measurements, which can vary quite a lot depending on prevailing conditions, citing a factor of three for *Austrominius modestus* versus three and a half to seven for three other species mentioned (Anderson 1994).

Size in Australasia

In its native range, the smallest juvenile *Austrominius modestus* recorded had a rostro-carinal diameter of 0.5 mm, while the maximum adult RCD was 13 mm (Moore 1944). The greatest height is 9 mm (Moore 1944) to 10 mm (Jones 1990), while the average size is c. 5 × 4 mm (Moore 1944). Juvenile *Austrominius modestus* show no trace of colour, being almost transparent (Moore 1944). In New Zealand, at Queen's Wharf, Port Nicholson, Wellington, Ralph & Hurley (1952) recorded that after four weeks of deployment, the diameter of *A. modestus*, on their subtidal (1.2 m below low-tide level) Oregon pine test blocks, ranged from 1.0–2.0 mm (average 1.5 mm), where the smallest individuals were found on vertical and silted areas. At Lyttleton, South Island, NZ, on subtidal panels that had been deployed for one month, the maximum RCD reached was 2.6 mm, but Skerman (1958) pointed out that they may not necessarily have been one month old (due to a lag in settlement), so they may attain larger sizes in a month. After six months on these panels, the maximum size attained by *Austrominius modestus* was 6.5 mm RCD. On the panels that had been deployed by Ralph & Hurley (1952) for 13 months, the maximum size was 6.0 mm, but the age of these was unknown.

Size in Europe

More research has been published on size and rates of growth of *Austrominius modestus* in its invasive than native range. Average RCD is similar to its native range, but a larger adult shell size (maximum RCD of 17 mm) has been recorded under certain environmental conditions in Europe (see subsequently). Tighe-Ford et al. (1970) found that the growth rates of recently settled *Austrominius modestus* in the laboratory were greater in flowing seawater in comparison to static seawater, despite the water being changed and food added in the latter situation. *Austrominius modestus* can show rapid growth when there is plenty of food available (Southward 2008), but usually has a slower growth rate than *Semibalanus balanoides* (Crisp 1964a). Crisp (1964a) gave a dry tissue weight increment of body (excluding shell) of 0.16–0.25 mg dry wt body d^{-1} (0.12–0.18 d^{-1}) (at 13–17°C). Rainbow & Wang (2001) pointed out that this is much higher than that measured in other species of barnacle, so, in their modelling of metal accumulation (see subsequently), they used much lower growth rate constants (0.002–0.01 d^{-1}), which had been determined in other barnacle species. In laboratory conditions, 15 weeks after settling, *Austrominius modestus* could measure 6 to 8 mm (Tighe-Ford et al. 1970), which is in the 'normal' size range (5–10 mm) of adult *A. modestus* suggested by Southward & Crisp (1963). Golléty et al. (2008) have carried out some of the most detailed work comparing the growth rates of intertidal *Austrominius modestus* and *C. montagui* at Roscoff, France, over a 13-month period, including calculating yearly size:weight allometric relationships and following the growth rates of different cohorts. *Austrominius modestus* showed a steadier growth than *Chthamalus montagui*, and the largest *C. montagui* reached 7.9 mm, in comparison to 9.4 mm for *A. modestus* (Golléty et al. 2008), comparable to the maximum size of 9.8 mm observed for subtidal *A. modestus* at Helgoland (Anger 1978). In The Netherlands, intertidal specimens could reach a maximum of between 6 and 8 mm in their first year and 11 and 12 mm in their second year, although one individual measured 12.2 mm (Hartog 1953).

Stubbings (1950) reported that subtidal specimens may reach a maximum of 4–5 mm in RCD at four weeks old in June–July, but in Helgoland, Germany, they reached only 3 mm after a month of settling, attaining 9.8 mm after one season (when water temperatures were 13–16°C, with the largest measured being 10.4 mm) (Anger 1978). Individuals at the edges of subtidal plates showed greater growth than those in the centre (Crisp & Davies 1955). Anger (1978) noted that the growth rates that he recorded were similar to those of Kühl (1954, 1963) for the German Bight area.

Growth and environmental conditions

Barnes & Barnes (1962) mentioned that, although *Austrominius modestus* is eurythermal, moderately high temperatures (e.g. 15–20°C) favour growth. The growth rate of *Austrominius modestus* was examined towards the northern part of its introduced range in Scotland, at Stranraer and Kirkcolm, where the annual temperature range was 4–16°C, and Millport, Isle of Cumbrae, in the Firth of Clyde, where winter temperatures were slightly higher, but maximum summer temperatures are lower than 16°C (Barnes & Barnes 1962). When growth was compared at different intertidal heights and subtidally (on a raft) and in muddy versus relatively open water conditions, growth took place at a fairly uniform rate in summer and autumn following settlement, but there was little growth in winter. Barnes & Barnes (1962) reported faster growth rates subtidally and lower on the shores; that is, *Austrominius modestus* that had settled in August had, by late autumn, reached a RCD of 8.6 mm on the raft and 6 mm at low tide level, but only 5 mm at the upper level (~2.7 m higher). The average size of adult specimens was 5–6 mm in Chichester harbour (Stubbings 1950) and was similar to that recorded for the species in Australia (Pope 1945) and New Zealand (Moore 1944), and in summer this size is reached in about two months. However, Bishop (1947) reported that, in June and July, in just 40 days, subtidal specimens in Chichester harbour could reach 6 mm, but grew less rapidly than *Amphibalanus improvisus*. However, Stubbings (1950) noted that the maximum size (9 mm) recorded in Chichester harbour was well below the 12.5–13.0 mm recorded in Australasia. He attributed the failure to reach the upper limit of size to the lower average surface water temperatures there, in all seasons, in comparison to their original habitat.

Growth rate was found to increase with access to previously unfiltered water and rapidly moving water, with individuals in fast-flowing water growing rapidly to reach a large size (10–15 mm) (Crisp & Davies 1955), which is larger than recorded in their native habitat. Even larger specimens were reported by Bishop (1954). These measured up to 17 mm and were found in Northern Finisterre, France, in narrow drowned river valleys, where there are large tidal ranges, which produce very fast currents. He suggested that this large size could be attained due to these very favourable environmental conditions, rather than age. Crisp & Patel (1961) discuss the potential reasons for growth rate slowing down after a certain size/maturity.

In south-west Ireland, *Austrominius modestus* recruits ultimately attained a larger opercular diameter than recruits of both native species, *Semibalanus balanoides* and *Chthamalus montagui* (Gallagher et al., unpublished data) (see Figure 2). The native species *Semibalanus balanoides* was found to display rapid growth in the first few months following settlement, allowing it to rapidly utilise space prior to the peak of *Austrominius modestus* settlement. This fast initial growth rate (see Plate 2) may provide the native species with a competitive advantage over *A. modestus,* allowing both species to persist in some locations. Plate 2 shows fast initial growth of *Semibalanus balanoides* and subsequent good survival of *S. balanoides*, in particular those that attained a large size initially. Continual settlement of *Austrominius modestus* can be observed, as can relatively high levels of adult mortality.

Crowding and growth: Anderson (1994) pointed out that crowding affects growth patterns (see 'Reproduction' subsequently also). He noted that the response to crowding of low-growing species, such as *Austrominius modestus*, is to grow over one another rather than becoming columnar, which is seen, for example, in *Chthamalus stellatus*.

Growth rates of breeding and non-breeding Austrominius modestus: Growth rates of *Austrominius modestus* vary depending on whether they are breeding. Crisp & Patel (1961) examined growth rates with age (from settlement to over 200 days, in summer to autumn) of 0+ non-breeding and breeding of *A. modestus* on panels continuously immersed in the Menai Straits, Wales. For both groups, growth was approximately linear with respect to time, until they reached 5–7 mm in RCD. Subsequently, those that could not breed (being isolated by >5 cm) then grew significantly faster and to a larger size than those that were able to cross-fertilise and breed, which they concluded

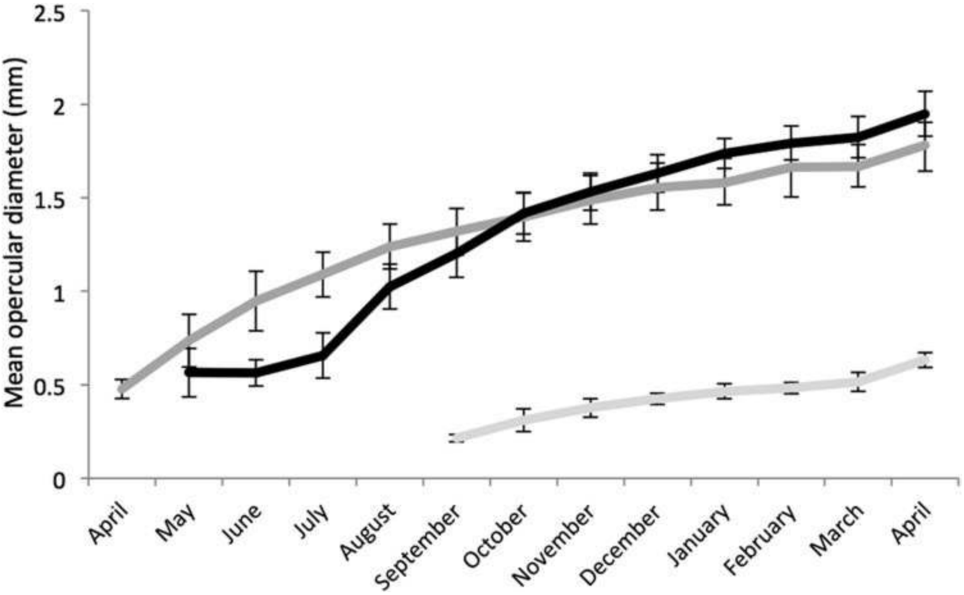

Figure 2 Mean (±SE) opercular diameter (mm) of *Semibalanus balanoides* (dark grey), *Austrominius modestus* (black) and *Chthamalus montagui* (light grey) at monthly intervals from April 2014–April 2015. Mean values were calculated from recruits in removal plots across six sites ($n = 108$ plots) in south-west Ireland.

was due to the loss of tissue in the form of eggs. After six months, the non-breeding individuals were ~10% larger in linear dimensions (except operculum) (see Table 8, p. 113 of Crisp & Patel 1961, for details), with a 30% greater volume and a total weight of 40% greater. Crisp & Maclean (1990) calculated the wet weight and volume index (L × B × H) of *Austrominius modestus* and found that it was closely correlated. Growth rates of these non-breeding and breeding *Austrominius modestus* on subtidal panels also varied when in potential competition with their own species or with *Semibalanus balanoides* (Crisp & Patel 1961). Although *Semibalanus balanoides* may be four times heavier than *Austrominius modestus*, growth of non-breeding individuals of *A. modestus* remained greater than breeding ones, confirming that the loss in weight previously was due to reproduction rather than competition for food.

Longevity: *Austrominius modestus* is likely short lived (Knight-Jones & Stevenson 1950) with a lifespan of just two to three years. Harms & Anger (1983) suggested less than two years, while Golléty et al. (2008) proposed at least 22–24 months, depending on the month in which recruitment

Plate 2 Photos showing growth and survival of *A. modestus* and *S. balanoides* over a 13-month period in removal plots at Ballyrisode, Co. Cork, Ireland, by M.C. Gallagher.

occurred. Crisp & Davies (1955) followed individuals on subtidal panels for 21 months, but this was under experimental conditions where new settlement was removed. Foster (1971b) noted that the highest specimens of *Austrominius modestus* on many shores are large specimens for this species, perhaps indicating that once they become established, they may live for long periods, but he did not suggest for how long they may live.

Growth in silty/muddy conditions: Crisp (1958) had suggested that since *Austrominius modestus* is euryhaline and often most abundant in muddy estuaries, they may be specially adapted to feed on detritus. However, Barnes & Barnes (1962) found that at moderately low temperatures, growth was equally good in muddy and open water areas. They suggested that this may indicate that they could use detritus and open coastal plankton equally well. Moore (1944) noted that 'Darwin picked on the most striking ecological attribute of *E. modestus*, its ability to withstand brackish and very muddy water'. Anon (1948) suggested that in its introduced range, it seemed to be able to withstand muddy waters in estuaries better than some native barnacle species. By 1979, *Chthamalus montagui* had disappeared from Mont St Michel, France, being replaced by *Austrominius modestus*, which was attributed to *A. modestus* being better adapted to the rapid silting-up of this part of the Bay of St. Malo (Crisp et al. 1981). One reason, along with its tolerance of low salinity, *Austrominius modestus* can survive in estuarine conditions is that its tough cirri can cope with the turbid conditions. Crisp & Davies (1955) noted that the fact that it can breed at a wide range of temperatures (see subsequently) makes it well suited to living in shallow estuaries and sheltered coasts in temperate latitudes.

Shell orientation: Although at settlement, orientation to the water current is negligible, as it grows, *Austrominius modestus* orientates itself to the water current, so that the carina points away usually from the current source, meaning that the cirral net faces the current (Crisp & Stubbings 1957). Most of the *Austrominius modestus* and *Balanus crenatus* on subtidal plates were orientated with their carinae at an acute angle to the water surface (Anger 1978). This orientation was due to light (Anger 1978) and the predominant sea surface current direction (Crisp & Barnes 1954, Crisp & Stubbings 1957). Barnes et al. (1951) found no observable change in orientation during growth in *Austrominius modestus*.

Endocrinology

The small amount of research to date on the endocrinology of *Austrominius modestus* has focused on the processes and substances controlling hatching, larval metamorphosis and moulting. Clare (1987) pointed out that some of the most detailed work on cirripede endocrinology concerns the histology of the neurosecretory centre and the processes that control moulting and egg hatching. McGregory (1967) examined the central nervous system for the presence of neurosecretory granules of a number of acorn barnacle species, including *Austrominius modestus*. He found that the neurosecretory granules, stained with paraldehyde fuchsin (PF), measured about 0.2 μm in diameter. Control of moulting involves ecdysteroids and a moult-inhibiting hormone. Clare (1987) mentioned that one of the first indications that ecdysteroids were present in barnacles was when unpublished research by D.B. Carlisle showed that extracts of adult *Austrominius modestus*, injected into Y-oran-ablated *Carcinus maenas*, induced the crabs to moult. Tighe-Forde (1977) found that two analogues of insect juvenile hormones (JHs) interfered with the development of *Austrominius modestus* larvae, suggesting that a JH or analogue controls larval moulting. When stage VI nauplii metamorphosed into cyprids, they were morphologically abnormal, retaining some naupliar characteristics, and were significantly smaller in size than usual (see Table I of Tighe-Forde 1977). When he then examined the effect of the two analogues on the metamorphosis of the cyprids, he found that many of the farnesyl methyl esther-treated cyprids were morphologically abnormal. The Ro-8-4314-treated cyprids did not show these abnormalities, but were in general larger than the control ones and in comparison to the control, significantly more of those that had metamorphosed into young adults were unattached.

Tighe-Forde (1977) suggested that these effects may be related to the physiological development of the larvae at the time of exposure. Mortlock et al. (1984) also reported abnormalities, but different to those found by Tighe-Forde (1977), when they exposed *Austrominius modestus* nauplii to another JH analogue, ZR 512. Metamorphosis of nauplii to cyprids and then to adults was accelerated at farnesol concentrations of 1 ppm. The hatching substance produced by the barnacle's own metabolism has been identified in *Austrominius modestus* and is covered in the 'Reproduction' section subsequently, along with the delay of ecdysis during brooding of the embryos.

Excretion

White (1992) and Anderson (1994) summarised what is known about excretion in barnacles, including the organs responsible and the main nitrogenous wastes. Most is known for *Semibalanus balanoides*, but White (1992) mentions Bubel's (1975) research on *Austrominius modestus*. In contrast to other mantle regions, the inner mantle hypodermis was found to show specialisations which were characteristic of a transportive epithelium, suggesting that they could function as a site of nitrogen release (Bubel 1975). The antennal glands are the excretory organs in the nauplii, and Walker (1973) described the frontal horns and associated gland cells of the nauplii of *Austrominius modestus*, *Chirona hameri* and *Semibalanus balanoides*.

Reproduction

Fertilisation

Austrominius modestus is an obligatory cross-fertilising hermaphrodite (Crisp 1950, Barnes & Crisp 1956), needing to be within a maximum of ~5 cm (i.e. the maximum extension of the penis, Barnes & Crisp 1956, Crisp 1958) from another individual to reproduce, unlike some other species of acorn barnacle which may self-fertilise in certain situations (see examples in e.g. Barnes & Crisp 1956, Barnes 1992). Flowerdew (1984) confirmed this obligatory cross-fertilisation when he found no evidence of inbreeding at up to nine loci. Similar to many other thoracican cirripede species, *Austrominius modestus* has a diploid count of 32 chromosomes, and the size of its nuclei and chromosomes at prometaphase (9.2 μm and 1.4–2.7 μm, respectively) are in the middle of the range of those species studied (Austin et al. 1958).

The mating group size of *Austrominius modestus* is generally four to seven, that is, mating involves up to seven 'males' donating sperm to a 'female', which is in line with it being a small barnacle in size, since they have the largest mating groups (Charnov 1987 citing Crisp as a pers. comm.). Foster & Nott (1969) described the sensory structures in the operculum of *Austrominius modestus* and how a functional female remains open when contacted by a penis, allowing penetration.

Age and size at breeding

In barnacles, sexual maturity is mainly a function of size but is also, to a limited degree, dependent on age (Crisp & Patel 1961). *Austrominius modestus* has been described as fast maturing and being able to breed at a very young age (Luckens 1975). Within its native range, in Ngataringa Bay, Auckland Harbour, New Zealand, Moore (1944) reported that they reached maturity and released larvae within two and a half to three months of settling. In its introduced range, reproduction can begin at an even younger age, with some fast-growing specimens in Great Britain containing embryos within as little as six to seven weeks of settlement (Crisp & Patel 1961) at a RCD as small as 3 mm, if continuously submerged, thus reaching maturity at a smaller size than *Semibalanus balanoides* (Crisp 1964b). Half of a studied population contained fertilised egg masses within 10 weeks of settlement and all by 12 weeks (Crisp & Patel 1961). Crisp & Davies (1955) noted that, by then, these young individuals had reached a breeding equilibrium, which was indistinguishable from older populations, unless the older barnacles were infected by the parasite *Hemioniscus balani* Buchholz (see subsequently). Stubbings (1950), as cited by Southward (2008), commented that during the summer, *Austrominius modestus* may reach maturity within eight weeks of settlement, which has also been seen in some individuals in Helgoland, Germany (Harms & Anger 1983). In Helgoland Harbour, some 0+ individuals on subtidal plates which had reached 3 mm in RCD were large enough to reproduce (Anger 1978), similar to that found by Crisp & Davies (1955) in Great Britain for a few of their continuously submerged specimens, most of which measured 4–6 mm in RCD. A similar young age of first reproduction has been seen in *Chthamalus anisopoma* and *Chthamalus fissus*, in California, at an age of ~six (Malusa 1986) and eight (Hines 1978) weeks, respectively, as well as some *Balanus* species (see references within Barnes 1989).

Terminology associated with the reproductive cycle

Crisp & Davies (1955) defined the various terms associated with the reproductive cycle of a single brood of *Austrominius modestus*. The brood period (T) is the time from one fertilisation (oviposition) to the next and consists of the fertilised period (T_F) (from oviposition to release of nauplii, i.e., the length of embryonic development) and the empty period (T_E) (from release of the nauplii to the next fertilisation and oviposition), while early embryonic development (T_D) is normally shorter than the fertilised period. See Crisp & Davies (1955) for the definition of other terms and how to calculate the fraction of the population with embryos and so on. In this paper, the definitions of egg and embryo follow Barnes (1989) from her review of egg production in cirripedes. The term egg refers to the fertilised ovum, from which in *Austrominius modestus* the stage I nauplius hatches. The term embryo refers to the young organism developing within the egg or embryonic capsule. Walker (1992) provides a good overview of the reproduction of barnacles in general, including the structure of the gonads.

Development of the gonads

The gonads of individuals in a population of *Austrominius modestus* are not necessarily synchronous (Crisp & Davies 1955), which is very different to *Semibalanus balanoides* and *Balanus balanus,* in which the gonads are in a uniform state at any given time. In the laboratory, Patel & Crisp (1960b) were able to induce a range of barnacle species to develop gonads within two to three weeks when fed and kept at an appropriate temperature. For *Austrominius modestus*, the lowest critical breeding temperature at which fertilised embryos were found was 8–9°C. Barnes (1989) noted the importance of temperature since it sets limits to reproduction, thus becoming ecologically important in the latitudinal distribution of cirripedes, but she warned that it can be difficult to distinguish the effect of temperature from latitude.

Subsequently we have summarised what is known about the development of the male and female gonads of *Austrominius modestus*, including the length of breeding season, the level of brooding (usually presented as %), the number of broods per year and what is known about how they vary in their native and introduced range with environmental parameters. However, much less has been published about any variation in the cycles of this species, especially regarding the development of the male gonads and ovary, than, for example, *Semibalanus balanoides*. There is plenty of scope for further targeted research, which would be particularly pertinent at the current known northern and southern limits of its introduced range. Barnes (1989) had noted that warm-water species with their northern limits of distribution in Europe may have more than one breeding cycle during warmer months but will have more cycles further south. The fact that reproduction can occur over a wide range of temperatures allows *Austrominius modestus* to thrive in sheltered coasts as well as in estuaries in its introduced range, where there can be wide fluctuations in temperature but an abundant food supply throughout most of the year (Crisp & Davies 1955). Although it is eurythermal, moderately high temperatures (e.g. 15–20°C) favour breeding (Barnes & Barnes 1962), as well as growth, as previously mentioned.

Crisp (1954) described the male and female reproductive organs of *Balanus balanus* (formerly *Balanus porcatus*) and provided scoring systems to stage the development of the testis tissue, vesiculae seminales and ovary, which have been adapted and modified for use in staging the gonad development of *Austrominius modestus* (see O'Riordan & Murphy 2000).

The male reproductive system

Austrominius modestus has been described as slightly protandrous due to the fact that male gonads can be found at smaller body sizes than the ovaries. In Great Britain, male gonads developed in *Austrominius modestus* at a RCD of 3 to 5 mm, with the testes and vesiculae seminales reaching full development in animals greater than 5 mm (Crisp & Patel 1961). Minimum size of first breeding has not been examined in Ireland yet. In Great Britain, those with a RCD of 5 mm or greater always had male gonads throughout the summer months. The same authors observed that crowded intertidal *Austrominius modestus* eventually developed male gonads at a smaller size and had longer penes than normal uncrowded subtidal *A. modestus* of the same size.

As far as the authors are aware, O'Riordan & Murphy (2000) is the only published paper examining the state of the testes and vesiculae seminales throughout the year, for either its introduced or native range. They compared the reproduction of *Austrominius modestus* over a 15-month period at three sites within a small bay in southern Ireland (51°50′N, 08°14′W): site one was adjacent to a the outlet pipe ('outfall') of a power-generating station, site two was toward the eastern part of the bay, while site three was where a freshwater stream (salinity of 0.1 to 0.6) ran into the southern part of the bay and where the lowest air and seawater temperatures were recorded. At site one, the salinity at low tide in the remaining water varied from 26.3–47.8 and air and water temperature were slightly higher than at the other two sites. The discharged seawater, which had been used for cooling the system, was 9–10°C above ambient. The testes and vesiculae seminales of *Austrominius modestus* showed an annual cycle of development, with the highest percentage with well-developed stages occurring in late summer, but moderately developed stages could be found in all months sampled at all three sites. In most months, a higher percentage of animals had well-developed testes than vesiculae seminales. The male gonads were least developed from October–December, most likely due to lack of food, after which they began to regenerate. The proportion of animals with well-developed testes was four times less at its peak at the outfall site than at the other two sites, and they only occurred in seven months. Each month, many of the barnacles at the outfall site lacked testes and vesiculae seminales, or the testes were poorly developed and vesiculae seminales were thin linear sacs with little sperm. Murray (2009) examined the state of the male gonads during a three-month period in summer 2009, at Lough Hyne Marine Nature Reserve, Cork, south-west Ireland. A higher proportion had moderately to well-developed testes and vesiculae seminales in late summer (August) than in early summer (June or July) (Murray 2009). For specimens collected in June from LWN near Plymouth, Great Britain, copulation in the laboratory occurred between 4 and 15°C (Southward 1955a). In south-west England, submerged specimens had somewhat reduced male organs in the late autumn and winter, but they were still present. Thus, reduced levels of brooding at this time of year may be due to lack of food for the re-development of the ovary (Crisp & Davies 1955). In comparison to the reserves needed for the ovary and egg masses, the loss of seminal fluid has been suggested to be either a negligible drain on resources or a common factor in both breeding and non-breeding specimens (Crisp & Patel 1961). However, Barnes (1992) noted that for samples taken in Arcachon Bay in France, the loss of semen results in a significant loss of body weight when the seminal vesicles are full.

Penis structure, extension and ecdysis: The penis of *Austrominius modestus* is minutely annulated, with a circlet of small setae distally, but it does not have a basidorsal point (see Figure 25K of Jones 1990). The penis of *Austrominius modestus* thus differs from balanids, in lacking this basidorsal point (Foster 1978). In Great Britain, Crisp & Patel (1961) measured the length of the penis with respect to the RCD, finding that in *Austrominius modestus* the penis was absent in very small animals, but it developed heterogonically in specimens of 3–5 mm diameter, thereafter growing more slowly. The penis of *Austrominius modestus* is much longer than its cirri, emerging between cirri I and II (Moore 1944), and fast beat cirral activity precedes the extension of the penis (Anderson 1994).

Within the Balanomorpha, the regression and/or loss of the penis seems to depend on how frequently the animals breed within a season and that the number of penis annulations follows the breeding season (Barnes 1992). In *Semibalanus balanoides*, which just produces a single brood per year, the first moulting after a period of anecdysis contains all of the tissues of the penis, and a new penis then gradually develops (Crisp & Patel 1958). However, Barnes (1992) found that in *Austrominius modestus* from Arcachon Bay, France, none were lacking a penis, but there was a greater percentage with penes with fewer annulations in March (40%), August (30%) and October (10%), and these penes had the appearance of regeneration rather than degeneration. However, she warned that the degeneration phase might have been missed due to the sampling regime. The maximum number of penis annulations recorded by Barnes (1992) for *Austrominius modestus* was 240. Further north, in southern Ireland, although they did not measure the number of penis annulations, a penis was present throughout the year in all of the more than 2000 specimens of *Austrominius modestus* examined over a 15-month period (O'Riordan & Murphy 2000). However, in summer 2009, and summer 2019, at Lough Hyne Marine Nature Reserve, Cork, Ireland, up to 20% and 24% respectively of samples lacked a penis (Murray, 2009; Swain, 2019). In winter 2019–20, a penis could not be found in between 2 and 39% of *Austrominius modestus* samples collected on shores in Cork (O'Sullivan 2020).

The spermatozoa of barnacles, unlike most other crustaceans, are flagellated and are usually immobile in the seminal fluid (Barnes & Crisp 1956), but the spermatozoa of *Austrominius modestus* (and *Semibalanus balanoides*) become extremely active either after being discharged through the penis into the mantle cavity of another individual or when treated with chelating agents, such as ethylene diamine tetra-acetic acid (Crisp, unpublished observation; cf. Fujii et al. 1955). Barnes et al. (1971) examined the spermatozoa and spermatogenesis of various cirripede species, including *Austrominius modestus*, while Klepal (1990) described both the spermatozoon and accessory droplets. The sperm ultrastructure and its phylogenetic significance have been described for 46 species of cirripedia, including a number of members of the Subfamily Elminiinae, but not *Austrominius modestus* (Healy & Anderson 1990). An accessory droplet is usually present in thoracican barnacles, with that of *Austrominius modestus* being represented by a thickening (Barnes et al. 1971). In April (1970), in Arcachon, France, all of the vesicular spermatozoa examined had either a very narrow non-refringent droplet (thickening) or were fully filiform, with only slight motility (Barnes et al. 1971).

The female reproductive system

The ovary and ovarian regeneration

Size of ova and ovarian development

In comparison to many other barnacle species (see Table III of Crisp 1954, and Table XV of Barnes 1992), the ova of *Austrominius modestus* are relatively small (see Table 1), ranging from 20–40 μm in the earliest stages up to 100–150 μm for a fully developed ovum (Crisp & Patel 1961) or a mean diameter of 125 μm (Crisp 1954). Although there are little published data on ova size in cirripedes, ovum size (volume) is known to be determined within very strict limits (see Crisp 1986 1987, Walker 1992). When reproductive energy is low (e.g. due to lack of food), it is the number of ova that is

Table 1 Size range of ova *A. modestus* when embryos were in different stages of development, adapted from Crisp & Patel (1961)

Size range of ova (μm)	Stages of development of embryos (see Crisp 1954)
20–40	1–4
30–60	5–7
40–100	8–10
70–120	11–12
80–120	13
100–150	Nauplii liberated

reduced, rather than their size (Patel & Crisp 1960b) and biochemical composition (Walker 1992). Barnes & Barnes (1965a,b) had noted that there is a marked effect of adult barnacle size on the size of ova and embryos.

The stage of development of the ovary can be determined by its colour and texture, and Crisp & Davies (1955) used a numbering system to describe the development of *Austrominius modestus*'s ovary, which followed Crisp's (1954) research on *Balanus balanus*. This and one used by Burrows (1988) for *Chthamalus* were later adapted and modified by O'Riordan & Murphy (2000) for *Austrominius modestus* (see their Table 1). However, with respect to the colour, Patel & Crisp (1960b) cautioned that if adult *Austrominius modestus* in the laboratory are fed with *Artemia* larvae, the colour of the newly developed ovary shows a pinkish tinge, instead of the normal yellow.

Samples of *Austrominius modestus* from southern Great Britain contained only a few individuals of ~3 mm RCD with any sign of ovarian development; embryos were rarely present in individuals less than 4 mm, with ovarian maturity occurring at ~6 mm (~40 days) (Crisp & Patel 1961), while, as mentioned previously, male gonads could be present from 3 mm. In southern Ireland, O'Riordan & Murphy (2000) found that, similar to the male gonads, the ovary of intertidal *Austrominius modestus* (all >4 mm RCD) showed seasonal changes, with the highest percentage with well-developed ovaries in the summer. Although less well-developed stages could be found throughout the year, it was in the winter months that the maximum proportion lacked any sign of ovaries. Similarly, in south-west England, Crisp & Davies (1955) noted that, for continuously submerged specimens on glass plates suspended 1.8 m below sea surface, the ovaries were small and poorly developed in late autumn and winter, but by the time the individual was fertilised, the ovarian tubules were nearly completely full of mature eggs. In April (1970), in Arcachon, France, most of the population had well-developed ovaries, with a small number with developing ovaries at a time when 23%–27% had embryo masses (Barnes et al. 1971). At Lough Hyne Marine Nature Reserve, Cork, Ireland, in summer 2009, the percentage with no ovary visible increased from June (13.4%), through July to August (63.4%). However, the percentage brooding embryos increased from June to August, suggesting that in June a batch of ova were fertilised, which developed as embryos in July and August, while another batch of ova were developing (Murray 2009).

Ovarian regeneration and the effects of food and temperature

If sufficient food is present, *Austrominius modestus* can breed continuously, with little or no interruption, with the immature ova developing as soon as nauplii are released from the embryo masses. The time taken to incubate the fertilised eggs determines the reproductive rate (Crisp & Patel 1961). Crisp & Patel (1961) showed that the smallest ova only occurred in *Austrominius modestus* that had early stages of fertilised eggs, while those which had the later stages had larger ova (see Table 1). *Austrominius modestus* eggs may be mature and ready to be fertilised as soon as the stage I nauplii are released, as seen in subtidal specimens in the Menai Straits, Wales (Crisp & Patel 1961), and intertidal populations in southern Ireland (O'Riordan & Murphy 2000). When food is present, the high reproductive rate is facilitated by the fast cirral beat of *Austrominius modestus*. However, further south, in south-west Britain, in submerged specimens in late autumn and winter, reduced levels of brooding were due to lack of food for the regeneration of the ovary (Crisp & Davies 1955). So in *Austrominius modestus*, fertilisation can occur at any time of year, as long as the ovaries have regenerated.

Reproduction can occur over a wide range of temperatures (6–20°C) in the wild, and reproduction may occur at even higher temperatures (Crisp & Davies 1955), but 15–20°C favours breeding. *Austrominius modestus* needs a sufficiently high temperature at the time of fertilisation, egg-laying and spawning, with 6.0–6.5°C being the critical temperature for the latter. In temperate areas of its invasive range, the gonads (testes, vesiculae seminales and ovary) show an annual cycle of development, with higher proportions with more well-developed gonads during summer months, but the gonads of individuals in a population are not necessarily synchronous.

Temperature affects the regeneration of the ovary. Crisp & Davies (1955) examined reproduction in continuously submerged specimens on glass plates suspended ~1.8 m below sea surface in south-west Britain, where temperatures increase in spring and early summer (range 5–18°C). They found that the ovary regenerated quickly, so that shortly after the nauplii were released, another set of eggs were fertilised to produce a new brood (Crisp & Davies 1955). However, in autumn and winter, the ovary may not regenerate for a long period of time, so a high proportion of the population will not contain embryo masses. They suggested that the fecundity of *Austrominius modestus* in south-west Britain is limited by the rate of development of the embryos in spring and summer but by nutrition in autumn and winter. Since they found that embryos were retained for a shorter time in spring and summer than in autumn and winter, they suggested that a rapidly maturing ovary at that time of year might stimulate naupliar release, but nauplii could still be released without ovarian regeneration. At similar temperatures, embryos will be released more quickly in spring than in autumn, because the barnacles are more well nourished, since more suspended food is available (Patel & Crisp 1960a).

Brood period (T) has been estimated to be as short as 14 days in the subtidal in the summer but longer in the intertidal and winter (up to 60–80 days) (Crisp & Davies 1955). During summer in the subtidal, the average brood period of 14 days was followed by hatching lasting ~10 days. But in winter, both brood and hatching periods were much longer (e.g. 60–80 days for the fertilised period T_F) and fluctuated more, even though normal development appears to occur at a wide range of temperatures. As long as enough food was available, they suggested that *Austrominius modestus* can breed down to a temperature of 6°C. Below temperatures of 6°C, embryonic development can continue, but at a very slow rate (Crisp & Davies 1955). Patel & Crisp (1960a) examined the rate of development of embryo masses, incubated outside the parent, of seven species of barnacles, at temperatures ranging from 3 to 32°C. The embryo masses of southern, intertidal and estuarine species displayed a wider range of temperature tolerance than northern, sublittoral and open coast species. *Austrominius modestus* showed embryo development at the widest range of temperature *in vitro*, from 3 to 32°C. However those at 3°C took over 50 days to develop (and were attacked by fungus) and were only liberated after the addition of a hatching substance. Development did not seem to be affected by brief periods near the freezing point. Those embryos which were removed from adults in the early stages of development failed to develop at 32°C, suggesting a greater sensitivity at these stages, since later-staged ones were able to complete development. The maximum rate of development occurred between 23 and 25°C, which they linked to the mean monthly seawater temperature (14–19°C) at the southern part of its introduced range (S. Portugal). They suggested that these relatively high temperatures may allow it to breed all year round in temperate waters, but this is currently not known and an area for further research. Patel & Crisp (1960b) slightly widened the optimum rate to 22–25°C, with 93% of the laboratory samples containing fertilised embryos at 25°C, versus only 54% and 35% at 9°C and 30°C, respectively. Barnes & Barnes (1962) commented that it takes 40 days for a brood to develop at 8–9°C, but that they occasionally found egg masses present in winter at their sites in Western Scotland.

Brooding of egg masses

Austrominius modestus may brood embryos throughout the year in both its native and introduced range, but this varies with location and latitude and maybe also salinity (see O'Riordan & Murphy 2000). Subsequently we describe how the length of brooding season, the level of brooding, the number of broods per year and fecundity vary with location and some key environmental parameters. Please see O'Riordan & Murphy (2000) for the scale for scoring the stage of development of the egg masses of *Austrominius modestus*. As they develop, the fertilised eggs, which are usually held in a pair of egg masses (see Plate 3, but see subsequently), change from white or a pale cream to yellow, grey, ochre, fawn brown.

When eggs have reached Stage 4 (and the egg masses are dark brown and kidney shaped), the eggs may be retained for quite a long time before release, although they can hatch immediately in the laboratory if removed from the parent.

Walker (1992) describes how a 'hatching substance' released by the adult barnacle causes the stage I nauplii to hatch from their embryo cases. Crisp et al. (1991) noted that although a hatching substance may not be essential in all barnacles, it is thought to be so in *Austrominius modestus* and *Semibalanus balanoides*. That used by *Austrominius modestus* is monohydroxyeicosapentaenoic acid (Hill et al. 1988) and is released by the adult into the mantle cavity, usually when the adult is well nourished but not when it is starved. Decayed remains of unhatched broods have been repeatedly found beneath a new brood in *Austrominius modestus* and *Semibalanus balanoides*, implying that sufficient hatching substance was not present (Crisp et al. 1991). They summarised (Table I therein, p. 64) the evidence for delayed and spontaneous hatching of mature eggs in nine species of barnacle, including some unpublished/pers. comm. data for *Austrominius modestus* and other species. Cawthorne & Davenport (1980) found that hatching only occurred at salinities above 21 with reduced salinities, causing the adults to retain the larvae, while fluctuations in temperature induced larval release in *Austrominius modestus* but not in *Semibalanus balanoides*. According to Crisp & Davies (1955) in *Austrominius modestus*, *Amphibalanus improvisus*, *A. amphitrite* and *Balanus crenatus*, all of which can produce more than one brood per year, oviposition never occurs until the previous brood is released; thus, never more than one brood of embryos can be found. However, O'Riordan & Murphy (2000) did find a single individual of *Austrominius modestus* (out of over 2000 examined) with two pairs of embryo masses in different stages of development (stages 3 and 4),

Plate 3 *A. modestus* removed from the substrate, showing a pair of kidney-shaped embryo masses, photo taken by M.C. Gallagher.

which showed no signs of decay. This is similar to '*Chthamalus stellatus*' (probably *Chthamalus montagui* since found high on the shore), where a few individuals out of several thousand had two sets of embryo masses (Crisp & Davies 1955). Three egg masses, instead of a pair, have been seen in one (out of 437) *Chthamalus stellatus*, while a single egg mass, instead of a pair, has been recorded in both *Chthamalus montagui* (2/234) and *Chthamalus stellatus* (4/437) (O'Riordan 1992, O'Riordan et al. 1995).

Brooding season in the native range: The brooding season of *Austrominius modestus* in Australasia has been described by a number of authors (e.g. Moore 1944, Powell 1947, Wisely & Blick 1964, Foster 1967a,b, Luckens 1970, 1975, 1976). In Auckland Province, New Zealand, Moore (1944) noted that stage I nauplii have been recorded in the mantle cavities throughout the year, and it was suggested that this may be the same all around the coast. Working at Leigh, Luckens (1975) described *Austrominius modestus* as a continuously breeding species. However, Barnes (1989) commented that, in New Zealand, within the optimum temperature range and in relatively stable conditions, there is some evidence of seasonal breeding periods superimposed on a general continuous low level of reproduction. This certainly seems to be the case for some other populations at Leigh, New Zealand (Foster 1967b), with peaks in the percentage brooding in February–March and August–October. However, no embryos were recorded in either year for the November samples (see Figure 3, p. 38 of Foster 1967b), but both immature and mature embryos were found in all months when brooding was present. Zauke et al. (1992) reported that for samples collected in May 1984, 100% of the *Austrominius modestus* samples attached to mangroves in Omaha Beach contained egg masses. From their 17 sites, further south in Auckland, the percentage brooding varied from 1% to 70%. At Omaha Beach, there was a slight positive correlation ($r = 0.478$) of fecundity with Cadmium levels. Based on settlement studies, further south in New Zealand, at Port Nicholson, Wellington, it was suggested that *Austrominius modestus* releases nauplii in autumn (Ralph & Hurley 1952). Further south again, at Lyttleton, spawning may take place throughout most, if not the whole, of the year (Skerman 1958). In samples collected from Garden Island, Sydney, SE Australia, there was evidence of low levels of breeding through most the year, except January and February (see Figure 7, p. 167, Wisely & Blick 1964), but eyed embryos (maximum of 21% of barnacles sampled) were present in seven months only. Although there was some evidence that nauplii were more liable to be released during the colder months of the year, small numbers were released during most of the year. However, it is uncertain whether the specimens examined were *Austrominius modestus*, since Foster (1982) subsequently described three species of the Subfamily Elminiinae from eastern Australia.

Barnes (1989) highlighted the potential effect of salinity on the breeding season of barnacles, especially in estuarine habitats or monsoon areas, referring to species of *Balanus* and *Chthamalus*, but not *Austrominius modestus*. Moore (1944) mentioned that in their native range, *Austrominius modestus* thrive at the edge of channels in mangrove forests, but the authors are unaware of any data on how variations in salinity in this habitat may affect their breeding cycle.

Brooding season in the introduced range in Europe: The brooding season (i.e. in what months of the year embryos occur) of *Austrominius modestus* in Europe has been mentioned by a number of authors (e.g. Knight-Jones & Waugh 1949, Crisp 1954, 1957, Crisp & Davies 1955, Wisely 1960, Crisp & Patel 1961, Stubbings & Houghton 1964, Barnes & Barnes 1966, 1968a, Harms 1984, Barnes 1992, O'Riordan & Murphy 2000, Macho 2006, Macho et al. 2010, Gallagher et al. 2016), although not all of the authors were able to sample throughout the year. Although *Austrominius modestus* can reproduce at a wide range of temperatures, breeding is most rapid at moderately high temperatures (Barnes & Barnes 1962), and, similar to its native range, at some locations, brooding can occur throughout the year. However, breeding of *Austrominius modestus* becomes seasonal at the northern limits of its distribution, where sea temperatures drop below 6°C (Barnes 1992). Gallagher (2016, Gallagher et al. in prep.) recorded the percentage of *Austrominius modestus* and *Semibalanus balanoides* that had embryo masses in March and November on the Isle of Cumbrae, SW Scotland. For *Austrominius modestus*, they found that a higher percentage of individuals were brooding in September, but this never exceeded 47%. The opposite trend was seen in the cold-water *Semibalanus balanoides*, with up to 100% of individuals brooding embryos in March, with <5% in September, which, being in an early stage, would overwinter in the mantle cavity. In Helgoland, Germany, *Austrominius modestus* breeds at 7–18°C in May–October, with the main period of hatching being between mid-July to mid-September when water temperatures are 16–18°C (Harms 1984). Yet when *Austrominius modestus* is held at a constant 12°C in the laboratory, individuals breed throughout the year (Harms 1984). Crisp & Chipperfield (1948) commented that *Austrominius modestus* breeds prolifically over the greater part of the summer, while Crisp & Davies (1955) noted that a high percentage of individuals in fast-flowing water can be found brooding in warmer months in Great Britain. In the 1950s, Crisp (1957) commented that it was the only barnacle species in Britain which has egg masses from which first-stage nauplii can be obtained throughout the year, at least in certain parts of the British coast (Wisely 1960). A number of authors have examined how reproduction can vary within a geographic region, such as Wales. Variability occurs between sites, even between closely located ones, but also between years. For example, at Menai Bridge, in North Wales, *Austrominius modestus* breeds and contains nauplii all year round (Crisp & Patel 1961, Foster 1971b), but nearby at Bangor Pier, embryos were found from March–October only (Austin et al. 1958). Further south in Wales, at Swansea, (Moyse, 1960), *Austrominius modestus* produced nauplii all the year round. This was also seen by the same author a few years later, when a high percentage of *Austrominius modestus* samples collected from the piles at Mumbles Pier, Swansea, Wales, had embryos at most times of year (Moyse 1963). Based on sampling of *Austrominius modestus* during the summer months in southern England and Wales, ~two-thirds of the mature population contained egg masses (Crisp & Patel 1961). According to Southward (2008), *Austrominius modestus* breeds throughout the year in southern England, but the rate reduces in the second half of winter and early spring. Patel & Crisp (1960a) commented that most of the embryos present in late January and February on the Essex Coast were ready to hatch, but would not do so until temperatures increased. By contrast, in Chichester Harbour (West Sussex), Stubbings & Houghton (1964) noted that brooding adults, with stage I nauplii present, had been recorded in February, but this was unusual and liberation of larvae occurred from April onwards. These authors pointed out that *Austrominius modestus* needs a sufficiently high temperature at the time of fertilisation, egg-laying and spawning, with 6.0–6.5°C being the critical temperature for spawning. Ross et al. (2003) noted that it is summer breeding. Even at similar latitudes, there can be variation in reproduction on different coasts. In southern England, there is variation in breeding between the east and west coasts. In south-west England, continuously submerged specimens could be found brooding embryos even in the coldest months, but this was not the case in south-east England (Crisp & Davies 1955). In south-west England, up to 80% of continuously submerged specimens were brooding in summer months (at temperatures as high as 23–25°C at Burnham-on-Crouch), decreasing in the late autumn and winter (down to 15%–20%) (Crisp & Davies 1955). For *Austrominius modestus* on experimental plates suspended ~2 m below sea surface, Crisp & Davies (1955) found no lunar (hence tidal) periodicity in the breeding cycle, and they suggested that this may be the same case for intertidal specimens, too. Tighe-Ford et al. (1970) noted that in southern England, the larvae develop from late spring to early autumn, but a small percentage contained egg masses in January and February, that is, during the winter. Crisp & Southward (1958) stated the main breeding period of *Austrominius modestus* in the English Channel as May-October-January.

In their westerly introduced range, in southern Ireland, embryos were found throughout the year, but there was a peak in the summer, with up to 90% brooding, although there was some variation between their three sites, with the percentage brooding in the outfall site being significantly lower (O'Riordan & Murphy 2000). Murray (2009) recorded a maximum of 53.3% of the sampled *Austrominius modestus* brooding embryos in June 2009. Similarly, Gallagher et al. found embryos in all but one month in Bullens Bay, Co. Cork, Ireland, in 2014–2015, but the level of brooding varied during the year (see Figure 3). The only other published data for Ireland are from further north.

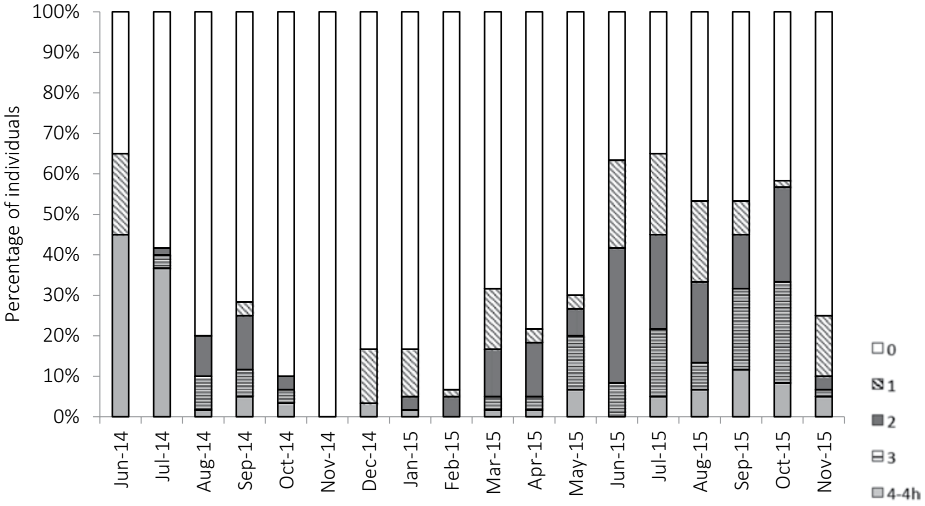

Figure 3 Percentage of *A. modestus* brooding embryos in different stages of development from Bullens Bay, Co. Cork, Ireland, in 2014–2015. Key on right-hand side of figure shows stage of development, from stage 0 (white) to stage 4-4h (stippled), using the scale of O'Riordan & Murphy (2000).

In Donegal, up to 45% were recorded brooding in June (O'Riordan 1996), but only a maximum of 28.5% in Galway Bay, between February and April (King et al. 1997).

Barnes (1992) described the breeding seasons of a number of species of barnacle in different parts of their range; however, the only location for *Austrominius modestus* was from Arcachon Bay in France, where she carried out sampling irregularly for several years beginning in 1965 ($n = 50–450$). All of the sampled *Austrominius modestus* had fertilised embryos in January and March, with nearly 100% in December (Barnes 1992). Barnes (1992) suggested that the high percentage in winter represented a population synchrony, following an autumn minimum, which may have been due to peculiar local nutrient conditions or greater competition for the amount available at this site. Synchronous breeding at this site was further supported by the release of all of the embryos in March and April and a low level or absence of egg masses during May and June. A reduction in body weight in April was suggested to be due to the barnacles not continuing to breed then, even though temperatures were much more favourable to gonadal development than in the winter. This may be a result of the local low nutrient conditions or greater competition for the available food. The body weight increased from April to June when a second brood was initiated, giving rise to a new maximum of gravid animals in July and August and consequent loss in body weight. The only other records of timing of reproduction in France and how it may vary with location were collected during surveys monitoring the spread and changes in abundance of *Austrominius modestus* on the continental coast (Barnes & Barnes 1965b, 1966, 1968b). Barnes & Barnes (1965b, 1966) reported only low levels of brooding, despite sampling in midsummer; for example, in Brittany, France, they found 0% brooding at St. Quay Portrieux (11th June), but egg masses were present at Port Blanc (15th June) and at Pornic on 16th June and 15th September 1963. Ten percent had egg masses at Ribadeo, Spain (3rd July 1963). In their survey of the French coast in 1967, some sites showed higher levels than four years previously, which may be because sampling was two months later (August). Barnes & Barnes (1968b) recorded the following percentages with egg masses: 25% at Talmont and in the Arcachon Basin, between 2% (on piles at La Jetée d'Eyrac) and 19% at Arcachon, 33%–50% at Port de Larros, 10% at Cassy, 17% at Arès, 32% at Bélisaire, 50% on pignots in Sableyre de Comprian and 15% at Pyla-sur-Mer. At Petit Nice, on exposed concrete blockhouses, south of the dunes at Arcachon, many of the *Austrominius modestus* had developing embryos in April 1971 (Barnes et al. 1972). Further south, in Ria de Arousa, NW Spain, it has been reported that *Austrominius modestus* can breed throughout the year (Macho 2006, Macho et al. 2010). Other species overlapping in the introduced range of *Austrominius modestus* in Europe may also have embryos present during the winter months, but the level of brooding is lower than when there are higher temperatures. At the known southern-most limits of its European range, (Gallagher, 2016, Gallagher et al., in prep.) recorded the percentage of *Austrominius modestus* that had embryo masses in February and August at Farol, Ihla de Culatra, Algarve, Portugal, as well as the percentage with different stages of egg development weekly over a four-week period in July-August, in comparison to the native *Chthamalus montagui* Both species had embryos present in February and August, but the levels of brooding were higher in *Austrominius modestus* (maximum = 67%). For both species on all four dates in July-August, stage 4 and 4 h embryos were present, but *Austrominius modestus* had a higher percentage of these, as well as having up to 85% with egg masses versus only 53% in *Chthamalus montagui.* O'Riordan & Ramsay (1999) reported that 60% of their sampled *Austrominius modestus* from Praia de Faro contained embryos in April.

Moyse (1963) linked the longer breeding season of *Austrominius modestus* (than *Semibalanus balanoides* and '*Chthamalus stellatus*') to the former's more catholic feeding habits. The larvae of *A. modestus* can be reared on both diatoms and flagellates, unlike the two other species. *Semibalanus balanoides* were reared successfully on diatoms, but not flagellates and vice versa for '*Chthamalus stellatus*', which is linked to their different geographic distributions and that of available food. These three species have distinct ranges in egg size, which has implications for the naupliar size and on the size of the phytoplanktonic species on which they feed in the wild (Barnes & Barnes (1965a).

Breeding and anthropogenic effects of temperature and salinity: In their introduced range, *Austrominius modestus* can be found in large numbers in estuarine areas, but the only published comparison of breeding in different salinity conditions in the field is that mentioned previously (O'Riordan & Murphy 2000). In southern Ireland, a significantly lower percentage of *Austrominius modestus* were brooding at their site of a warm-water outfall from a power station, where a wide range of salinities were recorded, than at another site nearby (O'Riordan & Murphy 2000). In contrast, Pannell et al. (1962) reported that the breeding season of *Austrominius modestus* was prolonged and extended into autumn in parts of Southampton water, which they suggested may have been a result of elevated warmer water conditions due to the activity of the Marchwood Power Station.

Variation in the number of broods

Although *Austrominius modestus* can have multiple broods per year, only a few publications have examined the number of broods in detail. Crisp & Davies (1955) pioneered the use of glass slides to examine *in vivo* the breeding of this species, which is possible because the embryo masses could be seen developing, as this species has a transparent membranous base. It would be useful to use similar methods to examine the age of first brooding and number of broods/year in other parts of *Austrominius modestus*'s introduced range, as well as in Australasia. This would be especially interesting at the current northern and southern limits of its introduced range. The range limits may be controlled by cold temperatures and out-competition by arctic-boreal barnacle species, but potentially lowered fecundity and desiccation effects on cyprids, metamorphs and maybe adults, at least intertidally, at the northern and southern limits, respectively.

Crisp & Davies (1955) described how reproduction in *Austrominius modestus* is characterised by a succession of broods, with the time taken for each brood to develop varying between individuals and season, with temperature being the main controlling factor. They estimated that in Great Britain, subtidal *Austrominius modestus* may produce 12 broods per year (but see subsequently), which is very different to the cold-water species *Semibalanus balanoides* and *Balanus balanus*, in which individuals only produce one brood per year. Other species (e.g. *Chthamalus stellatus* and *C. montagui*) overlapping in the introduced range of *Austrominius modestus* in Europe may also produce multiple broods per year. However, the maximum number of broods per year was usually two in 1+ individuals (O'Riordan et al. 1992), but zero to two in their first summer after settlement. This was seen through following individuals using experimental plates similar to Crisp & Davies (1955), rather than calculating based on the state of the gonads or embryos in a population. Crisp & Patel (1961) estimated that between mid-July until December, their experimental subtidal *Austrominius modestus* population in Menai Straits, Wales, could have 8 to 10 broods. They noted that the last brood of the season for a 0+ individual would be the heaviest. In western Scotland, where temperatures are only moderate (maximum 15–16°C), in its first year, *Austrominius modestus* may only produce one or two broods and only two or three broods per year in subsequent years (Barnes & Barnes 1962). However, further south, in Ria de Arousa, NW Spain, where it has been reported that *Austrominius modestus* can breed throughout the year, it was estimated that it can produce 18–22 broods per year (Macho 2006, Macho et al. 2010).

Fecundity

Austrominius modestus shows great/remarkable fecundity (Knight-Jones & Waugh 1949, Crisp & Davies 1955) or prolificacy (Darwin 1854, Moore 1944, Bishop 1947, Knight-Jones 1948). To date, little work has examined fecundity of *Austrominius modestus*, but no difference was found from Scotland to Portugal (see details subsequently). It is known that *Austrominius modestus* has smaller broods than many other barnacle species, but this may be compensated by producing multiple broods per year. In crustaceans, the number of eggs carried by a parent at any one time is a function of the size of the parent, but in barnacles it varies also with age, food supply and crowding. Barnes & Barnes (1968b) defined barnacle fecundity as the number of eggs produced per given increase in weight of the adult (slope of the adult size – egg number regression) per unit time. For *Austrominius modestus* (based on collections for Stranraer, Ribadeo, Silloth, Portosin, Pornic, Pontevedra, Croix de Vie and Nazaré), Barnes & Barnes (1968b) gave this as 1800 eggs per 1.0 mg dry body weight. This weight represented a moderate-sized individual. No significant differences in fecundity between site or region were found for *Austrominius modestus* (from Scotland to Portugal) and four other barnacle species (*Amphibalanus amphitrite, Perforatus perforatus*, *Euraphia depressa* and *Pollicipes cornucopia*), unlike their results for *Amphibalanus improvisus*. They suggested that the lack of variation was because the first five species occur in a relatively narrow range of ecological conditions, so egg production is similar.

In order to compare the reproductive efficiency of different barnacle species which may vary greatly in adult size, Barnes & Barnes (1968b) suggested using the number of eggs produced per increase of 50 µg dry body weight (N). This can be multiplied by the egg volume (V) to give the product ($N \times V$), which can be multiplied by the number of broods (B), when known, to give the metabolic efficiency of egg production (NVB) (the rate at which a given increment of body weight produces egg tissue). For *Austrominius modestus*, using samples collected from Stranraer, Scotland, they multiplied the number of eggs per increase of 50 µg dry body weight (87.5) by an egg volume of 2.05×10^{-6} mL, giving a product of 179. These authors then used Crisp & Davies (1955) data for *Austrominius modestus* living on continuously submerged plates, with presumably excellent nutritional conditions. If 14 days is assumed the minimum time required to produce a brood, some 26 broods could be produced a year; giving a NVB of 4654 (i.e. 26 × 179). When this value was corrected to compare with the eight-month period of brooding of *Semibalanus balanoides*, the metabolic efficiency of egg production was similar. However, because the eggs of *Austrominius modestus* are much smaller than those of *Semibalanus balanoides*, *A. modestus* produces more nauplii per unit weight of egg tissue. Crisp (1987) pointed out that a small brood size may be counterbalanced by warm-temperate species being able to produce multiple broods. Barnes & Barnes (1968b) noted that the smaller eggs of *Austrominius modestus*, which are produced in successive though smaller broods, can settle and reach maturity quickly and so contribute to further egg production, giving this eurythermal species a tremendous advantage over *Semibalanus balanoides*. This is one of the mechanisms facilitating its initial rapid spread. The potential ability to produce larvae over a longer period of the year than *Semibalanus balanoides* is also advantageous (Leloup & Lefevere 1952).

Crisp (1960b) suggested that the high temperatures and prolonged summer that occurred in 1959 in Great Britain may have allowed individuals to breed for a longer period of the year, resulting in increased fecundity. Greater fecundity boosted the spread of *Austrominius modestus* on both the east and west coasts, including the Firth of Clyde, Scotland, towards its northern limit, after little change in the previous five years.

Barnes & Barnes (1968b) pointed out that when comparing the overall egg production of different species and the potential competition for space on the substratum, it is necessary to consider the size (age) structure of the population as well as other factors. Also, they suggested that within the littoral, *Austrominius modestus* broods much less frequently than the every 14 days seen in the sublittoral. Barnes et al. (1971) estimated that in Arcachon, France, egg production of *Austrominius modestus* was 6.26 g dry weight per m^2 surface area per year.

With respect to fecundity over a lifespan (although how long *Austrominius modestus* lives in different conditions is not known yet), Crisp & Davies (1955) estimated that if *A. modestus* lives for three breeding seasons, having an average number of 500 nauplii in each brood, and 12 broods per season, the total output of nauplii would be ~18 000 per individual.

Crowding and food supply: Another factor affecting reproduction is when crowding among individuals reduces food supply. In laboratory conditions, fecundity increased with access to unfiltered, flowing seawater, but when starved, no fertilisation occurred and release of larvae was delayed (Crisp & Davies 1955). Even so, the normal cycle resumed a few weeks after being returned to non-filtered seawater (Crisp & Davies 1955). Crowding (and thus less available food) delayed the onset of breeding, but egg masses were found in smaller *Austrominius modestus* (but of about the same age) than in uncrowded individuals (Crisp & Davies 1955, Crisp & Patel 1961). According to Crisp (1959a), Clegg (unpublished observation) found that eggs of *Austrominius modestus* developed from a fairly early stage (Stages 5–9, Crisp 1954) in seawater *in vitro* without difficulty and hatched.

Barnacle age, size and egg production: As mentioned previously, *Austrominius modestus* can start breeding at a very young age, but Barnes (1989) pointed out that age can also affect the number of eggs produced. Crisp & Patel (1961) suggested that for a given weight, the weight of egg masses and number of eggs was less in small (younger) barnacles than in larger (older) ones. Crisp & Davies (1955) said that their subtidal experimental *Austrominius modestus* approached maturity at a RCD of 4–7 mm, but they found that under experimental conditions, those with a RCD measuring >6 mm were more fecund (i.e. bred more frequently) than those between 5–6 mm, which in turn were more fecund than those between 3–5 mm.

Sterility and age: Unlike some other barnacle species, there is no evidence to suggest that fecundity of *Austrominius modestus* decreases with age. Crisp & Davies (1955) reported that at least some subtidal *Austrominius modestus* in their third summer contained embryos, and there was no significant difference in breeding behaviour when compared with younger, but mature, individuals. This is despite the fact that at this age, they would have already produced 30–40 broods. They pointed out that a similar lack of sterility with age had previously been seen in *Balanus balanus*, but *Semibalanus balanoides* does show sterility (Moore 1935).

Moulting and breeding: The relationship between breeding and ecdysis has been examined under laboratory conditions for a number of acorn barnacle species, including *Austrominius modestus* (Crisp & Patel 1958). All of the species studied had a prolonged intermoult period when the barnacle had embryo masses present, but still moulted. For *Austrominius modestus*, similar to three other species studied (*Balanus crenatus*, *Perforatus perforatus* and '*Chthamalus stellatus*') where embryonic development is relatively fast, especially at higher temperatures, normal moulting resumed shortly after incubation. The moulting rate was dependent on food supply and temperature, but the normal intermoult period for these species was only 6–10 days. However, Patel & Crisp (1961) gave similar intermoult periods for *Balanus crenatus* (11–13 days at 10–11°C) and *Semibalanus balanoides* (10–12 days at 8–12°C) but only 6 to 7 days (at 14–16°C) for *Austrominius modestus.* In *Austrominius modestus* and *Balanus crenatus*, there was no detectable influence of the moulting phase on the frequency of copulation (and hence fertilisation), and this occurred with equal ease at any time of the cycle, which was different to *Semibalanus balanoides*. Patel & Crisp (1961) reported that very few *Austrominius modestus* moulted 24 hours before liberation, but during the period 12–24 hours after liberation, the moulting rate was very high. When unfertilised, the intermoult period of *Austrominius modestus* was an average of 5.4 days, while this was 15.2 days if starved. If fertilised, the intermoult periods of *Austrominius modestus* only varied by a day (15 if fed versus 16 if starved), although the latter small difference was not seen in *Balanus crenatus*. In the laboratory, the moulting rate increased linearly from 4 to 23°C and was similar whether the animals were well fed or starved. The latter also occurred in *Perforatus perforatus*, but this pattern was not observed in starved ‘*Chthamalus stellatus*’ and *Amphibalanus amphitrite* (Patel & Crisp 1960b).

Egg shape and size

Crisp (1987) reviewed the shape and size of eggs of cirripedes and suggested that both may be useful as taxonomic characters. Barnes (1989) described the shape of fertilised eggs of barnacles as ovoid, with the width being narrower at one end, giving a tapering shape, which Crisp (1987) called ‘typically pyriform’. The shape (length/breadth) changes from egg through to stage VI nauplius, which is similar in *Austrominius modestus* as a range of *Balanus* species (Crisp 1987). Table 2 shows data from Crisp (1987) on the shape of *Austrominius modestus* eggs and nauplii. There are differences between the species that produce lecithotrophic versus planktotrophic larvae (i.e. *Austrominius modestus*), with the former having much more globular eggs, but usually fewer in number in a brood (Barnes 1989).

At least five independent factors influence variation in egg size within a species of cirripede (see Crisp 1987, for a detailed discussion): stage of development, temperature, genetic differences, individual variation and also variation within an egg mass (Crisp 1987, Barnes 1989). The greatest amount of information is available for the arctic-boreal *Semibalanus balanoides*, especially with respect to genetic, individual and environmental factors other than temperature. The size of eggs of warm-water species (that can breed continuously above a critical temperature when plenty of food is present) is greatly influenced by temperature (Patel & Crisp 1960b, Crisp 1987). Most of the published data (see Table 3) for egg size in *Austrominius modestus* gives the dimensions of the mature egg (stage 4 embryo) before it has hatched (stage I nauplius). Crisp (1976) flagged that the volume of unhatched stage 1 nauplii will be smaller than that of the hatched stage I nauplii, since the nauplii are tightly packed inside the egg case. For *Austrominius modestus*, Crisp (1987) gives an egg volume of 1.53×10^{-6} mL for the maximum size before release. This egg volume is relatively small and is in line with other warm-temperate species, which is linked to the higher environmental temperature and also the small size of the adult and hence the mantle cavity (Crisp 1987). Patel & Crisp (1960b) showed the sizes of eggs at all stages of development: from stage 1 (early development, from newly laid to a few cells), 2 (multicellular) to 3 (from the appearance of limb buds to the presence of limbs and spines), to stage 4 (nauplii eye present to hatching, 4 h) under different temperature regimes in the laboratory (see Table 3). They found that all four of the southern/warm-water species tested (‘*Chthamalus stellatus*’, *Amphibalanus amphitrite* var. *denticulata*, *Perforatus perforatus* and *Austrominius modestus*) produced larger embryos from ova when maintained experimentally at low temperatures than they do at high temperatures. They attributed this to different rates of

Table 2 Shape S (= Length/Breadth) of the egg and stage I–VI nauplius of *A. modestus*, according to Crisp (1987, Table II, p. 5) (line 1) and Foster (1967b) (line 2)

Egg	Nauplius I	Nauplius II	Nauplius III	Nauplius IV	Nauplius V	Nauplius VI
2.040	2.000	2.480	2.050	1.920	1.810	1.820
–	2.08	2.36				

Table 3 The resultant mean (±SE) length (mm), breadth (μm) and volume of eggs of *A. modestus*, from stage 1–7 and to 8–13, when parents, which were fed, were kept under different temperature regimes in the laboratory (based on Table 4 of Patel & Crisp, 1960b).

	Stage 1–7*			Stage 8–13*		
Mean T.	Length	Breadth	Volume	Length	Breadth	Volume
9°C	214±2.6	107±0.84	1.28	241±4.00	120±2.60	1.82
15°C	202±1.7	102±0.65	1.10	232±1.80	112±0.86	1.53
20°C	189±5.8	97±0.50	0.93	226±1.25	113±0.78	1.51
25°C	184±1.4	94±0.50	0.85	214±1.25	109±0.80	1.33

*See Crisp (1954) for detailed description of stages of eggs, but in 1–7, the egg is early stage, up to the yolk being divided with three to six or more yolk cells, (~stage 1–2 of O'Riordan & Murphy, 2000) while the egg in stage 8–13 is from the appearance of limb buds to the hatching of the larvae (~ stage 3–4 h of O'Riordan & Murphy, 2000).

differentiation, with slower rates at lower temperatures resulting in a larger size and vice versa. The volume of embryos increased from early to late development, mostly due to increasing length.

For cold-water, arctic-boreal acorn barnacle species, fertilised embryos decrease in size with decreasing latitude, that is, from colder to warmer waters (Crisp 1954, 1959a). The embryos of the arctic-boreal *Semibalanus balanoides* were larger where winters were severe and summers relatively cold, irrespective of the latitude (Barnes & Barnes 1965a). They suggested that the change of egg size within a warm-water or eurythermal species over a similar latitudinal range is much smaller than for *Semibalanus balanoides*, which they attributed partly to the rapid breeding cycle, so that any given generation of eggs is subjected to the effect of temperature for only a short time, which would be the case for *Austrominius modestus*.

To remove any influence on the early stages of development prior to fertilisation, Patel & Crisp (1960b) transferred fertilised eggs, at early, middle and late stages of development, from three parents. They then examined the effect of three different temperatures on subsequent stage I nauplius size (length, breadth and derived volume) of released naupliar stage I when embryos were incubated *in vitro*. They suggested that temperature affected both the ova and subsequent embryo and hence naupliar stage I size. Although there was variation in nauplius size, even within a brood, Patel & Crisp (1960b) reported that those that developed *in vitro* at the highest temperatures (23°C) resulted in the smallest nauplii I, and those transferred at the earliest stage resulted in the greatest loss in volume (see Table 4), which Crisp (1987) attributed to an increase in metabolic rate resulting in extra consumption of reserves. For *Austrominius modestus*, O'Riordan & Murphy (2000) found that eggs within a brood were all at the same stage of development, which they attributed to the relatively small and thin egg mass, which, as suggested by Patel & Crisp (1960a), may allow uniform development.

Larval stages

Austrominius modestus has six naupliar stages, followed by a single cypris stage, which is adapted morphologically for site selection and settlement. The stage I nauplius, which is non-feeding (Foster 1967b) and moults to the stage II nauplius, occurs for a very short time only, from just a few hours (Foster 1967a), to 24 hours in the laboratory (Knight-Jones & Waugh 1949). The maximum length of time that an individual naupliar larva of *Austrominius modestus* can remain in the water column before metamorphosing into the non-feeding cypris stage is unknown, but the minimum time from stage I nauplius to cyprid has been calculated for laboratory-reared larvae to be six days (see e.g. Moyse 1963, Foster 1967a,b, Barker 1976). Combining his data on rearing larvae in the laboratory and long-term temperature data, Harms (1984) predicted the duration for the larvae to develop into

Table 4 Influence of temperature on mean (±SE) length (µm) and breadth (µm) of resultant stage I nauplii of *Austrominius modestus* when the fertilised eggs, at different stages of development, have been removed from individual parents and then reared *in vitro* at 11, 16 or 23°C

		11°C		16°C			23°C		
Parent no.	Stage of egg*	Length	Breadth	Length	Breadth	% Loss	Length	Breadth	% Loss
1	3–4	268±1.5	116±0.5	252±2.5	115±0.6	7.7	229±3.9	108±1.3	26.0
2	6–7	259±1.1	118±0.9	247±2.6	114±0.8	11.0	232±5.6	112±1.4	20.0
3	8–9	260±1.1	118±1.2	252±2.0	119±2.4	1.0	246±0.5	114±0.7	12.0

Note: Stage = stage of development* of transferred eggs at the start of the experiment, % loss = percentage loss of volume of eggs in comparison to egg developed at 11°C (based on Table 5 from Patel & Crisp 1960b) and Table VI from Crisp (1987).
*See Crisp (1954) for detailed description of stages of eggs, but in 3–4, the yolk is undivided, and in 6–7, the yolk is divided with three to six or more yolk cells, while 8–9 is from the appearance of limb buds to the presence of limbs, but the setae are absent or not evident.

cyprids in the wild in the Helgoland area. He suggested 30 days in spring, but only 14 days in August. Since they have a shorter planktonic life, the larvae of species of barnacle that inhabit relatively sheltered areas, such as *Austrominius modestus*, have smaller larvae than species from oceanic and exposed coastal areas (Moyse 1963).

Numerous authors have reared the nauplii of *Austrominius modestus* in the laboratory, and a smaller number describe how to rear the cyprids. Subsequently we discuss some of the most important findings arising from this work, focussing on variations in rates of development and survival using different diets, temperatures and salinity, as well as how these affected the size of the resultant nauplii, cyprids and metamorphs.

Nauplii

Description of the nauplii

Knight-Jones & Waugh (1949) were the first authors to describe the morphology of the larvae of *Austrominius modestus*, based on the hatching in the laboratory of stage I nauplii which had been obtained from adults and from plankton samples. They measured the total length, greatest breadth of nauplii and carapace length (including length of spines). When a carapace fold was present, they found that the greatest breadth was the most useful measurement for identifying the various naupliar stages, since the carapace length is affected by the degree of flexure of the abdomen. They gave the setation formulae for the antennule, antenna and mandible for all six naupliar stages (see Table 5), accompanied by detailed drawings and the description of the naupliar stages. They described how a combination of the size, shape, limb setation and labrum of the naupliar stages could be used to distinguish *Austrominius modestus* from the larval stages of other barnacle species occurring in British waters. A very useful key for the identification of stage II–VI nauplii of common barnacles of the British Isles is that of Ross et al. (2003), who used Knight-Jones & Waugh's (1949) descriptions and measurements of *A. modestus*. They pointed out that although both *Austrominius modestus* and *Perforatus perforatus* nauplii have a trilobed labrum, those of the former can be distinguished by the fact that the medial lobe of the labrum extends out much further than the two lateral lobes (in comparison to only slightly in *P. perforatus*), as well as other differences, for example, in cephalic shield size and shape and the stubby frontolateral horns in stages IV–VI. Ross et al. (2003) included scanning electron microscopy (SEM) of the ventral surface and the medial lobe of the labrum of a stage VI nauplius of *Austrominius modestus*.

In order to be able to identify the larvae of different species of barnacle in the water column by morphology, it is necessary to rear them in the laboratory to be sure of the parentage and then

Table 5 Setation formula (follows Bassindale 1936) of the appendages of the nauplii of *Austrominius modestus* reared by Barker (1976) from adults collected in Leigh, Auckland, New Zealand, based on his Table 2

Stage	Antennule	Antenna	Mandible
I	0.**4**.2.1.1	0.**1**.4–0.**3**.2.2.2.G	0.**1**.3–0.**3**.2.2.2.G
II	0.**4**.2.1.1	0.**2**.5–0.**3**.2.2.3.G (0.**1**.6–0.**3**.2.2.3.G)	0.**1**.3–0.**3**.2.2.2.G
III	1.**4**.2.1.1	0.**2**.5–0.**3**.2.2.4.G (0.**1**.6–0.**3**.2.2.4.G)	0.**1**.4–0.**3**.3.3.3.G
IV	1.1.**4**.2.1.1	0.**2**.7–0.**5**.3.2.4.G	0.**1**.4–0.**4**.3.3.3.G
V	1.1.1.**4**.2.1.1.1 (2.1.**4**.2.1.1.1)	0.**3**.8–0.**5**.3.2.4.G	0.**1**.5–0.**4**.4.4.3.G
VI	1.1.1.**4**.2.1.2.1 (2.1.**4**.2.1.2.1)	0.**4**.8–0.**5**.3.2.4.G	0.**1**.5–0.**4**.4.4.3.G

Note: Bold numbers refer to terminal setae. The formulae on brackets are those differences found by Knight-Jones & Waugh (1949), which are explained in the text below.

describe their main characteristic features. Stage I and II nauplii of *Austrominius modestus* and six other species from New Zealand samples, reared in the laboratory from stage I nauplii taken from the mantle cavity of adults, were described by Foster (1967b). A combination of features, such as carapace shape and length/width ratio, as well as form of the labrum, allow these different New Zealand species to be distinguished. Following on from the work of Knight-Jones & Waugh (1949), Foster (1967b) noted that the labrum of stage II nauplius of *Austrominius modestus* with its distinct protruding middle lobe and relatively short but forwardly facing front-lateral horns are distinguishing characteristics from other New Zealand species. Subsequently, Barker (1976) reared all of the naupliar stages (and cyprids) of six of the same species (including *Austrominius modestus*) and developed a key to distinguish between the nauplii of these species. Although Knight-Jones & Waugh (1949) had described the larvae of *Austrominius modestus*, they were from European adults. In the New Zealand specimens, Barker (1976) mentioned some differences in setation from earlier descriptions; however, this was probably due to a different interpretation of what constitutes a group of setae, rather than a structural difference in the larvae (Barker, 1976), as the text diagrams of Knight-Jones & Waugh (1949) indicated identical setation to New Zealand nauplii (see Table 5). Egan & Anderson (1985) suggested that some of the discrepancies, with respect to larval setation between Knight-Jones & Waugh (1949) and subsequent authors, may be also a consequence of different techniques of microscopy. For instance, Jones & Crisp (1954) noted the presence of a spine on the endopod of the mandible in *Austrominius modestus* larval stages collected in the plankton from four southern British estuaries and an extra seta in the form of a stub on the mandibular exopod in stage II nauplii of *A. modestus*, which were unreported by Knight-Jones & Waugh (1949). It is also possible that phenotypic traits are polymorphic at different locales.

In summary, Barker (1976) (p. 145 therein and Figure 6, Tables 2 and 3) succinctly describes the distinguishing features of the nauplii of *Austrominius modestus* as ‘Carapace triangular, length less than twice the width. Short posterior spines present in IV–VI. Short fronto-lateral horns directed anteriorly in II–VI. Frontal filaments present in stages II–VI. Abdominal process and caudal spine weakly developed in I, the former half the length of the latter in II, two-thirds the length in IV–VI. Labrum trilobed, with a median lobe extending well beyond lateral lobes’.

The paper on larval development of *A. covertus* and *Hexaminius popeiana* includes a useful table describing the features that can be used to distinguish stage II, IV and V nauplii of *A. covertus* and *Austrominius modestus* as well as the nauplii of *H. popeiana* when they co-occur in Australian waters (Egan & Anderson 1985), but there were no known distinguishable differences between stage I nauplii or the cyprids, and the limb setation has to be examined to distinguish their stage III nauplii.

Frontal horns, filaments and sensory function: Walker (1973, 1974) described the frontal horns and associated gland cells and the frontal filament complexes of the nauplii of *Austrominius modestus*, *Chirona hameri* and *Semibalanus balanoides*. The frontal horns of naupliar stages I and II *Austrominius modestus* are only about a third of the size of those of *C. hameri*, but they have a similar external appearance and have ventral perforations, while those of *Semibalanus balanoides* are much shorter and lack the perforations. However, for the three species, the associated gland cells of all naupliar stages and the frontal horns of naupliar stages III–VI are morphologically similar.

The frontal filaments have a pressure and/or orientation sensing function (Walker 1974). Stage I nauplii are strongly photopositive at liberation (Wisely 1960), and this is still the case for stage II nauplii of *Austrominius modestus* (Crisp & Ritz 1973). The latter authors showed the loss of dark adaptation of stage II nauplii of *Austrominius modestus* when subjected to white light in the laboratory. Tighe-Ford et al. (1970) had noted that nauplii are positively phototactic and, subsequently, Barnes & Klepal (1972) determined the spectral sensitivity of the naupliar eye of dark-adapted stage I nauplii of *Austrominius modestus* and *Semibalanus balanoides* and found maximum sensitivity for positive phototaxis between the wavelengths of 520–530 nm (blue-green). The photic response of the cyprids of *Austrominius modestus* is particularly interesting, since this species can settle both intertidally and sublittorally.

Use and effects of different culture conditions on naupliar development

Temperature, diet and salinity

Different culture conditions, in particular temperature, diet and salinity, affect rates of development, survival and the resultant size of the larvae. Moyse (1960), working in Swansea, Wales, noted that *Austrominius modestus* larvae in the laboratory can tolerate considerable fluctuations of temperature. At 20 ± 3°C, when *Austrominius modestus* nauplii were reared using different species and densities of flagellates and diatoms, a unialgal diet of the diatom *Skeletonema costatum* was found to be very successful, but nauplii fed on the diatom *Phaeodactylum closterium* took longer to develop, while those fed certain species of flagellates seemed to have thin cuticles and were unable to moult properly (Moyse 1963). A link between the geographical distribution of barnacle species and the diet of the larvae is possible, with those of cold-water species (with widely spaced setules) developing well on diatoms, while those of warm water (with a fine-meshed filter) develop better on flagellates (Moyse 1963). According to Stone (1989), *Austrominius modestus* has an intermediate distribution, so the larvae can survive on both larger diatoms and smaller flagellates, which may facilitate breeding and larval production throughout the year. However, *Austrominius modestus* larvae survived better on diatoms at cooler temperatures, but at warmer temperatures, flagellates promoted survival. By contrast, the nauplii of *Semibalanus balanoides*, whose larvae are released in spring, do better on diatoms (Stone 1986). Anderson (1994) pointed out that the retention of a moderate mesh size of 3–4 μm on the basal antennal setae of the nauplii of *Austrominius modestus* and *Perforatus perforatus* allows them to exploit a mixed diet.

Stone (1986, 1988, 1989) carried out some of the most detailed experiments using six different feeding regimes and different diets for the nauplii of *Austrominius modestus*, examining how these affected the rates of development and survival, as well as the sizes of the resultant nauplii (culture temperature was 18 ± 0.2°C, with a salinity of 35). Development was fastest when nauplii were fed a uniagal diet of the small flagellate *Isochrysis galbana* for the first four days, followed by a uniagal diet of the larger flagellate *Rhodomonas* sp. from days five to nine, but a mixed diet of these two species throughout gave higher survival (Stone 1988). These differences may be due to an increase in the mesh size of the antennal filter during growth of the nauplii. Stone (1988) reiterated the importance of the antennal endopodite for feeding in the nauplii and that the intersetular distances affect what size of particles can be captured. Of the total area covered by setae on the endopodite, there was a greater coverage of finely spaced setules (<5 µm apart) in the stage II (36.3 9%) vs stage VI (13.92%) nauplius of *Austrominius modestus*. The closest intersetular spacing on the antenna in stage II *Austrominius modestus* was 2 µm, with some spaced 3 or 4 µm apart in stage II and VI, but with the maximum spacing being 13 µm (see Figure 3, p. 26, Stone 1989). These results supported the suggestion that nauplii collect their food by means of filtering appendages rather than by localised currents alone, with the larvae selecting larger-sized particles as they grow (Stone 1988, 1989). Significant differences in carapace length and width of Stage IV and V nauplii occurred when they were fed different diets, with larger larvae resulting when larger algal cells were fed in the later stages of development (Stone 1988). According to Stone (1989), Walker et al. (1987) observed nauplii of *Austrominius modestus* (and *Semibalanus balanoides*) when they were restrained and found that the feeding mechanism relied on the recovery stroke of the antennae, which brought food particles within reach of the mandibles on their backward stroke. The mandibles then pushed the particles towards the labrum. In her test of ten different diets for *Austrominius modestus* nauplii, Stone (1989) found that diets containing the dinoflagellate *Prorocentrum micans* resulted in deformities of the ventral thoracic process in stage IV–VI nauplii.

The previous experiments comparing different diets used constant temperatures, while other authors tested the effects of a number of temperatures on the rate of development of the nauplii of *Austrominius modestus*. In the laboratory, nauplii develop at different rates depending on the temperature, but there is conflicting evidence as to what temperature is best, which may be linked to where the adults are collected. In their native range, Barker (1976) collected adults from the Leigh area, Auckland, New Zealand, and used *Skeletonema costatum* to rear *Austrominius modestus* and tried three different temperatures (20, 25 and 30°C). All six naupliar stages were cultured at 25°C, but the culturing took longer than at 20°C (e.g. stage VI after eight days vs five days at 20°C), and only the first two stages appeared at 30°C. Tighe-Ford (1977) had also successfully reared nauplii at 20°C, using *S. costatum*. In their introduced range, Harms (1984) reared larvae from stage I nauplii taken from adults that were collected in the intertidal of Helgoland. In contrast to Barker (1976), of the four constant water temperatures tested (at a salinity of 31–33), it was at the highest experimental temperature (24°C) that the larvae of *Austrominius modestus* developed quickest (~seven days) and showed the lowest mortality, although 24°C could be close to the nauplii's upper temperature limit (Barker 1976), since Tighe-Ford et al. (1970) had found 23°C to be lethal for the nauplii of *Austrominius modestus*. The ingestion rate of *Austrominius modestus* larvae has been found to increase with temperature (Harms 1987), maximum ingestion rate of the nauplii occurring at alga concentrations of >100–150 μl^{-1} (Yule 1986).

Temperature and swimming activity of Austrominius modestus nauplii

Temperature affects the swimming activity of *Austrominius modestus* nauplii reared in the laboratory, with their limb beat movements changing when food is present (Yule 1984, 1986). The rate of limb beat of stage II nauplii of *Austrominius modestus* was 7.2 beats per second at 20°C (Yule 1984) (see Anderson 1994, Table 8.2 for a comparison with 14 other barnacle species), while the mean limb beats per second of stage IV nauplii increased from 5 to 30°C, with a twofold increase from 5 to 15°C (i.e. a Q_{10} of 2.00). From 5 to 25°C, *Austrominius modestus* spent a greater percentage of time swimming (in the tested 5-min periods) than *Semibalanus balanoides* and *Chirona hameri*, with greater disparities as the temperature increased. At the lower temperatures, some of the *Austrominius modestus* were swimming continuously for the 5 minutes, showing no significant difference in the percentage time swimming even when monitored for six (at 20°C) to seven (at 15°C) hours. The average swimming stroke rate of *Austrominius modestus* decreased slightly as the temperature and limb beat frequency increased, which Yule (1984) suggested may, along with its eurythermy, have aided the colonization of north-temperate shores by this species that originated in the subtropical waters of New Zealand.

Size of the nauplii

The size of the adult of a barnacle species affects the size of ova and embryos, which then follows through to the naupliar size (Barnes & Barnes 1965a). Since size may be used to initially distinguish the nauplii of *Austrominius modestus* from those of other barnacle species, it is important to consider how size may vary depending on the laboratory rearing conditions and be aware that size (and colour) of cultured larvae may differ from 'wild' larvae collected from the plankton (Barker 1976). Small stage I and II naupliar larvae (measuring 110–140 µm (length including spines of 240–260 µm, respectively), as well as a few measuring 150–170 µm (length including spines of 360–430 µm), were obtained only from the laboratory (from adults collected in southern England) (see Table 6a) (Knight-Jones & Waugh 1949). Larger larvae of *A. modestus* were produced at lower temperatures (10°C vs 20°C) in the laboratory, although they took longer to develop (see Tables 1–3 of Tighe-Ford et al. (1970), for measurements and Table 4 for a comparison with Knight-Jones & Waugh 1949). Barnes & Barnes (1965a) give a measurement of 192 µm long for a fully ripe egg (containing the stage I nauplius) of *A. modestus* from Pontevedra, Spain (42°25′), which is similar to that given by Crisp (1954) (93 µm wide × 190 µm long). The size of a Stage I nauplius at 125 × 250 µm (so a volume [*V*] of 2.05×10^{-6} mL) is larger than species of *Chthamalus* but smaller than *Semibalanus*, *Balanus* and *Tetraclita* species (see also Crisp 1987). It was suggested that a reduction in embryo, and hence naupliar, size might be associated with euryhaline behaviour, since those of *Amphibalanus improvisus* ($V = 1.26 \times 10^{-6}$ mL) had the smallest balanid embryo (Barnes & Barnes 1965a). However, the volume of the embryos of *Amphibalanus eburneus* ($V = 3.18 \times 10^{-6}$ mL) and *Austrominius modestus* are not that small, but this may be because although these two species are euryhaline, they are probably less so than *Amphibalanus improvisus*. In plankton samples from the Burnham-on-Crouch district, Knight-Jones & Waugh (1949) reported no appreciable difference in size between those liberated during the early and later parts of the season, but later stages were much more variable in size than earlier stages. Stage I nauplii of *Austrominius modestus* collected from the plankton in New Zealand measured 150 × 360 µm, while cultured stage I nauplii were smaller, measuring 100–110 × 210–230 µm (Barker 1976) or 120 × 250 µm (Foster 1967a,b). Please see Tables 6a and 6b for differences in the size of larvae cultured in Great Britain vs New Zealand. Stone (1988 and 1989) found differences in size of stage IV–VI nauplii reared using different diets (see her Figure 1, 1988, and Table III, 1989) (when temperature was 18 ± 0.2°C and a salinity of 35). Please see 'Physiology and Function' regarding laboratory experiments on the effects of salinity on the development of nauplii). Similar to Tighe-Ford et al. (1970), Harms (1986) noted that stage VI nauplii grew bigger at low temperatures and attained their maximum

Table 6a Size in µm of larvae of *Austrominius modestus*, acc. to Knight-Jones & Waugh (1949), based on laboratory and plankton samples (June–July 1948 from Burnham-on-Crouch district)

	Carapace		
Stage	Greatest width	Length	Total length
I	110–140	–	240–260
II	150–170	–	360–430
III	180–200	210–250	350–430
IV	220–250	290–350	390–500
V	260–310	340–440	450–570
VI	330–410	420–550	480–710
Cyprid	–	540–560	–

Note: Length and total length include the caudal spines.

Table 6b Size of larvae (µm) of *Austrominius modestus* reared by Barker (1976) and Foster (1967b), col. 4, 5 and 6 in New Zealand

	Carapace				
Stage	Width	Length**	Width	Length	Length/width
I	100–110	210–230	120	250	2.08
II	150–160	360–380	150	360	2.36
III	180–200	410–450			
IV	220–240	280–290**			
V	270–290	340–370**			
VI	350–370	440–480**			
Cyprid	230–260	510–580			

Note: Length** in stages IV, V and VI excludes the caudal spines and Foster (1967a,b) col. 4, 5 and 6.

size at a salinity of 30 (Helgoland). Nauplii from the two New Zealand populations sampled were smaller than those from Helgoland, with the smallest being those from adults from the relatively cool South Island site of Portobello (Harms 1986).

Occurrence in the plankton timing and distribution

Larval navigation

During the pelagic phase, the larvae of barnacles respond to various environmental variables (see e.g. Crisp 1974 for a description of barnacle and other marine invertebrate navigation). In Wellington Harbour, Port Nicholson, New Zealand, the aggregation of *Austrominius modestus* nauplii was positively correlated with water temperature but negatively with salinity (Cassie 1959a,b, 1960, 1962), while Martin & Foster (1986) found that the larvae of *A. modestus* were retained almost completely within Mahurangi Harbour in New Zealand. It was discovered that nauplii of *Austrominius modestus* in the photonegative condition can be made photopositive (resulting in them swimming upwards) after a positive change in hydrostatic pressure, but they do not respond to negative pulses or a fall in pressure (Knight-Jones & Qasim 1966). In northwest Europe, Crisp (1958) had shown how the rate of spread of *A. modestus* could be explained by relating the larval life in the plankton to eddy diffusion.

Timing of occurrence in the plankton in European waters

The timing and peaks in abundance of *Austrominius modestus* nauplii in the plankton varies with location, occurring throughout the year in some locations, but more seasonally in others. *Austrominius modestus* nauplii occurred in the plankton near Helgoland, Germany, from May to the end of October, but they were most abundant in July and August (Harms 1984). Further south, Lang (1980) mentioned the probable seasonal occurrence of nauplii of *A. modestus* in the plankton in Great Britain from April–November but questioned whether they are present in December–March. However, they have been found around the island of Anglesey, North Wales, throughout the year, but there were higher abundances in late summer and autumn (Bennell 1981). During weekly sampling in 1979–1981 of the plankton SW of the Isle of Man, Salman (1982) noted that the larvae of *A. modestus* were very rare. Further south, in Southampton water, plankton were sampled at fortnightly to monthly intervals at two stations, Calshot and Marchwood, in 1954–1959, as part of research on the impact of warmed water from Marchwood Power Station. During the summer, the plankton was dominated by barnacle larvae, especially those of *A. modestus* (Pannell et al. 1962). In the latter years of the study, there were higher numbers of *A. modestus* larvae, which they attributed to increased nutrient supply (run-off from the River Test) and a larger area for attachment (and hence more breeding stock) due to dock and port installations nearby. They also found that the higher densities also continued for a longer time into early autumn. As mentioned previously under 'Reproduction', the elevated temperatures may have allowed *Austrominius modestus* to extend its breeding season and hence supply of nauplii (Pannell et al. 1962). Burrows (1988) carried out plankton sampling in Plymouth Sound from June–September in 1983 (weekly–fortnightly) and 1984 (weekly). *A. modestus* nauplii were found throughout this time, but large numbers of stage VI nauplii only occurred from the end of July in 1983 and September 1984, which was reflected in settlement patterns on the shore. However, small numbers of stage VI nauplii occurred throughout the sampling period, which caused Burrows (1988) to suggest that larval release in *A. modestus*, in comparison to some other species of barnacle, may be induced by factors less obviously related to sea temperature. Ross et al. (2003) stated that *A. modestus* nauplii are common from May to October but can be found all year round. Similar to Burrows (1988), Ross et al. (2003) found large numbers of *A. modestus* nauplii in their samples from Plymouth, collected in July, August and September. Ross (2001) noted a clear differential distribution of the nauplii of *A. modestus* and other barnacle species in the plankton around Plymouth which mirrors the adults, but did not give any details. No significant differences in the abundance of stages II and III nauplii of *A. modestus* occurred between ebb and flood tide (Burrows 1988), which is similar to what Wolf (1973) had found for cyprids. Burrows (1988) also found that on certain dates, *A. modestus* nauplii were the least dispersed (and lost fewer larvae) of the barnacle species examined (contrasting sharply especially with the nauplii of the exposed coastal species *Chthamalus stellatus*), which is similar to what Martin & Foster (1986) had found in New Zealand in a semi-enclosed water body, like the Plymouth Sound. In the partially mixed Ria de Arousa (Galicia, NW Spain), *A. modestus* larvae were present in the estuary during the whole year, but there were variations in peak abundance between the sampling years (1999–2001) (Macho et al. 2010). Based on their sampling at seven stations within the estuary, *A. modestus* larvae were most abundant in the inner part, showing marked larval retention inside the estuary, reflecting adult distributions in the intertidal zone, similar to what had been seen by Ross (2001) in the Plymouth Sound.

Use of larvae for laboratory studies

Due to the availability of stage I nauplii in brooding adult *Austrominius modestus* throughout the year, at least in some locations in Great Britain, and the ease of rearing them to the cypris stage in the laboratory (Crisp 1957, Holland 1987), the cyprids of *A. modestus* have been used as test species in antifouling and biofouling tests, while the nauplii have been utilised to investigate the cycling of planktonic organic matter in marine food webs. Wisely (1960) refined some of the techniques to rear them in the laboratory in the winter months in Great Britain, while Neal et al. (1986) examined how lipid changed when the faecal pellets of *A. modestus* nauplii were 'repackaged' into bigger pellets during coprophagous feeding by adult *Calanus helgolandicus*. Not only were characteristic algal hydrocarbons totally removed during feeding by the *A. modestus* nauplii, but also most of the dietary polyunsaturated fatty acids, but changes to dietary sterols were less marked. They suggested that such 'repackaging' during coprophagy may result in a higher direct input of C_{28}–C_{29} sterols to marine sediments than herbivory. Vay et al. (2001) examined digestive enzyme levels during development in the larvae of *A. modestus*.

Cyprids

Description and identification

A combination of carapace shape, pigmentation and relative size can be used to distinguish *Austrominius modestus* cyprids from those of other barnacle species occurring in European (e.g. Knight-Jones & Waugh 1949, O'Riordan et al. 2001) and Australasian (Barker 1976) waters. The cyprids of *A. modestus* are colourless to a pale straw colour and of glassy transparency (Knight-Jones & Waugh 1949, Norris & Crisp 1953). Following the work of Knight-Jones & Waugh (1949), Norris & Crisp (1953), Barker (1976) and Tighe-Ford (1977), O'Riordan et al. (2001) summarised the diagnostic carapace shape of the cyprid of *Austrominius modestus* as elongated, with a *sharp angle between dorsal and ventral surface at anterior end*; posterodorsal margin rises steeply to an angle then evenly curved; narrowly curved posterior end. The carapace is dorso-ventrally compressed, and it has a fusiform shape (Barker 1976, p. 145 and 6, Tables 2 and 3 therein). Al-Yahya (1991) reared the cyprids of *Austrominius modestus* and other species of barnacle in the laboratory (at 20 ± 2°C) and described their comparative external morphology. He provided some of the most detailed descriptions of the whole cyprids and key features, using scanning electron microscopy (see his Plates 4.20 and 4.22), as well as dimensions. The SEMs include the antennular attachment disc and organs which the cyprids use to selectively explore a surface before attachment and settlement (see subsequently). See also Jensen et al. (1994a,b) and Moyse et al. (1995) for more SEM studies of the cyprids, and Elfimov (1995) regarding the cyprid carapace. Tables 4.1 and 4.2, Figures 4.3 and 4.4 and Plates 4.20 and 4.22 of Al-Yahya (1991) are invaluable to distinguish the cyprids of nine species of barnacle that occur in the waters around Great Britain, while O'Riordan et al. (2001) tabulated (Table 1 therein, p. 310) those of cyprids of intertidal barnacles in European waters. The position of the eyes appears to vary according to the degree of extension of the antennules (Barker 1976).

Cyprid size in the plankton and laboratory cultured

Cyprids of *Austrominius modestus* collected in the wild or cultured under different conditions in the laboratory vary to some extent in length and width. Having reared the cyprids of six species of New Zealand barnacle in the laboratory, Barker (1976) flagged that size alone is an unreliable character to distinguish cyprids of different species, due to great variation, even when cultured in identical conditions, and those from the plankton are often larger. Some of the differences in the size range of cyprids seen in the wild are due to the effect of adult barnacle size on the size of ova and embryos, which then follows through to naupliar and cyprid size (Barnes & Barnes 1965b).

Cyprids of *A. modestus* collected from the intertidal at Roscoff, NW France, in late summer 1997 and 1998, which were distinguished from the cyprids of other species by their carapace shape, measured between 450 and 625 μm in length (O'Riordan et al. 2001). Those collected by Wolf (1973) from the plankton in the Dutch Wadden Sea in May 1967 were towards the smaller size, with a mean length of 444 ± 15 μm by 216 ± 11 μm ($n = 100$), while those from September 1967 measured 450 ± 16 μm by 217 ± 11 μm ($n = 40$). Cyprids collected from the plankton in the River Crouch, Essex, southern England, were larger (540–560 μm), and only showed a 20 μm variation in length, but others from the east coast of England varied between 500 and 600 μm (Jones & Crisp 1954 cited in Wolf 1973).

Cyprids cultured in the laboratory in Great Britain varied in size depending on the temperatures at which that had been reared as well as the location from where the adults had been collected. Those reared by Al-Yahya (1991) measured 467–552 μm by 191–247 μm, with a L/H ratio of 2.33, while cyprids reared in Wales, for SEM studies, ranged in length from 470–550 μm, with a mean of 510 μm (Moyse et al. 1995). Cyprids were larger when reared at 10°C (535–646 μm by 212–273 μm; mean 587 and 245 μm) than at 20°C (515–576 μm by 232–273 μm; mean 545 and 254.5 μm) (Tighe-Ford et al. 1970) or varied from a mean of 472.2–562.0 μm by 221.5–277.8 μm (Tighe-Ford 1977), while those reared in New Zealand by Barker (1976) at 20°C measured 510–580 μm by 230–260 μm. On average, cyprids of *A. modestus* are about 100 μm smaller than those of than those of *Perforatus perforatus* (Mean length 698 ± 53.2 μm) (Norris & Crisp 1953).

Length of time to development to the cypris stage and effects of different diets and temperatures

Similar to the nauplii, the rate of development to the cypris stage is affected by different diets, temperatures and light conditions. Moyse (1960) described how to successfully culture *Austrominius* *modestus* cyprids in the laboratory. He reared stage I nauplii taken from the mantle cavities of adult *A. modestus* to cyprids in six days at 22°C and in any month of the year, which is much shorter than the time it takes for the cyprids of *Semibalanus balanoides* or '*Chthamalus stellatus*' to develop. Comparing the success rate and length of time to the cypris stage of *Austrominius modestus*, using different species and densities of flagellates and diatoms, cyprids were obtained within five days, using a unialgal diet of the diatom *Skeletonema costatum* (Moyse 1963). These cyprids successfully settled, metamorphosed and grew to adult size (8 mm) on the same diet, while it took ten days and fewer cyprids were produced when fed the diatom *Phaeodactylum closterium*. It took Walker (1973) slightly longer (seven to nine days) to rear cyprids of *Austrominius modestus* from Stage I nauplii taken from the mantle cavities of adults in at 20°C, while it took Al-Yahya (1991) seven days.

Wisely (1960) investigated the effect of a number of different temperatures and flow rates, but used *Phaeodactylum tricornutum* supplemented with dried liver powder, and obtained over 3000 settling cyprids, with the first cyprids appearing after 15 days. Nauplii and cyprids were reared at the same temperature using *Skeletonema costatum* (Tighe-Ford 1977), but juvenile hormone analogues affected the size of the cyprids (see details previously in 'Physiology and function'). In the laboratory, larger cyprids of *A. modestus* were produced at lower temperatures, but they took longer to develop (21 to 34 days at 10°C vs 11 to 17 days at 20°C, with a diet of *Skeletonema costatum*), but cyprids were obtained after six days at 20°C (Tighe-Ford et al. 1970). Barker (1976) collected adults from the Leigh area, Auckland, New Zealand, used *S. costatum* to rear *Austrominius modestus* and tried three different temperatures (20, 25 and 30°C) but only got cyprids at 20°C and after six days. Tighe-Ford et al. (1970) agreed with Moyse (1963) that food was a critical factor for fast rearing of the cyprids. At 16°C, the cyprids could be obtained after 12 days when there was constant light, but it took 17 days in the dark, which might have been due to greater availability of food in the former conditions, whereby the diatoms could multiply (Tighe-Ford et al. 1970). Mortlock et al. (1984) determined the effects of farnesol on the last stage nauplii and cyprids of *A. modestus*. Metamorphosis of nauplii to cyprids and then to adults was accelerated at farnesol concentrations of 1 ppm. Finally, it was observed that in laboratory conditions when kept in shallow dishes, the cyprids of *A. modestus* may become trapped in the surface film, which was suggested to be due to the cuticle of the cyprid being strongly hydrophobic (Knight-Jones 1953).

Cyprids in the plankton

Although non-feeding (instead they use their stored lipid globules), barnacle cyprids are highly active, swimming for up to several weeks (Crisp 1974). As mentioned previously with respect to the nauplii, the authors are unaware whether any researchers have calculated how long the relatively small cyprids of *Austrominius modestus* can survive in the water column, but there are some published data on where and when they occur in the plankton. In the Wadden Sea, *Austrominius modestus* cyprids showed a groupwise occurrence at sampling depth, but this grouping appeared to be independent of the tide, but the need for more data was pointed out (Wolf 1973). No significant correlations in numbers of cyprids of *A. modestus* were found with chlorinity, silt, sand, total suspended matter or current velocity, which was very different behaviour to the cyprids of two other species studied (*Amphibalanus improvisus* and *Balanus crenatus*) (see Figure 8, p. 30, and Table XII, p. 31, of Wolf 1973). There was only a slight association of the cyprids with warm water, which suggested that they may have a slightly lower density than the seawater, which could affect their distribution in the water column (Wolf 1973). As mentioned previously, this is different to what Cassie (1959a,b, 1960, 1962) had found for stage V and VI naupliar stages of *A. modestus* in New Zealand, but this could be due different larval stages showing different behaviours. Unfortunately, Wolf (1973) did not separate VI stage nauplii into species of barnacles, but he identified cyprids of *A. modestus* in samples collected in May 1967, September 1967 and September 1969, but no *A. modestus* cyprids were recorded in the July 1967 sample. On shores studied in Plymouth, the cyprids of *A. modestus* occurred around the same time as those of *Chthamalus montagui* and *C. stellatus* in 2002 and 2003, and although their size overlapped, they could be distinguished clearly (Jenkins 2005).

Settlement and recruitment

Settlement

The moment when a planktonic larva attaches to a substrate can be defined as settlement (Keough & Downes 1982). Given the sessile nature of metamorphosed barnacles, the settlement location is very important; however, the point of attachment on a substrate is not entirely fixed, and barnacles can exhibit limited mobility (up to a few times their own diameter) when subjected to lateral pressure (Crisp 1960a). Barnacle larvae can settle on a variety of surfaces, but cyprids exhibit a preference for settling in grooves or depressions (Crisp & Barnes 1954). Using *Semibalanus balanoides* as their model organism, Hills & Thomason (1996), carried out some of the most detailed research on settlement surfaces, not just their type, but also roughness, texture ISO, contour and so on and created a 'Potential Settling Sites' index. *Semibalanus balanoides* settlement was found to be higher on rough as opposed to smooth surfaces (Hills & Thomason 1998).

Hills & Thomason (1996) outlined two processes controlling barnacle settlement. The first is oceanic currents, which transport barnacle larvae and control the locality where a cypris larva will settle. As long as the cyprids are physiologically ready to settle (Whillis et al. 1990), once present in this locality, the cypris larva will locate a suitable substrate, which is the second controlling factor, to settle on. Cyprids possess antennules, with many sensory organs. The cyprid carries out an exploratory walk (see e.g. Knight-Jones & Crisp 1953), attaching itself to the substrate at various locations via the antennules, presumably to test the adhesive nature of the surface (Crisp 1985), and leaving behind footprints of adhesive material, which may be used as settlement cues for other cyprids (Moyse & Knight-Jones 1967, Crisp 1974, 1985). The cypris larvae investigate the substrate from a broad scale to fine scale, with increasing attention given to substrates approaching the point of final attachment (Rainbow 1984).

Barnacles exhibit gregarious settlement, with cyprids readily settling where adult barnacles already exist. *Austrominius modestus* was the first barnacle species in which this was demonstrated (Knight-Jones & Stevenson 1950). This adaptation is advantageous, as their presence indicates a low risk of early mortality and thus a suitable habitat for survival; however, the tendency to settle close to adults of the same species should be stronger than different barnacle species, given the importance of cross-fertilisation and reproductive success (Patel & Crisp 1961, Moyse & Knight-Jones 1967, Crisp 1990). This is particularly important in species which are obligatory cross-fertilisers, such as *A. modestus*, which, as mentioned in 'Reproduction', requires another individual to settle within ~5 cm to allow copulation and fertilisation. The need for enough individuals to settle near one another to allow copulation was termed the 'critical breeding density' by Crisp (1958) and is one of the factors that slowed the speed of the spread of *A. modestus* in Europe.

Barnacles have the ability to distinguish between individuals of the same species or different species during settlement (e.g. Barnett & Crisp 1979, Barnett et al. 1979, Moyse & Hui 1981, Crisp 1990). Arthropodin, which is the settling factor responsible for elucidating gregarious settlement responses, is found in high concentrations in the integument of arthropods and is especially abundant in animals with recently formed cuticles, such as a newly settled barnacle or one which has just moulted (Crisp & Meadows 1962). It is possible that the very high moulting rate that occurs shortly after the release of larvae (which follows a long intermoult period when brooding embryos (see 'Reproduction' section)) promotes the settlement of other larvae in the water column at this time. No evidence of chemotaxis to arthropodin was found in barnacle cyprids when they are in the water column, since it was only when they alighted on treated surfaces that the cyprids showed a response.

Settlement of Austrominius modestus in response to its own and other species

In field experiments, settlement of *Austrominius modestus* is much higher on glass slides bearing *A. modestus* than on bare glass slides and on glass and slates plates placed in shelly areas, where barnacles are numerous, than those deployed in muddy areas where barnacles are absent. However, occasional individuals will settle in areas where settlement is sparse, which allows the colonization of new areas, and gradually other individuals will settle near these pioneers (Knight-Jones & Stevenson 1950). The gregarious behaviour not only facilitates reproduction, but also brings cyprids to habitats where other individuals have survived, thus reducing wastage through individuals settling in unsuitable localities and in isolation (Knight-Jones 1953). Cyprids respond more to the arthropodin of their own species, but that of related species evokes a similar, but less effective, response (Crisp & Meadows 1962). For both *A. modestus* and *Semibalanus balanoides*, lower concentrations of extracts (Crisp & Meadows 1962), or the presence of the same species of adult on stones (Knight-Jones 1955), induced higher settlement of its own species in comparison to the extract/presence of the other. Extracts of ‘*Chthamalus stellatus*’ induced some settlement of *Semibalanus balanoides*, but was less effective than extracts of *S. balanoides*, *Balanus balanus* or *Austrominius modestus* in descending order of effectiveness (Crisp & Meadows 1962). *Balanus crenatus* also caused settlement of *Semibalanus balanoides* (Knight-Jones 1955). Similarly, Larman & Gabbott (1975) found that *Austrominius modestus* cyprids readily settled on slates treated with extracts of both *Semibalanus balanoides* and *A. modestus,* while *S. balanoides* cyprids showed a preference for slates treated with *S. balanoides* extracts. Whillis et al. (1990) noted that there was little evidence for a graded systematic response to allospecific arthropodins, with *Chthamalus montagui* showing twice as much settlement in response to conspecific proteins, but no significant difference between the arthropodins of *A. modestus* and *Semibalanus balanoides.* The cyprids of *Austrominius modestus* often settle in close proximity to adult barnacles, both *A. modestus* adults and other barnacle species (Hui & Moyse 1982). Since *Austrominius modestus* is less discriminating than, for example, *Semibalanus balanoides*, as demonstrated by the fact that *A. modestus* cyprids can be induced to settle in response to ovalbumin, but not *S. balanoides* or *Balanus crenatus* (Larman & Gabbott 1975), it will settle in areas which are colonized already by other species and hence facilitate its spread, while Moyse & Hui (1981) noted that it may be adaptive, at least in some situations, for *Semibalanus balanoides* cyprids to settle near *Austrominius modestus* spat or adults, rather than conspecifics, since *S. balanoides* can outcompete *A. modestus* for space (Crisp 1964a,b).

Gregariousness and spacing: Although the cyprids of *Austrominius modestus* are gregarious during settlement (e.g. Knight-Jones & Stevenson 1950, Knight-Jones & Crisp 1953, Anger 1978), they may space themselves out during settlement (e.g. Crisp 1961, Knight-Jones & Moyse 1961, Moyse & Hui 1981), seeking bare spaces (Connell 1961a) and rarely touch their own species (Knight-Jones & Moyse 1961), including other recently settled *A. modestus* spat (Hui & Moyse 1982). However, Barnett et al. (1979) and Barnett & Crisp (1979) had reported that they were gregarious even at very close range, but Moyse & Hui (1981) pointed out problems with their experiments and conclusions. Hui & Moyse (1982) examined *A. modestus*’s settlement near spat of four different sizes, as well as adults of five different lengths. They found that territorial spacing occurs when the established individual is below 2 mm long. Settlement in the ‘straddling’ position is common when the established individual is over >3 mm long, whilst there is a combination for the 2–3 mm category. Furthermore, larger sizes (above 2.5 mm) were found to be increasingly attractive, for example, with 0.695 spat per adult in the >4 but <5 mm category, versus only 0.093 in the >2.5 but <3 mm (see Table 3 and Figure 1 therein).

Moyse & Knight-Jones (1967) reported that both *Semibalanus balanoides* and *Austrominius modestus* tend to space themselves out during settlement. They suggested that the short generation time of *A. modestus* reduces the chance of new recruits being able to reproduce before being crushed or lifted off by the adults. The reason for maintaining distance between *A. modestus* spat is that they offer no mechanical protection, suffer high mortality and grow quickly, posing a competitive threat (Hui & Moyse 1982). This spacing out prevents overcrowding and smothering (Knight-Jones 1951, Knight-Jones & Moyse 1961). Furthermore, this behaviour during settlement may be a factor contributing to the spread of *A. modestus*, as individuals which do not settle within dense aggregations of their own species will not necessarily be at a disadvantage (Larman & Gabbott 1975), provided there are other *A. modestus* individuals in close enough proximity to facilitate cross-fertilisation. When there is dense settlement and rapid growth, *A. modestus* may form hummocks, within 8 to 10 weeks of settling, but more settlement can still occur between and on top of the existing barnacles in the hummock (Luckens 1975). Leslie (1968) noted that on New Zealand shores, *A. modestus* has a tendency to occur in clusters.

Effect of substrate type on settlement of Austrominius modestus

Austrominius modestus is able to settle on a wider range of substrates, both natural and man-made, than some other barnacle species. It has been suggested that for *A. modestus*, the type of substrate is immaterial if conditions are otherwise suitable (Moore 1944). In its native range, *A. modestus* had been recorded on rock, concrete, iron and wood, in addition to living plants, algae, cirripedes, bivalves, gastropods, crabs, loricates and ascidians, as well as a brachiopods (Moore 1944, Luckens 1975). Zauke et al. (1992) added gravel and lava to this list of substrates for adults collected in Auckland, New Zealand. In its introduced range, *A. modestus* has been recorded similarly on numerous types of substrates, including on gastropod molluscs, crabs, tunicates, flotsam and jetsam (Hartog 1953), such as plastic litter in the Shetland Islands (Barnes & Milner 2005), as well as on *Semibalanus balanoides* and its own species. *Austrominius modestus* (and *Balanus crenatus*) were found on intertidal peat beds on the beach of Raversijde, Belgium (Jocqué & Van Damme 1971). *Austrominius modestus* does show some preferences, since where contiguous wood and iron surfaces were available, the wood was colonized much the faster (Moore 1944). Kathiresan & Bingham (2001) commented that some species of Subfamily Elminiinae appear to prefer mangroves over other substrates in South Australia, with *A. modestus* being recorded on the pneumatophores of the white mangrove tree *Avicennia marina* (Womersley & Edmonds 1958, Hutchings & Recher 1982, Bayliss 1982). In Cork Harbour, Ireland, a few *Austrominius modestus* individuals were recorded fouling on the test of another introduced species, the Korean sea squirt *Styela clava* (K. Swain & A. Greer, pers. obs. in May 2019), although Moore (1944) noted that *Austrominius modestus* favours moving, as opposed to sessile, animals as hosts. *Austrominius modestus* occurs on oysters and mussels in New Zealand (e.g. Ralph & Hurley 1952, Foster 1978) as seen in Ireland, too. In turn, *A. modestus* may itself form a suitable substrate, and in New Zealand, *A. modestus* is one of the substrata on which the barnacle *Chamæsipho columna* may occur (Moore 1944).

A number of types of substrate have been deployed as settlement panels for *Austrominius modestus*. The readiness of *Austrominius modestus* to settle (and stay attached) on glass plates was used to study its gregarious settling and brooding (Knight-Jones & Stevenson 1950, Crisp & Davies 1955). More cyprids were lost from smooth glass than frosted, suggesting a benefit of indentations, albeit small, for cyprid attachment and subsequent survival (Knight-Jones & Stevenson 1950). Crisp & Barnes (1954) labelled this tactile response rugotropic. In the summers of 1947–1949, in Burnham-on-Crouch, Great Britain, smooth slate plates that had been deployed to monitor oyster spat recruitment were usually covered by *A. modestus* within a few days (Knight-Jones 1948). When settlement was low, the cyprids tended to settle first in groups, but when it was very heavy, they noted that their distribution on these smooth plates was remarkably even. Demonstrating their rugophilic response, they noted that *Austrominius modestus* settled particularly abundantly in scratches and when there were surface irregularities. For *A. modestus*, slate panels were used also by Crisp &

Meadows (1962), while others tried roughened perspex (O'Riordan, unpublished), plexiglass (Anger 1978, Harms & Anger 1989) or Bakelite (Crisp & Barnes 1954).

Effects of biofilms on Austrominius modestus

Not only the surface itself and the presence/trace of other barnacles may be important to induce *Austrominius modestus* to settle, but also other organisms. Biofilms have both an inhibitory and stimulatory effect on *A. modestus* settlement (Hills & Thomason 1996), which is dependent on biofilm age (Neal & Yule 1994a,b). Relatively thin, dense multispecies biofilms associated with a high shear regime (83 s^{-1}) gave increased tenacity by *A. modestus* (and *Perforatus perforatus*) cyprids in comparison to relatively thick, less dense biofilms associated with a low shear regime (15 s^{-1}) (Neal & Yule 1994a,b). Although tenacity was significantly greatest for high-shear films for both species, *Austrominius modestus* cyprids attached as strongly to low-shear films as they did to unfilmed surfaces, but *Perforatus perforatus* showed better attachment to the latter. Differences between the two barnacle species towards the same biofilm suggested that differential settlement may play a more substantial role in the distribution and zonation than does post-settlement mortality (Neal & Yule 1994a,b). Furthermore, *A. modestus* showed a preference for long-immersed surfaces (see Table 4 in Skerman 1958), especially those with *A. modestus* already present. Panels which had been immersed only one month had a maximum of 26 *Austrominius modestus* per 100 cm^2 versus over 900 per 100 cm^2 on one that had been immersed two months.

Orientation of Austrominius modestus to light

Austrominius modestus orientates to light at settlement, and no rotation occurs during metamorphosis (Barnes et al. 1951). Although in deep grooves this orientation may be a response to light, in shallow grooves it is due to a rugophilic response (Barnes et al. 1951). Cyprids of *A. modestus* were found to prefer to settle on the illuminated upper side of horizontal opaque panels, being photopositive but geonegative at settlement, while *Semibalanus balanoides* settled preferentially on the undersides (Crisp & Ritz 1973). Crisp & Ritz (1973) noted that previously Barnes et al. (1951) had found higher settlement of *Austrominius modestus* on the lower surface of a horizontally exposed panel, but Crisp noted that he and his co-authors at that time had not monitored the light intensity on either side of the panel. When the numbers of spat and adults of four barnacle species, including *A. modestus*, were monitored on south- and north-facing surfaces at eight different heights above chart datum in Warwick Bay, Dale, Pembrokeshire, the zonation of the *A. modestus* spat agreed with those of the adults, with highest densities of spat and adults at 2.7 m above CD, but densities of both were lower on north-facing surfaces (adults: 50 per 100 cm^2 vs 300 per 100 cm^2; spat: 10 per 100 cm^2 vs 100 per 100 cm^2) (Moyse & Knight-Jones 1967).

Although barnacle cyprids are known to be selective in their settlement, they cannot delay settlement indefinitely and become less discriminative with age and in extreme cases may lose their ability to metamorphose (see e.g. Knight-Jones 1953).

Timing and level of settlement

The timing and abundance of settlement vary with location. In Australasia, in its native range, juveniles were found to be plentiful always (Moore 1944), with settlement occurring at any time of year in Auckland, both intertidally and subtidally (Luckens 1975). Elsewhere, in New Zealand, at Queen's Wharf, Port Nicholson, Wellington, settlement of *Austrominius modestus* was monitored on subtidal (1.2 m below low-tide level) Oregon pine test blocks (Ralph & Hurley 1952). Those which were deployed just for a single month showed settlement with a density of $\sim$4 cm^{-2} in May, the month of highest settlement. On long-term blocks, deployed for 13 months, only a few *A. modestus* were found, which was attributed to a failure to survive. *Austrominius modestus* was moderately common in May, July, October and November, but only rare in April, suggesting that the temperature may not have been an important factor (Ralph & Hurley 1952). Other fouling species (but not any other barnacle species) persisted on the blocks during this time, although no single species became dominant. At the same site, *A. modestus* was recorded also on wharf-piles and the mussel *Mytilus planulatus* (Ralph & Hurley 1952). At Lyttleton, South Island, New Zealand, settlement occurred on subtidal plates from March–November (none from December–February), but the peak settlement, in autumn and spring, was thought to be related to seasonal abundances of food for the plankton (Skerman 1958). However, cyprids were found enmeshed in polyzoan colonies in January and February, which, although not identified in the laboratory, were thought to be *Austrominius modestus*. The austral summer high temperatures during January and February were not thought to have restricted spawning or larval development, since *A. modestus* settles prolifically during these months in Auckland Harbour, where summer temperatures are an average 3°C to 4°C higher than Lyttelton (Skerman 1958). Instead, other species attached to the panels, for example, the polyzoan *Bugula* sp., may have competitively depleted the settlement and affected the growth rate of *Austrominius modestus* in certain months, either by drastically reducing the food supply in their vicinity or by mechanically fouling their opercular plates (Skerman 1958).

In its introduced range, *A. modestus* has been described as having a remarkably long settlement season (Knight-Jones & Waugh 1949), lasting longer than some of the native species (e.g. see Figure 4 for a comparison of the timing of settlement of *Semibalanus balanoides*, *A. modestus* and *Chthamalus montagui* at sites in SW Ireland in 2014 and 2015). This provides it with an increased likelihood of encountering free substrate suitable for settlement. However, this trait is not always advantageous, since high densities of *Austrominius modestus* can produce small individuals with slow growth and maturation rates. In Great Britain, the native species *Semibalanus balanoides*, which occupies a similar part of the intertidal zone as *Austrominius modestus*, settles approximately one month prior to the peak of *A. modestus* settlement, allowing the native species to utilise any substrate made available during the winter months (Crisp & Davies 1955). However, it has been suggested that *A. modestus* exhibits adaptations which compensate for a later settlement than *Semibalanus balanoides* (usually in April and May, when there is plenty of bare space) (Harms 1984, citing Lewis 1964). These adaptations include settling for a longer period; for example, in Helgoland, Germany, *Austrominius modestus* settlement (sum of individuals settled on panels during the subsequent one-month period) takes place from June to October (Harms & Anger 1983) at higher shore levels than *Semibalanus balanoides* (Kühl 1954), as well as subtidally from June to October and March–April (Anger 1978, Harms & Anger 1983, 1989). At many locations on the German coast, settlement was found to occur from May–June to October–November (Kühl 1963). In Den Helder, in the Dutch Wadden Sea, *Austrominius modestus* settlement begins in May and continues until late in the year (Wolf 1973), which, according to Wolf (1973) is similar to that recorded in Portsmouth, in southern England (Houghton & Stubbings 1963), and on the east coast of England (Knight-Jones & Waugh 1949). On shores where they co-occur and where there is no modifying effect of wave action, *A. modestus* can survive 30–60 cm higher than *Semibalanus balanoides*, which is probably dependent on the chance occurrence of favourable conditions during emersion (Foster 1971a,b). A longer settlement season gives *Austrominius modestus* a greater chance than *Semibalanus balanoides* of settling, growing and surviving high on the shore (Foster 1971a,b). In a ten-year study, the settling intensity and settling success of *Austrominius modestus* varied between years, with lower levels in springs following unusually cold winters, when adult populations in the German Bight were decimated (Harms & Anger 1989). On subtidal panels, barnacles (*A. modestus* and *Balanus crenatus*) covered up to 70%–100% of the surface at the end of the season (Harms & Anger 1989). During their surveys monitoring the spread and changes in abundance of *Austrominius modestus* on the continental coast in 1963, Barnes & Barnes (1965b, 1966) noted if spat were present: in France, they found them on 15th June

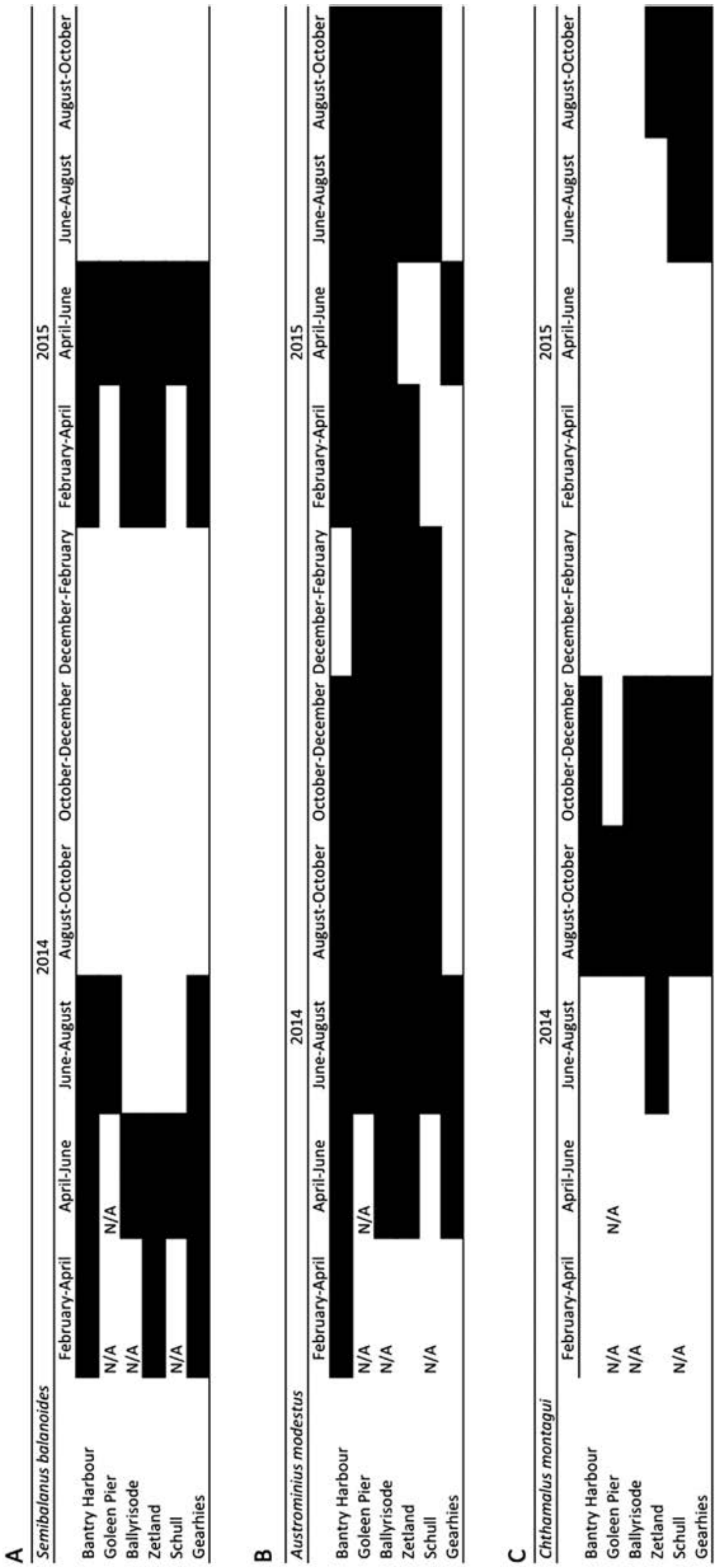

Figure 4 Timing of settlement of *S. balanoides*, *A. modestus* and *C. montagui* at sites in SW Ireland in 2014 and 2015.

at Pornic, in the Arcachon Basin at La Pointe Lavergne and on pignots in the upper part of the Chenal du Gujan and in Spain at Villaviciosa (30th June) and at Costa Nova do Prado, Portugal, on 11th July 1963.

Variation in the length of the settlement season with latitude in its introduced range: There are differences in the length of the settlement season of *Austrominius modestus* with latitude, with shorter seasons further north. For example, in Scotland, settlement was negligible on sites on the west coast except during the summer (Barnes & Barnes 1962), while on test panels immersed at Rosyth, in 1960, it occurred in late summer–early autumn (August, September and October) (Hemingway-Jones 1961). Further south, at Menai Bridge, North Wales, it was suggested that it was mostly in the summer months (May–September), with main peaks in June–July, but none was detected during winter (December–March) (Wisely 1960), but another author proposed that season did not restrict settlement of *A. modestus* there (Foster 1971b). At Menai Bridge, *A. modestus* could settle much higher than *Semibalanus balanoides*, with, in April 1968, the extreme highest specimens of *Austrominius modestus* occurring 40 cm above those of *S. balanoides* on a sheltered shore (Foster 1971b). In the Menai Straits, Anglesey, on transects that were monitored from 1974–1979, fluctuations in *Austrominius modestus* were recorded, with peaks of *A. modestus* abundance occurring when that of *Semibalanus balanoides* were relatively low (Bennell 1981). Although the cyprids of *Austrominius modestus* could be found in the plankton and on the shore at most times of year, the numbers were much less than the latter species. The timing of the peak of settlement of *A. modestus* varied greatly between years, with juveniles being most abundant from July to September in four years of the study but between October to December in two other years (1975 and 1977) (Bennell 1981). In south-east England, a similar season was seen as in North Wales, but the settlement was lighter there (Wisely 1960). In Burnham-on-Crouch, in 1948, settlement of *A. modestus* and *Amphibalanus improvisus* occurred with varying intensity from May to September but with most settling during this period being *Austrominius modestus* (Knight-Jones & Waugh 1949). The onset of settlement was thought to be related to a low sea water temperature of 14–15°C (Stubbings & Houghton 1964). In Chichester Harbour, which was described as muddy, with a high salinity, with little freshwater influx, *A. modestus* settled on subtidal panels (at a depth of 60–90 cm) from May to October between 1945–1949, but peak settlement was between June and September. In 1955, low levels of settlement were recorded also in late November/early December (seawater temperature was 7.2–8.3°C) (Stubbings & Houghton 1964). On weekly collected panels, between 1950 and 1955, settlement lasted between 16 and 22 weeks, with two peaks of settlement, a month to six weeks apart, in some years, while in other years, there just seemed to be one (Stubbings & Houghton 1964).

The number of settlers

The number of *Austrominius modestus* settlers can vary with time of year, location, depth, length of deployment and substrate. In Helgoland harbour, a maximum of 0.73 cm^{-2} were recorded on one-month subtidal panels in late August–September (Anger 1978). In Chichester Harbour, west Sussex, Great Britain, an average settlement of 31 cm^{-2} was seen in July 1945 on subtidal (60–120 cm deep) Bakelite panels, eight times higher than that seen at Wellington, New Zealand, on panels deployed at a similar depth (Ralph & Hurley 1952). Stubbings & Houghton (1964) recorded a total annual settlement varying from 10 919 to 140 891 (see Table 9 therein). The maximum settlement of *A. modestus* on one of the subtidal panels was 20 cm^{-2}. In 1952, in Brixham Harbour, South Devon, settlement was 0.01 cm^{-1} (Crisp & Davies 1955), but up to 50–100 cm^{-1} of spat could be recorded after just a week in June and July in the River Crouch in Essex. In Essex also, Waugh (1957) recorded up to 230 cm^{-2} on smooth slates. In southern Ireland, at Lough Hyne Marine Nature Reserve (LHMNR) (Ireland's only marine nature reserve), Lawson et al. (2004) found that intertidal settlement of *A. modestus* was highest from April–May and August–September, with settlement being over 300 times higher than that of *Semibalanus balanoides.* One of the reasons for its success there is the high water retention levels within the lough, as well as elevated temperatures in comparison to outside the lough, which may allow higher reproduction and retention of larvae. Gallagher et al. (2017) reported that although *Austrominius modestus* is the dominant barnacle in the intertidal at LHMNR, native barnacle species still co-exist with it there. Please see Watson et al. (2005) subsequently regarding intertidal and subtidal barnacle recruitment and survival at the Lough.

Post-settlement factors

Usually, barnacle settlement occurs over a much broader area than that eventually occupied by adults, as there are a variety of factors influencing the settled larvae or spat post settlement. In addition to these post-settlement factors, some species display zonation within the plankton, which may influence location of settlement, and patterns of zonation on the shore (Grosberg 1982). The availability of space for settlement is the factor which ultimately controls population size (Crisp 1960a). Settlement success can be determined by competitive interactions; initially, there is competition between larvae for suitable attachment substrates, and following this, developing juveniles are subject to competition from neighbouring barnacles (Svensson et al. 2006).

Based on his finding of very large specimens of *Austrominius modestus* in a drowned river valley with very strong tidal currents in northern France, Bishop (1954) suggested that the most advantageous site for barnacles to settle are those where the water movement is as great as they can tolerate. However, with respect to wave-exposed shores, Crisp (1958) suggested that cyprids of *A. modestus* do not settle there, rather than settling and then suffering post-settlement mortality due to wave action (but see previously regarding their shell structure) or predation. It was noted that since mortality of the cyprids and young adult stages of *Semibalanus balanoides*, *Austrominius modestus* and especially *Balanus crenatus* occurs naturally and regularly during intertidal emersion in dry weather, colonization of higher shore levels by these species depends on the coincidence of settlement with a sustained period of humid conditions of emersion (Foster 1971a). Maybe this is the same for *Austrominius modestus* in the hot, dry conditions of southern Portugal, its currently recorded southern introduced limit. It would be interesting to examine whether there is any difference in the rates of settlement of cyprids, successful metamorphosis and recruitment of *A. modestus* and native species at different latitudes in its introduced range, including whether there are any differences in success with day versus night attachment, as was done for chthamalid cyprids (Cruz et al. 2005).

Despite the profound structural reorganisation that is involved, barnacle cyprids require in general less than 24 hours to metamorphose into the metamorph (Crisp 1974). Under laboratory conditions, it has been reported that the cyprid *A. modestus* can metamorphose in a much shorter time, from less than four (Knight-Jones 1953, Knight-Jones & Crisp 1953) to eight (Crisp 1974) hours, although Tighe-Ford et al. (1970) noted that it occurred normally within three days. Walker (1970) had described the cement apparatus used to attach to the substrate of *A. modestus*, along with the cement apparatus of two other species of barnacle.

Recruitment

Recruitment has been defined as the number of individuals surviving for a certain amount of time, in the case of barnacles usually 30 days following settlement (Jenkins 2005). The ability of a species to colonize an area can be estimated by measuring its recruitment rate over a certain time period (Keough & Downes 1982), and panels and areas of cleared rock have been used by various authors to examine barnacle recruitment. The recruitment of *Austrominius modestus* was examined on artificial structures in cleared areas ranging in size from 6 to 25 cm^2 (Bracewell et al. 2013). Higher recruitment was seen in the larger plots, increasing until a maximum density was reached, after which there was a decline in settlement. This study confirmed that *A. modestus* has the ability to

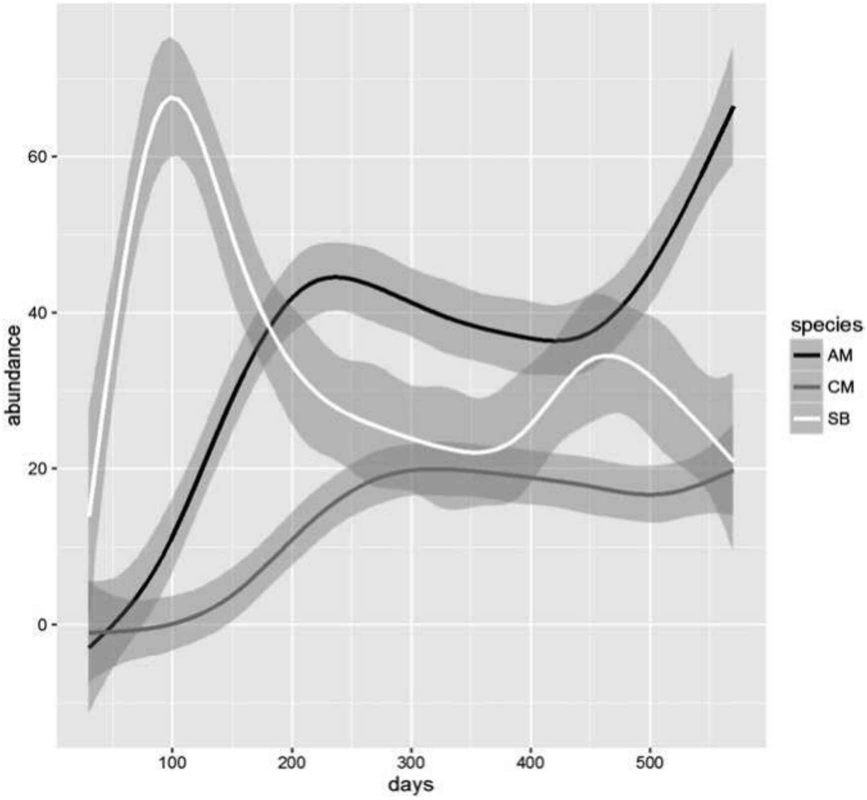

Figure 5 Number of recruits in clearance plots over an 18-month period – numbers are an average for all field sites and all shore heights sampled in south-west Ireland. AM, *A. modestus*, CM, *C. montagui*, SB, *S. balanoides*.

rapidly colonize free space made available, in this case in the form of an artificial substrate (see also Bracewell et al. 2012).

As mentioned previously, barnacle larvae are known to show a preference for rough as opposed to smooth surfaces and often settle in depressions or grooves on the substrate (Crisp & Barnes 1954), and this can affect recruitment and survival. In particular, chthamalid recruitment and survival has been shown to be higher on rougher surfaces (Coombes et al. 2015). Research by Gallagher et al. (in prep) found that, in contrast to natural rocky shores in south-west Ireland, *Austrominius modestus* by far outnumbered native barnacle species on the majority of intertidal artificial structures surveyed. Densities of 228.2 *A. modestus* per 100 cm^2 were recorded on artificial structures in south-west Ireland, while native species only attained maximum densities of 161.1 per 100 cm^2 (*Chthamalus montagui*) and 32.5 per 100 cm^2 (*Semibalanus balanoides*) (see Figure 5). At the southern introduced limit of *Austrominius modestus*, while this species was found to be most abundant on an artificial structure (Farol, Ihla de Culatra, Algarve) at a mean density of 92.9 per 100 cm^2, it was by far outnumbered by the native *Chthamalus montagui* at the same site (752.0 per 100 cm^2) (Gallagher et al., unpublished data). Similarly, on the Isle of Cumbrae, Scotland, close to the northern introduced limit of *Austrominius modestus*, the native species *Semibalanus balanoides* by far outnumbered *Austrominius modestus* on artificial structures surveyed (Gallagher 2016).

Not only the size but also the type and age of the available substrate may be important. The majority of newer piers and slipways surveyed by Gallagher et al. (2015) were constructed from smooth concrete with few cracks or crevices, though over time, erosion of the substrate may produce a more heterogeneous surface. Older structures were composed of a rough conglomerate mixture or large stones, both of which have many cracks and crevices, which may be a factor promoting the recruitment and survival of native species. This may be due to the sheltered conditions created by the artificial structures themselves, which would promote the abundance of *A. modestus*, or it may be due to the ability of *A. modestus* to settle on smooth substrata, while natives prefer rough surfaces. At a site seaward of the Biological Station at Roscoff, France, Gollëty et al. (unpublished poster, 2008) reported higher densities of *A. modestus* on a concrete block (mean ± SE: 67 305 ± 16 371 m^{-2}, max. 84 960 m^{-2}) than on a granite boulder (mean ± SE: 16 923 ± 4680 m^{-2} versus 18 135 ± 4643 m^{-2} for *Chthamalus montagui*), which she suggested could be due to the predominantly smooth surface of the former. The concrete block was dominated by *Austrominius modestus*, with only about 1% cover of other barnacle species (*Chthamalus montagui* and *Semibalanus balanoides*) (Gollëty et al. 2008). In the summer of 1997 and 1998, on a wall which was a mixture of natural stone and concrete at Roscoff, near Gollëty et al.'s (2008) site, O'Riordan et al. (2001) had found cyprids and adults of *Austrominius modestus*, *Chthamalus montagui* and *C. stellatus*, as well as adult *Semibalanus balanoides*. Gollëty et al. (2008) reported that in 2005, the recruitment period of *Austrominius modestus* occurred from late spring to the middle of autumn, with two peaks in June, another important one in August and a small one in October.

Levels of recruitment of *A. modestus* have been seen to vary also with intertidal shore height and subtidal depth. At Lough Hyne Marine Nature Reserve, SW Ireland, recruitment and survival were examined on machined-slate panels at 0 m (~two-hour emersion per tidal cycle), 6 m depth and 12 m depth at two sites with different flow regimes, over a three-year period (Watson et al. 2005). *A. modestus* was the species of barnacle that dominated the intertidal panels and had higher levels there than subtidally, with a maximum mean of ~two recruits cm^{-2}, but with significant differences between seasons. Although *A. modestus* recruited to the subtidal monthly and seasonal panels, none were present on the subtidal annual panels; instead, *Balanus crenatus* and *Verruca stroemia* dominated the latter, highlighting the importance of post-recruitment processes to the survival of *Austrominius modestus* subtidally (Watson et al. 2005). In the English Channel, recruitment of four species of barnacle, including *A. modestus*, was recorded in cleared vertical patches, with highest counts occurring along the coast of Sussex, with greatest recruitment at Selsey Bill (a mean of 16 and a maximum of 23 cm^{-2}). Generally recruitment was greater at the lowest of the three shore levels (MHWN, MTL and MLWN) (Herbert et al. 2007). Further north, in subtidal samples in Helgoland, Germany, recruitment was recorded from June–July to September–October (Anger 1978). Meadows (1969) reported 51% mortality of recently recruited (maximum of two months old) *A. modestus* on subtidal panels (60–120 cm below MLWS) at Rosyth, Scotland, which was lower that recorded for *Semibalanus balanoides* (90% and 83% from two other sites, Greenock and Mallaig).

Health status, natural enemies and anthropogenic threats

The health status of *Austrominius modestus* has been described briefly in a range of studies, but no definitive overview of potential parasites or pathogens has been compiled to date. While parasites and disease in the marine environment are increasing, a definitive overview of the health status of this barnacle species has not been carried out. However, this in part may be due to a lack of focus on this aspect of its biology which would require a range of diagnostic tests to do a full screen with large sample sizes and over a range of geographic locations. Of the studies that have been carried out, there has been a focus on the role of barnacles as reservoirs or potential predators of parasites.

Bacteria, including coliforms

Clements et al. (2013) screened a range of barnacle species including *Austrominius modestus* for a range of coliform species to determine if barnacles attached to mussels could act as reservoirs for human coliforms. They found that *A. modestus*, which had outcompeted native species in some of the areas being studied, contained much higher levels of coliforms relative to the native species and could act as reservoirs for these bacteria – potentially being transferred to mussels which would ultimately be consumed.

Other studies have focused on the control of bacteria in the culture of various barnacle life stages. Bacteria may develop during the rearing of larvae, so researchers often try to counteract this by adding antibiotics, for example, 0.01% chloromycetin (Barnes & Barnes 1974) or 0.4 mL of Crystamycin solution (Barker 1976, Tighe-Ford 1977) or penicillin-streptomycin solution (e.g. Stone 1988, 1989).

Commensals or potential parasites

Of those commensals or potential parasites that have been described most, one in particular, a microparasite, is the isopod *Hemioniscus balani*. Generally, this isopod, a parasitic castrator of a number of native barnacle species, disrupts egg production. Reports of the presence of this isopod are variable, as is the impact. Crisp & Patel (1960) examined the influence of the parasite *H. balani* on the moulting rhythm of *Austrominius modestus* collected from the Brixham, South Devon, location where Southward & Crisp (1954) had found a high level of infection. Although Crisp & Davies (1955) had shown that this parasite can cause castration in *A. modestus*, the presence of the parasite had no significant effect on the moulting rhythm of *A. modestus* or on that of the other three species tested. They examined ten *Austrominius modestus*, of which 50% were infected. In the large *Perforatus perforatus*, the parasite was shed with the cast (and may explain the low levels of *Hemioniscus balani* recorded in this species), but this did not occur in *Austrominius modestus* or the other two species.

During 1940–1950, when temperatures around Britain increased, there was an increase in the incidence of *H. balani* in the cold-water *Semibalanus balanoides*, as if the latter species had become more susceptible to infection (Little & Kitching 1996). Crisp & Molesworth (1951) reported that the incidence of infection by *Hemioniscus balani* was >50% in *Austrominius modestus* and *Amphibalanus amphitrite* in some areas of South Devon and South Wales, Great Britain. In their survey of the French coast in (August) 1967, at La Jetée d'Eyrac, at Arcachon, Barnes & Barnes (1968a) noted that ~2% of *Austrominius modestus* had a parasite resembling *Hemioniscus*. O'Riordan & Ramsay (1999) did not find any present *Hemioniscus balani* in the *Austrominius modestus* samples that they examined from Setúbal or Praia de Faro in 1998, nor was it found by the same authors at Alvor in 2013 (O'Riordan & Ramsay 2013), but barnacles were sampled in March/April only.

Another parasite that is found in *A. modestus* is the eugregarine *Nipyxioides elminii*, which occurs in the intestine (Ormières 1983). Goedknegt et al. (2015), in a study of disease risk under climate change scenarios, particularly temperature change, found that *Austrominius modestus* significantly reduced cercarial stages of the trematode *Renicola roscovita* in mussel beds (*Mytilus edulis*) through filtration, and this relationship was temperature dependent, with increased predation with increasing temperature. Cysts of the trematode *Maritrema gratiosum* (formerly *Maritrema arenaria*) have been recorded in *Austrominius modestus* at a number of locations in Ireland and Scotland (Gallagher 2016, Gallagher et al. in prep., Swain, 2019).

Overgrowth by other species

A number of species have been recorded overgrowing *Austrominius modestus*. On the upper reef at West Tamaki Head, Auckland Harbour, New Zealand, although some *A. modestus* could survive several months, being nearly completely covered by the mussel *Xenostrobus pulex*, eventually they were smothered by the carpet of mussels, underlain by silt (Luckens 1964, 1975). Similarly, the Auckland rock oyster *Saccostrea* (*Crassostrea*) *glomerata* often smothered *Austrominius modestus*, as well as other barnacle species (e.g. *Chamaesipho columna* and *Epopella plicata*) by growing over them. However, if, when the oyster spat had settled, there was little rock surface free (due to heavy barnacle cover), the attachment of the oysters became less secure over time, and they could be easily removed by the activity of other organisms. Some of the best evidence for interspecific competition for space was between *Austrominius modestus* and the alga *Corallina officinalis* on both vertical and horizontal cleared rock surfaces (Luckens 1964, 1975). Although *Austrominius modestus* settled first, it was smothered by *Corallina*. On transparent plexiglass panels, suspended at a depth of 1 m below a raft in Helgoland Harbour, Germany, overgrowing, mostly by the colonial ascidian *Botryllus schlosseri*, caused high mortality of *Austrominius modestus* in October 1977 (Anger 1978).

Predation

In its invasive range, a number of species have been shown to selectively predate native species before *Austrominius modestus*. It was reported that the nudibranch *Onchidoris* selected *Semibalanus balanoides* and neither it nor the dogwhelk *Nucella* predated on *Austrominius modestus* (Potts 1970), but Barnett (1979) showed that *Nucella lapillus* would predate on *Austrominius modestus*. However, in laboratory experiments, *Nucella lapillus* took greater numbers of *Semibalanus balanoides* than *Austrominius modestus*, unless the whelks had been starved (for ten months) (Barnett 1979). *Nucella* drilled the opercular valves significantly more often when predating on *Semibalanus balanoides* but prised open *Austrominius modestus*, suggesting that *Semibalanus balanoides* may be able to close its valves more securely or with greater force, hence the need for drilling. It was proposed that selective predation by *Nucella lapillus* on *Semibalanus balanoides*, rather than *Austrominius modestus*, may explain some of the initial success of *A. modestus* in NW Europe, as it could utilise bare space for settlement and then establishment, created by the mortality of *Semibalanus balanoides* (Crisp 1958). The preference for *S. balanoides* may be due to ingestive conditioning to the native barnacle species, or it may be because *S. balanoides* has a larger average size (Barnett 1979), which is in line with Connell’s (1961a,b, 1970) classic research, where *Nucella lapillus* selected *S. balanoides* rather than the smaller *Chthamalus*.

Pollution and heavy metals

It has been suggested that *Austrominius modestus* can tolerate pollution more than most native species in Great Britain (Crisp 1958), thriving in dirty harbours, where other species are uncommon (Little & Kitching 1996). Rainbow (1987) has described the levels of heavy metals in barnacles, including information about which ones are stored versus excreted or used and their value as biomonitors of trace metals in coastal waters, since higher body concentrations are accumulated where there is greater availability in the environment. Zinc is accumulated by barnacles as zinc phosphate granules, which, according to Rainbow (1987), may be a form of detoxification, thereby storing the zinc in a metabolically unavailable form. Please see Thomas & Ritz (1986) for the composition of elements in the ‘zinc’ granules in *A. modestus*. Rainbow & White (1989) gave concentrations (ppm dry weight) for four heavy metals in the body of *A. modestus* collected from a single site, Southend, Essex, England: 4900–11 700 Zinc, 20–169 Copper, 244–1382 Iron and 41–50 Cadmium. Rainbow (1985) and Pullen & Rainbow (1991) have examined heavy metal levels in *A. modestus* from the same site, while Al-Thaqafi & White (1991) investigated the effect of shore position and environmental metal levels on body metal burdens from two sites in Wales – Menai Straits and Anglesey. Please see levels listed in Table 1 (pp. 410–411) of Rainbow (1987) for comparison with other barnacle species and Table 4 of Zauke et al. (1992) for metal concentrations in ten species of barnacles from different regions of the world.

The assimilation efficiencies of four heavy metals were compared when adult *A. modestus* (collected from Southend) were fed different phytoplankton and zooplankton (a copepod collected from Hong Kong waters) diets (Rainbow & Wang 2001). Assimilation efficiencies differed for three of the metals, and there were variations between the different diets. Modelling of the accumulation of Cadmium and Zinc by *A. modestus* predicted that >97% of each of the accumulated metal had been derived from dietary ingestion, with <3% from the dissolved phase. The interaction between Cadmium and Zinc accumulation in *A. modestus* has been examined also (Elliott et al. 1985). Rainbow & Wang (2001) noted that the assimilation efficiencies of certain trace elements from its diet tended towards lower values for *A. modestus* than *Amphibalanus amphitrite* and *Balanus trigonus* (see their Table 3, p. 245). They suggested that this may indicate differences in the digestive physiology of the two families, that is, Austrobalanidae versus Balanidae. Zauke et al. (1992) examined Cadmium, Lead, Copper and Zinc levels in adult *Austrominius modestus* collected from 17 sites in two harbours in the Auckland area of New Zealand and from a site at Omaha Beach, ~60 km north. In general, the metal concentrations in *A. modestus* were towards the lower end in comparison to European studies. They suggested that the high concentrations of Cadmium in the samples from the study's mangrove site (Omaha Beach) may be due to the naturally increased bioavailabilities of certain metals in mangrove systems.

In recent years, a number of authors have used *A. modestus* as a model or test species in pollution studies. In New Zealand, *A. modestus* was investigated as a possible indicator of water quality (Okemwa 1999), while in southern England, the effects and toxicity of chromated copper arsenate (CCA) wood preservative was tested for a range of invertebrate fouling organisms, including *A. modestus* (Brown & Eaton 2001, Brown et al. 2001). Greater settlement occurred on non-treated panels, but *A. modestus* was one of the species which was dominant on the treated panels. Hill & Holland (1985) examined the influence of oil shale on intertidal organisms. They found that *A. modestus* and *Semibalanus balanoides* were induced to settle. They suggested that fractionated extracts of the oil shell containing metalloporphyrins acted in a similar manner to arthropodin, binding the proteins associated with the cyprid attachment disc.

Geographic distribution and changes (historic and future predictions with climate change)

The spread of *Austrominius modestus* is one of the best-documented examples of the spread of a marine animal to a new range (Barnes & Barnes 1965b), and there have been many published records of its dispersal and abundance on European coasts, in particular from the time of its initial introduction to Europe until the late 1960s (e.g. see Lewis 1964). Its spread is a good example of the effect of ship fouling in extending the range of a species (Pyefinch 1950). As well as shipping (both adults fouling on hulls and larvae in ballast water), other vectors possibly responsible for remote dispersal of *A. modestus* are flying boats (M. Barnes pers. comm. in Eno et al. 1997) and shellfish, while marginal dispersal is through the pelagic larval stages. O'Riordan (2010) summarised its spread country by country, with relevant references and notes in the distribution table and the section on 'History of Introduction and Spread', so subsequently we have just summarised its spread, given the key references for its spread and highlighted any recent changes. The first published record of this species in Europe was in Great Britain, by Bishop (1947), who recorded very large numbers on the Admiralty Raft moored in the mouth of Chichester Harbour in July 1945. However, according to Crisp (1948), Bishop had seen it there in 1944, and Bishop (1951) stated that it was first discovered in British waters in 1944. Even so, when Stubbings (1950) re-examined collections made in 1944 of fouling organisms from ships, he suggested that *A. modestus* may have been present in the Portsmouth area since 1943, while Crisp (1958) thought that it could have been there since 1939. It is believed that *A. modestus* was transported to Britain via shipping, evidence for this coming from live specimens of *A. modestus* found on a ship in Liverpool which had returned from Australia and New Zealand (Bishop 1947). Crisp (1948) reported *A. modestus* in Essex in autumn 1945, suggesting that, based on their size, they had settled in spring of 1945. Crisp & Chipperfield (1948) also recorded *A. modestus* from the south coast in 1945. In summary, the distance between the initial locations of colonization, along with the subsequent extent of range expansion, led Stubbings (1950) to suggest that *A. modestus* was well established prior to 1945, but the Second World War may have prevented the early stages of the introduction of this species from being recorded in British waters (Crisp 1958).

It was suggested by Crisp (1958) that the initial settlements in British waters must have been of a large number of individuals, which subsequent research confirmed (Flowerdew 1984, Dando 1987). An electrophoretic examination of *A. modestus* from ten European versus three Australasian populations found that the allele frequencies in all samples were similar (Flowerdew 1984). The genome of European *A. modestus* was entirely representative of the Australasian population, indicating that over the 40 years since its establishment, natural selection and genetic drift did not produce any changes great enough to produce genetic variation. There must also have been little differential selection on the European populations compared to those in the southern hemisphere. No significant differences in allele frequencies were seen between samples from Scotland to northern Spain (Flowerdew 1984) or between Cork Harbour and Bantry Bay, southern Ireland (O'Regan 1980).

There are many records following the spread of this species in Great Britain (see Southward 2008, for a summary of its distribution in Great Britain) that describe the spread of the species. In 1948, *A. modestus* was established, but not common, in the Helford River, Cornwall, on oyster grounds (Knight-Jones 1948). *Austrominius modestus* was not present on Skomer Island in the Bristol Channel during a survey in 1946 (Bassindale 1947), being first reported in the Bristol Channel at Blue Anchor (see Bassindale 1947) and near Cardiff by 1947, but in low abundances, indicating that *A. modestus* was just becoming established at this location (Purchon 1947). By 1948, *A. modestus* was the dominant barnacle in the intertidal zone and more widespread than native species of barnacles in the south-east of Great Britain. Additionally, it was found in areas unoccupied by native barnacle species, for example, Maldon beach (Knight-Jones 1948) or co-habiting on artificial substrates with native species (e.g. on pier piles in the Mersey estuary [Corlett 1948]). In Chichester Harbour, *A. modestus* was noted to be the most abundant barnacle species in the harbour by the 1950s (Stubbings & Houghton 1964). In 1952, two specimens were recorded at Ramsey, on the Isle of Man, where, by 1955, it was common and present further south (see Bruce et al. 1963). By 1957, *A. modestus* was recorded to be present in the Plymouth area (Marine Biological Association 1957), while Crisp & Southward (1959) examined its spread up until 1959. In 1963, it was absent from the open coast of the Dale Roads area of Pembrokeshire but was recorded as spreading within Milford Haven and increased in abundance at Watwick Bay and Dale Point (Moyse & Nelson-Smith 1963). *Austrominius modestus* was common in the Blackwater and Colne estuaries in the south-west of England, being the dominant barnacle in the Blackwater estuary in the 1960s (Davis 1967). Since the 1970s, there have been few new reports on the distribution and abundance of this invasive species in Britain. *Austrominius modestus* was most common in sheltered areas of North Wales, in particular in the Menai Strait. Although *A. modestus* occurred all around Anglesey, it was most common in sheltered areas of North Wales, and only in the Menai Strait did it make a significant contribution to barnacle cover (Bennell 1981). In the inner Bristol Channel, *A. modestus* was recorded from large boulders of Porlock Bay in 1980 (Hiscock 1986). Larvae of *A. modestus* were reported to be rare in waters off the Isle of Man in the early 1980s (Salman 1982). The most northerly records in Great Britain are from a number of sites in the Shetland Islands, as reported by Hiscock et al. (1978), where it had disappeared by 1986, but it has been found there recently attached to drifting plastic (Barnes & Milner 2005). It has been recorded on Scottish islands, such as the Isle of Cumbrae (Connell 1955, O'Riordan et al. 2009) and the Outer Hebrides (Howson et al. 1994).

Southward (1991) examined how the intertidal abundance of *A. modestus* had changed over 40 years in south Devon (Cellar Beach, River Yealm) from its first record there in 1948. Although it increased in abundance in the 1950s, it then stabilised at a low level of abundance. There were large fluctuations in density, which were not directly related to temperature, but may instead be due to the number of larvae available for settlement. Southward (1991) suggested that these larvae could have originated from breeding populations in the sublittoral or in the Tamar and Plym estuaries, where lowered salinity encouraged greater densities than in the River Yealm. Arenas et al. (2006) recorded *A. modestus* to be present at 66% (8) of their 12 sites surveyed using a rapid assessment survey on the south coast of England during 2004.

Based on 1954–1956 surveys, in the eastern part of the English Channel, *Semibalanus balanoides* was replaced in sheltered harbours and bays by *Austrominius modestus,* but *A. modestus* was common only in the estuaries and harbours in the west (Crisp & Southward 1958). Initially, headlands, such as Peveril Point, Portland Bill and Cap la Hague (at the tip of the Cotentin Peninsula), being more wave exposed, presented hydrographic barriers to its westward spread, slowing its spread by marginal dispersal. Hemingway-Jones (1961), citing Crisp & Southward (1953), suggested that *A. modestus* cannot disperse further than 48 km by marginal (coastal dispersal) and that they might spread 20–30 km per annum along an open coast. When the abundance of four species of barnacles at three heights in the intertidal along the central south coast of England was surveyed between 1994 and 1999, including sites previously surveyed by Crisp & Southward (1958), Crisp et al. (1981) and Southward (unpublished), Herbert et al. (2007) found that *A. modestus* was most common in the eastern English Channel, especially near estuaries (see their Figure 5). The maximum abundance was 4 cm^{-2} (at MHWN, at Southsea). At some sites east of Portland Bill, abundance was similar to that recorded some 40 years earlier (Crisp 1958, Crisp & Southward 1958). However, further west at Lyme Regis, where between 1948 and 1958 the species was absent, it was now ‘occasional’, and at Brixham, it was ‘abundant’ when previously it was ‘occasional’.

Following its introduction to Great Britain, this species spread rapidly along European coasts (e.g. Crisp 1958, Harms & Anger 1983), but cold winters constrained its spread. *A. modestus* was noted to be common on the southern North Sea coast of The Netherlands by Boschma in 1948, having been first recorded from The Netherlands in 1946 (van der Meulen 1946, Bishop 1947, Boschma 1948, Leenhouts 1948a,b, Hartog 1953, 1955), but may have first settled at the Hook of Holland in 1945 (Hartog 1953). Please see Figure 2, p. 13, of Hartog (1953) for its spread along the Dutch coast up to 1951. It had spread to Belgium by 1950 (Hartog 1953, Leloup & Lefevere 1952). It was found in France in 1950 also (Hartog 1953, Bishop 1954), but may have been in Normandy since 1944 (Hartog 1956) and was recorded settling in large numbers in Roscoff, Brittany, in summer 1952 (Hartog 1953, Drach pers. comm. in Bishop 1954). It was recorded in Helgoland in 1954 (Hartog 1959, Kühl 1963), the Isle of Sylt in 1955 (Kühl 1963) and had reached its northern continental border in southern Denmark by 1978 (Theisen 1980, Harms & Anger 1989). The Danish Wadden Sea was recorded as the northern limit of *A. modestus* in Europe at that time (Theisen 1980), but it died out there during the cold winters (Jensen & Knudsen 2005). Cuxhaven by Kühl (1963) also reported sensitivity to cold winters. Similarly, in some shores in France (Barnes & Barnes 1966), a severe winter in 1962–1963 caused high mortality, as well as in *Perforatus perforatus* (80%–90%) and ‘*Chthamalus stellatus*’ (5%–90%) (Barnes & Barnes 1966). However, it was recorded there every year between 2004 and 2008, being found near the eastern entrance to Limfjord in 2007 (Jensen 2009), so less cold winters allow it to re-establish in areas. In Helgoland, in the German Bight area, it has become dominant, although native species continue to persist (Franke & Gutow 2004, Reichert & Buchholz 2006, Witte et al. 2010). In Danish waters, *Austrominius modestus* now extends through the Limfjord (Jutland) and into the N.W. Kattegat (J.G. Lützen & H. Glenner, in prep., pers. comm. to O’Riordan, 28th November 2019).

Similar to its gradual spread northwards, *A. modestus* gradually colonized southwards. Crisp & Southward (1958) suggested that in 1954–1956, the European range of *A. modestus* extended from the south-west of Scotland to France, but it had actually been recorded in Galicia, northwest Spain, in 1955 (Fischer-Piette & Prenant 1956). Based on a survey in 1954, *A. modestus* was well established on the French coast from the Rade de Brest to the estuary of the Jaudy and from Cap de la Hague to the Belgian border (Bishop & Crisp 1957). Single specimens were found at some other locations along the French coast, though not further south than St. Jean-de-Luz. The authors remarked that even though there was suitable habitat and high levels of shipping activity, this species had not spread further south at that time. Bishop et al. (1957), Bishop & Crisp (1958), Fischer-Piette & Prenant (1956) and Crisp & Fischer-Piette (1959) provide other records of the occurrence of *A. modestus* on the French coast. Additional surveys carried out in 1957 reported increases in the abundance of *A. modestus* around Concarneau and Lorient (Crisp 1959b). It was suggested that the French populations were not established via spread from Belgium and The Netherlands, but they were separately established via shipping from Britain (Bishop & Crisp 1957). Additionally, the establishment of *A. modestus* in The Netherlands was unlikely through dispersal from France, but a separate colonization event (Bishop & Crisp 1957). Surveys in the 1960s monitored its progress south (e.g. Fischer-Piette & Forest 1961, Fischer-Piette 1963, 1964, 1965, Barnes & Barnes 1965b, 1966). *Austrominius modestus* was first recorded in Arcachon, France, in 1964 (Barnes & Powell 1966), following which it became highly abundant, being the most common barnacle species at this location, having smothered natives in some locations, colonizing areas previously unoccupied by native barnacle species (Barnes & Barnes 1968a). *Austrominius modestus* was established further north in the Baie de St. Malo (Barnes & Barnes 1969), though the coast north of Granville was thought not to be ideal for the establishment of this species, and only a small population survived there. South of Arcachon, *A. modestus* was established at St. Jean-de-Luz (Barnes & Barnes 1969). In 1971, *A. modestus* was found further south on the French coast, including Socoa, near the border of north-west Spain (Barnes et al. 1972). When its abundance was surveyed on 17 shores, between Calais and the Gulf of Malo, Cotentin Peninsula (Herbert et al. 2007), including sites previously surveyed by Crisp and Southward (1958), Crisp et al. (1981) and Southward (unpublished), *A. modestus* had increased by between one or two orders of magnitude on the west side of the Cotentin Peninsula compared to in 1954 when Crisp & Southward (1958) reported the barnacle as 'rare' or 'occasional'. In the 2001 and 2002 surveys, it was not found at one of the French sites surveyed and was 'abundant' at just one site, Calais, the most easterly site of those that they surveyed. This species is present in the Bassin de Thau, on the French Mediterranean coast, extending its known eastern European limit (O'Riordan & Ramsay 1999, citing Zibrowius, pers. comm.). However, Buckeridge & Newman (2010), also citing Zibrowius (pers. comm.), pointed out that the Thau population is small and may depend on yearly imports of oysters from the Atlantic coast of France. Back in 1968, Barnes & Barnes (1968a) had indicated the importance of activities associated with oyster cultivation for its spread within the Arcachon Basin, France.

A single individual was recorded in South Africa in 1949 (on an experimental plate at a depth of ~60 cm in Cape Town Docks); however, the species did not become established in this area (Sandison 1950). Tøttrup et al. (2010) described *A. modestus* as being a 'naturalised' member of European intertidal habitats. Although it has not yet been reported from the coasts of America, the reason for which remains unclear, it is expected to become established there in the future, if it has not already done so (Carlton et al. 2011).

The spread of *A. modestus* along the Atlantic coasts of Spain and Portugal between 1955 and 1963 was well documented (Barnes & Barnes 1965b, Fischer-Piette & Prenant 1956, 1957, Fischer-Piette & Forest 1961). In 1963, the southern limit of this species in Europe was recorded as São Martinho de Porto, Portugal (Barnes & Barnes 1965b). Eno et al. (1997) suggested erroneously that it occurred as far south as Gibraltar, citing Barnes & Barnes (1966), but although Gibraltar is the station furthest south that Barnes & Barnes (1966) surveyed in Spain (as well as surveying Huelva, Cadiz and Barbate along this coast), they do not mention *A. modestus* occurring there. They refer back to their earlier paper (Barnes & Barnes 1965b) for the detailed distribution and abundance levels for *A. modestus*, where they categorically state that in 1963, it was not found on the southern coasts of Spain (or France). Intertidal surveys on seven shores from Tarifa to Almuñecar, in Andalusia, Spain, in January 2018 failed to find any *A. modestus* (O'Riordan & Ramsay, unpublished). O'Riordan & Ramsay (1999) confirmed its southern European continental limit in Portugal to be Faro. Currently, the European range of *A. modestus* is from Scotland (The Shetlands) and Denmark in the north to Ilha de Culatra, near Faro, Portugal (Gallagher unpublished), in the south and two locations in the Mediterranean Sea (Zibrowius pers. comm., Casellato et al. 2007). The most easterly location reported is by Casellato et al. (2007), who recorded it in their surveys of subtidal (22–24 m deep) ‘tegnúe’, rocky outcrops in the Gulf of Venice, in the Northern Adriatic Sea, Italy, carried out between 2002–2003; however, this record has not been reported in the ICES WGITMO national reports, and this depth is much deeper than the species has been found elsewhere. A single specimen was found at Funchal marina, Madeira, in May 2005 (Wirtz et al. 2006), so it was listed as not established there (Chainho et al. 2015). Boaventura (2000) and Boaventura et al. (2002) did not mention the occurrence of *A. modestus* on any of the 27 rocky shores that they surveyed in spring 1997. As part of the INSPECT project, Cruz & Castro (2011) surveyed 24 sites on the Portuguese coast for *A. modestus* in spring/summer of 2010 and 2011. Its occurrence was mostly associated with ports and estuaries, and they recorded three new locations for it on the western Portuguese coast (Cruz & Castro 2011, pers. comm. to R. O’Riordan). Gallagher (2016) surveyed 18 shores in the Algarve in 2014 and found *A. modestus* present on all but two of the shores. However, when O’Riordan & Ramsay (unpublished) resurveyed 12 of the same shores in May 2018 and April 2019, *A. modestus* was absent from six of these shores.

At the limits of the geographical range of a species, the abundance and exact range can fluctuate (Southward & Crisp 1956). These fluctuations can often be linked to environmental changes, and by investigating this, the relative importance of these factors in determining the species distribution can be determined. Unpublished research carried out by Gallagher et al. examined the factors controlling the success of *A. modestus* at its southern limit in the Algarve and close to its northern limit on the Isle of Cumbrae, Scotland (see previously re: Shetland Islands as well). At the northern location, strong competition exhibited by the native species *Semibalanus balanoides* during years of good settlement for this species was limiting the abundance of *A. modestus*, while at the southern limit, it seems likely that desiccation stress, or some other stress, at the settlement and recruitment stage is limiting the abundance of *A. modestus*. Previously, it had been suggested that high temperatures were responsible for restricting it to the lower shore of some Atlantic shores in SW France and in some rias in Spain (Barnes & Barnes 1966, Barnes et al. 1972).

Ireland is the most westerly location of *A. modestus*, where it was first recorded in 1957 (Beard 1957). O’Riordan (1996, 2002, 2010) described its spread around the coast in the subsequent 50 years. The intertidal distribution and abundance of *A. modestus* around the Irish coast changed between the 1950s and 2003 (Simkanin 2004, Simkanin et al. 2005). It was found on 57 of the 63 sites resurveyed, and its abundance showed an overall increase, especially along the east coast. The significant increase of *A. modestus* over this period of time was suggested to be a classic example of a successful invasion, reflecting a rapid colonization of a new area unrelated to climate change (Simkanin 2004). However, studies have shown that climate change may indirectly affect the interactions between introduced and native species by causing increased stress in native populations (Occhipinti-Ambrogi & Savini 2003) and earlier recruitment in introduced species (Stachowicz et al. 1999), thus facilitating the expansion of non-native organisms. Although Simkanin (2004) cautioned that this apparent increase may be an artefact due to operator error, rather than a change due to natural or anthropogenic reasons, other studies supported that *A. modestus* has increased its range significantly around the Irish coast (O’Riordan 1996). Subsequent reports describing increases in the abundance of *A. modestus* with warming sea surface temperatures (e.g. Lawson et al. 2004, Allen et al. 2006, Witte et al. 2010) have suggested that *A. modestus* could be an ‘ecological sleeper’ (Witte et al. 2010), with the potential for further increases in abundance towards the northern part of its invasive range with predicted climate change. While this may be the case in the middle and northern parts of the invaded range of *A. modestus*, data collected in the Algarve (Gallagher 2016) make it unlikely that warming temperatures will facilitate an increase in the abundance of this species at very southerly locations. Although *A. modestus* appears as tolerant as *Chthamalus montagui*, its restriction to lower on the shore than *C. montagui* towards the south of its range may be because the temperature conditions are becoming too extreme (Barnes et al., 1972). Some surveys of the intertidal Moroccan coasts during spring tides have been carried out recently by researchers from the University of the Algarve (pers. comm. to R. O'Riordan, May 2018). It will be interesting to see whether *Austrominius modestus* is present in any of their catalogue of photographs from these shores, which would experience higher temperatures than in the Algarve.

Ecosystem structure

Although invasive species generally have negative associations, it is not always the case in reality, and there have been very few recorded extinctions due to competition from invasive species, and where extinctions do occur, it is generally between trophic levels, for example, predator and prey (Davies 2003). A review by Katsanevakis et al. (2014) noted that many invasive species have both positive and negative impacts and that the positive impacts are largely underestimated. Species richness is not necessarily an indicator of ecosystem function (Schwartz et al. 2000); therefore, if *Austrominius modestus* reduces the number of native barnacle species, this may not alter ecosystem function, provided that *A. modestus* plays the same functional role as those native species. The overall impact of *A. modestus* on the dynamics of rocky shore communities in Great Britain has been small (Raffaelli & Hawkins 1996). It simply replaced some individuals of a group or a guild of co-occurring barnacles (e.g. *Chthamalus montagui*, *C. stellatus* and *Semibalanus balanoides*), which were seen to fluctuate in abundance over a 40-year period from 1951–1991, changing sea temperature being one of the potential factors involved (Southward 1991).

Austrominius modestus has been found to coexist with native barnacle species at multiple locations (e.g. see Gallagher et al. 2015, 2016, 2017). This could be facilitated in various ways, for example, *A. modestus* and native barnacle species display distinct patterns of zonation and generally occupy different parts of the shore. Colonization of different parts of the shore reduces direct competition between the species, allowing them to coexist. Differences in the timing and extent of the reproductive periods of the native and invasive species are also likely to be a contributing factor in the coexistence of these species, with *A. modestus* and native barnacle species essentially utilising different temporal niches. It was noted that where *A. modestus* started to become dominant, it was probably because of greater fecundity and prolonged breeding and settling seasons, enabling prior colonization of vacant sites on the substrate (Foster 1970). Shinen & Navarrete (2014) reported that the barnacles *Notochthamalus scabrosus* and *Jehlius cirratus* coexist neutrally. They found that a lottery for space during settlement largely determined the distributions of the two species. Small, nonsignificant and probably ephemeral fitness differences, which were inconsistent across the tidal gradient, probably provided enough niche differentiation to allow coexistence (Shinen & Navarrete 2014).

Within three years of settling in parts of the Firth of Forth, Scotland, *Austrominius modestus* had started to outnumber the former dominant species *Semibalanus balanoides* (Hemingway-Jones 1961). Sometimes later settlements of *Austrominius modestus* attached amongst spat of *Semibalanus balanoides*, and because the latter were faster growing and took up lateral space, the *A. modestus* have to project themselves above the *S. balanoides* (Crisp 1960a). If these *Austrominius modestus* survived, they could grow rapidly, mature early and could cause the underlying *Semibalanus balanoides* to become silted up and smothered (Crisp & Davies 1955, Crisp 1960a). Towards the northern part of its introduced range, such as western Scotland, where winter temperatures are low and summer temperatures are only moderate, native *S. balanoides* may be at an advantage in competition with *Austrominius modestus*, since at these temperatures, brood production by the latter species is relatively low (Barnes & Barnes 1962). However, further south, the ability of *A. modestus* to reproduce and settle throughout the year, unlike *Semibalanus balanoides*, gives it a greater chance to settle high on the shore and grow during more favourable climatic conditions (Foster 1971a,b). Settlement over the autumn and winter, when desiccation stress is less, may establish the ascendancy in intertidal distribution, with the upper limit being maintained by those individuals which grow sufficiently to reach a size which will protect them from lethal dehydration when adverse emersion conditions arise at that level (Foster 1971a,b).

Working with mathematical colleagues, the authors (Gallagher et al., 2020), have modelled the colonization of space by *Semibalanus balanoides* and *Austrominius modestus* in 1) communities where the species are initially present at different densities, 2) on a novel substrate and 3) under the scenario of future climate change. The time difference between the peak of *Semibalanus balanoides* reproduction and *Austrominius modestus* reproduction is the key factor in determining whether the two species coexist or outcompete one another. The longer the time period, the more *Semibalanus balanoides* is favoured. This is most likely because this allows *S. balanoides* more time to utilise space, especially as the recruits grow more quickly; thus, there is a lower likelihood of them being displaced by *Austrominius modestus.* A key factor with respect to the occurrence of a novel substrate is when it becomes available relative to their respective reproduction and recruitment. Finally, based on the models, the gradual warming of waters, which would positively affect *A. modestus*'s reproduction, generally favours *A. modestus*, leading to a reduced density of *Semibalanus balanoides* and eventually its extinction. Interestingly, for some parameter values, a more complex scenario is plausible due to warming, which may favour *S. balanoides* first, but then the trend reverses again, leading to the complete elimination of *S. balanoides.*

Since native barnacle species have a lower tolerance of disturbance, *Austrominius modestus* can achieve high abundance in harbours and ports on both artificial and natural substrates and occur at shore levels where native species would outcompete it on rocky shores. At the lower shore, on European shores, there is some competition for space between *A. modestus* and the native *Balanus crenatus* and *Amphibalanus improvisus* (Crisp 1958, Kühl 1963, Foster 1970), as well as higher up with *Semibalanus balanoides* (Kühl 1963). However, in the case where there are no native barnacle species present, *Austrominius modestus* is capable of colonizing the entire range of the intertidal zone (as well as subtidally), though not at exposed locations. Similarly, because *A. modestus* can tolerate low salinities and turbid waters, Barnes & Barnes (1968b) suggested that in some very protected areas in harbours or quiet bays (in SW France and southern Spain), where the water was very turbid and the salinity was relatively low, '*Chthamalus stellatus*' could be restricted to higher shore levels due to competition with *Austrominius modestus* (see also Barnes & Barnes 1966), as well as *Amphibalanus improvisus and Amphibalanus amphitrite. Austrominius modestus* competes with all of the other species of barnacle in Belgian waters (Kerckhof 2002).

Determining the functional role of *A. modestus*, and comparing this with native barnacle species, is of key importance in determining the ecosystem level impact of *A. modestus. Austrominius modestus* plays a similar functional role to natives (Olenin et al. 2007). However, while it has not been investigated in detail, there is some evidence that the *A. modestus* may differ from the native species in its utilisation of food resources (Southward 1955a,b, Moyse 1963, Stone 1989, Harms 1999). This may be due to differences in rate of cirral beat (Southward 1955a,b), potential differences in diet (Stone 1989) and contribution of larvae to the plankton community. If so, these could mean that *A. modestus* plays a different role to native barnacle species, which could facilitate niche partitioning, but this is currently speculative. There are some known key differences in the niche occupied by *A. modestus* and native barnacle species, which also play an important role in facilitating coexistence (see Figure 6).

Austrominius modestus is most often found in sheltered, estuarine areas, with highest abundances at the middle and low shore levels. This species can persist in areas that are subject to high levels of disturbance, due to its opportunistic nature, which is typical of invasive species (see Figure 7). Although the native species *Semibalanus balanoides* is also found at the middle to low shore, *S. balanoides* is more tolerant of wave-exposed conditions and less tolerant of estuarine conditions (especially low salinities) in comparison to *Austrominius modestus. Chthamalus montagui* dominates at the high shore level, generally at more wave exposed locations (but being replaced by the native *Chthamalus stellatus* on the most exposed shores) and does not have a

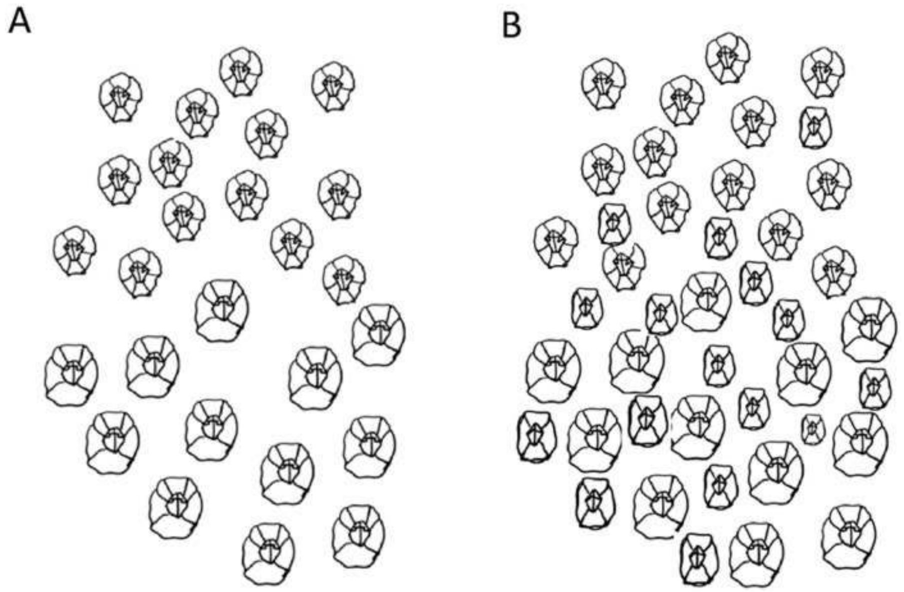

Figure 6 Generalised illustration of typical distribution of barnacles on the shore (high to low = top to bottom) (A) prior to *A. modestus* invasions and (B) after. See Figure 7 for the identity of the three species.

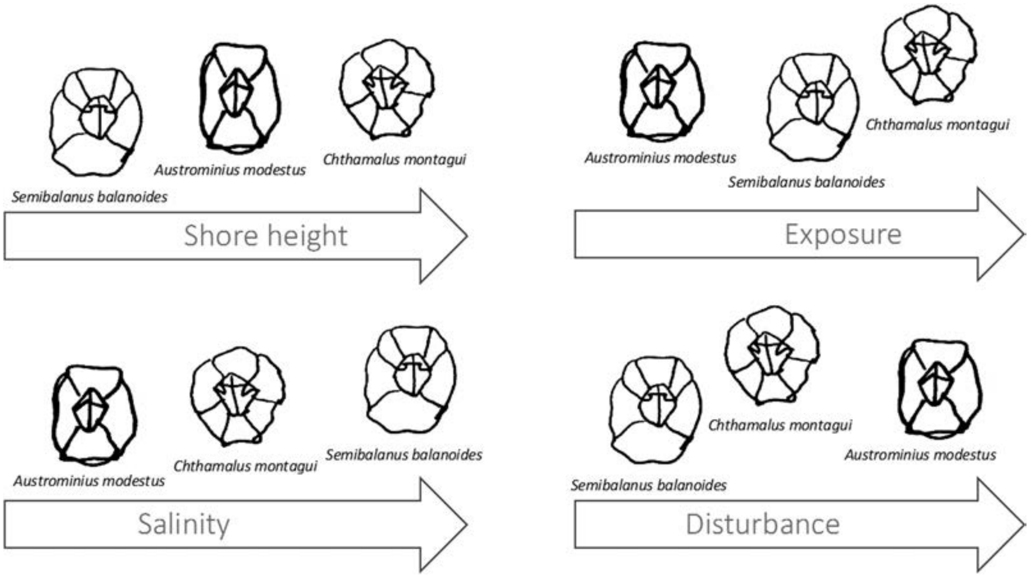

Figure 7 Indication of the varying tolerance levels of *Austrominius modestus, Semibalanus balanoides* and *Chthamalus montagui* to four different environmental variables as they increase from low (left of figure) to high (right of figure)

high tolerance of estuarine conditions. When the distribution of barnacles at three shores height on two sheltered and two exposed intertidal shores was examined in the Plymouth region, it was chthamalids that dominated, with *Austrominius modestus* reaching a maximum of 25% (Jenkins 2005). However, high densities of *A. modestus* have been recorded at some locations; for example, between 1959 and 1965, *A. modestus* was one of the most important organisms on the sea walls in the intertidal of the Blackwater estuary and adjacent waters in Essex, as well as on stones and shells amongst the muddy sand, being very common in the Colne estuary, mostly on the lower and middle shore but also subtidally. In the Blackwater estuary, it was the dominant barnacle species, reaching densities of up to 3750 individuals per m^2 (Davis 1967). Forty years later, at one of their sites in Roscoff, France, Gollety et al. (2008) recorded densities of 84 960 *A. modestus* m^{-2}, which they said was comparable to the densities seen for the other commonly occurring intertidal barnacles, *Chthamalus montagui*, *C. stellatus* and *Semibalanus balanoides*, on Atlantic European shores. They mentioned that common to abundant densities can be observed along the coasts of Brittany, France, with densities from 13 040 to 77 200 m^{-2} around Roscoff, while Barnes (1971) recorded 40 000 *Austrominius modestus* m^{-2} in the Arcachon Basin.

As mentioned previously (see section on Substrate type for *A. modestus* under 'Settlement and recruitment'), *A. modestus* is known to attach to a wide range of substrata, including other living organisms. In its native range in New Zealand, it was reported that it could smother and kill mangrove seedlings (Moore 1944). It is currently not known if there is a similar effect of smothering on native species in its invaded range through either competition for space or even smothering. In the early years after it was reported in Great Britain, concern was expressed because it was found to settle prolifically on panels during and after oyster spatfall so that it was competing more keenly with the young spat than any native barnacle species or sessile forms, and poor growth of young oyster spat was attributed to competition with *A. modestus* (Knight-Jones 1948). Although oyster spat could grow over and smother nearby *A. modestus*, the resultant oysters became misshapen and stunted. At that time, there was concern that it might cause problems for oyster cultivators in France and The Netherlands, where they were using artificial spat collectors exposed at low tide (Knight-Jones 1948), but there is nothing subsequently in the literature about this potential conflict. Settlement of *A. modestus,* as well as other barnacle species, on oysters and edible winkles was also reported to be a problem for the shellfish industry in Great Britain. Fouling by *A. modestus* caused complaints by sellers of winkles there (Anon 1948), for example, in West Mersea (Knight-Jones 1948), since the trade was accustomed to receiving clean winkles and most of the fouling was due to *Austrominius modestus*. There were complaints from oyster dredgers who had to remove *A. modestus* before selling (Knight-Jones 1948). Finally, concern was expressed that *A. modestus* might retard the recovery of oyster beds on the east coast of England, which had been affected by non-native *Crepidula fornicata* and *Urosalpinx cinerea*, followed by a severe winter (Knight-Jones 1948).

The question remains whether the presence of *Austrominius modestus* has a negative impact on ecosystem function. If not, and this species carries out the same functional role as native barnacles, its presence could potentially be seen as positive, as it could act as a replacement for *Semibalanus balanoides* under future climatic situations if *S. balanoides* dies out. The presence of generalist non-native species may contribute to ecosystems that are better able to cope with future environmental change (Witte et al. 2010). In the absence of this non-native species, only chthamalid barnacles would be present. There are some indications that there are differences between *Austrominius modestus* and native barnacle species that could have the potential to alter ecosystem function, but this needs to be confirmed. Baird et al. (2012) assessed the impact of *A. modestus* (and another invasive species there, the Pacific oyster *Crassostrea gigas*) on the structure and function of the entire intertidal region of the Sylt-Rømø Bight ecosystem (~87% of the Bight was declared a World Heritage Site by UNESCO in July 2009). Quantified network models with carbon (a surrogate for energy) were constructed to represent three different time periods. Changes in system attributes between 1995 and 2007 were ascribed to the impact of the invasive species on organisation and function of the system. For example, when there was a high biomass (1.3 and 15 gC m^{-2} of *Austrominius modestus* and *Crassostrea gigas*, respectively) of these two invasive species in 2007 (having increased from virtually zero in 1995), they accounted for ~35% of the total phytoplankton uptake, which then impacted lower trophic levels. However, the biomass of both species declined by 2010, following an unseasonably cold 2009/2010 winter, to only 0.12 and 0.6 gC m^{-2}, respectively.

Overall, the presence of generalist non-native species and the absence of specialist native species may lead to negative impacts on local biodiversity. In this specific case, it is important to consider the potential positives of the presence of *Austrominius modestus* but also to be aware that this species could have increased negative impacts at certain locations in the future. Hence, we encourage researchers to carry out more work on the biology and ecology of this species in its native range but especially at the current limits of its introduced range.

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TOWARDS AN OPTIMAL DESIGN FOR ECOSYSTEM-LEVEL OCEAN OBSERVATORIES

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Abstract Four operational factors, together with high development cost, currently limit the use of ocean observatories in ecological and fisheries applications: 1) limited spatial coverage, 2) limited integration of multiple types of technologies, 3) limitations in the experimental design for *in situ* studies, and 4) potential unpredicted bias in monitoring outcomes due to the infrastructure's presence and functioning footprint. To address these limitations, we propose a novel concept of a standardised 'ecosystem observatory module' structure composed of a central node and three tethered satellite pods together with permanent mobile platforms. The module would be designed with a rigid spatial configuration to optimise overlap among multiple observation technologies, each providing 360° coverage of a cylindrical or hemi-spherical volume around the module, including permanent stereo video cameras, acoustic imaging sonar cameras, horizontal multibeam echosounders, and a passive acoustic array. The incorporation of multiple integrated observation technologies would enable unprecedented quantification of macrofaunal composition, abundance, and density surrounding the module, as well as the ability to track the movements of individual fishes and macroinvertebrates. Such a standardised modular design would allow for the hierarchical spatial connection of observatory modules into local module clusters and larger geographic module networks providing synoptic data within and across linked ecosystems suitable for fisheries and ecosystem-level monitoring on multiple scales.

Keywords: Ocean observatories, Ocean technology, Ecological monitoring, Networks, Coenoclines, Deep-sea, Behaviour, Optoacoustic technologies, Passive acoustic, Fish sounds, Cyber interfaces

Introduction

Ocean observatories have become important resources for oceanographic observations around the world and consist of networks of instruments primarily designed to collect data on oceanographic and geophysical conditions in real time over long durations (Tunnicliffe et al. 2003, Schofield & Glenn 2004, Aguzzi et al. 2012, Gould et al. 2013). However, increasingly, observatories are becoming useful tools for biologists interested in animal behaviour, ecosystem ecology, and fisheries applications (ACT 2007, Aguzzi et al. 2011b, 2015a, Barns et al. 2013). Four operational factors, besides development costs, limit applicability of existing ocean observations systems for use as tools in fisheries and ecosystem level applications: 1) limited spatial coverage, 2) limited integration of multiple types of technologies (i.e. multiple modalities of observation), 3) limitations in the experimental design for *in situ* studies, and 4) potential unpredicted bias in monitoring outcomes due to the infrastructure's presence and functioning footprint. These limitations have slowed the spread of ocean observatory use for fisheries and other ecological applications (e.g. benthopelagic connectivity), highlighting the need for efforts to improve observatory design (e.g. Handegard et al. 2013, Locascio et al. 2018).

The objective of this review is to show how ocean observatories, combined with other observational sampling technologies, can be better designed from fisheries and ecology perspectives for the monitoring of marine ecosystems and their connectivity through coenoclines (i.e. gradients of communities) formed along depth, latitude, and geographic gradients. What is unique about the suggested approach is that systems would be designed from the beginning for ecosystem-level observations on large spatial and temporal scales and would be replicated in many locations for global coverage. In order to meet these objectives, observatories need to be highly standardised and produce quantitative observations that are comparable among locations and over time. The present review presents a concept of standardised modular platform design that is intended to stimulate discussion and refinement within the scientific community. The ecosystem observatory module (EOM) concept (hereafter simply referred to as the 'module') consists of a central node and three tethered satellite pods (hereafter referred to as 'satellites'). A modular design means that the platforms should be designed so that they can be prefabricated, and therefore produced at lower cost, but be flexible enough to allow customisation and implementation in different habitats. Such a design serves two purposes: first, it provides directly comparable data among different locations, and second, it will encourage wider implementation of observatories around the globe. Most of the instrumentation proposed for each module has already been developed and implemented in some existing cabled observatories, though significant improvements in capabilities and reduction in cost are needed (see review in Aguzzi et al. 2019). In addition, much of the software needed to realise large-scale observatory networks that are useful to fisheries scientists, resource managers, and ecologists are still in the early stages of development (Allken et al. 2018, Juanes 2018, Marini et al. 2018a,b). Therefore, the development of data delivery systems that are accessible to a wide range of stakeholders from different disciplines and backgrounds is of vital importance for the effective use of ocean observatories for fisheries and ecological applications (Pearlman et al. 2019). It is therefore important to design data packaging and delivery systems in concert with the observatory structural and instrumentation design, rather than as an afterthought.

The implementation of permanent monitoring systems should deliver data on animal movement across habitat gradients (Aguzzi et al. 2015a) and energy flux interchange (Thomsen et al. 2017), providing measures of ecosystem functioning (Aguzzi et al. 2019). Time series of visual counts for different species by different monitoring modules and their satellites of a network may provide spatially meaningful representations of a population's abundance fluctuations when data are summed (i.e. scaled) together (Aguzzi et al. 2019). Spatiotemporal variations in population abundances could then be used to track the status of ecosystem services such as fisheries resources. Major requirements for ecosystem-level ocean observatory networks include 1) spatial quantification of organism abundance, density, and biomass through cross-referencing of data obtained from multiple observation technologies; 2) quantification of the impact of the observatory structure and operation of its instruments on the local biota; 3) a design for use of observatories as *in situ* laboratories; 4) spatial clustering of observatories/devices to optimise observation on multiple spatial scales over appropriate coenoclines; 5) integration of ocean observatory data with observational data collected through other sampling methodologies (e.g. ship, satellite, drifter, and buoy-based surveys and animal-borne devices); 6) automatic data processing, such as detection of fish images or sounds to enhance data analysis by end-users; and 7) seamless presentation of multiple data streams to end-users that are synchronised in time across all instruments within a module and ultimately across all module locations.

This review starts with a brief summary of ocean habitat connectivity to provide context, followed by a description of a proposed ecosystem observatory system, including modules, components, and ways of combining modules into clusters and networks to allow monitoring along habitat gradients and coenoclines. A description of monitoring modelling and forecasting of observatory data is followed by an explanation of how observatories could be integrated with animal-borne technologies and the cyber developments needed to support monitoring networks accessible to users of different backgrounds. The final section is a rationale for the incorporation of observatory systems into commercial developments such as windfarms and oil platforms (e.g. Fujii & Jamieson 2016) to serve as partial mitigation for potential ecosystem impacts by extending marine ecosystem monitoring capability beyond what would otherwise be financially feasible.

Background: Ecosystem connectivity

Current ocean observatories have limited applicability to fisheries and ecosystem monitoring, in part because marine habitats exhibit complex linkages that operate on many different scales. A brief summary of ocean ecosystem connectivity helps to provide context for the rationale for highly standardised observatories that are organised in hierarchical spatial configurations to enhance quantification of ecosystem attributes along habitat gradients or coenoclines.

Researchers have long known that marine ecosystems are intricately linked through passive and active mechanisms for matter and energy transference. For example, estuaries serve as an important direct and indirect source of nutrients for coastal marine waters and thereby help to sustain coastal and deep-water fisheries (e.g. Teal 1962, Haines 1979, Nixon 1980, Odum 1980, Pomeroy & Wiegert 1981, Dame et al. 1986). Passive processes involve bi-directional fluxes of nutrients, pollutants, and plankton carried by water movements such as runoff, river flow, tides, up- and down-welling, storm events, and dense shelf-water cascading, all acting along a habitat gradient from freshwater to coastal areas and to the deep sea (Figure 1; Canals et al. 2006, Afonso et al. 2014, Puig et al. 2014, Rogers 2015, Thomsen et al. 2017). Active processes also contribute to energy/matter transference in the form of rhythmic and arrhythmic population movements across seabed and water column depth gradients, such as diel vertical migrations (DVMs), which represent the largest natural daily movement of biomass on the planet (e.g. Graeme et al. 2010, Doya et al. 2014, Aguzzi et al. 2015b, De Leo et al. 2018; Figures 1 and 2).

Mechanisms that regulate nekton distribution and movements along bathymetric and latitudinal coenoclines are similar and involve interactions between environmental (e.g. temperature gradients and cyclic fluctuations) and biological conditions (e.g. food and shelter availability and predation risk) (see reviews in Rountree 1992, Deegan et al. 2000, Rountree & Able 2007, Aguzzi & Company 2010, Aguzzi et al. 2011a). Horizontal linkages have been referred to as the ‘chain-of-migration’ (Rountree 1992, Deegan et al. 2000, Rountree & Able 2007), while vertical migrations have been referred to as the ‘ladder-of-migration’ (Vinogradov 1953, 1955, 1971). Mechanisms for linkages along a depth coenocline from the photic to dysphotic pelagic zones and the deep-sea benthos include ‘organic rain’ (Vinogradov 1971, McCave 1975, Honjo 1980, Alldredge & Silver 1988, Thomsen et al. 2017), ontogenetic (i.e. with size or life-stage) vertical migration of organisms (e.g. Merrett 1978, Wakefield & Smith 1990, Kobari et al. 2008, De Leo et al. 2018), and cyclic vertical migrations such as observed in the deep scattering layers (DSLs, Vinogradov 1953, Marshall 1971, Longhurst 1976, Mauchline 1980, Aguzzi & Company 2010, Naylor 2010, Aguzzi et al. 2017). In particular, rhythmic depth strata movements similar to DVMs also occur within the benthic boundary layer across shelves and slopes by endobenthic burrowing organisms (Aguzzi & Company 2010). Indirect

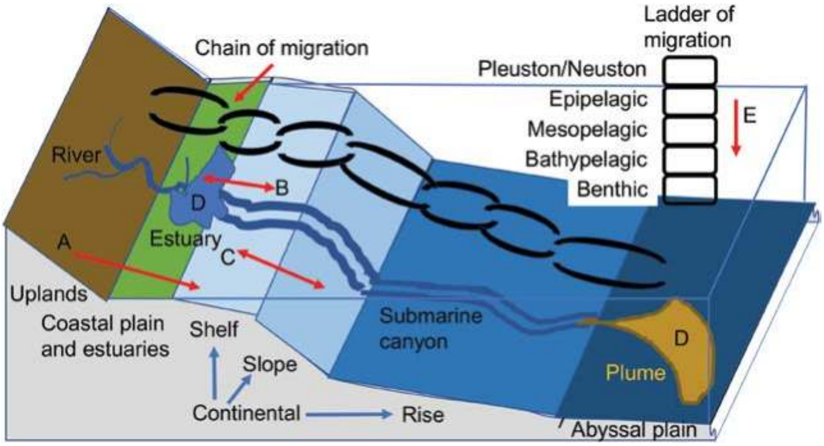


Figure 1 Example of some major linkages among habitats distributed along horizontal and vertical coenoclines connecting terrestrial to deep-sea ecosystems along a large river system. Major linkages are provided by a chain-of-migration connecting habitats horizontally, while a ladder-of-migration connects vertical habitats through ontogenetic and cyclical movements of organisms (see Figure 2). Other mechanisms of linkage include: (A) run-off from land to sea; (B) nutrient, detritus, and organism 'outwelling' and corresponding 'inwelling'; and (C) upwelling/downwelling occur largely due to water movements such as tides and storms; (D) deposition occurs where water velocity slows to allow precipitation of suspended materials and entrapment and mortality of organisms, as well as faecal deposition of migrating organism; and, finally, (E) organic and inorganic rain.

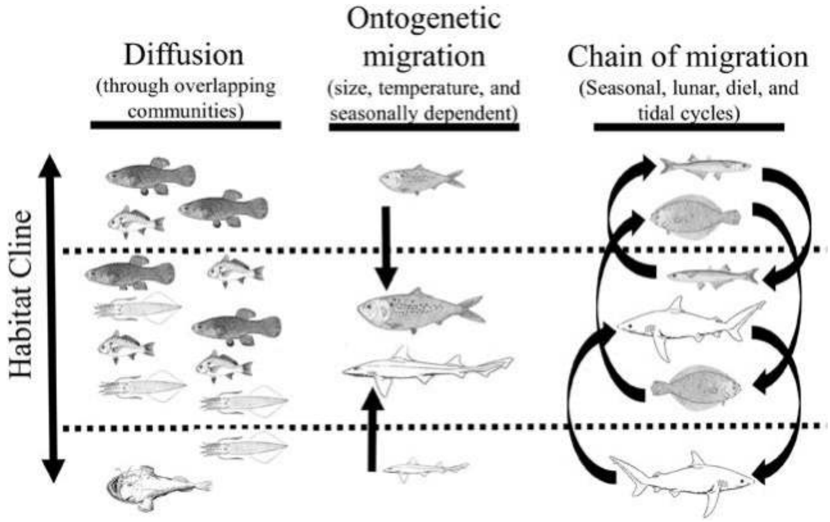


Figure 2 Example of mechanisms of energetic linkages among adjacent habitats or ecosystems through the distribution and movements of organisms. Major mechanisms include diffusion, ontogenetic migration, and chain-of-migration. Diffusion results from trophic transfer of energy among overlapping assemblages and is poorly understood. Ontogenetic migration results from movements of organisms among habitats as they grow and can be size, environmental condition (such as temperature), or seasonally mediated. The chain-of-migration (and analogous ladder-of-migration) results from rhythmic movements of organisms among habitats on seasonal, lunar, diel, or tidal cycles. The smallest links in the chain are between adjacent habitats, but links from direct movements of organisms can occur on any spatial scale among habitats located along the same coenocline. Major mechanisms of energy transfer include predator–prey interactions, spawning, faecal deposition, and local mortality.

day-night synchronisation of biological activity in deep-sea aphotic realms may also occur due to the movements of deep-scattering layer organisms (e.g. Irigoien et al. 2014). These rhythmic movements may also be accompanied by changes in background illumination at the seabed, when species making up the scattering layers are bioluminescent (i.e. bioluminescence panoramas; Aguzzi et al. 2017).

All these types of ontogenetic and rhythmic (e.g. diel and seasonal) movements produce energy fluxes that affect the functioning of ecosystems connected through a coenocline (Rountree & Able 2007, Aguzzi et al. 2011a; Figures 1 and 2), which are difficult to quantify with isolated ocean observatories. Accordingly, any technological development dedicated to ecosystem exploration, monitoring, and ultimately management (*sensu* Danovaro et al. 2017) should be planned by combining Lagrangian sampling strategies (i.e. capable of tracking individuals and population movements) as well as Eulerian approaches (i.e. a 'snapshot' capable of characterising locally the community changes produced by species displacements). For the former strategy, large-scale movements of animals are being studied through telemetry via satellite (Hussey et al. 2015). Nevertheless, only a few environmental parameters (e.g. depth and salinity) and no other ecological features (e.g. species interactions) are measured as explanatory factors of behaviour. For the latter strategy, a virtually holistic environmental monitoring approach is possible, but typically at a fine scale, which can be difficult to scale up to larger systems (Aguzzi et al. 2019). Accordingly, a merger of both strategies would be possible by the establishment of networks of monitoring stations that allow animal and population tracking at a high rate in a simultaneous fashion across large geographic scales and across latitudinal and depth gradients.

In this context, fisheries scientists have recognised the need to move from single species to ecosystem-based management approaches, but progress has been slow due to the complexity of coenoclines and the difficulty of obtaining synoptic data on appropriate scales (e.g. Marshall et al. 2018). Fishery management agencies can simultaneously advocate tracking and quantifying stocks as a monitoring action required to inform management measures and implement no-take zones (Maxwell et al. 2015). This point is crucial, as many essential fish habitats (EFHs, e.g. spawning or nursery areas) are not permanent; thus, the establishment of fishery restricted areas (FAO 2018) or other spatial management measures for fish and habitat protection could follow an adaptive approach (Walters 2007). Such a spatially dynamic approach will require different pathways for technological development in species and ecosystem monitoring. Such an approach is currently being pursued in the development of a cross-communication capability between cabled observatories and animal-borne technologies (e.g. hydrophones for acoustic tag recognition; Hussey et al. 2015).

Marine strategic areas are defined as ecologically iconic zones where multiannual surveying, as carried out by vessel-oriented technologies, is strongly recommended for scientific or management purposes (Aguzzi et al. 2019). Data on species demographic indicators (e.g. density, size and biomass), community composition (i.e. richness), and the effects of environmental controls on biodiversity obtained in this way for one iconic zone could be scaled to other areas with similar geomorphologic and oceanographic features as similar seascapes (Danovaro et al. 2017). Relevant areas have been and continue to be instrumented with different types of pelagic and benthic multiparametric platforms as part of observational networks (Tunnicliffe et al. 2003, Barnes et al. 2013), providing different levels of monitoring capability and manipulative interventions (e.g. ONC 2019, OOI 2019). However, such large networks could be improved by the development of the ecosystem observatory module design, with its increased focus on obtaining temporally and spatially overlapping data from multiple observation technologies.

Observatories are invasive technologies that produce noise, lighting, and motions that can be foreign to the habitat under study. In addition, it is important that observatories be designed to better understand their invasive impact to comply with international legislation (e.g. underwater noise as an ecological descriptor; Audoly et al. 2016, 2017). Therefore, there is a need for observatories to have built-in capabilities to monitor their own effect on the surrounding habitat and biota. The

EOM design seeks to provide self-monitoring capabilities for two reasons: 1) measurement bias and 2) degree of impact by the structures' presence and functioning on the local environment (typical sizes of the main components of observatory systems are likely to be around 3–5 m on each side and 2–4 m in height). Since any observatory will function as an artificial reef and thereby modify the local habitat characteristics that are being measured (Vardaro et al. 2007, Blanco et al. 2013), more attention is needed to understand the attraction, repulsion, and residency effects of the structures and their operations (e.g. pan-tilt camera motor noise, mobile platform noise, and illumination at imaging) on sessile and motile species and their interactions with each other (e.g. the establishment of fouling communities on the structure could influence the local trophic structure). Over time, such developments can result in enough changes that the observatory data will no longer reflect the habitat that it was designed to observe.

The ecosystem observatory module

A conceptual schematic of a proposed ecosystem observatory module and its components is provided in Figure 3, and the function of each sensor and component device is outlined in Table 1. Standard components of each module would include: 1) central node and associated instruments, 2) mobile platforms, 3) three satellite pods, 4) a passive acoustic array, 5) a spatial configuration and software to optimise cross-referencing among observational data, and 6) autonomous instruments. Optionally, some modules would be enhanced with the addition of a pelagic satellite to collect data on sea-surface and water-column organisms and conditions.

The central node and its instruments

The central node serves as the primary instrumentation platform, power supply, and data link for the module. It also houses dockage, data transfer links, and power supply for three types of mobile

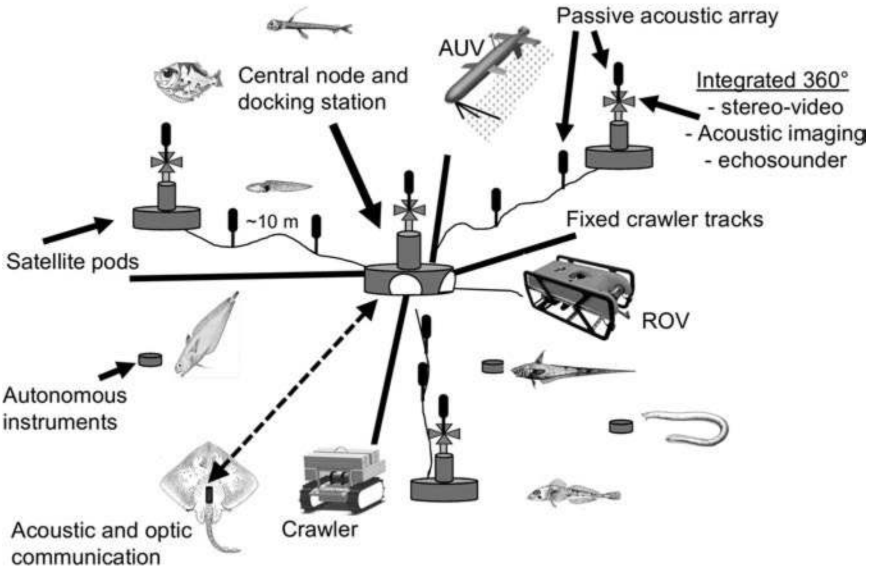


Figure 3 Schematic illustration of the proposed standard ecosystem observatory module consisting of a central node, three satellites, AUV, ROV and crawler mobile platforms and their dockage, and various autonomous devices. Hydrophones on the central node and each satellite form a 3-dimensional passive acoustic array. Crawlers would operate on predetermined tracks lines to reduce their impact on the substrate.

Table 1 Optoacoustic-image and passive acoustic sensors installed on the standard cabled ecosystem observatory module and its associated mobile docked platforms

Components	Instruments	Purpose
Central node	Multiple	Module power supply, data deposition and transmission, instrument platform, and mobile dockage platform.
	Hydrophones	Passive acoustic monitoring, including recording of environmental noise, system noise, and biological sounds over the biologically relevant frequency range of 1 Hz to 150 kHz. Component of the module's 3-dimensional passive acoustic array for sound source location; cross-reference with video, acoustic imaging sonar, and echosounder for species identification, tracking, and target strength quantification.
	Stereo-video cameras	Video recording of conditions and organisms over 360° around the central node to determine the size and spatial location of individual organisms. Use for identifying or confirming the source of sounds, targets in the acoustic image, and bioacoustic echosounder targets.
	Pan-tilt HD cameras	User-controlled video cameras with pan-tilt control, zoom capability, and lighting control, for use in investigating selected field of view areas, infrastructure elements, and to zoom in on selected passive acoustic, acoustic image, and echosounder targets for identification and behavioural observations.
	Acoustic imaging sonar cameras	Recording the presence and movements of animals in a 360° cylindrical volume surrounding the central node during all visibility conditions; cross-reference with passive acoustic array source location, stereo camera location, pan-tilt cameras, and echosounder targets for species identification, tracking, and target strength quantification.
	Rotary horizontal multibeam echosounder	Bioacoustic echosounder to quantify distribution of organisms in the water column within a 360° zone surrounding the central node and extending outward for a radius of 100–800 m. Cross-reference with passive acoustic array source location, stereo camera localisation, and pan-tilt cameras, for species identification, tracking, and target strength quantification.
	Environmental sensor package	Continuous recording of habitat variables, for example, pressure, temperature, salinity, current speed and direction, methane, oxygen, nitrates, pH, chlorophyll, and turbidity.
	Acoustic and optic receivers and transponders	Acoustic receivers for animal- and instrument-borne telemetry signals. Also including receivers for acoustic modem-based or optical communication and data transmission. In some cases, transponders can be used for two-way communication with animal- and instrument-borne devices.
	Crawler and dockage	Placing and servicing autonomous devices and satellite experimental payloads; conduct physical and biological sampling in the area surrounding central node along fixed and predetermined tracks.
	ROV and dockage	Central node servicing; place and service autonomous devices and satellite experimental payloads, conduct physical and biological sampling in area surrounding node, conduct video transect surveys, document fouling organism and species associations with infrastructure, investigate unknown targets detected by observation technologies.
	AUV and dockage	Conduct benthic habitat and biota distribution mapping transects around the central node and throughout area between modules within an observatory cluster. Investigate unknown echosounder targets beyond the range of the crawler and ROV and of video and acoustic imaging sonar ranges.

(*Continued*)

Table 1 (*Continued*) Optoacoustic-image and passive acoustic sensors installed on the standard cabled ecosystem observatory module and its associated mobile docked platforms

Components	Instruments	Purpose
Satellite pods	Hydrophones	Passive acoustic recording of ambient sounds (see previously). Components of the module's passive acoustic array for sound localisation.
	Stereo-video cameras	360° calibrated visual recording of organisms (see previously) around the satellite and cross-reference with observational data from the central node.
	Pan-tilt video cameras	User-controlled video cameras (see previously). Also, to supplement and cross-reference observational data from the central node instruments.
	Environmental sensors	Record microdistribution of physical parameters (see previously) expected to vary within the module area.
	Experiment or observation payload	Exchangeable 'plug-and-play' payload containing instruments for user-designed data collection or experimentation, such as settlement trays with different substrates (e.g. carbon, wood, or bones and even litter), experimentation on light effect on species, tagging, and so on.
Autonomous devices	Mission dependent	Stand-alone sound recorders, cameras, cages, mesocosms, and other devices to be placed by ROV or crawler to monitor short- and long-term conditions at a specific location such as monitoring a fish nest or sessile invertebrates. Other possible devices include animal collection traps and stand-alone small-scale experimental packages.

platforms (Figure 3, Table 1). Standard observation instruments on the central node would include stereo video cameras, acoustic imaging sonar cameras (e.g. dual-frequency identification sonar: DIDSON), and bioacoustic echosounders, as well as a passive acoustic system capable of recording sounds over a biologically relevant bandwidth (1 Hz to 150 kHz). In order for these systems to provide observations useful for ecosystem-level monitoring, they must provide spatially and temporally quantifiable data. For example, pan-tilt high-definition cameras that are often standard on observatories are not conducive to the collection of occurrence data on even a presence/absence level because the direction, depth, and angle of the field of view are constantly changing and hence the absence of organisms cannot be determined.

To achieve the desired quantification, the module should be designed so that each technology provides 3-dimensional data over 360° around the module and overlaps with others to the maximum degree possible (Figure 4). However, each device will have different ranges, beam angles, and time resolutions which must be integrated to provide seamless views to the end-user (see section on cyber developments subsequently). Comparison of data from the overlapping 3-dimensional views provides the ability to cross-reference data to improve identification and measurement accuracy (Figure 4). Stereo video cameras should be used to obtain the 360° view around the central node because they also provide 3-dimensional location and organism size data (Bosch et al. 2019). Although we are not aware of previous stereo video camera applications on existing observatories, they have been widely used in fisheries and ecological applications, including deep-sea applications (e.g. Harvey & Shortis 1998, Shortis et al. 2008, Williams et al. 2010, 2018, Bonin et al. 2011, Merritt et al. 2011, Shortis & Abdo 2016). It is important that these devices not be under user control, because they must provide the maximum stability of views over time (i.e. constant field of view within the device's limits). However, it is advisable for each module's central node to contain at least one pan-tilt video camera under user control to allow the examination of specific phenomena (e.g. burrow emergence of different individuals or rate of access to carrion) and to help validate the identification of organisms observed with the fixed video or other observation instrument.

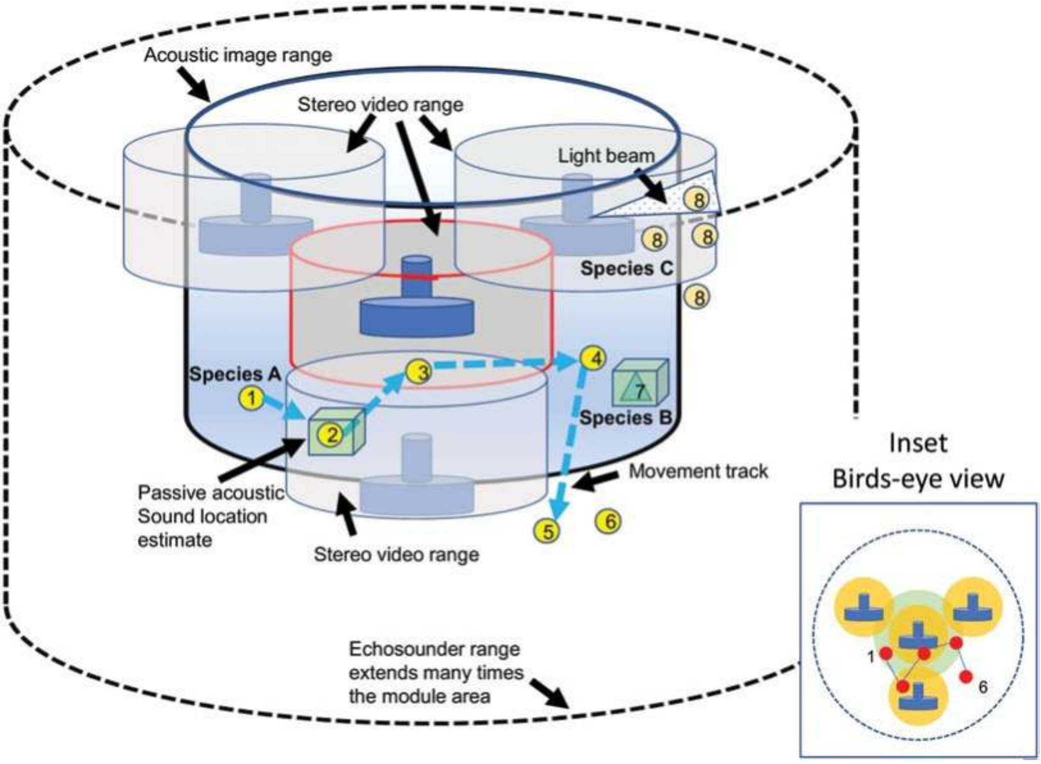


Figure 4 Schematic 3-dimensional illustration (not to scale) of the spatial configuration of the central node and satellites of a module and the overlap among video, acoustic imaging sonar, and echosounder spatial coverage areas (inset provides a bird's-eye-view of the spatial configuration). Integration of multiple 3-dimensional observation modalities in a module provides cross-referencing data to identify and track organisms. (1–6) a single individual of species A is tracked as it moves through the module area. Changes in echosounder target strength due to orientation changes can be quantified by comparison of different observations at each location, enhancing our ability to determine fish identification from target strength data. (1) Silent individual detected by echosounder and acoustic imaging sonar, provides target strength, orientation, location, and size estimates. (2) Same individual produces sound loud enough to be localised by the passive acoustic array, actual location and identification confirmed by stereo-video, acoustic image, and echosounder. Sound received level can then be corrected for exact location to obtain sound source level and detection range. (3) Now silent, it is detected by stereo video, acoustic imaging sonar, and echosounder from the central node, as well as stereo-video from a satellite. (4) The individual moves out of camera range but continues to be tracked by acoustic imaging sonar and echosounder. (5) As the individual leaves the module area, it continues to be tracked by echosounder. (6) Separate individual of species A is detected on echosounder only, but target strength consistency of species A at other locations permits accurate attribution to species within the wider area covered by the echosounder. (7) A second unknown species is detected by acoustic imaging sonar and echosounder and is identified based on localisation on a known sound. (8) The reaction of multiple fish of species C to light is quantified by acoustic imaging sonar and echosounder.

Mobile platforms

Three types of mobile platforms would be docked at the central node of each module, including a seafloor 'crawler', neutrally buoyant remotely operated vehicle (ROV), and autonomous underwater vehicle (AUV). Although there is some redundancy among ROV, AUV, and crawler platforms, each provides unique capabilities and disadvantages. All three types of platforms are useful for surveying habitat and organism distribution surrounding the module, and each can be used to investigate specific phenomena observed around the module and can aid in the identification of unknown targets detected by the video, acoustic imaging sonar, echosounder, and passive acoustic array.

ROVs and AUVs are both mobile assets; the AUV has a much greater range and is not limited by its tether. In contrast, although hampered in some ways by a tether, the ROV has manipulative capabilities (i.e. by robotic arms), can carry larger payloads, and can be directly controlled by a user in real time. The AUV provides the best mechanism for mapping and monitoring habitat and biota (benthic and pelagic) of the area surrounding a module and the larger area encompassed by the module's satellites. In addition to providing habitat-mapping capabilities of the area immediately surrounding the central node, the ROV can also be used to place autonomous instruments, exchange satellite payload packages, and service all infrastructure components of the module (Sivčev et al. 2018). The ROV can also be equipped with push-corers in order to sample sediments. The ROV's high mobility also allows important functions such as the monitoring of the fouling community, interactions of organisms with the infrastructure and its instruments, and faunal residence (e.g. sheltering).

A drawback of both AUVs and ROVs is that thrusters must be in operation even when hovering at a station, thus creating high levels of noise and turbulence that limit their ability to conduct unbiased sampling and observations at a specific location for any period of time (Rountree & Juanes 2010; Durden et al. 2016a). An important, but often overlooked, noise problem with ROVs is that their acoustic tracking and guidance systems produce intense broadband noise that may influence animal behaviour and can also bias measurements of the acoustic properties of biological sounds (Rountree & Juanes 2010). In addition, the intense tracking pings make it harder for a human user to process soundscape data (R.A. Rountree pers. obs.). Another drawback of ROVs is the need for lights for operations (Rountree & Juanes 2010). The main limitations of AUVs are related to the development of suitable docking infrastructures that can provide for data downloading and fast inductive recharging of batteries to increase AUV operating time.

A crawler can more effectively conduct point-census surveys that can provide data at specific locations for extended time periods (minutes to hours), during which noise production and turbulence can be substantially reduced compared with the other mobile platforms. A drawback to the crawler is its physical disturbance of the benthic habitat and impact on benthic organisms along its movement track, but this can be reduced to a narrow strip of seabed by limiting the crawler to a constant corridor for displacement (Chatzievangelou et al. 2016). Since such potential impacts would be magnified in the area around a permanent observatory, we recommend that crawlers be operated on predetermined and constant tracks to minimise habitat disturbance (Figure 3).

Tethered satellite pods

The three standardised satellites of each module would have several functions: 1) provide observational redundancy and spatial overlap of observations with the central node observations to assist in organism detection, identification, and development of 3-dimensional distribution maps in the area surrounding the module (Figure 4), 2) provide observation of biotic responses to the central node and its mobile platform presence and operations; and 3) serve as platforms for changeable instrument packages designed to address specific research hypotheses.

A central premise of the proposed ecosystem observatory module design is that it includes multiple modalities of observation that are synchronised in time and provide the maximum spatial overlap. Therefore, the spatial configuration is dependent on optimising the overlap among the systems under local conditions, as well as limitations of tethering with regard to ROV and crawler access to the satellites. In many locations, satellites placed at 120° intervals and at distances on the order of 10 m from the central node would be most suitable (Figure 4). Minimally, each satellite would be equipped with stereo video cameras capable of capturing a 360° cylindrical or hemispherical view around the satellite. Ideally, they would also include the same acoustic imaging sonar and bioacoustic echosounder instruments as those on the central node, but at the present time, these systems are prohibitively costly to achieve the ideal redundancy and overlap within the module area. As these technologies advance sufficiently to allow cost-effective 360° coverage, they should be added to the satellites to improve spatial overlap over a larger area surrounding the central node.

Observational data obtained by the satellites of the area surrounding the central node and by the central node of the area surrounding each satellite would provide a powerful means of determining faunal interactions with the structures, including behavioural reactions to instrument operations (e.g. lights and sounds, Figure 4).

Ocean observatories should be thought of as permanently instrumented areas where scientists of different backgrounds have an opportunity to perform manipulative experiments, favouring iconic environments such as the deep sea, for example, and resulting in a transition from a still largely descriptive science toward a more experimental, hypothesis-driven, approach. In order to better serve as platforms for hypothesis-driven research objectives, the satellites need to be designed with an infrastructure that allows for ‘slide-in slide-out’ exchange of experimental payloads for hook-up to power and data transfer. Examples of potential payloads might include settlement trays, experiments on the response of biota to artificial light regimes (useful for behaviour studies but also to examine the impact of observatory lights), observation of biota response to bioluminescent light, response to various baits, response to sound playback experiments (useful to understand behaviour and also the impact of observatory generated noise on the biota), experimental attempts to mark or tag biota through ingestion of tags or automatic capture, tag and release mechanisms (having the dual purpose of studying fish movements and residency and using the observatory structure as habitat), the effects of new colonised substrates on species and succession experiments, habitat manipulation experiments such as predator exclusions, microcosm and mesocosm experiments, and many other possibilities.

Passive acoustic array

Passive acoustic monitoring of fishes and invertebrates has become an important tool in fisheries and ecosystem studies (Rountree et al. 2006, Luczkovich et al. 2008); however, inherent problems have slowed its more widespread application, including lack of catalogues of fish sound data (Rountree et al. 2002), lack of information on source levels and detection ranges, and lack of sufficiently developed autodetection software (Rountree et al. 2006, Luczkovich et al. 2008). The use of multiple observation technologies to aid in the *in situ* validation of sound source identity, source level, and detection ranges is in its infancy (Rountree et al. 2003, Rountree 2008, Rountree & Juanes 2010), but a combination of using a passive acoustic array with video for the *in situ* identification of unknown fish sounds has recently been demonstrated (Mouy et al. 2018). The application of passive acoustic arrays for localisation and cross-reference with other forms of observation on ocean observatories are particularly promising, especially in the deep sea where many fishes possess sonic muscles that are presumably used for sound production (Rountree et al. 2012, Wall et al. 2013). Calls for the increased use of passive acoustics for fishes and invertebrates to be incorporated into ocean observing systems have been made at workshops for decades (Rountree et al. 2003, ACT 2007, R.A. Rountree pers. obs.), but implementation has been slow (Locascio et al. 2018). It should be emphasised that incidental sounds produced by fishes and invertebrates as by-products of movement, feeding, or physiological processes can be important markers of species identity and useful for monitoring temporal and spatial patterns in the associated behaviour (Rountree et al. 2006, 2018). Thus, passive acoustics can be a useful tool for monitoring both vocal and non-vocal organisms and their behaviours at observatories.

Because of the potential importance of passive acoustic monitoring as an important tool in ocean observatories, it is essential to include a hydrophone array in the EOM design. At the minimum, hydrophones should be placed on the central node and each satellite to create a four-element 3-dimensional array that can localise sounds originating near the central node. However, a greatly improved ability to localise the low-amplitude sounds created by many fishes and invertebrates could be achieved by placing compact arrays of six hydrophones on each element (*sensu* Mouy et al. 2018) or by placing additional hydrophones at intervals along the tethers from the central node to each satellite (Figure 3).

Stand-alone sensors and other devices

Autonomous instruments and recording devices (e.g. Corgnati et al. 2016, Marini et al. 2018a) deployed and serviced by the mobile platforms would be incorporated into the area surrounding the module to provide unique data on biota in the surrounding habitat and additional opportunities for *in situ* experimentation (Figure 3). For example, autonomous video recorders could be placed close enough to individual fish nest sites, or individual sessile invertebrates, to use short-range infra-red lighting to make long-term observations on microhabitat use, behaviour, and species associations. Autonomous instruments could also be used to measure gradients in conditions at increasing distances from the central node or specific satellites in an effort to quantify the effects of habitat heterogeneity on animal presence and habitat use and the observatory's influence on environmental conditions, habitat structure, and organism distribution (i.e. to distinguish between natural variation and artefacts resulting from effects of the module). Many other types of autonomous devices can be envisioned to carry out hypothesis-driven experiments, such as small mesocosms, settlement trays, exclusion cages, and benthic animal traps.

Importance of observation data overlap

Time synchronisation and spatial overlap of all observation data, within the resolution limits of each type of instrument, within a standardised spatial configuration, is one of the most important attributes of the proposed ecosystem observatory module design, as it allows for the cross-referencing needed for species detection, identification, and tracking (Figure 4). Consideration of how best to optimise the spatial coverage and overlap of observation data and how it can be packaged for users should be part of the design process for implementation of the EOM concept.

Ideal spacing between the central node and satellites is determined by optimising overlap among spatial coverage of all instruments for local conditions. Stereo video cameras provide the highest accuracy of species identification, size, and location in the area surrounding the module but are limited to periods of natural or artificial lighting during hours of darkness or in the aphotic zone. Acoustic imaging sonar provides accurate location of targets but poorer species identification (Aguzzi et al. 2019). However, it is not limited by lighting. Horizontal multibeam echosounders provide highly accurate 3-dimensional location over a large spatial area surrounding the module, but identification is limited by the accuracy of back-scatter target strength data, which are influenced by fish size and orientation to the acoustic beam, creating uncertainty in multispecies scenarios (Juanes 2018). Sounds detected by the passive acoustic array can be used to identify species when sounds are well known, but until detailed catalogues of fish and invertebrate sounds become available, most sounds detected and localised will be from unknown sources.

Cross-referencing of echosounder data with acoustic imaging sonar, video, and passive acoustic data can provide valuable validation of target strength data for organisms and thereby enhance biomass estimations around the observatory, as well as providing target strength data for other independent conventional bioacoustics surveys (e.g. traditional fisheries pelagic surveys that rely on accurate target strength data for bioacoustic assessment of fish stocks). Similarly, cross-referencing of acoustic imaging sonar with echosounder, video, and passive acoustic data can provide identification validation of acoustic image targets in the near field (ranges of up to the limit of visibility) and echosounder targets in the far field (ranges up to 1000 m). Finally, cross-references of unknown sounds localised by the passive acoustic array with video, acoustic imaging sonar, and echosounder data can provide sound source identification and quantification of source level and detection range (Rountree 2008, Mouy et al. 2018).

Simultaneous observations from all technologies would make it possible to track organisms continuously as they move around the module (Figure 4). Therefore, at each location, data on changes in fish orientation and location can be used to quantify their influence on echosounder target strength. As more and more data are compiled, accuracy of identification and tracking and estimates of fish size, abundance, density, sound source level, and sound detection range can be improved. A 360° view around the observatory by multiple observation technologies allows users to estimate the abundance of biota per unit volume while correcting for movements of individual fish and other organisms. A fish swimming in circles around the structure can be counted accurately as one individual, rather than multiple individuals moving in and out of a video field of view. To obtain these type of data, modules must be configured with satellites in close enough proximity to provide adequate coverage of mobile biota (Figure 4).

Optional pelagic satellite

The ecological monitoring of modules can be significantly enhanced by the addition of surface and water-column assets that can combine benthic observations with water-column and surface observations to monitor both surface-associated organisms and conditions as well as those of the water column (Figure 5). Besides providing a monitoring capability of the pelagic ecosystems, ecosystem observatory modules enhanced with a pelagic satellite can provide unprecedented information on pelagic-benthic ecosystem connectivity. This can be accomplished by placing a buoyed surface platform in contact with a module via an instrumented mooring line. Surface buoys and mooring lines have the potential capacity for numerous instruments to be distributed throughout the water column to synoptically monitor fine-scale hydrographic and biogeochemical parameters as, for example, corrosive (i.e. low pH, high pCO_2) oxygen minimum zone waters that intrude seasonally onto continental shelf-edge zones (Juniper et al. 2016). Instruments can be either fixed (e.g. Bahamon et al. 2011) or movable as yo-yo systems for fish monitoring from decommissioned platforms (Fujii & Jamieson 2016). They can also serve as access platforms to allow some types of maintenance of observatories placed on the seabed (depending on depth and conditions).

Each buoy would be fitted with a weather station, microphone, and video camera to monitor surface conditions and shipping activity (e.g. Aguzzi et al. 2011b, OBSEA 2019). Recordings of aerial noises associated with weather, sea state, and shipping can be validated by the video and compared with simultaneous acoustic recordings from hydrophones to provide important insight into the source of underwater sounds and help to quantify noise impacts on the aquatic soundscape. The surface buoy would also support downward-projecting video, acoustic imaging sonar, and echosounder instruments to provide similar capabilities to those of the bottom mounted instruments and hence valuable data on pelagic components of the ecosystem. All instruments would be connected to the cabled observatory for data transmission and power supply, with no need for satellite communication.

The development of a new cargo elevator technology (Figure 5) would allow the rapid delivery and retrieval of instruments and materials to and from the module. For example, in combination with the module's ROV or crawler, scientists could deliver a new experimental payload to one of the satellites and remove the old unit. Another example would be to deliver fresh bait to a baited camera system or to retrieve organisms captured by instruments at the module. An elevator system could dramatically increase our ability to deploy and retrieve materials to the module because it would no longer depend solely on the use of expensive ship-based submersibles or ROV bottom time.

Pelagic satellites can also be used as docking and communication stations for specially adapted aerial drones (Figure 5). One of the most important applications of drones would be to map spatial and temporal distributions of marine birds, mammals, turtles, and large pelagic fishes (e.g. Toonen & Bush 2018). Pleustonic and neustonic components of the ecosystem could also be mapped,

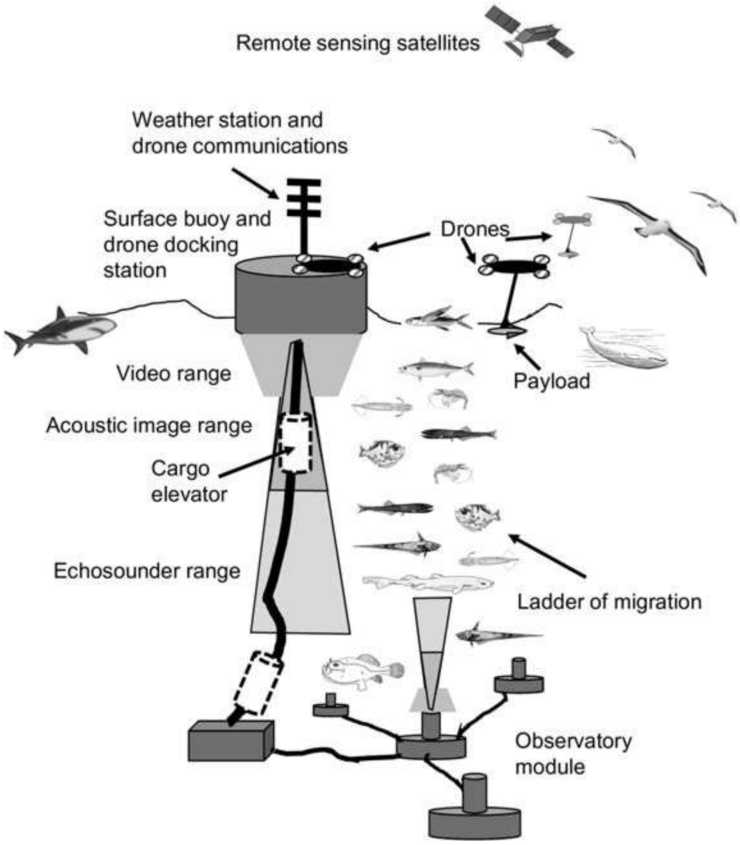


Figure 5 Schematic of an ecosystem observatory module enhanced with a pelagic satellite composed of a surface buoy and associated instruments to monitor vertical distribution of organisms and physical properties. The surface buoy would be equipped with downward-looking video camera, acoustic imaging sonar system, and echosounder similar to those deployed on the benthic module components. It would also include a microphone and 360° video to capture above-water audio and video data of weather and shipping conditions for correlation with underwater recordings. The mooring line would be variously equipped with monitoring instruments at different depths and a cargo elevator system to transport materials, such as new scientific payloads for satellite nodes between benthic and surface systems. The pelagic satellite includes a drone system to map aerial (e.g. birds) and aquatic megafauna (mammals, fish, turtles), as well as neustonic and pleustonic organisms and pollutants. Drones can also be used to carry an instrument payload such as a hydrophone or fluorometer and other instrumentation for spatial mapping.

including distributions of jellyfish, *Sargassum*, and other surface organisms and the development of windrows. In addition, they can map the distribution of organic matter subsidies, including kelp and marine mammal carcasses, and also track pollution, such as floating plastics, oil slicks, and other buoyant pollutants. This can also be crucial to monitor alien species and forecast potential areas of invasion, as plastic debris and other floating materials contribute to the transfer of non-native species (Vetger et al. 2014). Drone systems are already being successfully developed to conduct passive acoustic surveys (Lloyd et al. 2017). A communication tower on the buoy would enable researchers to communicate with the drones through a relay from the cabled observatory and also provide short-range communication with research ships and aircraft.

Satellite remote sensing has become an important tool in oceanography and fisheries monitoring (e.g. Santos 2000, Blondeau-Patissier et al. 2014), but ground-truthing of data is critical for accurate interpretation and modelling (Congalton 1991). The Southeast Atlantic Coastal Ocean Observing System (SEACOOS) included a pilot study of the potential for integration of satellite remote sensing and ocean observation systems (Nelson & Weisberg 2008), which found that coordination among data providers, management, modellers, and users was a critical bottleneck. Field validation efforts are important but expensive and difficult to coordinate. Observatory-based drone sampling can also be used to enhance satellite remote sensing programs by conducting some types of coordinated field validation sampling. Ecosystem observatory-based drones could provide a more cost-effective tool for obtaining oceanographic data for a wide range of measurements from sea surface temperature to primary production in order to tune satellite data interpretation and modelling. Some drones could be equipped with a payload of specialised equipment for specific projects, such as a chlorophyll fluorometer, or for deployment of sonobuoys, drifters, and expandable vertical profilers. Thus, integration of ocean observatories with remote sensing satellite systems can improve the accuracy of spatial mapping of large-scale environmental conditions.

Ecosystem observatory module clusters and networks

To be able to provide meaningful ecological data at different spatial scales (i.e. from local conditions to geographic areas) accounting for key factors such as habitat heterogeneity along a coenocline (e.g. Rex & Etter 2010, Lecours et al. 2015, Zeppilli et al. 2016), local modules should be associated into a spatial hierarchy of clusters and networks, called ecosystem observatory module clusters and ecosystem observatory module networks. Adopting a highly reproducible module design for observatories should reduce costs and allow for replication of data at different locations.

The spatial configuration of modules within clusters and clusters within networks is critical to providing spatial and temporal overlap among the various observation technologies required for cross-referencing and validation. Experiments are needed to determine the optimal configuration under local conditions. In these experiments, a minimum of three modules within clusters and three clusters within networks are needed to ensure at least minimal coverage and overlap. A cluster design of three modules separated on the order of hundreds of metres would be an effective way to scale up data collection from individual sites to habitat (Figure 6). At distances of hundreds of metres, bioacoustics coverage among the modules in a cluster would overlap to provide the ability to estimate water-column biota density in a homogenous fashion over a large area (0.5–1 km^2 or more; Figure 6) and to quantify the effect of module structure and operations on biota occurrence and behaviour. Cross-reference data from each module would greatly improve the accuracy of the identification and density estimation of biota within the cluster area, but well outside of individual modules, and allow for detailed benthic habitat mapping over the larger area encompassed by the cluster. Such coverage would facilitate accurate faunal abundance and density estimates necessary for fisheries and other applications and reduce observatory bias on measurements due to attraction and avoidance responses of organisms to the observatory structures.

Finally, advanced AUV capabilities would enable the AUV to be used to map habitat and benthic biota distributions between and among modules within the cluster. In some scenarios, all modules within a cluster might share one AUV that patrols among them and can dock at any module. In other scenarios, AUVs provided by each module would provide the cluster with multiple AUVs for more rapid and detailed mapping. Observational data obtained from the AUV tracks can further increase our ability to validate the identity of bioacoustic and passive acoustic targets outside of the modules but within the cluster area. In some cases, AUVs might be programmed to investigate passive acoustic or echosounder targets beyond the range of the other observational instruments within a cluster area to improve identification and density estimates. Where feasible, an observatory cluster would include one module equipped with a pelagic satellite that could provide drone support for the entire cluster to enhance studies of vertical connectivity from the surface to the benthos at the cluster location.

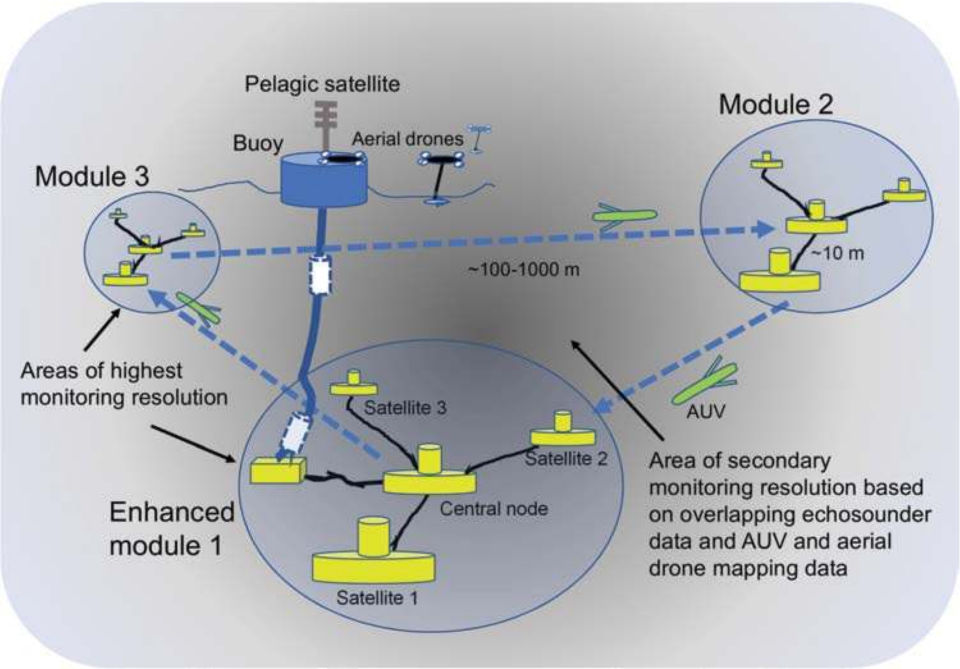


Figure 6 Schematic illustration of an ecosystem observatory module cluster designed to provide synoptic data on differing spatial scales within the cluster area. Three or more modules should be arranged in geometric clusters to allow detailed spatial comparisons within a larger spatial array. Spacing between modules is dependent on local conditions, AUV range, and optimal echosounder coverage. Clusters with module spacing allowing for overlap among bioacoustics echosounders, with greatest overlap in the centre of the cluster, enable highly accurate identification of water column organisms over a large spatial area. One or more AUVs would be designed to navigate among modules in the cluster to map habitat and organism distributions within the cluster area and provide additional ground-truth data for organism identification based on their target strength. Demersal and benthic organism and habitat mapping resolution is greatest around the modules but is also high within the wider area encompassed by the observatory module cluster.

Sentinel system

Observatory systems combining multiple EOM clusters along a coenocline form a ‘sentinel system’ observatory network (Figure 7). A minimum of three EOM clusters (i.e. nine modules arranged in a spatial hierarchy) would be needed to elevate the monitoring network from examination of local habitats to ecosystems and large geographic regions (Figure 7). It should be clear that such a sentinel system would ideally be one component of a larger monitoring effort that coordinates data from conventional ship, satellite, buoy-based, and animal-borne survey programmes. For example, establishing a sentinel system composed of clusters (each of which provides high-resolution monitoring on a scale of 0.5–1 km^2) in the upper and lower sections of a major estuary (e.g. the Chesapeake Bay) and another on the continental shelf just offshore would be effective at monitoring movements of coastal fishes that utilise the estuary as seasonal feeding or nursery grounds. Similarly, deployment along coastlines can provide information on the timing of seasonal movements of fishes and habitat connectivity along migration corridors. Sentinel systems would be useful to monitor migration patterns of fishes and invertebrates by documenting first detection, last detection, and residence period at different points along the gradient. Such a system would also be useful for monitoring the invasion of organisms into new territories (Juanes 2018) by placing clusters along the predicted invasion pathway.

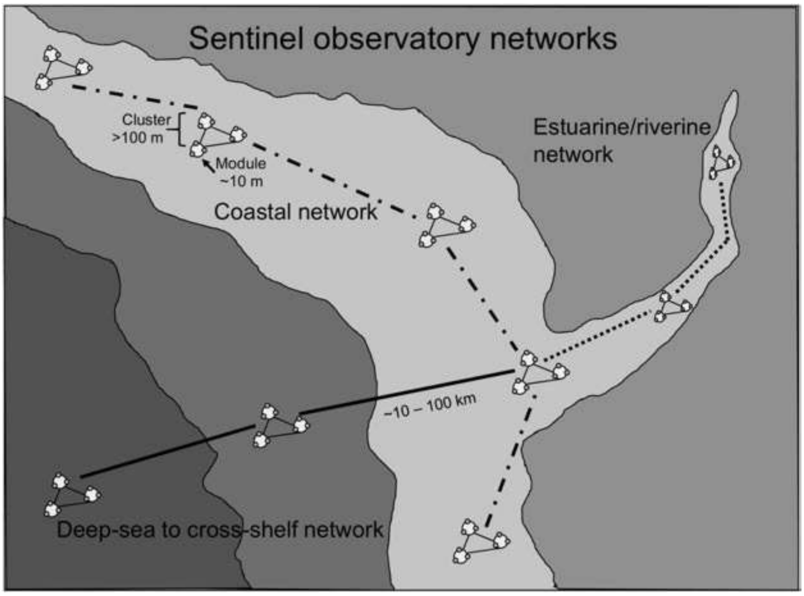
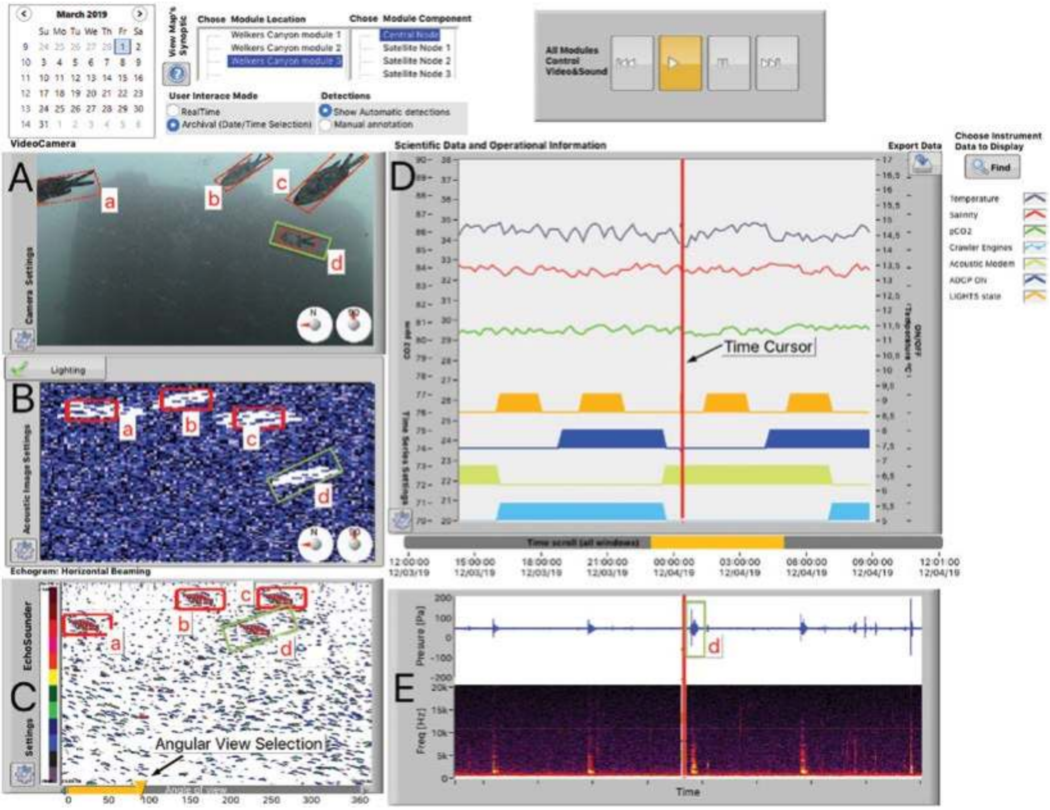


Figure 7 Sentinel ecosystem observatory networks (not to scale) composed of multiple module clusters distributed across a habitat gradient or coenocline occurring from estuarine/riverine areas to coastal zones and the shelf, down to the deep-continental margin of the slope and abyssal plain.

Ecosystem surveillance, modelling, and forecasting

Fixed and mobile platforms allow for an experimental approach to the study and monitoring of ecosystem functioning at different spatiotemporal scales (over kilometres and years). The combination of stereo video, acoustic imaging, and echosounder imaging provides the ability to quantify abundance, size, and biomass of organisms over a wide size range, as well as to identify multiple types of behavioural reactions to natural or artificial stimuli. In addition, the simultaneous acquisition of biochemical and oceanographic data can inform researchers of potential causative factors for observed behaviour and abundance patterns. However, automatic processing of the high volumes of data generated by the observatories would be essential. Automated detection and classification methodologies based on the various observation technologies are rapidly advancing (e.g. Allken et al. 2018, Juanes 2018, Marini et al. 2018b). However, we suggest that the concept of an ecosystem observatory user data interface would greatly enhance the application, testing, and quality control of detection algorithms by providing a simple computer interface for user-aided system learning (see ‘Cyber developments in support of monitoring networks’ section subsequently; Figure 8).

Ecosystem observatory networks can be used to estimate local species abundances derived from the image-based identification and counting of individuals, made possible through integration of multiple observation technologies (see Figures 4 and 8). In addition, the methodology provides an ability to develop size-class frequency data and species biomass estimation based on the estimated size and counts of individuals (Durden et al. 2016b). Cross-referencing of data from ROV, crawler, AUV, and echosounder data with validation data from each module provides the ability to obtain standardised abundance and biomass data for the entire observatory network area (Figures 4, 6 and 7). Simultaneous monitoring of a large suite of environmental factors such as temperature, turbidity, chlorophyll concentration, and other biochemical factors, together with fine-scale temporal and spatial distribution patterns of organisms, would provide important data on environmental regulators of species population structure and behavioural patterns. Temporal patterns in species



Chose Module Location: Welkers Canyon module 1 / Welkers Canyon module 2 / **Welkers Canyon module 3**

Chose Module Component: **Central Node** / Satellite Node 1 / Satellite Node 2 / Satellite Node 3

User Interace Mode: ○ RealTime ● Archival (Date/Time Selection)

Detections: ● Show Automatic detections ○ Manual annotation

Figure 8 Hypothetical user interface of data from an ecosystem observatory module, composed of the central node plus the three satellites. All data windows (A–E) play in time simultaneously, as indicated by the time cursor in the scientific data and passive acoustic sound windows (D–E). Video, acoustic image, and echosounder displays show only the portion of the 360° area surrounding the module which has been selected by the user, with the angular view selection bar common to all three (below C). However, when the playback is paused, the user can simultaneously scroll through all 360° surrounding the module in the video, acoustic image, and echosounder windows (A–C). The overlapping observation modalities and integrated visual displays are a powerful tool for examining correspondences among environmental conditions, observatory operations, and animal behaviour. When autodetection is available for one or more of the observation technologies, the user can validate detections in other windows, for example, targets 'a–d' are detected in video (A), acoustic image (B), and echosounder data (C). Data from each instrument can then be compiled to provide the most accurate information on species identification, 3-dimensional location, size, and target strength together with environmental conditions at the time of detection. In addition, sound source targets localised by the passive acoustic array and shown in the sound window (sound labelled 'd' in E) can be identified by its corresponding location in the other windows (A–C).

richness, abundance, biomass, size-class structure, and role of environmental regulators within an observatory network, supplemented with data from other monitoring programmes, could provide the raw data needed to develop ecosystem modelling and forecasting programs for the habitat or region surrounding the network.

Data from multiple observatory networks could then be linked to make comparisons among areas, populations, and environmental regulatory factors to develop regional and ultimately global monitoring programmes. Spatially representative and long-term monitoring provides the ability to distinguish between population/community regulation by repetitive phenomena (e.g. rhythmic abundance variations due to seasonal environmental changes and ontogenetic migrations, spawning migrations; Aguzzi & Company 2010, Aguzzi et al. 2011a) from long-term (decadal and longer) processes such as shifts in species distributions due to climate change and changes in resource exploitation. If the information obtained from the observatory network system and associated modelling and forecasting programs is automated, it may be possible to develop ecosystem alarm protocols that detect anomalies in ecosystem parameters that might signal undesired environmental states such as impending population collapse of keystone species.

Integration of benthopelagic networks with animal-borne technologies

Cross-connection of ecosystem observatory module networks with free-moving animal-borne sensor (ABS) technologies can also be envisaged. Inclusion of technology into the module design that allows communication with independent ABS (Figure 3) is particularly promising for obtaining data on animal behaviour as well as data from animal-borne environmental monitoring programmes (see, for example, the Animal Telemetry Network Implementation Plan 2016–2021, NOC 2016). Presently, data loggers connected to animals are getting ever more miniaturised (e.g. Nassar et al. 2018) and still primarily store oceanographic information about travelled seascapes (Wilmer et al. 2015, Fehlmann & King 2016) but only limited ecological information on intra- and interspecific interactions experienced by the traveller. This weakness is being corrected in part by the development of animal-borne cameras. Animal-borne video collection directly allows the derivation of ecological information based on what is seen by individuals during their displacements (Moll et al. 2007). Moreover, the progressive miniaturisation of implant components will eventually allow camera installation on animals of very different sizes (although filming may be constrained at night or in deep water).

If both the observatory module and animal-borne technologies are capable of two-way communication, then data-intensive video-sampling by animal-borne technologies can be enhanced by dumping data to the observatory, thereby freeing up data storage and increasing their useful lifespan. Similarly, modules can be tuned to receive telemetric data from tagged animals freely moving across depths and basins (Hussey et al. 2015). This cross-communication can complement the monitoring capability of already existing pelagic and coastal-shallow networks (e.g. OTN 2019). Presently, for the development of technological tracking of epibenthic animals carrying an acoustic emitter, displacements can be measured into a network of moored receiving hydrophone stations (Rotllant et al. 2014, Tuck et al. 2015). Such development is necessarily limited by the range of hydrophone detection capabilities and could be potentially expanded when animal tracking is assisted by moving platforms, delivering real-time data on their positioning. Tracking expansion is presently pursued by using wave-gliders and AUVs (e.g. Lin et al. 2016, Masmitja et al. 2017).

Cyber developments in support of monitoring networks

Networks of fixed and mobile units for coordinated ecological monitoring require not only hardware development but a concomitant suitable cyber architecture for data communication, processing, storage, and visualisation of interrelated multidisciplinary data of different types (Florea & Buiu 2017). Moreover, cyber infrastructures should provide proper ‘virtual research environments’ (VREs), which can be described as online collaborative environments that allow open access and program development for best science practices (Martin et al. 2019, Morris et al. 2019, Pearlman et al. 2019). These VREs should be built on top of interrelated multiparametric data access platforms similar to those developed for the Ocean Networks Canada Web services application program interface (API) and Sandbox tool set (Rempel & Cabrera 2018). It is critical that such VREs serve as libraries of multiparametric data (e.g. imaging, acoustics, physical, biochemical) derived from the observatories, as well as open-source automated classification and statistical analysis programs.

As ecology researchers increasingly deploy embedded sensor networks, they are being confronted with an array of challenges in capturing, organising, and managing large amounts of data (Borgman et al. 2007). User navigation into network data banks and analysis capability requires the design of efficient interfaces between people and computers. Such a design should include all steps of information flow, from data collection at each sensor and platform to its global elaboration. This type of information flow framework is well described by ecoinformatics (Michener & Jones 2012), which arose from the need to integrate environmental and information sciences to provide the language tools and standardisation practices necessary to access and analyse massive amounts of heterogeneous data (e.g. by developing data banking).

Data integration would include several disciplines related to information technology that allow control of data collection, processing, integration, and use in VRE systems by multiple sensor technologies. The sensor web enablement (SWE) approach defined by the Open Geospatial Consortium (OGC) standards (Del Río et al. 2018, Chaturvedi & Kolbe 2019) is a low-level specification of functionalities that allow any kind of compliant sensor to interact with other sensors, with human users, or with properly defined intelligent services. Networks of SWE-compliant sensors allow for a remote interaction by simply triggering them on and off or by changing their acquisition configuration in order to adapt the monitoring activities for specific purposes. The intelligent services capable of interacting with the SWE-compliant sensors are generally defined according to the Internet of Things (IoT) technology paradigm (Qin et al. 2016, Čolaković & Hadžialić 2018), which refers to the capability of making content and services understandable by devices without human involvement. To achieve this goal within the marine science and technology community, data science methodologies (Skiena 2017) based on artificial intelligence should be capable of extracting the relevant content from the acquired data, then using this content for interacting with the SWE-compliant observatory or for populating appropriate data repositories (e.g. the Copernicus or the SeaDataNet initiatives). For example, data acquired by SWE sensors and managed by intelligent services could be of the biophony (sounds of known fishes, cetaceans, birds, unknown biological sounds, etc.), the geophony (natural sounds like wind, rain, thunder, waves, etc.), and the anthropophony (noise from ships, seismic surveys, and the observatory itself), which would then be utilised by sound type classification software to document spatial and temporal patterns in sound occurrence and correlations between biophony and anthrophony to assess noise impacts. SWE sensors could similarly be used for biogeochemical data or visual data acquired by stand-alone devices capable of communicating the relevant acquired information (Marini et al. 2018a).

Since all marine monitoring networks are increasingly service- and end-user oriented, their data management cyber infrastructures are also being upgraded to retrieve, store, and process data in real time, acting as a cognitive system for data interpretation for humankind (Shenoi et al. 2015). Systems should enable any end-user worldwide to investigate ecological processes via interactive web interfaces, allowing navigation into banks of multiparametric 'big' biological and environmental data (Figure 8). Responses should be visualised in the form of synthetic graphic outputs, highlighting significant global trends and cause–effect relationships. Such visualisation would be based on high-level data science activities performed within VRE capable of allowing non-expert users to compose complex workflows based on tools with high technological and scientific content (Buck et al. 2019). Data output could be based on automated time series analysis (Aguzzi et al. 2012, Skiena 2017, Recknagel & Michener 2018) as well as on multivariate statistics, which would then allow modelling of biological responses to key environmental variables. The use of such powerful software tools on big biological and environmental data will transition ocean observatory systems from a largely observational to a more quantitative monitoring platform for ecological and fisheries applications.

Data flow management from multiple observation technologies

It is critical that data streams from all the observation instruments and sensors be synchronised and maintained as relationally integrated data that are interoperable with other observation networks (e.g. the ONC's Oceans 2.0 program; ONC 2019). Data should be enriched with the appropriate semantic information that allows their retrieval by semantic-based search engines (Aguzzi et al. 2015a). A user annotating events in one dataset should be able to seamlessly populate the same annotation in all other data streams (Figure 8). For example, a user marking the location of a sound in the hydrophone recording should be able to locate the corresponding data position automatically in video, acoustic image, echosounder, and environmental datasets (e.g. 'd' in Figure 8). Although observatories currently provide metadata containing information on observatory instrumentation functioning performance, maintenance status and functioning history, data quality assurance and control, calibration, and other aspects (e.g. ONC 2019), this may not be sufficient for end-users who are not capable of cross-referencing all this information automatically, because it must first be downloaded and integrated by the users themselves.

A user interface that provides all module data integrated together in an interactive visual display would be a powerful tool for researchers (Figure 8). For example, a user viewing a video would immediately see not only environmental and other observational data but also the activity state of all instrumentation (e.g. lights on, rotary motor active, ADCP active, ROV thrusters on or off). Comparison of data from the overlapping 3-dimensional views in video, acoustic image, and echosounder windows provides the ability to cross-reference data to improve identification and measurement accuracy. For example, if a video detector identifies targets 'a' to 'd', its 'ghost' target can be displayed in the acoustic image and echosounder windows to look for matches or to compare with automatic detections in those datasets. That will help a user determine if some detections are valid or to identify unknown detection targets. The user could then download a dataset containing all the attributes of the target based on the different observation types as well as corresponding environmental and operational state data. Such information can provide valuable clues to understand species response to the observatory and potential biases in behavioural observations, in addition to providing data on biotic responses to environmental conditions and the raw data necessary to compile species abundance and volume density maps. The ability to download data seamlessly in these kinds of relational datasets is of the utmost importance to encouraging widespread utilisation of observatory data among scientists, resource managers, and educators.

Observatory integration within commercial development projects

Scientists around the world struggle to obtain funding for even small observatory systems. The cost of observatory infrastructure, such as the platform and dedicated data/power transmission cables to shore, often constitutes the largest expense and greatly limits observatory capabilities. Offshore development projects (e.g. telecommunication cables, wind farms, tidal/current turbines, and oil/gas platforms) provide a unique opportunity for advancement of ocean science if government and industry leaders have the foresight to integrate ocean observatory systems into offshore development design (e.g. Danovaro et al. 2017). It is hoped that current large scientific actions are being conceived at higher institutional levels to combine the two visions and design offshore energy systems that can provide both much-needed renewable energy and also much-needed ocean observatory systems (e.g. see DELOS and LoVe initiatives as reviewed by Aguzzi et al. 2019). Offshore energy development can provide platforms for many EOMs at a location and thus the ability to construct large EOM cluster networks capable of delivering an unprecedented view of underwater life to scientists, fishers, and the public. Further, because power and data cables are a necessary part of the energy delivery system, scientists could have a fully functional data transfer network to shore already in place. If commercial industries incorporated observatory systems into project design from the beginning, rather than post-construction, and consider the advantages of an improved public image, the cost of required environmental monitoring and mitigation would likely be more palatable.

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ECOSYSTEM SERVICES AND DISSERVICES OF MANGROVE FORESTS AND SALT MARSHES

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Abstract Coastal wetlands such as mangrove forests and salt marshes provide a range of important benefits to people, broadly defined as ecosystem services. These include provisioning services such as fuelwood and food, regulating services such as carbon sequestration and wave attenuation, and various tangible and intangible cultural services. However, strong negative perceptions of coastal wetlands also exist, often driven by the perceived or actual ecosystem disservices that they also produce. These can include odour, a sense of danger, and their real or perceived role in vector and disease transmission (e.g. malaria). This review provides an introduction to the ecosystem services and disservices concepts and highlights the broad range of services and chdisservices provided by mangrove forests and salt marshes. Importantly, we discuss the key implications of ecosystem services and disservices for the management of these coastal ecosystems. Ultimately, a clear binary does not exist between ecosystem services and disservices; an ecosystem service to one stakeholder can be viewed as a disservice to another, or a service can change seasonally into a disservice, and vice versa. It is not enough to only consider the beneficial ecosystem services that coastal wetlands provide: instead, we need to provide a balanced view of coastal wetlands that incorporates the complexities that exist in how humans relate to and interact with them.

Keywords: blue carbon, coastal protection, coastal wetland, cultural ecosystem services, environmental policy, environmental service, wave attenuation

Introduction

Coastal wetlands are found along low-energy shorelines worldwide, with distinct but overlapping geographical distributions. Mangrove forests are restricted to the tropics, subtropics, and some warm temperate locations, covering 137,600 km^2 in 2010 (Bunting et al. 2018). Salt marshes are predominantly found in temperate and subarctic regions, though extensive salt marshes are also found in the tropics and subtropics, where they may form an ecotone with mangrove forests. The global area of salt marsh is poorly constrained, particularly due to uncertainty in the distribution of tropical salt marsh, though this ecosystem is conservatively estimated to cover 41,700–54,900 km^2 globally (Ouyang & Lee 2014, McOwen et al. 2017).

The distribution of coastal wetlands overlaps with a zone of disproportionately high population densities (Neumann et al. 2015); thus, many populations rely on coastal wetlands for the benefits or 'ecosystem services' that they provide. Ecosystem services are most commonly conceptualised into three groups of benefits to people: provisioning services (materials directly extracted from the ecosystem, such as timber and medicinal products), regulating services (the regulation of ecosystem processes such as wave attenuation and carbon sequestration), and cultural services (ranging from tourism and recreation to aesthetic and spiritual values). These services are sustained through a range of supporting ecosystem services, such as pollination and photosynthesis. More recently, ecosystem services have been further conceptualised as *Nature's Contributions to People,* with greater emphasis on the role of culture and local knowledge (Díaz et al. 2018).

While the ecosystem services concept has been successful in promoting the importance and value of the environment, it has often faced criticism for being too anthropocentrically focused, for overemphasising economic valuation, for oversimplifying complex ecosystem processes and functions (Schröter et al. 2014, Saunders & Luck 2016), and for not encompassing the real and perceived negative impacts that ecosystems can have on human wellbeing, termed 'ecosystem disservices' (McCauley 2006, Vaz et al. 2017). Disservices provided by coastal wetlands include being a source of pests and diseases (Claflin & Webb 2017) danger (Friess 2016), and odour (Knight et al. 2017). Disservices have received relatively little attention among coastal wetland scientists compared to ecosystem services (*sensu* von Döhren & Haase 2015). Incorporating disservices into the broader environmental policy and decision-making framework, however, allows for a more holistic understanding of a stakeholder's preference for and interactions with the environment. Studying disservices also encompasses a broader set of ecosystem processes and functions that may not be the same as those producing ecosystem services (Blanco et al. 2019).

This review takes a holistic view of human interactions with coastal wetlands that incorporates both ecosystem services and disservices. We do this by conducting an in-depth literature review of the broad range of ecosystem services and disservices produced by mangrove forests and salt marshes (as conceptualised in Figure 1). We also discuss how ecosystem services and disservices can be managed to achieve effective coastal wetland conservation outcomes.

History of the ecosystem services and disservices paradigms

History of the ecosystem services concept

The reliance of humans on the benefits of nature has long been known, with Plato (~400 BC) recognising spatial trade-offs between upstream deforestation for timber and downstream impacts on soil erosion and water scarcity (Daily 1997). Notions of this relationship were later introduced in the book *Man and Nature* (Marsh 1864) which by the 1960s spurred collaborative efforts between ecologists and economists leading to the use of terms such as 'environmental services' (Wilson & Matthews 1970), 'natural capital' (Schumacher 1973), and 'nature's services' (Westman 1977). In particular the term 'ecosystem services' (Ehrlich & Ehrlich 1981) quickly gained traction in the 1980s–90s, culminating in two seminal publications Daily (1997) and Costanza et al. (1997). The Millennium Ecosystem Assessment (MEA 2005) later defined categories of ecosystem services and mainstreamed the concept into national and international policy. In order to increase the utility of the concept, subsequent initiatives have refined the definitions and categories of ecosystem services (e.g. the European Union's Common International Classification of Ecosystem Services [CICES] and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]) and

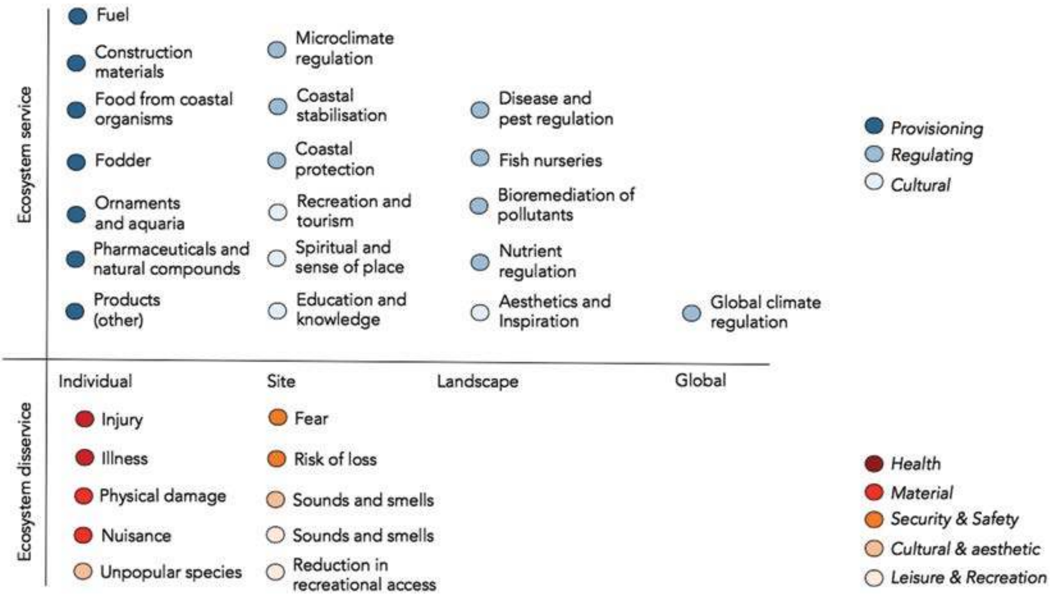

Figure 1 A conceptual diagram of ecosystem services and disservices in coastal wetlands.

communicated them to different audiences such as businesses (e.g. The Economics of Ecosystems and Biodiversity [TEEB] framework).

Critiques of ecosystem services and the emergence of the ecosystem disservices concept

The concept of ecosystem services has received considerable criticism (Schröter et al., 2014) for its anthropocentric view of nature, inconsistencies between valuation schemes (Gómez-Baggethun et al. 2010, Braat & de Groot 2012), and ethical issues related to the commodification and economic valuation of nature (McCauley 2006, Turnhout et al. 2013). Additionally, by focusing on ecosystem benefits, the concept of ecosystem services has also been critiqued for its positive bias and inability to reflect negative components i.e. ecosystem disservices (Lyytimäki & Sipila 2009, Dunn 2010, Lele et al. 2013).

Similar to ecosystem services, ecosystem disservices have been described for centuries through various historical descriptions (e.g. Friess 2016 for coastal wetlands). Ecosystem disservices, however, are a much more recent academic concept compared to ecosystem services (Blanco et al. 2019), so typologies and frameworks are not as clearly defined. Disservices were first categorised according to aesthetic, safety, security and health, economic, and mobility disservices (Lyytimäki et al. 2008) and then financial costs, social nuisances, and environmental pollution (Escobedo et al. 2011). Shackleton et al. (2016) have undertaken one of the more rigorous ecosystem disservice typologies, defining disservices as the 'functions, processes, and attributes that resulted in perceived or actual negative impacts on human wellbeing and describing many of the important considerations for their categorisation. Others have subsequently expanded this and categorised disservices into health, material, security and safety, cultural and aesthetic, and leisure and recreation disservices (Vaz et al. 2017).

Ecosystem disservices have themselves been criticised for oversimplifying complex ecosystem processes, hampering conservation efforts, and potentially leading to undesirable economic outcomes and justifications (Dunn 2010, Lyytimäki 2015). A desire to consider disservices within the dominant ecosystem services framework, however, represents a fundamental paradigm shift in understanding human-environment interactions, recognising that nature can have both beneficial and harmful impacts on human wellbeing, both of which must be managed (Shackleton et al. 2016, Schaubroeck 2017). In reality, ecosystem services and disservices are not binary but can influence stakeholders at the same time or in the same location (Saunders & Luck 2016).

Ecosystem services of coastal wetlands

Coastal wetlands provide a range of ecosystem services that support human wellbeing in a number of ways. These include provisioning services such as food from fisheries and plant products, fuels, and fibre; regulating services such as coastal protection through wave attenuation, water quality improvements to nearby coastal areas through nutrient assimilation and sediment trapping, and climate regulation via carbon sequestration and storage; and cultural ecosystem services such as recreation, education, and spiritual value (Table 1). Cultural ecosystem services are particularly understudied in coastal wetlands, in part because they are non-material, often intangible, and rarely remain constant (Thiagarajah et al. 2015, Queiroz et al. 2017).

Provisioning ecosystem services

Construction materials

Coastal wetlands are an important source of materials for construction. This ecosystem service is particularly provided by mangrove forests, as their durability, hardness, and resistance to rot and pests make trees such as *Rhizophora* spp. a highly desirable source of timber for subsistence and commercial purposes (Uddin et al. 2013, Friess 2016). At the subsistence level, mangrove forests provide timber for the construction of houses, fencing, and boats (Knox & Miyabara 1984, Palacios & Cantera 2017). *Rhizophora* spp. are commonly used for home construction in South and Southeast Asia and South America, though *Heritiera fomes* and *Excoecaria agallocha* were also historically used in the Sundarbans of Bangladesh and India (Bandaranayake 1998). *Avicennia* spp., *Xylocarpus* spp., and *Barringtonia asiatica* are preferred for boat building in the Pacific islands, while *Sonneratia alba* is preferred in Madagascar (Bandaranayake 1998). Similarly, mangrove-associated plants (often shrubs), and many salt marsh species (e.g. *Juncus kraussii*, *Spartina alterniflora*, and *Phragmites* spp.) provide thatch used in the construction of farmhouses and homes (Russell 1976, Köbbing et al. 2013, Cunningham 2015). Fronds of the palm *Nypa fruticans* are a common roofing material in Indonesia and Malaysia, known as *attap* (Baba et al. 2013).

Commercially, the large-scale mangrove forestry trade was instrumental in the expansion of Spanish naval fleets in Central America in the 19th century (López-Angarita et al. 2016). Mangrove trees were the primary material to construct telecommunication poles, without which the reach of telecommunications in some parts of East Africa and Asia would have been limited (Semesi 1998). Despite the wider availability of timber resources today, mangrove timber continues to be extracted, often for fencing posts. Poles may be the product of thinning during mangrove forestry operations for the production of charcoal.

Fuel

Many mangrove species, particularly those in the *Rhizophora* genus, are highly valued as a source of fuelwood and charcoal, because their high calorific value makes them a preferred fuel source compared to other trees (Bandaranayake 1998). *Rhizophora* spp. are slow-burning and release a high amount of heat with little smoke (Walters et al. 2008). Historically, mangroves were used as fuel for trade ships connecting European and Asian markets (Friess 2016), and naval fleets in Latin America (López-Angarita et al. 2016). Their importance to the Spanish empire was such that mangrove wood

Table 1 Summary of major ecosystem services provided by coastal wetlands

Ecosystem service	Description	Examples of benefit
Provisioning ecosystem		
Construction materials	Timber and construction materials derived from coastal wetland trees, shrubs, and associated flora	Mangroves such as *Rhizophora* spp. are used as a source of timber due to their hardness, pest-resistance, and rot-resistance properties (Palacios & Cantera 2017) The common reed, *Phragmites australis,* has long been used as both roof and wall thatch (Köbbing et al. 2013). Other saltmarsh species have been used for a similar use (Russell 1976)
Fuel	Energy sourced from coastal wetland biomass	Mangroves such as *Rhizophora* spp. are used directly as fuel or converted to charcoal due to their high calorific value (Malik et al. 2015) The common reed, *Phragmites australis,* is used as a source of fuel, burned after pelletisation, or used as a raw fuel source for methane production (Köbbing et al. 2013, Wichmann 2017)
Products (other)	The extraction of wild or farmed biota for human use	Tannins are extracted from mangrove bark used in the preservation of leather (Higake 1987) and dyeing textiles and fabrics (Punrattanasin et al. 2013) The mat rush, *Juncus kraussii*, is used in basket weaving, bedding, and the production of various wedding crafts and handicrafts for export in southern Africa (Cunningham 2015)
Food from coastal wetland organisms	Extraction of coastal wetland faunal biomass	Numerous fish and shellfish species are caught or gleaned from mangroves and salt marshes for food (Carney 2017, Castagno 2018)
Ornaments and aquaria	Extraction of biota for decoration, fashion, handicraftand souvenirs,, and so on or for display in aquaria	Juvenile fish, crustaceans, amphibians, and snakes can be extracted from mangroves and salt marshes for use in aquaria (Sandiliyan 2016)
Fodder	Biomass used to feed domesticated animals	Mangrove biomass is used for cattle fodder in East Africa (Semesi 1998). Saltmarsh grasses are used for cattle fodder in Australia and Canada (Rogers et al. 2006, Gedan et al. 2009)
Pharmaceuticals and natural compounds	Extraction of coastal wetland biota in order to produce medicines or pharmaceuticals	Ecteinascidin 743, derived from the mangrove ascidian *Ecteinascidia turbinata*, is used as an anti-cancer drug in the treatment of soft tissue sarcoma (Newman & Craig 2004). Compounds extracted from mangrove tissue can also be used as an insecticide (Bandaranayake 1998) Saltmarsh spp. have been used to treat gastrointestinal issues (especially *Salicornia* spp.) and are recognised for their potential anti-inflammatory, anti-oxidant, and anti-cancer properties (Rhee et al. 2009, Oueslati et al. 2012)

(*Continued*)

Table 1 (*Continued*) Summary of major ecosystem services provided by coastal wetlands

Ecosystem service	Description	Examples of benefit
Regulating ecosystem services		
Global climate regulation	Carbon sequestration and storage by salt marshes and mangroves (known as 'blue carbon'), particularly in their soils	In mangroves, mean carbon sequestration rates range from 174–224 gC m^{-2} $year^{-1}$ (Alongi 2012, Hopkinson et al. 2012), and carbon stocks are estimated to be on average 956 TC ha^{-1} (Alongi 2014) In salt marshes, carbon sequestration rates range from 57–218 gC m^{-2} $year^{-1}$ (Chmura et al. 2003, Hopkinson et al. 2012), and carbon stocks are estimated to be on average 593 TC ha^{-1} (Alongi 2014)
Microclimate regulation	Cooling of local climate by evapotranspiration and changes in albedo	Mangrove vegetation can cool local temperatures (Beserra de Lima & Galvani 2013) through evapotranspiration, and to a lesser extent, this effect may be expected in salt marshes
Coastal protection	Dampening or reduction in the intensity of hydrodynamic energy by vegetation and topography	Coastal wetlands contribute to coastal protection by attenuating wave energy, though this is non-linear with coastal wetland width (Koch et al. 2009). Mangrove vegetation can reduce incoming wave heights by 80% (Brinkman 2006) Saltmarsh vegetation can reduce storm surge wave height by ~20% (Möller et al. 2014)
Coastal stabilisation	Soil conservation within the ecosystem	The complex above-ground root structures of many mangrove species contribute to sediment trapping (Krauss et al. 2003) and reduced erosion Similarly, in salt marshes, high above-ground shoot density and dense rooting networks result in both trapping of sediments and limited erosion (Stumpf 1983)
Bioremediation of pollutants	Contribution of coastal wetland biota to the removal of pollutants through storage, dilution, transformation, and burial	The nutrient and heavy metal retention ability of mangrove forests contributes to their use in the treatment of wastewater (Tam & Wong 1993) Similarly, salt marshes are also able to improve coastal water quality by removing heavy metals from industrial wastewater, including Zn, Pb, and Cu (Caçador et al. 1996)
Nutrient regulation	Storage, internal recycling, processing, and acquisition of nutrients	Mangroves such as *Sonneratia* spp. can reduce nutrients such as nitrites, ammonia nitrogen, and reactive phosphorus from water by as much as 89%, 86%, and 38%, respectively (Huang et al. 2012) Nutrient cycling and N and P assimilation by *Spartina* and *Sarcocornia* saltmarsh spp. contributes to reducing eutrophic conditions (Sousa et al. 2010)
Fish nurseries	Provision of refuge habitat and nursery grounds which are crucial for survival in early life stages of commercial, recreational, and other ecologically important species	Mangrove forest extent is linked to offshore fisheries catches (Whitfield 2017) and are particularly important nurseries for emperor fish (*Lethrinus* spp.) in many parts of Indonesia, Japan, and west Africa (Nakamura & Sano 2004, Unsworth et al. 2009) Salt marshes have historically been important nurseries for blue crab (*Callinectes sapidus*) fisheries in the Gulf of Mexico (Rees 1963)

(*Continued*)

Table 1 (*Continued*) Summary of major ecosystem services provided by coastal wetlands

Ecosystem service	Description	Examples of benefit
Cultural ecosystem services		
Recreation and tourism	Provision of natural landscapes that supply an appropriate space for recreational activities, which can enhance physical and mental health and wellbeing	Mangrove forests provide opportunities for leisure activities such as fishing, boating, and social gatherings (Queiroz et al. 2017) and are hotspots for nature-based tourism (Uddin et al. 2013) Common recreational activities in salt marshes include bird watching, hiking, watersports, and wildfowling (Feagin et al. 2010, Jones et al. 2011)
Aesthetic appreciation and artistic inspiration	Provision of visual, aural, tactile, or olfactory enjoyment and/or a source of inspiration for artistic creations from natural landscape scenery and features	Mangrove forests have provided artistic inspiration for paintings (Cumming 2008) The tranquillity of salt marshes has been expressed via sculpture, poetry, and books (Wiegert & Pomeroy 1981, Seabrook 2012)
Scientific and educational knowledge	Ecosystems (or their features) which provide the opportunity for the development of scientific research, knowledge systems, and environmental education practices	Mangrove forests and salt marshes support a variety of opportunities to further the understanding of wetland ecosystems on a local and regional level, such as educational school visits and the engagement of local communities through an expanding network of wetland education centres (Ramsar Convention Secretariat 2010), and on a global scale through the publication of scientific research papers and other forms of scientific value (Greenberg et al. 2006)
Spiritual and cultural heritage and sense of place	Provision of specific areas of religious, spiritual, or cultural significance or social value, including World Heritage Sites, folklore, lifestyle values, media specifically associated with culture and heritage	Spiritual festivals such as Rush Mela (Uddin et al. 2013) and celebrations of other deities (Jalais 2014) are held within mangroves by local communities Areas in South Carolina, US, are revered as a ‘sacred’ by Gullah Geechee people, who hold strong cultural and heritage ties to tsalt marshes (Seabrook 2012)

Figure 2 Local-scale mangrove harvesting for charcoal, Tanakeke Island, Indonesia. (Photo by Jared Moore [National University of Singapore].)

became part of the tax or 'tribute' that indigenous communities had to pay the Spanish king (López-Angarita et al. 2016). Today, some small-scale charcoal production is conducted at the community level, which can have negative impacts on local mangroves if not regulated effectively (Brown et al. 2014; Figure 2). Most charcoal production, however, is produced through large forestry concessions, with complex supply chains that produce charcoal for national and regional markets. For example, Matang Mangrove Forest Reserve in Malaysia has been managed for forestry purposes since 1902, and produces as much as 179 tonnes of biomass per hectare each year from harvested plots (Ismail et al., 2017). Forestry production in Matang is not without consequence, however, as species diversity and wood yields have declined over time (Goessens et al. 2014).

Few saltmarsh species are used as fuel sources, but the common reed, *Phragmites australis,* is commonly used as a source of fuel by direct burning, being made into fuel pellets, or used to produce biogas via anaerobic digesters (Köbbing et al. 2013, Wichmann 2017). This is most popular in northern Europe and north-eastern North America.

Food from coastal wetland organisms

Many coastal communities depend on coastal wetlands for subsistence, owing to the wide variety of biodiversity they support, including offshore fisheries, invertebrates (Figure 3), mammals, birds, and plants (Hutchison et al. 2014). For many coastal communities, fish and shellfish derived from these ecosystems are the main source of dietary protein (e.g. Carney 2017). Mangroves and salt marshes provide fish and other marine species with vital spawning grounds and nurseries to raise their young and provide a habitat for shellfish, such as oysters and snails, thus supporting a highly productive and diverse food source. Historically, the food security afforded by mangrove forests may have led to the settlement of nomadic Middle East communities along the coast ∼6500 years ago, as interior areas became more arid and less productive (Biagi & Nisbet 2006). More recently, fisheries derived from mangrove forests (e.g. Aburto-Oropeza et al. 2008) and salt marshes (e.g. Castagno 2018) constituted significant contributions to subsistence and commercial markets, such that coastal wetlands are

Figure 3 Examples of coastal wetland organisms used for food, including dried fish in Sulawesi, Indonesia (a); prawns in Sumatra, Indonesia (b); mangrove crabs in New Caledonia (c); and octopus in Madagascar (d). (Photos by authors.)

valued at over USD \$1,000 ha^{-1} yr^{-1} for fisheries alone (De Groot et al. 2012, Costanza et al. 2014). In many instances, the abundance and exploitation of food resources creates a number of livelihood opportunities (Siar 2003, Glaser & Diele 2004, Magalhães et al. 2007; Figure 3).

Plant resources extracted from coastal wetlands are also an important food source. In mangrove forests, sap from the Nypa palm (*Nypa fruticans*) is commonly tapped to produce sugar, vinegar, or alcohol, and its fruits are used for food in both raw and processed forms (Hamilton & Murphy 1988). The fruits and propagules of *Bruguiera* spp., *Sonneratia* spp., and *Avicennia* spp. are all used to produce flour for baking, and the leaves of *Acanthus* spp. are used for tea (FAO 1996). In salt marshes, *Salicornia* spp. are collected for use as a vegetable or the base for vinegar and fermented beverages (Patel 2016).

Pharmaceuticals and natural compounds

Chemical extracts from coastal wetland organisms are widely used in many parts of Asia, Africa, Latin America, and the Caribbean, both in traditional and modern medicine, to treat a range of ailments including asthma, skin diseases, diabetes, cancer treatments, inflammation, tumours, viruses, ulcers, and animal venom. The medical properties of coastal wetland vegetation are typically concentrated in their leaves, fruits, flowers, roots, seeds, and resins, but recently, biomolecules are also being identified and extracted from otherwise overlooked components of the coastal wetland ecosystem, including microbes, fungi, algae, insects, and herpetofauna (Bandaranayake 1998, Cunningham 2015). Within traditional medicine, extracts from *Bruguiera* spp. are used by local communities in the treatment of tumours and viral infections (Knox & Miyabara 1984). Extracts from *Xylocarpus* spp., *Ceriops* spp., and *Rhizophora* spp. have also been used in the treatment of diarrhoea and haemorrhaging (Bandaranayake 1998). In pharmaceuticals, HIV-1 inhibitors have been characterised from the mangrove associate, *Calophyllum inophyllum* (Patil et al. 1993). Antiviral, analgesic, and anti-parasite biomolecules have been identified from *Avicennia* spp. and used in the treatment of leprosy, hepatitis, and smallpox (Majumdar & Patra 1979, Sharma & Gard 1996, Ito et al. 2000).

The use and exploration of saltmarsh vegetation for medicinal biomolecules is not as advanced as for mangrove forests. However, recent biomolecular studies have highlighted the potential of saltmarsh flora as a resource for biomolecules with broad application in modern medicine. For instance, extracts from the saltmarsh *Salicornia herbacea* show potential application as an antibacterial, antidiabetic, antiproliferative, antioxidant, anti-inflammatory, and in diabetes treatments (Patel 2016). *Salicornia herbacea* extracts have also been traditionally used in the treatment of gastrointestinal ailments and obesity (Rhee et al. 2009). *Suaeda fruticosa* has also been evaluated for a variety of antioxidant, anti-inflammatory, and anti-cancer compounds (Oueslati et al. 2012).

Regulating ecosystem services

Global climate regulation

Coastal wetlands contribute to the regulation of the global climate through their ability to sequester and store carbon dioxide from the atmosphere. High productivity (Odum 1959) coupled with low decomposition rates (Patrick & DeLaune 1977) in their anoxic soils results in a predominantly net positive balance between aboveground and belowground tissue, litter production, and organic matter decomposition (Charles & Dukes 2009). This high productivity results in mangrove forests and salt marshes sequestering and storing 3–5 times more carbon per hectare than other vegetated ecosystems (Chmura et al. 2003, Donato et al. 2011).

In mangrove forests, mean carbon sequestration rates range from 174–224 gC m^{-2} $year^{-1}$ (Chmura et al. 2003, Alongi 2012, Hopkinson et al. 2012), and carbon stocks are estimated to average 956 Mg ha^{-1} (Alongi 2014). In salt marshes, carbon sequestration rates are estimated to be slightly lower, ranging from 57–218 gC m^{-2} $year^{-1}$ (Chmura et al. 2003, Hopkinson et al. 2012), with their resulting carbon stocks estimated to average 593 Mg ha^{-1} globally (Alongi 2014). Several factors contribute to the global variation in carbon sequestration rates and stocks observed in both ecosystems. At the largest scale, climate (temperature, precipitation and potentially extreme weather events) determines the productivity of the wetland ecosystem and the amount of biomass that is produced (Sanders et al. 2016, Feher et al. 2017, Simard et al. 2019). More locally, coastal geomorphology is a key factor in determining carbon sequestration rates and stocks through the import of nutrients from rivers or other sources, tidal regime, and underlying substrate (Rovai et al. 2018, Twilley et al. 2018). Carbon sequestration rates and carbon stocks are thus highly variable across space, and their quantification requires a sound understanding of large-scale climatic influences and local-scale edaphic conditions (e.g. geomorphology, temperature, freshwater availability) and species composition.

At national and international policy levels, mangrove forests and salt marshes have been described as ‘blue carbon’ ecosystems, alongside seagrasses (Lovelock & Duarte 2019) and tidal freshwater forested wetlands (Krauss et al. 2018). Blue carbon ecosystems have received a large amount of attention globally for their ability to sequester and store carbon. However, scale is crucial in assessing the contribution of blue carbon to global climate regulation. The ability of coastal wetlands to regulate carbon is highest at the plot scale (Figure 4a) but largely insignificant at the

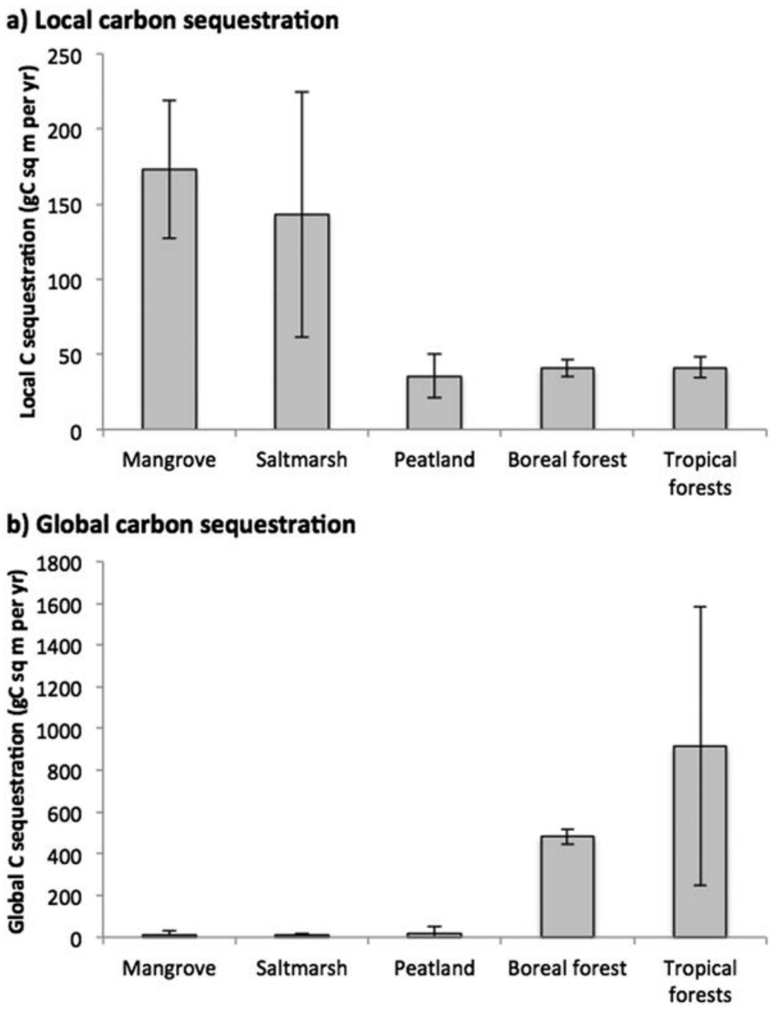

Figure 4 Comparison of carbon density for mangroves, salt marshes, and selected terrestrial ecosystems at the plot scale (a) and the global scale (b). (Data from Taillardat et al. 2018. *Biology Letters* 14, e20180251.)

global scale (Figure 4b). Combined, mangrove forests and salt marshes only account for ~0.8% of global carbon sequestration by vegetated ecosystems, due to their smaller global extent compared to other terrestrial ecosystems with a lower per hectare carbon density (Taillardat et al. 2018). It is at the national scale (for countries with long coastlines) where mangroves and salt marshes may have the most impact on climate regulation.

Coastal protection

Coastal wetlands provide protection to people and property by buffering the impact of storm surges and coastal flooding (Guannel et al. 2016, Hochard et al. 2019). This is particularly important given that over 625 million people lived in the coastal zone in 2000 with an expected increase to more than 1 billion by 2060 (Neumann et al. 2015). Mangrove forests and salt marshes protect shorelines by reducing incoming wave energy through reflection and dissipation. Dissipation occurs largely as a result of the friction generated by the physical structure and roughness of vegetation (including pneumatophores, aerial roots, trunks, and stems) (Mazda et al. 2006, Wamsley et al. 2010).

Under normal tidal and weather conditions, mangroves attenuate wave energy and wave height over short distances. *Rhizophora*-fringed mangrove forests can reduce wave energy and wave heights by as much as 71% and 79%, respectively (Brinkman 2006). *Sonneratia* spp. can attenuate as much as 50% of incoming wave energy within a distance of 100 m (Mazda et al. 2006). In addition to forest width, tree density and species are also key factors in determining the rate of attenuation; in mixed-species mangrove forests, low-density mangrove forests composed of *Avicennia* and *Sonneratia* spp. attenuated 83% less wave energy compared to high-density *Rhizophora*-dominated forests under normal conditions (Horstman et al. 2014).

Under extreme tidal or coastal hazard conditions (i.e. tsunamis and large storm surges), the effectiveness of mangroves to protect coastlines remains unclear given the paucity of empirical observations. This is particularly the case for tsunami events. The 2004 Southeast Asian tsunami spurred huge research interest in the role of mangroves in attenuating high-magnitude waves, particularly after early studies correlated lower levels of tsunami damage with larger areas of mangroves in front of coastal communities (e.g. Danielsen et al. 2005, Kathiresan & Rajendran 2005). However, subsequent analyses have tempered conclusions about the role of mangroves in attenuating tsunami waves, due to misinterpretation of potential causal mechanisms and the role of slope and distance from shore, rather than mangrove cover alone (Kerr et al. 2006). While their role in protecting against tsunami events may be limited, there is a general consensus that mangroves can still confer resilience to the coast and offer greater protection to human life and property than unvegetated coasts under storm conditions (Hochard et al. 2019), such as the Odisha tropical cyclone in 1999 (Das & Vincent 2009).

Salt marshes under normal conditions attenuate as much as 85% wave energy compared to 28% for unvegetated tidal flats (Möller et al. 1999, Möller & Spencer 2002, Yang et al. 2008). Trait differences among different species of salt marsh species (e.g. stem height, flexibility, density, leaf characteristics, and stem diameter) directly influence the extent of wave attenuation (Möller 2006, Rupprecht et al. 2017). For instance, an area of *Spartina alterniflora* attenuated wave energy 2.5 times greater than *Scirpus mariqueter*, likely due to its greater height and biomass providing greater resistance (Yang et al. 2008, Ysebaert et al. 2011).

Similar to mangroves, there are few empirical observations of wave attenuation by salt marshes under extreme conditions. Large-scale flume studies suggest that even a thin fringe of saltmarsh vegetation can attenuate storm surge waves by as much as 20% while still remaining resilient to damage caused by waves (Möller et al. 2014). The degree to which saltmarsh vegetation can attenuate extreme waves is species specific (Rupprecht et al. 2017), with implications for the upscaling of results from low species diversity flume studies to more complex field settings. As a long-term coastal buffer, water depth thresholds may limit the utility of salt marshes in building coastal resilience (Möller et al. 2001), especially when compared to much taller and more rigid mangrove trees. As such, a larger area of salt marsh is required to attenuate the equivalent amount of hydrodynamic energy as a mangrove stand (Doughty et al. 2017). Salt marshes are also vulnerable to bank erosion due to normal waves and tidal cycles, which eventually results in the collapse of marsh edges and the long-term deterioration of the salt marsh (Möller 2006, Tonelli et al. 2010, Fagherazzi et al. 2013).

Coastal stabilisation

In tandem with the direct protection of coastlines, mangroves and salt marshes can mitigate coastal erosion and reduce the vulnerability of people and property (Arkema et al. 2013). Under normal conditions, mangroves and salt marshes stabilise sediments through a number of mechanisms. Roots and shoots resist and slow the flow of water promoting the deposition of suspended sediment and inhibiting its resuspension (Furukawa & Wolanski 1996, Christiansen et al. 2000). Sediments are then mixed with organic matter and consolidated within interlocking belowground roots, a process which further binds sediments and slows rates of erosion by preventing sediments from being entrained and lost by near-bed currents (Feagin et al. 2009). Over time, these processes can lead to the vertical and lateral build-up of land through accretion. Vertical accretion in mangroves can be as much as 12 mm yr^{-1} in some locations (Alongi 2008), and the role of vegetation in encouraging sediment deposition means that accretion rates inside the coastal wetland can be several times higher than accretion in neighbouring unvegetated areas (Marani et al. 2007). Thus, coastal ecosystems provide an ecosystem service by reducing the vulnerability of people and property to coastal erosion by consolidating intertidal surfaces through sediment deposition, stabilisation, and accretion.

Consequently, in areas where vertical accretion rates contribute to positive surface elevation changes in minerogenic systems that exceed projected sea-level rise (SLR), coastal wetlands have been suggested as a possible natural mitigation measure to coastal flooding and erosion. Saltmarsh species (such as *Spartina alterniflora*) have been exported globally (from North America to coastlines across South America, Europe, South Africa, and China) over the last two centuries (Ainouche & Gray 2016). This species was chosen because it has many of the characteristics of a wetland pioneer species: it is fast-growing, can grow in the low intertidal zone, has high stem density that encourages sedimentation, and quickly creates a dense root mat that consolidates sediments (Friess et al. 2012). The growth strategy of *S. alterniflora* is so successful that the species is now invasive beyond the locations where it was originally introduced, with expensive control and eradication programmes required for its removal (e.g. Jardine & Sanchirico 2018).

Nutrient regulation

Related to processes that trap and stabilise suspended sediments in coastal wetlands are co-occurring nutrient regulating ecosystem services. Coastal wetlands are highly productive systems with a strong influence on nutrient cycling and regulation in the coastal zone, which translates into two distinct ecosystem services. First, mangrove forests and salt marshes act as a crucial link between terrestrial and marine ecosystems and can account for an integral portion (sometimes >40%) of dissolved nitrogen exported to coastal waters (Valiela 1995). Thus, coastal wetlands provide an ecosystem service by enriching and regulating broader estuarine and coastal food webs that humans rely on through detrital production and nutrient processing (Boesch & Turner 1984, Turner 1993). Second, land-use change and terrestrially derived organic pollution mean that coastal wetlands receive large inputs of nutrients (Tobias et al. 2001). Mangrove forests and salt marshes alleviate these impacts and improve water quality by transforming, recycling, and removing excess nutrients, such as nitrogen and phosphorus, from the water column (Mitsch et al. 2001). Nitrogen is mostly absorbed as nitrates by coastal wetland plants, either from the available pool of nitrates or due to the activity of nitrogen-fixing bacteria (Craft 1997).

Removal rates of nutrients by coastal wetlands and their soils are influenced by temperature, soil moisture, species and age, soil redox, density, hydrology, geomorphology, and other edaphic conditions (Feller et al. 1999, Cott et al. 2018, Bourgeois et al. 2019). Among salt marshes, *Sarcocornia* spp. and *Atriplex* spp. are efficient at nitrogen removal, whereas *Spartina* spp. are best suited for the removal of phosphorus (Sousa et al. 2010). Pioneer vegetation tend to be net importers of nutrients, whereas older vegetation are net exporters (Hughes & Paramor 2004, Lovelock et al. 2010). These factors result in high spatial variability of ecosystem service provision.

Fish nurseries

Transient and resident communities of fishes and invertebrates utilise mangrove forests and salt marshes for food, shelter, and refuge (Nagelkerken et al. 2015, Whitfield 2017). Many of these species are important to commercial fisheries (Lugendo et al. 2007, Nagelkerken 2009). Complex root and stem structures create shelter for juveniles from larger predators, which alongside high food abundance creates an environment that can support high densities of juveniles (Verweij et al. 2006, Nagelkerken et al. 2010). This forms the basis of the nursery ecosystem service, where higher densities of juveniles can be found in coastal wetlands, which contributes to fish and invertebrate catches and associated food security (Nagelkerken 2009).

Evidence is available for this ecosystem service for both mangrove forests and salt marshes. Mangrove forests have long been recognised as a nursery area, especially to tropical reef fish (Mumby et al. 2004, Nagelkerken et al. 2008, Unsworth et al. 2009). Some species of fish may also prefer certain subhabitats over others for their nursery functions, such as the preference of *Avicennia* spp. pneumatophores over *Rhizophora* spp. prop roots for some fish species (Rönnbäck et al. 1999). Salt marshes support blue crab (*Callinectes sapidus*) fisheries, historically one of the largest commercial fisheries in the Gulf of Mexico, United States (Thomas et al. 1990). Similarly, significant higher densities of penaeid shrimp inhabit salt marsh-dominated estuaries than unvegetated habitats (Raoult et al. 2018).

The role of coastal wetlands as a nursery habitat, however, is not without controversy. Connectivity between coastal ecosystems makes it difficult to attribute nursery services to a single ecosystem such as a mangrove forest or a salt marsh, and it is difficult to prove if such a service is permanent or if fish use coastal wetlands as a nursery opportunistically (Whitfield 2017). Correlations between offshore fish catches and coastal wetland extent are not always statistically significant (Loneragan et al. 2005), and where correlations do exist, they may be driven by broader estuary characteristics rather than the coastal wetland itself (Manson et al. 2005). While more research is required to better quantify the nursery function of coastal wetlands, it is clear that mangroves and salt marshes are a key component of the coastal seascape for a wide variety of aquatic species.

Cultural ecosystem services

Recreation and tourism

Recreation and tourism opportunities are some of the most common cultural benefits that people derive from coastal wetlands (Himes-Cornell et al. 2018), which as an industry contributes substantially to local economies. Costanza et al. (1997) estimated the global value of recreational services (which was partially calculated from usage fees) to be US\$815 billion yr^{-1}, of which US\$574 billion yr^{-1} could be attributed to wetlands. Recreational and tourism opportunities in mangrove forests and salt marshes range from the non-extractive such as walking, photography, bird watching, social gatherings, and ecotourism (Davidson et al. 2017, Queiroz et al. 2017) to the extractive, such as fishing and hunting (Kelleway et al. 2017). Underpinning this service in many instances is the rich biodiversity that coastal wetlands support (Feagin et al. 2010, Uddin et al. 2013). For example, the Sundarbans mangroves are home to over 300 species of flora and 425 species of fauna, some of which are endangered flagship species, such as the Royal Bengal tiger (Biswas et al. 2007). Its biodiversity value saw parts of the Sundarbans recognised as a UNESCO World Heritage Site, which has helped promote tourism opportunities (Salam et al. 2000); the Tiger Reserve alone attracted almost 175,000 visitors and permits in 2015 (Bhattacharyya et al. 2018). The revenue from ecotourism has provided substantial economic benefits to the surrounding area and fostered community management (Khanom et al. 2011, Uddin et al. 2013). Similarly, salt marshes and adjoining mudflats are often visited for their high biodiversity. Salt marshes support large numbers of migratory and resident birds, which has made them popular among tourists and birders (Burger et al. 1995, Klein et al. 1998, Myatt et al. 2003). Feagin et al. (2010) attributed differing recreational values to various zones within the salt marsh, with the salt flat and the high marsh recording high values for birding and hunting, owing to their being prime bird habitat, and the low marsh flagged as high value as the habitat supported recreational fishing activities.

Aesthetic appreciation

The aesthetic quality of a landscape can have a positive effect on human wellbeing and health (Hermes et al. 2018) by fostering mental rejuvenation, triggering positive emotions, and improving moods, whilst nurturing social interaction and advocating physical activity (Chang et al. 2008, Russell et al. 2013). Coastal wetlands have aesthetic appeal, as they have particular features that are unique in evoking a sense of true wilderness (Smardon 1978). This allows mangrove forests and salt marshes to be iconic and perceived as examples of outstanding beauty, bolstered by their relative scarcity in many landscapes.

Mangroves are an integral part of the coastal landscape that uniquely exist at the intersection of land and sea, and within this broad context are viewed as a place for rest and reflection by many (Kaplowitz 2001, Rönnbäck et al. 2007, Queiroz et al. 2017). The mystery and complexity of the extensive vistas of intricate waterways and dense mangrove canopies (Odum et al. 1982) have also been the motive for musical compositions, such as a composition in Australia titled *Mangrove*, by Peter Sculthorpe in 1979 and artwork by Sidney Nolan and Ian Fairweather in 1961, which conjured imagery of this 'alien environment' (Cumming 2008).

Salt marshes are similarly highly valued for their natural beauty (Wiegert & Pomeroy 1981, Casagrande 1997a) and have an enduring history of influencing landscape painting, literature (such as *The Snow Goose* by Paul Gallico), and poetry (such as *The Marshes of Glynn* by Sidney Lanier). These sources provide romanticised accounts of the vast expanses of wilderness and natural beauty of coastal wetlands or the wildfowl associated with the landscape (Jones et al. 2011, Seabrook 2012).

Spiritual value and sense of place

Many groups attach spiritual or religious value to coastal wetlands. With many local communities having lived alongside neighbouring coastal wetland ecosystems for generations, the traditional rights, practices, and knowledge gained from their plural interactions are invariably intertwined in the culture of these communities (Diegues 2002, Walters et al. 2008). In some instances, spiritual values are attributed to specific coastal wetlands, resulting in these sites being considered holy or sacred (Verschuuren 2006).

The spiritual value of mangrove forests materialises from peoples' contact with nature and is enhanced by specific components of the system, such as the spiritual significance of water and heightened sense of wilderness that people may experience in this unfamiliar habitat (Queiroz et al. 2017). In Brunei, cultural and spiritual beliefs are inextricable from the maintained practice of traditional lifestyles and customs (Islam & Yahya 2017). Similarly, in the Sundarbans, spiritual festivals such as Rush Mela (Uddin et al. 2013) and celebrations of other deities (Jalais 2014) still continue within the mangroves by local Hindu communities. Additionally, the use of mangrove roots in totemic carvings seen to be of spiritual value is widespread in cultures spanning Indonesia to northern Australia, a practice that continues today (Kelleway et al. 2017).

Both mangrove forests and salt marshes can provide spiritual value and a sense of place for communities that have traditionally been displaced or marginalised. Local accounts for salt marshes of the Gullah Geechee community who have lived on the Sea Islands from North Carolina to Florida since the 1600s describe how the area holds particular importance for the descendants of slaves, as a 'sacred place' where their history, heritage, and culture were founded in the salt waters and marshes and, as such, held physical, emotional, and spiritual roots of their present day existence (Seabrook 2012). Similarly, in coastal Louisiana, Cajuns, Native Americans, and escaped slaves utilised the extensive coastal wetlands as their home (Gramling & Hagelman 2005). These productive habitats provided both abundant resources and protection to marginalised communities and continue to contribute to their modern culture and sense of place.

The value of coastal wetland ecosystem services

Methods of ecosystem service valuation

The promotion of ecosystem services in recent decades was often triggered by the realisation that these crucial benefits are underestimated in decision-making (Hein et al. 2006). As such, ecosystem service valuation has become a prominent field in both ecological economics and environmental science (Atkinson et al. 2012). The complex and numerous ecosystem services provided by coastal wetlands require ecosystem service valuation to take a multifaceted approach using myriad market and non-market approaches (Birol et al. 2006, Table 2).

Despite our increasing knowledge of coastal wetland ecosystem services, values attributed to these services are not well represented in the literature (Himes-Cornell et al. 2018). In general, it is understood that both mangroves and salt marshes are undervalued economically (Brander et al. 2012). Coastal wetlands can be difficult to value because they are ‘public goods’, and society cannot be excluded from receiving that service, nor can the use of a benefit by one beneficiary alter how it is provided to another (Brander et al. 2012). Complications arise when attempting to value such services, as their underlying ecological functions vary spatially and temporally and may also have a degree of connectivity which should be considered during any valuation exercise (Barbier et al. 2011).

Coastal wetland ecosystem services are further undervalued in decision-making because many are ‘non-market’ goods and therefore difficult to quantify in purely monetary terms. An analysis of coastal ecosystem service valuation studies shows that market value analysis of provisioning services was much more common than the valuation of regulating or intangible cultural services (Himes-Cornell et al. 2018). Cultural ecosystem services such as inspiration for art, culture, and design are particularly underrepresented and undervalued (Himes-Cornell et al. 2018).

Table 2 Economic valuation methods for coastal wetland ecosystem services

Ecosystem service	Economic valuation methods											
	MA	PFA	NFI	R/SC	COI	TCM	HP	CV	CE	DAC	PGL	DEC
Provisioning services												
Construction materials	X											
Fuel	X											
Products (other)	X											
Food from coastal wetland organisms	X											
Ornaments and aquaria	X											
Fodder	X											
Pharmaceuticals and natural compounds	X											
Regulating services												
Global climate regulation		X		X						X	X	X
Microclimate regulation		X		X						X	X	X
Coastal protection	X	X		X						X	X	X
Coastal stabilisation	X	X		X						X	X	X
Bioremediation of pollutants				X	X					X		
Nutrient regulation				X	X							
Fish nurseries	X	X	X					X	X			
Disease and pest regulation				X	X			X	X			
Cultural services												
Recreation and tourism						X	X	X	X			
Aesthetic appreciation and artistic inspiration								X	X			
Scientific and educational knowledge								X	X			
Spiritual and cultural heritage and sense of place								X	X			

Source: Adapted from Birol et al. 2006. *Science of the Total Environment* **365**, 105–122.

Abbreviations: (PFA), production function analysis; (NFI), net factor income; (R/SC), replacement/substitution cost; (MA), market analysis; (COI), cost of illness; (TCM), travel cost method; (HP), hedonic pricing; (CV), contingent valuation method; (CE), choice experiment method; (DAC), damage avoidance costs; (PGL), productivity gains and losses; (DEC), defensive expenditure costs.

Estimating the global value of coastal wetlands

Despite the limitations outlined previously, several studies have attempted to aggregate values for coastal ecosystem services at national to global scales (Brouwer et al. 1999, Woodward & Wui 2001, Brander et al. 2006, 2012). Most large-scale ecosystem service valuations are conducted using benefit transfer, assuming a constant unit of ecosystem service value per hectare of each type of ecosystem, which is then multiplied by the area of each ecosystem type to produce aggregated totals (Batker et al. 2008). This approach is useful when trying to aggregate values on a national or international scale using scarce data; however, it assumes that an ecosystem provides services uniformly across its range. For coastal wetlands, ecosystem status and service provision vary significantly across space due to population density (Rao et al. 2015) and climatic (e.g. Ouyang et al. 2017, Simard et al. 2019) and geomorphological variation (Twilley et al. 2018).

The first notable study to estimate global coastal wetland ecosystem service value was conducted by Costanza et al. (1997), which valued mangrove forests and tidal marshes at US\$9,990 ha^{-1} yr^{-1} (US\$1995, converted to US\$13,786 ha^{-1} yr^{-1} in US\$2007; Costanza et al. 2014). More recently, values were aggregated again by De Groot et al. (2012), who estimated the global value of ecosystem services provided by coastal wetlands as high as US\$193,843 ha^{-1} yr^{-1} (US\$2007). The substantial increase in ecosystem service value estimated by the latter study does not necessarily indicate an increase in the value of ecosystem services over time but is instead more likely a reflection of an increase in research effort coupled with more robust analysis techniques (Costanza et al. 2014).

Ecosystem services and coastal wetland policy

Another way to understand the value of coastal wetland ecosystem services is to see how they have been used and valued by policy makers. Several international policy initiatives have incorporated the ecosystem services provided by mangrove forests and salt marshes. For example, the Ramsar Convention on Wetlands (2018) describes how the ecosystem services of coastal wetlands can contribute substantially to all of the United Nations' Sustainable Development Goals (SDGs). The SDGs are a set of 17 priorities established to help countries improve sustainable economic development, ensure social safeguards, and encourage environmental protection. Many coastal wetland ecosystem services contribute to livelihoods, which can help countries move towards achieving SDG 1 (*End Poverty*). The provisioning services of coastal wetlands also contribute to the achievement of SDG 2 (*End Hunger*). The carbon sequestration potential of coastal wetlands makes them suitable for achieving SDG 13 (*Climate Action*), while coastal wetlands also contribute to fisheries and healthy oceans (SDG 14, *Life Below Water*).

Blue carbon is being increasingly discussed in the context of global climate change policies, such as Article 5 of the Paris Agreement of the United Nations Framework Convention on Climate Change. While mangrove forests and salt marshes may not substantially impact the global carbon cycle, their contributions to carbon sequestration may be important at the national scale for countries with long coastlines and lower carbon emissions (Taillardat et al. 2018).

The coastal protection services of coastal wetlands contribute to the aims of the Sendai Framework for Disaster Risk Reduction, a recent initiative by the United Nations Office for Disaster Risk Reduction to increase interdisciplinary collaboration and opportunities for risk reduction against hazards (Aitsi-Selmi et al. 2015). The use of the natural environment to reduce hazard risk through 'ecological engineering', 'building with nature', 'ecosystem-based adaptation', or 'grey-green infrastructure' (Morris et al. 2018, 2019) are attempts to achieve the aims of the Sendai Framework by promoting ecological disaster risk reduction (eco-DRR) through the use of ecosystem services that sustainably regulate hazards (Faivre et al. 2018). Wetlands can be incorporated into broader integrated coastal management planning to reduce risk to coastal hazards (Wanger et al. 2020).

Ecosystem disservices of coastal wetlands

Ecosystem disservices are largely understudied in most ecosystems, and this is especially the case for coastal wetlands. As such, categorisations and frameworks are less developed compared to the larger field of ecosystem services, and we still lack an operationable and locally adaptable classification of ecosystem disservices (Blanco et al. 2019). This review utilises and adapts one of the most recent ecosystem disservice frameworks (Vaz et al. 2017) to allow broad comparability with existing ecosystem service frameworks. Ecosystem disservices have been divided into five categories: *health ecosystem disservices* include the direct or indirect negative impacts of biota and their existence on human physical and/or mental health and wellbeing; *material ecosystem disservices* are those that cause a nuisance or physical damage to built infrastructure; *security and safety ecosystem disservices* are those that directly or indirectly disrupt physical, personal, national, or financial safety and security; *cultural and aesthetic ecosystem disservices* represent the direct or indirect impacts of an ecosystem that contribute to cultural and spiritual disconnection with the environment; and *leisure and recreation ecosystem disservices* are those that reduce the demand for recreational opportunities. Examples of these categories are given in Table 3. There is substantial overlap between ecosystem disservice categories, and the fuzzy and perceived nature of many ecosystem disservices means that they may span several categories at once (Vaz et al. 2017).

Health ecosystem disservices

Specific components of mangrove forests and salt marshes have the potential to cause physical or mental harm to people, whether through injury, illness, or distress. Such components may include plants (e.g. thorns), animals (insects, aggressive interactions with macrofauna such as crocodiles and monkeys), or diseases that may be present in these environments.

It was long considered that coastal wetlands were a source of diseases such as malaria, though the exact mechanism by which disease was transferred has changed. Disease was originally associated with their odour; indeed, the etymology of the word ‘malaria’ involves the Italian phrase for ‘bad air’ (Hempelmann & Krafts 2013). For nearly 2000 years, it was assumed that diseases were transmitted from mangrove forests and salt marshes through their odour of decaying organic matter, or ‘miasma’. For example, colonial explorers in the Zambezi Delta in East Africa considered miasmatic air emanating from mangroves to carry the ‘death-germ’ (Rankin 1890). Colonial explorers in Central America considered mangroves to be ‘generating unhealthy miasmata’ (Fitzroy 1853), which may have limited efforts to construct a canal or railroad across the isthmus. The miasma theory was supported by respected scientists at the time such as Alexander von Humboldt, resulting in the wide acceptance of the theory (Browne 1944). It was only with the advent of modern medicine and germ theory that diseases were understood to be bacterial or viral in origin and transferred by vectors such as mosquitoes (particularly *Aedes vigilax, A. camptorhynchus, A. albopictus, Verrallina butleri*, and *Culex sitiens*) instead of bad air (Hempelmann & Krafts 2013). Thus, while diseases are still a disservice caused by coastal wetlands, the perceived mechanism by which this disservice operates has changed.

Mosquitoes are common in coastal wetlands, supported by components of the ecosystem such as vegetation, standing water, microtopographic variation, and moist substrate (Dwyer et al. 2016, Rowbottom et al. 2017). Mosquitoes and associated vector-borne diseases remain a common public health concern today and can have substantial impacts on wellbeing and economic productivity. Several integrated mosquito control strategies are employed to reduce this ecosystem disservice in urban and peri-urban areas. This includes the application of chemical larvicides, reduction of ecosystem components (such as standing water) that encourage larval growth, and creating buffer areas between coastal wetlands and human settlements (Dwyer et al. 2016).

Table 3 Summary of direct or indirect, perceived, and/or actual ecosystem disservices provided by coastal wetlands

Real or perceived ecosystem disservices	Description	Examples of disservice
Health ecosystem disservices: affecting human physical or mental health		
Injury, irritation, or reaction	Negative interaction with plants, animals, or abiotic components caused by exposure, consumption, and/or contact	Death and/or injuries sustained by wildlife or habitat encounters; examples in mangroves include: crocodile attacks, snake bites, cuts by sharp or uneven vegetation (Friess 2016) Biting insects are often a serious nuisance and source of irritation in and near salt marshes (Scott & Littig 1962)
Illness, infection, viral, or disease	Physical or emotional discomfort, pain, or incompetence caused by exposure, consumption, transmission, or interaction with flora, fauna, bacteria, viruses, or zoonotic infections or diseases	Coastal wetlands provide habitat for vectors of malaria (Dunn 2010) Salt marshes and surrounding estuaries can harbour vibrio bacteria, especially in shellfish populations, that may result in illness if consumed (Colwell et al. 1981)
Material ecosystem disservices: damaging the human built environment		
Physical damage	Physical damage to built infrastructure caused by ecosystem components	Saltmarsh wrack deposition can lead to clean-up costs (beaches, lawns, docks) and unsightly and less available beaches (Gisselman 2014) and may result in allowing unwanted species to invade an area
Nuisance	Irritants to built infrastructure	Animal excrement or leaf litter from coastal wetland organisms can stain pavements and jetties (Vaz et al. 2017)
Security and safety ecosystem disservices: disrupting physical, personal, national, and/or financial stabilisation		
Fear of habitat, pests, plants, and/or animals	Feeling of unsettlement when provoked by nature	In early accounts, mangrove forests were described as ‘dark, gloomy, and dangerous’. These actual and/or socially constructed negative perceptions were caused by fear of unknown habitats, wildlife, and indigenous peoples (Friess 2016) Salt marshes were associated with danger and higher crime rates (Casagrande 1996)

(*Continued*)

Table 3 (*Continued*) Summary of direct or indirect, perceived, and/or actual ecosystem disservices provided by coastal wetlands

Real or perceived ecosystem disservices	Description	Examples of disservice
Risk of loss or harm	Financial deficits acquired by way of physical or environmental functions, processes, and/or attributes	Diseases associated with mangroves can lead to decreased financial wellbeing due to healthcare costs and inability to work (Knight et al. 2017) High density grazing of Arctic-breeding geese in coastal salt marshes disturbs and exposes the soils to erosion and flooding and can release carbon emissions (Buij et al. 2017)
Cultural and aesthetic ecosystem disservices: impacting mental, cultural, and spiritual interactions with nature		
Sounds, smells, or sights of biota, landscapes, or seascapes	Reduction, disruption, or inhibition of cultural and spiritual interactions with nature	Historical accounts often described mangroves as ‘dark’, ‘gloomy’, ‘fetid’, and ‘dismal’ (Friess 2016). Mangroves often form dense vegetation, and today landowners may feel that this blocks their view of the landscape/seascape nearby (De Luca 2015) Both mangrove forests and salt marshes are commonly described as having foul odours. Derived from the anoxic conditions of coastal wetlands, sulphurous compounds result in a ‘rotten-egg’ smell and are often seen as unpleasant and decrease lifestyle amenity (Gurran 2008, Harty 2009, Friess 2016)
Unpopular species	Ecosystem components that are a religious, traditional, or cultural taboo	Some coastal wetland animal species are associated with evil spirits (Jalais 2014)
Leisure and recreation ecosystem disservices: inhibiting physical interactions with nature		
Sounds, smells, or sights of biota, landscapes, or seascapes	Reduction, disruption, or inhibition of recreational interactions with nature	See *Cultural and aesthetic ecosystem disservices*
Reduction in recreational access	Ecosystem components that reduce recreational opportunities due to perceived or actual nuisance or injury	Presence of mosquitoes may reduce demand for recreation

Source: Adapted from Vaz et al. 2017. *Ecosystem Services* **23**, 94–107

Security and safety ecosystems disservices

Ecosystem disservices related to security and safety are those that have the potential to disrupt a person's physical, personal, or financial stability. These can be actual or perceived situations of hardship and can range from feelings of uneasiness to remorse. Since this disservice is largely cultural and perceived, the magnitude of this disservice differs between individuals.

Due to their dynamic position in the margin between the terrestrial and marine zones, coastal wetlands have long been viewed with suspicion, particularly by those who were not familiar with these ecosystems. For example, British explorers in West Africa during the mid-1800s described mangroves as impenetrable and dark due to the density of foliage and roots, all of which contributed to the coastal landscape feeling sombre (Bacon 1842). Many salt marshes have been viewed as places of crime, dangerous due to pollution, or, similar to mangroves, 'gloomy' in nature (Casagrande 1996). One such study showed almost half of respondents perceived their nearby salt marsh to be a dangerous place due to crime (Casagrande 1997b).

Safety and security disservices extend beyond perceived notions of insecurity to threats to physical safety. Historically, mangroves were avoided by explorers because they were considered to be home to 'dangerous' indigenous populations who would attack ships (e.g., see accounts by Smith & Dalrymple 1860). This ecosystem disservice was particularly apparent during the exploration of the Australian coast by British explorers, where aboriginal groups would use mangroves to retreat or remain from view (e.g. Birtles 1997).

Cultural and aesthetic ecosystem disservices

Similar to cultural ecosystem services, cultural, material, and aesthetic disservices are difficult to categorise and measure because they are influenced by sociodemographics, experiences and knowledge, and personal or spiritual beliefs. Different individuals may or may not find particular landscapes aesthetically pleasing. Such views and perceptions vary greatly among individuals, so the type and level of ecosystem disservice experienced differs from person to person (Lyytimäki et al. 2008). While there is strong evidence to suggest that the stark nature of coastal wetlands inspires substantial levels of aesthetic ecosystem services in many people what is considered 'aesthetically appealing' differs between individuals. This means that some stakeholders consider such coastal wetlands to produce aesthetic disservices due to their bleakness. Historical colonial expeditions often described novel mangrove forests as 'dark', 'gloomy', 'fetid', and 'dismal' (Friess 2016), and explorers noted that mangrove forests had 'few attractions to the lover of the picturesque' (Rankin 1890) because of the primeval look caused by their dense root systems. Similarly, salt marshes were considered 'bleak, appalling, boundless, treeless landscapes' (Zwart 2003).

Aesthetic disservices have also provided literary inspiration, in a similar manner to aesthetic ecosystem services. Charles Dickens drew inspiration from the Thames marshes in the United Kingdom for the bleak and solitary wilderness as a backdrop for an angry sky in the opening chapters of the novel *Great Expectations* (Hynes 1963). Such an example highlights how the aesthetic disservice provided by coastal wetlands can act as a broader negative metaphor.

Consequences of ecosystem disservices

Historical coastal wetland loss

Ecosystem disservices can influence the action of stakeholders to a greater degree than ecosystem services (Blanco et al. 2019), and coastal wetlands are a great example of this. Historically, coastal wetlands have seen high rates of loss due to anthropogenic influences. Coastal wetlands were often perceived as wastelands with little economic value and the source of ecosystem disservices and thus were converted to land for agriculture, aquaculture, and industry. It is believed that up to 87% of the world's freshwater and coastal wetlands have been lost since 1700, with 35% of all coastal wetlands lost since 1970 (Ramsar Convention on Wetlands 2018).

The conversion of coastal wetlands has been practiced in North America, Europe, Africa, China, and elsewhere for centuries to millennia (Bertness et al. 2004, Davidson 2014, Knight et al. 2017). In Europe, urbanised coastlines now account for >50% of coastlines in the Mediterranean Sea, and 15,000 km^2 of coastal wetlands, tidal flats, and other coastal features have been converted in the Wadden Sea alone (Airoldi & Beck 2007). In China, at least 5,352 km^2 of coastal wetlands have been lost since 1978, and remaining coastal wetlands have been subject to pollution, degradation, and overexploitation (Meng et al. 2017). In North America, coastal wetland loss has been dramatic in both urban environments (e.g. Boston: >75% loss of coastal wetlands, Bromberg & Bertness 2005), as well as on the regional scale (e.g. northern Gulf of Mexico: 0.86% loss per year from 1955–1978, Baumann & Turner 1990). Loss and degradation due to agriculture has been common both via direct conversion or through use of coastal wetlands for livestock grazing (Gedan et al. 2009).

In comparison to salt marshes, large-scale mangrove forest loss occurred relatively recently, with coarse estimates suggesting that ~35% of the world's mangrove forests were potentially lost between 1980 and 2000 alone (Valiela et al. 2001). Approximately 1 million hectares of mangroves in Indonesia have been lost since 1800 (Ilman et al. 2016), 12%–25% of all of Thailand's mangroves were lost to shrimp ponds from 1961–1993 (Dierberg & Kiattisimkul 1996), and there was 12% total mangrove loss in Southern and Southeastern Asia from 1975 to 2005 (Giri et al. 2008). The majority of this mangrove loss has resulted from agriculture, aquaculture, and urbanisation (Giri et al. 2008). Encouragingly, rates of mangrove loss have reduced globally since the turn of the 21st century and are now only 0.3%–0.6% per year, though some countries such as Myanmar and Malaysia still experience rates of deforestation that are substantially above the global average (Hamilton & Casey 2016).

While coastal wetland loss has been significant through direct conversion for economic gain, other reductions in wetland area have occurred due to explicit attempts to reduce their ecosystem disservices, such as for the control of mosquito populations (Knight et al. 2017). Thought to be a haven for disease-carrying mosquitoes coastal wetlands have often been subject to intensive ditching and efforts, particularly in North America, Australia, and Europe (Dale & Hulsman 1990). For example, draining efforts lead to the digging of dikes and drainage ditches in 95% of coastal wetlands in the northeast United States as part of efforts to reduce mosquito populations (Buchbaum 2001).

Negative public perceptions of coastal wetlands

With an increasing knowledge of the ecosystem services coastal wetlands provide to communities, it would be expected that public perceptions of these ecosystems would now be different from the historical perceptions that drove coastal wetland loss. While this may be largely true, a negative perception of coastal wetlands still remains with many people today because of the long history of ecosystem disservices discourse associated with these ecosystems. The now common American political phrase 'drain the swamp' has its origin in ecosystem disservices, where the odour and mosquitoes associated with freshwater and coastal wetlands are used as a metaphor for lobbyists and bureaucrats. This phrase has a long history, and authors have argued that draining the swamp is associated with a masculine, colonial mindset of taming the wilderness and conquering nature and its disservices (Giblett 1996).

Lingering negative perceptions of coastal wetlands may be due in part to their poor advertising. A survey of major international media outlets by Duarte et al. (2008) showed that 73% of all newspaper articles on coastal ecosystems focused on coral reefs. Salt marshes and mangrove forests accounted for only 6.5% and 20% of newspaper articles, respectively. The media is a key channel to communicate the importance of coastal wetlands and challenge perceptions of disservices. Since Duarte et al.'s study, coastal wetlands have continued to be in the news, though still not to the degree of other coastal ecosystems. A rapid search of the Google News platform (a news aggregator and search engine) in June 2018 showed that of ∼434,900 articles written about coastal ecosystems, 85% of articles focused on coral reefs, and only 8.7% and 6.5% of articles were written about salt marshes and mangrove forests, respectively. Poor representation in the media may affect the communication of ecosystem services, providing a challenge to tackling common misconceptions of coastal wetlands linked to ecosystem disservices.

Managing ecosystem services and disservices holistically

Ecosystem services are a key approach to support environmental conservation, so highlighting and quantifying ecosystem disservices has been considered by some to hinder conservation efforts (Lele et al. 2013). Ignoring ecosystem disservices in environmental management, however, may be counterproductive, since ecosystem disservices strongly influence stakeholders' decisions (Blanco et al. 2019) and increase the likelihood of (often unanticipated) negative interactions between ecosystems and people. For example, if a disservice such as odour from a mangrove forest is not defined and characterised by managers, then it is harder to plan for its mitigation or management. Disregarding ecosystem disservices can cause local stakeholders not to buy into management decisions such as coastal wetland restoration (Handel 2016).

Instead of ignoring ecosystem disservices entirely, management may be more successful if disservices are integrated into a more holistic framework of ecosystem management and stakeholders are educated to understand ecosystem disservices, why they occur, and how they can be managed. Knight et al. (2017) propose a conceptual framework for integrating coastal wetland ecosystem services and disservices for better decision-making. Based on 30 years of experience of salt marsh management in southeastern Australia, it allows managers to enhance ecosystem service provision while mitigating potential disservices.

Incorporating disservices into a holistic framework of environmental management also allows managers to understand the tradeoffs caused by their decision-making. In order to make a reasoned and informed decision regarding any potential tradeoffs, managers should ensure that they have enough information to do so. To realistically consider all consequences of management decisions made in trade-off scenarios, it is pertinent to not only consider the valuation of ecosystem services but also of ecosystem disservices.

Future research directions

The field of coastal wetland ecosystem services has attracted huge recent research interest, and, as a result, our knowledge in this area is relatively advanced. However, significant knowledge gaps still remain, particularly around the quantification of intangible cultural ecosystem services and the integration of ecosystem disservices into ecosystem services frameworks:

a. *Cultural ecosystem services*. In general, little is known about cultural ecosystem services compared to other ecosystem service categories, and this is even more the case when considering coastal wetlands (Queiroz et al. 2017). A consideration of cultural ecosystem services is essential because they are a clear link between ecosystems and people and so may be some of the most important to consider during coastal management. A strengthened research focus on cultural ecosystem services will give us a more holistic view of the contribution of coastal wetlands and provide more evidence for their conservation, especially in urban settings where coastal wetland-human interactions are greatest.

b. *Value of ecosystem services.* Scientific knowledge of the full range of ecosystem services that coastal wetlands provide has become increasingly advanced, and for most services, we have clear methods with which to quantify them. A range of methods are also now available to value coastal wetland ecosystems services, but the majority of regional and global syntheses of coastal wetland value still rely on a small number of data points, make various assumptions about data quality and transfer, and assume that the value of coastal wetland ecosystem services is uniform across space. More valuation studies are needed in different coastal settings across the globe to better represent the huge spatial variation inherent in coastal wetland ecosystem service provision and value.
c. *Ecosystem disservices.* Ecosystem disservices have only been conceptualised as an academic research area relatively recently compared to ecosystem services. This is particularly the case for coastal wetlands, where research has been dominated by the ecosystem services paradigm. Ecosystem services have been an established framing for coastal wetlands research for decades, and this review has highlighted that our knowledge of several coastal wetland ecosystem services could be considered to now be quite strong. Ecosystem disserviceshave not received the same amount of attention generally, and this is especially the case for coastal wetlands. The recent introduction of generic ecosystem disservices frameworks (e.g. Vaz et al. 2017) may begin to stimulate ecosystem disservices research in coastal wetlands in the same way that the Millennium Ecosystem Assessment (MEA 2005) did for ecosystem services.
d. *Interactions between ecosystem services and disservices.* Future research needs to close the conceptual and management gaps between ecosystem services and disservices and better integrate them for more holistic coastal management and decision-making. We support recent calls by Blanco et al. (2019) to do this, and there are several steps that can allow this to happen. First, we must acknowledge that coastal wetland disservices can exist in a given management location, and the various disservices that could affect management should be identified. Identified disservices must then be quantified through a variety of techniques. To utilise this information, existing ecosystem services frameworks need to be adapted so that they are more holistic and allow appropriate weighting between services and disservices.

Conclusions

Coastal wetlands have long been considered negatively in history and popular culture, focusing on the perceived and actual ecosystem disservices that they may cause or the economic returns that can be derived by converting these apparent coastal wastelands that have no explicit value themselves. However, coastal communities have also long utilised coastal wetlands for their tangible and intangible ecosystem services, and stakeholders and policy makers are now clearly valuing them for the benefits they provide to coastal societies. The range of ecosystem services provided by coastal wetlands covers broad categories from provisioning to cultural services and can have very high monetary and non-monetary values for coastal communities. As such, coastal wetlands are strongly promoted on the international policy stage for their roles in protecting against natural hazards, sequestering and storing our carbon emissions, and providing goods and materials to support the livelihoods of nearby communities.

As coastal populations continue to increase and human-environment interactions become more common in the coastal zone, there is a need for a more balanced view of coastal ecosystems. This balanced view should take into account the services that coastal wetlands provide alongside the disservices that they cause. Ecosystem disservices have strongly influenced salt marsh and mangrove forest management historically, leading to a view that coastal wetlands have limited value, and incentivising their subsequent large-scale draining. However, it is now important that, in a new age of ecosystem services research, focus doesnot swing too far in the other direction. Ultimately, a binary 'services versus disservices' discourse does few favours for coastal wetland management. Instead, holistic frameworks should embrace and manage the complexity inherent in myriad positive and negative interactions between coastal wetlands and people, in order to find management interventions that encompass the true value of these important coastal systems.

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THE OCEANOGRAPHY AND MARINE ECOLOGY OF NINGALOO, A WORLD HERITAGE AREA

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Abstract The Ningaloo coast of north-western Australia (eastern Indian Ocean) hosts one of the world's longest and most extensive fringing coral reef systems, along with globally significant abundances of large marine fauna such as whale sharks. These characteristics – which have contributed to its inscription on the World Heritage list – exist because of the unique climatic, geomorphologic and oceanographic conditions. The region is hot and arid, so runoff of water from land is low, facilitating clear water that allows corals to grow close to the shore. The poleward-flowing Leeuwin Current is an important influence, bringing warm water and generally suppressing coastal upwelling. During the austral summer, strong southerly winds generate the equatorward-flowing Ningaloo Current on the inner shelf – this current facilitates sporadic upwelling events that enhance concentrations of nutrients, which in turn enhance pelagic primary productivity that supports the reef's biota. The coast has experienced several marine heatwaves since 2011 that have caused mortality of corals and probably seagrass, albeit relatively less than elsewhere along the coast. Wind-generated surface waves break over the fringing reef crest, causing cooling currents that tend to dampen warming – although this mechanism seems not to have prevented some areas from experiencing damaging heat, and corals in places that do not receive the wave-generated currents have experienced substantial mortality. Herbivores, from fish to green turtles, are abundant, and in the lagoon, extensive stands of large brown algae provide an important habitat for newly recruited fish. There has been a decline in abundance of some fish. Predictions of future pressures include a weaker but more variable Leeuwin Current and increased human use. The ability of Ningaloo's

ecosystems to withstand growing pressures will depend partly on the rate and magnitude of global warming but also on actions that manage local pressures from increasing human use. These actions will rely on continued science to provide the evidence needed to identify the pressures, the changes they create and the ways that we can mitigate them.

Introduction

Ecologists have long noted that the tropics, conventionally defined as the latitudes between the tropics of Cancer and Capricorn (~23.4° N and S of the equator, respectively), host a greater diversity of species than other regions (Barlow et al. 2018). In particular, the diversity of three marine habitat-forming taxa – corals, seagrasses and mangroves – is highest in the tropics. This diversity is especially high in the 'Coral Triangle', which encompasses Indonesia, Malaysia, Papua New Guinea, Philippines, Solomon Islands and Timor-Leste (Hoeksema 2007). This region hosts most of the world's species of reef-building corals, seagrasses and mangroves and a very high proportion of the world's species of fishes and other taxa associated with these habitats. The area covered by these three habitats is declining (Waycott et al. 2009, Polidoro et al. 2010, Hughes et al. 2018), with cascading impacts on the species that inhabit them and the human societies that rely on them.

All three of these habitats are pantropically distributed (and also extend into cooler latitudes). Coral reefs tend to occur mostly between the latitudes of 30°S and N, a distribution which is largely determined by the thermal tolerances of scleractinian (hard) corals and their endosymbiotic dinoflagellates (zooxanthellae: Spalding et al. 2001). These thermal tolerances are now being regularly exceeded, causing corals to bleach (a process in which the zooxanthellae are expelled), which is followed by death if the corals do not regain the zooxanthellae (Hoegh-Guldberg 1999, Hughes et al. 2018). This process, in concert with numerous other injuries arising from poor water quality and direct destruction, has led to a decline in the number and quality of coral reefs worldwide (Spalding & Brown 2015).

Most of the world's coral reefs are already threatened in some way by human activities (Burke et al. 2011, Hughes et al. 2018). One coral reef that has so far mostly escaped the worst degradation is Ningaloo, a predominantly fringing reef that abuts the arid coast of north-western Australia, a thousand or so kilometres south-west of the Coral Triangle. Ningaloo has been relatively unscathed by the global pressures that have caused degradation of many coral reefs (although not every part of Ningaloo has escaped, which we review later in this paper). It is one of only three (of 29) World Heritage–listed coral reefs not expected to experience bleaching at least twice per decade by 2041 (a frequency that is likely to cause total mortality) under Representative Concentration Pathway (RCP) 8.5 climate projections (Heron et al. 2017); however, the same models predict that bleaching will occur at least twice per decade after 2041. This deferral of the fate predicted for so many other coral reefs is due to multiple contributing influences, including unique weather and oceanography and relatively low rates of human use, which we review here. These characteristics make Ningaloo globally important, because a high abundance and diversity of coral (and associated taxa) might persist there after other coral reefs have been severely affected.

Ningaloo is contained within the Ningaloo Coast World Heritage Area (NCWHA), which includes land and sea, and was inscribed in part because of the high diversity of corals and coral-associated species, the globally important annual aggregations of whale sharks and the high abundances of large marine fauna like sea turtles and elasmobranchs (http://whc.unesco.org/en/decisions/4278; accessed 15 March 2019). Much of Ningaloo, including the coral reef and surrounding marine habitats, also falls within marine parks and reserves managed by state (Western Australia) and national (Australia) governments (Figure 1); of this, much is within highly protected 'no-take' (IUCN Category II) reserves (e.g. 34% of the area within the state-managed Ningaloo Marine Park, and 4.8% of the nationally managed Ningaloo Marine Park, is within IUCN Category II reserves).

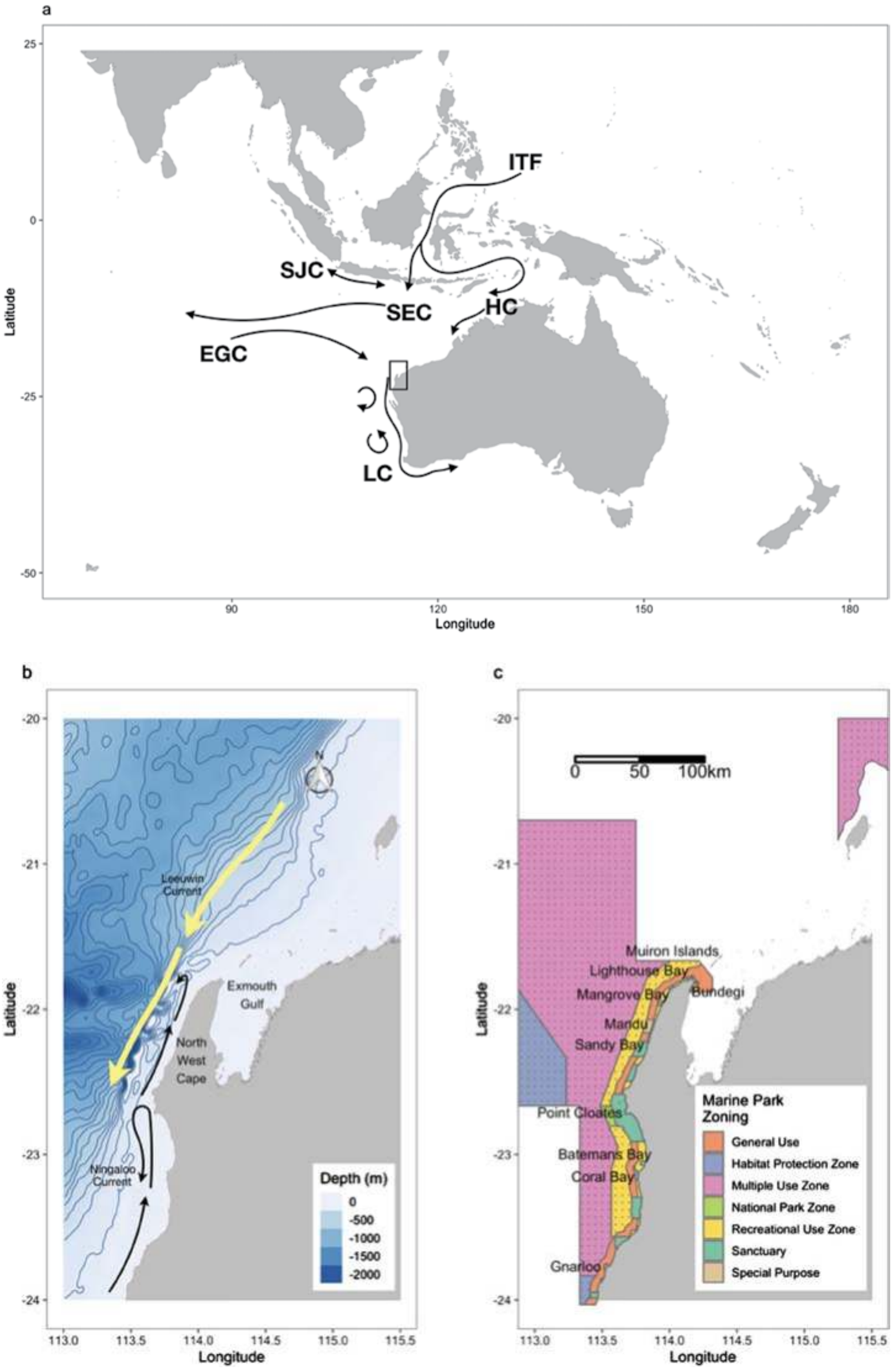

Figure 1 (a) Location of Ningaloo (black rectangle) relative to the major oceanographic currents in the region (EGC, East Gyral Current; ITF, Indonesian Throughflow; HC, Holloway Current; LC, Leeuwin Current; SEC, South Equatorial Current; SJC, South Java Current); (b) bathymetry of Ningaloo, and approximate position of the Leeuwin and Ningaloo Currents and (c) the state and Commonwealth marine park zones (Commonwealth marine park zones are speckled).

In this review, we synthesise more than four decades of research at Ningaloo, placing the knowledge gained in the context of the Indo-Pacific region and coral reefs globally. We critically evaluate our current knowledge about the underpinning climate, geomorphology and oceanography at Ningaloo and the biology and ecology of the habitat-forming taxa (such as corals, seagrass and mangroves) and associated biota, with particular emphasis on the taxa that were fundamental to its inscription on the register of World Heritage Areas. As part of this, we examine the threats Ningaloo faces and the features which have helped its coral reefs survive so far and consider whether we should expect these features to persist into the future. We use the term 'Ningaloo' to refer broadly to the area encompassed by the marine parts of the NCWHA, but because many of the relevant ecological processes span boundaries, we also include information from areas immediately adjacent.

The setting: Climate, oceanography and geomorphology

The coral reefs at Ningaloo encompass ~300 km of coast (2 degrees of latitude, 21°40 S to 23°34 S), south from North West Cape in north-western Australia (eastern Indian Ocean) (Figure 1). The Muiron Islands, ~15 km from North West Cape, also have well-developed coral reefs, and we include them in this review. The region is hot and arid, with mean daily maximum air temperatures exceeding 37°C in the austral summer and mean monthly rainfall less than 50 mm all year (Figure 2). Mean monthly potential evaporation exceeds 120 mm all year – on average, potential evaporation is 12 times higher than rainfall. Most rainfall occurs within episodic events associated with tropical low-pressure systems, including cyclones, of which 15 have passed over or adjacent to Ningaloo since 1970 (Figure 3). As a result, there is usually little or no terrestrial runoff, so inshore waters are clear, and corals grow only a few metres from the mean low tide mark in many places.

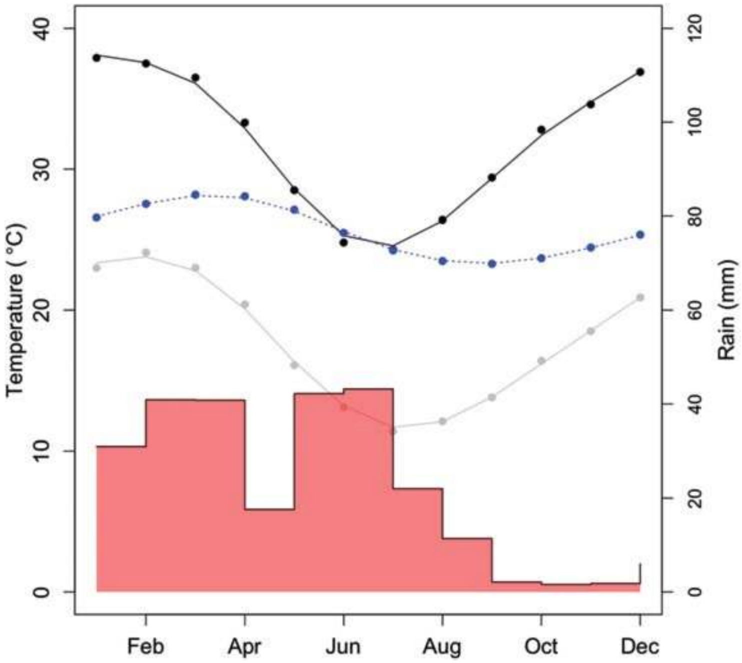

Figure 2 Mean daily maximum (black line) and minimum (grey line) air temperature, mean sea surface temperature (dotted blue line) and mean monthly rainfall (red bars). (Air temperatures and rainfall are from Bureau of Meteorology records from 1970–2018 measured at the Learmonth weather station; sea surface temperatures are from NOAA for 113.5°E, 21.5°S from 1981–2010.)

Cyclones also bring extreme wind conditions, which have the potential to cause significant damage (winds from Cyclone Vance in 1999 were measured at 267 km h^{-1}; http://www.bom.gov.au/cyclone/history/vance.shtml, accessed August 13, 2019). However, the typical wind conditions are also important at Ningaloo – the west side of North West Cape experiences regular strong afternoon sea breezes, exceeding average speeds of 6.6 m s^{-1} (23.7 km h^{-1}) in summer months. These winds bringing cooler water to the reef and facilitate localised upwelling, processes that tend to protect the corals from extreme warming events (Woo et al. 2006).

Situated at the southern edge of the Indo-Pacific warm pool (De Deckker 2016), the ocean currents off Ningaloo are strongly influenced by climate variability in the Indo-Pacific (Zinke et al. 2014). The major oceanographic feature in the region is the poleward-flowing Leeuwin Current (Cresswell & Golding 1980), which is driven by a meridional (i.e. north-south) pressure gradient in the south-eastern Indian Ocean, which in turn is partly caused by the Indonesian Throughflow. This process overrides the normal equatorward flow direction expected for a current on the eastern boundary of an ocean, which would normally bring cooler water. Instead, the Leeuwin Current is a downwelling current, transporting relatively warm, low-salinity (<35.4‰) tropical water southwards (Domingues et al. 2006, Feng et al. 2015).

The Leeuwin Current conveys Pacific Ocean influences into the Indian Ocean through Kelvin and Rossby waves which propagate through the Indonesian archipelago and down the western Australian coast (Feng et al. 2003, Feng et al. 2004, Wijffels & Meyers 2004). These influences include the El Niño-Southern Oscillation (ENSO: the variation in sea surface temperature and wind in the tropical eastern Pacific) and the Interdecadal Pacific Oscillation (long-term increases and decreases in ocean temperature in the Pacific). In 2010–11, a strong La Niña (the phase of ENSO which is associated with cooler water temperatures in the tropical eastern Pacific) caused an unusually strong Leeuwin Current which, combined with a cessation of normal wind patterns, instigated an unprecedented marine heatwave, the 'Ningaloo Niño', off the west coast of Australia

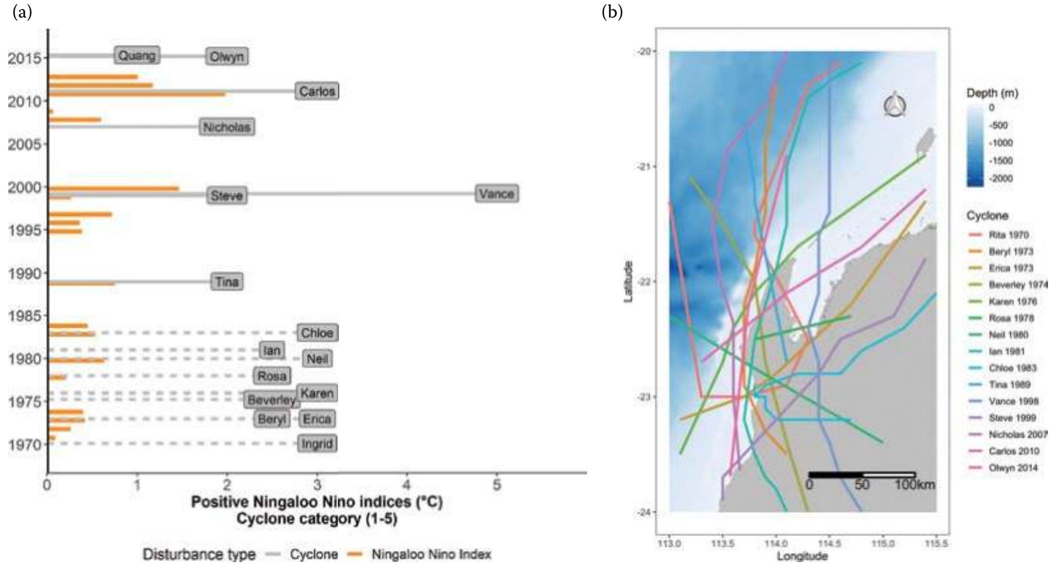

Figure 3 (a) Timeline of two types of ecological disturbance at Ningaloo: cyclones and anomalously high water temperatures. Ningaloo Niños are the strong warming events identified in Feng et al. (2015) from a scaled January–February Ningaloo Niño index. The length of the bar gives an indication of the relative magnitude of the high temperature anomalies (no meaning for the cyclones). (b) Tracks for tropical cyclones that passed over Ningaloo between 1970–2018. (Bureau of Meteorology.)

(Feng et al. 2013; Figure 3). Marine heatwaves in the region can also start from conditions associated with reduced cloud coverage (which causes increased solar radiation) and a weakened Australian monsoon (which causes reduced evaporation) in the Indonesian-Australian basin north of Ningaloo (Benthuysen et al. 2018).

The Leeuwin Current typically contains very low concentrations of dissolved nutrients (e.g. <0.2 μM nitrate), but nutrients can be enhanced during episodes of coastal upwelling. A regular deepening of the mixed layer (within which turbulence mixes the water from the surface to a given depth) in autumn, probably because of a combination of acceleration of the current and heat loss leading to cooler sea surface temperature, also increases nutrient concentrations (Rousseaux et al. 2012). Episodes of coastal upwelling are associated with the Ningaloo Current, a northward-flowing current that runs inshore of the Leeuwin Current, parallel to Ningaloo reef (Taylor & Pearce 1999, Hanson et al. 2005) (Figure 1). The Ningaloo Current brings water with higher nutrient concentrations (up to 2–6 mM nitrate, which is still about an order of magnitude lower than large upwelling systems) onto the continental shelf adjacent to Ningaloo (Hanson et al. 2005). The upwelling is caused by strong southerly winds that occur during late summer and early autumn and by anticlockwise Leeuwin Current eddies in cooler seasons (Rossi et al. 2013, Xu et al. 2015, Zhang et al. 2016). Around northern Ningaloo, the continental shelf is very narrow (in places <10 km wide), so the upwelled water is close to the reef. Upwelling can also be enhanced during El Niño events, when the thermocline (which correlates with the nutricline) is raised closer to the surface (Furnas 2007).

These seasonal or episodic increases in concentrations of dissolved nutrients appear to be important for pelagic primary production. The composition of phytoplankton in the two currents is also different, with the Leeuwin Current dominated by picoplankton, while the Ningaloo Current is dominated by haptophytes and diatoms (Hanson et al. 2007). It seems likely that the nutrients and plankton associated with both upwelling and deepening of the mixed layer are important for reef biota, but the high concentrations of phytoplankton that result from the deepening of the mixed layer in autumn might be more important (Wyatt et al. 2012, Wyatt et al. 2013). Phytoplankton are also food for the zooplankton that probably sustain the seasonal aggregations of whale sharks, but the rates of secondary production are quite low, and trophic pathways remain poorly understood (Hanson & McKinnon 2009, Molony et al. 2011).

An ecologically meaningful feature of water circulation at Ningaloo is wave-induced water flow across the reef and through the lagoon (Figure 4b). Waves breaking on the reef crest cause currents that flow across the reef flat, into the lagoon (Hearn 1999), and then exit the lagoon through reef channels (Figure 4d). Current speeds increase with wave height and are also strongest when tides are 0.2–0.4 m below the mean water level (Taebi et al. 2011). Higher sea levels, such as during La Niña conditions (or in a scenario of sea level rise without concomitant increases in the height of the reef surface), would tend to reduce the wave-driven circulation and increase the amount of time it takes to flush the lagoon (Taebi & Pattiaratchi 2014).

The wave-driven flows across the reef are important for bringing nutrients and food particles. As water flows across the reef, chlorophyll concentrations decline (Wyatt et al. 2010), with many different phytoplankton taxa being removed (Patten et al. 2011), presumably by corals and other suspension feeders. When conditions are favourable for upwelling, the reef appears to be a net nutrient sink, while when upwelling is absent, it is a net source (Wyatt et al. 2012). Since the main oceanographic features (the strength and depth of the Leeuwin Current and the episodes of upwelling) are quite seasonal, it is probable that this is reflected in the ecology of the reef, but our knowledge of these patterns remains scarce.

The wave-driven flows are also an important influence on water temperature over the reef and lagoon. Sea surface temperatures at Ningaloo vary from ~24–26°C on average (Falter et al. 2014; see also Figure 2) and have warmed over the last century by perhaps more than 1°C (Kuhnert et al. 2000, Zinke et al. 2015), but lagoon water can be cooled as waves bring water over the reef and into the lagoon.

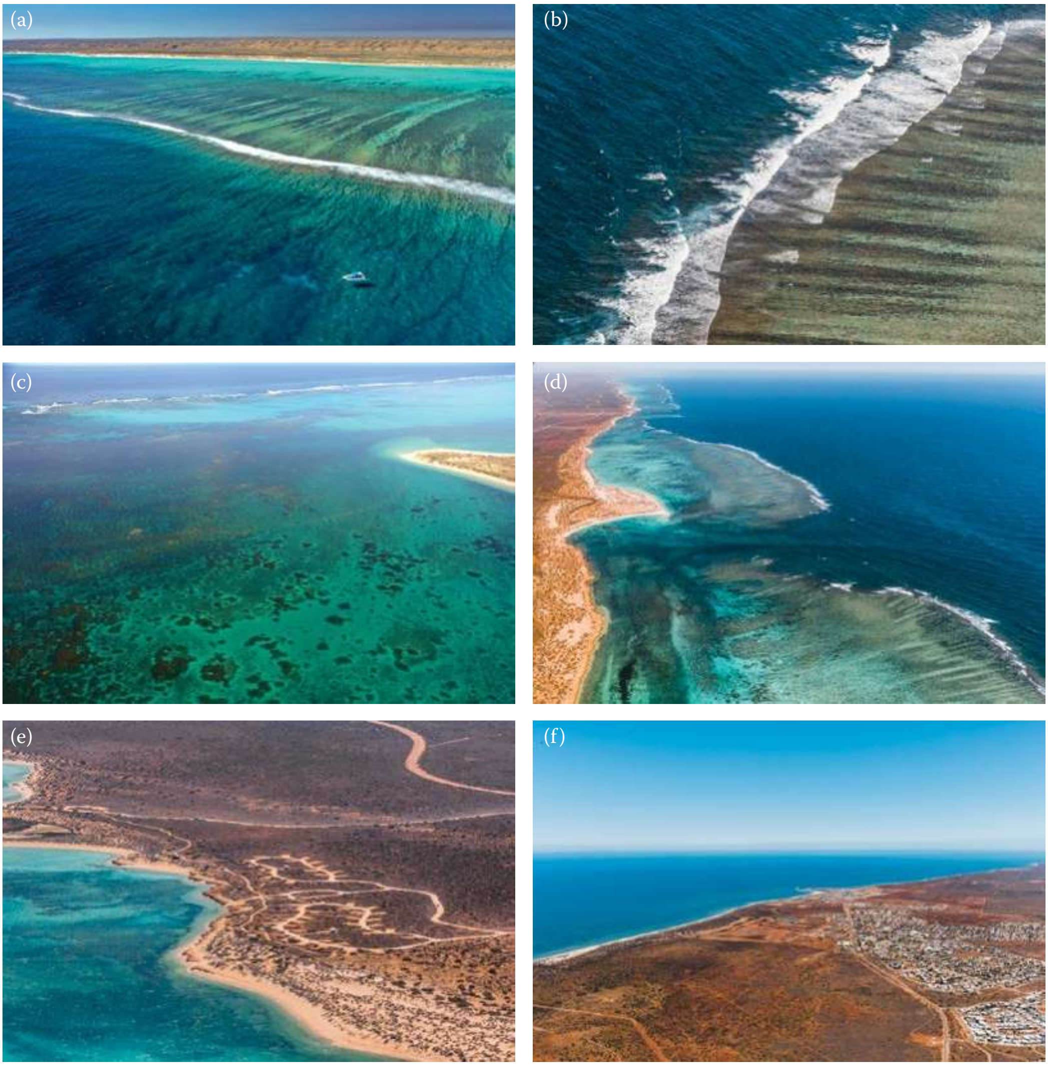

Figure 4 Aerial perspectives of Ningaloo. (a) View from the reef slope towards the lagoon in unusually calm conditions (photo credit: Nick Thake); (b) waves breaking over the reef (photo credit: Violeta Brosig); (c) lagoon with coral bommies (photo credit: DBCA); (d) between sections of the reef at Ningaloo (photo credit: Violeta Brosig); (e) camping area at Osprey Bay (photo credit: Violeta Brosig); (f) town of Exmouth looking towards Exmouth Gulf (photo credit: Violeta Brosig).

Much of Ningaloo is composed of fringing reefs, with a shallow (usually <5 m deep) sand- and low relief limestone-dominated lagoon which is up to 6 km wide, a reef flat (usually <150 m wide) and a reef slope to approximately 30–35 m depth, often characterised by spur-and-groove formations (Cassata & Collins 2008: Figure 4a, Figure 5a). In several sections, the reefs are not contiguous, particularly in the southern parts and on the eastern side of North West Cape, where the reefs are mainly patch reefs (Twiggs & Collins 2010). The geomorphology has a profound influence on the distribution of the major benthic habitat-forming organisms (Figure 5a–g), with hard corals dominating the reef flat and reef slope in depths shallower than 40 m, macroalgae dominating the lagoons and unconsolidated sediments interspersed with patches of suspension-feeding sessile invertebrates occurring in deeper areas (Kobryn et al. 2013, Turner, Babcock et al. 2018).

Corals: The foundation of the reef

Up to 217 species of scleractinian corals have been recorded from Ningaloo (Veron & Marsh 1988, Veron 1995), although this number is likely to be an underestimate (Richards & Rosser 2012). The number of species is similar to that of other parts of north-western Australia (Veron 1995, Richards & Rosser 2012), but numbers drop markedly south of Ningaloo, with the exception of relatively high diversity at the offshore Houtman-Abrolhos Islands, where there are at least 184 species (Veron & Marsh 1988, Veron 1995). Although the number of species is fairly typical for a coral reef at this latitude, the extensive development of the coastal fringing reefs is remarkable (Wilson 2013), and Ningaloo constitutes one of the world's longest and most extensive fringing reef systems. Crustose coralline algae (CCA) are also major sources of reef accretion, while other taxa such as hydrocorals from the genus *Millepora* appear to contribute in wave-exposed or high-current locations, such as in reef passes. Around the Muiron Islands, soft corals (Alcyonaria) are relatively more abundant (Cassata & Collins 2008) and might also make a significant contribution as habitat providers.

Ningaloo's habitats have been mapped using airborne hyperspectral surveys (Kobryn et al. 2013) and multiple discrete habitat types identified (Figure 5). On the seaward side, at the base of the reef slope (~35 m), the living coral is dominated by encrusting, plate-forming and sub-massive morphs (Turner, Babcock et al. 2018). The percentage cover of living coral at these depths is low (<1%) relative to that reported from similar depths on other coral reefs (Khang et al. 2010). However, many of those studies have been carried out at oceanic locations surrounded by deep water with high water clarity, which allows light – a fundamental requirement of all reef-building corals – to penetrate to greater depths (Turner et al. 2017). At Ningaloo, the reef structure stops at around 35 m, where it transitions to flat, sediment-covered continental shelf. At these depths (~40 m), low light (1.9% of surface photosynthetically active radiation; Turner, Babcock et al. 2018), which is probably caused by the presence of phytoplankton and resuspended sediment in the water, likely limits the abundance of living coral (Turner, Thomson et al. 2018). The percentage cover of living coral on the reef slope increases to ~15% at around 25 m; acroporid corals are relatively less abundant here, and poritid corals dominate. Percentage cover of living coral peaks at 3 m, where it approaches 20% and the coral assemblage is dominated by Acroporidae (Turner, Thomson et al. 2018). The shallow reef slope and the reef flat (Figure 5b), which extend up to several hundred metres either side of the reef crest, are characterised by high percentage cover of CCA (~80%) and living coral (~20%, mainly digitate Acroporidae). This transitions to a shallow (~1 m deep) inner reef flat where the percentage cover of living coral can be as high as 90%, with an assemblage dominated by tabular *Acropora*, mainly *A. spicifera* (Figure 5b). Colonies of this species are fragile and can only develop to their full extent on parts of the reef that are sheltered from strong water motion. The reef flat transitions to the back reef (~2 m deep) where the percentage cover of living coral is 20%–50%, and the assemblage is also dominated by *Acropora*, but is taxonomically and structurally more diverse, containing arborescent and corymbose forms of *Acropora* and greater numbers of massive corals such as Faviidae (Cassata & Collins 2008). The sandy-bottomed lagoon is populated by sparsely distributed colonies of coral growing attached to underlying limestone pavement and by large patch reefs ('bommies') in deeper areas (3–15 m) (Cassata & Collins 2008; Figure 4c). These bommies are frequently associated with (and probably formed around) massive *Porites* colonies, which are often substantially eroded and colonised by multiple taxa of other corals.

The species composition and morphology of corals are also strongly influenced by temperature and hydrodynamic forces, including extreme events such as marine heatwaves and cyclones. Both have influenced coral abundance within the last decade (Gilmour et al. 2019). The abundance of corals has declined substantially in some areas, less in others, and in others has remained relatively unchanged (Depczynski et al. 2013, Holmes et al. 2017; Figure 6). Bundegi, a reef in Exmouth Gulf on the eastern side of North West Cape, suffered from marine heatwave-induced coral bleaching in

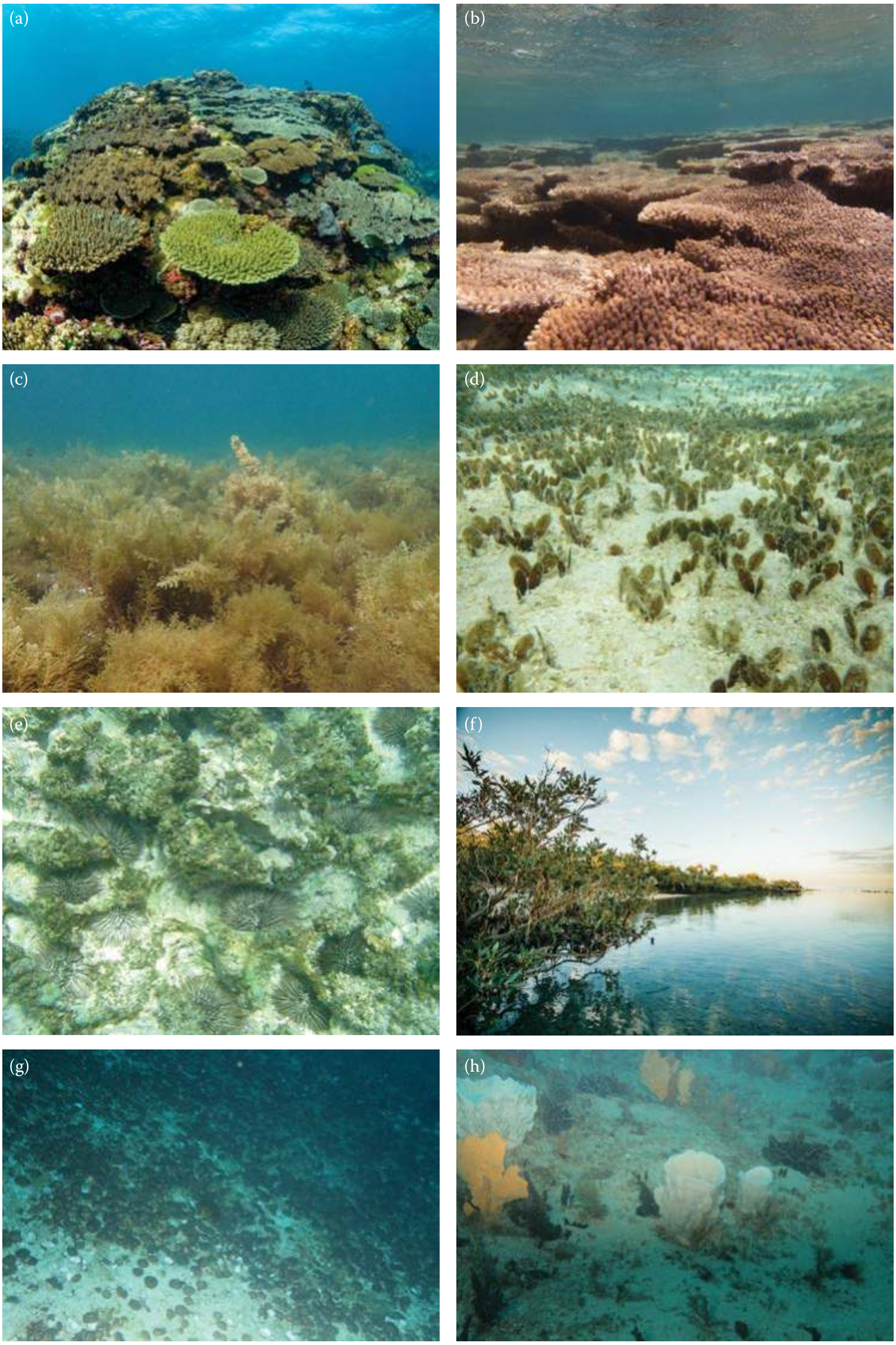

Figure 5 Some of the main habitats present at Ningaloo. (a) Reef slope, (b) reef flat, (c) macroalgae in lagoon, (d) seagrass in lagoon, (e) low-relief limestone with high densities of *Echinometra mathaei*, (f) mangroves (photo credit: Violeta Brosig), (g) dense aggregations of solitary coral *Diaseris* at ~40 m seaward of the reef slope and (h) assemblage of suspension feeders at ~42 m seaward of the reef slope.

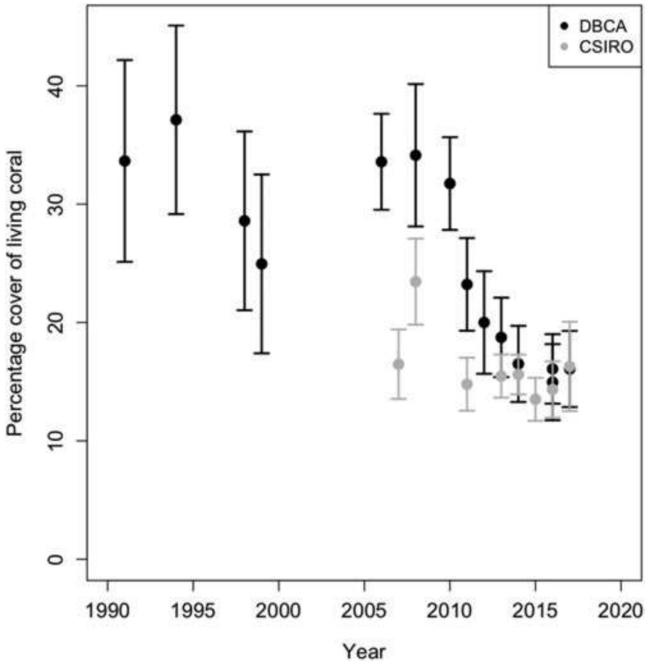

Figure 6 Percentage cover of living coral from 1991–2017, derived from photographs of benthos along transects from long-term ecological research at Ningaloo. DBCA surveys were conducted in back reef and lagoon; CSIRO surveys were conducted in reef flat. (Redrawn from Gilmour, J et al. 2019. *Coral Reefs* **38**, 651–667.)

2011, causing living coral abundance to decrease by up to 95%, while corals at the Muiron Islands decreased by around 50% from a similar event in 2012–2013 (Depczynski et al. 2013, Holmes et al. 2017). In contrast, many reefs on the western side have survived the heatwaves relatively intact, probably because of the cooling effects of the wave-driven currents as they pass over the reef. However, the abundance of corals in some sheltered locations south of Point Cloates has declined steadily since 2011 (Holmes et al. 2017), and localised decreases in coral cover have also occurred north of Point Cloates (e.g. Vanderklift et al. 2019). Cyclones might have caused some mortality, but the declines are coincident with major warming events and seem most likely to be caused by water temperatures exceeding thermal thresholds. Poor water quality has been implicated in degradation of some coral reefs elsewhere, but at Ningaloo, even turbidity associated with high runoff from extreme rainfall events caused no apparent change in percentage cover of living coral (Lozano-Montes et al. 2017).

Over smaller spatial extents (tens of kilometres), localised declines in coral cover have been linked with periodic disturbances. At Coral Bay, multiple episodes have occurred in which accumulations of coral spawn cause anoxia and subsequent mortality of corals (Simpson et al. 1993, van Schoubroeck & Long 2007). Patterns of mortality have typically been patchy even within the bay, and areas with slow currents (high water residence times) were the worst affected. There was recovery from 9% to >40% after 15 years at the worst affected sites (Shedrawi et al. 2017), in contrast to observations at Bundegi, where there has been little recovery following heat stress and cyclones in 2011 (Holmes et al. 2017).

Biological interactions, such as competition, disease and predation, also have the potential to influence the abundance and composition of corals. The incidence of disease at Ningaloo has been estimated to be less than 3% (Onton et al. 2011), which is similar to the background levels of disease reported in other studies of Indo-Pacific scleractinian corals (Willis et al. 2004, Page et al. 2009, Raymundo et al. 2009), suggesting disease has not been a major cause of mortality. Indeed, the majority of diseased corals from an area with a similar incidence (range: 0%–7.3%) – Barrow Island, approximately 150 km to the north-east of Ningaloo – recovered within weeks and without mortality (Stoddart et al. 2019). Competition between corals is also unlikely to be a major influence, because percentage cover of living coral is less than 50% in most places. The dense stands of tabular *Acropora spicifera* on reef flats are exceptions to this overall pattern, but these areas are almost monospecific, so any competition is likely mostly intraspecific. Macroalgae can attain high biomass on the reef despite the low nutrients and abundant herbivores, so competition between corals and macroalgae might be important. Experimental exclusion of fish in one study led to a proliferation of tall macroalgae, which in turn reduced coral recruitment (Webster et al. 2015). This implies that herbivory by fish is probably an important process that facilitates high coral cover. Other experimental studies of herbivory by fish at Ningaloo support this inference (Doropoulos et al. 2013, Michael et al. 2013).

Outbreaks of the coral-eating gastropod *Drupella cornus* were first noted in the mid-1980s, causing coral mortality as high as 75% in some areas, and leading to extensive loss of coral cover by 1987 (Turner 1994a). *D. cornus* were most commonly recorded on caespitose or corymbose morphs of *Acropora* and reached their highest abundances (up to 19.4 ind. m^{-2}) on the back reef and reef flat (Turner 1994a). The abundance of *D. cornus* appeared to peak around 1989, when they were recorded in high densities throughout the reef (Turner 1994b). The causes of this outbreak remain unknown; variability in abundance can be high, but average densities recorded in the most recent surveys have been mostly <1 ind m^{-2} (Holmes et al. 2017). The overall density at Mandu between 2007 and 2016 was 0.14–0.6 ind m^{-2}, below the estimated outbreak threshold of $\sim$0.95 ind m^{-2} (Bessey et al. 2018). Other known problematic corallivores, such as the crown-of-thorns starfish *Acanthaster solaris*, are rare at Ningaloo.

The accretion and growth of reefs at Ningaloo appear to vary from reef to reef. Although the rate of historical reef growth has been low (Twiggs & Collins 2010), contemporary estimates are in the range of other coral reefs – the mean net carbonate accumulation rate is 2.46 ± 2.01 kg^{-1} $CaCO_3$ m^{-2} yr^{-1} (Perry et al. 2018). This is higher than many other coral reefs in the central (1.41 ± 3.02 kg^{-1} $CaCO_3$ m^{-2} yr^{-1}) and western Indian Ocean (1.71 ± 2.02 kg^{-1} $CaCO_3$ m^{-2} yr^{-1}), where corals have experienced significant mortality (Perry et al. 2018). Fast-growing corals (e.g. *Acropora* and *Pocillopora*) are responsible for the bulk of calcium carbonate production (Perry et al. 2018), but other calcifiers such as CCA are probably more important in wave-exposed areas, where they are abundant (Cassata & Collins 2008). The parrotfish *Chlorurus microrhinos* and the sea urchin *Echinometra mathaei* (Figure 5e) are likely to be the main bioeroders, accounting for up to 95% of the total mass of carbonate excavated from Ningaloo each year (D. Thomson & M. Haywood, unpublished data).

Estimates of net calcium carbonate accumulation (i.e. calcification minus erosion) for Ningaloo are positively correlated with the percentage cover of living coral. The highest rates of carbonate accumulation occur on reefs on the western side of North West Cape (Perry et al. 2018), where the percentage cover of living coral is high (>25%) and the coral assemblage is dominated by *Acropora* and *Pocillopora* (Turner, Babcock et al. 2018). For corals such as these, which have branching and tabulate species, rates of linear extension are a reliable predictor of carbonate production. Linear extension rates for tabulate *A. spicifera* are 12.4 ± 1.4 cm^{-1} yr^{-1} at north-western Ningaloo and 10.5 ± 1.2 cm^{-1} yr^{-1} at north-eastern Ningaloo (Stimson 1996), which is high for tabulate *Acropora* (Pratchett et al. 2015). These high growth rates, combined with their high abundance, support the prediction that they are responsible for most of the production of carbonate material. The lowest rates of net carbonate accumulation occur where coral cover is generally low (<10%) and the reef is dominated by CCA and relatively slow-growing corals such as Poritidae and Faviidae. The high net carbonate accumulation rates suggest Ningaloo's reefs have the potential to keep pace with moderate rates of sea level rise over the next 30 years (Perry et al. 2018).

Recovery of reefs after disturbances can occur solely by regeneration from fragments (Hughes 1987), but reproduction and recruitment are vital to the long-term survival of coral reefs (Hughes et al. 1999). This is particularly the case for Acroporidae, which, while often the first corals to be affected by storms or bleaching, are also early colonisers which are important for the recovery of damaged reefs (Doropoulos et al. 2015). The majority of Acroporidae are known to participate in mass spawning (the synchronous release of gamete bundles for external fertilisation), which occurs in autumn at Ningaloo, after full moons between late March and early April (Gilmour et al. 2016). A small proportion of acroporid species are thought to spawn in spring or summer, although the details of these and many other species are not well known, because field observations have been concentrated during the known mass spawning period (Gilmour et al. 2016).

Recruitment of corals at Ningaloo has not been well studied, but a study of coral recruitment onto tiles placed at multiple depths from 3–40 m revealed that the greatest number of settlers was at 25 m, with very little settlement at 40 m (Turner, Thomson et al. 2018). The number of recruits averaged <2.5 dm^{-2} (100 cm^{-2}), which is almost an order of magnitude lower than recruitment measured at coral reefs elsewhere using the same methods (e.g. Hughes et al. 1999, Smith et al. 2005) and is also lower than measurements prior to the 2011 bleaching (Holmes et al. 2017). This low recruitment might mean that corals at Ningaloo would recover slowly from disturbances that cause bleaching and subsequent mortality – this has indeed been the case at Bundegi. This inference is supported by hydrodynamic particle dispersion modelling, which shows that Ningaloo probably receives larvae from the reefs farther north (Feng et al. 2016). Furthermore, the amount of larvae that are transported to Ningaloo varies from year to year, and supply varies among individual reefs, such that recovery times of many reefs are likely to be decades or longer (Boschetti et al. 2019).

Beyond corals: Macroalgae and seagrasses of Ningaloo

Macroalgae, including filamentous turf, cover more than 50% of the seafloor at Ningaloo (Kobryn et al. 2013), particularly within the lagoons (Figure 5c), where large meadows of canopy-forming macroalgae can be found (Cassata & Collins 2008). Fucalean algae from the family Sargassaceae are the main canopy-forming taxa, particularly those from the genera *Sargassum* and *Sargassopsis*, though other brown algae such as *Lobophora* and *Dictyota* are also common (Fulton et al. 2014). In the summer months, the density, height and percentage cover of canopy-forming Sargassaceae increases (Wilson et al. 2014, Lim et al. 2016), and these are highest during La Niña years when water temperatures are warmer (Wilson et al. 2018a,b). Seasonal changes in abundance of macroalgae are closely aligned with water temperature, with biomass typically peaking in February and March when water is warmest (Fulton et al. 2014). There is, however, considerable spatial variation in the composition of macroalgae beds from place to place (Wilson et al. 2014).

In the lagoon, away from coral bommies or reef structure, herbivory is negligible (Verges et al. 2011, Downie et al. 2013) and consumption of macroalgae is mainly by small herbivores that inhabit the macroalgae, such as the parrotfish *Leptoscarus vagiensis* (Lim et al. 2016) and green turtles *Chelonia mydas* (M. Vanderklift, unpublished data). Most uneaten biomass detaches in the early autumn months (Fulton et al. 2014), and the detached thalli form wrack within nearby subtidal and intertidal habitats, or rafts on the sea surface. Both processes probably provide an additional source of nutrients for fauna in adjacent or distant habitats (Fulton et al. 2019), although the relative importance of this process at Ningaloo is unknown.

On the reef, macroalgae range from tall taxa with bushy morphs (like *Sargassum* and *Turbinaria*) to small filamentous taxa; the latter typically grow mixed with sediment and detritus in a combination often called the 'epilithic algal matrix' (Wilson et al. 2003). Compared to many other coral reefs, the interactions between algae, corals and herbivores on the reef has been little studied at Ningaloo. On the reef flat, herbivore exclusion experiments (cages) led to marked increases in the biomass of macroalgae (Webster et al. 2015). Other evidence also suggests that herbivory is likely to be an important determinant of the composition and distribution of macroalgae. Bare 'halos' around patch reefs indicate intense herbivory by fish inhabiting the reefs (Downie et al. 2013). Browsing acanthurids (surgeonfish) and kyphosids (drummer) are the main consumers of tall macroalgae like *Sargassum* (Michael et al. 2013), and proximity to reefs facilitates access to macroalgae in the lagoon by reef-dwelling fish (van Lier et al. 2018). Acoustic telemetry of the drummer *Kyphosus bigibbus* (Pillans et al. 2017) demonstrated that schools of fish on adjacent patch reefs have distinct core areas of use which did not overlap despite very similar habitats. Home range estimates of *K. bigibbus* (mean 95% KUD = 1.61 km^2) are the largest values for a herbivorous coral reef fish recorded to date.

Seagrasses are another important marine plant in sheltered waters at Ningaloo (Figure 5d) and are likely to be a key food and habitat source for some species. For example, the distribution of seagrass is likely to be a primary influence on the distribution of dugong *Dugong dugon* (Holley et al. 2006). Up to 12 species of seagrass occur at Ningaloo. Three species appear to have their northern-most distribution limits at Ningaloo: *Posidonia coriacea* (observed growing in Batemans Bay), *Amphibolis antarctica* (observed near the Muiron Islands) and *P. australis* (drift samples observed at several locations at Ningaloo) (Van Keulen & Langdon 2011, M. Vanderklift unpublished observations; https://naturemap.dpaw.wa.gov.au, accessed 5 March 2019).

On the east side of North West Cape, in Exmouth Gulf, the composition and abundance of seagrass varies from year to year, and the variation appears to be related to a pattern of disturbance (from events like cyclones and marine heatwaves) and recovery (Loneragan et al. 2013, Vanderklift et al. 2016). These fluctuations have implications for other parts of the ecosystem: for example, declines in abundance of dugong (Gales et al. 2004) and brown tiger prawns *Penaeus esculentus* (Loneragan et al. 2013), followed loss of seagrass due to Cyclone Vance.

Variation in abundance and composition of seagrass tends to be less at Bundegi and the Muiron Islands. At Bundegi (in Exmouth Gulf), the abundance of seagrass tends to be highest in late summer and lowest in winter, while at South Muiron Island, abundance of *Halophila ovalis* and *Thalassia hemprichii* remained low during 2.5 years of surveys (Vanderklift et al. 2016).

Other than abundance, the ecology of seagrasses at Ningaloo remains poorly known. The small-leaved *H. ovalis* has been observed flowering at Bundegi in summer, but the importance of seeds and asexual reproduction in maintaining populations is unclear. However, patterns of moderate to high genetic diversity in *H. ovalis* suggest that both sexual reproduction and vegetative growth are present (McMahon et al. 2017). Genetic diversity in *Halodule uninervis* is more variable – *H. uninervis* from Exmouth Gulf are genetically distinct from those in the central and eastern Pilbara – and patterns imply that some populations probably rely on vegetative growth (McMahon et al. 2017). *T. hemprichii* at the Muiron Islands are genetically diverse and exhibit moderate to high connectivity with populations in the Pilbara, a pattern which might be due to dispersal of propagules (McMahon et al. 2017).

Patterns of growth and consumption relative to other places are also poorly known. At Coral Bay, mean photosynthetic rates of 12 ± 0.68 mg O_2 g DW hr^{-1}, with a temperature optimum at about 27°C, were recorded for *H. ovalis* (Said 2017), comparable to the rates recorded for this species and *Halophila spinulosa* in other tropical reef systems (Mohammad et al. 2006), but about four times higher than for the same species from temperate sites. Rates of production of *A. antarctica* at Ningaloo are high compared to a cool temperate region, but rates of consumption are also higher, and ~30% of leaf production is consumed by herbivores – especially fish (Verges et al. 2018).

Mangroves are not abundant on the coast west of North West Cape, but there are some significant stands of mangroves in the southern reaches of Exmouth Gulf. Three species of mangroves are present: *Avicennia marina* (the grey mangrove), *Rhizophora stylosa* (the red mangrove) and *Bruguiera exaristata* (the rib-fruited mangrove, which is rare). *A. marina* is the most abundant species. A small mangrove forest at Mangrove Bay appears to be vulnerable to sea level changes associated with ENSO, and two dieback events have coincided with extremely low sea levels and associated increases in soil salinity, which also seemed to result in reduced reproductive success (Lovelock et al. 2017).

The mangroves are used by a range of marine species, but perhaps one of the more unique features is a trophic subsidy whereby kangaroos which feed on adjacent grasslands transfer nutrients into mangroves when they shelter in the shade the trees provide during the day (Reef et al. 2014).

Mobile inhabitants of the reef: Fish and invertebrates

Ningaloo hosts at least 500 species of fishes from 234 genera and 86 families (Allen 1980, May et al. 1983, Hutchins 1994, CALM 2005), though the true number may be much higher. Underestimates may have resulted from studies at Ningaloo relying primarily on visual surveys of a restricted group of families, and so many cryptic and nocturnal species may not have been recorded (Hutchins 1994, Hutchins 2001, Babcock et al. 2008, Watson et al. 2010). Nonetheless, endemism is low, and most species are widely distributed across the tropical Indo-Pacific or temperate Australia (Hutchins 2001). There are also latitudinal gradients with the number of species declining from north to south, with distinctive assemblages at the geographic extremes: Bundegi, the Muiron Islands, Lighthouse Bay (all in the north) and Gnaraloo (in the south), which all differed from the central west coast of North West Cape (Babcock et al. 2008).

As well as latitudinal and regional patterns, the composition of fish assemblages varies across the reef from the reef slope towards the lagoon (Babcock et al. 2008), a pattern which is consistent with fringing reefs elsewhere in the world (Chabanet et al. 1997, Núñez-Lara et al. 2005). This is at least partly due to differences in structural complexity (Wilson et al. 2012), but depth (Fitzpatrick et al. 2012) and wave energy (Fulton et al. 2005) are also likely to be important influences. More species have been recorded from the reef slope than the other reef zones (Babcock et al. 2008).

Compared to the species from shallow habitats, there is very little information about the species that inhabit deep water at Ningaloo. Many of these species are slow growing and long lived and tend to aggregate around isolated patches of favourable structure. In deep water, the majority of unique species have been recorded from areas with assemblages of suspension feeders. The composition of fish assemblages was best predicted by a combination of benthos (filter feeders, macroalgae, sand or rubble zones) and depth (Babcock et al. 2008).

Relatively more research has been done further north on the North West Shelf, because of the commercially important trap and trawl fisheries (e.g. Moran & Stephenson 2000, Newman 2002), but there are some important differences in bathymetry and oceanography (e.g. the continental shelf is much wider north of Ningaloo: Wilson 2013), as well as a long history of trawling in parts of the North West Shelf that has probably changed the biota (Sainsbury 1991); these differences limit the extent to which knowledge can be transferred. Two large submarine canyons (Cape Range Canyon and the Cloates Canyon) extend offshore from the Ningaloo coast – these features remain largely unexplored.

In a survey of fish encompassing depths from 1–110 m, Fitzpatrick et al. (2012) found that the number of species and abundance declined with increasing depth, but average length and trophic level increased. For some species, larger (and presumably older) individuals were found in deeper habitats, a pattern which implies that there might be ontogenetic changes in habitat use.

In an extensive study of demersal fish assemblages south of 21°S, Williams et al. (2001) used nets to survey continental slope habitats in 200–1500 m. They identified a northern shelf break assemblage in 200–310 m depths off Ningaloo, characterised by five species (some not yet identified) that were almost exclusively found in this area (*Squalus* sp. D, *Chlorophthalmus* sp. B, *Lepidotrigla* sp. A, *Lepidotrigla* sp. B and *Citharoides macrolepidotus*). The remainder of species found in this area comprised a variety of tropical fishes whose range extends south from NW Australia (Williams et al. 2001).

Overall, estimates of fish biomass based on underwater visual census (788 kg ha^{-1}, Wilson et al. 2018a) are similar to those from other well-enforced no-take marine reserves in the Indian Ocean (McClanahan et al. 2009) but are less than the 1,000 kg ha^{-1} expected in the total absence of fishing (MacNeil et al. 2015). There tend to be more individual fish and species of fishes inside sanctuary zones, but differences in the number of species are not maintained after controlling for the number of individuals (Vanderklift et al. 2013).

The first documented surveys of fish assemblages at Ningaloo Reef were conducted by Ayling & Ayling (1987) in Sandy Bay in 1987. These surveys included counts of some species targeted by recreational fishers and revealed high densities of two species of lethrinids (emperors): *Lethrinus nebulosus* and *L. atkinsoni* (Ayling & Ayling 1987). Surveys have continued and become more frequent and widespread in the region, with most data collected since 2005 (Cresswell et al. 2019). Babcock et al. (2008) compared results from surveys in 2006–07 with those of previous surveys (Ayling & Ayling 1987, Westera et al. 2003) and found lower abundance of lethrinids, suggesting that their abundance has declined over time. Ten years of surveys by Vanderklift et al. (2019) support this, finding parallel declines inside and outside the Mandu Sanctuary Zone. The abundance of Labridae (wrasses) and Chaetodontidae (butterflyfish) have also declined, while other families, including parrotfish and surgeonfish, do not appear to have changed. Various plausible explanations for the observed declines exist, including fishing, localised declines in the abundance of coral and long-term climate variability (Holmes et al. 2017, Wilson et al. 2017). However, attributing causes is complicated when some trends may be part of long-term cycles – necessitating a deeper understanding of processes influencing mortality and recruitment.

There is some evidence that declines are not limited to fish. A commercial fishery (hand collection by snorkel diving) for rock lobster *Panulirus* spp. (mainly *P. cygnus*) existed at Ningaloo in the 1950s and 1960s and supported at least one full-time professional fisher (Halkyard 2005). Anecdotal reports describe a single diver harvesting 20–30 kg of lobsters within 30 minutes. The commercial fishery ceased to operate in the 1970s, by which time catches were declining (Halkyard 2005), and abundances remain low (Depczynski et al. 2009). The reason behind a lack of recovery in abundance of lobster decades after the closure of the commercial fishery is not clear, although changes in ocean currents might have contributed to ongoing low abundance by influencing recruitment (Ningaloo is the northern distribution limit of *P. cygnus*).

The majority of fish recruitment at Ningaloo likely occurs on the back reef and in the macroalgae that are abundant in the lagoon (Wilson et al. 2010, Depczynski et al. 2013, Wilson et al. 2017). Fish recruitment is probably lower in shallow depths on the reef slope (Depczynski et al. 2013), while little is known about recruitment processes in slope habitats deeper than 20 m.

Some settlement of fish larvae can occur all year (Wilson et al. 2014), but most settlement at Ningaloo is coincident with increasing seawater temperatures during the austral summer (McIlwain 2002, 2003). Much of this occurs between November and January (Meekan et al. 2001, McIlwain 2003), but spawning and settlement of some reef-associated species have also been recorded in February (McIlwain 2002, Wilson et al. 2016), indicating that recruitment may continue through to March or even April (Wilson et al. 2018b). The temporal differences in settlement intensity probably reflect variation in reproductive strategies among taxa, as well as environmental influences.

Spatial and temporal patterns in fish settlement at Ningaloo are influenced by variation in regional oceanography. Wilson et al. (2016) found differences in recruitment patterns between Bundegi, the western coast north of Point Cloates, and the western coast south of Point Cloates. This is probably because the southward-flowing Leeuwin Current, the northward-flowing Ningaloo Current and the tidally influenced local currents of the Exmouth Gulf shape the strength and timing of larval supply. Temporal variability in the strength of these currents can have a major influence on supply of fish larvae, with recruitment along the west coast of Ningaloo closely correlated with the

Southern Oscillation Index (SOI) and strength of the Leeuwin Current during the summer months (Wilson et al. 2017, Wilson et al. 2018a).

Large invertebrates are also conspicuous at Ningaloo, but knowledge about them is limited. Small giant clams *Tridacna maxima* can be abundant on intertidal platforms and some parts of the reef and likely experience considerable variation in recruitment and mortality (Black et al. 2011). Sea urchins, especially the burrowing urchin *Echinometra mathaei*, can be abundant in some habitats (Johansson et al. 2010), but unlike many other coral reefs, there is little evidence that sea urchins are a major influence on the abundance of macroalgae.

Connectivity among the various habitats facilitates the use of a broad array of resources by fish at Ningaloo and includes diurnal (Pillans et al. 2017), seasonal (Lim et al. 2016, Babcock et al. 2017) and ontogenetic movements (Wilson et al. 2010, Fitzpatrick et al. 2012) by individuals among habitats. In the early 1990s, 66% (of 1,781) of tagged individual *Lethrinus nebulosus* and *L. atkinsoni* were recaptured within 5.5 km of where they were tagged after ~2.5 years (Moran et al. 1993). A few individuals had moved 110 km within three months of the release, and none were recaptured more than 148 km away. Recent research has used arrays of acoustic receivers (Pillans et al. 2009) and showed that although both juvenile and adult *L. nebulosus* had relatively small home ranges (mean 95% Kernel Utilisation Distribution [KUD] = 8.5 km^2), more than 60% of the 84 individuals tagged moved beyond the boundary of the 28 km^2 array of acoustic receivers (Pillans et al. 2014, Babcock et al. 2017). These studies provided strong evidence for long-distance spawning movements (>130 km) by *L. nebulosus,* which are among the farthest recorded for any species of coral reef fish. Movements of individuals tagged during spawning aggregations suggested that spawning aggregations occur adjacent to reef passages and the reef slope and occur after quarter moons between October and December. The study provided strong evidence that only large fish (>50 cm FL) participate in these movements during the spawning season, implying that a large proportion of fish above the minimum legal size (41 cm) do not spawn. A significant proportion of individual *L. nebulosus* also exhibit patterns of movement associated with time of day and tide (Babcock et al. 2017).

The unique megafauna of Ningaloo

Ningaloo is home to a large suite of marine megafauna, including sharks, turtles, whales, dolphins, dugongs and manta rays (Preen et al. 1997). The diversity and abundance of Ningaloo's megafauna was an important contributor to its inscription as a World Heritage Area. Whale sharks have predictable seasonal aggregations at Ningaloo (Wilson et al. 2001, Meekan et al. 2006), and together with manta rays and humpback whales form the basis of an economically important ecotourism industry at Ningaloo (Davis et al. 1997, Catlin & Jones 2010, Venables et al. 2016, Huveneers et al. 2017).

Two species of dolphins are resident at Ningaloo, the Indo-Pacific bottlenose dolphin *Tursiops aduncus* and the Australian humpback dolphin *Sousa sahulensis* (Allen et al. 2012, Jefferson & Rosenbaum 2014). Both species are relatively commonly seen in the coastal waters of Ningaloo, often in mixed-species groups (Hunt 2018). The density of *S. sahulensis* is the highest recorded, and it exhibits site fidelity and residency (Hunt et al. 2017, Hunt et al. 2019).

Humpback whales *Megaptera novaeangliae* and pygmy blue whales *Balaenoptera musculus brevicauda* migrate past Ningaloo each year on their way to breeding grounds further north, and back again (Chittleborough 1965, Jenner et al. 2001, Double et al. 2014). Like elsewhere in the world, the number of humpback whales was significantly reduced by whaling, which continued in Western Australia until 1963 (including at Ningaloo until 1957). The population has recovered rapidly since the species was protected (Bejder et al. 2015), and humpback whales have now been downgraded from vulnerable to conservation dependent in Western Australia. Exmouth Gulf is a resting area, particularly for females and their calves on their journey back to the Antarctic (Chittleborough 1965, Jenner et al. 2001). While the Kimberley has been recognised as the main calving and breeding area for this population of humpback whales (Jenner et al. 2001), calving areas have become less well defined in Western Australia with the recovery of this population, and an increasing number of calves are being born at or near Ningaloo each year (Irvine et al. 2018). Killer whales *Orcinus orca* prey on humpback whale calves and are regularly present during the southern migration of humpback whales each year (Chittleborough 1953, Pitman et al. 2014).

White sharks *Carcharodon carcharias* are another potential predator of humpback whales. Although Ningaloo is near the northern range limit of white sharks for the coast, tagged individuals have been sporadically detected by acoustic receivers at Ningaloo during most of the year. The reasons white sharks travel to Ningaloo remain largely unknown, but migration for reproduction is unlikely because all acoustic detections in this area have been of juvenile or subadult individuals, nor do patterns in direction and timing of movement suggest that they follow migrating humpback whales (McAuley et al. 2017).

White sharks are just one of a diverse suite of elasmobranchs known to occur at Ningaloo, which supports among the most abundant and diverse shark and ray fauna found anywhere (Stevens et al. 2009, Vanderklift et al. 2014). Stevens et al. (2009) documented 47 species of elasmobranchs (30 sharks and 17 rays) in the state-managed Ningaloo Marine Park alone but estimated that there could be up to 118 species, based on the distribution of Australian elasmobranchs (Last & Stevens 2009).

The abundance and distribution of elasmobranchs at Ningaloo seems to be influenced by human activities. Commercial shark fishing is not permitted at Ningaloo west of 114°06E (the longitude of North West Cape), so Ningaloo is potentially an important refuge for species that are captured by this fishery, especially dusky shark *C. obscurus* and sandbar shark *C. plumbeus*. Sharks also interact with fishers frequently, with more than 10% of fish captured by fishers on the western side of North West Cape depredated by sharks and depredation occurring on more than a third of fishing trips across Ningaloo (Mitchell et al. 2018).

Individual dusky sharks tagged between Perth and Ningaloo moved freely between 21.7°S and 35.4°S, undertaking movements of up to 2,000–3,000 km per migratory event. The probability of these individuals being detected at Ningaloo was high in the austral winter–spring and low (males) to moderate (females) during the austral summer–autumn (Braccini et al. 2017). Indeed, the majority of detections were from Ningaloo (Braccini et al. 2017).

Some species move even further: one tiger shark tagged with a satellite tag at Ningaloo moved as far north as Sumba, Indonesia, and as far south as Esperance, on the south coast of Australia (Stevens et al. 2009). Acoustically tagged tiger sharks have demonstrated that some individuals appear to be nomadic, because they are only detected for a few months each year as they pass through Ningaloo, while others stay at Ningaloo for up to five years (Stevens et al. 2009, R. Pillans, unpublished data).

The lagoon provides an important nursery habitat for several species, including giant shovelnose ray *Glaucostegus typus*, blacktip reef shark *Carcharhinus melanopterus,* grey reef shark *C. amblyrhynchos,* nervous shark *C. cautus* and sicklefin lemon shark *Negaprion acutidens.* Acoustic tagging of neonates and juveniles of multiple species of sharks and rays showed that *N. acutidens* was the only species that displayed consistent use of shallow lagoon as a nursery (Oh et al. 2017a). Of the rays tagged, some juvenile *G. typus*, cowtail stingray *Pastinachus atrus* and porcupine ray *Urogymnus asperrimus* remained within the shallow lagoon, but others departed within a few months of tagging (Cerutti-Pereyra et al. 2014). However, the majority of these findings are based on few individuals, limiting their ability to conclusively determine the importance of habitats as nursery areas.

At Mangrove Bay, most (10 out of 13) tagged neonate blacktip reef sharks departed a 28 km^2 array of acoustic receivers within 16 days and had relatively large ranges (mean 95% Kernel Utilisation Distribution of 11.2 ± 12.5 km^2). In contrast, most (17 out of 23) tagged neonate sicklefin lemon sharks remained within the array for more than 30 days and had smaller ranges located close to where they were captured (mean 95% KUD = 4.8 ± 6.1 km^2) (Oh et al. 2017b). Both species showed strong preference for inshore sandflats but also spent time in mangroves, macroalgae-covered limestone pavement and shoreline reefs; they actively avoided reef slope and sandy lagoon habitats. A similar study of juvenile and adult nervous sharks revealed a small home range (50% and 95% KUD of 0.66 and 3.64 km^2, respectively) with a strong preference for mangrove habitats, but, again, few individuals were used ($n = 12$), and most ($n = 7$) were resident for less than 40 days (Escalle et al. 2015).

Differences in residence and home range of grey reef sharks between Mangrove Bay and Coral Bay suggest habitat may influence movement (Speed et al. 2012, Speed et al. 2016). Speed et al. (2012) reported that five adult female blacktip reef sharks showed a preference for shallow inshore water during the warmest parts of the day which resulted in their body temperature being $\sim$1°C warmer than mean water temperature and suggested this was evidence of behavioural thermoregulation, with grey and blacktip reef sharks detected more frequently in shallow inshore waters in the afternoon. Vanderklift et al. (2014) found that more frequent observations of blacktip reef sharks on the reef flat at dusk (from camera deployments and an agent-based model) were corroborated with more detections of acoustically tagged animals on the reef flat at dusk. The maximum density of blacktip reef sharks estimated by Vanderklift et al. (2014) was 20–90 ind km^{-2}, which is amongst the highest densities recorded for this species and further highlights the importance of Ningaloo for elasmobranchs.

Overall, the diet of elasmobranchs at Ningaloo is poorly known. Many species of rays forage in soft sediments for invertebrates, and their diet overlaps, with annelids dominating the diets of the majority of species (*Pastinachus atrus*, *Taeniura lymma*, *Neotrygon kuhlii*, *Urogymnus asperrimus*), while crustaceans dominate the diet of *Himantura uarnak* (O'Shea et al. 2013). The foraging activities of rays result in significant bioturbation, with an estimated $\sim$42% of the shallow (mean depth of 5.6 cm) intertidal soft-sediment area turned over by stingrays annually (O'Shea et al. 2012).

One elasmobranch for which Ningaloo has become renowned is the whale shark *Rhincodon typus*, the only member of the family Rhincodontidae and the largest fish in the world, attaining lengths exceeding 16 m (Borrell et al. 2011). Distributed throughout tropical and warm temperate seas, but rare everywhere, large numbers of whale sharks aggregate at Ningaloo each year between March and July (Mau & Wilson 2007, Holmberg et al. 2008, Sleeman, Meekan, Wilson et al. 2010), although some whale sharks are present all year (Norman et al. 2016, Reynolds et al. 2017).

The aggregations of whale sharks at Ningaloo coincides with the period when the Leeuwin Current is strongest, and there tend to be more whale sharks in La Niña years when the Leeuwin Current is particularly strong (Sleeman, Meekan, Fitzpatrick et al. 2010, Taylor & Pearce 1999, Wilson et al. 2001). Concentrations of dissolved nutrients (and therefore phytoplankton abundance) are also highest at this time of year, and during La Niña years, observations imply that whale shark aggregations are linked to periods of enhanced primary production (Wyatt et al. 2010, Rousseaux et al. 2012). Rousseaux et al. (2012) also inferred that rates of consumption of phytoplankton by zooplankton were probably high, providing a plausible link to the taxa that whale sharks feed on. The inference is supported by frequent observations of whale sharks near reef passes (Anderson et al. 2014), which are places where primary production tends to be high (Wilson et al. 2002). Nevertheless, our broader understanding of the mechanisms through which oceanographic conditions and phytoplankton production influence whale shark abundance remains poor.

The regularity and predictability of whale shark aggregations at Ningaloo led to it becoming one of the first places where ecotourism focused on in-water interactions with this species. Established in 1989, the industry grew swiftly, and the number of people swimming with whale sharks each year increased to nearly 30,000 by 2017 (Rob & Barnes 2017). The total direct expenditure by tourists in the whale shark industry in 2014 was estimated to be over $AUD11.5 million per year, with an additional $AUD12.5 million spent in the region by tourists for whom the opportunity to snorkel with whale sharks was the primary motivation for their trip (Huveneers et al. 2017).

The whale sharks that visit Ningaloo are mostly males (74%–85%), the majority of which are immature – there are no records of neonates or individuals <3 m (Arzoumanian et al. 2005, Meekan et al. 2006, Norman & Stevens 2007, Sequeira et al. 2016). Sexually mature males make up less than 10% of individuals, and mature females (at or exceeding published size at maturity) constitute <1% of individuals encountered (R. Pillans, unpublished data). Sex- and age-specific philopatry by whale sharks is also observed in other regions (Graham & Roberts 2007, Rowat & Gore 2007). To date, there has been no evidence of whale sharks mating at Ningaloo (Holmberg et al. 2008).

Four studies have estimated temporal trends in abundance for whale sharks at Ningaloo, with varying conclusions reached from different approaches (Bradshaw et al. 2007, Bradshaw et al. 2008, Holmberg et al. 2008, 2009). Using a capture-mark-recapture framework on 159 individuals of known sex and size, Bradshaw et al. (2007) estimated that 10 of 16 models yielded declining abundance (estimated changes in relative abundance ranged from 0.87 to 1.26 yr^{-1}). In contrast, Holmberg et al. (2008), also applying a capture-mark-recapture framework but on a larger dataset (representing 355 individuals over a 13-year period between 1995 and 2008), estimated an increasing trend in relative abundance of 1.12 yr^{-1} ($\mathrm{SE} = 0.06$).

The variation in estimates of trends in abundance are also found in published trends in size. Bradshaw et al. (2008) found that estimates of length from the ecotourism industry declined between 1995 and 2004, but Holmberg et al. (2009) suggested that the decline in size was due to increased recruitment of smaller animals. Estimates from these types of models provide information about the philopatric portion of the broader whale shark population but do not account for the remainder, which might not visit Ningaloo during their life. The discrepancy between studies that seek to answer an important question in conservation ecology (and for the regional economy) indicates that alternative methods are required.

More than 8% of whale sharks observed at Ningaloo had scars consistent with vessel strike (Speed et al. 2007). Combined with the severity of some wounds, this might suggest that vessels pose a threat, although the magnitude of this threat is not known. There are no direct threats from fishing in Australian waters, but targeted fisheries that operated in the northern Indian Ocean in the 1990s are likely to have influenced abundance. It is possible that observed declines in genetic diversity (Vignaud et al. 2014) resulted from high levels of historical harvest in the northern Indian Ocean (Anderson & Ahmed 1993, Fowler 2000, Pravin 2000). Despite protection, continued illegal harvest has been documented in parts of the eastern Indian Ocean (White & Cavanagh 2007, Riley et al. 2009).

Vignaud et al. (2014) suggested that whale sharks exist in two distinct populations with minimal connectivity – the Indo-Pacific and the Atlantic Ocean. Other studies have suggested that there is sufficient gene flow to prevent sub-populations occurring within the Indo-Pacific (Schmidt et al. 2009, Castro et al. 2007). However, there is limited evidence from records of individuals identified from photographs that animals move between aggregation sites within each population (Rowat & Gore 2007, Speed et al. 2007, Brooks et al. 2010).

The uncertainty in estimates of abundance and knowledge of threats highlights the usefulness of understanding whale shark movement patterns. Tagging studies can help resolve these movements. There have been ~49 published tracks of whale sharks tagged with satellite tags at Ningaloo (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Sequeira et al. 2013, Norman et al. 2016, Reynolds et al. 2017), and there are an additional ~50 individuals for which data have not yet been published (zoatrack.org/projects, http://www.seaturtle.org/tracking/?project_id=1112). The longest published track is 261 days (Norman et al. 2016), but unpublished data include three tracks over 300 days (R. Pillans, unpublished data).

Whale sharks tagged at Ningaloo show long-distance movements, including to Indonesia and Timor Leste (R. Pillans unpublished data,), with the extent of movements between 12–35°S and 100.9–121.72°E (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Norman et al. 2016, Reynolds et al. 2017). However, most satellite-tagged whale sharks have remained within 300–400 km of Ningaloo (Wilson et al. 2006, Sleeman, Meekan, Wilson, et al. 2010, Norman et al. 2016, Reynolds et al. 2017). Long-distance movements away from Ningaloo have been primarily northwards, towards Christmas Island, Java and the Timor Sea (Wilson et al. 2005, Wilson et al. 2006, Sleeman, Meekan, Wilson et al. 2010, Norman et al. 2016), as well as west as far as the Arafura Sea and Gulf of Carpentaria (Sleeman, Meekan, Wilson et al. 2010, R. Pillans unpublished data). Norman et al. (2016) also reported that a whale shark photographed off Borneo in 2007 was positively identified at Ningaloo in 2011 and 2012. This may reflect immigration, as no images of this animal were present prior to 2007. Southwards movements are less common, but some have been detected off Perth (Norman et al. 2016, R. Pillans unpublished data). For all published records of animals tagged with satellite tags at Ningaloo, the extent spans 26.5 degrees of latitude (5.5° to 32°S; >4,000 km) and 55 degrees of longitude (85° to 145°E). The reasons individuals move in a particular direction or for a particular distance are very poorly understood. Sleeman, Meekan, Fitzpatrick, et al. (2010) (2010) found that movement of satellite-tagged individuals was independent of near-surface currents and weakly correlated with sea-surface chlorophyll-*a* concentrations.

Although movements away from Ningaloo are poorly understood, there seems little doubt that whale sharks visit Ningaloo to feed. At Ningaloo, whale sharks have been observed feeding on tropical krill *Pseudeuphausia latifrons* (Gunn et al. 1999, Wilson et al. 2001, Taylor 2007), and this species has been identified in faecal samples of three individuals (Jarman & Wilson 2004). Marcus et al. (2016) found differences in fatty acid composition between years, suggesting variability in the prey consumed, perhaps when travelling both to and from Ningaloo Reef and while resident at Ningaloo. Resolution of where and when they feed has been assisted by tags with the ability to record and transmit water temperature and the depth that individuals swim to. Although some studies have implied deep foraging (Meekan et al. 2015), recent high frequency depth and temperature records, combined with accurate GPS data from whale sharks tagged at Ningaloo, suggest limited foraging at depths >200 m (R. Pillans, unpublished data).

Gleiss et al. (2011) used tags with different types of sensors to demonstrate that ascents always showed significant lateral acceleration, while descents were largely passive (they glide down and swim up). Whale sharks dived deeper at night than during the day but exhibited ram filter feeding at the surface during sunset and the first few hours of night, with sharks spending approximately 8 min per day in this position. Observations indicated these individuals were also feeding on *P. latifrons*. Thums et al. (2013) analysed temperature and depth data from four sharks and demonstrated that prolonged dives into deep, cool water were followed by long surface times and hypothesised that this behaviour was in response to thermoregulation. Additional data from long-term tag deployments are required to better resolve fine-scale behaviour associated with feeding, migrating and resident animals.

The big herbivores: Dugongs and turtles

Ningaloo and Exmouth Gulf also host populations of dugong *Dugong dugon* and turtles. Preen et al. (1997) estimated that there were 7–9,000 turtles (primarily green turtles *Chelonia mydas* and almost certainly an underestimate) and 1,000 dugong at Ningaloo from aerial surveys, estimates comparable to the Great Barrier Reef (Marsh & Saalfeld 1989, Marsh et al. 1994, Preen et al. 1997). Dugong abundance is lower at Ningaloo than at Shark Bay (Preen et al. 1997, Gales et al. 2004), but the proximity of these two World Heritage Areas (~400 km between North West Cape and Shark Bay) allows dugong to move between them in response to loss of seagrass habitat following catastrophic events (Gales et al. 2004, Holley et al. 2006).

Six of the world's seven species of turtles have been recorded at Ningaloo, and four of these (green turtles *Chelonia mydas*, loggerhead turtles *Caretta caretta,* hawksbill turtles *Eretmochelys imbricata,* flatback turtles *Natator depressus*) nest on the adjacent beaches. The population of green turtles in the North West Shelf stock is one of the largest in the world (Limpus 2007), and the beaches of the Ningaloo Marine Park contain a high percentage of the nests of the south-eastern Indian Ocean populations of loggerhead and green turtles (Baldwin et al. 2003, Casale et al. 2015).

Each year, nesting is dominated by green (~17,000 tracks) and loggerhead turtles (~2,000 tracks) (Whiting 2016). The sparse nesting by hawksbills (~400 tracks) reflects that Ningaloo is located at the southern margins of their nesting distribution for Western Australia. The most concentrated area of green turtle nesting is along the northern beaches and Muiron Islands, while loggerhead nesting is concentrated along beaches further south (Bungelup, Jane's Bay, Gnaraloo) and on South Muiron Island. Yearly surveys of nesting turtle tracks and nests have occurred since 2001; there is no increasing or decreasing trend in the number of tracks during this time, but there is substantial inter-annual variation (Whiting 2016).

Although resident turtles at Ningaloo exhibit relatively restricted movements (certainly green turtles: M. Vanderklift & R. Pillans, unpublished data), nesting females can migrate hundreds or even thousands of kilometres (Waayers et al. 2019, Table 1). The post-nesting migrations of green turtles tagged at Ningaloo have ranged from Shark Bay to the south (25°40 S; 400 km) to Kimberley in the north (16°50 S; >1,000 km), while loggerhead turtles have ranged even further, as far as the tip of Cape York in eastern Australia (DBCA, unpublished data). In turn, a small number of tag returns (from thousands of individuals tagged at nesting beaches and from Exmouth Gulf) have indicated that turtles resident at Ningaloo nest elsewhere in the Pilbara (Prince 1993, Prince et al. 2012).

Turtles are particularly sensitive to a changing climate, both directly through the influence that temperature exerts on the probability of a hatchling being male or female and indirectly through impacts on food resources and erosion of nesting beaches. The pivotal temperature for Ningaloo green turtles is 29.2°C (obtained from *in vitro* incubations in a laboratory); both males and females were produced between 27.9 and 30.4°C, gradually transitioning to all males at lower temperatures and all females at higher temperatures (Stubbs & Mitchell 2018).

Turtles (primarily green and hawksbill) were commercially harvested at Ningaloo until 1973, when the practice was banned. Although tens of thousands of turtles were harvested in the years prior to closure, exploitation was relatively late compared to elsewhere in the world (Halkyard 2014). Nevertheless, it probably led to locally depleted abundances (Halkyard 2014).

Table 1 Satellite tracking deployments for sea turtles initiated within Ningaloo Marine Park

Year	Source	Species	Sex	N	Habitat (B, W)	Distance L	Distance G
2007–2008	Ningaloo http://www.seaturtle.org/tracking/?project_id=265	L	F	9	B	1,559	–
2013	Ningaloo http://www.seaturtle.org/tracking/?project_id=814	G	M, I	2	W	–	–
2015–2019	Ningaloo http://www.seaturtle.org/tracking/?project_id=1101	G	F, M, I	35	B, W		189 (B), 4 (W)
2016	Muiron Islands http://www.seaturtle.org/tracking/?project_id=1176	L	F	5	B	1,900	
2016, 2017	Gnaraloo (1149) http://www.seaturtle.org/tracking/?project_id=1149	L	F	12	B	300	
2018	Muiron Islands, Ningaloo (1341) http://www.seaturtle.org/tracking/?project_id=1341	L, G	F	25	B	596	101

Abbreviations: L, loggerhead turtle; G, green turtle; F, female; M, male; I, immature; N, individuals; B, beach; W, water.

Note: Distance is the median displacement distance (in km, straight line between start and end point) for individuals which transmitted for >100 d. Habitat is where turtles were captured for tagging (beach or water).

Human use

Although the resident human population at Ningaloo is low (a combined population of <3,000 people in Exmouth and Coral Bay: Figure 5.4f), more than 150,000 people visit each year, most of whom visit for tourism (Jones et al. 2011; Figure 5.4e). A large proportion of these tourists engage in activities that interact with the marine ecosystem, including fishing and snorkelling, as well as interactions with wildlife such as whale sharks (Smallwood et al. 2012). These activities are managed through a suite of measures. The Commonwealth and state marine parks include spatial zones that include IUCN Categories II, IV, V and VI. Places where recreational fishing can occur are controlled by these zones, and the number and size of fish that can be caught and retained is controlled by a suite of regulations which include species-specific boat, bag, possession and slot (size) limits. Tour operators involved in wildlife interactions are licensed and are required to follow codes of conduct (Department of Parks & Wildlife 2013).

Recreational fishing is a popular activity and includes fishing from the shore and from private and charter boats (Smallwood & Beckley 2012, Lynch et al. 2019). Commercial fishing has been restricted in this area since the 1970s and does not occur at present (Marriott et al. 2012, Gaughan & Santoro 2018). Recreational fishing is predominantly line fishing; effort is concentrated in a few areas and occurring mostly from April to October (Smallwood & Beckley 2012).

Although data on recreational fishing effort and catch have been collected periodically since the late 1990s, different survey objectives and methods make comparisons between surveys difficult, and so broad trends are challenging to identify. In addition, these surveys are designed to provide catch and effort estimates for large fishery management units, which makes the data difficult to interpret in the context of local patterns. The most commonly caught and retained species by recreational fishers are emperors (Lethrinidae) and cods (Serranidae), with spangled emperor *Lethrinus nebulosus* and Chinaman rockcod *Epinephelus rivulatus* – both of which tend to occur in shallow water – the most commonly recorded species (Marriott et al. 2012, Ryan et al. 2017). Demersal species that inhabit deeper habitats, such as goldband snapper *Pristipomoides multidens* and rankin cod *Epinephelus multinotatus*, have been consistently recorded in recreational catches since 2011–12 (Ryan et al. 2013, Ryan et al. 2017, 2015).

Estimated retained catches of *L. nebulosus* from boat-based recreational fishers in the Gascoyne Coast bioregion (within which Ningaloo is located) were similar in 1998–99 and 2007–08 (16,000 vs 15,000 individual fish: Marriott et al. 2012). Most *L. nebulosus* are caught north of Coral Bay, with an expansion into offshore areas evident from 1998–99 to 2007–08 (Marriott et al. 2012). It is not possible to directly compare these studies with Ryan et al. (2017) because survey methods were different, but retained catches of *E. rivulatus, P. multidens* and *E. multinotatus* were steady between 2011–12 and 2015–16 at Ningaloo, while the estimated retained catch of *L. nebulosus* at Ningaloo was lower in 2015–16 (2,887 individual fish; SE ± 686) than 2011–12 (7,973 individual fish; SE ± 1,328: Ryan et al. 2017).

Participation in whale shark tourism has steadily increased, with more than 30,000 attendees on tours to snorkel with whale sharks in 2018 (Figure 7). Management frameworks have so far proved effective. For example, analyses of the potential impacts of ecotourism activities yielded no evidence that people swimming with them affected the likelihood of a whale shark being re-encountered or the residence time of individual whale sharks at Ningaloo (Sanzogni et al. 2015). There is some evidence that whale sharks change direction more often in the presence of tours but little to suggest this has long-term effects on their behaviour (Raudino et al. 2016).

Ecotourism at Ningaloo also includes tours to observe and swim with manta rays and humpback whales. Tours to swim with manta rays began in the early 1990s; operators of these tours can choose to abide by a voluntary code of conduct, but Venables et al. (2016) suggested that a management approach similar to that applied to the whale shark tourism industry would be useful. Tours to swim with humpback whales began in 2016, with a trial to determine whether it could develop into an

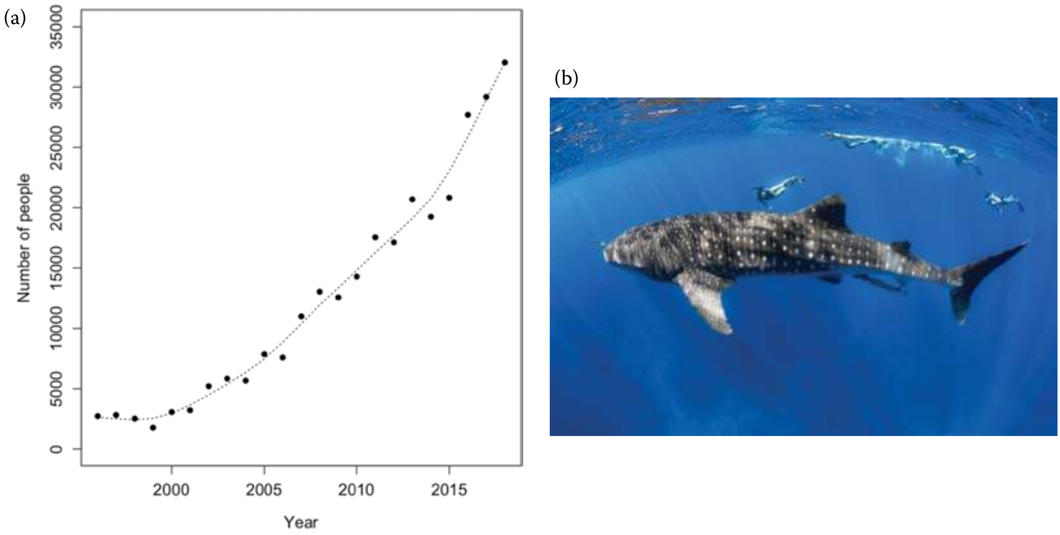

Figure 7 (a) Total numbers of passengers swimming with whale sharks on licensed tours in Ningaloo Marine Park. (Data from Wilson & Barnes. 2018.) (b) Tourists swimming a whale shark at Ningaloo Reef (photo credit: Violeta Brosig).

economically and ecologically sustainable industry; participation increased from approximately 2,300 passengers in 2016 to 3,185 passengers in 2018 (Department of Biodiversity Conservation and Attractions, unpublished data). Evidence suggests that application of best-practice principles can ensure minimal impacts to whales while enhancing safety and satisfaction of tour participants (Sprogis et al. 2020).

The future of Ningaloo

As with coral reefs globally, Ningaloo is facing increasing pressure from the combined effects of climate change and increasing human use (Fulton et al. 2011). Downscaled climate models tend to predict a weaker Leeuwin Current, especially in winter (resulting from a predicted reduction in the amount of water passing through the Indonesian Throughflow, which is in turn a result of a predicted weakening of winds in the tropical Pacific), with a deeper thermocline and more sporadic upwelling by the 2060s (Brinkman 2011, Sun et al. 2012). The downscaled models tend to predict larger changes than global climate models (Sun et al. 2012), a prediction which seems to be supported by empirical evidence using δ^{18}O in coral cores, which indicate a ~1.5°C increase in water temperature at Ningaloo over the last century, a rate of increase which is faster than the global average (Kuhnert et al. 2000).

Heron et al. (2017) used global climate models to predict that water at Ningaloo will reach temperatures warm enough to cause coral bleaching each year by 2049, and twice each decade by 2041 – a frequency that is almost certainly too high for corals to recover between warming events. The faster rates of warming yielded by downscaled models and evidence from coral cores mean that this might occur sooner. Exacerbating the likely increase in the frequency of bleaching is the potential for reduced supply of larvae from weaker currents, because the coral reefs to the north are likely to be sources of larvae for Ningaloo (Boschetti et al. 2019), and coral abundance on these reefs has already been significantly reduced (Gilmour et al. 2019, Haywood et al. 2019).

Warmer water will also generate effects beyond the direct influence on bleaching. Contemporary water temperatures at Ningaloo are not favourable for development of crown-of-thorns, a major predator of corals on the Great Barrier Reef and some other places, including the Montebello Islands located just 100 km north of Ningaloo (Haywood et al. 2019, Keesing et al. 2019), but rare at Ningaloo. Water temperatures at Ningaloo are near the threshold above which larvae develop (~28°C), but as temperatures warm, the probability of larvae surviving and developing will increase, in turn increasing the probability of an increase in abundance of adults (Henderson & Lucas 1971, Johnson & Babcock 1994).

If corals survive, their calcification rates should enable them to keep up with sea level rise (Perry et al. 2018), but this may be compromised if the abundance of bioeroders increases substantially. In parts of the western Indian Ocean, sea urchins such as *Echinometra mathaei* have become abundant, probably because the abundance of predatory fish that eat them has been reduced by unsustainable rates of fishing (McClanahan 1995, 2008). At Ningaloo, there is no obvious correlation between the abundance of *E. mathaei* and the abundance of its predators (Babcock et al. 2008), but the abundance of lethrinids (one of the predators of *E. mathaei*) is decreasing (Vanderklift et al. 2019).

Other primary producers will also likely be affected by increasing water temperatures. The abundance of seagrasses, primarily *Halophila* spp., has been reduced by extreme events in Exmouth Gulf (with marine heatwaves or cyclones the likely cause), but recovery has occurred within a few years (Loneragan et al. 2013, Vanderklift et al. 2016). Some seagrasses, such as *Amphibolis antarctica*, have their northernmost distribution limits at Ningaloo. *Amphibolis* experienced widespread mortality in 2011 at Shark Bay, south of Ningaloo, due to an extreme marine heatwave and impacts are still evident almost ten years later (Arias-Ortiz et al. 2018). The effects of this event on *A. antarctica* at Ningaloo are poorly known, but reports suggest it is vulnerable to climate extremes at Ningaloo as well (Van Keulen 2018).

Mangroves can adapt to sea level rise if there is sufficient space for them to expand, but over shorter timeframes they will also suffer from climate variability. For example, mangroves on the western Ningaloo coast experienced mortality during periods of very low sea level during which salinity in the underlying soil increased (Lovelock et al. 2017). The balance between long-term trends and short-term variability in sea level, and availability of space to expand into, will determine their future at Ningaloo, but which will be the primary influence is unknown. Some older trees have died at Mangrove Bay this century (Lovelock et al. 2017), but studies based on aerial imagery over a relatively short period (<10 years) indicate that the small stands at Mangrove Bay have increased in spatial extent, although they have experienced some canopy loss (Holmes et al. 2017).

Changes to upwelling might influence whale sharks and manta rays, but their reliance on food resources supported by upwelled nutrients is not well understood, and so predictions are necessarily speculative. Increasing air temperature will increase sand temperatures: the pivotal temperature in an *in vitro* laboratory incubation of green turtle hatchlings from Ningaloo was ~29°C (Stubbs & Mitchell 2018), which was the mean sand temperature recorded by Trocini (2013) in 2006–2008 at Ningaloo, who also recorded temperatures exceeding 33°C in the last third of incubation periods for more than half of the nests surveyed. The nesting success of turtles can also be reduced by erosion of beaches during cyclones: predictions for cyclones are very uncertain, but most global models predict a greater proportion of stronger cyclones, although not necessarily a greater frequency (Walsh et al. 2016).

Ningaloo will also face increased pressure from growing human use (Fulton et al. 2011): most visitors to Ningaloo are from Western Australia, a state whose population will potentially more than double by 2066 (with a projected range of 3.6–5.9 million, http://www.abs.gov.au). A growing number of visitors will result in increasing need for coastal infrastructure, and decisions will need to be made about whether such infrastructure is consistent with ensuring the sustainable use of Ningaloo. At present, we know little about the ability of Ningaloo's ecosystems to absorb additional pressures. For example, trends in fish abundance indicate that some taxa might not readily absorb additional fishing effort, and understanding how to balance sustainable rates of effort with the aspirations of visitors to fish will require sound information about the ecology and biology of the species (Fulton et al. 2011).

While current estimates of growth of the resident population of Exmouth are not considered large (increasing from 2,536 residents in 2012 to an estimated 4,604 in 2051 under a 'high growth scenario'; Gascoyne Development Commission, 2015), the number of tourists that visit Ningaloo is likely to increase. It is difficult to accurately estimate rates of visitor use because there are multiple entry points along 300 km of coastline. However, long-term increases in the number of people participating in tourism activities suggest continued growth in visitation is likely. For example, tourists visiting Ningaloo to swim with whale sharks on licensed tours have increased steadily since 1996 (Wilson & Barnes 2019: Figure 7).

Predatory feral animals (red foxes *Vulpes vulpes*, and possibly cats *Felis catus*) have been a substantial source of mortality of turtle hatchlings in the past. Feral animal control programs (including baits) targeted at protecting turtle rookeries along the Ningaloo Coast have been effective in significantly reducing predation on nests and hatchlings by feral animals to levels approaching zero (Markovina 2017).

Ningaloo, in common with many of the world's coral reefs, is experiencing steadily increasing pressures, which are now manifesting in changes to some components of the ecosystem, including declining abundances of corals and fish. It experiences seasonal winds, upwelling and wave-driven currents, which tend to dampen the impacts of ocean warming. Well-enforced regulations provide some protection from the pressures of increasing human use. However, the presence of taxa at their northern range limits, and the possibility that even relatively small changes could breach thresholds (such as the thermal tolerance of corals and crown-of-thorns larvae), mean that even relatively small changes in temperature could generate unanticipated outcomes. The extensive effort to elucidate the ecology of Ningaloo in recent decades has provided much knowledge, but there are still key processes we do not understand. Generating better knowledge (including traditional ecological knowledge) about these processes and how they respond to the pressures of climate change and human use through well-coordinated research, and translating that knowledge into practical actions, will be critical for the future of Ningaloo.

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PRIORITY SPECIES TO SUPPORT THE FUNCTIONAL INTEGRITY OF CORAL REEFS

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Abstract Ecosystem-based management on coral reefs has historically focussed on biodiversity conservation through the establishment of marine reserves, but it is increasingly recognised that a subset of species can be key to the maintenance of ecosystem processes and functioning. Specific provisions for these key taxa are essential to biodiversity conservation and resilience-based adaptive management. While a wealth of literature addresses ecosystem functioning on coral reefs, available information covers only a subset of specific taxa, ecological processes and environmental stressors. What is lacking is a comparative assessment across the diverse range of coral reef species to synthesise available knowledge to inform science and management. Here we employed expert elicitation coupled with a literature review to generate the first comprehensive assessment of 70 taxonomically diverse and functionally distinct coral reef species from microbes to top predators to summarise reef functioning. Although our synthesis is largely through the lens of the Great Barrier Reef, Australia, a particularly data-rich system, it is relevant to coral reefs in general. We use this assessment to evaluate which taxa drive processes that maintain a healthy reef and whether management of these taxa is considered a priority (i.e. are they vulnerable?) or is feasible (i.e. can they be managed?). Scientific certainty was scored to weight our recommendations, particularly when certainty was low. We use five case studies to highlight critical gaps in knowledge that limit our understanding of ecosystem functioning. To inform the development of novel management strategies and research objectives, we identify taxa that support positive interactions and enhance ecosystem performance, including those where these roles are currently underappreciated. We conclude that current initiatives effectively capture many priority taxa but that there is significant room to increase opportunities for underappreciated taxa in both science and management to maximally safeguard coral reef functioning.

Introduction

Coral reefs have changed profoundly over recent decades due to cumulative impacts from local (e.g. fisheries, water quality) and global (i.e. ocean warming) stressors. While continued exposure to extreme events could stimulate some level of adaptive capacity and resilience in surviving cohorts (Maynard et al. 2008, Hughes et al. 2019a, b), reef recovery and persistence will be variable at local and global scales (Guzman & Cortes 2007, Graham et al. 2011b, Glynn et al. 2015, Bento et al. 2016, Mumby et al. 2016, de Bakker et al. 2017, Mellin et al. 2019). It is estimated that up to 90% of coral reefs may disappear as soon as 2050 if global emissions are not curbed in line with improved local management strategies to resolve mounting pressures (Wilkinson 2006, Albright et al. 2016a, Schleussner et al. 2016, van Hooidonk et al. 2016, Harvey et al. 2018, Hughes et al. 2018a).

High-biodiversity systems, like coral reefs, are suggested to have broader systemic resilience to environmental perturbation through increased trait diversity and functional redundancy (Boucher 1997, Bellwood et al. 2004, Hooper et al. 2005, Micheli & Halpern 2005, Ferrigno et al. 2016, McWilliam et al. 2018). Species-poor ecosystems, in contrast, may be particularly susceptible to collapse following the loss of just a few key species (Mumby et al. 2008). One of the foremost examples of this exists for Caribbean reefs, where loss of a predominant grazing herbivore (a diadematid sea urchin) resulted in undesirable algal growth and catastrophic, largely irreversible, phase shifts towards macroalgal and cyanobacterial reefs (Hughes 1994, Gardner et al. 2003, Mumby et al. 2006a, Brocke et al. 2015, de Bakker et al. 2017). Even in high-diversity ecosystems, the loss of key species can result in ecological changes that impair critical processes and services, including resource use, fisheries productivity and carbonate accretion (McClanahan et al. 2002, Kennedy et al. 2013, Holbrook et al. 2015, Rogers et al. 2015, 2018a, Mora et al. 2016, Harborne et al. 2017, Mumby 2017, Clements & Hay 2019).

Coral reefs are complex ecosystems with a great diversity of players, including microbes, algae, sponges, corals, other invertebrates and fishes (Reaka-Kudla 1997, Fisher et al. 2015). While high biodiversity is considered the hallmark of healthy and productive ecosystems, many studies highlight the critical importance of a small subset of species in maintaining ecosystem functioning through a range of positive interactions (Halpern et al. 2007, Naeem et al. 2012, Shaver & Silliman 2017, Renzi et al. 2019), their broad distributions and high abundances or high degree of specialisation with limited functional redundancy (Power et al. 1996, Piraino et al. 2002, Bellwood et al. 2004, Hooper et al. 2005, Mouillot et al. 2013). Corals, for example, are major contributors to calcification and reef building, but some species contribute disproportionately to coral recovery and coverage (e.g. *Acropora*) (Johns et al. 2014, Ortiz et al. 2014, 2018), while others contribute more to rates of reef building in high-sediment regions (e.g. *Turbinaria*) (Browne 2012, Morgan et al. 2016). Beyond corals, microbial organisms underpin many ecosystem processes (Glasl et al. 2018a), benthic invertebrates and cryptobenthic fishes are at the foundation of fisheries productivity (tertiary production) (Depczynski & Bellwood 2003, Kramer et al. 2015, Brandl et al. 2018, 2019), planktivorous fishes partition their feeding activity into different reef zones (Hamner et al. 1988, Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005), some herbivorous fishes are more important in controlling fouling macroalgae (Bellwood et al. 2004, Mumby et al. 2006a, 2014, Hoey & Bellwood 2009, 2010b, Loffler et al. 2015a) and predatory fishes can alter reef community structure (Almany & Webster 2004, Rizzari et al. 2014, Stier & White 2014, Palacios et al. 2016b, Stier et al. 2017). As biodiversity conservation is often based on broad-scale habitat protection through marine reserves (Maynard et al. 2016, Mellin et al. 2016), ensuring that specific provisions for key species are incorporated could enhance effectiveness of management strategies (Halpern et al. 2007, Naeem et al. 2012, Shaver & Silliman 2017, Richards & Day 2018).

The biology and ecology of coral reef species are generally well understood, but information on reef ecosystem functioning is largely weighted towards hard (scleractinian) corals and reef fishes (Bellwood & Choat 1990, Bellwood et al. 2004, 2017, 2019, Munday et al. 2009b, Stuart-Smith et al. 2013, McClanahan et al. 2014, Pratchett et al. 2015, Bourne et al. 2016, Konow et al. 2017, Bierwagen et al. 2018, Brandl et al. 2018, McWilliam et al. 2018), overlooking many other species important to a functioning ecosystem. A growing number of studies provide comprehensive reviews of the significance of alternative groups to reef functioning, including for microorganisms (Mouchka et al. 2010, Charpy et al. 2012, Garren & Azam 2012b, Thompson et al. 2015, Hernandez-Agreda et al. 2017), sponges (Wulff 2006, Bell 2008, Maldonado et al. 2015, Pawlik et al. 2018), algae (McCook et al. 2001, Tribollet 2008, Nelson 2009, Connell et al. 2014), phyto- and zoo-plankton (McKinnon et al. 2007, Ferrier-Pages et al. 2011), echinoderms (Birkeland 1989, Pratchett et al. 2014, Purcell et al. 2016a) and coral-associated invertebrates (Castro 1976, Stella et al. 2011b). Some also review specific ecological processes on coral reefs, such as bioerosion (Hutchings & Kiene 1986, Sammarco 1996, Tribollet 2008), calcification and carbonate accretion (Allemand et al. 2011, Tambutte et al. 2011, Bertucci et al. 2013, Kennedy et al. 2013), herbivory (Cvitanovic et al. 2007, Mumby 2009a, Bonaldo et al. 2014, Puk et al. 2016), foraging associations (Lukoschek & McCormick 2000), cleaning symbioses (Cote 2000, Vaughan et al. 2017) and certain modes of predation like corallivory (Cole et al. 2008, Rotjan & Lewis 2008, Konow et al. 2017, Rice et al. 2019). As coral reefs degrade, a growing body of literature also draws focus on the environmental stressors threatening biological processes and reef functioning, including climate change (Hoegh-Guldberg et al. 2007, Atkinson & Cuet 2008, Baker et al. 2008, Pratchett et al. 2008b, Przeslawski et al. 2008, Graham et al. 2011b, Harley et al. 2012, Andersson & Gledhill 2013, Munday et al. 2013b, Albright et al. 2016a, Anthony 2016, Hoey et al. 2016a, Camp et al. 2018a, Espinel-Velasco et al. 2018, Harvey et al. 2018), storms and cyclones (Harmelin-Vivien 1994), water quality (Fabricius 2005, McKinley & Johnston 2010, Brodie et al. 2012, Browne et al. 2012, Erftemeijer et al. 2012, Wear & Thurber 2015, Hairsine 2017) and anthropogenic stressors more generally (Wilkinson 1999, Brodie & Waterhouse 2012, Ban et al. 2014b, Uthicke et al. 2016, Harborne et al. 2017, Richards & Day 2018). However, the majority of these studies are still focussed on corals and fishes.

While a wealth of empirical data and literature reviews address ecosystem functioning on coral reefs, they are typically targeted at specific taxa, processes and/or stressors. What is lacking is a comparative assessment across the diverse range of taxonomic and functional groups of coral reef species to synthesise available knowledge to inform science and management. Given global degradation of many coral reefs, it is not only timely but imperative to ask whether key species that support ecosystem functioning are being adequately protected. To date, the paradigm in ecosystem restoration has been to reduce the negative effects of physical stress, human impacts and/or species interactions (e.g. invasions), but explicit recognition of positive species interactions is critical to conservation success (Halpern et al. 2007, He et al. 2013, Shaver & Silliman 2017, Thomsen et al. 2018, Renzi et al. 2019, Zhang & Silliman 2019). Identifying and protecting species of particular importance is essential for the conservation of coral reefs and in providing targeted information to safeguard species, biodiversity and functioning in a future ocean (McClanahan et al. 2014, Rogers et al. 2015, Richards & Day 2018).

Here we employed expert elicitation coupled with an extensive compilation of the literature to create a hierarchy of key coral reef taxa – from microbes to top predators – that support reef functioning. As a particularly data-rich system, our synthesis is focussed on the Great Barrier Reef (GBR), Australia, but is relevant for coral reefs globally. We assessed taxa based on their contributions to ecosystem processes and functioning and examined their perceived vulnerability and manageability to improve the holistic management of GBR species, values and processes. Specifically, we assessed which taxa drive processes that maintain a healthy reef and address whether management is considered a priority (i.e. are they vulnerable?) or feasible (i.e. can they be managed?). Elicitation results were used to guide compilations of the literature for key taxa outlined at various levels of ecosystem processes, functioning and stressors. This includes case-specific compilations for key species (tabular corals, branching corals, microorganisms, crustose coralline algae [CCA], turf algae, herbivorous parrotfishes, crown-of-thorns starfish [CoTS]) and novel candidates (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated decapods, detritivorous fishes).

Scientific certainty was addressed so that data-deficient groups were not overlooked in our analysis with the objective to highlight novel cases. We also present five case studies to address current gaps in knowledge that limit our understanding at various levels of ecosystem functioning on the GBR. Case study themes were nominated by our expert panel during workshop discussions, and consensus decisions were made to reflect the multidisciplinary expert assemblage, including 1) invertivory, 2) the carbonate budget, 3) microbial links to water quality, 4) recreational spearfishing and 5) the CoTS juvenile life stage. We conclude by outlining the desired outcomes for both science and management to support and protect priority species regarding ecosystem functioning on coral reefs using a framework that can be expanded to guide future integrated and holistic management.

Defining 'key' species

There is some confusion and debate regarding the definition of 'key' versus 'keystone' species (Piraino & Fanelli 1999, Valls et al. 2015). Keystone species (Paine 1969) are those that have a large, disproportionate effect on their community relative to their abundance (Power et al. 1996). The 'keystone' archetype was applied to an intertidal marine predator that shaped community assemblages despite their low relative abundance (Paine 1969) but is not exclusive to top-down processes (Mills et al. 1993). Yet notably, species that drive ecosystem processes, energy flows and/or functioning can be abundant and dominant and thus should not be included in the 'keystone' typology (Paine 1995, Piraino & Fanelli 1999). Here, we refer to 'key' species as those with explicit roles in ecosystem functioning regardless of their relative abundance This facilitated our analysis across a diverse range of coral reef species at various levels of taxonomy and functioning, whether comparatively rare or abundant. This is particularly important given the challenges associated with identifying key species and quantifying their roles in high-diversity ecosystems (Gotelli et al. 2011, Pigot et al. 2016), including coral reefs (Maire et al. 2018). Critically, species' roles in ecosystem functioning are dynamic, and species and their interactions have variable inputs and outputs over space and time (Piraino et al. 2002, Bellwood et al. 2019, Williams & Graham 2019).

Ecosystem functioning on coral reefs

Ecosystem functioning (Jax 2005) refers to the range of natural processes and components that contribute to the production and exchange of energy and materials (Srivastava & Vellend 2005, Pacala & Kinzig 2013, Bellwood et al. 2019), sustain and fulfil life (Daily et al. 1997) and provide goods and services for human use (de Groot et al. 2002). Despite the diversity of interpretations in the literature, the overarching typology of ecosystem functioning considers the natural properties and processes that work to support an ecosystem and their direct or indirect anthropogenic benefits (de Groot et al. 2002, Jax 2005, Srivastava & Vellend 2005, Farnsworth et al. 2017). In the marine environment, ecosystem functioning depends on interactive physical (e.g. waves, currents, sediment, light), chemical (e.g. nutrient cycling, ocean pH, salinity) and ecological (e.g. primary production, herbivory, predation, calcification) processes. While we recognise that physical and chemical processes are essential components of coral reefs, a species' contribution to ecosystem functioning is inextricably linked to its ability to perform ecological processes (Figure 1). To identify species – or functional groups of species – that are disproportionately important to the maintenance of coral reef functioning, this review focussed on key ecological processes.

We examined species' contributions to a range of ecological process that scale up to support habitat (e.g. reef accretion) and production (e.g. fisheries) functioning (Figure 1). Together, these form the foundations of coral reefs through 1) habitat provisioning and the stocks of energy and material (e.g. calcification, bioerosion) and 2) the production and fluxes of energy and materials across ecosystem networks (e.g. trophic transfers, photosynthesis, nutrient uptake) (de Groot et al. 2002, Srivastava & Vellend 2005, Kennedy et al. 2013, Harborne et al. 2017, Bellwood et al. 2019). These effectively incorporate the construction (and destruction) of the biogenic reef structure – the fundamental framework of coral reefs (Wild et al. 2011) – and trophic pathways and interactions across the food web (Figure 1). Habitat and production functioning encapsulate the most important goods and services provided by coral reefs, scaling up to benefit coastal protection and fisheries production (Moberg & Folke 1999, Harborne et al. 2017). They are fundamental attributes of outstanding universal value (OUV) and contribute to the values and integrity of coral reefs, including for the World Heritage property of the GBR (GBRMPA 2014c).

Due to a growing number of local and global stressors, irreversible shifts in the ecological processes that maintain coral reefs are already measurable, including for those that support habitat

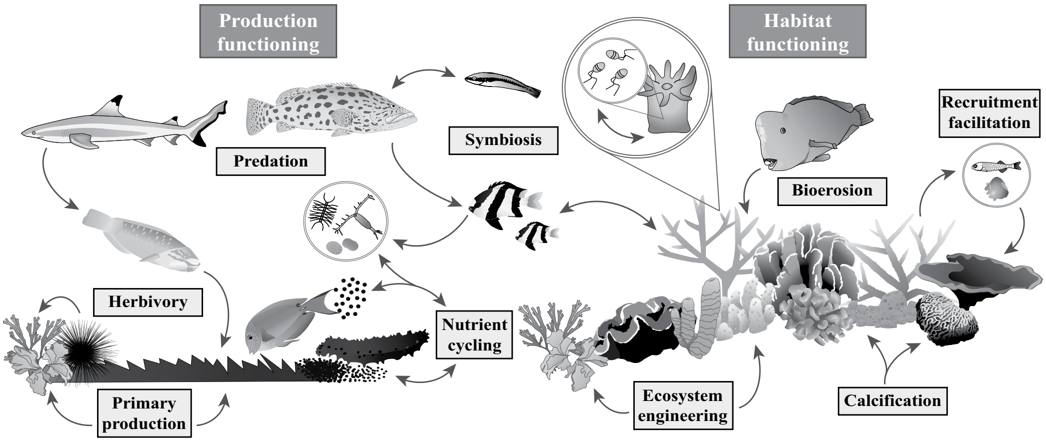

Figure 1 Simplistic representation of the nine key ecological processes considered here in support of habitat and production functioning on coral reefs.

and production functioning (De'ath et al. 2012, Cinner et al. 2016, 2018, Hughes et al. 2018b, Richardson et al. 2018, Rogers et al. 2018a). Some examples include changes to processes that support: 1) calcification and bioerosion rates, which impact reef community composition, reef accretion and the net carbonate budget (Silverman et al. 2012, 2014, De'ath et al. 2013, Dove et al. 2013, DeCarlo et al. 2015, Albright et al. 2016b, 2018, Perry & Harborne 2016, Manzello et al. 2017, Schönberg et al. 2017, Cyronak et al. 2018); 2) herbivory and algal growth that results in phase shifts away from coral towards algal-dominated reefs (Ceccarelli et al. 2006, Hughes et al. 2007b, Mumby 2009b, Burkepile & Hay 2010, Cheal et al. 2010, Hoey & Bellwood 2011, Bellwood et al. 2012b, Adam et al. 2015a); 3) impaired recruitment opportunity and success, which limits reef growth and persistence across generations (Doropoulos et al. 2012b, Doropoulos & Diaz-Pulido 2013, Hughes et al. 2019a) and 4) antagonistic population outbreaks of predatory species with impacts on live coral cover (Endean 1982, Brodie & Waterhouse 2012, De'ath et al. 2012, Baird et al. 2013, Pratchett et al. 2014, Hoey et al. 2016b). Such shifts in the coral reef archetype will continue to have serious repercussions on ecosystem resilience and recovery and in how we shape current and future management practises (Knowlton 2012, Uthicke et al. 2016, van de Leemput et al. 2016, Osborne et al. 2017, Stuart-Smith et al. 2018). With this in mind, we provide a framework to rationalise priority species and processes that work to support coral reefs at their highest levels of functioning in a changing environment.

Methods

Expert elicitation

Quantifying the importance of species to ecosystem functioning is challenging and complex, especially for high-diversity ecosystems like rainforests and coral reefs. A number of studies have addressed this at specific levels of taxonomy and functioning, including for lichen assemblages within soil ecosystems (Gotelli et al. 2011), avian traits regarding plant-frugivore interactions (Pigot et al. 2016) and the influence of coral reef fishes on live coral cover and socio-environmental services (Maire et al. 2018). Yet for coral reefs, functional ecology lacks a clear definition and empirical evidence on the assumed links between reef taxa and processes (Williams & Graham 2019). Further, knowledge of reef functioning is largely weighted towards certain taxonomic and functional groups (e.g. corals and fishes; Bellwood et al. 2004, 2017, 2019, Stuart-Smith et al. 2013, Bierwagen et al. 2018, McWilliam et al. 2018). Given the breadth of our analysis, we employed expert elicitation to facilitate a comparative assessment of the ecological roles of a diverse array of coral reef taxa – from microbes to top predators – and broad spectrum of ecosystem processes and functioning.

Expert elicitation can provide valuable insight and data to inform science and decision-making, particularly when there are significant limitations and inconsistencies in scientific knowledge (Morgan et al. 2001, Knol et al. 2010, O'Leary et al. 2011, Polasky et al. 2011, Runge et al. 2011, Martin et al. 2012, Ban et al. 2014b, Morgan 2014, Rogers et al. 2015). Experts were selected from a literature search and using background knowledge of coral reef ecologists currently involved in research in the focal region, the GBR, Australia. Using a snowball approach, experts were invited to participate in the project, ensuring a multidisciplinary assemblage with expertise across taxonomic groups, levels of ecosystem functioning and environmental stressors. A total of 18 experts were directly involved in project development, scientific workshops and/or the elicitation process. This size pool is within the lower ($n = 3$; Clemen & Winkler 1999) and upper ($n = 60$; de Franca Doria et al. 2009) ranges for the expert elicitation process (Ban et al. 2014b). Given the level of involvement and knowledge provided through the elicitation process, experts were included as co-authors.

Our expert elicitation process conformed to the Investigate, Discuss, Estimate, Aggregate (IDEA) protocol, which was designed to improve the accuracy of expert judgement (Burgman 2016, Hemming et al. 2018). In short, in a two-day workshop, we convened our panel of GBR experts, where they were first asked to *Investigate* knowledge and information on key coral reef taxa across a range of processes, functioning and threats. Attempts at compiling and formulating this information into questions and evidence were then open to feedback. Experts were encouraged to *Discuss* interpretations and results to promote critical thinking and reduce ambiguity. These two stages provided the framework of further project and survey development before experts completed an official independent *Estimate* scoring stage. Expert responses and scores were then *Aggregated* to produce mean data across responses. Specific details on project and survey development, and data handling and aggregation, can be found in the following sections.

Project and survey development

In the two-day workshop with our expert panel, we identified 70 functionally and taxonomically distinct groups of marine species common on the GBR (Figure 2). Functional groups remained broadly defined but were occasionally refined to individual species with explicit and well-documented roles (e.g. CoTS). Subsequent in-depth examination was intended for high-ranking groups at later stages of the project through targeted literature searches. Some taxa were excluded (e.g. marine reptiles, mammals, seabirds), as these groups are often rare on the GBR and/or already intensively addressed and managed (see: Stoeckl et al. 2010b, Birtles et al. 2014, GBRMPA 2014b,c, Richards & Day 2018, Risch et al. 2019). Many species within these taxa are of OUV and are critical to the way the World Heritage Convention is implemented on the GBR (GBRMPA 2014c), with key social and economic value, particularly regarding tourism (Stoeckl et al. 2010a,b, Marshall et al. 2018, Curnock et al. 2019). The exclusion of these species does not devalue their contributions to a functioning ecosystem (e.g. Graham et al. 2018, Savage 2019, Tavares et al. 2019) or their necessity to be considered in context of social, cultural and economic values for holistic management (GBRMPA 2014a,c).

As the world's largest coral reef ecosystem, the GBR is an amalgamation of bioregions with their own, often unique, dynamics (McCook et al. 2010, Day 2016) and governance (Day 2002, Brodie & Waterhouse 2012, Morrison 2017). Due to the sheer size and diversity of the GBR, our expert panel chose to focus attention on the functioning of classical reef slope and reef crest habitats, as these are typically the most diverse and coral-rich ecosystems that support the greatest range of services (Mumby et al. 2008, Harborne et al. 2017). This refined approach acknowledges the exclusion of other important and interconnected biomes of coral reefs (e.g. mangroves, seagrass meadows, interreefal areas) (GBRMPA 2004, 2014b,c, van de Koppel et al. 2015, Sievers et al. 2019), including deep (or mesophotic) reefs (Bridge et al. 2012, Harris et al. 2013, Turner et al. 2017), but was employed to ensure a targeted research design to inform the holistic management of GBR species, values and processes. There is the opportunity to build on the current framework of biological functioning in future work to include other important coral reef biomes and give greater consideration to social, cultural and economic values.

A methodology to assess functionally important species was developed by our scientific panel during the workshop (Figure 3; Table 1) in a series of stages framed by the IDEA protocol for expert elicitation (as previously) (Burgman 2016, Hemming et al. 2018). Outcomes were used to construct annotated online surveys that operated under three main criteria:

1. Functional importance: a process-based assessment of species' contributions to ecosystem processes and functioning.
   Question: Who contributes most to ecosystem functioning on the GBR?
2. Vulnerability: an assessment of the sensitivity and exposure of species to current and near-future stressors and their likely recoverability.
   Question: What species are most vulnerable on the GBR, and do they require protection?
3. Manageability: an assessment of the probable effectiveness and feasibility of a management intervention in the context of biological functioning.
   Question: Is management feasible for important species?

Figure 2 Taxonomic and functional groups partitioned in this assessment with examples in parentheses. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and Hutson et al. (2018). Note: 1) dinoflagellate Zooxanthellae are not considered part of the 'phytoplankton'; 2) it is understood that foraminifera are not corals; 3) zooplankton includes groups outside of the Crustacea (e.g. larvaceans, chaetognaths, salps).

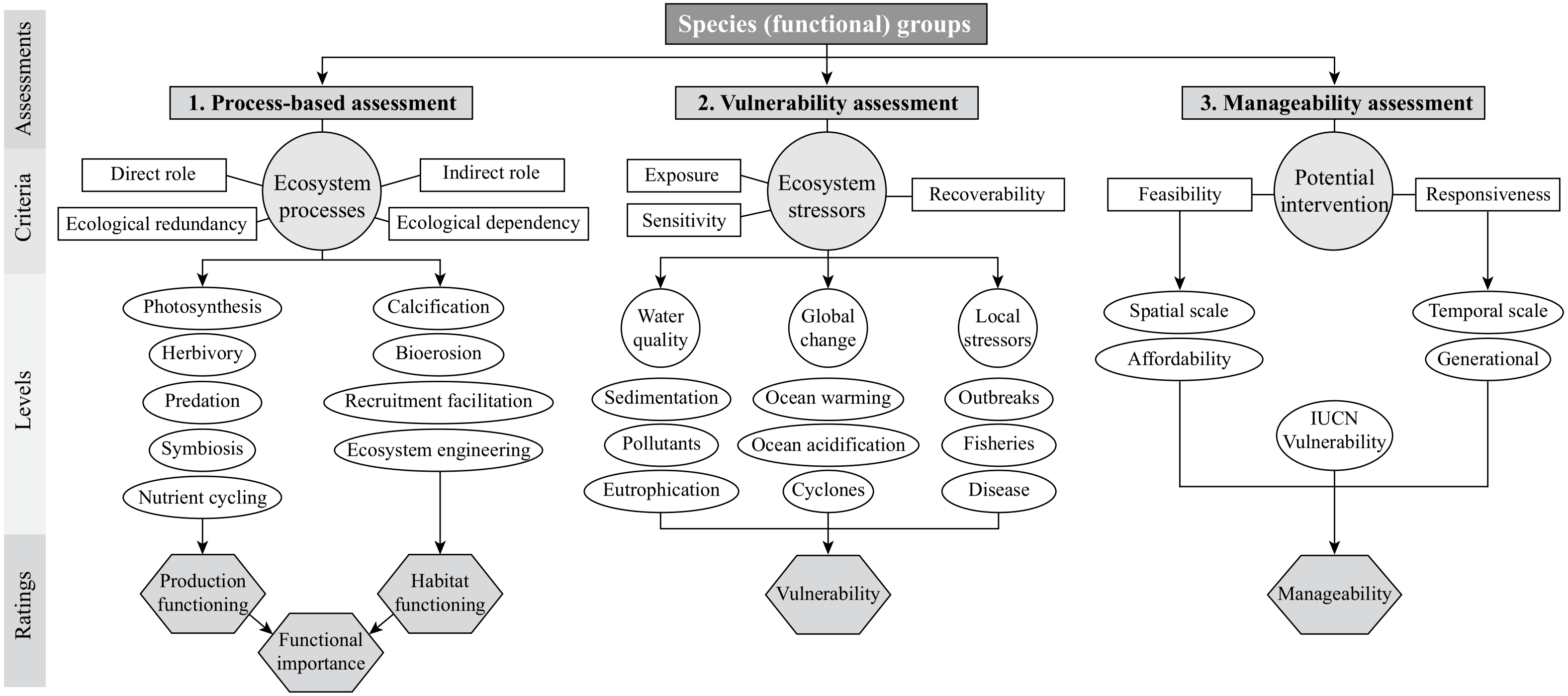

Figure 3 Framework outlining the assessment criteria employed to identify and rank priority species in support of ecosystem functioning based on their 1) functional importance (process-based assessment), 2) vulnerability and 3) manageability.

Table 1 Criteria used to score 70 functional groups on their (A) functional importance, (B) vulnerability and (C) manageability on the GBR.

Dynamic	Category	Score	Notes
A. Functional importance			
Direct contribution	None	0	No direct role performing the process
	Low	1	Directly contributes to the process but is not a key player
	High	2	Ecologically significant contribution to the process
Indirect facilitator/mediator	None	0	No real indirect effect on others performing the process
	Low	1	Some level of impact on the process; competition, mutualism
	High	2	Specific impact; key predator, top-down/bottom-up control
Redundancy	None	0	Critical and specific performing the process or in mediating it
	Low	1	Some level of replaceability, similar species performing the process
	High	2	Replaceable in its role performing the process
Dependency	None	0	Self-sufficient in performing the process
	Low	1	Some level of dependence to perform the process
	High	2	Reliant on other organisms to complete the process
Certainty	Low	0.25	Little empirical work and expert knowledge
	Medium	0.50	Some empirical work and expert experience
	High	0.75	Extensive work and/or experience
B. Vulnerability			
Sensitivity (S)	Sensitive	−2	Highly sensitive to the stressor
	Slight impact	−1	Partial negative impacts
	No impact	0	Not affected
	Slight gain	1	Partial benefit from stressor
	Beneficial	2	Stressor is highly beneficial
Exposure (E)	None	0	Not exposed to the stressor
	Low	1	Low exposure, low likelihood of exposure
	High	2	Highly exposed, highly likely to be exposed
Potential Recoverability (PR)	Low	0.25	Unlikely to recover before next event
	Medium	0.50	Some level of recoverability
	High	0.75	Highly likely to recover before next event
Certainty	Low	0.25	Little empirical work and expert knowledge
	Medium	0.50	Some empirical work and expert experience
	High	0.75	Extensive work and/or experience
C. Manageability			
Responsiveness	None	0	Species/populations unlikely to change following intervention
	Low	1	Some response predicted through action
	High	2	Action is likely to have a strong effect on populations
Feasibility	None	0	Broad scale, not affordable, inefficient, impossible
	Low	1	Plausible but likely restricted to some locations/populations
	High	2	Very possible, with good scope-cost benefits
Information	None	0	Little existing work, hard to monitor
	Low	1	Some work exists, monitoring possible (but patchy)
	High	2	Extensive work exists, easy to monitor

Surveys to address these criteria were developed online using the Surveymonkey platform and were open for several weeks (July–August 2018). Surveys were targeted at our expert panel, but responses remained anonymous. A low-range scoring system (e.g. none/low/high) was employed to reduce ambiguity in responses (see Table 1), as qualitative words and broad scoring ranges are prone to subjectivity and uncertainty (Morgan et al. 2001, Morgan 2014). Space for comments and feedback was provided throughout the surveys, which is outlined as a critical elicitation process to ensure expert knowledge is accurately captured and interpreted (Martin et al. 2012, Hemming et al. 2018). A total of 16 survey responses were completed across our taxonomic and functional groups, with equal-weighted averages taken across expert responses. Group averages are simple but can be effective in producing estimates of elicitation (Martin et al. 2012). Scores were checked and calibrated against the literature and empirical data (where possible) to reduce subjectivity and bias. This proved particularly effective during the *Discuss* stage of the IDEA framework (Hemming et al. 2018). Scoring criteria are explicitly outlined for each assessment (Figure 3; Table 1).

Extensive literature searches were conducted by the primary author between March 2018 and June 2019 using online databases, including Web of Science and Google Scholar. Experts involved in the elicitation process had the opportunity to recommend relevant literature through the IDEA framework, but the review process remained largely independent of the expert panel. Peer-reviewed research and review articles pertaining to the 70 species groups and various levels of ecosystem processes, functioning and/or environmental stressors, as addressed in this review, were of focus. As a particularly data-rich system, literature explicitly related to the GBR was targeted, although we included relevant information for coral reefs more generally. Particular attention was given to species groups that scored highly at specific levels of ecosystem processes, functioning and/or stressors to benchmark results against peer-reviewed literature. This process aided in the interpretation of expert results and response accuracy (Hemming et al. 2018). We outline discrepancies between expert responses and the literature when evident, particularly for groups that scored highly despite receiving comparatively marginal representation in the literature. Independent literature searches were also conducted for each of the five case studies integrated in this review.

Scoring criteria

Functional importance: A process-based assessment

Contributions of organisms to ecosystem processes (e.g. calcification, bioerosion, herbivory, predation; Figure 1) drive and support ecosystem functioning (e.g. reef accretion, habitat complexity, energy/trophic transfers) and services (e.g. coastal protection, fisheries, tourism). The first stage of our surveys elicited experts to score the contribution of 70 taxonomic and functional groups of coral reef species (Figure 2) to nine ecosystem processes considered critical to ecosystem functioning (Figures 1 and 3). These processes were selected due to their broad representation in the literature and current consideration in management reports for the GBR (GBRMPA 2014b). These nine processes scale up to support habitat and production functioning, which are fundamental to the future of coral reefs in terms of reef construction, trophic pathways and ecosystem services (de Groot et al. 2002, Harborne et al. 2017). All ecosystem processes were considered equally important to ensure that all were represented at their highest levels; that is, no process was weighted as more important to a functioning ecosystem.

Species groups were scored based on their direct and indirect contributions to each process (Figure 3; Table 1A). This was intended to capture both the immediate contribution of an individual to a process (e.g. hard corals to calcification) and, equally important, their indirect facilitation and/or mediation of the process (e.g. algae to herbivory), as indirect effects are fundamental to the complexity of ecosystem functioning and to conservation outcomes (Wootton 1994, 2002, Dulvy et al. 2004, Jordán et al. 2008, Bergstrom et al. 2009, Ritchie & Johnson 2009). Species groups were also scored based on their ecological redundancy and dependency on a per-process basis (Figure 3; Table 1A), as species interactions and functional diversity can highlight critically important taxa (Petchey & Gaston 2002, Mouillot et al. 2013, 2014). Expert scores were compiled and average scores calculated for each functional group–ecosystem process combination. Finally, experts were elicited to rate the level of confidence (i.e. certainty; Table 1A) in their scores for each functional group. These scores were used *post hoc* to weight final scores for management recommendations.

Scores for direct (D) and indirect (I) contributions were combined as a measure of the magnitude (M) of the role of each functional group to each ecosystem process, using the equation:

$$M = (D + I)^2$$

This equation worked under the assumption that direct and indirect effects were equally important to ecosystem processes and functioning. Scores were squared to elevate organisms that scored highly for any given process and to amplify even the slightest differences among expert responses. Scores for magnitude, redundancy and dependency were then categorised and ranked for each species–process combination (Table 2). For magnitude, the top and bottom 33rd percentile of scores were classed as 'high' and 'low', respectively, with the remaining scores classed as 'intermediate' (Table 2). Thus, rankings were relative to the range of scores within each process. We worked under the assumption that magnitude was the most important score for determining the importance of species groups; that is, how much they contribute (directly or indirectly) to the process outweighed their ecological redundancy and/or dependency (Table 2). Examples of 'high' magnitude scores existed in algal turfs to primary production, branching and tabular corals to calcification and piscivorous fishes to predation. Examples of 'low' magnitude scores were worms to primary production and piscivorous fishes to calcification.

Redundancy and dependency were used as mediators of scores for magnitude. Species with 'low' (or no) ecological redundancy (average scores ≤1) were considered more important for targeted management (Table 2), as this suggests specialisation and irreplaceability in their roles (Hooper et al. 2005, Jain et al. 2014, McWilliam et al. 2018). Species with 'high' redundancy (average scores >1) were deemed replaceable and were down-weighted (Table 2). For example, triton snails had low redundancy for the predation process, as they are essential predators of CoTS, while other predatory molluscs were considered to have higher redundancy in this process. Species groups with 'low' dependency (average scores ≤1) were considered more important than those with 'high' dependency (Table 2), under the assumption that they can effectively perform their roles exclusive of others and are thus better candidates for targeted management. Conversely, dependent species were down-weighted (Table 2), as their ecological performance requires inclusion of other species with implications for management efficacy.

Table 2 Ranking scheme for functional groups based on their magnitude, redundancy and dependency in the context of nine key ecosystem processes on the GBR

Rank	Magnitude	Redundancy	Dependency
1	H	L	L
2	H	L	H
3	H	H	L
4	H	H	H
5	M	L	L
6	M	L	H
7	M	H	L
8	M	H	H
9	L	L	L
10	L	L	H
11	L	H	L
12	L	H	H

Abbreviations: H, high; M, intermediate; L, low.

Ranks were determined on a per-process basis. Within this scoring scheme, a functional group with the highest magnitude of contribution to an ecosystem process but the lowest ecological redundancy and dependency would rank the highest: an 'essential provider'. Conversely, a low-contributing group with high redundancy and dependency would rank the lowest; a 'leech'. Total functional importance (FI) was then calculated across the $i = 9$ process rankings using a sum of squares equation:

$$FI = \sum_{i=1}^{9} (13 - x)^2$$

where x is the rank score for each process. This ensured that highly ranked groups (i.e. $x = 1$) received higher final scores, and that those ranked highly for just one process were recognised. This also ensured that no species scored a complete zero (i.e. when $x = 12$). Final values for FI were square root transformed to normalise data. FI was calculated in the same manner for habitat and production functioning separately. Scores for expert scientific certainty were examined *post hoc*. Final values for FI with high certainty were considered top priority, while scores that were largely uncertain were up-weighted under precautionary principles.

Assessing the vulnerability of coral reef species

Ecosystems are considered healthy if they are able to maintain (or recover) structure and functioning in the face of external pressures (Costanza & Mageau 1999). To understand potential threats to functioning on the GBR, pertinent current and near-future (2050 outlook; [DEE 2015, GBRMPA 2018b]) stressors were workshopped (Figure 3). Parallel to scoring functional importance, experts were elicited to score the 70 functional groups (Figure 2) based on their vulnerability to nine critical stressors (Figure 3) in line with previous projects, elicitation processes and reviews (Ban et al. 2014a,b, Uthicke et al. 2016, Harborne et al. 2017). The Intergovernmental Panel on Climate Change (IPCC) Vulnerability Framework (IPCC 2007) formed the basis of this assessment, which uses the sensitivity and exposure of an individual, as well as its potential to recover, to calculate its total vulnerability (Figure 3; Table 1B).

Experts scored species groups based on their known (and anticipated) sensitivity, exposure and recoverability to each of the nine pertinent stressors (Figure 3). Sensitivity (S) was scored across a range of positive to negative scores (Table 1B), as some species may benefit from a particular stressor (e.g. ocean warming on algal growth, herbivore abundance due to overfishing of predators), while others may be severely impacted (e.g. calcification due to ocean change, sea cucumbers due to overfishing). However, since our focus was to identify vulnerable species for management, scores that suggested positive effects from a stressor ($S > 0$) were counted to have no effect (i.e. not sensitive; $S = 0$). Exposure (E) was considered generally for typical reef habitats (e.g. reef crest, reef slope) but was assessed differently for inner reefs and offshore regions on the GBR, as some stressors, such as those related to water quality, are often more significant on inshore reefs proximal to terrestrial influence (Devlin & Brodie 2005, Wooldridge et al. 2006, Brodie & Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, MacNeil et al. 2019, Mellin et al. 2019).

Potential impact (PI) was calculated from average expert scores for each stressor–functional group combination, using the equation:

$$PI = (S \times E)^2$$

This calculation assumes that sensitive groups that are not exposed to a stressor ($E = 0$) are not vulnerable, as for groups that are exposed but not at all sensitive ($S = 0$). PI was calculated for each of $i = 9$ stressors, and total vulnerability (V) was then calculated across all stressor values, using the equation:

$$V = \frac{\sqrt{\sum_{i=1}^{9} PI}}{PR}$$

This framework ensured that species with high potential recovery (PR) were down-weighted under the assumption that management would be less necessary for species likely to recover. Conversely, V would be greater for species with low PR under the assumption that they would require greater management attention to improve recovery chances. Experts also scored the certainty of their scores for each functional group here (Table 1B), which was used *post hoc* to address the validity of vulnerability scores. Final rankings suggesting high vulnerability with high certainty were considered the most critical to address. Vulnerable species groups with a low-rated level of certainty could also be examined under precautionary principles so that data-deficient groups were not overlooked.

Final scores for V and FI were combined to identify key species where both factors were high. The relative impact (Imp) of our nine stressors was also calculated by multiplying V and FI for each species-process-stressor combination:

$$Imp_{\text{species}} = V_{\text{stressor}} \times FI_{\text{process}}$$

From this template, we could determine the proportional impact that each stressor was considered to have on each functional group at their highest level of functioning. This was also calculated for each ecosystem process-stressor combination. The proportional impact of a given stressor would be weighted higher by taxa scored to be more functionally important. Conversely, the proportional impact of a stressor would be less driven by species with marginal importance. This information could be used to identify combinations of species, stressor and/or processes that may be most critical to address and protect.

Assessing the manageability of coral reef species

Each functional group was assessed in context of its relative manageability on the GBR. This assessment was in context of the biological roles of each species group and was not an assessment of other attributes such as social, cultural and economic values. These additional attributes would be important to consider if building out from the current framework. Experts were elicited to score groups based on their likely 1) responsiveness to management intervention, 2) feasibility of implementation (affordability, geographic scale, etc.) (Figure 3) and 3) availability and attainability of information (i.e. monitorability) (Table 1C). Conservation status (e.g. IUCN Red List species) was also considered *post hoc* to address 'at risk' populations (Richards & Day 2018) (Figure 3).

Manageability (Mg) was calculated using average expert scores for responsiveness (R) and feasibility (F), using the equation:

$$Mg = (R + F)^2$$

Scores for information/monitorability were not included in this calculation under the assumption that functionally important and vulnerable species should be a priority regardless of their ability to be monitored. Thus, the predicted ability for species to respond to management (R) and feasibility (F) of implementation formed the foundations of our Mg calculation (Figure 3). Groups were categorised as a high priority for management if they were in the top 66th percentile of scores for Mg, while those in the bottom 33rd percentile were deemed lower management priorities. Top-scoring organisms for functional importance, vulnerability and management priority were considered top candidates overall. High scoring groups that were considered lower priority for management would be highlighted as groups that may require innovative approaches.

Incorporating uncertainty

Experts were elicited to score the certainty of their scores for functional importance and vulnerability. Certainty was scored categorically as low (0.25), medium (0.50) or high (0.75) (Table 1A, B). These scores were used *post hoc* to support our recommendations, particularly when scientific certainty was comparatively high or low. High certainty solidified the merit of our recommendations, particularly for highly ranking functional groups. Under precautionary principles, scores that were uncertain were highlighted so that functional groups that 'slipped through the cracks' in our ranking system due to data deficiencies were not missed. Thus, low-ranked functional groups had the potential to be elevated in their importance and/or vulnerability if certainty was low.

Knowledge gaps in ecosystem functioning on the Great Barrier Reef

Formal expert elicitation is a structured and transparent methodology that effectively addresses uncertainties in scientific knowledge (Knol et al. 2010, Polasky et al. 2011). In addition to the scoring criteria previously, critical knowledge gaps in our understanding of reef functioning were made evident by our expert panel. Consensus decisions on the most logical, feasible and important knowledge gap themes were made, which were developed into five subprojects that reflect our multidisciplinary expert assemblage across taxonomic groups, levels of ecosystem functioning and environmental stressors on the GBR. Within the lifetime of this project, teams of researchers addressed these knowledge gaps, which are presented here as case studies that highlight pivotal species (and groups of species) at specific levels of ecosystem functioning to directly inform this project and future research;

1. Invertivory on the GBR: a poorly understood link in the trophic chain.
2. Addressing the carbonate budget for the GBR.
3. Microbial communities as indicators of water quality on the GBR.
4. Functional impacts of recreational spearfishing on the GBR.
5. Juvenile CoTS 'in waiting': the missing link in population and connectivity models.

Results and discussion

Species of particular functional importance on the GBR are outlined subsequently using an ecosystem process-based assessment for 70 distinct groups (Figure 2). Rankings for functional importance are provided at various levels of ecosystem functioning, 1) for each ecosystem process, 2) for habitat and production functioning and 3) combined overall (Figure 3). Additional rankings are outlined for species groups based on their perceived vulnerability to nine key environmental stressors on the GBR and for their relative manageability (Figure 3). Final scores are presented across these three components and weighted to scientific certainty. Note that all levels of ecosystem processes were considered equally important to a functioning reef to reflect all species and processes at their highest level of functioning.

Process-based assessment

Top-ranked species groups within each process are outlined in Table 3. Scores are discussed, interpreted and/or supported in the following sections through case-specific reviews of the literature available for coral reefs, primarily the GBR, at various levels of ecosystem processes and

Table 3 Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
Microbes	Phototrophic	4	7	7	4	4	7	4	4	7
	Host-associated	2	7	7	4	2	2	2	2	4
	Chemoautotrophic	4	7	7	4	4	6	4	4	4
	Heterotrophic	4	7	7	4	4	8	4	4	4
Algae	Phytoplankton	2	7	7	2	7	7	5	11	5
	Algal turfs	2	3	7	2	7	7	2	8	2
	Leathery	8	3	7	8	7	5	11	4	11
	Foliose	4	3	7	8	7	5	11	4	2
	Calcareous	6	3	7	6	7	2	11	8	5
	CCA	2	5	7	6	7	2	11	4	2
Sponges	Heterotrophic	7	7	7	6	4	7	7	3	3
	Phototrophic	3	7	7	6	4	7	7	3	3
	Boring	3	7	7	10	4	4	2	6	4
	Cryptic	7	7	7	6	4	3	3	5	3
Coral	Tabular	4	7	7	2	2	2	7	2	2
	Staghorn	4	7	7	4	4	4	7	2	2
	Branching (other)	4	7	7	8	4	4	11	4	2
	Massive	4	7	7	8	2	4	11	2	4
	Encrusting	4	11	7	8	4	4	7	4	4
	Free-living	8	11	7	8	4	8	11	8	8
	Soft corals	4	7	7	4	2	7	11	4	8
	Foraminifera	8	11	11	8	4	4	7	12	12
Worms	Nematodes	11	11	7	7	8	7	3	7	11
	Nemertea	11	11	7	7	8	7	3	7	11
	Polychaetes	11	11	3	7	8	7	3	7	7

(*Continued*)

Table 3 (*Continued*) Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
	Spirobranchus	11	11	8	11	4	7	3	7	5
Crustaceans	Decapods (H)	7	3	7	7	8	7	7	7	7
	Decapods (P)	11	11	3	7	7	7	7	7	11
	Coral-associated	7	11	4	6	2	2	3	8	7
	Barnacles	11	11	7	11	8	7	7	7	7
	Stomatopods	11	11	3	7	8	7	3	7	7
	Cleaner shrimp	7	11	8	10	6	5	11	7	5
	Infauna	7	7	3	7	8	7	7	7	7
	Zooplankton	7	3	3	2	7	7	11	11	11
	Parasitic	11	11	7	7	8	7	11	11	11
Molluscs	Gastropods (H)	7	3	7	7	7	3	7	7	7
	Gastropods (P)	11	7	3	7	7	3	7	7	11
	Triton snails	7	7	1	7	5	3	7	5	11
	Drupella	7	11	7	7	7	3	7	7	7
	Tridacnidae	7	7	7	7	8	3	7	7	3
	Bivalves	7	7	7	8	7	3	7	7	3
	Chitons	7	7	7	7	7	3	3	7	7
	Cephalopods	11	7	1	7	8	7	7	7	11
Echinoderms	Seastars (H)	7	3	7	7	7	7	7	7	11
	Seastars (P)	11	11	7	7	7	7	7	7	7
	CoTS	7	3	3	7	7	3	3	7	7
	Sea cucumbers (DF)	7	7	7	5	8	5	7	7	11
	Sea cucumbers (SF)	7	11	7	11	7	11	7	11	11
	Sea urchins (regular)	7	3	7	7	7	3	3	7	7
	Sea urchins (irregular)	7	7	7	11	7	7	7	7	11
	Brittle stars	7	7	7	7	7	7	7	7	11

(*Continued*)

Table 3 (*Continued*) Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
	Feather stars	7	11	11	11	7	7	7	7	11
Fishes	Cryptobenthic	7	7	3	2	8	11	11	7	7
	Farmers	7	2	9	8	7	5	9	3	2
	Scrapers (scarids)	7	4	9	4	11	5	3	3	1
	Browsers (nasos)	7	4	9	8	11	5	11	7	3
	Browsers (siganids)	7	4	9	8	11	5	11	7	3
	Browsers (other)	7	4	9	8	11	5	11	7	3
	Bolbometopon	7	2	7	6	11	5	3	1	3
	Excavators (other)	7	2	5	8	11	5	3	3	3
	Detritivores	7	2	9	1	11	7	11	7	5
	Planktivores	11	9	7	7	11	11	11	11	5
	Corallivores	11	9	7	11	11	7	11	7	9
	Invertivores (labrids)	7	11	4	7	11	11	7	7	9
	Invertivores (other)	7	7	7	7	11	11	5	7	11
	Invertivores (lutjanids)	7	5	7	11	11	11	5	7	9
	Eels	11	6	5	5	11	11	11	7	7
	Piscivores (residents)	11	8	4	7	11	11	11	7	7
	Piscivores (transients)	11	7	3	7	11	11	11	7	9
	Cleaner wrasse	7	5	5	10	2	5	9	6	5

Note: Shading denotes highest scores; 1st = dark, 2nd = mid, 3rd = light.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

functioning. Results met expectations in many cases, but due to our assessment of both direct and indirect effects, and ecological redundancy and dependency, we highlight novel and sometimes unexpected players. This interpretation was supported through the evaluation of peer-reviewed literature, outlined for groups that received high scores despite comparatively marginal attention in the literature.

Primary production

Algal turfs, phytoplankton, CCA and host-associated phototrophic microbes were the top-ranked groups for primary production (Table 3). Approximately 70% of the carbon fixed by primary producers on the GBR originates from phytoplankton (Furnas & Mitchell 1987, 1988, McKinnon et al. 2007). Typical of tropical ecosystems, phytoplankton communities on the GBR are diverse, including a range of diatoms, dinoflagellates, cyanobacteria and picophytoplankton, which form the baseline of pelagic food webs (Revelante & Gilmartin 1982, Revelante et al. 1982, McKinnon et al. 2007, Davies et al. 2016). Microbial metabolic pathways are involved with 59%–100% of the net primary production on coral reefs, including within the phytoplankton (Arias-Gonzalez et al. 1997, Silveira et al. 2017). This sweeping contribution to primary production is captured here for all microbial groups ($FI \geq 4$). Host-associated phototrophic groups (e.g. Symbiodiniaceae) ranked highest, owing to their niche role facilitating productivity and organic carbon cycling in corals (and other hosts) (Silveira et al. 2017) and supporting the physiology, ecology and evolution of coral reefs (LaJeunesse et al. 2018).

Turf algae are critical primary producers in oligotrophic coral reef waters, exhibiting high mass-specific rates of productivity (Adey & Goertemiller 1987), though we acknowledge the high diversity and ubiquitous nature of this group. Turf growth and productivity can be enhanced by high wave energy (Roff et al. 2019) and nutrient enrichment with links to water quality (Vermeij et al. 2010, Gordon et al. 2016a), particularly on inshore reefs of the GBR (Lam et al. 2018). Turf algae are rapid colonisers of bare substrates on coral reefs, particularly in degraded systems (Roth et al. 2018). Although they have a relatively low biomass per unit area and typically only reach heights of ~1 cm, algal turfs have a rapid turnover and can shape coral reef communities from cryptic species diversity (Carpenter 1985, 1986, Klumpp et al. 1988, Klumpp & McKinnon 1989, Klumpp & Pulfrich 1989, Enochs 2012, Enochs & Manzello 2012) to herbivore assemblages on reef flats (Bellwood et al. 2018). The contribution of algal turfs to net primary production on the GBR is 100–500 $g.C.m^{-2}.yr^{-1}$ for both inshore and offshore habitats (Klumpp & McKinnon 1992, Russ 2003), lower than estimates for fleshy macroalgae (e.g. *Sargassum*; 1000 $g.C.m^{-2}.yr^{-1}$) (Schaffelke & Klumpp 1997). Turfs often persist as constant grazing by herbivores prevents overgrowth by larger, fleshy seaweeds (e.g. *Sargassum*) (Diaz-Pulido & McCook 2008). However, once established, species such as *Sargassum* are highly resilient to physical and biological removal with implications for altered trophodynamics and production functioning on degraded reefs (Loffler & Hoey 2018). The contradiction in ranks between turf and macroalgal groups here may reflect the relatively low biomass of fleshy macroalgae across much of the offshore area of the GBR.

Primary production by CCA is similar to that by turf algae (Chisholm 2003, Diaz-Pulido & McCook 2008, Lewis et al. 2017). Despite lower direct contributions to primary production, algal turfs and CCA ranked higher than fleshy macroalgae due to a suggested lower redundancy with expansive assemblages at scales from centimetres to kilometres (Harris et al. 2015). Turfs and CCA dominate the epilithic algal matrix (EAM) across the GBR, with direct links to total benthic and grazer (i.e. fisheries) productivity (Klumpp & McKinnon 1992, Russ 2003, Littler & Littler 2007, Arnold et al. 2010), and recruitment dynamics (Doropoulos et al. 2017a,b).

Interestingly, no group scored the top ranking ($FI = 1$; Table 3), attributing to the broad ecological redundancy in primary production across and within functional groups, and/or dependency of some species on others to complete this role (i.e. host-associated phototrophic microbes). Corals are active primary producers through their association with their microbial partners (Zooxanthellae;

Symbiodiniaceae, and endolithic algae) but scored lower here (FI ≤ 4), as they have high levels of dependency and generally lower rates of production than most algae. Experts noted that the contribution of corals to photosynthesis was considered largely redundant, as it would be readily replaced by algal productivity.

Herbivory

Farming (e.g. damselfishes) and excavating (e.g. parrotfishes) fishes were the highest-rated groups for herbivory (FI = 2; Table 3). Farming damselfishes are well recognised for their role regulating the growth and composition of algal assemblages within their territories (Ceccarelli et al. 2001, 2011, Hata & Kato 2004, Hoey & Bellwood 2010c), where they shape benthic coral reef communities (Ceccarelli et al. 2001, Ceccarelli 2007, Casey et al. 2015a) and reef fish behaviour and assemblages (Eurich et al. 2018). Densities of herbivorous fishes and intensity of herbivory can be influenced by proximity to reef structure. Distinct grazing halos around reef structures are a physical indication of top-down behavioural interactions between herbivores and predators (Sweatman & Robertson 1994, Madin et al. 2011, Downie et al. 2013, Ollivier et al. 2018), particularly for species that are closely associated with reef refugia, including farming damselfishes.

Nominally herbivorous parrotfishes are typically attracted to the endolithic algal growth on dead coral surfaces, and their scraping and excavating feeding behaviour promotes reef bioerosion (Clements et al. 2017). The green humphead parrotfish, *Bolbometopon muricatum*, is one of the largest roaming herbivores on coral reefs. Its high score for herbivory here is likely a reflection of its functionally explicit contribution to reef bioerosion through its feeding ecology. Despite being a nominal herbivore, each individual ingests around 5 tonnes of structural carbonate per year (around half is living coral) (Bonaldo et al. 2014). Replacement of the functional roles of *B. muricatum* by other species is unlikely (i.e. low ecological redundancy), as observed on some coral reefs where this species has experienced extreme population declines from overfishing (Myers 1999, Donaldson & Dulvy 2004).

All nominally herbivorous reef fishes scored highly for their magnitude of contribution to the herbivory process (FI ≥ 4). Certain species of scrapers (e.g. parrotfishes) and browsers (e.g. rabbitfishes, unicornfishes) are considered particularly important herbivores at various scales across the GBR, with several key species highlighted in the literature: *Naso lituratus*, *N. unicornis*, *Siganus canaliculatus*, *S. doliatus*, *Calotomus carolinus*, *Kyphosus vaigiensis* (Hoey & Bellwood 2009, 2010a, Hoey et al. 2013, Loffler et al. 2015a,b, Streit et al. 2015). Their slightly lower-ranked importance for herbivory here (Table 3) may reflect an arguably broader level of ecological redundancy in the scrapers and browsers compared to excavators on the GBR. However, dietary groupings of nominal herbivores do not necessarily reflect taxonomy (Choat et al. 2002), and key herbivorous species appear to have specialised traits in their feeding ecology that can have specific and dynamic influences on algal communities at local and regional scales (Bellwood et al. 2006a, Hoey & Bellwood 2009, Wismer et al. 2009, Johansson et al. 2013, Loffler et al. 2015a, Streit et al. 2015, Loffler & Hoey 2018). Caution must be taken when assuming functional redundancy among herbivorous fishes, particularly when generalising within the common nominal feeding modes (Bejarano et al. 2017).

Interestingly, detritivorous fishes, including blennies and surgeonfishes, ranked among the highest for herbivory despite having a lower magnitude of contribution (direct and indirect) than nominally herbivorous groups (Table 3). As scored by experts, this may be an artefact of the low functional redundancy of detritivores, which are outlined in the literature as fundamental components of nutrient pathways and the transfer of energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014). Regardless, this group represents ~40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). The surgeonfish *Ctenochaetus striatus* was highlighted by experts as particularly important. This is supported in the literature, which describes the active role of *C. striatus* in removing sediment and detritus from the EAM, indirectly facilitating herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015). Detritivores can be key nuclear species that affect the behaviour and distribution of other species and provide high contributions to the export of nutrients across reefs from sand flats to hard reef structure (Lukoschek & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & Mumby 2012). Interestingly, detritivores and other functional groups (including herbivores) can supplement their diet with a range of other food sources (e.g. invertebrates, microbes, diatoms), which have a higher protein, fatty acid and/or total energy content than their primary food source (Montgomery & Galzin 1993, Choat et al. 2002, 2004, Clements et al. 2009, 2017, Hernaman et al. 2009, Kramer et al. 2013). Notably, diet partitioning and selectivity are currently underestimated for many nominal detritovores and herbivores (Choat & Clements 1998, Clements et al. 2017).

Most benthic algal groups scored highly for herbivory (FI = 3) due to their role as food for herbivores, demonstrating the importance of assessing indirect effects in ecosystem functioning. This was not captured in expert responses for phytoplankton, which are ubiquitously important for grazers in the plankton, including early life stages of most marine invertebrates and fishes (Hamner et al. 1988, Furnas et al. 2005, McKinnon et al. 2005, 2015). Zooplankton, and a range of other invertebrates (sea urchins, decapods, gastropods, seastars), scored highly for herbivory (FI = 3; Table 3). Pelagic grazers, such as copepods, larvaceans and salps, provide the fundamental links in production and energy flow to higher order consumers. Mesozooplankton (the medium-sized zooplankton) can graze ~40% of the production by phytoplankton in oligotrophic regions (Calbet 2001), including essentially all production in certain size classes, yet zooplankton may still be food limited in the oligotrophic waters of the GBR (McKinnon & Thorrold 1993, McKinnon et al. 2005, Skerratt et al. 2019).

Many micro- and macro-invertebrates occupy specific functional space, but since they typically have a lower magnitude of herbivory compared to reef fishes, their roles often go unappreciated (Brawley & Adey 1981, Klumpp & Pulfrich 1989, Altman-Kurosaki et al. 2018). Sea urchins are top herbivores on some coral reefs, usually after populations of herbivorous fishes and/or urchin predators are depleted through fishing (Ogden & Lobel 1978, Carpenter 1986, McClanahan 1988). Echinoids are often considered keystone species, with a range of contributions to reef ecosystem functioning (Birkeland 1989). Detrimental coral-algal phase shifts can occur in their absence, as documented in the Caribbean (Carpenter 1990, Mumby 2006, Mumby et al. 2006b). Some sea urchin species are also outplanted as biocontrol (e.g. *Tripneustes*) to maintain invasive algal growth on some reefs (Conklin & Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018). Other benthic herbivores (e.g. trochus snails, diogenid hermit crabs, amphipods) can be active in areas not accessible to reef fishes, particularly in the cryptic reef framework, limiting algal growth and facilitating coral recruitment in refugia from higher order grazers (Brawley & Adey 1981, Coen 1988, Klumpp & Pulfrich 1989, Doropoulos et al. 2012b, 2016). Conversely, grazing by some herbivorous invertebrates may disrupt coral recruitment and regeneration, as posited for the blue starfish, *Linckia laevigata* (Laxton 1974b), but there is surprisingly little information available on the ecology of this vibrant well-known species.

Predation

Somewhat unexpectedly, the top-ranked groups for the predation process were triton snails and cephalopods (FI = 1; Table 3). Triton snails, specifically the giant triton, *Charonia tritonis*, are among the largest mobile predatory invertebrates on the GBR and are a key predator of adult CoTS (Endean 1969, Pratchett et al. 2014, Cowan et al. 2017, Hall et al. 2017). Expert scores for triton snails are likely a reflection of this niche role in predation, especially as CoTS population control is a prime management focus on the GBR (Pratchett et al. 2014, Babcock et al. 2016a, Hoey et al. 2016b). CoTS population outbreaks have been attributed to the removal of *C. tritonis* from the GBR in the mid-1900s (the 'predator removal hypothesis'), although controlled laboratory experiments suggest they only consume ~0.7 CoTS ind^{-1} $week^{-1}$ and that they also target a range of other marine invertebrates (Pearson & Endean 1969). Regardless, their ranking here reflects this important predatory niche, which has been addressed for the GBR in depth previously in the context of conservation and CoTS outbreak management (Hall et al. 2017).

Interestingly, invertivorous fishes did not score highly in the predation process (Table 3), including those that target CoTS at various life stages (e.g. emperors, pufferfishes, triggerfishes) (Cowan et al. 2017). It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), including many with specialised feeding mechanisms and roles, such as tuskfishes (*Choerodon*) (Jones et al. 2011), cleaner wrasses (*Labroides*) (Grutter 1997) and rockmover wrasses (*Novaculichthys*) (Wainwright et al. 2002). The lack of consideration of invertivores by experts here may reflect the broad ecological redundancy of this group at this level of functioning and, importantly, the data gaps regarding empirical observations of invertivory on the GBR (Case Study 1).

Cephalopods also received the top score for the predation process (FI = 1), despite the literature being largely restricted to their taxonomy and diversity (Roper & Hochberg 1987, Norman 1992, Norman & Finn 2001, Rosa et al. 2019). Surprisingly little information exists on their functional ecology on the GBR and in general (Ponder et al. 2002). The ecological importance of cephalopods is perhaps mostly presumed from their fast growth rates (Pecl & Jackson 2008), broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & Bennett 2008). The relatively high feeding rates and densities of squid and other cephalopods have the potential to control recruitment dynamics of many commercially and ecologically important fishes (Hunsicker & Essington 2008). Changes to predatory-prey dynamics of cephalopods could have ecosystem-level implications (Pecl & Jackson 2008, Spady et al. 2014, 2018, Rosa et al. 2019). Benthic shallow-water octopuses are likely key predators within the reef matrix where large predatory fishes cannot access. Their behaviours are complex for an invertebrate and can involve interesting mutualistic hunting relationships with predatory fishes such as coral trout (Vail et al. 2013). Moray eels (muranids) occupy a similar niche in the reef matrix and demonstrate the same hunting mutualism (Vail et al. 2013) but were rated slightly lower for the predation process by experts here (FI = 5). Overall, trophic interactions in cryptic habitats are difficult to quantify and are poorly characterised.

Cryptobenthic fishes, which also occupy the reef matrix, rated highly for predation (FI = 3), despite the lack of empirical information on their taxonomy and ecological roles (Bellwood et al. 2019, Brandl et al. 2019). This group, which includes the gobies, represent around half the total number of reef fishes on the GBR, with around 8% of this population consumed daily (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018), producing almost 60% of the consumed reef fish biomass (Brandl et al. 2019). Representing some of the smallest marine vertebrates, cryptobenthic fishes are fundamental to predation processes and production functioning as prey. They are also important crypto-invertebrate predators in the reef framework (Goatley et al. 2017), particularly of microcrustaceans (e.g. copepods) (Case Study 1).

Copepods are the most speciose group in the zooplankton on the GBR and are at the base of marine food webs that directly and indirectly support fisheries production (McKinnon & Thorrold 1993, McKinnon et al. 2005). It is estimated that the flux of zooplankton to the coral reef ‘wall of mouths’ is ~0.5 kg m^{-1} d^{-1} (Hamner et al. 1988), with extrapolations that suggest copepod production across the entire GBR is >630,000 tonnes carbon yr^{-1} (McKinnon & Thorrold 1993, McKinnon et al. 2005, 2007). Zooplankton scored high within the predation process (FI = 3), given their fundamental contribution to reef trophodynamics. Plankton occupy the largest coral reef habitat – the pelagic ecosystem – and are key to ecosystem functioning (McKinnon et al. 2007). It should be noted that this broad-scale pelagic context stretches beyond the typical reef habitat examined here for targeted management recommendations.

CASE STUDY 1: INVERTIVORY ON THE GREAT BARRIER REEF: A POORLY UNDERSTOOD LINK IN THE TROPHIC CHAIN

Hannah Sheppard-Brennand, Maria Byrne, Jessica Stella, Kennedy Wolfe

It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), but data gaps remain regarding invertivory on benthic mobile invertebrates (BMIs) including crustaceans, gastropods, worms and echinoderms. In this case-specific review of over 550 studies, only 35 reported nominally invertivorous fishes to incorporate BMIs in their diet on the GBR. This included 174 species from 20 families (Figure CS1.1; Appendix 1 on the book website), ~10% of the total known number of fish species on the GBR. This diversity spans a range of life stages, sizes, morphologies and feeding modes and exceeds that of herbivorous (178 species from 9 families; Cvitanovic et al. 2007), detritivorous (24 species from 5 families; Wilson et al. 2003) and corallivorous (128 species from 11 families; Cole et al. 2008) fishes on the GBR. Quantitative measures of invertivory on BMIs were only found for 18 families in 33 studies, including three families that consumed <10% invertebrates (Acanthuridae, Blennidae, Siganidae). This highlights the paucity of direct observations and quantification of fish invertivory on BMIs. It should be noted that this does not include fishes that target CoTS, as this has already received considerable attention (see Cowan et al. 2017). Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR, including a focus on quantifying direct measures of invertivory, prey availability and trophic transfers from the benthos to higher order taxa to enhance production functioning.

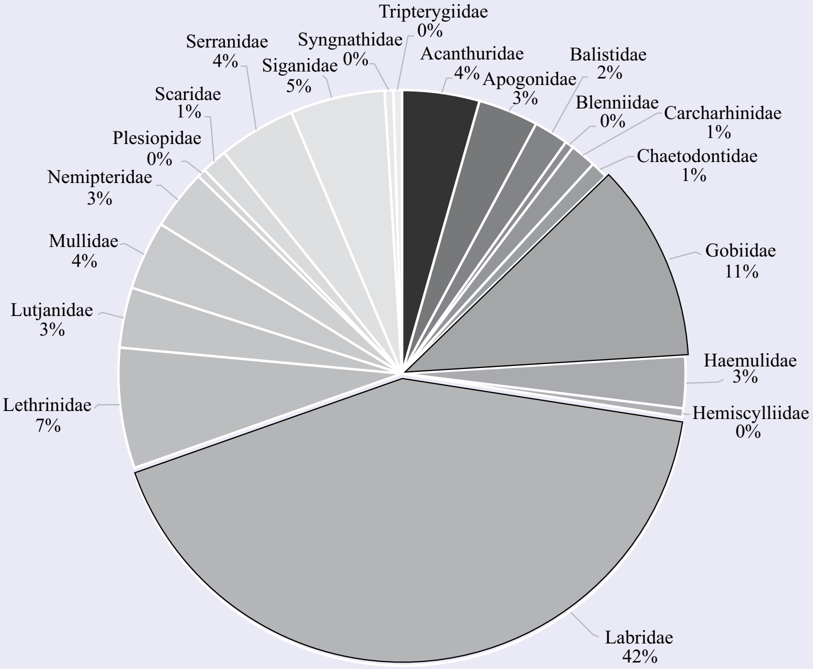

Figure CS1.1 Proportion of coral reef fishes and sharks (by family) that are reported to consume benthic mobile invertebrates on the GBR.

The greatest diversity of invertivores came from the Labridae (wrasses), followed by the Gobiidae (gobies) (Figure CS1.1). Labrids are one of the most functionally and ecologically diverse groups of fishes on coral reefs and account for the highest biomass of invertivores on the GBR (Williams & Hatcher 1983, Bellwood et al. 2006b, Kramer et al. 2015). While this may suggest high functional redundancy (Bellwood et al. 2006b), labrids exhibit the greatest range of specialised feeding mechanisms and species with key roles; for example, tuskfishes (*Choerodon*) use tools to break open mollusc shells (Jones et al. 2011), cleaner wrasses (*Labroides*) target gnathiid isopods over other parasites (Grutter 1997), rockmover wrasse (*Novaculichthys*) overturn the benthos to access hidden prey (Wainwright et al. 2002). Cryptobenthic fishes (e.g. gobies) represent around half the total number of reef fishes on the GBR, are particularly important predators of microcrustaceans (e.g. copepods) and themselves provide direct trophic pathways to higher order consumers (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019). Apogonids (cardinalfishes) and a range of other nocturnally active species (e.g. reef sharks, epaulette sharks, sweetlips and emperors) are functionally significant invertivores at night, particularly regarding larger crustaceans (e.g. Malacostraca) (Marnane & Bellwood 2002, Boaden & Kingsford 2012).

For species where invertivory was quantified (Figure CS1.2), ~40% were obligate consumers of invertebrates. Crustaceans were the predominant prey across all families of invertivorous fishes (Figure CS1.2). Annelid worms represented the greatest proportion of the diet of the Hemiscylliidae (epaulette sharks) and Mullidae (goatfishes) (Figure CS1.2), but this was only quantified for one species in each family. Many species not classified as nominal invertivores in the literature are documented to ingest significant amounts of benthic invertebrates (e.g. carnivores: *Cheilodipterus quinquelineatus* and *Carcharhinus melanopterus*, >35% of stomach contents; herbivores and detritivores: *Amblygobius phalaena* and *Bathygobius fuscus*, >15%; carnivores/piscivores: *Lethrinus nebulosus*, >50%) (Appendix 1 on the book website). Detritivores and other functional groups may supplement their diet with invertebrates to avail of the higher protein and energy content (Hernaman et al. 2009, Kramer et al. 2013).

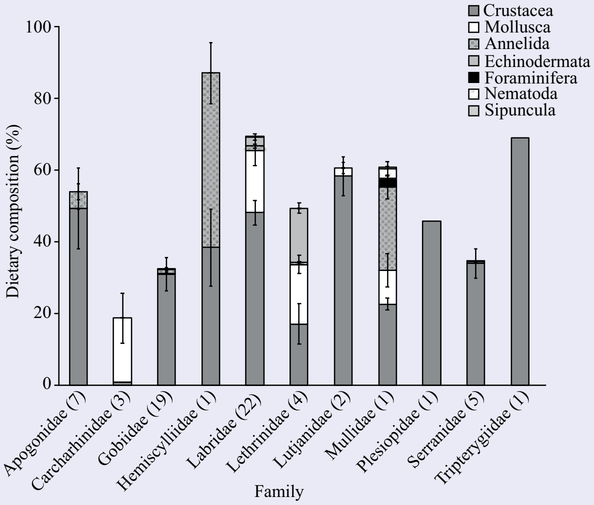

Figure CS1.2 Mean proportion (±SE) of invertebrates (by phyla) in the diet of nominally invertivorous fishes (by Family). Number of species are indicated in parentheses after family name. Note only 11 of 18 families are presented as other data were not comparable.

Notably, the zooplankton group also comprises the macro- and mega-plankton, which includes the larger-bodied (>200 mm) cnidarian and ctenophoran jellyfishes. This group has explicit roles in ecosystem functioning through their typically carnivorous predation on smaller zooplankton groups (Hutchings et al. 2019) and as an important food source themselves (Ates 1988, 1991, Purcell & Arai 2001). Jellyfish blooms are increasingly documented around the world, including on the GBR, with impacts on ecosystem stability and functioning (Hutchings et al. 2019). Cubozoans (box jellyfish and *Irukandji*) are a particularly important group on the GBR resulting from their socioeconomic impacts on inshore reefs through their sometimes fatal envenomation (Huynh et al. 2003, Kingsford et al. 2012, Gershwin et al. 2014).

In context of the 'wall of mouths' (Hamner et al. 1988), planktivorous fishes (e.g. damselfishes, fusiliers, anthias) scored surprisingly low (FI = 7), despite their well-appreciated roles transferring carbon (in plankton) from the water column into trophic networks, especially within close proximity of reef structure and refugia (Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005) and their contribution as prey to a multitude of species (Hamner et al. 1988, 2007, Johansen & Jones 2013). The unexpectedly low score for planktivorous fishes may, in part, reflect their broad ecological redundancy, as they represent >20% of all coral reef fishes and account for >60% of the total fish biomass (Bellwood & Hughes 2001, Bellwood et al. 2004). It is also possible that experts scored the predation process from a top-down perspective, resulting in lower scores for many intermediate-level predators, including the planktivores and invertivores. Similarly, corals did not score highly for predation (FI ≥ 7), likely due to their broad redundancy regarding this process and propensity to switch between autotrophy and heterotrophy to meet energy requirements (Anthony & Fabricius 2000, Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015). This ability is highly dynamic depending on species and location, with some corals on turbid inshore reefs 10–20 times more heterotrophic than their counterparts in oligotrophic waters (Anthony 2000, 2006).

Other invertebrates, including predatory polychaete worms, crustaceans (decapods, stomatopods, infauna) and molluscs (e.g. *Conus*, nudibranchs), ranked highly (FI = 3). Both pelagic and benthic micro- and cryptopredators provide the foundations of energy transfer to higher trophic levels (Goatley et al. 2017). This includes impressive cases for key benthic predators like mantis shrimp (*Odontodactylus*) (deVries et al. 2016, Goatley et al. 2017) and cone snails (*Conus*) (Kohn 2015), which can be highly specialised physically and/or chemically to target larger vertebrate prey. Harlequin shrimp (*Hymenocera*) and a number of other predatory invertebrates may be important cryptic predators, including of the juvenile life stage of CoTS hidden in the reef and rubble framework (Glynn 1984, Cowan et al. 2017, Keesing et al. 2018). Nudibranchs can influence benthic cyanobacterial productivity through top-down effects on key herbivores (Geange & Stier 2010), and sponge-feeding nudibranchs sequester chemical defences that can alter fish feeding behaviour (Proksch 1994, Becerro et al. 1998, Ritson-Williams & Paul 2007). Nudibranchs are among the most abundant spongivores on coral reefs, but their low relative densities limit their ability to shape sponge abundance and distributions (Powell et al. 2015).

CoTS also ranked among these invertebrates for the predation process (Table 3), as top corallivores with extreme predatory potential during population outbreaks (Pratchett et al. 2014). Outbreaks aside, CoTS adults can consume up to 250 cm^2 of live coral per day (Chesher 1969, Glynn 1973), around 2–5 times the rate of other similarly sized corallivorous starfish, such as *Culcita novaeguineae* (Glynn & Krupp 1986, Birkeland 1989). Non-*Acanthaster* predatory asteroids scored lower for predation (FI = 7), although their selective feeding habits can influence the relative abundance of some coral species (Glynn & Krupp 1986). A recent (but rare) outbreak of *Culcita schmideliana* in the Maldives was associated with 24% mortality of juvenile acroporid and pociloporid corals, hindering postbleaching reef recovery (Bruckner & Coward 2019). The boom-and-bust population characteristic typical of echinoderms attributes to the ephemeral nature of their ecological roles and impacts (Birkeland 1989, Uthicke et al. 2009). Even the nominally herbivorous sea star, *Linckia* *laevigata*, is reported to feed on live coral, but this behaviour is rare, with little documented impact as their stomachs are relatively small (Laxton 1974b).

Large predatory reef fishes (transients and residents) were among the highest scoring fishes within the predation process but were rated lower by experts than a range of other taxa (Table 3). This is in line with suggestions in the literature that top-down forces on the GBR are weak (Rizzari et al. 2015, Casey et al. 2017). While top-down effects of predatory reef fishes can alter reef fish recruitment and community structure (Webster & Almany 2002, Almany 2004b, Almany & Webster 2004, Rizzari et al. 2014, Palacios et al. 2016a,b), their relative rarity and limited links across trophic networks can reduce their overall functional importance (Roff et al. 2016, Casey et al. 2017). In contrast to common ecological theory, there is a degree of ecological redundancy in the mesopredator group on the GBR, which includes the sharks (Rizzari et al. 2015, Frisch et al. 2016b). Most reef-associated sharks do not act as apex predators but instead function as mesopredators along with a diverse group of coral reef fishes (Roff et al. 2016). Interestingly, resident fishes (e.g. coral trout) scored lower (FI = 4) than transient predatory fishes (e.g. sharks, barracudas) (FI = 3). As reflected in expert scores, this may be associated with the dependency of resident predators on habitat refugia (Rogers et al. 2014, 2018b). Hunting regularity and success are typically greater in resident reef fishes, but transient predators can be the primary source of mortality for non-reef associated fishes (Hixon & Carr 1997, Almany 2004a).

Nutrient cycling

Detritivorous fishes were the highest-ranked group regarding nutrient cycling (FI = 1; Table 3). They are outlined in the literature as fundamental components of nutrient pathways transferring energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014) and in the export of nutrients and detritus from sand patches across the calcified reef structure (Lukoschek & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & Mumby 2012). Blennies are considered key detritivores on the GBR, representing ~60% of this trophic group's density in some habitats (Wilson 2001) and exhibiting incredible population productivity with estimates that <1% survive for more than one year (Wilson 2004). This is similar for cryptobenthic fishes (e.g. gobies) (FI = 2), which are super abundant and highly productive and provide direct links from the hidden and largely inaccessible reef matrix to higher consumers (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018). The small size (<50 mm length) and rapid population turnover of cryptobenthic fishes reflect their niche roles in top-down trophodynamics within the reef matrix and bottom-up pathways that support fisheries productivity (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019). The high scores for blennies and gobies here capture their critical roles in coral reef trophodynamics.

Phytoplankton and turf algae also scored highly for nutrient cycling (FI = 2) at the baselines of pelagic and benthic productivity, respectively (Furnas & Mitchell 1987, 1988, Klumpp & McKinnon 1992, Russ 2003, Littler & Littler 2007, McKinnon et al. 2007). In the context of productivity, *in situ* growth rates of dominant phytoplankton species range from one to several doublings per day, resulting in fast growth rates and substantial contributions to nutrient cycling. Phytoplankton species are important in nitrogen fixation, particularly *Trichodesmium*, which form extensive cyanobacterial rafts (Revelante & Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Similarly, turf algae are particularly important in the fixation of nitrogen on coral reefs. Much of the nitrogen in coral reefs is 'fixed' (made biologically available) by blue-green algae within the EAM, which have rapid growth rates and are intensively grazed, distributing nitrogen and other nutrients throughout the reef (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). On turf and macroalgal-rich reefs, microbial community density and diversity increase with the potential to shape nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019).

All four functional groups of microbes, as nominally partitioned here, also scored highly (FI = 4). Microbial communities are key drivers of large-scale biogeochemical processes in the oceans (Falkowski et al. 2008), with fundamental roles in mediating nutrient cycling (e.g. phosphorus, nitrogen) (Charpy et al. 2012, Tout et al. 2014, Ferrier-Pages et al. 2016) and influencing water quality (Glasl et al. 2017, 2018a). Impressively, host-associated microbes (the 'coral microbiome') (FI = 2) can provide >90% of a coral's nutritional requirements (Muscatine & Porter 1977, Bourne et al. 2016). While the ecological contribution of the coral microbiome is poorly understood, it appears to be inextricably linked to the passage and cycling of nutrients (carbon, nitrogen, sulphur, phosphorus, vitamins) and overall reef productivity (Bourne et al. 2016).

Tabular corals (FI = 2) were ranked higher than the remaining coral groups (FI = 4–8) by our expert panel. Based on the literature, this is likely a result of the broader importance of tabular corals regarding rapid reef growth and post disturbance recovery (Connolly & Muko 2003, Ortiz et al. 2014, 2018). In the context of nutrient cycling, the relative contribution of autotrophy and heterotrophy in corals is variable, dynamic and plastic (Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015). A range of coral species, including some acroporids and pocilloporids, exhibit higher rates of heterotrophy in turbid environments near shore compared to the same species in oligotrophic waters offshore (Anthony 2000, Anthony & Fabricius 2000). Soft corals tend to dominate the turbid waters typical of nearshore reefs on the GBR, suggesting regional specificity in functional importance between coral taxa (Fabricius 1997, Fabricius & De'ath 2001a). Some soft coral species are even herbivorous, feeding predominantly on phytoplankton – an important consideration that can shape community structure on eutrophic inshore reefs (Fabricius et al. 1995, Fabricius & De'ath 2008).

Interestingly, sponges rated fairly low (FI ≤ 6), despite their well-documented roles in benthic-pelagic coupling and detrital pathways (de Goeij et al. 2013, Mumby & Steneck 2018). This discrepancy between expert scores and peer-reviewed evidence is important to note. This may be a result of the lack of information available for sponges (particularly cryptic species) on Pacific reefs, as most information on the trophic ecology of sponges is derived from the Caribbean (Wilkinson 1983, 1987, Mumby & Steneck 2018).

The highest-scoring mobile invertebrates to nutrient cycling were the zooplankton (FI = 2; Table 3), which include a diversity of pelagic crustaceans (e.g. copepods and mysids), doliolids, salps, larvaceans (Appendicularia) and chaetognaths. Zooplankton are intermediate trophic levels in pelagic food webs, linking primary production by phytoplankton with higher-order taxa, and thus support oceanic and coastal fisheries. Zooplankton are also key players in benthic-pelagic coupling, as they are consumed by benthic fishes and invertebrates, including corals (Bishop & Greenwood 1994, Marnane & Bellwood 2002, Holzman & Genin 2003, Holzman et al. 2005). An estimated 25%–100% of particulates in the water column fall to the benthos each day, making planktonic groups and the faeces and marine snow they produce, important components of benthic functioning (i.e. benthic-pelagic coupling) (McKinnon et al. 2007, Alongi et al. 2015, Lonborg et al. 2017). There are also demersal zooplankton that migrate between the benthos and water column daily with important roles in nocturnal trophodynamics (Jacoby & Greenwood 1988). Zooplankton can be highly abundant with distinct cross-shelf community assemblages (Sammarco & Crenshaw 1984, Williams et al. 1988, McKinnon & Thorrold 1993, McKinnon et al. 2005). Their biomass is greatest inshore and around shallow reef areas in the southern and central GBR and is greater in summer months (Russell 1935, Skerratt et al. 2019). Appendicularia have been found to grow faster than any other multicellular organism (Hopcroft & Roff 1995) and can be nearly as abundant as copepods on coral reefs, where they are important food source for planktivores and fish larvae (Noda et al. 1992, Llopiz 2013, Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016).

Most benthic mobile invertebrate groups scored low, with deposit-feeding sea cucumbers (FI = 5) and coral-associated decapods (FI = 6) among the highest ranked groups (Table 3). As reflected by expert scores here, these groups are commonly underappreciated in their roles compared to reef fishes and corals. Sea cucumbers have been coined the 'vacuum cleaners' of the reef (Samyn & Tallon 2005), with functionally important roles in bioturbation, carbonate chemistry and nutrient cycling and a strong influence on benthic productivity and infaunal community structure (Uthicke & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Purcell et al. 2016a, Lee et al. 2017, Wolfe & Byrne 2017a, Wolfe et al. 2018). In terms of ecosystem functioning, the relative importance of sea cucumbers would likely be greater in lagoon systems, outside of the focal coral reef habitat here. Coral-associated decapods (e.g. Tetraliidae, Trapeziidae) have direct relationships with their hosts, typically acroporid and pocilloporid corals (Stella et al. 2011b, Gonzalez-Gomez et al. 2018). They play important roles utilising large amounts of coral mucus, recycling detritus and organic matter (Glynn 1983, Hutchings 1983, Stimson 1990), and even physically defending their coral host from predators (e.g. CoTS, *Drupella*) (Pratchett 2001, Stella et al. 2011b). Their high dependency on their coral host (and thus highly localised benefits) worked to lower their overall score here.

Symbiosis

As organismal symbioses are defined by interactions and interdependency, it was not possible to receive the highest score for this process within our scoring scheme. Top-rated (FI = 2) functional groups for symbiosis were microbes (host-associated phototrophic), corals (tabular, massive, soft), decapods (coral-associated) and fishes (cleaner wrasse) (Table 3). The coral microbiome (i.e. coral-associated microbes) can exist at densities exceeding one million cells per cm^2 of host tissue (Garren & Azam 2012a), with diversities in the thousands in some host species (Mouchka et al. 2010, Blackall et al. 2015, Bourne et al. 2016). The best-known coral symbionts are photosynthetic dinoflagellates within the Symbiodiniaceae, which can reach densities $>10^6$ cm^{-2} of host tissue (Garren & Azam 2012a, Bourne et al. 2016). These microbes are at the foundation of coral reefs, particularly in their relationships with benthos-dominating species such as corals, sponges and algae, where they are pivotal to host fitness through nutrient provisioning and waste removal pathways (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Ferrier-Pages et al. 2016, Glasl et al. 2016, 2018b, Ramsby et al. 2018b). Coral holobionts are at the core of a healthy coral animal – and coral reef – sometimes providing corals with almost all of their nutritional requirements (Muscatine & Porter 1977, Bourne et al. 2016), including up to 100% of their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008). The relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016). All corals scored highly (FI ≥ 4), reflecting their important symbioses, not only with microbial communities, but also their diverse and fundamental associations with a range of reef taxa spanning from worms to fishes that depend on corals as habitat. Recent observations suggest that soft corals (FI = 2) may be particularly important in providing reef structure post disturbance (i.e. bleaching), with potential to promote fish diversity and density at a critical time of recovery (Ferrari 2017).

Corals co-exist with a great diversity of symbiotic reef biota. Coral-associated decapods are strongly bound to their coral hosts, where they can increase coral growth, deter predators, and even reduce disease in their coral host (e.g. *Cymo*, *Tetralia*, *Trapezia*) (Glynn 1980, 1983, Pratchett 2001, Stella et al. 2011b, Pollock et al. 2013). Christmas tree worms (*Spirobranchus*) also scored highly (FI = 4), with similar coral-host associations, enhancing water circulation across coral polyps, influencing coral nutrition, growth and recovery (Strathmann et al. 1984, Dai & Yang 1995, Ben-Tzvi et al. 2006), and aiding in the protection of corals from predators (e.g. CoTS) (DeVantier et al. 1986, Rowley 2008). However, corals exist in the absence of these associates, meaning they may not be functionally imperative. Similar to corals, giant clams (Tridacnidae) host symbiotic autotrophs that can provide >50% of the individual's carbon needs for both respiration and growth, superseding their need for heterotrophy through filter-feeding as they grow (Klumpp et al. 1992). This symbiotic association was not captured for giant clams here (FI = 8), which may reflect the coral-centric interpretation of symbioses in expert scores.

For the reef fishes, cleaner wrasses (*Labroides*) scored highest (FI = 2). Cleaners, particularly *L. dimidiatus* on the GBR, have highly developed interspecies communication and 'cleaning' services, removing ectoparasites, dead skin and mucus from their clients (Grutter & Poulin 1998, Bshary &

Grutter 2002). Ranging from small fishes to charismatic megafauna, clients frequent cleaning stations to ensure their bodies are well maintained and parasite free. This service has been documented to reduce stress hormones in the client (Soares et al. 2011) and increase fish density, diversity, size (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011), recruitment (Sun et al. 2015) and cognitive performance (Binning et al. 2018). Cleaner wrasses may also be self aware – a hallmark of cognition and intelligence (Kohda et al. 2019). Cleaner wrasses appear to fill an ecological niche with little ecological redundancy, but more information is needed on other cleaning species (e.g. *Lysmata* shrimp, other fishes) (Cote 2000, Vaughan et al. 2017) and how their symbioses scale up to support greater reef functioning.

Calcification

Microbes (host-associated phototrophic), calcifying algae (CCA, calcareous species) and corals (tabular) scored highest for their roles in calcification (Table 3). The influence of the coral microbiome on coral health and functioning is widely appreciated in the literature (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Glasl et al. 2016, 2018b), and their functional ranks by experts here even outweighed some coral species. Corals are largely dependent on their microbiome for their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008), and restructuring of reef communities occurs when this symbiotic relationship breaks down (i.e. coral bleaching) (Fitt et al. 2001, Bourne et al. 2016, Hughes et al. 2018b, Stuart-Smith et al. 2018). Coral calcification provides the framework and complexity of the reef, so not surprisingly, most corals scored highly (FI ≥ 4). Tabular corals were considered the most functionally significant contributors to calcification on the GBR, owing to the rapid growth characteristic of acroporids (Pratchett et al. 2015, Anderson et al. 2017, 2018), including those on turbid inshore reefs (Thompson & Dolman 2010, Browne 2012, Browne et al. 2013, Rocker et al. 2017). Acroporids (including tabular corals) generally exhibit the highest calcification rates, with the greatest influence on the carbonate budget (Case Study 2). In addition, the redundancy of key tabular corals could be considered relatively low, with just three species considered common on the GBR: *Acropora hyacinthus*, *A. cytherea* and *A. clathrata*.

Calcification by CCA can be particularly fast in shallow-water habitats (up to 10 kg $CaCO_3$ m^{-2} yr^{-1}) (Kinsey 1983, Chisholm 2000), where they can completely dominate benthic cover (90%–100%) (Atkinson & Grigg 1984, Glynn et al. 1996). CCA calcification in deeper (≥6 m) reef slope habitats (as focused on here) is likely to be slower (≤ 5 kg $CaCO_3$ m^{-2} yr^{-1}) (Chisholm 2000, Lewis et al. 2017). Calcareous algae (e.g. *Halimeda*) contribute to the production of marine sediments and can be major contributors to beach and lagoonal sediments (Marshall & Davies 1988, Delaney et al. 1996), with carbonate production around 2.2 kg $CaCO_3$ m^{-2} yr^{-1} (Drew 1983). While this is lower in comparison to calcification by scleractinian corals (Case Study 2), such as *Porites* (>10 kg $CaCO_3$ m^{-2} yr^{-1}) (Cooper et al. 2008, De'ath et al. 2009), the breakdown of calcareous alga can be much faster and can rapidly fill interreefal space. Overall, hard scleractinian corals are calculated to be responsible for ~95% of carbonate production on the GBR, with CCA accounting for the remaining 5% (Case Study 2).

The contribution of non-coral, non-algal species to reef carbonate production (i.e. calcification) was not captured in Case Study 2, as other calcifiers are not captured in the long-term monitoring programme, and/or their contributions are often comparatively marginal. Little is known of the contribution of very small but highly abundant calcifying invertebrate groups (e.g. micro-molluscs and foraminiferans), many of which are yet to be named. For many of these taxa, their contributions to calcification are often overlooked but can be presumed from their presence in carbonate sands. For example, benthic and pelagic Foraminifera can make considerable contributions to the carbonate budget of coral reefs (Langer et al. 1997, McKinnon et al. 2007, Fujita et al. 2009, Doo et al. 2017, Hamylton et al. 2017) and are particularly important attributes in lagoon and reef sediment facies (Yamano et al. 2002, 2015, Wilson & Vecsei 2005, Sarkar et al. 2016, Schmitt & Gischler 2017). Large benthic foraminiferans (e.g. *Marginopora*, *Baculogypsina*) can be the single most important contributors to mass sediment production on

CASE STUDY 2: ADDRESSING THE CARBONATE BUDGET OF THE GREAT BARRIER REEF

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Coral reefs exist in a dynamic state between reef construction (calcification) and destruction (erosion). The balance between these processes (i.e. the carbonate budget) can be used as a key metric to assess reef health and forecast the ability of reefs to cope with environmental change (Perry et al. 2008, 2018, Kennedy et al. 2013, Mace et al. 2014). Some studies have quantified the rates of carbonate production (e.g. Kinsey 1983, Browne et al. 2012, Silverman et al. 2012) and bioerosion (Kiene & Hutchings 1994, Osorno et al. 2005, Hoey & Bellwood 2008) in specific taxa and/or locations on the GBR. Variability in these rates is the result of complex interactions between these processes and terrestrial influences (e.g. water quality) (Mallela & Perry 2007), reef metabolism (e.g. calcification and dissolution, and photosynthesis and respiration) (DeCarlo et al. 2017, Woodroffe et al. 2017), reef topography and hydrodynamics (Vargas-Ángel et al. 2015) and ocean change (Kennedy et al. 2013, Shaw et al. 2016, Manzello et al. 2018, McMahon et al. 2019). For example, net ecosystem calcification dropped by 46% on a reef flat at Lizard Island, GBR, between 2009 and 2016, immediately after a mass-bleaching event (McMahon et al. 2019). Such dramatic changes in reef-scale calcification rates would impact reef functioning. Ocean change stressors are likely to retard reef carbonate systems at the global scale (Dove et al. 2013, Kennedy et al. 2013, Manzello et al. 2017, Albright et al. 2018, Cyronak et al. 2018), though examples of resilience and recovery at local scales are promising (Manzello et al. 2018). Critically, current carbonate budget estimates are largely restricted to specific regions (Yamano et al. 2000, Suzuki et al. 2001, Browne et al. 2013, Hamylton et al. 2013, 2014, 2017), making it imperative to upscale this information to establish a baseline carbonate budget at the whole-of-reef scale in the face of global change.

Carbonate production and bioerosion rates were calculated from coral cover reported for 37 reefs across the southern GBR between 2017 and 2019 using the long-term monitoring programme (LTMP) data provided by the Australian Institute of Marine Science (AIMS) (Jonker et al., 2008). Southern reefs were selected as this analysis spanned a period of time when coral cover was in serious decline on the northern GBR (Hughes et al., 2017b, 2018b). This is an important consideration with regard to spatial and temporal changes in the carbonate budget of the GBR in future work. Data for coral cover were combined with published extension, production or erosion rates sourced from the ReefBudget website (http://www.exeter.ac.uk/geography/reefbudget) and other publications for the GBR (Drew, 1983; Musso, 1994; Osorno et al., 2005; Hoey & Bellwood, 2008; Pratchett et al., 2015; Anderson et al., 2017; Razak et al., 2017; Rocker et al., 2017). Total carbonate production of each reef was calculated with a model derived from geometric growth forms of corals. Estimates were derived from rates of carbonate production (or accretion) by hard corals and calcareous algae (CCA, articulated calcareous red algae, *Halimeda* and *Peyssonnelia*). Carbonate removal (bioerosion) by parrotfishes (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) was calculated using density and size records in the AIMS LTMP fish transect dataset. Secondary bioerosion by micro- and macro-borers (including polychaetes, sipunculans, sponges [e.g. *Cliona*] and molluscs) was estimated using experimental data from the GBR (Kiene & Hutchings, 1994; Osorno et al., 2005; Chazottes et al., 2017).

Hard coral assemblages contributed to approximately 95.5% of the total reef carbonate production (calcification) across all reefs on the GBR, with the remaining 4.5% contributed by calcareous algae, including CCA, *Halimeda* spp., *Peyssonnelia* spp. and calcareous red algae

Table CS2.1 Mean rates (±SE) of carbonate production, bioerosion and carbonate budget in the southern GBR

		$kg\ m^{-2}\ yr^{-1}$
Production	Primary (corals)	6.36 ± 0.52
	Secondary (algae)	0.30 ± 0.03
	Total	6.66 ± 0.54
Bioerosion	Primary (parrotfish)	−4.18 ± 0.53
	Secondary (micro/macroborers)	−0.42 ± 0.02
	Total	−4.60 ± 0.53
Carbonate budget		2.07 ± 0.77

(Table CS2.1). *Acropora* species exhibit the greatest calcification rates on the GBR compared to other carbonate producers (i.e. non-*Acropora* corals and calcareous algae) (Figure CS2.1). Total carbonate production ranged between 0.49 and 12.97 kg m^{-2} yr^{-1} in the southern GBR (Table CS2.1). Mean bioerosion rates, driven almost entirely by grazing parrotfishes (Figure CS2.1), ranged between 0.69 and 19.0 kg m^{-2} yr^{-1}) (Table CS2.1). Overall, the total carbonate budget ranged from –14.9 to 12.05 kg m^{-2} yr^{-1} with a mean of 2.1 ± 0.8 kg m^{-2} yr^{-1}, suggesting a positive carbonate budget in the southern GBR (Table CS2.1). How the relative abundance of different coral taxa contributed to the observed variability in the carbonate budget will be important to differentiate in order to determine potential thresholds in coral cover to maintain reef resilience and recovery in a future ocean.

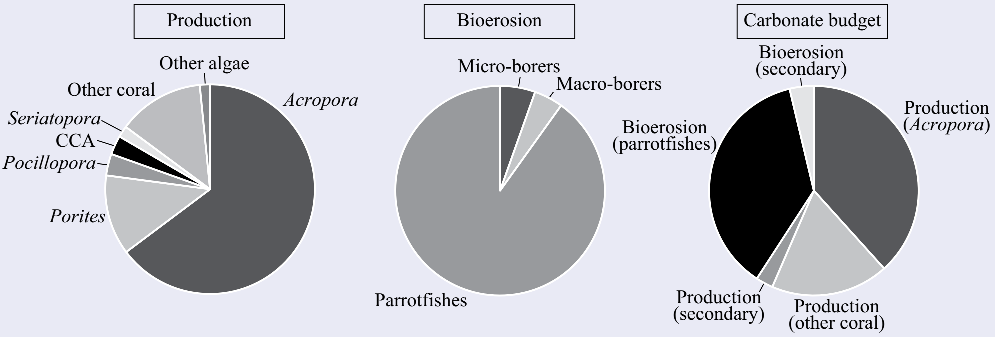

Figure CS2.1 Proportional mean rates of production (calcification), bioerosion and the total carbonate budget by key groups in the southern GBR between 2017 and 2019 (AIMS LTMP).

the GBR where they can make up >60% of biogenic sediment (Yamano et al. 2000, Dawson & Smithers 2014, Dawson et al. 2014). As such, foraminiferans received their highest score across all processes for calcification (FI = 4).

Coral-associated decapods scored highly for the calcification process (FI = 2), which emphasises the importance of looking beyond direct roles when evaluating ecosystem functioning. While the direct magnitude of calcification by decapods is likely to be minimal at best, the influence of coral-associated crabs in regulating coral mucus can enhance the growth and survival of their coral hosts

(Glynn 1983, Hutchings 1983, Stimson 1990). They can also have pronounced effects on corals by reducing fouling algal epibionts (Coen 1988). These symbiotic benefits, which facilitate coral calcification, upregulated coral associates within this process compared to other crustaceans.

Molluscs generally scored highly (FI = 3), but as for crustaceans, they have lower direct contributions to calcification compared to corals. Calcification in Mollusca is perhaps greatest for giant clams (Tridacnidae), with some species reaching >120 cm across and weighing >200 kg (Rosewater 1965). Calcifying zooplankton such as pteropods and heteropods (molluscs) are relatively uncommon in GBR waters, although the pteropod *Cavolinia longirostris* can form aggregations in summer (Russell 1935). Corallivorous molluscs (e.g. *Drupella*) have indirect impacts on calcification through coral predation (Cumming 1999, 2009, Glynn & Enochs 2011), as for CoTS (FI = 3), which have been attributed to >40% of the decline in coral cover on the GBR (De'ath et al. 2012). Sea urchins (e.g. *Diadema*) scored similarly due to their indirect role in the balance between reef accretion and erosion through their herbivorous grazing (Birkeland 1989, Alvarado et al. 2016), as well as the direct calcification of their tests and spines. In addition, during winter when algal production slows down on Caribbean reefs, up to 25% of the diet of *Diadema antillarum* can be derived from living scleractinian corals (Carpenter 1981), an unsuspected coral predator.

Bioerosion

No group received the top ranking for bioerosion, reflecting the high redundancy within this process (Table 3). Host-associated phototrophic microbes, algal turfs and boring sponges scored highest (FI = 2). A diversity of bacteria, fungi and endolithic algae ('microborers') biochemically penetrate live and dead coral and CCA substrates (Golubic et al. 1981, 2005, Tribollet 2008, Hutchings 2011, Diaz-Pulido et al. 2014, Reyes-Nivia et al. 2014). These groups represent somewhat hidden bioerosion pathways operating on micro-biological scales on and within the reef matrix (Hutchings 1986, Glynn & Manzello 2015). All groups of microbes scored highly (FI ≥ 4), with significant roles in carbonate dissolution–calcification processes. Cyanobacteria are estimated to be responsible for 18%–30% of sediment dissolution of coral reef and lagoon sediments on the GBR (Tudhope & Risk 1985). Epilithic (surface) microfloral (e.g. algal turfs) and microbial communities can shape bioerosion pathways and biological community structure (Chazottes et al. 2002). Microborers are often the primary agents of bioerosion in the first year following coral mortality, which promotes larger bioeroding grazers (e.g. parrotfishes) to dominate in the years to follow (Tribollet et al. 2002, Tribollet & Golubic 2005). However, the contributions of microborers to net reef erosion are difficult to quantify, and large knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & Manzello 2015). Likewise, there is a need to quantify and distinguish the contribution of microbial metabolic processes from that of purely thermodynamic and chemical processes (e.g. low saturation of interstitial seawater with respect to calcium carbonates, e.g. omega undersaturation) to the rates of internal biological carbonate erosion (e.g. Reyes-Nivia et al. 2014). Both biological and chemically driven processes are fundamental for an accurate quantification of erosion rates of reef cements.

Boring and cryptic sponges ranked as important bioeroders (FI = 3). The most important genera of siliceous sponges to bioerosion are *Cliona*, *Anthosigmella* and *Spheciospongia* (Wilkinson 1983, Schönberg 2000, Fang et al. 2017). Sponges can be the most significant invertebrate bioeroders on coral reefs, with *Cliona* species reported to contribute up to 23 kg $CaCO_3$ m^{-2} yr^{-1} (Neumann 1966, Glynn & Manzello 2015). Around 2%–3% of the carbonate skeleton is dissolved in this process, with the remainder passed on as sediments (Glynn & Manzello 2015). In extreme cases, sponges can also infest and kill live coral colonies (Lopez-Victoria et al. 2006, Marulanda-Gomez et al. 2017). *Cliona* and non-*Cliona* sponges are the only bioeroding invertebrates captured in the AIMS LTMP dataset, as densities of other cryptic bioeroding invertebrate species are hard to quantify. The lack of spatially explicit data on these groups makes it difficult to upscale their contributions to bioerosion and reef carbonate budgets (Case Study 2). This might explain why bioeroding molluscs (e.g.

lithophagid bivalves, boring clams) scored low for bioerosion here (FI = 7) despite their documented contribution to bioerosive and biocorrosive processes (Hutchings 1986, Lazar & Loya 1991, Krumm 1999, Londono-Cruz et al. 2003, Chen et al. 2013, Schönberg et al. 2017).

All groups of worms ('macroborers') scored highly for bioerosion (FI = 3), but as an incredibly diverse assemblage, they are likely to have diversity and redundancy in their biological and ecological roles. The first suite of macroeroders to proliferate in dead coral substrate are typically short-lived polychaetes (e.g. *Polydora*, fabriciniids), which can be extremely abundant, followed by longer-lived polychaetes (e.g. Cirratulidae, Eunicidae, Sabellidae) (Hutchings et al. 1992, Hutchings 2011). In high densities (up to 80,000 ind. m^{-2}), these worms can contribute to erosional losses around 0.7–1.8 kg $CaCO_3$ m^{-2} yr^{-1} (Davies & Hutchings 1983). *Spirobranchus* (Serpulidae) scored highly among the other worm groups, but, importantly, they do not bore into live coral directly. Instead, these worms stimulate corals to grow around their thinly calcified tubes, where they can have significant indirect effects on calcification, bioerosion and the deterrence of some corallivores (DeVantier et al. 1986, Rowley 2008, Hutchings et al. 2019).

A range of other mobile invertebrates also scored highly (FI = 3; Table 3). Mean bioerosion rates of chitons on One Tree Island, southern GBR, were 0.16 kg $CaCO_3$ ind^{-1} yr^{-1} (Barbosa et al. 2008). At high densities, chitons may have an equivocal role in carbonate erosion budgets as other macroeroders like sea urchins and parrotfishes, namely in the intertidal. Regular sea urchins (e.g. diadematids, echinometrids) contribute to erosion rates >10 kg $CaCO_3$ m^{-2} yr^{-1} on some reefs (Glynn & Manzello 2015, Alvarado et al. 2016), but rates on the GBR are comparatively low, perhaps due to comparatively healthy fish populations regulating urchin densities (Sammarco 1985). CoTS scored among these invertebrates, possibly as its consumption of live coral promotes colonisation by bioeroders on dead coral surfaces altering the biological character of the reef (Glynn & Manzello 2015).

Scraping and excavating parrotfishes scored highly for bioerosion (FI = 3). Most of these nominally herbivorous fishes are attracted to the endolithic algal growth on dead corals, with substantial bioerosion resulting from their feeding behaviour (Clements et al. 2017). Some species also target live coral in >50% of the diet (e.g. *Bolbometopon muricatum*) (Bonaldo et al. 2014). Parrotfishes are generally the greatest contributors to bioerosion on coral reefs and are key drivers in total reef carbonate budgets (Case Study 2) (Perry et al. 2012a). Calculations in Case Study 2 suggest that 25 species of parrotfishes from five genera (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) are responsible for almost all of the bioerosion in the southern GBR. Excavating parrotfishes (*Bolbometopon* and *Chlorurus* spp.) are typically the most significant external bioeroders on coral reefs, contributing to erosion rates over 32 kg $CaCO_3$ m^{-2} yr^{-1} on the GBR (Hoey & Bellwood 2008), with significant contributions to sediment production (Bellwood & Choat 1990, Bellwood et al. 2003). *Bolbometopon muricatum* alone accounts for around 87.5% of the erosive processes and almost all of the live coral predation by parrotfishes on outer-shelf reefs of the GBR (Bellwood et al. 2003, Hoey & Bellwood 2008).

Ecosystem engineering

Bolbometopon scored highest by experts regarding ecosystem engineering (FI = 1; Table 3). This was influenced by the low redundancy of this species, which is supported in the literature, given its functionally explicit role as a mass excavator of live and dead coral, particularly on outer-shelf reefs (Hoey & Bellwood 2008, Bonaldo et al. 2014). Other parrotfishes also scored highly for this role (FI = 3) but were down-weighted due to a comparatively higher redundancy across the group. In healthy systems on the GBR, parrotfish bioerosion can balance net reef accretion (calcification) (Hoey & Bellwood 2008) and has the potential to drive a negative carbonate budget (Case Study 2), especially following disturbance Farming damselfishes scored along with the parrotfishes for their roles in shaping algal communities and coral reef growth within their territories (Ceccarelli et al. 2001, 2011, Hata & Kato 2004, Ceccarelli 2007, Casey et al. 2015a). This can further impact reef fish behaviour and community structure (Eurich et al. 2018). Damselfishes seem to exhibit a positive association with both coral habitat and predators (e.g. coral trout) across the GBR (Emslie et al. 2019), with impacts on coral growth, resilience and recovery (Chase et al. 2014, 2018).

Corals (tabular, staghorn, massive) and host-associated phototrophic microbes scored highly (FI = 2). This reflects the symbiotic relationship between the coral and its microbiome and the fundamental importance of both to the construction of the reef (Bourne et al. 2016). The rugosity and complexity of branching and tabular corals, including acroporids and pocilloporids, provide critical refugia that support the diversity of coral reefs (Hixon & Menge 1991, Cheal et al. 2008, Harborne et al. 2012, Rogers et al. 2014, 2018a,b). Different coral species support different fish communities (Holbrook et al. 2008, 2015, Messmer et al. 2011), suggesting that coral and fish biodiversity are tightly linked. For example, tabular coral formations provide particularly important shelter for larger predatory fishes, which inspires competition, predation and community dynamics and scales up to support fisheries productivity (Pratchett et al. 2008a, Kerry & Bellwood 2012, 2015a,b, 2016, 2017). However, tabular and branching corals typically have ephemeral life history traits (Tanner et al. 1996), and the loss of particular coral species can have disproportionate impacts on reef fish assemblages and biodiversity (Messmer et al. 2011, Holbrook et al. 2015). The influence and importance of specific functional and morphological coral groups is dynamic over time and space (McWilliam et al. 2018, Bellwood et al. 2019).

Exhibiting high recruitment rates, tabular corals (e.g. *Acropora hyacinthus*) are key to the growth, maintenance and recovery of coral reefs (Connolly & Muko 2003, Ortiz et al. 2014, 2018, Yadav et al. 2016). Staghorn corals (e.g. *Acropora muricata*) are commonly regarded as fast-growing 'weedy' species, as they have greater calcification rates but exhibit disturbance-prone 'boom-and-bust' characteristics (Knowlton 2001, Graham et al. 2014, Anderson et al. 2017). Massive corals (e.g. *Porites*) are slow growing, but their broader resilience and longevity are important characteristics regarding long-term reef accretion, persistence and recovery (Baldock et al. 2014, Ortiz et al. 2014, 2018, Yadav et al. 2016). Some corals (e.g. *Turbinaria*) may be more resilient to turbid conditions on inshore reefs, where their functional importance is likely to be comparatively greater in the absence of other groups (Anthony 2006, Browne 2012, Browne et al. 2013). In response to mass coral bleaching and mortality on the GBR (Hughes et al. 2018b), brooding *Pocillopora* (grouped here within 'other branching corals') replaced broadcast spawning acroporids as the predominant recruitment taxon for the first time recorded (Hughes et al. 2019a) and may emerge as key features in the current reef recovery trajectory owing to transgenerational plasticity and adaptation through local retention of brooding reproductive modes (Torda et al. 2013a,b, 2017).

Sponges also scored highly for ecosystem engineering, particularly larger conspicuous groups (heterotrophs, phototrophs) (Table 3). In addition to providing structural complexity to a reef (Maldonado et al. 2015), marine sponges host a diverse microbiome, which can occupy up to 35% of sponge volume and impact host defence, metabolism and resilience to perturbation (Simister et al. 2012, Webster & Taylor 2012, Taylor et al. 2013). It is not surprising that all microbe groups also scored highly (FI ≥ 4). Although scoring lower for ecosystem engineering than other sponge groups (Table 3), the role of cryptic and boring sponges to reef and rubble consolidation is well appreciated (Wulff & Buss 1979, Wilkinson 1983, Hutchings 2011), with important inferences for settlement, recruitment and recovery on coral reefs (Biggs 2013). This is similar for CCA (Matsuda 1989, Diaz-Pulido & McCook 2008, Arnold et al. 2010, Doropoulos et al. 2012a), which scored among the highest algal groups (FI = 4). The role of a range of taxa (e.g. CCA, algae, sponges and microbes) in the biogenic cementation and consolidation of degraded reef rubble habitat is likely to be critical to reef functioning and recovery in a future ocean (Johns et al. 2018), but this remains poorly characterised.

Recruitment facilitation

Parrotfishes scored highest for recruitment facilitation (FI ≥ 3; Table 3). As previously, the bulk excavation of both live and dead coral by scraping and excavating parrotfishes is an important process for bioerosion and ecosystem engineering. Parrotfish feeding scars are hypothesised to facilitate settlement of corals and a range of other species through the excavation of live coral polyps and/or removal of epilithic algae from hard surfaces (Bellwood & Choat 1990, Bonaldo & Bellwood 2009, Bonaldo et al. 2014). This may also be true for grazing invertebrates like sea urchins (Dart 1972). Farming damselfishes also scored highly (FI = 2), due to their territorial behaviour that influences coral recruitment and juvenile survival (Gleason 1996, Gochfeld 2010, Doropoulos et al. 2013, Casey et al. 2015a), as well as community dynamics of larger reef fishes (Ceccarelli et al. 2001). Generally, herbivores play functionally diverse roles in recruitment facilitation owing to their diet, behaviour and distribution on the reef (Dart 1972, Doropoulos et al. 2013).

The roles of algae in recruitment facilitation are diverse, including indirect pathways through herbivory and feeding scars (Dart 1972), adding structural complexity free from the coral polyp 'wall of mouths' (Hamner et al. 1988) and/or biochemical settlement cues (e.g. CCA, macroalgae) (Heyward & Negri 1999, Harrington et al. 2004, Birrell et al. 2008b, Arnold et al. 2010, Doropoulos et al. 2012a, 2013, Brooker et al. 2016b). While turf and macroalgal growth can impair the recruitment of coral reef species (Birrell et al. 2008a, Diaz-Pulido & McCook 2008, Arnold et al. 2010, Johns et al. 2018), it has been posited that the benefits of macroalgae in protecting juvenile corals from predation by species such as parrotfishes may outweigh the negative impacts of algal growth on coral settlement and coral-algal competition (Venera-Ponton et al. 2011). Interestingly, the presence of CCA can prevent such undesirable algal growth to facilitate recruitment processes (Vermeij et al. 2011, Gomez-Lemos & Diaz-Pulido 2017).

Tabular and branching corals scored highly (FI = 2), as increased complexity provides refugia on coral reefs, facilitating the settlement, recruitment and survival of corals, fishes and other marine species (Patton 1994, Ohman et al. 1998, Pratchett et al. 2008a, Shima et al. 2008, Wilson et al. 2008, Coker et al. 2014, Yadav et al. 2016, Gallagher & Doropoulos 2017). Shading by tabular corals can reduce the settlement success of autotrophic species (e.g. corals, algae) and alter benthic community compositions towards heterotrophs (e.g. bryozoans, other invertebrates) (Baird & Hughes 2000). Sponges (FI ≥ 4) also influence settlement and recruitment, perhaps most importantly in their ability to consolidate benthic habitat (e.g. rubble). Coral rubble is an important settlement and recruitment habitat, and unconsolidated rubble can reduce coral settlement and recruit survival, hindering reef recovery (Wulff & Buss 1979, Fox et al. 2003, Fox & Caldwell 2006, Biggs 2013, Johns et al. 2018).

Interestingly, bivalves including giant clams and bed-forming species like oysters scored highly (FI = 3). The structural refugia they provide can facilitate settlement of juvenile fishes and a diversity of other organisms, increasing their protection and survival post settlement, particularly when coral cover is low (Beukers & Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). Shell and 'bed' construction by giant clams and other bivalves offers structural complexity to the reef that provides substrate for colonisation by a diversity of holobionts, epibionts, commensal and ectoparasitic organisms (Neo et al. 2017). In this context, the low scores for bivalves regarding symbiosis (FI = 8) and ecosystem engineering (FI = 7) are surprising but may be considered marginal in terms of reef construction compared to corals. Further, the functional roles of bed-forming species are likely to be greater in intertidal and estuarine habitats (e.g. oysters), beyond the target habitat explored here.

Functional importance rankings

In this section, we provide a ranking across our 70 functionally and taxonomically distinct groups, creating a hierarchy of species in terms of their total functional importance from our ecosystem process-based assessment. Using the scores elicited by experts on a per-process basis (as previously), we produced three sets of ranks for each group's relative importance to: 1) production functioning (i.e. primary production, herbivory, predation, nutrient cycling and symbioses), 2) habitat functioning (i.e. calcification, bioerosion, ecosystem engineering and recruitment facilitation) and 3) total ecosystem functioning (i.e. all nine processes combined) (greater detail can be found in the methods). These ranks are presented in Table 4.

Table 4 Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

Taxa	Functional group	Production functioning	Habitat functioning	Total functioning
Microbes	Phototrophic	10	27	17
	Host-associated	2	1	1
	Chemoautotrophic	11	12	9
	Heterotrophic	12	25	13
Algae	Phytoplankton	6	41	22
	Algal turfs	1	10	3
	Leathery	36	43	41
	Foliose	20	24	18
	Calcareous	21	28	28
	CCA	15	9	6
Sponges	Heterotrophic	30	17	24
	Phototrophic	16	18	15
	Boring	22	8	11
	Cryptic	31	5	10
Coral	Tabular	3	4	2
	Staghorn	13	7	4
	Branching (other)	23	13	19
	Massive	17	14	12
	Encrusting	35	16	25
	Free-living	45	65	62
	Soft corals	5	44	26
	Foraminifera	59	52	59
Worms	Nematodes	64	38	54
	Nemertea	65	39	53
	Polychaetes	46	29	40
	Spirobranchus	61	26	48
Crustaceans	Decapods (H)	33	45	38
	Decapods (P)	41	53	51
	Coral-associated	19	15	16
	Barnacles	69	46	65
	Stomatopods	47	30	39
	Cleaner shrimp	60	42	52
	Infauna	34	47	37
	Zooplankton	4	68	34
	Parasitic	66	69	70
Molluscs	Gastropods (H)	27	31	30
	Gastropods (P)	38	40	36
	Triton snails	9	33	21
	Drupella	55	32	47
	Tridacnidae	48	19	33
	Bivalves	49	20	32
	Chitons	42	21	31
	Cephalopods	26	54	45
Echinoderms	Seastars (H)	28	55	46
	Seastars (P)	62	48	58
	CoTS	14	22	14

(*Continued*)

Table 4 (*Continued*) Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

Taxa	Functional group	Production functioning	Habitat functioning	Total functioning
	Sea cucumbers (DF)	39	49	49
	Sea cucumbers (SF)	63	70	68
	Sea urchins (regular)	29	23	23
	Sea urchins (irregular)	56	56	57
	Brittle stars	43	57	50
	Feather stars	68	58	66
Fishes	Cryptobenthic	8	62	35
	Farmers	32	11	20
	Scrapers (scarids)	37	2	7
	Browsers (nasos)	50	34	44
	Browsers (siganids)	51	35	43
	Browsers (other)	52	36	42
	Bolbometopon	25	3	5
	Excavators (other)	24	6	8
	Detritivores	7	50	29
	Planktivores	67	66	67
	Corallivores	70	60	69
	Invertivores (labrids)	53	61	61
	Invertivores (other)	57	59	60
	Invertivores (lutjanids)	58	51	56
	Eels	40	63	55
	Piscivores (residents)	54	64	64
	Piscivores (transients)	44	67	63
	Cleaner wrasse	18	37	27

Note: Shading denotes ranks; 1st = dark, 2nd = mid, 3rd = light.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

Species that scored highly within just one ecosystem process were not necessarily ranked highly in terms of total functional importance (e.g. cephalopods) (Table 4). Similarly, species that scored well within either production or habitat functioning separately may not have ranked highly overall (e.g. zooplankton, cryptobenthic fishes, detritivorous fishes) (Table 4). Only those that scored highly across multiple processes, and those contributing to both production and habitat functioning, would achieve a high final rank (Table 4). For specific details within each process with support from the literature, refer to the sections previously.

Vulnerability rankings

Vulnerability of our 70 functional groups was assessed in context of their biological functioning in the typical reef slope and reef crest habitats on the GBR, with a primary focus on offshore reef regions (Table 5). Inner-reef regions were assessed separately, as exposure to some stressors (particularly those related to water quality) is most significant inshore (Devlin & Brodie 2005, Wooldridge et al. 2006, Brodie & Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, Mellin et al. 2019), where recovery rates are impaired (MacNeil et al. 2019). Thus, we specifically contrast results for water quality stressors between inshore and offshore regions (Table 6). Vulnerabilities to each of our nine key stressors were considered equal, though we note that some stressors are likely to have greater and broader impacts at local and global scales and that all stressors will occur in synergy with cumulative and multifaceted impacts (Halpern et al. 2008, Brown et al. 2014, McClanahan et al. 2015, Uthicke et al. 2016, Harborne et al. 2017, Wolff et al. 2018).

Climate change Changes in the global climate are occurring faster than anticipated (IPCC 2018, Xu et al. 2018). The greatest potential impacts across our 70 functional groups were suggested for ocean warming and ocean acidification, followed by cyclones (Table 5). This indicates that climate-related stressors were the primary concern of GBR experts, as demonstrated previously (Ban et al. 2014b). This is in line with the widespread coral bleaching events documented across the GBR over recent years (Hughes et al. 2017b, 2018b,c), with alterations to reef community assemblage and structure (Stuart-Smith et al. 2018), trophodynamics (Hempson et al. 2018a,b), reproduction (Hughes et al. 2019a), community calcification (McMahon et al. 2019) and reduced recovery rates (Osborne et al. 2017, MacNeil et al. 2019) already observed, including for deep (or mesophotic) reefs (Frade et al. 2018). Rates of change in ocean chemistry are also likely to be steeper on the GBR than currently projected by the IPCC (Mongin et al. 2016b), perhaps even more so for inshore reefs (Uthicke et al. 2014). Further, cyclones will have significant spatial and temporal impacts across the GBR (Wolff et al. 2016, Cheal et al. 2017, Mellin et al. 2019). The only comprehensive solution to reduce the impact of global change on coral reefs, and globally, is to rapidly decrease anthropogenic emissions of CO_2, but the future of coral reefs is dependent on both local and global action on local and global stressors (Kennedy et al. 2013, Albright et al. 2016a, Hoey et al. 2016a).

There will be spatial variability in the responses of reef organisms to climate change stressors, owing to thermal histories, local adaptation and regional disparities in exposure (Uthicke et al. 2014, Siboni et al. 2015, Hughes et al. 2018b, Stuart-Smith et al. 2018). Intertidal and coastal organisms may be less susceptible to future conditions owing to their current exposure to diel fluctuations (e.g. pH, temperature, oxygen), while offshore and open-ocean organisms may be most vulnerable, as they typically experience the most constant conditions (Byrne 2011, Jarrold et al. 2017, Jarrold & Munday 2018, Wolfe et al. 2020). Transgenerational plasticity may enable some marine organisms to acclimatise over several generations, enhancing adaptive responses, poleward migration and reef resilience in the face of climate change (Byrne et al. 2020, Torda et al. 2017).

Host-associated microbes scored among the most vulnerable to climate change stressors, particularly for ocean warming (Table 5). The sensitivities and responses of free-living microbes (independent of a host organism) are often starkly different and can be important bioindicators of reef health regarding temperature, nutrients and sedimentation (Case Study 4) (Hansen et al. 1992, Falkowski et al. 2008, Glasl et al. 2017, 2018a). Biota permanently in the plankton (e.g. copepods, pteropods), which typically have short generation times, may have resilience in their ability to respond to changes in ocean conditions compared to species with longer generational turnover (McKinnon et al. 2007). Zooplankton were considered more vulnerable to climate change stressors than phytoplankton (Table 5), but impacts will be highly variable across the diversity of these two groups. Anthropogenic stressors and their interactions will impact phyto- and zooplankton growth, development, physiology, abundance and distribution, altering blooms, benthic-pelagic coupling and functioning (Huntley & Lopez 1992, Edwards & Richardson 2004, Richardson & Schoeman 2004, Kirby et al. 2007, Gao et al. 2012, Häder & Gao 2015, Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016). Indirect influences of climate change on oceanographic processes (e.g. currents, upwelling, etc.) are suggested to drive vulnerabilities in the plankton across the GBR region, as reviewed by McKinnon et al. (2007). Any alteration to phytoplankton or zooplankton abundance, composition, productivity and timing of occurrence is likely to have a cascading effect on higher trophic levels and functioning of the GBR (McKinnon et al. 2007).

For coral reef fishes, current evidence suggests that increased water temperature will be a major determinant of future assemblages through habitat degradation and direct effects on larval dispersal, recruitment, physiology and behaviour (Munday et al. 2009b, Hoey et al. 2016a). The

Table 5 Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

Taxa	Functional group	Warming	Acidification	Cyclones	Fisheries	Disease	Outbreaks
Microbes	Phototrophic	9.0	1.0				
	Host-associated	16.0	4.0			1.0	
	Chemoautotrophic	4.0	1.0				
	Heterotrophic	9.0	1.0				
Algae	Phytoplankton						
	Algal turfs	1.0					
	Leathery	1.0		2.3			
	Foliose			0.3			
	Calcareous	4.0	4.0	2.3			
	CCA	9.0	9.0				
Sponges	Heterotrophic	1.0	7.1	16.0	1.0	1.0	
	Phototrophic	1.0	1.0	16.0	1.0	1.0	
	Boring	0.4		0.3		1.0	
	Cryptic	1.0	1.0	1.0		1.0	
Coral	Tabular	16.0	9.0	16.0	0.1	2.8	16.0
	Staghorn	16.0	9.0	16.0	0.4	2.8	16.0
	Branching (other)	16.0	9.0	16.0	0.1	1.8	16.0
	Massive	16.0	6.3	1.8	0.1	1.8	1.8
	Encrusting	16.0	6.3	1.8	0.1	1.8	2.8
	Free-living	12.3	6.3	4.0		1.8	1.8
	Soft corals	12.3	4.0	11.1	0.1	1.0	
	Foraminifera	4.0	6.3	7.1		0.4	
Worms	Nematodes						
	Nemertea			0.3			
	Polychaetes			0.3			
	Spirobranchus	9.0	4.0	1.0		1.0	
Crustaceans	Decapods (H)	9.0	16.0				
	Decapods (P)	16.0	16.0	0.3			
	Coral-associated	16.0	16.0	9.0			0.3
	Barnacles	9.0	9.0				
	Stomatopods	9.0	9.0	0.3			
	Cleaner shrimp	9.0	16.0	1.0			
	Infauna	1.0	9.0	0.3			
	Zooplankton	9.0	16.0	0.3			
	Parasitic	4.0	9.0	0.3			
Molluscs	Gastropods (H)	16.0	16.0				
	Gastropods (P)	9.0	7.1	1.0			
	Triton snails	9.0	7.1	1.0	0.3		
	Drupella	16.0	16.0	0.3			
	Tridacnidae	16.0	16.0	16.0	1.0		
	Bivalves	16.0	16.0	4.0	1.0	1.0	
	Chitons	9.0	9.0	1.0			
	Cephalopods	1.0	4.0	0.3	2.3		
Echinoderms	Seastars (H)	9.0	4.0				
	Seastars (P)	9.0	1.0	1.0			
	CoTS	1.0	9.0	1.0			
	Sea cucumbers (DF)	9.0	4.0	2.3	16.0		
	Sea cucumbers (SF)	9.0	1.0	1.0	1.0		

(*Continued*)

Table 5 (*Continued*) Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

Taxa	Functional group	Warming	Acidification	Cyclones	Fisheries	Disease	Outbreaks
	Sea urchins (regular)	9.0	16.0				
	Sea urchins (irregular)	9.0	16.0	0.3			
	Brittle stars	9.0	4.0	0.3			
	Feather stars	9.0	4.0	1.0			
Fishes	Cryptobenthic	11.1	4.0	11.1			1.8
	Farmers		1.8	7.1			
	Scrapers (scarids)		1.8	0.1	0.1		
	Browsers (nasos)		1.8	0.4	0.1		
	Browsers (siganids)		1.8	0.4	0.4		
	Browsers (other)		1.8	0.4	0.4		
	Bolbometopon	1.8	4.0	1.8	0.4		
	Excavators (other)		1.8	1.8	0.1		
	Detritivores	0.4	1.8	7.1			
	Planktivores	11.1	4.0	11.1			2.8
	Corallivores	16.0	11.1	2.8			4.0
	Invertivores (labrids)	4.0	4.0	1.8	0.1		
	Invertivores (other)	4.0	4.0	1.8	1.8		
	Invertivores (lutjanids)	4.0	4.0	1.0	0.4		
	Eels	7.1	4.0	1.0			
	Piscivores (residents)	11.1	4.0	2.8	16.0		
	Piscivores (transients)	7.1	4.0	1.8	16.0		
	Cleaner wrasse	7.1	1.8	11.1			

Note: Exposure was considered in context of offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

positive associations between a great diversity of reef fishes and their coral habitat exemplifies the fundamental importance of coral as the foundation of healthy reef communities (Coker et al. 2014, Pratchett et al. 2018, Emslie et al. 2019). Thus, there are specific concerns for species that depend on corals as a food source and/or for shelter, including coral-associated decapods (Stella et al. 2011a,b), and corallivorous, planktivorous and cryptobenthic fishes (Munday 2004, Pratchett et al. 2004, 2008b, Wilson et al., 2006 2014, Cole et al. 2010, Bellwood et al. 2012a, Hempson et al. 2018c, Rice et al. 2019) (Table 5). Specialist and obligate corallivorous fishes (e.g. butterflyfishes and tubelip wrasses) are likely to be highly impacted by the combined impacts of global change through prey depletion, starvation and even reduced sociality and reproductive potential (Pratchett et al. 2004, Berumen & Pratchett 2006, Cole et al. 2008, 2010, Graham et al. 2009, Thompson et al. 2019), while their feeding adds further pressure on coral condition (Cole et al. 2009). Butterflyfish (Chaetodontidae) abundance and species richness seem to be primarily influenced by bottom-up drivers making physical changes to their coral habitat a significant concern (Brooker et al. 2016a, Leahy et al. 2016). Yet, trophic and foraging plasticity as documented for a range of coral reef fishes, including some considered to be specialist obligate feeders, will likely offer some resilience in a degraded reef setting (Wen et al. 2016, Hempson et al. 2017, Karkarey et al. 2017, Letourneur et al. 2017, Feary et al. 2018, Zambre & Arthur 2018). The close contact relationships

Table 6 Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

		Inshore			Offshore		
Taxa	Functional group	Nutrients	Sediments	Pollutants	Nutrients	Sediments	Pollutants
Microbes	Phototrophic		4.0	16.0		1.0	
	Host-associated	16.0	9.0	16.0	4.0	2.3	
	Chemoautotrophic			9.0			
	Heterotrophic			9.0			
Algae	Phytoplankton		1.0	9.0		0.3	
	Algal turfs		1.0	9.0		0.3	
	Leathery		1.0	4.0		0.3	
	Foliose		9.0	4.0		2.3	
	Calcareous		9.0	4.0		2.3	
	CCA	4.0	16.0	9.0	1.0	4.0	
Sponges	Heterotrophic		7.1	11.1		1.8	
	Phototrophic		16.0	11.1		4.0	
	Boring		7.1	9.0		1.8	
	Cryptic		9.0	16.0		2.3	
Coral	Tabular	12.3	9.0	1.6	3.1	2.3	
	Staghorn	12.3	9.0	1.6	3.1	2.3	
	Branching (other)	12.3	7.1	1.6	3.1	1.8	
	Massive	6.3	6.3	1.6	1.6	1.6	
	Encrusting	6.3	9.0	1.6	1.6	2.3	
	Free-living	4.0	6.3	1.6	1.0	1.6	
	Soft corals	4.0	9.0	1.6	1.0	2.3	
	Foraminifera		6.3	2.3		1.6	
Worms	Nematodes						
	Nemertea						
	Polychaetes						
	Spirobranchus		4.0	9.0		1.0	
Crustaceans	Decapods (H)			4.0			
	Decapods (P)			4.0			
	Coral-associated		4.0	9.0		1.0	
	Barnacles		4.0	4.0		1.0	
	Stomatopods			4.0			
	Cleaner shrimp			4.0			
	Infauna			1.0			
	Zooplankton		1.0	4.0		0.3	
	Parasitic			1.0			
Molluscs	Gastropods (H)		1.0	4.0		0.3	
	Gastropods (P)			4.0			
	Triton snails			4.0			
	Drupella			4.0			
	Tridacnidae		9.0	4.0		2.3	
	Bivalves		1.0	4.0		0.3	
	Chitons						
	Cephalopods	1.0		4.0	0.3		
Echinoderms	Seastars (H)		1.0	4.0		0.3	
	Seastars (P)			4.0			
	CoTS			1.0			
	Sea cucumbers (DF)			4.0			

(*Continued*)

Table 6 (*Continued*) Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

			Inshore			Offshore	
Taxa	Functional group	Nutrients	Sediments	Pollutants	Nutrients	Sediments	Pollutants
	Sea cucumbers (SF)		1.0	4.0		0.3	
	Sea urchins (regular)		1.0	4.0		0.3	
	Sea urchins (irregular)			1.0			
	Brittle stars			1.0			
	Feather stars			4.0			
Fishes	Cryptobenthic	0.4	4.0	7.1	0.1	1.0	
	Farmers		11.1	7.1		2.8	
	Scrapers (scarids)		16.0	4.0		4.0	
	Browsers (nasos)		7.1	4.0		1.8	
	Browsers (siganids)		7.1	4.0		1.8	
	Browsers (other)		7.1	4.0		1.8	
	Bolbometopon	0.4	11.1	4.0	0.1	2.8	
	Excavators (other)		16.0	4.0		4.0	
	Detritivores	1.8	7.1	4.0	0.4	1.8	
	Planktivores	0.4	4.0	7.1	0.1	1.0	
	Corallivores	7.1	11.1	4.0	1.8	2.8	
	Invertivores (labrids)		7.1	7.1		1.8	
	Invertivores (other)		7.1	7.1		1.8	
	Invertivores (lutjanids)		4.0	4.0		1.0	
	Eels	1.8	7.1	4.0	0.4	1.8	
	Piscivores (residents)	4.0	7.1	7.1	1.0	1.8	
	Piscivores (transients)	1.8	7.1	7.1	0.4	1.8	
	Cleaner wrasse	0.4	1.8	4.0	0.1	0.4	

Note: Exposure was considered in context of inshore and offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

between host-associated fishes (e.g. damselfishes) and coral refugia can enhance water circulation (Goldshmid et al. 2004), which can moderate bleaching susceptibility of the coral host itself (Chase et al. 2018).

In extreme cases, the abundance and richness of reef fishes may decline >60% following extensive collapse of reef habitat and structure (Pratchett et al. 2018). Resident predatory fishes that depend on reef structure, including the top fisheries targets on the GBR (coral trout), show a range of vulnerabilities to projected future conditions at both larval and adult life stages (Munday et al. 2013a, Johansen et al. 2014, 2015, Clark et al. 2017, Messmer et al. 2017, Pratchett et al. 2017b). In the context of direct effects, unable to meet the energetic costs of living in a warmer environment, larger-bodied coral trout may be more heavily impacted than smaller-sized individuals, with significant ramifications to fisheries and functioning (Messmer et al. 2017, Scott et al. 2017b). Indirectly, the dependency of resident predatory fishes on tabular corals in particular presents a concerning case where changes in habitat functioning through the loss of coral complexity could have cascading impacts on fisheries production functioning (Kerry & Bellwood 2012, 2015a,b). Conversely, cephalopod populations are proliferating globally (Doubleday et al. 2016), as recognised in the increasing trends in cephalopod fisheries catches (Caddy & Rodhouse 1998, Rodhouse et al. 2014). Cephalopods did not score as vulnerable here (Table 5), in line with global trends and suggestions that they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

Herbivorous fish groups were considered generally resilient, with densities of some grazing species (e.g. parrotfishes) even documented to increase postdisturbance, perhaps due to the increased algal production that typically follows coral mortality (Diaz-Pulido & McCook 2002, Cheal et al. 2008, 2010, Wilson et al. 2009, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c, Roth et al. 2018). However, grazing intensity can decline in line with reduced coral cover as denser algal growth outweighs and minimises the impact of grazers, and simplified habitat complexity increases predation exposure (Cheal et al. 2010, Bozec et al. 2013, Pratchett et al. 2018, Rogers et al. 2018a). The functional roles of the diversity of nominally herbivorous species will vary depending on algal density and the state of the reef (Chong-Seng et al. 2014). Habitat degradation reduces postsettlement success of corals, and shifts towards algal-dominated systems may limit reef recovery (Roth et al. 2018). Coral-algal phase shifts have documented impacts on fisheries productivity (Ainsworth & Mumby 2015, Rogers et al. 2018a), and herbivores protected from fisheries activity in no-take areas may enhance reef recovery (Mumby et al. 2014, Chung et al. 2019). While changes in ecosystem states are a dynamic process (van de Leemput et al. 2016), in general, resilience and recovery of coral reefs will depend on the reversibility of seaweed blooms postdisturbance, with grazing herbivores deemed particularly critical (Arthur et al. 2006, Bellwood et al. 2006a, Hughes et al. 2007b, Diaz-Pulido et al. 2009, Adam et al. 2011, 2015b, Doropoulos et al. 2013, Bonaldo et al. 2014, Mumby et al. 2014, Bennett et al. 2015, Graham et al. 2015). Effective herbivore management through herbivore management areas (HMAs) is an emerging resilience-building tool in response to widespread and severe coral bleaching events (Chung et al. 2019).

Sponge-dominated reefs may increase in occurrence in a future ocean (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham & Bell 2018), although for *Cliona*, the most abundant bioeroding sponges on the GBR, densities and benthic cover have not increased, and trends are likely to be site specific (Ramsby et al. 2017). Interestingly, phototrophic sponges appear to be more resilient to ocean warming and acidification than their heterotrophic counterparts, which may influence community structures towards phototrophic species (Bennett et al. 2017, 2018). Stark increases in the density of the colonial ascidian, *Didemnum molle*, have also been documented following warming and widespread coral bleaching on the GBR, perhaps linked to reduced competition for space and nutrients and/or reduced predation pressure (Tebbett et al. 2019). It will be increasingly important to determine the competitive relationships between non-coral phase shift drivers (e.g. algae, sponges, ascidians) and how they alter trophic pathways and energy flows on future coral reefs (Norstrom et al. 2009, Maldonado et al. 2015, Bell et al. 2018, Tebbett et al. 2019).

For other marine invertebrates, additive stress from corallivorous gastropods (e.g. *Drupella*) and sea stars (e.g. CoTS, *Culcita*) through coral predation may reduce the resilience and recovery of corals to climate change stressors (Bruckner et al. 2017, Shaver et al. 2018, Bruckner & Coward 2019, Keesing et al. 2019). Marine worms were not considered vulnerable to any stressor, except for *Spirobranchus* to ocean warming, owing to its dependence on live coral substrate and a range of coral-host associations (Strathmann et al. 1984, DeVantier et al. 1986, Dai & Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008), though increased water circulation close to the coral surface as caused by *Spirobranchus* may decrease host susceptibility to bleaching (Strathmann et al. 1984), as posited for other coral-associated groups (Chase et al. 2018).

Ocean warming

Marine organisms are more vulnerable to warming than terrestrial taxa, making increasing ocean temperatures one of the most broadly confronting contemporary stressors (Richardson & Schoeman 2019). The effects of warming on coral reefs are most pronounced, as tropical species already exist within narrow thermal tolerance ranges at their upper limits (Hoegh-Guldberg 1999, Pörtner & Farrell 2008, Pandolfi et al. 2011, Hoey et al. 2016a). While there are high levels of variability in species responses and tolerances to climate change stressors, changing temperature regimes are likely to have significant impacts on species ranges, reproduction, physiology, taxonomy and diversity, productivity and functioning.

Recent temperature-induced bleaching events have had catastrophic impacts on coral reefs globally. On the GBR, back-to-back warming anomalies over 2016 and 2017 resulted in mass bleaching and mortality of corals, particularly in the northern sections of the reef, where coral cover decreased by >80% (Hughes et al. 2017b, 2018b). This has contributed to significant alterations to whole-reef community structure and patterns of reproduction and recruitment (Hughes et al. 2018b, 2019a, Stuart-Smith et al. 2018).

Host-associated phototrophic microbes and most coral groups rated among the most vulnerable to ocean warming (Table 5). Thermal sensitivity of the coral holobiont is well established, with the expulsion of microbial symbionts from the coral host following extended exposure to warm conditions (Brown 1997, Fitt et al. 2001, Bourne et al. 2008, 2016, Baird et al. 2009). This results in a range of physiological and ecological impacts on corals – the coral bleaching phenomenon – with similar effects on other zooxanthellate-host organisms, including tridacnid clams (Buck et al. 2002, Leggat et al. 2003), sponges (Vicente 1990), sea anemones (Lesser et al. 1990) and algal species including CCA (Anthony et al. 2008). Bleaching impairs the transfer of nutrients from the zooxanthellae to the host, impacting tissue development, skeletal growth, biomass, fecundity and autotrophy while increasing susceptibility to disease and host mortality (Szmant & Gassman 1990, Glynn 1996, LeTissier & Brown 1996, Fitt et al. 2001). Yet the relative abundance and local adaptation of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016, Barfield et al. 2018).

Specific coral species and morphologies are documented to be more heavily impacted by ocean warming, with branching and tabular groups (acroporids, pocilloporids) typically most prone to bleaching (Gleason 1993, Baird & Marshall 1998, 2002, Marshall & Baird 2000, Obura 2001, McClanahan et al. 2004, Adjeroud et al. 2005, Thompson & Dolman 2010, Kennedy et al. 2018). Yet these faster-growing corals are critical to postbleaching recovery (Adjeroud et al. 2009, Linares et al. 2011, Ortiz et al. 2014, 2018), and there may be some resilience to the coral bleaching phenomenon through thermally tolerant zooxanthellae and microbiomes (Berkelmans & van Oppen 2006, Epstein et al. 2019b), switches to heterotrophic feeding (Grottoli et al. 2006, Ferrier-Pages et al. 2011), intraspecies resilience across life stages (Putnam et al. 2010, Alvarez-Noriega et al. 2018) and adaptive responses owing to genomic history (Howells et al. 2013, Bay & Palumbi 2015, Dixon et al. 2015, Quigley et al. 2018). High levels of connectivity, most notably in the south poleward direction, along the GBR may facilitate the genetic migration and spread of warmer heat-tolerant alleles to higher latitudes as the climate warms (Poloczanska et al. 2013, Matz et al. 2018).

Ocean acidification

Changes in ocean chemistry (e.g. pH and carbonate ions) are attributable to increased anthropogenic CO_2 in the atmosphere and corresponding CO_2 dissolved by the world's oceans (Kleypas et al. 1999, Caldeira & Wickett 2005, Orr et al. 2005). Resultant decreases in seawater pH and the reduced availability of carbonate ions will directly impair the ability for calcifying organisms to develop their skeletons and shells, including for corals (Hoegh-Guldberg 2005, Przeslawski et al. 2008, De'ath et al. 2009, Anthony et al. 2011b, Fabricius et al. 2011, Wild et al. 2011, Connell et al. 2013, Dove et al. 2013). Coral reefs are among the most sensitive ecosystems to changes in ocean chemistry, as they are fundamentally dependent on calcification to support both habitat and production functioning (Hoegh-Guldberg 2005, Anthony et al. 2011b, Albright et al. 2016a).

CCA ranked as the most vulnerable algal group to climate change stressors, while other algae may benefit from waters higher in temperature (warming) and CO_2 (acidification), with a competitive advantage over corals (Diaz-Pulido & McCook 2002, Diaz-Pulido et al. 2007, 2009, 2011b), though this is not the case for all macroalgae (Bender et al. 2012, 2014a). CCA may even be more sensitive than some corals, exhibiting greater skeletal dissolution due to its high magnesium-calcite carbonate form, and reduced productivity, diversity, growth and survival when exposed to ocean acidification and/or warming (Anthony et al. 2008, Nelson 2009, Diaz-Pulido et al. 2012, Ordonez et al. 2014, McCoy & Kamenos 2015, Cornwall et al. 2019). Variability in natural conditions as driven by diel cycles (particularly in the intertidal) may heighten the sensitivity of CCA to decreases in ocean pH, converse to that suggested for organisms exposed and adapted to naturally extreme conditions (Camp et al. 2018a, Johnson et al. 2019). For example, it is suggested that large benthic Foraminifera show varied responses to ocean change stressors due to their exposure to extreme conditions in shallow-water intertidal environments (Fujita et al. 2011, Doo et al. 2014, Schmidt et al. 2014, 2016, Prazeres et al. 2015). However, any impact on the ability for foraminiferans to calcify will have long-term impacts on reef carbonate dynamics and sediment processes (Dawson et al. 2014).

Records of skeletal growth of massive *Porites* corals indicate a measurable decrease in coral calcification on the GBR over the past few decades (De'ath et al. 2009, 2013) but with high spatial and temporal variability in trends (D'Olivo et al. 2013) and potentially just reflecting short-term responses to thermal stress events (Cantin & Lough 2014). Reduced calcification rates have also been reported for a range of branching corals on the GBR and elsewhere, including for acroporids and pocilloporids (Manzello 2010, Pratchett et al. 2015, Anderson et al. 2017, 2018) and in total carbonate budgets (Case Study 2). Structural branching coral forms are possibly more vulnerable to ocean acidification than robust massive forms (Fabricius et al. 2011, Madin et al. 2012). There are also notable changes in the diversity of the coral microbiome under acidified conditions, which may have concomitant implications for reef structure, recruitment and total functioning (Mouchka et al. 2010, Krause et al. 2012, Doropoulos & Diaz-Pulido 2013, Webster et al. 2013a,b, 2016, Grottoli et al. 2018, Wee et al. 2019). However, the coral microbiome can enhance the transgenerational adaptive plasticity of corals in support of reef adaptation and resilience (Torda et al. 2017, Webster & Reusch 2017).

Coral reefs may switch to a state of net dissolution in the coming decades due to changes in ocean temperature and chemistry, with significant impacts on net ecosystem calcification (Silverman et al. 2012, 2014, Albright et al. 2013, 2018, Kennedy et al. 2013, Cyronak et al. 2018, Eyre et al. 2018, McMahon et al. 2019), sediment dynamics (Eyre et al. 2014, Cyronak & Eyre 2016) and reef recovery (Osborne et al. 2017). On Lizard Island, GBR, net ecosystem calcification decreased by ~46% between 2009 and 2016, measured immediately after extensive coral bleaching (McMahon et al. 2019). Parallel to decreases in calcification, bioerosion rates are accelerating in line with ocean change, which is itself emerging as a significant stressor in terms of reef health and future reef resilience (Reyes-Nivia et al. 2013, DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). The total carbonate budget across the GBR may soon be in a state of net dissolution and erosion, as may already be the case for some reefs (Case Study 2). This trajectory indicates that the GBR may enter a critical negative state in which erosive processes surpass carbonate accretion in a changing ocean, with critical impacts on habitat and production functioning, as suggested for other reefs (Kennedy et al. 2013, Manzello et al. 2017). However, the ability for some bioeroding organisms, like clionid sponges, to persist in a future ocean may also be impacted (Achlatis et al. 2017, Fang et al. 2018, Ramsby et al. 2018a).

Most marine invertebrate groups rated as highly vulnerable to the impacts of ocean warming and acidification (Table 5), with an abundance of research and reviews documenting survival bottlenecks across life-history stages, particularly for calcifying marine larvae and adults (Przeslawski et al. 2008, Byrne 2011, Bhadury 2015, Przeslawski et al. 2015, Espinel-Velasco et al. 2018). Tropical sea urchin larvae are considered among the most vulnerable (Byrne et al. 2013). Unsurprisingly, calcifiers were considered the most vulnerable to ocean acidification here (Table 5). Yet the effects of ocean acidification and the energetic stress of hypercapnia extend well beyond the calcification process, being observed to cause a range of sensory, cognitive and behavioural abnormalities across reef invertebrate and fish life histories (Munday et al. 2009a, 2012, 2014, Briffa et al. 2012, Devine et al. 2012, Domenici et al. 2012, Allan et al. 2013, Watson et al. 2014, 2017, Ferrari et al. 2017, Jarrold et al. 2017, Espinel-Velasco et al. 2018), as well as altered predatory-prey dynamics (Munday et al. 2010, Allan et al. 2013, Heinrich et al. 2016, Watson et al. 2017, Spady et al. 2018). Ocean acidification will also impact settlement success on coral reefs through changes in the nature and distribution of suitable settlement cues and substrates, including CCA and biofilm (Doropoulos et al. 2012a, Doropoulos & Diaz-Pulido 2013, Espinel-Velasco et al. 2018).

Ocean acidification may even enhance certain processes, including bioerosion rates (Reyes-Nivia et al. 2013, Enochs et al. 2015, Schönberg et al. 2017), with potential impacts on reef carbonate budgets (Wisshak et al. 2014, Manzello et al. 2017). Light intensity may work to ameliorate the negative effects of acidification on photosynthesising species like corals (Dufault et al. 2013, Wall et al. 2017) and giant clams (Watson 2015). Tropical deposit-feeding sea cucumbers may partially mediate or buffer the impacts of ocean acidification through their bioturbation activity and contributions to reef biogeochemistry (Schneider et al. 2011, 2013, Wolfe et al. 2018). This has been posited for the mega-consumer and excreter of coral carbonates *Bolbometopon muricatum* (Goldberg et al. 2019), but this remains poorly addressed for parrotfishes in general. Seagrasses, macroalgae and a range of other species may also contribute to the biogenic buffering of reef carbonate chemistry owing to their relative roles in the balance between photosynthesis (i.e. O_2 production) and respiration (i.e. CO_2 production) (Anthony et al. 2011a, McCulloch et al. 2012, Smith et al. 2013, Cornwall et al. 2014, Mongin et al. 2016a, Page et al. 2016, DeCarlo et al. 2017). This presents a potential management strategy through *in situ* cultivation of macroalgae (Mongin et al. 2016a).

Cyclones

While tropical cyclones and storms are not expected to increase in occurrence in a changing climate, they are predicted to increase in severity (Lough 2007). The likelihood of more intense cyclones within timeframes of coral recovery by the mid-century presents significant global threat to coral reefs and those that depend on them (Cheal et al. 2017). Cyclones were suggested to have the strongest impact on sessile marine invertebrates: branching corals (tabular, staghorn, other species), sponges (heterotrophic, phototrophic) and giant clams (Tridacnidae) (Table 5). Zooplankton scored low, yet cyclone and storm events can drive homogenisation of zooplankton communities with potential knock-on effects to higher trophic levels (McKinnon et al. 2003). At the whole-reef scale, mean rates of coral loss on the GBR are projected to be $-0.67\%\ y^{-1}$, largely attributed to cyclone damage (Mellin et al. 2019). At the colony level, morphology plays an important role in the biophysical impacts of cyclones, which are often most severe for fragile branching corals compared to robust massive forms (Woodley et al. 1981, Connell et al. 1997, Hughes & Connell 1999, Adjeroud et al. 2005, Madin 2005, Madin & Connolly 2006, Madin et al. 2014).

The long-term effects of cyclones (i.e. habitat degradation) may have the greatest impact on coral reef fishes and fisheries production (Cheal et al. 2002), but impacts will vary across communities depending on species, depth ranges and exposure gradients (windward, protected) (Ceccarelli et al. 2016). Site-attached reef fishes (e.g. cryptobenthics, damsels, planktivores, cleaner wrasse) scored as the most vulnerable fish groups to cyclones (Table 5). Small fish species that rely on corals for survival may be particularly vulnerable to the habitat loss and increased predation pressure attributed to cyclone damage (Lassig 1983, Harmelin-Vivien 1994, Coker et al. 2009, Ceccarelli et al. 2016). Conversely, resident predatory fishes, which also depend on coral habitat, may be largely resilient to a range of environmental disturbances on the GBR (Emslie et al. 2017). Damselfish assemblages have generally been well retained within their respective regional settings on the GBR, with assemblage degradation only associated with major coral losses (Emslie et al. 2019). Operating on site-specific cleaning stations, cleaner wrasse populations were documented to decline by 80% following a sequential cyclone and El Niño (warming) event on Lizard Island, GBR (Triki et al. 2018). Following extensive habitat loss due to tropical Cyclone Ita, some invertivorous fishes increased in biomass (the titan triggerfish [*Balistoides viridescens*], darkspot tuskfish [*Choerodon monostigma*] and sidespot goatfish [*Parupeneus pleurostigma*]), suggesting they may benefit from novel resources made available for exploitation postdisturbance (Brandl et al. 2016). Grazing fishes (e.g. detritivores, parrotfishes) may help to maintain fish diversity postdisturbance on some reefs (Wilson et al. 2009, Ceccarelli et al. 2016).

Fisheries Ultimately, management of climate change stressors depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functioning and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Overfishing is considered one of the greatest local threats to coral reefs (Jackson et al. 2001, Garcia & Moreno 2003, Bellwood et al. 2004, Newton et al. 2007, Cinner et al. 2016, 2018). Our partitioning of species here to broader taxonomic and functional levels does not fully encapsulate species-specific vulnerabilities to overfishing but rather the groups most broadly at risk. Impacts from fishing were greatest for predatory reef fishes (resident and transient) and for deposit-feeding sea cucumbers (Table 5). While fishing intensity is relatively low at regional scales, commercial fisheries have increased in effort (~40%) and catch (~50%) since the 1990s (Mapstone et al. 2004). Regardless, fin-fish fisheries are generally well managed on the GBR (Williamson et al. 2004, DEE 2017), with reef resilience enhanced through marine park zoning (Mellin et al. 2016). Unlike on other reefs globally, the fishing of herbivores is marginal on the GBR.

The primary fin-fish species targeted on the GBR is the coral trout (*Plectropomus* spp.), considered here as a resident piscivore. An estimated 749 tonnes of coral trout are commercially harvested from the GBR each year, with >100,000 additional individuals harvested by recreational spear and line fishers annually (DEE 2017). Globally, many *Plectropomus* populations are in decline due to the combined effects of overfishing and habitat degradation (Frisch et al. 2016a). On the GBR, coral trout, and a range of other predatory fishes, benefit from no-take zones through increases in biomass, density and size compared to sites open to fishing (Williamson et al. 2004, Heupel et al. 2009, Miller et al. 2012, Emslie et al. 2015, Casey et al. 2017, Castro-Sanguino et al. 2017, Frisch & Rizzari 2019), including in the context of recreational spearfishing (Case Study 3). No-take reserves also preserve the natural behaviour of coral trout, with potential influences on genetic and social structures (Bergseth et al. 2016). In a global context, the status of *P. leopardus* was recently re-evaluated from a Near Threatened to a Least Concern species (Choat & Samoilys 2018), and its fishery on the GBR is well monitored and managed (DEE 2017). For some larger target species, such as sharks, illegal harvest in no-take zones may continue to have significant impacts on population structures (Stevens et al. 2000, Davis et al. 2004, Robbins et al. 2006, McCook et al. 2010, Bergseth et al. 2017, Weekers & Zahnow 2018, Frisch & Rizzari 2019). The Queensland shark control programme also contributes to the extraction of these predators, with around 500–700 sharks removed from Queensland waters each year (QGSO 2019). There has been a regional depletion of shark populations over the past half-century since the onset of this control programme, with concurrent declines in body size and probability of encountering mature individuals, suggesting sharks on the Queensland coastline are more vulnerable to exploitation than previously thought (Roff et al. 2018).

Deposit-feeding sea cucumbers are particularly prone to overfishing due to their ease of collection and general lack of scientific information on their biology and ecology to empower management (Uthicke et al. 2004, Purcell et al. 2013). The sea cucumber (bêche-de-mer) fishery currently operating on the GBR has a history of exploitation, with trends of sequential population declines across species with high market value (Eriksson & Byrne 2015), and continued occurrence of illegal harvest inside the Marine Park bounds (Conand 2018). In 2004, a rotational harvest scheme was implemented as a management tool, but concerns have been raised regarding its effectiveness, as recovery of depleted populations may still be marginal, and caches of high-valued species continue to decline (GBRMPA 2014b, Purcell et al. 2016b). At least ten sea cucumber species found on the GBR are listed as Vulnerable to Extinction on the IUCN Red List for Threatened Species (Conand et al. 2014, Purcell

CASE STUDY 3: FUNCTIONAL IMPACTS OF RECREATIONAL SPEARFISHING ON THE GREAT BARRIER REEF

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Of the recreational fishing methods, spearfishing is a small but contentious component (Godoy et al. 2010, Young et al. 2015). Given the well-documented impacts of line fishing from discarded pollution, lost gear, the requirement of bait and frequent levels of bycatch, spearfishing may be considered the more sustainable practise (Frisch et al. 2008). Yet in a comparison between line and spearfishers on the GBR, despite a similar catch composition and landing fewer fish overall, the mean size of fish caught by spearfishers was significantly greater (Frisch et al. 2008). Spearfishing is a highly selective method where participants can target specific individuals based on species and size, with limited impacts on non-target species (Dalzell et al. 1996, Bejarano et al. 2014). So, while spearfishing may have a seemingly smaller impact on the marine environment, selectivity towards large individuals (that are likely fecund) and particular trophy species may result in negative impacts to viable breeding stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, 2012, Godoy et al. 2010). For example, just three years after the introduction of spearfishing on an inshore reef near Townsville, vast decreases in the number (54%) and size (27%) of coral trout (*Plectropomus* spp.) – the primary fisheries target on the GBR – were recorded (Frisch et al. 2012). There is potential for recreational line and spearfishing to have broadly equivalent impacts on the marine environment (Frisch et al. 2008), but the lack of information on spearfishing often causes it to be overlooked in fisheries management (Johansson et al. 2013, Pavlowich & Kapuscinski 2017), as for recreational fishing in general.

A survey of over 140 spearfishers active on the GBR was conducted to determine which functional groups of coral reef fishes were preferred by spearfishers. From a list of 22 common GBR fishes (Table CS3.1), spanning nominal herbivores ($n = 8$), invertivores ($n = 3$) and piscivores ($n = 11$), coral trout (*Plectropomus* spp.) were outlined as the preferred targets (Figure CS3.1), as in recreational line-based and commercial fisheries on the GBR (Leigh et al. 2014, DEE 2017). The coral trout fishery on the GBR is considered well managed (DEE 2017), which is reflected in the recent re-evaluation of this group from Near Threatened to Least Concern (Choat & Samoilys 2018). Nominally piscivorous species (including Lutjanidae, Lethrinidae and *Plectropomus*) represented ~75% of the preferred catch of spearfishers, while nominal herbivores were lesser preferred (Figure CS3.1). This may be associated with the campaign aimed at spearfishers to limit herbivore catches on the GBR to protect species that reduce algal growth and support reef health and functioning (GBRMPA 2016, 2018a). Tuskfishes (*Choerodon* spp.) were the preferred invertivores (Figure CS3.1), which are broadly distributed across the GBR (Platten et al. 2002, Fairclough et al. 2008). As a Near Threatened and monandric protogynous hermaphroditic species where males only occur in the largest size bracket (Fairclough & Nakazono 2004), the black-spot tuskfish (*C. schoenleinii*) may be particularly vulnerable to the selectivity of spearfishing. Interestingly, the venus tuskfish (*C. venustus*) can alter its sex ratio in response to overfishing (Platten et al. 2002). Regardless, the reproductive biology of tuskfishes has resulted in rapid population declines on other coral reefs owing to overfishing (Ebisawa et al. 1995, Cornish 2003, Fairclough & Nakazono 2004).

While spearfishing has the potential to impact viable fish stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, 2012, Godoy et al. 2010), the Queensland (and Australian) spearfishing community has been highly responsive to previous management campaigns and exhibits self-regulatory and monitoring approaches that are vital to fisheries conservation and advocacy

Table CS3.1 List of species included in surveys of spearfishers operating on the GBR

Family	Species	Common names	Guild	IUCN listing	Size at maturity (cm)	Max size (cm)	Legal catch size (cm)	Legal bag limit	References
Acanthuridae	*Acanthurus dussumieri*	Eyestripe surgeonfish	H	LC	N/A	54	25	5	
	Naso unicornis	Bluespine unicornfish	H	LC	30–35	70	25	5	DeMartini et al. (2014)
Scaridae	*Bolbometopon muricatum*	Green humphead parrotfish	H	V	65	130	25	5	Chan et al. (2012)
	Cetoscarus bicolor	Bicolour parrotfish	H	LC	30	50	25	5	
	Chlorurus bleekeri	Bleeker's parrotfish	H	LC	N/A	49	N/A	N/A	
	microrhinos	Steephead parrotfish	H	LC	37	70	N/A	N/A	Barba (2010)
	Scarus ghobban	Blue-barred parrotfish	H	LC	41	90	25	5	Mellin et al. (2007)
Siganidae	*Siganus lineatus*	Goldlined rabbitfish	H	LC	19–24	43	N/A	N/A	Longenecker et al. (2014)
Labridae	*Choerodon schoenleinii*	Black-spot tuskfish	I	NT	25	100	30	6	Fairclough & Nakazono (2004)
	venustus	Venus tuskfish	I	LC	24	65	30	6	Platten et al. (2002)
Lethrinidae	*Monotaxis grandoculis*	Bigeye seabream	I	LC	27.5	60	25	5	
	Lethrinus miniatus	Redthroat emperor	P	LC	36.1	90	38	8	
	xanthochilus	Yellowlip emperor	P	LC	42.4	70	25	5	Carpenter et al. (2016)
Lutjanidae	*Aprion virescens*	Green jobfish	P	LC	44.9	112	38	5	
	Lutjanus argentimaculatus	Mangrove jack	P	LC	57	150	35	5	
	johnii	Golden snapper	P	LC	44	97	35	5	Kamali et al. (2006)
	rivulatus	Maori seaperch	P	LC	40	80	25	5	Longenecker et al. (2014)
	sebae	Red emperor	P	LC	54.2	116	55	5	
	Macolor niger	Black and white snapper	P	LC	38	75	25	5	Longenecker et al. (2014)
Serranidae	*Epinephelus cyanopodus*	Purple cod (Blue Maori)	P	LC	31–35	122	38	5	Lau & Parry Jones (1999)
	Plectropomus leopardus	Coral trout	P	LC	32–17	120	38	7	Choat & Samoilys (2018)
Rachycentridae	*Rachycentron canadum*	Cobia	P	LC	75	200	70	2	Babatunde et al. (2018)

Notes: Data obtained from the online FishBase resource, unless otherwise stated. Legal limit data are taken from the Department of Agriculture and Fisheries, Queensland Government.
Abbreviations: H, herbivore; I, invertivore; P, piscivore; LC, least concern; V, vulnerable; NT, near threatened; N/A, data not available.

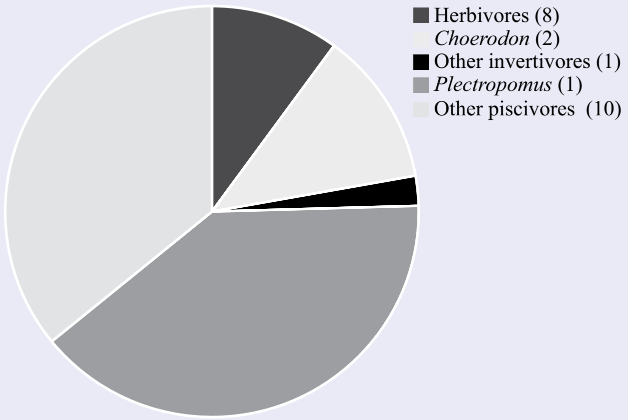

Figure CS3.1 Contribution of select coral reef fishes to the estimated catch of spearfishers active on the GBR. Number of species in each group in parentheses.

(Young et al. 2014, 2016, GBRMPA 2016). We highlight the importance of 1) educating groups on spearfishing-selectivity for species with vulnerable reproduction (e.g. coral trout, tuskfishes) and 2) monitoring catch trends for key species within the spearfishing community to inform self-regulation. Quantitative data on catch sizes, target species and catch per unit effort are needed, particularly for target species and those with vulnerable reproductive biology.

et al. 2014, Richards & Day 2018) and three species of teatfish are proposed to be listed in CITES Appendix II (Di Simone et al. 2019). There is particular concern for the black teatfish (*Holothuria whitmaei*), as its fishery, which was closed in 1999 due to widespread overharvest (Uthicke et al. 2004, Eriksson & Byrne 2015), may be reopening (DAF 2018) without fisheries-independent data to indicate whether populations have recovered. Quantitative information on bêche-de-mer populations along and across the GBR is imperative to inform management independent of fisheries.

Interestingly, no other group scored as vulnerable to fisheries. A range of fishing-related impacts are documented on the GBR, resulting from derelict fishing gear that can entangle corals and increase disease susceptibility (Williamson et al. 2014a), anchor and vessel damage (Beeden et al. 2014a, Kininmonth et al. 2014), frequent by-catch from commercial fisheries (Hill & Wassenberg 2000) and illegal practises in no-take zones (Davis et al. 2004, Arias & Sutton 2013, Williamson et al. 2014a, Bergseth et al. 2015, Weekers & Zahnow 2018). The impact of recreational spearfishing is assessed in detail in Case Study 3. We acknowledge that assessment beyond the broad taxonomic and functional groups examined here is necessary to determine specific impacts from fisheries on the GBR. It will also be important to assess fisheries operating outside of coral habitat, including soft-bottom, interreefal, coastal and intertidal habitats where many commercially important invertebrates on the GBR are targeted, including prawns and scallops (Gribble 2003, Courtney et al. 2008, 2015, GBRMPA 2014b). Future work should also consider social, cultural and economic values of fisheries targets on the reef.

Population outbreaks There are a range of species, particularly non-coral marine invertebrates, that exhibit marked population fluxes on coral reefs (Norstrom et al. 2009). The boom-and-bust phenomenon of the Echinodermata is well documented (Uthicke et al. 2009). On the GBR, outbreaks of *Acanthaster* cf. *solaris* (CoTS) are the most extensive, destructive and researched outbreak candidate, gaining considerable traction in reef management (Westcott et al. 2016, Sweatman &

Cappo 2018). As scored here, population outbreaks (namely in consideration of CoTS) were outlined to have the greatest potential impact on tabular, staghorn and other branching corals (Table 5). *Acropora* and *Montipora* are the preferred coral genera of CoTS across the Pacific (Laxton 1974a, Pratchett et al. 2014, Westcott et al. 2016), though even the less-preferred coral species are consumed during extreme outbreaks or when food is scarce (Chesher 1969, Pearson & Endean 1969). At the whole-reef scale, corallivory by CoTS in outbreak densities has been attributed to ~42% of the declines in live coral cover on the GBR (De'ath et al. 2012). However, this statistic is likely to be much lower at present in light of extensive coral bleaching in 2016 and 2017 (Hughes et al. 2017b, 2018b,c).

Outbreaks of other marine invertebrates have received considerably less attention on the GBR and in general. High densities of *Drupella* sp. (Muricidae) can have significant impacts on reef condition, documented to reduce live coral cover by >75% on some reefs (Turner 1994, Scott et al. 2017a). Their effects can be even more significant following bleaching-induced coral mortality, which can impact coral resilience and recovery (Bruckner et al. 2017, Keesing et al. 2019), similar to other corallivorous gastropods, including *Coralliophila* (Muricidae) (Shaver et al. 2018) and *Dendropoma* (Vermetidae) (Smalley 1984, Shima et al. 2010). While these gastropods are present on the GBR, such extensive impacts have not been documented (Cumming 2009). Stark increases in the density of the colonial ascidian *Didemnum molle* were recently documented on Lizard Island following pervasive coral bleaching (Tebbett et al. 2019). While corallivorous species like CoTS and *Drupella* have direct impacts on the persistence of corals through predation, rapid expansions of opportunistic sessile organisms, like these ascidians, can impact reef recovery and resilience through competition for food and space and potential toxicity (Bak et al. 1996, Tebbett et al. 2019). Even at highly localised scales, population outbreaks of alternative opportunistic invertebrates, including sea cucumbers and sea stars, can have repercussions on coral recruitment, recovery and functioning (Zhang et al. 2018, Bruckner & Coward 2019). Ecosystem states are dynamic in terms of time and space (van de Leemput et al. 2016), and phase shifts beyond the typical coral-algal model are increasingly common as reefs degrade (Norstrom et al. 2009).

In general, there has been little documentation of extensive impacts from invasive or introduced species in the marine environment of the GBR, with a greater representation and impacts documented for mainland and island habitats (GBRMPA 2014b).

Diseases Diseases are poorly understood for corals and other marine species on the GBR, despite documentation of widespread proliferation in some cases (Richardson 1998, Willis et al. 2004, Roff et al. 2011, Shore & Caldwell 2019). Disease proliferation in other marine environments is a portent of the devastating impacts and rapid rate of spread that can occur, including the *Diadema* die-off in the Caribbean (Hughes 1994, Mumby et al. 2006b, Feehan & Scheibling 2014) and sea star wasting disease on the US west coast (Bates et al. 2009, Hewson et al. 2014, Eisenlord et al. 2016, Montecino-Latorre et al. 2016). While expert scores were considerably lower for disease than for a number of other stressors, acroporids (tabular and staghorn) rated as the most vulnerable to disease (Table 5). White Syndrome primarily impacts tabular acroporids compared to other coral species and functional forms (Hobbs & Frisch 2010, Hobbs et al. 2015). Coral disease can reduce net growth rates of corals, particularly tabular acroporids, by ~20% (Roff et al. 2008, Maynard et al. 2011).

In the marine environment, disease proliferation is largely induced by temperature anomalies (Bruno et al. 2007, Harvell et al. 2007, Sato et al. 2009, 2011, 2016, Maynard et al. 2011, Ruiz-Morenol et al. 2012, van de Water et al. 2016, Chen et al. 2017) but can also be expedited by plastic pollution (Lamb et al. 2018), runoff and sedimentation (Haapkyla et al. 2011, Pollock et al. 2016), cyclone damage (Sato et al. 2018), tourism (Lamb & Willis 2011, Lamb et al. 2014, van de Water et al. 2015) and fisheries activity (Diaz-Pulido et al. 2009, Page et al. 2009, Graham et al. 2011a, Williamson et al. 2014a, Lamb et al. 2015, 2016). While the transmission of coral disease between individuals and among populations remains understudied (Shore & Caldwell 2019), it seems that any considerable stressor can enhance disease susceptibility on coral reefs, particularly inshore on the GBR (MacNeil et al. 2019). Disease management on the GBR focuses on continued research and monitoring of disease outbreaks to inform local response plans (Maynard et al. 2011, Beeden et al. 2012). To date, it seems that Australia's biosecurity strategies regarding terrestrial, agricultural and human-based diseases typically receive greater attention in contingency planning (Craik et al. 2017).

Water quality Water quality stressors (nutrients, sediments, pollutants) were not considered severe threats in the context of offshore reefs (Table 6), assumedly driven by low exposure at distance from the coastline. This is most likely because the three water quality stressors assessed here are closely related to aeolian processes. Water quality scores did not consider impacts from other sources of pollution, including shipping, noise pollution, plastics and oil and gas. Broader consideration of these pollution types should be considered in future work. When assessed in context of nearshore reefs, nutrients, sediments and pollutants were considered to have greater impacts across our functional groups (Table 6).

Declining water quality is considered one of the greatest threats to the long-term health of the GBR but most critically for inshore reefs (Brodie & Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). While consistent exposure to poor water quality may render inshore reefs more resilient (Browne 2012, Perry et al. 2012b), they typically exhibit slower rates of growth and recovery (MacNeil et al. 2019, Mellin et al. 2019). Microbial groups scored among the most vulnerable to water quality stressors, particularly host-associated groups (Table 6). Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 2018a), with populations that vary in response to external conditions (e.g. season, water quality) and habitat type (Kelly et al. 2014, Tout et al. 2014, Angly et al. 2016, Frade et al. 2016, Agusti et al. 2019). Such environmental parameters can drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR (Case Study 4).

Spatially, nutrient (e.g. chlorophyll *a*) levels on the GBR typically increase from north to south and from outer to inner coastal regions, supporting bottom-up processes from the plankton along these gradients (Skerratt et al. 2019). It appears that dissolved inorganic nitrogen, primary production, phytoplankton biomass and zooplankton grazing are elevated in La Niña years, driven by greater average winds, rainfall and river discharge (Skerratt et al. 2019). A range of species in the plankton (e.g. copepods, Appendicularia) are reported to increase in abundance on anthropogenically disturbed reefs, possibly due to increases in terrestrial runoff and nutrients (Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016).

Sediment loads on inshore reefs were considered a significant stressor for many of the species examined here (Table 6), in line with the literature (Bainbridge et al. 2009, 2014, Brodie et al. 2013, Tsatsaros et al. 2013, Waterhouse et al. 2013). Only a small proportion of land-derived sediment reaches mid- to outer-reefs on the GBR (Bartley et al. 2014). Sediments can have a range of impacts on coral reef communities through elevated turbidity gradients, reduced light availability and the physical smothering of sessile organisms, and fine sediments typically have greater impacts on coral reefs than course sediments (Erftemeijer et al. 2012). On the GBR, macroalgal and bioeroding communities show a positive relationship with suspended sediment concentrations, contrasting the negative relationship observed for coral and CCA cover (Fabricius & De'ath 2001b, 2004, Fabricius et al. 2005, Hutchings et al. 2005, Bessell-Browne et al. 2017b). Sediments and high turbidity alter reef structure, reproduction, larval success, recruitment, bioerosion and species interactions on inshore reefs (Babcock & Davies 1991, Fabricius 2005, 2005, Hutchings et al. 2005), with extensive dredging activity posing considerable risk (Erftemeijer et al. 2012, Jones et al. 2016, Bessell-Browne et al. 2017a, Pineda et al. 2017b, Tebbett et al. 2017d).

Sessile and filter-feeding invertebrates are possibly most susceptible to sediment loads, including corals, sponges and giant clams (Elfwing et al. 2003, Przeslawski et al. 2008). However, some nearshore reefs appear resilient to turbidity, maintaining relatively rapid accretion rates and high

CASE STUDY 4: MICROBIAL COMMUNITIES AS INDICATORS OF WATER QUALITY ON THE GREAT BARRIER REEF

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Microorganisms are fundamental drivers of biogeochemical cycling in coral reef ecosystems (Gast et al. 1998, Bourne & Webster 2013b) and are critical to the health of keystone marine invertebrates, including corals (Bourne et al. 2016). The current lack of available microbial data collected at sufficient spatial and temporal resolution hinders our capacity to identify the contributions that microbes make to a functioning reef and reef resilience (Dinsdale et al. 2008). Faced with the growing impacts of rapid climate change (Hughes et al. 2017a, Osborne et al. 2017), identification of microbial taxa that contribute to a healthy reef is critical. This case study synthesises available information on pelagic microbial communities across GBR regions (Table CS4.1; Figure CS4.1). Relative microbial abundances were used to identify patterns in communities along inshore to offshore gradients in the context of riverine floodwaters and water quality plumes (Angly et al. 2016).

Pelagic microbial communities across the GBR respond in a deterministic way to environmental fluctuations and drivers. This means that microbial community dynamics can be modelled to better understand how ecosystem functioning can predict changes to reef health and redress knowledge gaps that may guide future interventions aimed at mitigating environmental stressors. For example, the cyanobacterial family Prochlorococcaceae is more common under oligotrophic conditions (offshore), while Synechococcaceae becomes increasingly dominant in nutrient-rich eutrophic waters (inshore) (Figure CS4.2) (Dinsdale et al. 2008). The relative abundance of these two groups varies between wet and dry seasons, as evidenced on the mid-shore Yongala reef, which switches from Prochlorococcaceae dominance to Synechococcaceae dominance in the wet season, likely owing to influence from terrestrial freshwater runoff (Figure CS4.2) (Dinsdale et al. 2008). These two photoautotrophic bacterial families have different capacities to use organic nitrogen (Scanlan & West 2002, Zubkov et al. 2003), and so the Prochlorococcaceae:Synechococcaceae relative abundance ratio can be used as an indicator for nutrient enrichment at a range of spatial and temporal scales (Figure CS4.2).

Table CS4.1 Summary of published and unpublished microbial 16S rRNA data sets for the GBR; BPA = BioPlatforms Australia (https://data.bioplatforms.com/).

Region	No. samples	No. locations	Rarefaction depth	Sequencing platform	Taxonomic assignment	Primer pair and refs	Reference
Tully	78	7	250	454	SILVA and Greengenes	pyroLSSU926F/ pyroLSSU1392R	Angly et al. (2016)
Burdekin	48	3	25,000	Illumina Miseq 2 × 300	SILVA	27F/519R	Glasl et al. (2019)
Coral Sea	9	6	100,000	Illumina Miseq 2 × 300	SILVA	27F/519R	BPA
Yongala (Burdekin)	97	1	30,000	Illumina Miseq 2 × 300	SILVA	27F/519R	BPA
Heron Island	16	4	50,000	Illumina Miseq 2 × 300	SILVA	515F/806Rb	Epstein et al. (2019a)
Mackay	8	4	1,350	454	GreenGenes	63F/533R	Alongi et al. (2015)

Another example of a microbial-based indicator exists in the ratio between Pelagibacteraceae and SAR86, which is negatively correlated with increasing nutrient levels. Levels of typical copiotrophs such as families OCS155, Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae could be modelled against levels of oligotrophs such as Pelagibacteraceae and SAR86 to generate new indices indicative of eutrophication (e.g. Haas et al. 2016). Typical opportunistic bacteria, including those exhibiting virulence towards benthic organisms (e.g. in the families Rhodospirillaceae, Rhodobacteraceae and Vibrionaceae), could also be used as indicators of reef health and/or degradation. Microbial baselines could be used to assess impacts from coastal eutrophication, anthropogenic disturbance and climate change, as microorganisms represent the first responders to environmental change and may mitigate or exacerbate the impacts of disturbance for higher trophic levels. How microbial assemblages translate to changes in benthic composition (macroalgal versus coral cover) and reef health requires attention (Glasl et al. 2019). Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients in the northern, central and southern GBR would enable a robust assessment of the microbial contribution to reef functioning and health.

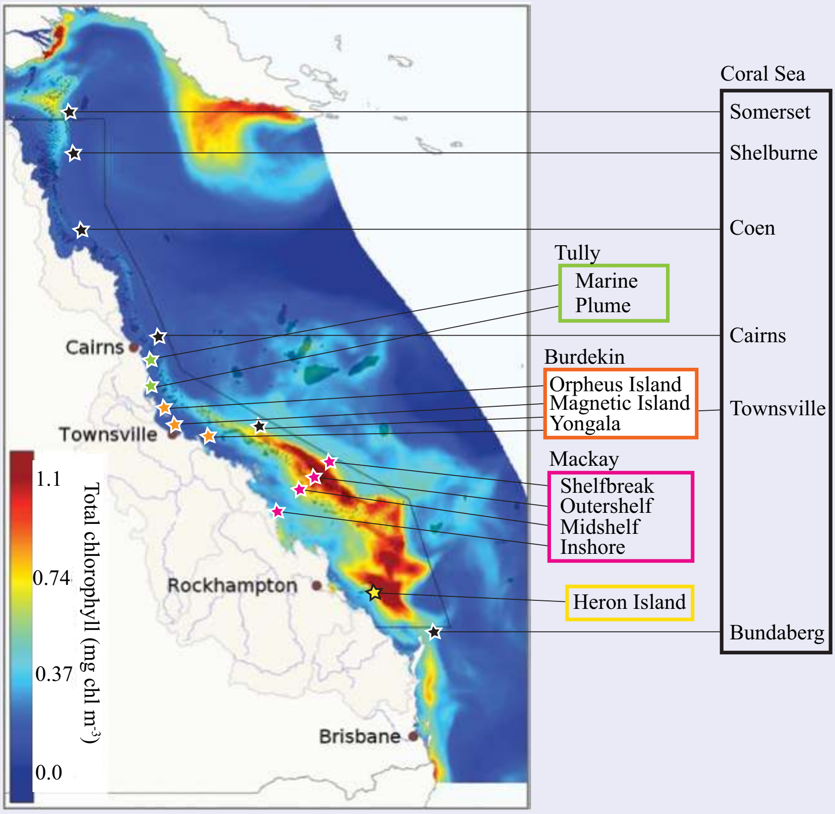

Figure CS4.1 Regions and locations on the GBR covered in the literature for pelagic microbial data sets (see Table CS4.1). Chlorophyll data obtained from eReefs (June 2016) (CSIRO GBR4 Hydrodynamic Model v2.0), with online map generation by AIMS.

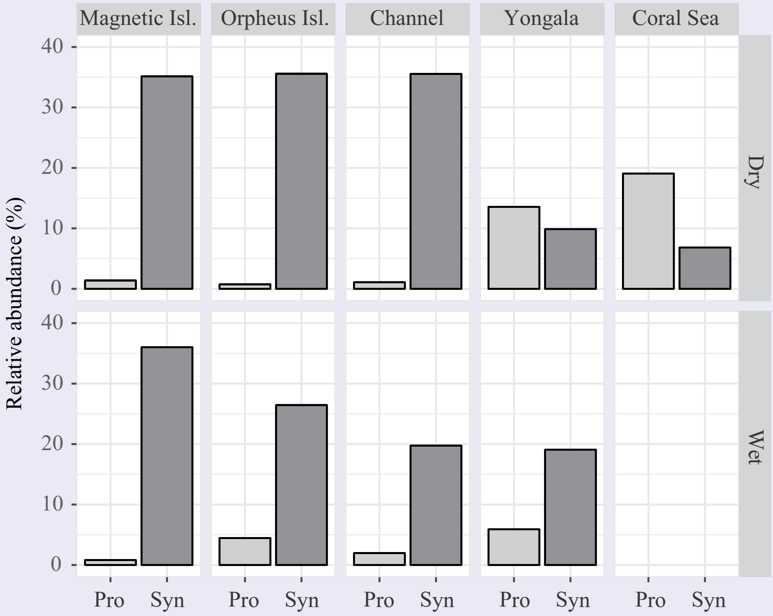

Figure CS4.2 Relative abundance of the cyanobacteria Prochlorococcaceae (Pro) and Synechococcaceae (Syn) during wet and dry seasons in the Burdekin region (see Figure CS4.1). Data provide comparison between inshore (Magnetic Island, Orpheus Island and Channel), mid-shore (Yongala) and open ocean (Coral Sea) regions. Coral Sea only sampled in dry season.

coral cover (Browne et al. 2010 2013, Browne 2012, Perry et al. 2012b) but with trade-offs in feeding regimes (Anthony 2000, Anthony & Fabricius 2000, Anthony & Connolly 2004), morphology (Browne et al. 2010, Padilla-Gamino et al. 2012, Duckworth et al. 2017) and skeletal density (Rocker et al. 2017). Sponges rated among the most vulnerable to sediments and pollutants (Table 6), yet both sponges and their microbiomes seem relatively resilient to high sediment loads on the GBR (Pineda et al. 2017b,c, Strehlow et al. 2017), and some species may even thrive (Bell et al. 2015). While responses are variable (Pineda et al. 2017a), the diversity of sponges, even at small cryptic scales, may offer some resilience to sediment and pollutant loads (Schönberg 2001, 2016). Increases in the benthic cover of *Cliona*, the most abundant bioeroding sponge on the GBR, are greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

For reef fish communities, increased suspended sediments can impact foraging, growth, larval development, behaviour and predator-prey interactions (Wenger et al. 2011, 2012, 2013, 2014). Foraging success of visual predators like planktivorous damselfishes can be significantly impaired in turbid environments (Wenger et al. 2012, Johansen & Jones 2013). Herbivorous fishes rated among the most vulnerable to sediments (Table 6), with some species shown to decrease grazing activity when sediments loads are too high in the EAM (Bellwood & Fulton 2008, Goatley & Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). This can be expedited by turf canopy height, whereby taller canopies trap sediments with negative impacts on herbivory and coral recruitment (Carpenter & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & Bellwood 2012, Clausing et al. 2014, Lam et al. 2018). Interestingly, some detritivores may be particularly important in removing sediment and detritus from the EAM, facilitating herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015).

Habitat degradation associated with coral bleaching and freshwater flood plumes (Williamson et al. 2014b) has been shown to drive dietary shifts in both juvenile (Wen et al. 2016) and adult (Hempson et al. 2017) coral trout. This trophic plasticity involved consumption of non-preferred fishes in line with changes in foraging behaviour (Wen et al. 2016) and prey biomass (Hempson et al. 2017). Although dietary adaptive capacity may mitigate short-term impacts of sedimentation and habitat degradation, it may result in a shortened and simplified trophic structure with a longer-term toll on ecosystem functioning (Graham et al. 2007, Estes et al. 2011, Hempson et al. 2017, Feary et al. 2018). These stressors impact predator-prey dynamics are particularly important to characterise, particularly for key fisheries targets with ontogenetic shifts in diet, like coral trout (Case Study 1).

Pesticides, herbicides, trace metals and agricultural nutrients (e.g. nitrogen, phosphorus) that influence eutrophication are commonly measured on nearshore reefs of the GBR at concentrations above Australian water quality guidelines (Lewis et al. 2009, 2012, Brodie & Waterhouse 2012, Waterhouse et al. 2012, Brodie et al. 2013). However, few toxic pollutants on the GBR approach harmful concentrations and, if so, are typically only recorded during short-term runoff pulses (van Dam et al. 2011). Further, there is limited empirical evidence on how pesticides scale up to impact inshore ecosystem processes, functioning and services (Fichez et al. 2005, van Dam et al. 2011, de Valck & Rolfe 2018). In the context of nearshore systems on the GBR, there is a lack of evidence that mangrove and seagrass biomes are negatively impacted by water quality stressors, but elevated nutrient levels, substrate availability and low grazing pressure suggest that nearshore benthic communities are shifting towards macroalgal abundance, with negative impacts on reef functioning (Schaffelke et al. 2005).

On the GBR, the herbicide Diuron has received considerable attention, which can impact photosynthesis, fecundity, larval development and survival in a range of groups, including corals, CCA, foraminiferans and sea urchins (Negri et al. 2005, Cantin et al. 2007, Magnusson et al. 2008, 2012, Shaw et al. 2009,). Regarding bottom-up effects, biofilms (EAMs) may be resilient to herbicides, but their community structure can be altered depending on exposure thresholds (Magnusson et al. 2012). *In situ* nutrient dosages of nitrogen and phosphorus impacted coral growth, recruitment and skeletal density but only when loading was high and generally with sublethal effects (Koop et al. 2001, Bell et al. 2007). Elevated nutrient levels can also enhance microbioerosion, making it imperative to manage water quality as coral reefs degrade (Chazottes et al. 2017). Most significantly, elevated nutrients have been attributed to CoTS outbreaks on the GBR through the enhancement of success in pelagic larval life stages, which has received considerable attention in the literature (Brodie et al. 2005, Fabricius et al. 2010, Wooldridge & Brodie 2015, Babcock et al. 2016a, Wolfe et al. 2017, Uthicke et al. 2018, Wolff et al. 2018), although the links are tenuous and unresolved (Pratchett et al. 2014, 2017a, Wolfe et al. 2017).

Rainfall is highly variable in northeast Australia, and there is no real consensus on projections for precipitation events in the coming decades (Whetton et al. 2005). However, the intensity of drought and rainfall events is expected to increase, elevating risks associated with flood events and water quality (Lough 2007, Lovelock & Ellison 2007, Adame et al. 2019). Overall, water quality stressors are likely to combine with other environmental factors with significant additive impacts, particularly in the context of thermal stress (Wooldridge & Done 2009, Negri et al. 2011, van Dam et al. 2011, Lewis et al. 2012, van Dam et al. 2012, 2015, Banc-Prandi & Fine 2019). Early monitoring of runoff loads, particularly following heavy rainfall and flood events, has resulted in tighter regulations and catchment management in the GBR region (Brodie & Waterhouse 2012, Brodie et al. 2012). Even though water quality issues have been a strong management focus on the GBR, current initiatives to improve or reverse pollutant loads are not being met (de Valck & Rolfe 2018). A better understanding of the direct impacts of pollutants (e.g. pesticides, metals, nutrients) on coral reef organisms, and the functioning and services they provide, is essential to ensure management goals are biologically relevant and postdisturbance recovery is supported (Fichez et al. 2005, van Dam et al. 2011).

Total vulnerability and recoverability

Using the IPCC Vulnerability Framework (IPCC 2007), corals were outlined as the most vulnerable across the nine stressors for both inner reef and offshore regions (Table 7). Vulnerability scores were generally higher for inner reefs compared to reefs offshore, owing to the additional impacts from water quality in close proximity to the coastline. Branching and tabular corals were rated the most vulnerable of our 70 groups but with tabular corals rated to have a higher level of recoverability (Table 7). Host-associated phototrophic microbes were the most vulnerable microbial group, considered especially vulnerable inshore, as for CCA (Table 7). The most vulnerable invertebrates were coral-associated decapods, several mollusc groups (particularly giant clams; Tridacnidae) and deposit-feeding sea cucumbers (Table 7). Piscivores (resident, transient) were considered the most vulnerable of the reef fishes with the lowest recovery potential (Table 7), strongly influenced by their potential to be impacted by fisheries (Table 5). Staghorn and massive corals were predicted to have the lowest recovery potential for corals, and the triton snail was rated lowest for recovery overall (Table 7). Once considered abundant, densities of triton snails on the GBR have remained extremely low since their extensive overharvest in the 1930s (Endean 1969, Endean & Stablum 1973, Hall et al. 2017). Deposit-feeding sea cucumbers were also suggested to have particularly low recovery potential (Table 7), as bêche-de-mer fisheries operating on the GBR follow global trends of overharvest with no fisheries-independent data available to suggest overfished populations have recovered (Eriksson & Byrne 2015, Purcell et al. 2016b).

Combined assessment of functionally important and vulnerable groups

In order to identify key species for targeted management on the GBR, we compared scores for functional importance against scores for vulnerability (Figure 4). Using the median values for both axes, four quadrants were established to represent priority targets (Figure 4);

1. Intervention (high priority): Functionally important and vulnerable groups that should be considered top priorities for management.
2. Intervention (low priority): Important groups that are not as vulnerable but may still be considered for management to conserve a functioning reef.
3. Protection: Vulnerable groups that were not considered as critical to reef functioning but may require protection to ensure they are not lost.
4. Monitor: Low-rated importance and vulnerability suggests little action may be needed, but populations should still be monitored, especially when certainty is low.

Not surprisingly, most coral groups scored highly for both measures and are considered top priority (Figure 4). Specifically, tabular and branching groups (staghorn, other) ranked highest. Host-associated phototrophic microbes also ranked as a top priority, although they were scored to be less vulnerable than these coral groups (Figure 4). The remaining microbial groups were considered lower priority owing to their low scores for vulnerability (Figure 4), despite free-living microbes (i.e. those in seawater or sediment) and bacteria emerging as important bioindicator tools for monitoring reef health (Case Study 4) (Glasl et al. 2017, 2018a), as for phytoplankton (Revelante & Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Coral-associated decapods ranked highly, along with a range of other invertebrates, including zooplankton, bivalves and giant clams, triton snails and other gastropods (herbivores, predators). Regular sea urchins (e.g. *Diadema*) also fell within this top priority space, perhaps due to lessons learned from the Caribbean (Hughes 1994, Mumby et al. 2006a,b). Top-priority algal groups were the calcifiers (CCA, calcareous) owing to their higher-rated vulnerabilities compared to the remaining algal groups. Despite their great contributions to a functioning reef, algal turfs and macroalgae were categorically considered low priority for management owing to lower-rated vulnerabilities (Figure 4). However, the opportunistic nature of

Table 7 Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

		Inner GBR		Outer GBR			
Taxa	Functional group	PI	V	PI	V	Recoverability	Certainty
Microbes	Phototrophic	30.00	40.00	11.00	14.67	0.75	0.75
	Host-associated	62.00	99.20	27.25	43.60	0.63	0.50
	Chemoautotrophic	14.00	18.67	5.00	6.67	0.75	0.63
	Heterotrophic	19.00	25.33	10.00	13.33	0.75	0.63
Algae	Phytoplankton	10.00	13.33	0.25	0.33	0.75	0.75
	Algal turfs	11.00	14.67	1.25	1.67	0.75	0.75
	Leathery	8.25	16.50	3.50	7.00	0.50	0.50
	Foliose	13.25	17.67	2.50	3.33	0.75	0.63
	Calcareous	23.25	46.50	12.50	25.00	0.50	0.50
	CCA	47.00	62.67	23.00	30.67	0.75	0.50
Sponges	Heterotrophic	44.33	76.00	27.89	47.81	0.58	0.50
	Phototrophic	47.11	80.76	24.00	41.14	0.58	0.50
	Boring	17.81	26.71	3.47	5.21	0.67	0.58
	Cryptic	29.00	49.71	6.25	10.71	0.58	0.50
Coral	Tabular	82.70	110.27	65.20	86.94	0.75	0.75
	Staghorn	83.03	147.62	65.53	116.51	0.56	0.69
	Branching (other)	79.81	116.09	63.73	92.70	0.69	0.69
	Massive	41.76	83.51	30.82	61.64	0.50	0.75
	Encrusting	45.51	66.19	32.51	47.28	0.69	0.69
	Free-living	37.87	55.08	28.62	41.63	0.69	0.56
	Soft corals	43.03	68.86	31.72	50.76	0.63	0.63
	Foraminifera	26.31	38.26	19.37	28.17	0.69	0.44
Worms	Nematodes	0.00	0.00	0.00	0.00	0.75	0.63
	Nemertea	0.25	0.33	0.25	0.33	0.75	0.38
	Polychaetes	0.25	0.33	0.25	0.33	0.75	0.38
	Spirobranchus	28.00	37.33	16.00	21.33	0.75	0.38
Crustaceans	Decapods (H)	29.00	38.67	25.00	33.33	0.75	0.38
	Decapods (P)	36.25	58.00	32.25	51.60	0.63	0.38
	Coral-associated	54.25	108.50	42.25	84.50	0.50	0.50
	Barnacles	26.00	34.67	19.00	25.33	0.75	0.38
	Stomatopods	22.25	29.67	18.25	24.33	0.75	0.38
	Cleaner shrimp	30.00	48.00	26.00	41.60	0.63	0.50
	Infauna	11.25	18.00	10.25	16.40	0.63	0.50
	Zooplankton	30.25	40.33	25.50	34.00	0.75	0.50
	Parasitic	14.25	19.00	13.25	17.67	0.75	0.50
Molluscs	Gastropods (H)	37.00	59.20	32.25	51.60	0.63	0.50
	Gastropods (P)	21.11	33.78	17.11	27.38	0.63	0.50
	Triton snails	21.36	56.96	17.36	46.30	0.38	0.50
	Drupella	36.25	48.33	32.25	43.00	0.75	0.63
	Tridacnidae	62.00	106.29	51.25	87.86	0.58	0.67
	Bivalves	46.00	73.60	38.25	61.20	0.63	0.63
	Chitons	19.00	25.33	19.00	25.33	0.75	0.50
	Cephalopods	19.61	26.15	7.75	10.33	0.75	0.50
Echinoderms	Seastars (H)	18.00	24.00	13.25	17.67	0.75	0.50
	Seastars (P)	15.00	20.00	11.00	14.67	0.75	0.50
	CoTS	12.00	16.00	11.00	14.67	0.75	0.75

(Continued)

Table 7 (*Continued*) Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

		Inner GBR		Outer GBR			
Taxa	Functional group	PI	V	PI	V	Recoverability	Certainty
	Sea cucumbers (DF)	35.25	70.50	31.25	62.50	0.50	0.50
	Sea cucumbers (SF)	17.00	22.67	12.25	16.33	0.75	0.50
	Sea urchins (regular)	30.00	40.00	25.25	33.67	0.75	0.50
	Sea urchins (irregular)	26.25	42.00	25.25	40.40	0.63	0.50
	Brittle stars	14.25	19.00	13.25	17.67	0.75	0.50
	Feather stars	18.00	24.00	14.00	18.67	0.75	0.50
Fishes	Cryptobenthic	39.56	52.74	29.11	38.81	0.75	0.67
	Farmers	27.11	36.15	11.67	15.56	0.75	0.67
	Scrapers (scarids)	22.00	29.33	6.00	8.00	0.75	0.67
	Browsers (nasos)	13.44	20.17	4.11	6.17	0.67	0.67
	Browsers (siganids)	13.78	20.67	4.44	6.67	0.67	0.75
	Browsers (other)	13.78	23.62	4.44	7.62	0.58	0.50
	Bolbometopon	23.56	40.38	10.89	18.67	0.58	0.75
	Excavators (other)	23.67	35.50	7.67	11.50	0.67	0.67
	Detritivores	22.22	29.63	11.56	15.41	0.75	0.58
	Planktivores	40.56	60.83	30.11	45.17	0.67	0.75
	Corallivores	56.11	96.19	38.44	65.90	0.58	0.58
	Invertivores (labrids)	24.11	32.15	11.67	15.56	0.75	0.67
	Invertivores (other)	25.78	44.19	13.33	22.86	0.58	0.67
	Invertivores (lutjanids)	17.44	34.89	10.44	20.89	0.50	0.58
	Eels	25.00	50.00	14.33	28.67	0.50	0.50
	Piscivores (residents)	52.11	104.22	36.67	73.33	0.50	0.58
	Piscivores (transients)	44.89	89.78	31.11	62.22	0.50	0.75
	Cleaner wrasse	26.22	34.96	20.56	27.41	0.75	0.63

Note: Values are shown for inner and outer reefs. Dark cells = top 10th percentile of scores (bottom 10th for recoverability); light cells = top 25th percentile.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders

these algal groups can drive phase shifts away from coral dominance, and for this very reason, they should not be ignored in management, particularly on inshore reefs where nutrient enrichment from water quality can enhance algal growth (Vermeij et al. 2010, Gordon et al. 2016a), including on the GBR (Schaffelke et al. 2005, Lam et al. 2018). Phototrophic and heterotrophic sponges were top-priority sponge groups, while the more functionally important cryptic and boring sponges were considered more resilient (Figure 4).

For the reef fishes, although scoring lower for their total functional importance compared to other fish groups, cleaner wrasse and cryptobenthic fishes were the only two fish groups to fall within the top priority space (Figure 4). For cleaner wrasse, which may not be the most directly important or vulnerable of the reef fishes, this score was largely attributed to their low ecological redundancy. Interestingly, those that were considered among the most functionally important groups (e.g. *Bolbometopon*, scarids, damselfishes, detritivores) were not considered highly vulnerable (low priority), while those that were the most vulnerable (e.g. piscivores, corallivores, planktivores) were not ranked among the key groups for maintaining a functioning reef (Figure 4). This highlights the importance of using a multi-level approach in assessing species' functionality.

For each group of species, we combined their functional importance per process and vulnerability per stressor in every combination to calculate the relative impact of each stressor at various levels

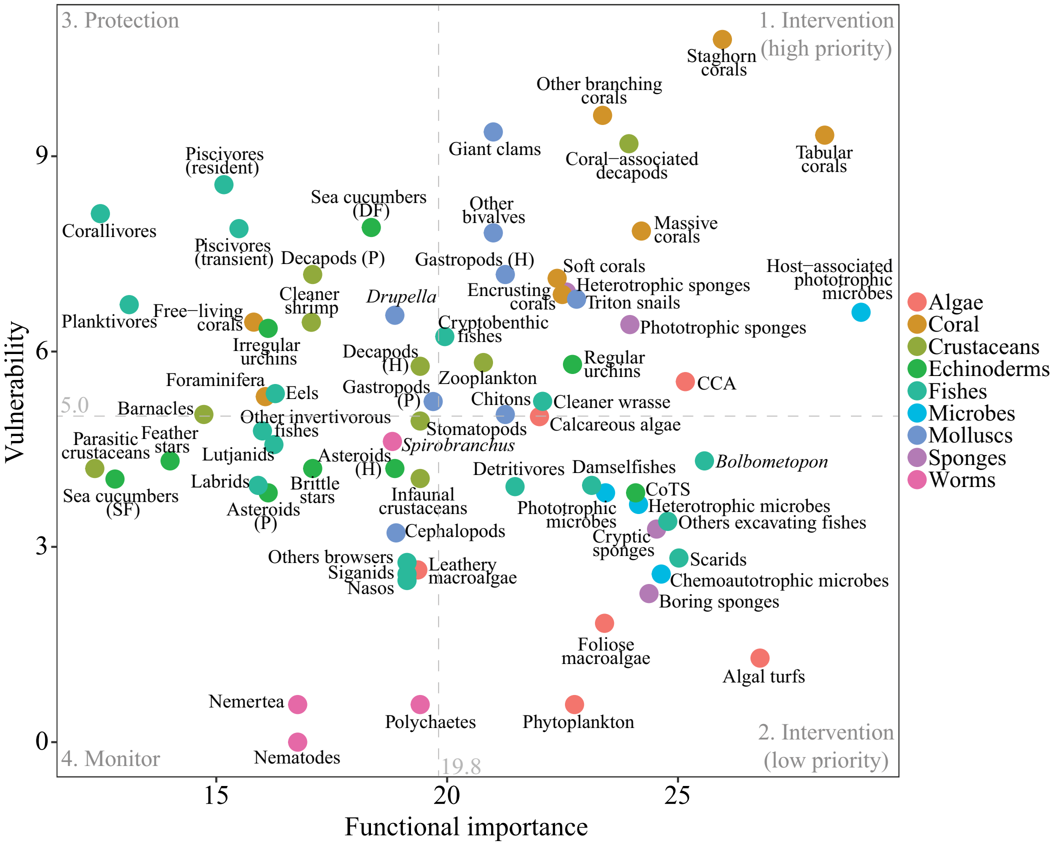

Figure 4 Assessment of the functional importance and vulnerability of 70 species groups. Dotted grey lines represent the median values for each axis creating four management quadrats; 1) Intervention (high priority), 2) Intervention (low priority), 3) Protection, and 4) Monitor. Colours represent taxonomic groups. H = herbivores, P = predators, DF = deposit feeders, SF = suspension feeders.

of taxonomy and ecosystem processes (see methods). This analysis presents weighted impacts of stressors for species at their highest levels of functioning and vulnerability. These data may be particularly useful in guiding where attention could be focussed to maintain highly weighted species-stressor-process combinations.

The proportional impact of each stressor varied across our taxonomic groups and between inner reef and offshore regions (Figure 5A,B). As previously, global change stressors (ocean warming, ocean acidification, cyclones) were considered to have the greatest potential impact overall, especially offshore (Figure 5B). On inshore reefs, the proportional impact of global change stressors on biological functioning was dampened by a greater influence from water quality stressors (nutrients, sediments, pollutants) (Figure 5B), as would be expected (Brodie & Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). This will likely be exacerbated as the intensity of rainfall events increases over the coming decades (Lough 2007). Interestingly, the proportional impact of water quality stressors superseded ocean change stressors on inshore reefs for some taxa (e.g. microbes, algae, sponges, fishes) (Figure 5A), attributing to the importance of addressing local management in conjunction with global stressors and a low-carbon economy (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Corals were the primary taxonomic group considered to be impacted by outbreaks, likely almost entirely in the context of CoTS on the GBR. Echinoderms and fishes

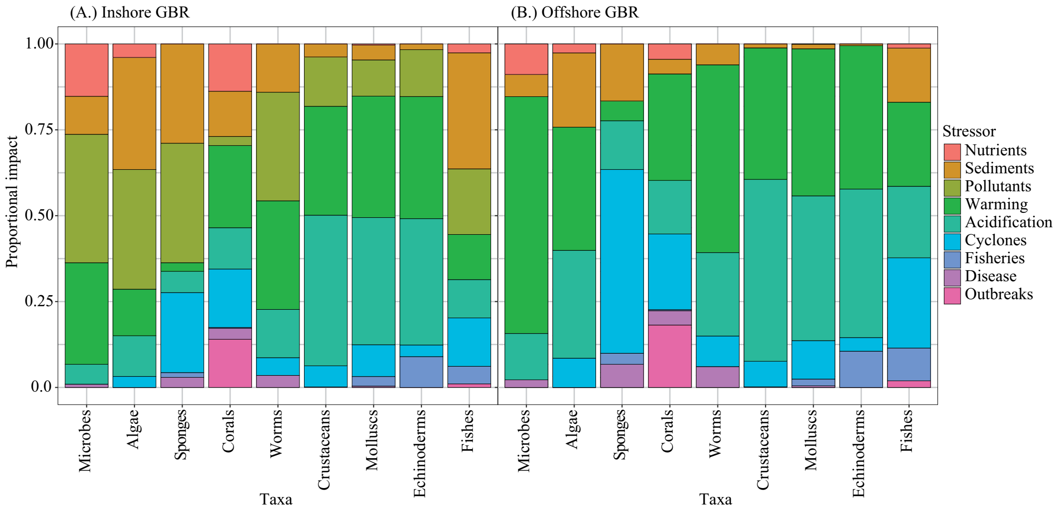

Figure 5 The proportional impact of each stressor on taxonomic groupings (A) inshore and (B) offshore. Each column represents the relative proportion of the functional importance and vulnerability of all species groups within the taxa-stressor combination.

were the major groups impacted by fisheries (Figure 5A,B). The functional contributions of sponges seemed disproportionately impacted by cyclones compared to other taxonomic groups, particularly offshore where there was less exposure to impacts from sediments and pollutants (Figure 5B).

This analysis was deconstructed at the level of our 70 functional groups, providing important information on the most critical stressors to consider when looking to maintain each species group at their highest level of functioning. For many of the mobile invertebrate groups (i.e. crustaceans, molluscs and echinoderms), the impact of ocean change stressors was greatest, even in context of inshore reefs (Figure 6), as reviewed for adult and larval life stages across this great diversity of species (Przeslawski et al. 2008, 2015, Byrne 2011). For most herbivorous fish groups (e.g. browsers, excavators and scrapers), water quality stressors, particularly sediments, were considered to have the greatest proportional impact on their functioning (Figure 6), including offshore (Figure 7). This is in line with the literature that suggests grazing activity can be significantly impaired when sediment loads are too high in their algal food source (Bellwood & Fulton 2008, Goatley & Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). As such, functioning of several algal groups, including turfs, was considered to be greatly impacted by sediment loads (Figures 6 and 7). Of the marine worms, only *Spirobranchus* was considered vulnerable to a number of stressors. Nemerteans and polychaetes were suggested to be almost entirely impacted by cyclones (Figures 6 and 7) – an artefact of their low-rated vulnerabilities as a whole. Scores for nematodes, nemerteans and polychaetes reflect the data gaps and uncertainty in the biology and ecology of these groups in a broader context of reef functioning and threat sensitivity. Fisheries were suggested to have a disproportionate impact on deposit-feeding sea cucumbers and were the major stressor impacting functioning of piscivorous fishes (resident and transient) (Figures 6 and 7). It would be important to partition these broad categories for piscivores at greater resolution in future work. Tabular, staghorn and other branching corals were the groups most impacted by outbreaks, with the functioning of some fish groups that depend on corals for shelter (i.e. corallivores, cryptobenthic, planktivores) also partially impacted. This reflects the ability for our scoring system to capture indirect impacts of stressors on reef functioning. Interestingly, water quality stressors seemed to have a broader and proportionately greater impact on functioning for many species than outbreaks, including offshore (Figure 7).

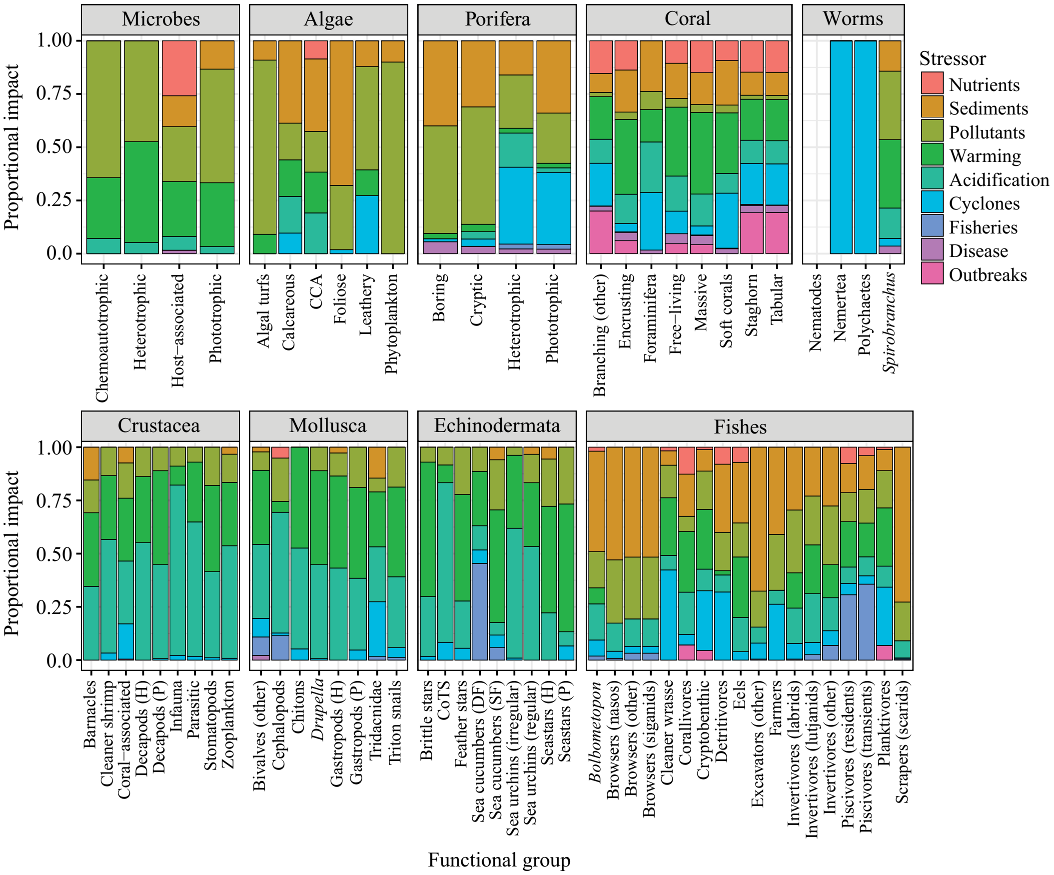

Figure 6 The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance inshore.

Process-level vulnerability

To examine the impact of our nine stressors on ecosystem processes, the additive functional importance and vulnerability of each taxa were calculated across each process-stressor combination. This allowed the determination of the relative impact of each stressor at the level of our nine ecosystem processes, which was weighted by species at their highest level of functioning. Despite the observed differences in the proportional impact of stressors on taxa separately (as previously), analyses at the level of ecosystem processes showed little variation in potential impact (Figure 8A, B). Global change stressors were calculated to have the greatest proportional impact on ecosystem processes, especially offshore (Figure 8B). As previously, impact from water quality stressors on ecosystem processes were proportionately greater inshore (Figure 8A). Though generally, there was little difference in the proportional impact of stressors between inshore and offshore habitats other than the added stress from pollutants (Figures 8–10). Few toxic pollutants on the GBR approach harmful concentrations and, if so, are typically only recorded during short-term runoff pulses near shore (van Dam et al. 2011).

This analysis became more informative when examined as a proportion of each stressor separately. The impact of fisheries was evidently greatest for the predation process (Figures 9 and 10), likely driven by combined importance and vulnerability of the two large predatory fish groups (residents and transients) at this level of functioning. This could be assumed to be driven by

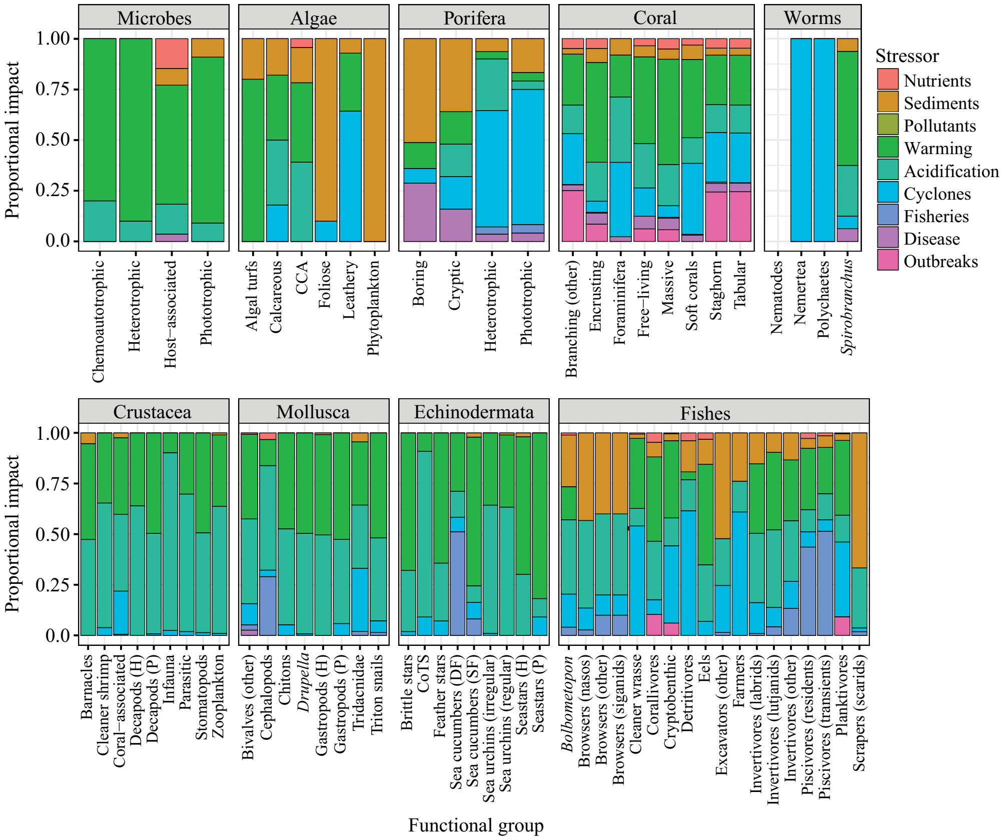

Figure 7 The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance offshore.

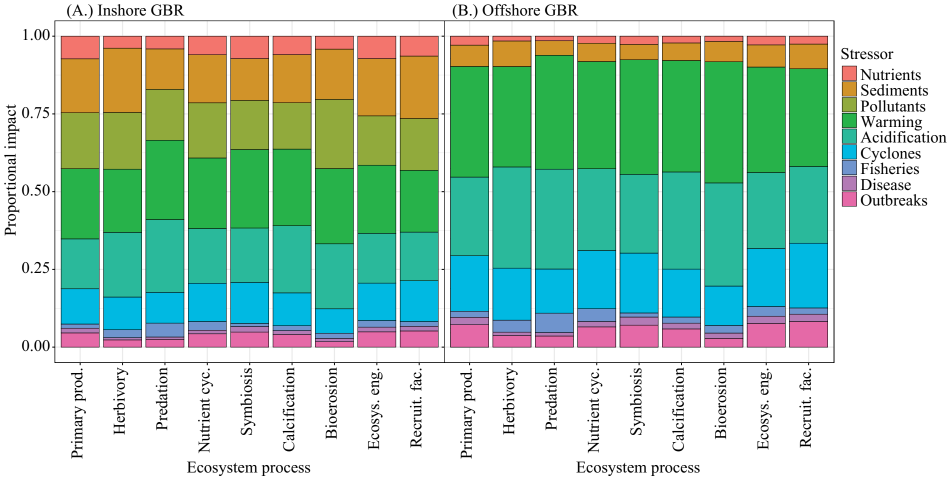

Figure 8 The proportional impact of each stressor on ecosystem processes (A) inshore and (B) offshore. Each column is a relative proportion of the functional importance and vulnerability of all species groups within each process-stressor combination.

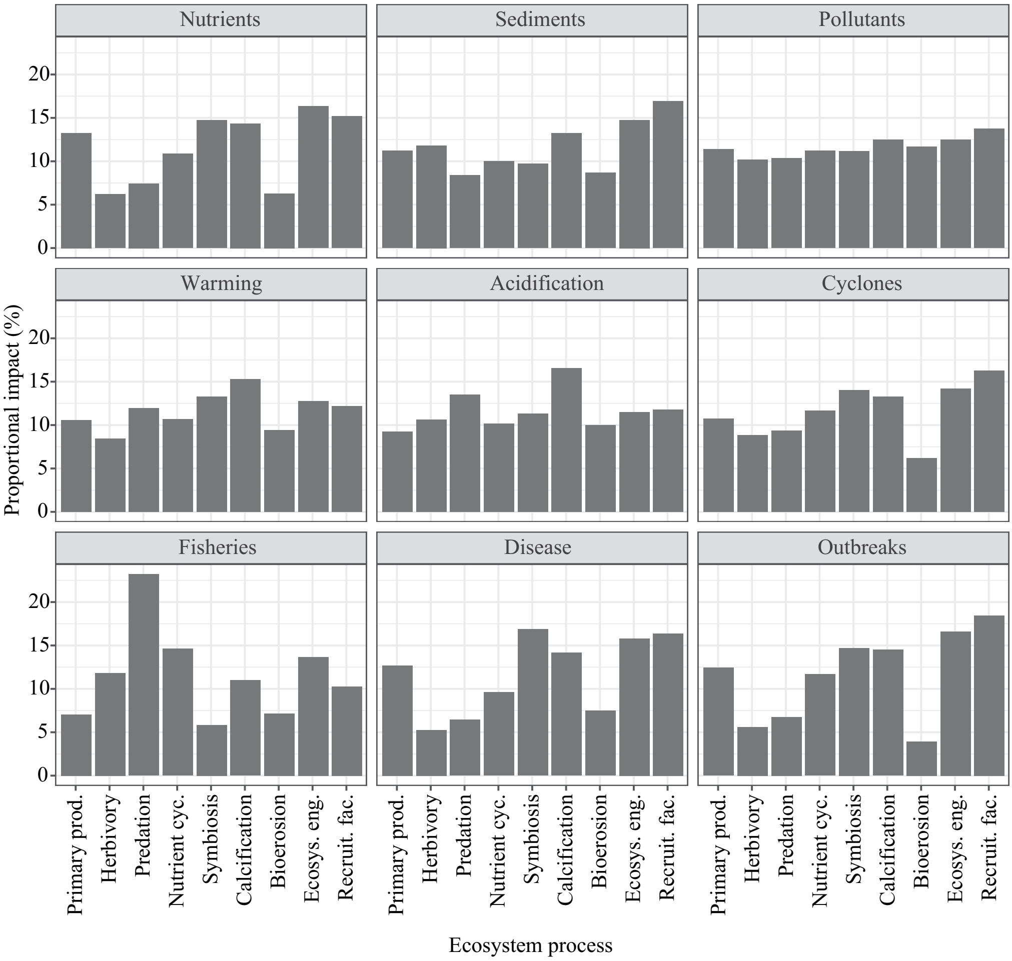

Figure 9 The proportional impact of each stressor on ecosystem processes in context of inshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor.

triton snails, which rated highest for predation in context of CoTS, but these gastropods were not considered vulnerable to fisheries here, as records of exploitation are only anecdotal (Endean 1969), and collection of *Charonia tritonis* on the GBR has been prohibited for several decades (Hall et al. 2017). Generally, stressors had the lowest proportional impact on the bioerosion process (Figures 9 and 10), in line with the literature suggesting bioerosion is likely to increase in a future ocean and is itself an emergent stressor on coral reefs (DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). Ocean acidification had the greatest proportional impact of species considered important for the calcification process (Figures 9 and 10), as would be expected. For a number of stressors (nutrients, warming, cyclones, outbreaks and disease), potential impacts were tightly coupled for symbiosis, calcification, ecosystem engineering and recruitment facilitation processes (Figures 9 and 10). This likely reflects the fundamental role of corals and their symbionts in the ecosystem process that support habitat functioning. Yet overall, the proportional impacts on many ecosystem processes within each stressor were relatively homogenous (Figures 9 and 10) attributed to the broad sweeping effects stressors can have in complex systems like coral reefs.

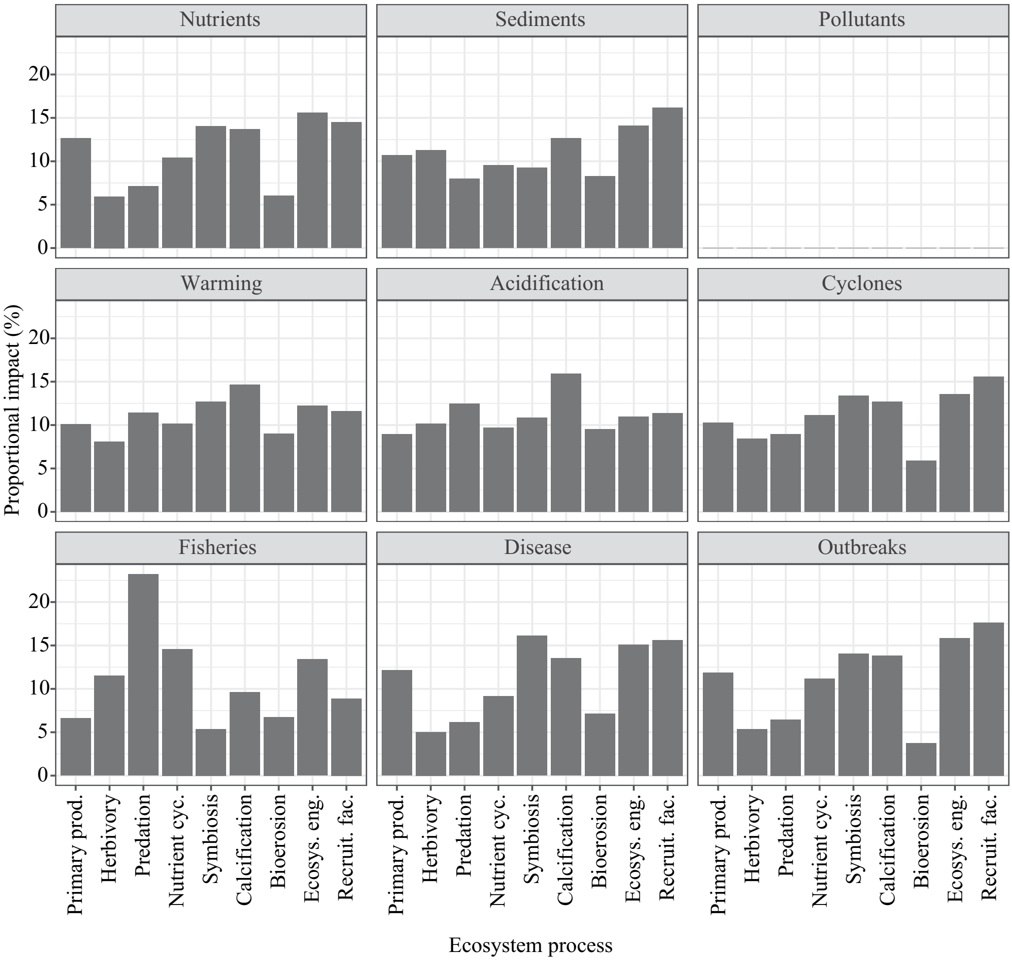

Figure 10 The proportional impact of each stressor on ecosystem processes in context of offshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor. Data absent for pollutants offshore due to null score for exposure (see methods).

Addressing manageability

Experts were elicited to rate species based on their potential responsiveness to management action and the feasibility of implementing management strategies (i.e. spatial scale, time, energy, cost) (see methods). Groups that scored in the top 66th percentile were categorised as a higher priority for management that would likely benefit from direct measures of protection or even represent cases where management has already proved effective. Those in the bottom 33th percentile were deemed lower management priorities that may indirectly benefit from broader-scale management schemes (e.g. marine zoning) and/or require innovative approaches. In any case, maintaining current systems of zoning and compliance provides a baseline to management to preserve species, functioning and biodiversity on coral reefs (GBRMPA 2014c, 2018b). Note that this assessment was in context of the biological functioning of each taxa and was not an assessment of other important elements in strategic assessments, including social, cultural and economic reef values (GBRMPA 2014c).

Interestingly, species that scored lowest for their functional importance and vulnerability on the GBR were also regarded as the least manageable (Figure 11). This may reflect expert bias and the

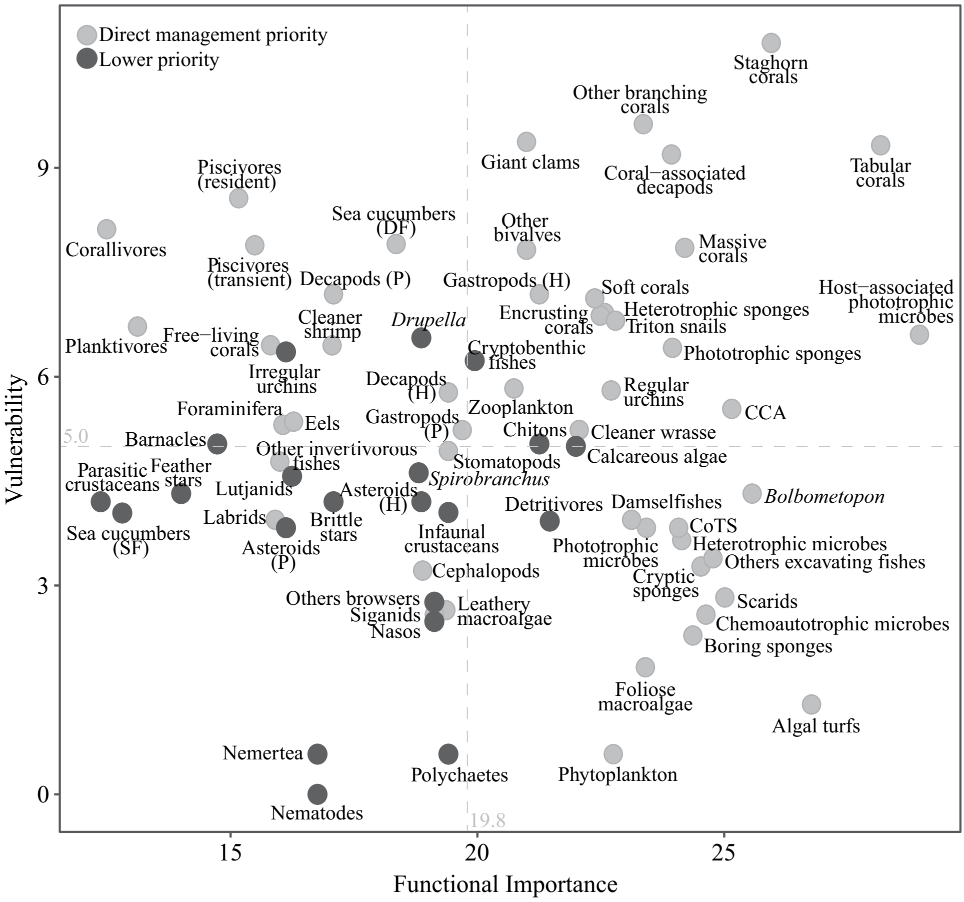

Figure 11 Perceived manageability of each species group relative to their rated functional importance and vulnerabilities on the GBR. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

assumption that important and vulnerable groups should be managed but also demonstrates strong support for the protection of highly rated groups. Invertebrates were most frequently considered unmanageable (Figure 11), reflecting the difficulties inherent in monitoring and managing small, often cryptic species. This was reflected in the Crustacea, where barnacles, infaunal species and parasites scored low, along with all four groups of marine worms (Figure 11). Five groups of reef fishes (cryptobenthics, *Naso* sp., other browsers, detritivores, lutjanids) rated as low priority (Figure 11), most likely stemming from the direct comparison of these groups to other reef fishes rather than their actual inability to be managed. In context of the biology of these groups, cryptobenthic fishes are incredibly diverse and abundant, with rapid population turnovers that ensure persistence against extreme predation pressure (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019), suggesting an inherent resilience. This is also true for the broad distributions and/or high densities of many detritivorous fishes, including blennies (Wilson 2000, 2001, 2004), and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Interestingly, microbes, which are ubiquitous and relatively poorly understood, were considered manageable candidates. This may reflect recent research suggesting that some groups (e.g. bacteria and free-living microbes in seawater or sediment) can be used as bioindicators to monitoring reef health, particularly regarding water quality (Case Study 4) (Glasl et al. 2017, 2018a) and potential Symbiodiniaceae community regulation in support of reef restoration (Quigley et al. 2018). All corals were considered manageable, including the non-coral group Foraminifera, as were phytoplankton and zooplankton (Figure 11).

Addressing scientific certainty

Scientific certainty, as expressed by our expert panel, varied among the 70 functional groups (Figure 12). Uncertainty was most evident for mobile marine invertebrate groups, reflecting the comparatively poor knowledgebase we have regarding non-coral invertebrates on the GBR and generally (Ponder et al. 2002, Przeslawski et al. 2008). While certainty was high for some key species, such as CoTS and bivalves, for most non-coral marine invertebrates, including marine worms, crustaceans and echinoderms, certainty was poor (Figure 12). Along with CoTS, scientific certainty was greatest for *Bolbometopon*, tabular corals and algal turfs, which have received great attention both in the literature and in this review. The lowest certainty for a reef fish group was for eels (muraenids) (Figure 12). Interestingly, certainty was relatively high for cephalopods despite surprising data deficiencies regarding the biology and ecology of this group on the GBR and elsewhere. Conversely, certainty was low for triton snails despite the body of literature devoted to this gastropod owing to

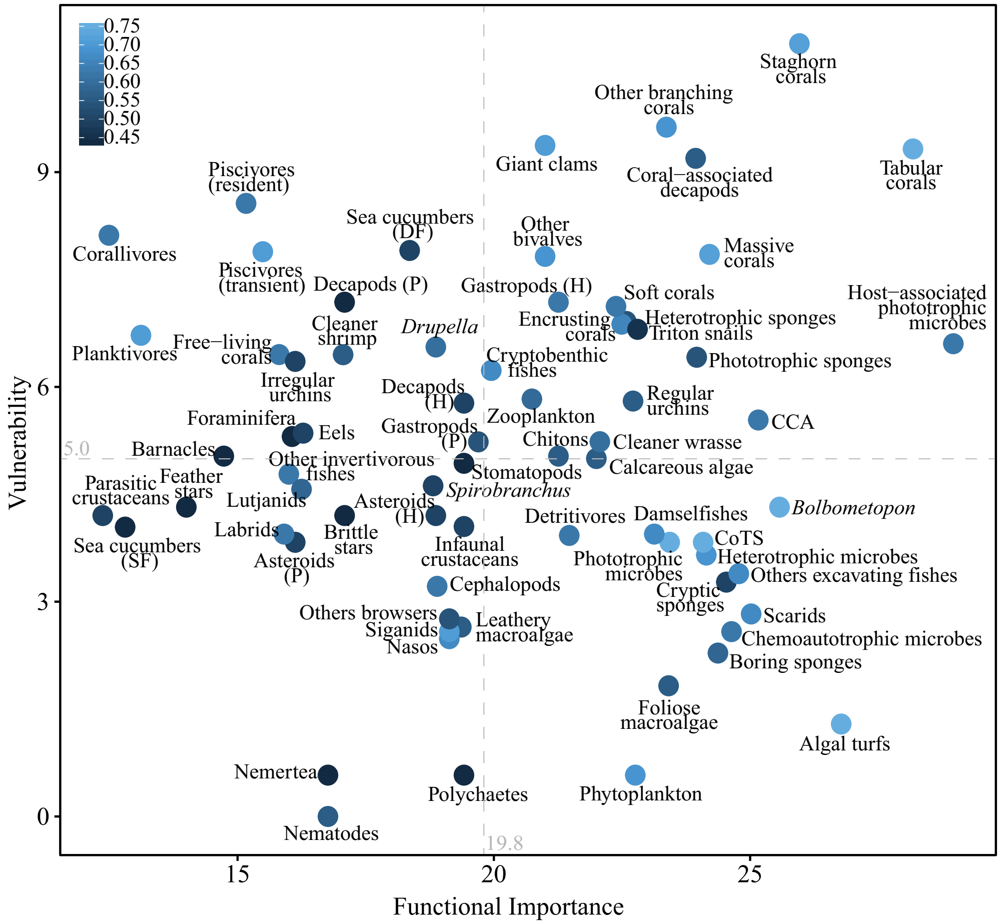

Figure 12 Scientific (expert) certainty in scores for functional importance and vulnerability of the 70 functional groups. Shading reflects scores of high (light) to low (dark) certainty. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

its role in CoTS predation (Endean 1969, Pratchett et al. 2014, Westcott et al. 2016, Cowan et al. 2017, Hall et al. 2017). The perceived depletion of *Charonia tritonis* on the GBR, and elsewhere, was the basis for the 'predator removal hypothesis' regarding CoTS outbreaks (Endean 1969). However, records of their exploitation are mainly anecdotal, and the lack of scientific data and official harvest records suggest these gastropods may have always been rare on many coral reefs (Hall et al. 2017). Regardless, triton snails were scored to have low potential recoverability (Table 7), as while limited data exists, exploitation has occurred for *Charonia* species on many coral reefs globally, where their numbers remain low (Salm 1978, Nijman et al. 2016, Hall et al. 2017).

These high or low relative values for certainty are highlighted here to inform and support our findings and recommendations – an important elicitation process (Knol et al. 2010, Polasky et al. 2011). For groups that scored highly overall with a high level of certainty, management seems most appropriate; that is, we are sure that they are functionally important, vulnerable and manageable on the GBR. Groups with comparatively low levels of certainty are briefly reviewed subsequently under precautionary principles so that no groups were overlooked due to data deficiencies, particularly for those where uncertainty was disproportionate to their relative importance and/or vulnerability. In most cases of uncertainty, we conclude that more empirical data are required to explicitly characterise their functional significance and vulnerabilities and to predict ecological consequences in their absence. The desired outcome for these data-deficient groups is to reduce uncertainty through increased research and monitoring.

Cryptic predators: Eels and octopuses

Due to the difficulties surveying the cryptic habitats they typically occupy, little data exist for muraenids (eels) on the GBR and reefs in general. They likely span many trophic levels, with adults ranging from just a few centimetres to >3 m, and from sandy-bottom to complex reef rubble and intertidal habitats (Böhlke & Randall 2000). Many muraenids actively hunt within the intricacies of the reef framework often inaccessible to other large predators, sometimes occupying nocturnal niches with diets that include fishes, crustaceans, worms and cephalopods (Hiatt & Strasburg 1960, Hixon & Beets 1993, Fishelson 1997, Young & Winn 2003, Gilbert et al. 2005). Unlike a diversity of other reef fishes, including large resident piscivores, muraenids optimise habitat use within the reef and rubble matrix (i.e. dead coral) rather than exhibiting dependence on live coral, suggesting they may fare better as coral reefs degrade. Yet how trophic pathways within the reef matrix scale up to fisheries productivity are poorly understood. As for muraenids, a broad knowledge gap is evident for cephalopods, particularly octopuses that exist in a similar trophic space. Benthic predators like octopuses and muraenids are likely key predators within the reef matrix where large predatory fishes cannot access, but this remains to be quantified. Data gaps for cephalopods are surprising given their broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & Bennett 2008). Surprisingly little information exists regarding their functional ecology on the GBR and in general (Ponder et al. 2002). Interestingly, cephalopod populations are proliferating globally, and they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

Deposit-feeding sea cucumbers

Although they have important roles in bioturbation, carbonate chemistry, nutrient cycling, benthic productivity and infaunal community structure (Uthicke & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Lee et al. 2017, Wolfe & Byrne 2017a, Wolfe et al. 2018), sea cucumbers may be more influential in lagoon systems – outside of the focal habitat here. Large deposit-feeding holothuroids are likely to have a greater influence on ecosystem-scale carbonate chemistry in closer association to reef structure (Schneider et al. 2013, Wolfe et al. 2018). As recognised by our expert panel, they are among the most vulnerable species to overfishing on the GBR (Uthicke et al. 2004, Purcell et al. 2013, 2016b, Eriksson & Byrne 2015), as globally recognised (IUCN Red List for Threatened Species) (Conand et al. 2014, Purcell et al. 2014, Richards & Day 2018). Empirical data on their recruitment and reproduction (e.g. Wolfe & Byrne 2017b, Balogh et al. 2019), and natural population densities, are essential to characterise before fisheries impacts on wild populations can no longer be differentiated. This is particularly true for the black teatfish (*Holothuria whitmaei*), in light of the recent discussions to reopen its fishery (DAF 2018) without any fisheries-independent data since its closure (owing to overfishing) in 1999.

Marine worms

This broad group boasts an incredible diversity across a range of functioning and taxa, from microscopic infaunal nematodes, to parasitic platyhelminths, to large predatory polychaetes, to sessile filter-feeders (Hutchings et al. 2019). For polychaetes alone, there are currently over 130,000 species recognised worldwide, but there has not yet been a comprehensive survey of the polychaetes, or marine worms, of the GBR. Marine worms are often highly cryptic, and new species are frequently identified when taking the time to look, as demonstrated from a two-week polychaete workshop on Lizard Island that described 91 new species (Aguado et al. 2015, Capa et al. 2015, Hutchings & Kupriyanova 2015). Bioerosion is perhaps the most well-documented functional role of marine worms on the GBR (Hutchings & Kiene 1986, Hutchings 2008), but the lack of spatially explicit information on their population densities across the GBR hinders the ability to upscale their contributions into carbonate budget calculations (see Case Study 2). The Christmas tree worm (*Spirobranchus*) has received specific attention in the literature, owing to the benefits it provides for its coral host (Strathmann et al. 1984, DeVantier et al. 1986, Dai & Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008). Marine worms are an important food source for many reef organisms, including invertivorous reef fishes (Case Study 1), but explicit trophic contributions are notoriously difficult to quantify for soft-bodied cryptic fauna, and attention to these gaps in knowledge is required.

Cryptic sponges

In general, the functional ecology of sponges is better documented on Caribbean reefs than for the Indo-Pacific, including the GBR (Wilkinson 1983, 1987, Maldonado et al. 2015, Mumby & Steneck 2018). Although conspicuous sponges ranked in the top-priority space, largely owing to their higher-ranked vulnerability (Figure 4), cryptic (and boring) sponges scored higher in their functional importance and are highlighted here under precautionary principles, owing to the uncertainty in their scores (Figure 12). Cryptic sponges can be the most significant invertebrate bioeroders on coral reefs (Neumann 1966, Glynn & Manzello 2015), a process likely to be accelerated in a future ocean (Wisshak et al. 2014). The contribution of cryptic sponges to reef and rubble consolidation is well appreciated (Wulff & Buss 1979, Wilkinson 1983, Hutchings 2011), facilitating recruitment processes and reef recovery (Fox et al. 2003, Fox & Caldwell 2006, Biggs 2013). Sponge aggregations can enhance local biodiversity through habitat provisioning, making it important to determine the competitive relationships between sponges and other phase-shift drivers (e.g. algae) and how changes in the dominance of these organisms may alter trophic pathways and energy flows on coral reefs (Maldonado et al. 2015, Bell et al. 2018). There may be interesting outcomes in a future ocean as sponge-dominated reefs become increasingly common (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham & Bell 2018), but possibly shifting from heterotrophic towards phototrophic communities (Bennett et al. 2017, 2018, Bell et al. 2018). For *Cliona*, the most abundant bioeroding sponge genus on the GBR, tolerance to ocean warming may be low (Ramsby et al. 2018a). Yet while clionid benthic cover does not appear to be increasing at the regional scale, it seems greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

Crustaceans

As for the marine worms, the functional and taxonomic diversity of crustaceans on the GBR is poorly characterised. Crustaceans are the most diverse marine arthropods and are often termed ‘insects of the sea’, spanning microscopic copepods, to parasitic isopods, to predatory decapods, to filter-feeding barnacles (Hutchings et al. 2019). Crustaceans are abundant in all habitats of the GBR, with ~1300 recorded species, but the cryptic nature of many of these groups makes them inherently difficult to examine and quantify (Ponder et al. 2002). This includes those that exist in the plankton, such as copepods, which are the most well-studied and important group numerically in the zooplankton in waters of the GBR, constituting ~80% of the mesozooplankton abundance (McKinnon & Thorrold 1993, McKinnon et al. 2005, 2007). Among the most broadly recognisable crustaceans are the decapods (crabs, shrimps and lobsters), owing to their larger size and commercial value. The dendrobranchiates (prawns) are not generally common on coral reef structures but are common in coastal and interreefal sediment habitats where they support an important trawl fishery on the GBR (Gribble 2003, GBRMPA 2014b). Stomatopods (e.g. mantis shrimp) are possibly the most flamboyant crustaceans on coral reefs, with vivid colouration, remarkable vision (Marshall et al. 1994, Porter et al. 2010) and active and aggressive ‘spearing’ and ‘smashing’ hunting techniques, sometimes targeting larger fish prey (deVries et al. 2016, Goatley et al. 2017, Hutchings et al. 2019). Owing to their association with corals, coral-associated decapods (e.g. *Trapezia*, *Tetralia*) have received considerable attention in the literature (see: Stella et al. 2011b), as reflected by a higher relative certainty in expert scores here (Figure 12). The contribution of crustaceans to marine food webs is fundamental and has gained slightly more traction than for the worms, as the hard exoskeletons of crustaceans are more easily identified in gut content analyses (see Case Study 1). However, explicit quantification of population productivity, bioavailability and trophic transfers of crustaceans to higher order predators is essential to our understanding of reef trophodynamics and production functioning.

Conclusions

Management of the Great Barrier Reef

Composed of ~3000 individual reefs, the GBR is possibly the most complex natural system in the world (Knowlton 2012, Day 2016). This coral reef ecosystem supports many high-value sectors, including trade, fisheries and tourism, estimated to provide ~AU$6 billion to the Australian economy annually (McCook et al. 2010, Stoeckl et al. 2011, Brodie & Waterhouse 2012, Knowlton 2012, O’Mahoney et al. 2017). Due to its global and ecological significance, the GBR has been managed as a national Marine Park since 1975 (GBRMP Act 1975) and in 1981 became the first coral reef to be granted World Heritage status by the United Nations Educational, Scientific and Cultural Organisation (UNESCO). Management has since focussed on resource use, with a particular devotion to the preservation of biodiversity (McCook et al. 2010) to maintain its OUV. The GBR Rezoning Plan (2004), implemented in July 2004, increased the area of the Marine National Park (Green) Zone from <5% to 33% of the total GBRMP area, enhancing protection of reefs from activities including shipping, fisheries and recreation (Fernandes et al. 2005, Day 2016). This scheme continues to demonstrate significant contributions to the management of biodiversity, ecosystem resilience and socioeconomic values, and so the GBR is often hailed for its gold standard for reef management (McCook et al. 2010, Day 2016).

Given the size of the GBR, spatial confines in jurisdiction have created complexity for ecosystem-based management on the reef, particularly involving land-based riparian and coastal activities (e.g. water quality, riverine discharge, port development) (Brodie & Waterhouse 2012, Day 2016). In addition, parts of the World Heritage Area of the GBR fall outside the Marine Park, further complicating jurisdictional boundaries and management (GBRMPA 2014c). While biodiversity conservation has historically been considered pivotal to ecosystem-based management of the GBR through successes in marine park zoning (Fernandes et al. 2010, McCook et al. 2010, Day 2016), it is increasingly necessary to target management provisions towards key taxa to support ecosystem functioning and stability in a future ocean (Richards & Day 2018).

In this comprehensive review guided by expert elicitation, we document a diversity of species that are critical to ecosystem functioning on the GBR. This presents the first attempt to rate and compare the functional importance, vulnerability and manageability of the incredible diversity of organisms on a coral reef spanning microbes to predatory fishes. As a result, functional groups remained relatively broad, but greater detail can be found in the following sections where priority groups and species are highlighted. It is noted that this assessment was through the lens of classical reef crest and reef slope habitats on the GBR and that whole-ecosystem management is necessary to maintain the integrity of the reef. Regardless, many of the attributes examined here, at the level of species, ecological processes and ecosystem functioning, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c) and for coral reefs in general. So here we provide a first step to inform holistic management approaches aiming to preserve important reef species, values and processes.

In the following sections, we reiterate findings in case-specific compilations of the literature for priority groups that met expectations (Who were the winners?) and provided novel cases (Who were the surprises?). Future work aiming to protect the biodiversity values of coral reefs may use the information compiled here to inform dynamic research and management to safeguard ecosystem functioning (Richards & Day 2018). We highlight suggested areas where management and/or science could increase monitoring and integrate novel approaches while commending current management success in spatial planning (Day 2002) and conservation initiatives (e.g. GBRMPA 2017, 2018a) on the GBR, which seem to effectively capture priority groups and functional entities. It appears that functional groups that met expectations may already benefit from specific incorporation in management initiatives and broad-scale habitat protection as offered by the GBRMP zoning system, as discussed in the following sections. Novel cases are outlined as those that may benefit most from this process-based assessment, as they are not specifically considered in current management strategies. In any case, a default management strategy should exist in education, which can enhance pro-environmentalism, self-efficacy, stewardship, compliance and the transfer of information regarding reef conservation (Zeppel 2008, Myers et al. 2012, Beeden et al. 2014b, Elmer et al. 2017, Vercelloni et al. 2018, Curnock et al. 2019).

Who were the winners?

Branching and tabular corals Of the coral groups addressed here, tabular, staghorn and other branching corals scored highest in combination for their functional importance and vulnerability on the GBR. The roles of branching and tabular corals in reef ecosystem functioning are fundamental and have been extensively documented. Throughout the Indo-Pacific, fast-growing branching species like *Acropora* and *Pocillopora* contribute most to rapid increases in coral cover (Connell et al. 1997, Pratchett et al. 2015), most notably during years without major disturbance events (Thompson & Dolman 2010). As addressed in Case Study 2, the relative contribution of corals of the *Acropora* genus to net ecosystem calcification outweighs that of other coral groups and calcareous algae, with the greatest contribution to the carbonate budget of the GBR. Reproduction, recruitment and growth rates of structural branching and tabular species are highly variable across time and space (Browne 2012, Browne et al. 2013, Pratchett et al. 2015, Anderson et al. 2017, Anderson et al. 2018), as they can be the most susceptible groups to a range of stressors, including coral bleaching (Baird & Marshall 1998, Marshall & Baird 2000, Loya et al. 2001) and ocean acidification (Fabricius et al. 2011, Madin et al. 2012). Yet they appear to be persistently key to rapid reef growth and postdisturbance recovery (Pearson 1981, Connolly & Muko 2003, Ortiz et al. 2014, 2018). Ensuring that species key to carbonate production, a positive carbonate budget and reef recovery are protected is a key focus of resilience-based management on the GBR (GBRMPA 2017, 2018a). Thus, current management strategies on the GBR are aligned with maintaining a key species identified in this process-based assessment.

Rates of recovery for coral assemblages are dependent on the relative contributions of new recruits and adult persistence (Connell et al. 1997, Linares et al. 2011, Gilmour et al. 2013, Pratchett et al. 2015). Following localised bleaching in the central GBR in 2001–2002, increases in coral cover up to 10% y^{-1} were primarily driven by tabular *Acropora hyacinthus*, almost entirely attributed to growth of existing corals (Linares et al. 2011). Recent mass-bleaching on the GBR resulted in significant declines in coral recruitment by ~89%, with brooding *Pocillopora* species replacing spawning *Acropora* in the recruitment panel for the first time documented (Hughes et al. 2019a). This supports the suggestion that *Pocillopora* species may be more thermally resilient (Epstein et al. 2019b), owing to the local adaptation required in brooding reproductive modes where gene flow is retained (Ayre & Miller 2004, Miller & Ayre 2004, Baums 2008, Torda et al. 2013a,b). It is increasingly important to determine how coral larval density and supply may scale up to support reef recovery (Doropoulos et al. 2017a, 2018). If the recovery trajectory of *Acropora* and other branching corals are increasingly compromised, then shifts in dominance towards more robust and resilient taxa (e.g. *Porites*) can be expected (Fabricius et al. 2011, Pratchett et al. 2015).

Branching and tabular corals are the preferred target of CoTS (Colgan 1987, Pratchett 2007), and so current CoTS control initiatives should be maintained in support of reef resilience (Westcott et al. 2016). Tabular corals are also more susceptible to coral diseases, including the epizootic White Syndrome (Roff et al. 2006, 2008, 2011, Hobbs & Frisch 2010, Maynard et al. 2011, Hobbs et al. 2015). The five diseases found to affect *A. hyacinthus* also increase in prevalence as water temperature warms (Willis et al. 2004). Due to their morphology, physical impacts from storms and cyclones, vessel groundings and anchor damage are often more significant for branching and tabular corals compared to other coral morphologies (Riegl & Velimirov 1991, Riegl & Riegl 1996, Connell et al. 1997, Hughes & Connell 1999, Dinsdale & Harriott 2004, Madin 2005). But while frequent, anchor damage is considered to have a relatively low impact across the GBR (GBRMPA 2014b, Kininmonth et al. 2014), and current management efforts are proving effective in reducing coral damage in high-use areas through increased awareness and stewardship (Beeden et al. 2014a).

As recognised here, and previously (Ortiz et al. 2014, 2018, GBRMPA 2017), tabular corals are paramount to the resilience of the GBR. However, there may be low ecological redundancy of key tabular corals on the GBR, with just three species considered common; *A. hyacinthus*, *A. cytherea* and *A. clathrata*. There should be continued momentum in the protection of tabular corals on the GBR (GBRMPA 2017, 2018a), in conjunction with research, long-term monitoring programmes and plans to operationalise resilience-based management (GBRMPA 2018b). Tabular corals are easily recognisable and render themselves important features for monitoring by citizen science groups and in education in support of increased awareness, compliance and protection at their greatest level of functioning.

Acropora hyacinthus often dominates the reef crest and shallow reef slope on the GBR and coral reefs throughout the Indo-Pacific (Veron 1986), where it exhibits both asexual and sexual reproduction (Wallace 1985, Smith & Hughes 1999). This species is listed as Near Threatened on the IUCN Red List of Threatened Species (Aeby et al. 2008), along with a range of other scleractinian corals on the GBR (Richards & Day 2018). Internationally, all corals are listed on CITES Appendix II, which restricts and controls trade of ‘at risk’ species, and are important attributes of OUV that contribute to the World Heritage status of the GBR (GBRMPA 2014c). Acroporids have historically been the main targets of coral fisheries on the GBR but with minimal impact on their populations (McCormack et al. 2005).

In situ enhancement of coral larval supply and recruitment is an emerging tool to replenish degraded reefs (Heyward et al. 2002, Cooper et al. 2014, dela Cruz & Harrison 2017, Doropoulos et al. 2019). Similarly, the culture of 'super corals' is an emerging management strategy aiming to enhance reef resilience and recovery via transplanting and outplanting of adapted corals (Auberson 1982, van Oppen et al. 2015, 2017, Barton et al. 2017, Beyer et al. 2018, Camp et al. 2018b, Forsman et al. 2018). There has been success transplanting fragments of *A. hyacinthus* and a range of other coral species onto reefs including in Japan (Okubo et al. 2005), the Maldives (Clark & Edwards 1995) and the Caribbean (Bruckner & Bruckner 2001, 2010, Ladd et al. 2018, 2019). However, there are potential limitations in larval seeding and transplant methods through altered coral-microbe communities and increased disease proliferation (Casey et al. 2015b), reduced species diversity and ecological functioning (Ladd et al. 2018, 2019), as well as spatial limitations at whole-reef scales. Regarding larval seeding techniques, enhancement of a diverse assemblage of coral species is imperative to reef recovery and functioning, and seeding from natural spawning slicks may offer promising opportunities for large-scale coral reef restoration (Heyward et al. 2002, Doropoulos et al. 2019). If targeted research on transplanting and outplanting corals for restoration were to develop further, then functionally important species like *A. hyacinthus* are suggested.

Microorganisms Microbial communities, spanning both host-associated (e.g. corals, sponges, algae) and free-living (e.g. seawater, sediments) taxa, drive biogeochemical cycles in the ocean and undertake numerous functions that underpin the health of coral reef ecosystems (Falkowski et al. 2008, Krediet et al. 2013). They are key to the remineralisation of organic matter and efficient recycling of nutrients, especially in oligotrophic tropical waters (Capone et al. 1992, Tribble et al. 1994, Rasheed et al. 2002, Wild et al. 2005, Ferrier-Pages et al. 2016). The role of microbes in marine invertebrate recruitment and settlement dynamics is also well recognised (Webster et al. 2004, 2011, Siboni et al. 2012a). Their sweeping ratings to ecosystem functioning here are not surprising, though most groups had lower-rated vulnerabilities on the GBR compared to other functional groups.

We outline host-associated phototrophic microbes (e.g. Symbiodiniaceae) as the most critical microbe group to consider in management to maintain a healthy reef, as they are inextricably linked to the survival of their coral hosts (Bourne et al. 2016). Importantly, the relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 2013, Stat et al. 2013, Bay et al. 2016), an important feature in a warming climate. As we become more aware of the functional roles of microbial communities on coral reefs, it is increasingly apparent that broad-scale community sequencing of the coral holobiont (coral host and microbial symbionts) is required in order to characterise metabolic pathways, coevolution and the acclimation/adaptation of coral reefs to environmental change (Bourne et al. 2016).

Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 2018a), with populations that vary in response to external conditions (e.g. season, water quality) and habitat type (Kelly et al. 2014, Tout et al. 2014, Angly et al. 2016, Frade et al. 2016, Agusti et al. 2019). Such environmental parameters can drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR (Case Study 4). Free-living microbes and bacteria in reef seawater and sediments may be more sensitive indicators of environmental change than coral-microbes (Glasl et al. 2019). Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters, which seems to be sensitive both at spatial and temporal scales (Case Study 4). Yet, despite this potential, we have a poor understanding of how microbes provide resilience and buffering across the greater reef system or how they could be used as early warning signals for tipping points as habitats degrade.

Given that microbes have great potential to be used as early warning signals, it would be highly beneficial to establish baseline conditions of the coral reef microbiome, from host-associates to free-living communities, as the current lack of data hinders our potential to use microbes in reef-monitoring programmes. Incorporating the coral reef microbiome into long-term monitoring schemes could provide useful information to assess and predict broader reef impacts from coastal eutrophication and climate change. This functional group is not part of a specific management initiative on the GBR at present, but programmes such as the Australian Marine Microbial Biodiversity Initiative (AMMBI) conducted by IMOS and Bioplatforms Australia (IMOS 2018) provide an opportunity to expand the sampling and biobanking of marine microbes. Currently, AMMBI includes just one site on the GBR, the Yongala, an iconic mid-shelf shipwreck (Brown et al. 2018). Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients of the GBR would enable a robust assessment of the microbial contribution to reef functioning and health. This would require a combination of analytical techniques (omic approaches: genomic and transcriptomic sequencing, metabolomics, epigenetics) to characterise communities, including *in situ* visualisation to link localisation with broader reef functioning.

Crustose coralline algae CCA was outlined as the most important and vulnerable of the algal groups, in light of the low-rated vulnerability of algal turfs and other macroalgal groups to ecosystem stressors. It is broadly understood that some CCA are important components of the EAM, aiding in reef consolidation (e.g. *Porolithon*) (Matsuda 1989, Diaz-Pulido & McCook 2008), shaping cryptobenthic communities within the reef matrix (e.g. *Mesophyllum*, *Lithothamnion*) (Enochs & Manzello 2012), and in coral recruitment facilitation (e.g. *Titanoderma*) (Heyward & Negri 1999, Harrington et al. 2004, Arnold et al. 2010, Diaz-Pulido et al. 2010, Doropoulos et al. 2012a, 2018). CCA are calculated to be the primary non-coral contributors to net carbonate production on the GBR (Case Study 2) and elsewhere (Bak 1976, Perry et al. 2012a). The functional roles of CCA may be particularly important on reef crests, where they can dominate benthic cover >90% (Atkinson & Grigg 1984, Glynn et al. 1996), including for vertical surfaces with lower rates of sediment accumulation (Kennedy et al. 2017, Duran et al. 2018). Surveys of CCA on the GBR indicate that communities vary considerably in abundance, diversity and composition across the continental shelf and suggest that shelf positioning, habitat, grazing and water quality (e.g. sediment deposition and nutrient loads) are key factors affecting their distribution (Fabricius & De'ath 2001b, Dean et al. 2015). To ensure CCA is preserved at its highest level of functioning, it seems important to maintain the key processes necessary for CCA growth, which primarily involves facilitating high rates of herbivory and reducing sediment loads.

At present, CCA may benefit from the GBRMPA zoning scheme through the protection of particular sections of reef from direct impacts, including anchor damage and fisheries activity, but this is regionally specific. Species-specific information on the distribution and relative abundance of key CCA taxa (e.g. *Titanoderma*, *Porolithon*) is limited, and these groups would benefit from consideration in long-term monitoring programmes. On the GBR, CCA taxa abundant on offshore reefs include *Neogoniolithon*, *Lithophyllum* and *Porolithon* species (Diaz-Pulido & McCook 2008), but generally, they are data deficient, and information is restricted to a few locations on the GBR (Dean et al. 2015). Taxonomic information is very scarce, and the cryptic diversity evident in even the most well-known genera (e.g. *Porolithon*) is quite high (Gabrielson et al. 2018). Attention to these knowledge gaps requires urgent action to ensure CCA can be directly incorporated in management schemes for consideration by local (e.g. GBRMPA) and global (e.g. IUCN Red List) protection agencies, especially for priority species with key roles, such as *Titanoderma* and *Porolithon*, which work to uphold the OUV of the GBR and coral reefs in general.

Some common GBR species (*T. pustulatum*, *P. onkodes*, *Neogoniolithon* sp.) have the remarkable capacity to deter settlement of seaweed spores, which may be an increasingly important feature on future coral reefs to minimise coral-algal phase shifts (Arnold et al. 2010, Vermeij et al. 2011, Gomez-Lemos & Diaz-Pulido 2017), especially considering the active removal of macroalgae is an emergent management strategy (Ceccarelli et al. 2018). *Titanoderma* spp. is one of the preferred substrates for coral settlement, with one experiment showing settlement rates to be 15 time higher on this species compared to other CCA (Harrington et al. 2004). How this translates at the ecosystem level *in situ* remains unclear. Ocean acidification may have direct impacts on coral reef settlement success through impacts on CCA (Doropoulos et al. 2012a, Doropoulos & Diaz-Pulido 2013, Espinel-Velasco et al. 2018), and so it seems critical to assess the potential ecosystem-level consequences that a loss of key coral settlement inducers could have on the recruitment success on coral reef species. Interestingly, coral larvae seem to show settlement preference towards red-coloured objects (e.g. plastic cable ties, buttons), compared to blue, green and white substrates, which reflects their propensity to settle to pink CCA and – at least in part – decouples the paradigm that settlement cues are solely biochemically driven (Mason et al. 2011, Gómez-Lemos et al. 2018). This may become an important consideration for reef restoration (Mason et al. 2011), particularly since CCA appear to be highly vulnerable to changes in ocean condition (i.e. warming and acidification), even more so than some coral species (Diaz-Pulido et al. 2007, 2012, Anthony et al. 2008).

Algal turfs and the epilithic algal matrix Algal turfs were rated the most functionally important group regarding production functioning, and third overall, but were considered largely resilient to the range of stressors examined here. For this very reason, this group is highlighted here under precautionary principles in context of algal phase shifts in a changing ocean (Roth et al. 2018). Algal turfs are an assemblage of minute, often filamentous, algae that exhibit fast growth, high productivity and rapid colonisation rates. Within the epilithic algal matrix, turfing species dominate surprisingly large proportions of coral reefs (Diaz-Pulido et al. 2016), where they are critical to primary production in oligotrophic waters (Adey & Goertemiller 1987, Klumpp & McKinnon 1989), harbour detritus and microorganisms (Wilson et al. 2003) and host a diversity of cryptic invertebrates (Kramer et al. 2012). While the taxonomy of turfs and EAMs is complex, offshore reefs are often dominated by the red alga *Ceramium punctatum* and the blue-green algal family *Nostococaceae* (Scott & Russ 1987), while inshore reefs are typically dominated by the green algae *Acetabularia calyclus* and *Cladophora fascicularis*, the filamentous brown algae *Sphacelaria* spp. and the *Falkenbergia* stage of the red alga *Asparagopsis taxiformis* (Diaz-Pulido & McCook 2008).

EAMs cover high proportions of reef flats (50%–80%) and reef slopes (30%–70%) on the GBR, with particularly high productivity in summer (Klumpp & McKinnon 1992). They lay the foundations for benthic production functioning, with particularly important roles in the fixation of nitrogen and its rapid distribution across trophic pathways (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). Rates of turf algal productivity strongly predict herbivore biomass (Carpenter 1986, Russ 2003, Tootell & Steele 2016), and, conversely, herbivores directly regulate turf canopy height (Carpenter & Williams 1993, Mumby et al. 2013a). Herbivorous grazers are suggested to consume around half of the total annual net production of the EAM, making it directly available to the food web (Hatcher & Larkum 1983, Klumpp & Polunin 1990), particularly on reef flats (Bellwood et al. 2018).

There can be interesting top-down and bottom-up drivers of turfing seascapes on coral reefs, including from wave exposure, nutrification, sedimentation and herbivory (Carpenter & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, Tebbett et al. 2017a, Roff et al. 2019). Variability in turf assemblages occurs at small spatial scales (Harris et al. 2015), with thresholds in canopy heights and sediment depths (>3 mm) found to reduce herbivory, alter turf metabolism and impair coral recruitment (Carpenter & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & Bellwood 2012, Clausing et al. 2014, Doropoulos et al. 2017a,b, Lam et al. 2018). There is compelling evidence that the canopy height of turf algae can predict productivity, sedimentation, herbivory, wave exposure and recruitment success, which could be an important attribute to monitor so as to establish spatial data for this priority group on the GBR and on coral reefs in general. Further, turfs are a more pertinent stress when combined with sedimentation and/or nitrification. How dynamic states in turf algal productivity (e.g. turf height), nutrification, sedimentation and wave exposure (hydrodynamics) interact to impact ecological functioning needs to be explicitly characterised. Precautionary measures should continue focus on water quality (e.g. eutrophication, sedimentation) in catchment and riparian management to facilitate natural moderation of turf growth through herbivory. Keeping turf canopy height low (<3 mm) is important for the successful recruitment of corals and other reef species (Roth et al. 2018).

Despite the lack of information on long-term trends in algal condition, major changes are expected to occur regarding their distribution, abundance and composition in a changing ocean, driving significant alterations to ecological functioning (Diaz-Pulido et al. 2007, 2011a). On turf- and macroalgal-rich reefs, the relative abundance and diversity of microbial communities also increase with the potential to influence nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019). Ocean acidification is likely to enhance algal turf productivity and biomass (Ober et al. 2016), cause shifts in epilithic communities to turfing and cyanobacteria assemblages (Diaz-Pulido & McCook 2002, Bender et al. 2014b) and increase rates of bioerosion and reef carbonate dissolution (Carreiro-Silva et al. 2005, Tribollet et al. 2006, Schönberg et al. 2017). Even marginal differences in turf canopy height impact micro-scale circulation and can alter turf metabolism and chemistry across diffusive boundary layers (Carpenter & Williams 1993). This will directly influence the balance between reef growth (calcification) and destruction (dissolution) in a future ocean, with predictions that coral reefs will switch to a state of net dissolution by the end of this century (Albright et al. 2018, Eyre et al. 2018). However, the raw contribution of microfloral borers to net reef erosion is difficult to quantify, and knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & Manzello 2015). Concerns over shifting carbonate budgets should address all forms of bioerosion, including rates within the EAM and endolithic algae, especially given the propensity for turf algae to rapidly colonise dead coral substrate following perturbation (Diaz-Pulido & McCook 2002) and that bioerosion rates are likely to increase due to environmental change, with significant impacts on reef health and resilience. Rates of carbonate dissolution within the reef matrix also need to be quantified, as these cements may be more responsive to changes in the saturation state of calcium carbonate under ocean acidification scenarios (Reyes-Nivia et al. 2013).

At present, the primary management objective regarding algal turfs on the GBR exists in the maintenance of herbivore assemblages, particularly those that regulate the EAM, to reduce algal growth and facilitate the competitive dominance of reef-building corals. While herbivores are not a common fisheries target on the GBR (e.g. Case Study 3), herbivore-centric management campaigns are already underway to minimise herbivore landings in support of reef resilience in a changing ocean (GBRMPA 2016, 2017). Additionally, *in situ* cultivation of some macroalgal species has been suggested as a potential management strategy to, at least in part, mitigate or buffer ocean acidification and its effects on coral reefs through biogeochemical functioning (Mongin et al. 2016a).

Crown-of-thorns starfish outbreaks (and triton snails) The pervasive impacts of coral predation by CoTS have been extensively documented (e.g. Pratchett et al. 2014, 2017a, Babcock et al. 2016a, Cowan et al. 2017, Wilmes et al. 2018). While high-density populations of CoTS can adversely affect whole reefs, their impacts at low densities are minor (Branham et al. 1971), as observed on the GBR for decades at One Tree Island (Maria Byrne, pers. comm.) and other largely unaffected reefs of the Capricorn Bunker Group (Sweatman et al. 2015). The driving forces behind CoTS population outbreaks are widely debated, but their extreme fecundity and reproductive potential (Uthicke et al. 2009, Babcock et al. 2016b, Rogers et al. 2017) and high levels of connectivity across the GBR (Matz et al. 2018) are likely strong determinants (Hock et al. 2014, 2017). Historically, research on the CoTS outbreak phenomenon has been significantly weighted towards the larvae (e.g. the nutrient runoff hypothesis; Lucas 1982) and adults (e.g. the predator removal hypothesis; Endean 1969), and management strategies and their implementation have developed in line with this research focus (Westcott et al. 2016).

For larvae, management has been centred on improving water quality in catchment areas to limit the potential success of early developmental stages in the plankton (Fabricius et al. 2010, Wolfe et al. 2015b, Wooldridge & Brodie 2015), although CoTS larvae appear to have high resilience to oligotrophy (Olson 1987, Wolfe et al. 2015a, 2017, Carrier et al. 2018) and the remarkable ability to clone in the plankton (Allen et al. 2019). Outbreaks are also documented on reefs not influenced by anthropogenically driven eutrophication, including on the GBR and elsewhere (Lane 2012, Miller et al. 2015, Roche et al. 2015). Yet in the absence of strong evidence to the contrary, precautionary measures should continue to focus on improving water quality across catchment areas to mitigate the potential for runoff-induced eutrophication to enhance larval success.

For CoTS adults, management on the GBR has included the protection of the once-overfished triton snail (*Charonia tritonis*) (Endean 1969, Cowan et al. 2017) and the active and labour-intensive removal or culling of adults (Pratchett et al. 2014), including innovative injection and detection methods (Dayoub et al. 2015, Moutardier et al. 2015, Bostrom-Einarsson & Rivera-Posada 2016, Bostrom-Einarsson et al. 2018). Current measures of control (e.g. the NESP Integrated Pest Management project; Westcott et al. 2016) are commended, and continued development of this and other such programmes is encouraged, including involvement with citizen science groups and in education. The high rankings for triton snails within this report, particularly for the predation process, reflect their perceived niche role as key predators of CoTS and their historical vulnerability to overharvest, as reviewed previously (see Hall et al. 2017). Biocontrol of CoTS populations through triton snail predation would be most effective when aiming to keep non-outbreak populations at low densities so as to lessen the potential for outbreaks to initiate (Hall et al. 2017). There is evidence that CoTS are less abundant in no-take fishing zones on the GBR and elsewhere (Dulvy et al. 2004, Sweatman 2008, McCook et al. 2010), suggesting that heavy fishing may encourage outbreaks through suppression of a multi-level trophic cascade (i.e. reduced predation pressure across various life stages) (Cowan et al. 2017). Yet the lack of information on the basic biology of CoTS of any age-class *in situ* means that the relationship between fishing and outbreaks remains elusive (Sweatman & Cappo 2018). Information is particularly limited for CoTS juveniles (Case Study 5), although recent work demonstrates high densities of juvenile CoTS can be detected (Wilmes et al. 2016, 2018, 2020), and that juveniles can survive for years before the ontogenetic shift to coral (Deaker et al. 2020a,b). Characterising this life stage may provide an important opportunity to improve the early detection of outbreaks and their management (Sweatman & Cappo 2018).

CASE STUDY 5: JUVENILE CROWN-OF-THORNS STARFISH ‘IN WAITING’: THE MISSING LINK IN POPULATION AND CONNECTIVITY MODELS

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Settlement of CoTS larvae is typically triggered by CCA or biofilm (Johnson et al. 1991, Wolfe et al. 2015b), where they begin their benthic life stage as small herbivorous juveniles, with an ontogenetic shift in diet to become coral predators as they grow (Yamaguchi 1974, Johansson et al. 2016, Kamya et al. 2018). As for the great diversity of marine invertebrates, the early life history stages of CoTS experience high mortality rates (Keesing et al. 2018, Wilmes et al. 2018). In order to seed a population outbreak of deleterious corallivorous adults, high survival rates of the herbivorous juvenile are required. However, the biology and ecology of juvenile CoTS are poorly characterised due to their highly cryptic nature.

In an experiment over 4.5 months (139 days), juvenile CoTS were raised on one of three diets: crustose coralline algae (CCA), *Amphiroa* sp. (calcifying algae) or biofilm (Figure CS5.1) and their growth rates quantified. As for adult CoTS, juveniles leave feeding scars on their algal food source (Figure CS5.1). Juveniles fed CCA and *Amphiroa* grew the same number of arms (Figure CS5.2A) and at the same rate until day 43, when those fed CCA began to grow faster

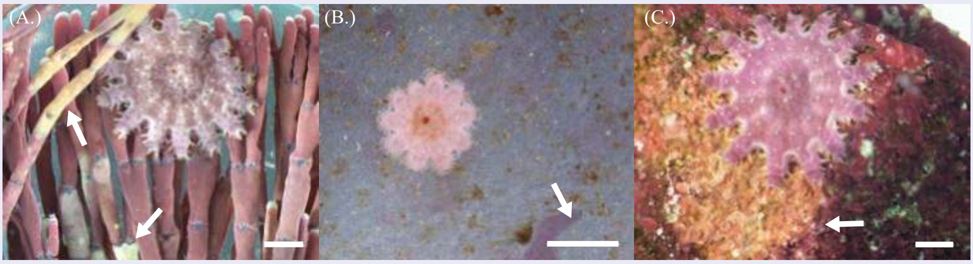

Figure CS5.1 Juvenile CoTS leave feeding scars (white arrows) on algal food sources; (A) *Amphiroa* sp., (B) biofilm and (C) CCA (scale bars = 2 mm).

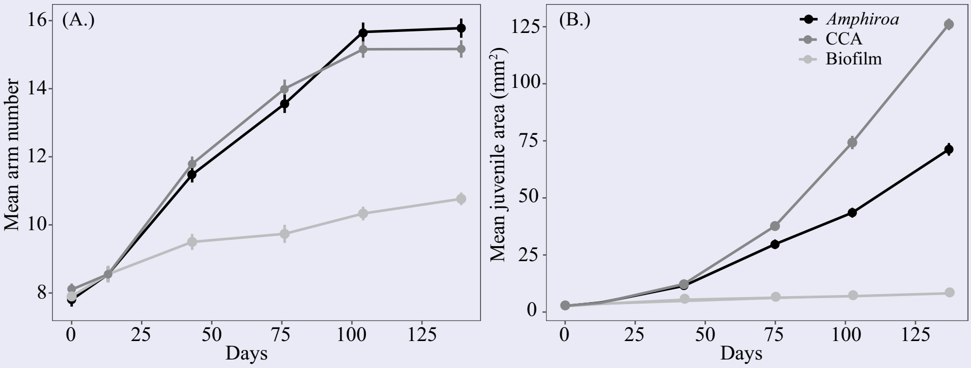

Figure CS5.2 Mean (±SE) (A) number of arms and (B) area of CoTS juveniles raised on one of three algal diets.

(Figure CS5.2B). Juveniles were able to consume and survive on biofilm, although growth was marginal (Figure CS5.2A,B). When offered a choice between the three diets, they selected either CCA or *Amphiroa* over biofilm, indicating that they can identify preferred food at this early life stage.

In general, CoTS have a broader diet range than previously recognised. Their ability to subsist on biofilm alone suggests that juvenile CoTS may be able to survive for extended periods of time in the coral rubble matrix (or other EAM habitat) following settlement and prior to their ontogenetic switch to corallivory. This may create a time lag across the larval–settlement–juvenile–outbreak continuum of the CoTS life history, which is currently uncaptured in population models. As juvenile growth rates are strongly linked to resource availability, current growth estimates that are largely based on laboratory cultures (e.g. Wilmes et al. 2016) may not reflect size-age relationships in nature. These 'juveniles in waiting' complicate our ability to understand the processes that drive CoTS outbreaks and require extra attention. Early warning signals for outbreaks may exist in the benthos through juvenile reserves, but where these exist remains largely unknown (Johnson et al. 1991, Wilmes et al. 2016, 2018). The characterisation of habitat preferences of CoTS juveniles has the potential to reshape how we survey, detect and manage CoTS on the GBR and on coral reefs in general.

Herbivorous parrotfishes There is a diverse but critical range of roles in the regulation and removal of algae by nominally herbivorous fishes in coral reef ecosystems (Bellwood et al. 2006a, Burkepile & Hay 2008, 2011, Steneck et al. 2017). In our process-based assessment, scraping and excavating parrotfishes were among the most ecologically significant, driven by their roles shaping habitat functioning (bioerosion, ecosystem engineering, recruitment facilitation). Parrotfishes are the primary contributors to bioerosion on the GBR, as on other reefs (Perry et al. 2012a), with the capacity to exacerbate the total carbonate budget through their bioerosive processes (Case Study 2). The potential for this activity to influence or buffer reef biogeochemistry would be interesting to quantify in context of ocean acidification, particularly for mass excavators such as *Bolbometopon* (Goldberg et al. 2019), as posited for deposit-feeding sea cucumbers (Schneider et al. 2011, Purcell et al. 2016a, Vidal-Ramirez & Dove 2016, Wolfe et al. 2018).

There may be limited functional redundancy among parrotfishes, which demonstrate spatial variability in their contributions to herbivory, bioerosion, ecosystem engineering and recruitment facilitation across GBR (Hoey & Bellwood 2008). *Bolbometopon muricatum*, one of the largest parrotfishes on coral reefs, appears to be most significant on outer-shelf reefs, while *Scarus rivulatus* (scraper) and *Chlorurus* spp. (excavators) are more important on inner- and mid-shelf reefs (Hoey & Bellwood 2008). *Bolbometopon muricatum* is listed as Vulnerable on the IUCN Red List owing to its susceptibility to overfishing globally (Dalzell et al. 1996, Aswani & Hamilton 2004, Donaldson & Dulvy 2004, Chan et al. 2012, Bejarano et al. 2013, 2014); though it is generally not fished on the GBR (Case Study 3). Recruitment of this species may also be vulnerable to habitat loss attributed to water quality issues (Hamilton et al. 2017). Other parrotfishes common on the GBR are listed as Data Deficient or Least Concern by the IUCN and are currently seldom targeted by commercial and recreational fishers on the GBR. While the impact from fisheries seems low for herbivores at present, there has not yet been an assessment on the total extractive use of herbivores for the GBR.

Changes in herbivory can result in undesirable shifts in coral reef ecosystems (Carpenter 1990, Newman et al. 2006, Bozec et al. 2013, Mumby et al. 2013b, 2016, Ainsworth & Mumby 2015, Graham et al. 2015, Roff et al. 2015), with natural reversals from algal dominance back to coral-dominated states rarely observed (Diaz-Pulido et al. 2009, Rasher et al. 2013). It appears that high-diversity reefs across the Indo-Pacific have a better capacity to recover from disturbance without entering an algal-dominated phase, as observed on Caribbean reefs (Roff & Mumby 2012), though alternate ecosystem states are dynamic in terms of time and space on coral reefs (van de Leemput et al. 2016). Most herbivorous fish groups were considered resilient to environmental stressors here, with densities of some grazers (e.g. parrotfishes) even documented to increase post disturbance, perhaps due to the increased algal production that typically follows coral mortality (Cheal et al. 2008, 2010, Wilson et al. 2009, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c). Removal of particular larger herbivores can even reduce coral recovery at least three-fold by allowing modest increases in some macroalgal genera that deter coral settlement (Doropoulos et al. 2016, Mumby et al. 2016). Long-term maintenance of reef habitat and production functioning requires sufficient parrotfish stocks (Mumby 2016). Protection through Herbivore Management Areas is an emerging resilience-building tool in response to severe coral bleaching on reefs where herbivores are key targets (Chung et al. 2019).

While herbivorous fishes were generally considered less vulnerable on the GBR than other functional groups, lessons learned from other coral reefs where they have been intensively overfished suggest that early protection should be considered to avoid shifting baselines (Bozec et al. 2016). In support of this, GBRMPA released a conservation initiative in 2016 aimed to deter fishers from targeting herbivorous groups, which act as ‘natural lawnmowers and keep seaweed levels under control by grazing’ (GBRMPA 2016, 2017). Maintaining herbivore assemblages, particularly those that regulate the EAM, would facilitate the competitive dominance of reef-building corals. In extreme cases of algal growth where intervention is necessary, protection of herbivores may be best coupled with active removal of macroalgae (Ceccarelli et al. 2018), though likely labour intensive. Outplanting of the native herbivorous grazing sea urchin, *Tripneustes gratilla*, to reduce the overgrowth of invasive algal species has been a successful management focus on Hawaiian reefs for over a decade (Conklin & Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018).

Wave exposure, nutrification and sedimentation can determine relationships between turf algal productivity and herbivory (Carpenter & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, Tebbett et al. 2017a, Roff et al. 2019), but tipping points need to be explicitly quantified to inform holistic management aiming to enhance the recruitment and the competitive dominance of reef-building corals. It is critical to note that the functional importance of key herbivores is dynamic with changing ecosystem states (Hempson et al. 2018c). For example, the removal of carbonates by mass-excavators (*Bolbometopon*) may be critical in systems where some corals dominate, but as fast-growing corals are lost and states shift to turf-dominance, species that regulate turfs would emerge as the key functional groups (Bellwood et al. 2019). Both research and management must be flexible to the dynamics of changing ecosystems to remain ecologically relevant.

Who were the surprises?

Chemoautotrophic microbes There is a growing awareness of the importance of chemoautotrophic microbes (e.g. Archaea) in many marine habitats. More information is known for this group in the water column, where they are highly prevalent and may have significant roles in carbon and energy cycling, particularly for the Thaumarchaeota of the Marine Group II Archaea (Jiao et al. 2010, Zhang et al. 2015, Angly et al. 2016, Liu et al. 2017). In benthic systems, they were probably first recognised as important components of the sponge microbiome, with specific roles in nitrogen and ammonia cycling (e.g. Thaumarchaeota, *Nitrospira*) (Taylor et al. 2007, Bayer et al. 2008, Webster & Taylor 2012, Bourne & Webster 2013a) and altered community dynamics following bleaching stress (e.g. *Crenarchaeota*) (Lopez-Legentil et al. 2008, 2010). In corals, a diverse endolithic community has also been identified, which is likely to be important for sustaining coral health through the exchange of nutrients, especially during periods of bleaching-related stress (Fine & Loya 2002). Motile archaeal communities are prevalent within the coral mucus and are likely involved in complex nutrient cycling (Kellogg 2004, Frade et al. 2016), while anaerobic methanotrophic Archaea (ANME) can be tightly coupled with nitrogen cycling and sulphate reduction in complex communities within coral polyps (Figure 13) (Wegley et al. 2007, Kimes et al. 2010, Bourne & Webster 2013a). There has also been an increased interest in microaerophilic and anaerobic processes within benthic substrates. Microbial communities vary between oxic (e.g. *Planctomycetaceae*, *Proteobacteria*) and anoxic (e.g. ANME) sediments, where they play functionally important roles in organic matter degradation and nutrient cycling (Figure 13) (Rusch et al. 2009, Rusch & Gaidos 2013).

To date, chemoautotrophic microbes have been poorly represented in the literature, owing to difficulties in culturing and detecting these groups. As such, their final ranking above phototrophic and heterotrophic microbes here is somewhat surprising. Archaeal communities are more strongly shaped by geography rather than host-specificity as displayed by other microbes and bacteria (Siboni et al. 2012b, Frade et al. 2016), although this may simply be an artefact of insufficient investigations that include archaeal-specific primers. On the GBR, prevalence of some chemoautotrophic microorganisms in the inshore lagoon system suggests seasonal variation in assemblages driven by floodwaters and consequent differences in water quality and suspended sediments (Case Study 4) (Angly et al. 2016), but improved detection and monitoring of microbial groups is required, including for spatially explicit Archaea.

Microbial communities can likely be used to provide early warning signals for ecosystem change (Bourne et al. 2016, Glasl et al. 2017, 2018a), but this emerging bioindicator tool requires further development. As in the microbes section above, chemoautotrophic microbes are not specifically included in a management strategy on the GBR, but AMMBI (Brown et al. 2018, IMOS 2018), and similar monitoring platforms provide the opportunity to expand sampling and biobanking of important marine microbe groups. If such monitoring requires a refined or targeted methodology, we recommend that this functionally important chemoautotrophic group be a prime candidate. In

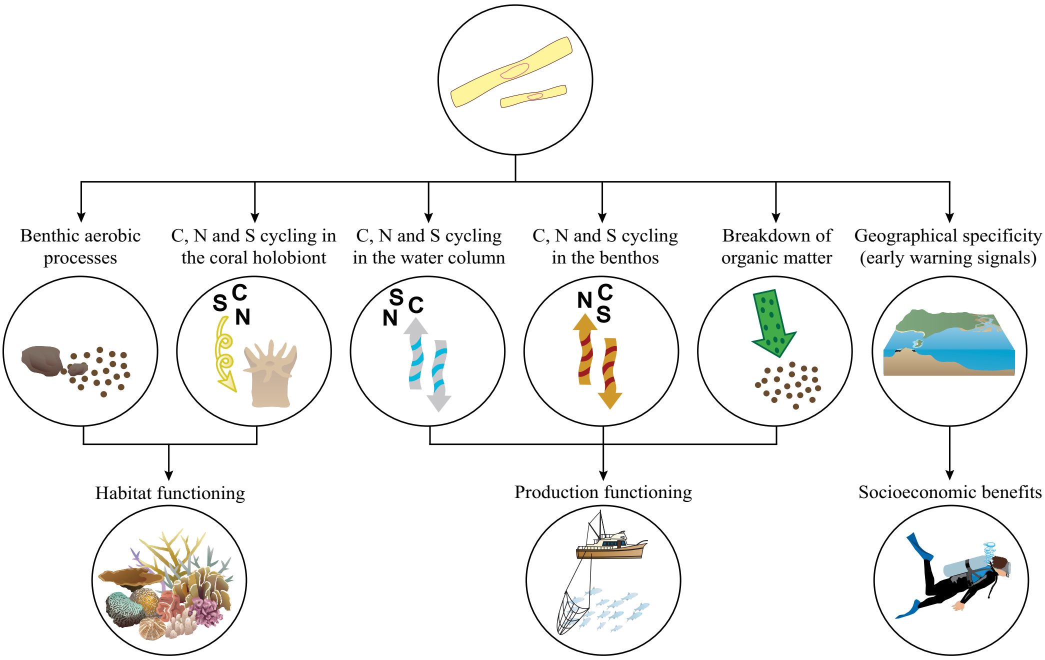

Figure 13 Schematic of the influences of chemoautotrophic microbes (e.g. Archaea) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

the meantime, precautionary measures should maintain focus on water quality while links between runoff (nutrients, sediments, etc.) and microbial assemblages are characterised.

Cleaner wrasse Cleaner wrasses were the only fish group that scored in the top priority quadrant for important and vulnerable species (Figure 4) that were also considered a higher-priority candidate for management (Figure 11). This ranking was likely upweighted by their low functional redundancy, as cleaner wrasse scored lower for most processes compared to other fish groups. Cryptobenthic fishes scored alongside cleaner wrasse in their combination of functional importance and potential vulnerability (Figure 4) but were deemed a lower priority for management compared to the other fishes examined (Figure 11), likely owing to their incredible display of population productivity for a vertebrate (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019).

The ecological importance of cleaning organisms and their cleaning stations in marine community dynamics has long been recognised, but is largely overlooked (Cote 2000, Vaughan et al. 2017). There are over 200 species of cleaner fishes from 106 genera, and over 50 species of cleaner shrimp from 11 genera, recorded to exhibit cleaning behaviour (Cote 2000, Vaughan et al. 2017). In context of the GBR, here we draw focus on the bluestreak cleaner wrasse (*Labroides dimidiatus*), as it has received considerable attention in the literature as a dedicated specialist cleaner. Though typically existing at very low densities, cleaner wrasse can shape reef fish assemblages through the active removal of deleterious ectoparasites, dead skin and mucus from client fishes (Figure 14). Parasitic gnathiid isopods rapidly reoccupy their fish hosts within 24 hrs on the GBR – where they are in high abundance – a process that requires clients to frequently return to cleaning stations (Grutter 1996, 2003). The effects of gnathiids on hosts vary, ranging from partial blemishes and lesions to death, with early life history stages of fishes most susceptible

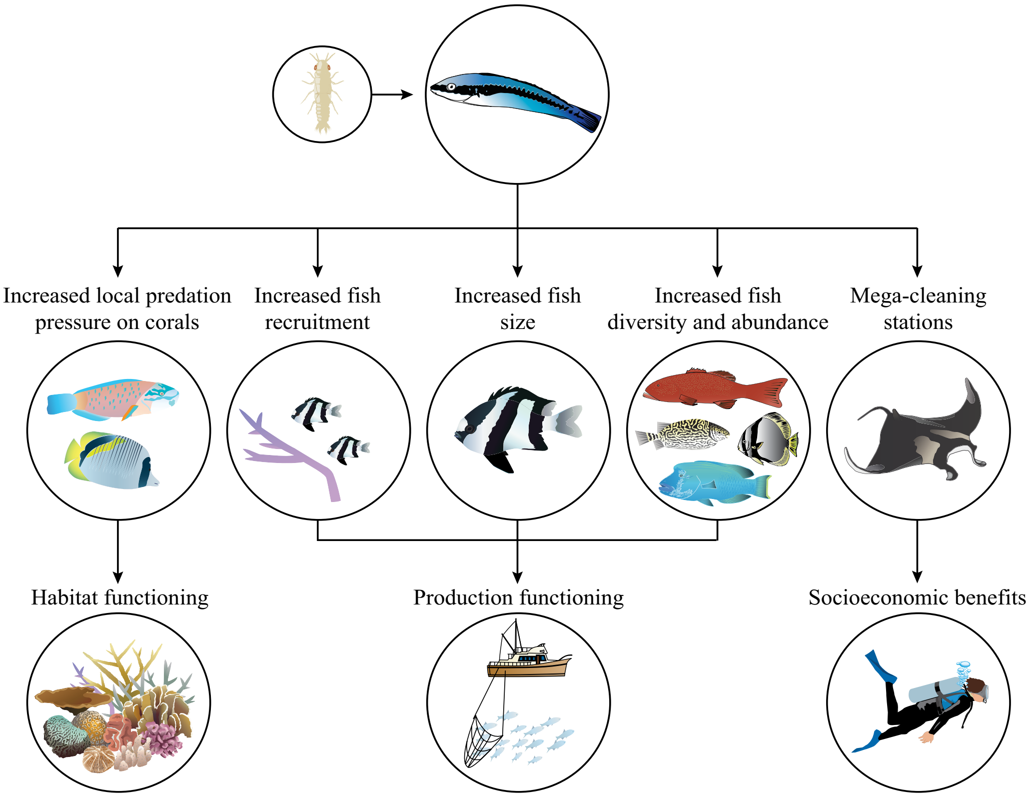

Figure 14 Schematic of the influences of cleaner wrasse (*Labroides dimidiatus*) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and (Hutson et al. 2018).

to parasitic micropredation (Grutter et al. 2008, 2011, Penfold et al. 2008, Sun et al. 2012, Jenkins et al. 2018, Duong et al. 2019).

Through the cleaning process, *L. dimidiatus* have been documented to reduce stress hormones in the client (Soares et al. 2011); increase fish size, density, diversity and survival (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011); encourage juvenile recruitment (Sun et al. 2015) and enhance fish cognitive performance (Binning et al. 2018) (Figure 14). In a series of long-term (>8 year) removal experiments on the GBR, some reefs were up to 66% lower in fish abundance and 33% less species rich in the absence of *L. dimidiatus* (Waldie et al. 2011), with a 27% increase in the size of a model damselfish (Clague et al. 2011). In the context of ecosystem functioning, the symbiotic relationship established between cleaners and a diversity of marine fauna is likely to improve production functioning on coral reefs (Figure 14) – although direct links to fisheries productivity are yet to be quantified. Cleaners also have the potential to influence habitat functioning indirectly by attracting excavating (e.g. parrotfishes) and corallivorous (e.g. butterflyfishes) species to cleaning stations, increasing the exposure of coral communities to bioerosion and predation processes (Adam 2012). How cleaners influence reef resilience and health beyond fish-fish interactions (i.e. coral growth, reef recovery) requires attention.

In the context of ecosystem services, cleaners attract a diversity of marine megafauna, including manta rays, turtles, mola mola, sharks and large predatory fishes, to specific reef locations (Oliver et al. 2011, Jaine et al. 2012, Couturier et al. 2014, 2018, Murie & Marshall 2016). Established 'mega stations' (cleaning stations that attract megafauna) are primary targets for recreational divers and tourist operators on reefs from Mozambique, through the Indo-Pacific and Caribbean, with direct socioeconomic benefits (Figure 14). Manta rays can spend ~8 hr per day engaging in cleaning activity, which inspire tourist hotspots (Marshall & Bennett 2010a,b, Rohner et al. 2013, Germanov et al. 2019). Additionally, their presence on cleaning stations can be used as indicators of environmental conditions of water quality, hydrodynamics and food availability (Armstrong et al. 2016, Barr & Abelson 2019). On the GBR, ecotourism in the southern-most coral cay, Lady Elliot Island, largely benefits from manta ray associations with cleaning stations (Couturier et al. 2014). Mega cleaning stations are also found on Osprey Reef in the Coral Sea (O'Shea et al. 2010), supporting high-revenue tourist operations (Stoeckl et al. 2010a,b). The influence of cleaners on regional- and global-scale socioeconomics seems so poorly appreciated, and their broader integration into ecosystem monitoring, citizen science and tourism initiatives seems important.

Little information exists regarding the vulnerabilities of cleaner wrasses. Globally, they are primary targets for the aquarium industry but are among the lowest survivors in amateur tank setups owing to their highly specialised diets and symbioses (Rhyne et al. 2017), though they are rarely harvested from the GBR (Roelofs 2008). *Labroides dimidiatus* is considered Least Concern by the IUCN (Shea & Liu 2010), but naturally existing at low densities with strong site fidelity, cleaner wrasse (and other cleaning organisms) may be particularly vulnerable to environmental perturbation (Rosa et al. 2014, Vaughan et al. 2017, 2018, Triki et al. 2018). Following the extreme weather events that affected the GBR during 2016, *L. dimidiatus* densities decreased by ~80% from long-term monitoring sites on Lizard Island (Triki et al. 2018). However, surveys beyond these long-term sites suggest *L. dimidiatus* may have increased in abundance around Lizard Island between 2011 and 15 (Ceccarelli et al. 2016). Though poorly characterised, it is probable that fast recovery of cleaner populations post disturbance would help re-establish cleaning interactions and the benefits they provide (Triki et al. 2018), particularly since gnathiid isopod densities show fast recovery post bleaching (Sikkel et al. 2019). It is important to understand how environmental stressors (e.g. bleaching) impact cleaners and their interactions on cleaning stations and to what extent a loss of cleaners would affect reef functioning.

The biological, functional and socioeconomic benefits of cleaning stations provide a strong case for the need to protect these localised habitats to maintain ecosystem functioning and the services cleaners support (Figure 14). At present, cleaner wrasse are not specifically protected on the GBR or elsewhere. We suggest that protecting cleaning stations as hubs of ecosystem functioning may be a more appropriate and successful management initiative than protecting the cleaners themselves. Owing to their site fidelity, local-scale assessments in support of reef resilience might assign some high priority to cleaners and cleaning stations as key features, as outlined in the GBRMPA Blueprint for Resilience regarding herbivores and tabular corals (GBRMPA 2017, 2018a).

Bivalves Giant clams (Tridacnidae) and other bivalves (e.g. oysters) scored surprisingly high for habitat functioning, driven by processes of calcification and recruitment facilitation. Shell and 'bed' construction by bivalves can contribute significant structural complexity to the reef, with both alive and dead structures encouraging recruitment and providing refugia for a diversity of symbiotic and commensal organisms, a particularly important feature when coral cover is low (Beukers & Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). This may be an increasingly important attribute to document and protect in a changing ocean. Shallow-water benthic bivalves are natural controllers of eutrophication and water quality through their filter-feeding processes (Figure 15), perhaps most importantly on nearshore reefs (Klumpp et al. 1992, Klumpp & Lucas 1994, Neo et al. 2015), enhancing an important aesthetic reef value (GBRMPA 2014c, Marshall et al. 2018, Vercelloni et al. 2018). Some bivalves are also important bioeroders, such as the boring clam, *Tridacna crocea*, which can dominate reef and intertidal areas on nearshore (e.g. Orpheus Island) and offshore (e.g. One Tree Island) reefs (Hutchings 1986). As bioerosive processes become more pervasive on coral reefs, knowledge gaps for non-parrotfish bioeroders on the GBR (including

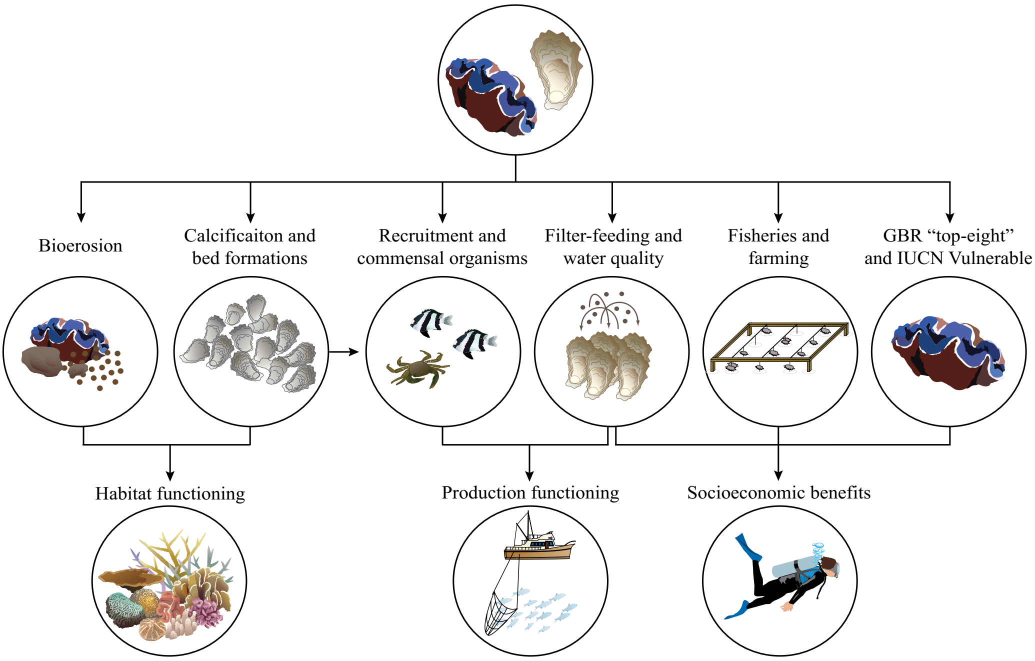

Figure 15 Schematic of the influences of bivalves (e.g. Tridacnidae, oysters) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

bivalves, sponges, microborers) should be filled to empower calculations on the total carbonate budget for the reef and predictions on future reef accretion and recovery processes.

As for corals, giant clams host zooxanthellae that aid in respiration and growth (Klumpp et al. 1992), but this makes them prone to bleaching under warm-water exposure (Buck et al. 2002, Leggat et al. 2003). As calcifying organisms, molluscs and their thinly calcified veliger larvae are among the most vulnerable to changing ocean temperature (warming) and chemistry (acidification) (Przeslawski et al. 2008, Byrne 2011, Przeslawski et al. 2015), including impacts on juvenile survival of some tridacnids (Watson et al. 2012). Ocean acidification may also accelerate bioerosion processes within bivalve bed formations (Wisshak et al. 2014), but suitably high levels of light may work to ameliorate the negative effects of ocean acidification on some tridacnids (Watson 2015). Improving water quality would enhance the potential for light levels to ameliorate the negative impacts of ocean change on photosynthetic tridacnids, particularly for nearshore populations.

Many commercially important bivalves have been decimated by local stressors such as fisheries and habitat and water quality degradation (Kirby 2004, Bersoza Hernández et al. 2018), including on the GBR (Gillies et al. 2015). The most important bivalve to fisheries on the GBR may be the saucer scallop, *Amusium japonicum ballotti*, which operates as a trawl-fishery with a range of management implications (Courtney et al. 2008, 2015), but this occurs beyond the focal reef-centric habitat investigated here. Oysters (*Saccostrea cucullate*, *Saccostrea echinate*, *Isognomon ephippium*, *Pinctada* spp.) and mussels (*Trichomya hirsuta*) may have once been significant reef formers on the GBR, particularly in the sheltered and intertidal habitats of estuaries, nearshore reefs and mangroves, but were also primary shellfish fisheries targets (Gillies et al. 2015, Lewis et al. 2015). Subtidal oyster reefs appear to be functionally extinct over their former range along the east coast of Australia (Beck et al. 2011), but the extent of this on the GBR is historically poorly characterised.

Giant clams, namely the larger species *T. gigas* and *T. derasa*, experienced heavy exploitation through poaching on the GBR (Pearson 1977, Dawson 1985), with all tridacnids consequently listed on Appendix II of CITES by 1985. Both *T. gigas* and *T. derasa* are also listed as Vulnerable on the IUCN Red List of Threatened Species (Wells 1996a,b, Richards & Day 2018). Giant clams are the only invertebrates listed in the 'top-eight' species to see on the GBR (https://www.barrierreefaustralia.com/info/great8/), a significant tourism drawcard. Experimental aquaculture and cultivation of *T. gigas* has occurred on the GBR previously (Orpheus Island) (Crawford et al. 1988, Lucas et al. 1989), with bed formations that still exist integrated in the reef framework today. Population transplants and aquaculture of functionally important bivalves deserves consideration to optimise benefits from the natural infrastructures of reef-forming molluscs, including fisheries production, shoreline protection, water filtration and tourism (Figure 15). Precautionary measures should maintain focus on water quality to enhance the resilience and survival of bivalves on the GBR and elsewhere.

Coral-associated decapods Coral-associated decapods are strongly bound to their coral host, where they take refuge from a range of reef and cryptic predators, including squirrel fishes, wrasses and eels (Hiatt & Strasburg 1960). From a bottom-up perspective, coral-associated crabs can form up to 70% of a reef fish's diet, particularly for species with specialised morphologies that can access prey items from the intricacies of the coral framework (Hobson 1974, Rinkevich et al. 1991). The most common and well-recognised coral-associated crabs on the GBR include the *Trapezia*, *Tetralia* and *Cymo*, which primarily occupy acroporids and pocilloporids (Stella et al. 2011b). Interestingly, *Trapezia* typically occupy pocilloporid corals, while *Tetralia* are found in acroporids (Patton 1983, 1994), where they are both often observed grazing on their host's live tissue, mucus or fat bodies (Stimson 1990, Rinkevich et al. 1991, Castro 2000, Castro et al. 2004). This grazing activity is not considered to have negative effects on their host, given these coral crabs generally exist at low densities (~2 individuals per colony) (Rotjan & Lewis 2008, Stella et al. 2010, 2011b). Obligate-dwellers are considered highly beneficial to their coral hosts, as they actively defend the host from predators, including CoTS, *Drupella* and *Dendropoma*, and contribute to the removal of excess sediment that would otherwise smother the corals (Figure 16) (Glynn 1980, 1983, Pratchett 2001, Stewart et al. 2006, Stier et al. 2010, Stella et al. 2011b). Further, some obligates (e.g. *Cymo*) have been shown to slow the progression of disease in their coral host (Figure 16) (Pollock et al. 2013).

Coral-associated crabs can have pronounced effects on their hosts by reducing fouling algal epibionts by >65% (Coen 1988). In an experiment that removed trapezid crabs from their coral host, whole-colony mortality occurred in up to 80% of crab-less hosts within a month (Stewart et al. 2006), but how the localised benefits of coral crabs scale up to ecosystem and socioeconomic levels is ambiguous. The benefits and feedbacks between coral-associates and their hosts through removal experiments requires greater attention, including how shifts in baseline habitat quality (i.e. coral health) may impact invertebrate communities and trophic links to fisheries productivity. In light of intensifying degradation of coral reefs, any direct benefits to corals through management, as offered through the GBRMPA zoning scheme, would surely support broader resilience of coral-associated organisms to environmental change. There is no specific protection or management initiative outlined for coral-associated decapods at present, which would prove difficult to implement and monitor given their small and cryptic nature. Broader protection of their coral habitat and education on the importance of coral-associated organisms to reef functioning are likely to be the most reasonable and effective management strategies for this group.

The survival of coral-associates is inextricably linked to that of their host, and so obligate associates are considered particularly vulnerable to changes in live coral cover (Caley et al. 2001, Stella et al. 2011a,b). Among the most sensitive corals to thermal stress are *Acropora* and *Pocillopora* (Loya et al. 2001, McClanahan et al. 2004, van Woesik et al. 2011), the typical host genera of coral crabs. For trapeziids, coral bleaching has been shown to impact their densities

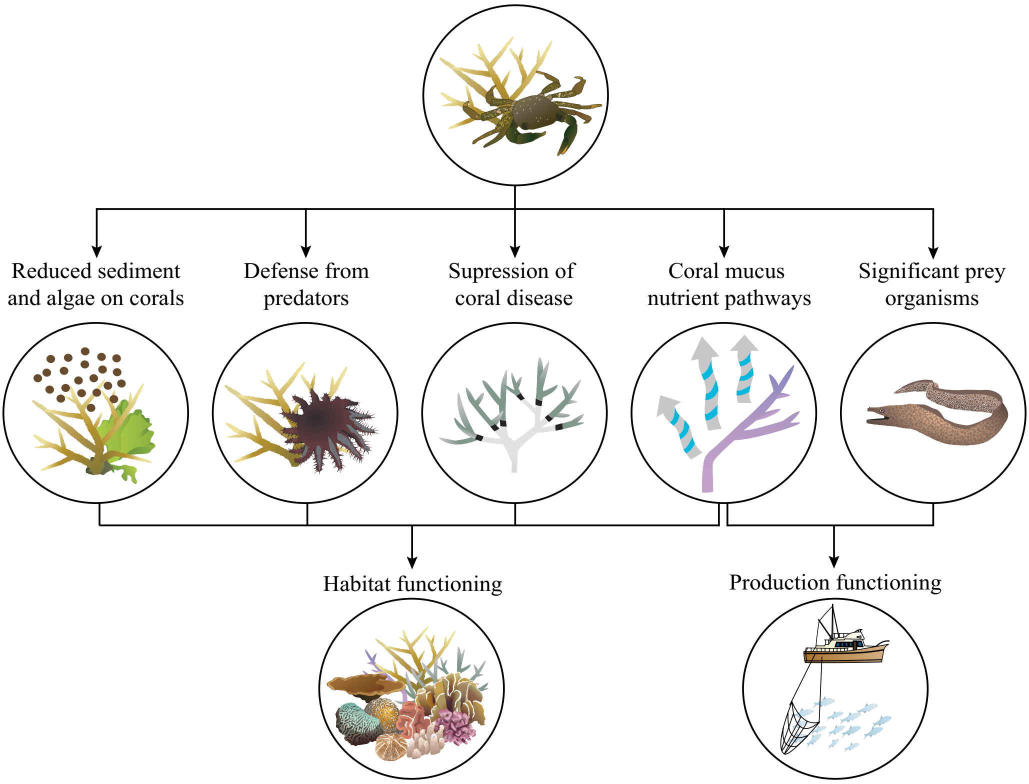

Figure 16 Schematic of the influences of coral-associated decapods on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

and reproduction, which intensifies inter- and intraspecies competition (Glynn et al. 1985, Stella et al. 2011a, 2014). There are records of some trapeziids occupying dead coral habitat, which could suggest unanticipated resilience in the ability for these coral-obligates to occupy degraded and dead coral habitats (Head et al. 2015). However, this is usually a result of saturated population densities and increased territoriality, which forces losing individuals to traverse dead coral and rubble habitats in search of suitable (and available) live coral habitat, a behavioural trait that renders them vulnerable to predation and hinders their ability to fulfil their novel roles in coral reef functioning (Stella et al. 2011b). The ability for coral-associated decapods to sustain their populations in alternative habitats during periods of coral recovery requires attention, including their potential to enhance reef resilience as corals recover, particularly when coral mortality occurs at large spatial scales.

Detritivorous fishes Although being rated as a critical functional group, especially regarding particular ecosystem processes (e.g. nutrient cycling), detritivorous fishes were not considered vulnerable nor a high-priority candidate for management. This is likely due to the broad distributions and/or high densities of predominant groups, including blennies (Wilson 2000, 2001, 2004) and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Regardless, detritivores are considered a key trophic group, representing ~40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). They are fundamental components of nutrient pathways through the transfer of energy from the EAM to secondary consumers (Figure 17) (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014). The rapid population turnover of blennies in particular

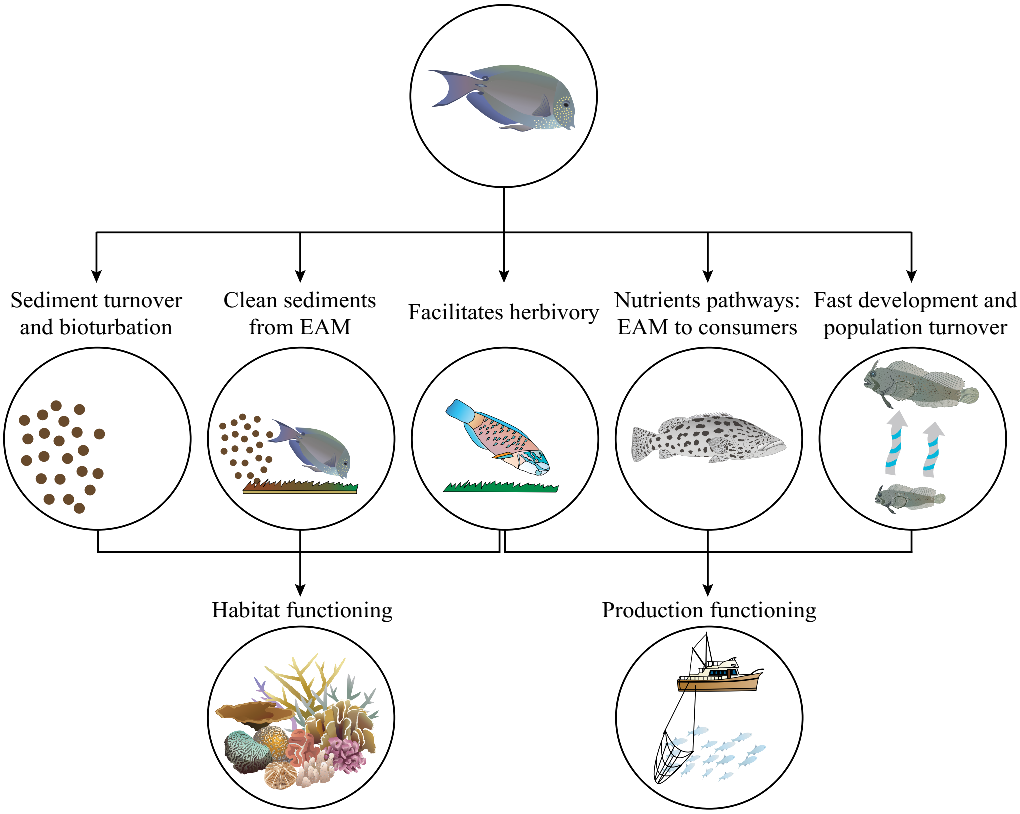

Figure 17 Schematic of the influences of detritivorous fishes (e.g. blennies, *Ctenochaetus striatus*) on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

(Wilson 2004), which can account for ~60% of detritivore biomass in some habitats (Wilson 2001), attributes to their key role in reef trophodynamics with links to fisheries productivity (Figure 17). Further, post disturbance and associated losses in coral cover and fish diversity may be maintained by detrital- and EAM-grazers (Wilson et al. 2009, Ceccarelli et al. 2016). Given the importance of detritivores to particular ecosystem processes, it could be important to characterise additional key contributors to detritivory and sediment processing, including for other fishes and invertebrates like deposit-feeding sea cucumbers.

One expert noted that their scores for detritivores were primarily in context of *C. striatus*. This species is one of the most abundant and important surgeonfishes on Indo-Pacific reefs, including on the GBR (Trip et al. 2008), through its contributions to detritivory and sediment dynamics (Purcell & Bellwood 1993, Goatley & Bellwood 2010, Krone et al. 2011, Cheal et al. 2013, Tebbett et al. 2017b,d, 2018). While feeding on components of the EAM (e.g. detritus, bacteria), *C. striatus* selectively brushes associated particles from algal turfs. They may have low functional redundancy in this role removing sediments (Tebbett et al. 2017b, 2018), which has been shown to facilitate herbivory by other species (Goatley & Bellwood 2010, Marshell & Mumby 2012, 2015), with potential roles regulating coral-algal phase shifts (Cheal et al. 2010). *Ctenochaetus striatus* are selective feeders with a preference for coarser sediments. Fine sediments appear to impact their feeding behaviour and associations with the EAM, with implications regarding their vulnerability to sedimentation, as produced by dredging activities or heavy storm events (Tebbett et al. 2017c,d, Bellwood et al. 2018);

other EAM-feeders may not be as fussy (Tebbett et al. 2017c). As some detritivores can be highly sensitive to sediment loads, improving water quality across catchment areas, including reducing impacts from dredging activity, are management strategies that would likely benefit this group.

Although considered Least Concern by the IUCN, *C. striatus* has been extensively fished from some reefs like American Samoa (Trip et al. 2008, Choat et al. 2012). The aggregative spawning behaviour exhibited by this species, including on the GBR (Robertson 1983), could have specific implications for their management regarding seasonal spawning closures. There is a recreational catch limit of five individuals and a minimum size limit of 25 cm on the GBR, but they are not heavily targeted and exhibit particularly fast growth rates to a distinct size (Trip et al. 2008, Choat et al. 2012). The biology of *C. striatus* may render them particularly resilient across their expansive range, given fishing intensity remains low (Trip et al. 2008). Specific consideration of key detritivores, such as *C. striatus*, in reef monitoring programmes is recommended to ensure that groups with important contributions to ecosystem functioning are well documented and safeguarded in a future ocean. Management and education initiatives may also be implemented for detritivores, as already exist for herbivores and tabular corals (GBRMPA 2017, 2018a).

Overview and synthesis

Ultimately, global protection of coral reefs depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functioning and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Explicit identification and protection of key species that support positive ecological interactions is imperative to conservation and in providing targeted information to safeguard species, biodiversity and functioning into the future (Halpern et al. 2007, McClanahan et al. 2014, Rogers et al. 2015, Shaver & Silliman 2017, Richards & Day 2018). We present a broad review of the literature for priority coral reef species on the GBR and for typical reef crest and reef slope habitats more generally. While whole-ecosystem management is necessary to maintain the integrity of coral reefs, many of the attributes examined here, at the level of species, ecological processes and ecosystem functioning, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c). The information here provides a first step to inform holistic management aiming to preserve important reef species, values and processes and the opportunity to build out from the current framework in context of biological functioning to other important coral reef biomes (e.g. mangroves, seagrass meadows, interreefal areas) and values (e.g. social, cultural, economic).

The preservation of biodiversity is critical to maintain coral reef functioning (Clements & Hay 2019), but we must augment the precautionary principle of conserving biodiversity with predictive science that informs practical and specific solutions (Naeem et al. 2012). Conservation success depends on the recognition and inclusion of specific taxa that support positive interactions, with disproportionate benefits to ecosystem functioning (Halpern et al. 2007, Shaver & Silliman 2017, Renzi et al. 2019). We present a range of desired outcomes for priority groups (tabular corals, branching corals, microorganisms, crustose coralline algae, algal turfs, crown-of-thorns starfish and herbivorous parrotfishes) to empower research and holistic management. In the context of the GBR, past and present management schemes (e.g. GBRMPA zoning [Day 2002, Fernandes et al. 2005, 2009], Blueprint for Resilience [GBRMPA 2017, 2018a]) are commended for their efforts, and momentum should be maintained. Novel taxa (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated crabs and detritivorous fishes) may benefit from consideration in these (or similar) initiatives, including expanding current research and monitoring programmes to effectively capture these groups to inform whole-system models. Many of these priority and novel taxa are distinct and identifiable, rendering themselves particularly attractive to future endeavours in education and citizen science, if not already captured. For novel candidates and groups where scientific certainty was particularly low (cryptic predators, deposit-feeding sea cucumbers, marine worms, cryptic sponges and crustaceans), empirical data on their roles in ecosystem functioning and vulnerability to the growing number of stressors on coral reefs are imperative to ensure that functioning is adequately safeguarded at its highest degree.

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Supplementary Tables are provided online at https://www.routledge.com/9780367367947

Appendix 1

List of fishes and reef sharks that consume invertebrates on the GBR, including their trophic level, life stage, feeding type and time of foraging activity.

Family	Species	TL	Life stage	Feeding type	Activity	References
Acanthuridae	*Acanthurus blochii*	D	A	Facultative	Diurnal	5
	Acanthurus lineatus	H/D	A	Facultative	Diurnal	5
	Acanthurus nigricauda	D	A	Facultative	Diurnal	5
	Acanthurus nigrofuscus	D	A	Facultative	Diurnal	5
	Acanthurus olivaceus	D	A	Facultative	Diurnal	5
	Ctenochaetus striatus	D	A	Facultative	Diurnal	5
	Naso unicornis	D	A	Facultative	Diurnal	5
	Zebrasoma scopas	H/D	A	Facultative	Diurnal	5
	Zebrasoma veliferum	H/D	A	Facultative	Diurnal	5
Apogonidae	*Apogon doederleini*	Mac	J/A	Obligate	Nocturnal	24
	Cheilodipterus artus	C	J/A	Facultative	Nocturnal	24
	Cheilodipterus quinquelineatus	C	J/A	Obligate	Nocturnal	24
	Nectamia fusca	Mic	J/A	Facultative	Nocturnal	24
	Ostorhinchus cyanosoma	Mac	J/A	Obligate	Nocturnal	24
	Pristiapogon exostigma	Mac	J/A	Obligate	Nocturnal	24
	Taeniamia leai	Mic	J/A	Facultative	Nocturnal	24
Balistidae	*Balistapus undulatus*	O	A		Diurnal	26, 35
	Balistoides viridescens	Mac	A		Diurnal	6, 35
	Pseudobalistes flavimarginatus	Mac	A		Diurnal	6
	Sufflamen chrysopterum	Mac	A		Diurnal	6
Blenniidae	*Salarias patzneri*	D	A	Facultative	Diurnal	34
Carcharhinidae	*Carcharhinus amblyrhynchos*	C	A	Facultative	Nocturnal	10
	Carcharhinus melanopterus	C	A	Facultative	Nocturnal	10
	Triaenodon obesus	C	A	Facultative	Nocturnal	10
Chaetodontidae	*Chelmon rostratus*	I	A		Diurnal	6, 26
	Heniochus monoceros	O/Mic	A		Diurnal	6
Gobiidae	*Amblygobius bynoensis*	H	J/A	Facultative	Diurnal	14
	Amblygobius decussatus	O/Mic	A	Facultative	Diurnal	19
	Amblygobius nocturnus	D	A	Facultative	Diurnal	9
	Amblygobius phalaena	H	J/A	Facultative	Diurnal	14
	Asterropteryx semipunctata	D	J/A	Facultative	Diurnal	9, 14, 19
	Bathygobius fuscus	D	A	Facultative	Diurnal	9
	Eviota sp. *C*	O/Mic	A	Obligate	Diurnal	9
	Eviota queenslandica	O	A	Facultative	Diurnal	9
	Eviota zebrina	O/Mic	A	Obligate	Diurnal	19
	Istigobius decoratus	D	A	Facultative	Diurnal	9
	Istigobius goldmanni	O/D	J/A	Facultative	Diurnal	9, 14
	Istigobius rigilius	O/Mic	A	Facultative	Diurnal	19
	Koumansetta rainfordi	H	A	Facultative	Diurnal	9
	Paragobiodon sp.	Cor	A		Diurnal	21

(Continued)

Family	Species	TL	Life stage	Feeding type	Activity	References
	Paragobiodons xanthosoma	Cor	A		Diurnal	21
	Paragobiodon echinocephalus	Cor	A		Diurnal	21
	Paragobiodon lacunicolus	Cor	A		Diurnal	21
	Pleurosicya muscarum	C/Mic	A	Facultative	Diurnal	9
	Priolepis nuchifasciatus	Mic	A	Obligate	Diurnal	9
	Trimma caesiura	O	A	Facultative	Diurnal	9
	Trimma striatum	Mic	A	Obligate	Diurnal	9
	Valenciennea longipinnis	Mic	A	Facultative	Diurnal	27
	Valenciennea muralis	Mic	J/A	Facultative	Diurnal	9, 14
Haemulidae	*Diagramma pictum*	C/Mac	A		Nocturnal	6, 17, 26
	Plectorhinchus albovittatus	Mac	A		Both**	6
	Plectorhinchus chaetodonoides	C/P	A		Both**	26
	Plectorhinchus chrysotaenia	Mac	A		Both**	6, 26
	Plectorhinchus gibbosus	Mac	A		Both**	26
	Plectorhinchus lineatus	Mac	A		Both**	6, 26
Hemiscylliidae	*Hemiscyllium ocellatum*	Mac	J/A	Obligate	Nocturnal	15
Labridae	*Anampses* spp.†	I	A		Diurnal	20
	Anampses caeruleopunctatus	I	A		Diurnal	2, 6
	Anampses neoguinaicus	I	A		Diurnal	2, 6, 26
	Bodianus spp.†	Mac	A		Diurnal	20
	Bodianus axillaris	Mac	A		Diurnal	6
	Bodianus loxozonus	Mac	A	Obligate	Diurnal	2
	Bodianus mesothorax	Mac	A		Diurnal	6, 26
	Cheilinus spp.†	Mac	A		Diurnal	20
	Cheilinus chlorourus	Mac	A		Diurnal	6, 25, 26
	Cheilinus fasciatus	Mac	A	Obligate	Diurnal	2, 6, 25, 26
	Cheilinus trilobatus	Mac	A		Diurnal	6, 25, 26
	Cheilinus undulatus	C/Mac	A		Diurnal	6
	Choerodon spp.†	Mac	A		Diurnal	20
	Choerodon anchorago	Mac	A	Obligate	Diurnal	2, 26
	Choerodon cephalotes	I	A		Diurnal	2
	Choerodon cyanodus	Mac	A	Facultative	Diurnal	2
	Choerodon fasciatus	Mac	A		Diurnal	6, 26
	Choerodon graphicus	P/Mac	A	Obligate	Diurnal	2
	Choerodon monostigma	Mac	A		Diurnal	6
	Choerodon schoenleinii	P/Mac	A	Obligate	Diurnal	2, 26, 35
	Choerodon sugillatum	I	A		Diurnal	2
	Choerodon vitta	I	A		Diurnal	2, 6
	Coris spp.†	Mac	A		Diurnal	20
	Coris aygula	Mac	A	Obligate	Diurnal	2, 6, 26
	Coris batuensis	Mac	A		Diurnal	6, 26
	Coris gaimard	Mac	A	Obligate	Diurnal	2, 6
	Cymolutes spp.†	NA	A		Diurnal	20
	Cymolutes torquatus	Mic	A		Diurnal	2
	Epibulus sp.†	C/Mac	A		Diurnal	20
	Epibulus insidiator	C/Mac	A		Diurnal	6, 25
	Gomphosus sp.†	Mic	A		Diurnal	20

(Continued)

Family	Species	TL	Life stage	Feeding type	Activity	References
	Gomphosus varius	Mic	A	Obligate	Diurnal	2, 6, 26
	Halichoeres spp.†	I	A		Diurnal	20
	Halichoeres chloropterus	Mac	A		Diurnal	6, 26
	Halichoeres hartzfeldii	Mac	A	Obligate	Diurnal	2
	Halichoeres hortulanus	Mac	A	Obligate	Diurnal	2, 6, 26
	Halichoeres marginatus	Mac	A		Diurnal	6, 26
	Halichoeres melanurus	Mic	R/A	Obligate	Diurnal	2, 6, 11, 19, 26
	Halichoeres melasmapomus	Mic	A		Diurnal	2
	Halichoeres miniatus	Mic	A		Diurnal	2
	Halichoeres nebulosus	Mic	A		Diurnal	6, 26
	Halichoeres nigrescens	Mic	A		Diurnal	6
	Halichoeres prosopeion	Mic	A		Diurnal	6
	Halichoeres trimaculatus	Mac	A		Diurnal	6
	Hemigymnus spp.†	I	A		Diurnal	20
	Hemigymnus fasciatus	I	J		Diurnal	2, 6, 26
		I	A		Diurnal	
	Hemigymnus melapterus	I	J		Diurnal	2, 6, 26
		I	A		Diurnal	
	Hologymnosus spp.†	C/Mac	A		Diurnal	20
	Hologymnosus doliatus	C/Mac	A		Diurnal	6
	Labroides spp.†	Mic	A		Diurnal	20
	Labroides bicolor	Mic	A		Diurnal	6
	Labroides dimidiatus	Mic	J	Obligate	Diurnal	2, 6, 12, 13, 26
		Mic		Both*	Diurnal	
	Labroides pectoralis	Mic	A	Facultative	Diurnal	2
	Labropsis spp.†	Mic	A		Diurnal	20
	Macropharyngodon spp.†	Mac	A		Diurnal	20
	Macropharyngodon choati	Mac	A		Diurnal	2, 6
	Macropharyngodon meleagris	Mac	A		Diurnal	6, 26
	Macropharyngodon negrosensis	Mac	A		Diurnal	2, 6
	Novaculichthys sp.†	Mac	A		Diurnal	20
	Novaculichthys taeniourus	Mac	A	Obligate	Diurnal	2, 6
	Oxycheilinus spp.†	C/P	A		Diurnal	20
	Oxycheilinus digramma	C/P	A	Obligate	Diurnal	8, 25
	Pseudocheilinops sp.†	Mic	A		Diurnal	20
	Pseudocheilinus spp.†	Mic	A		Diurnal	20
	Pseudocheilinus evanidus	Mic	A		Diurnal	2, 26
	Pseudocheilinus hexataenia	Mic	A		Diurnal	2, 6
	Pseudocheilinus octotaenia	Mic	A	Obligate	Diurnal	2
	Pseudodax sp.†	Mac	A		Diurnal	20
	Pseudodax moluccanus	Mac	A		Diurnal	6
	Pseudojuloides spp.†	Mac	A		Diurnal	20
	Pseudojuloides cerasinus	Mac	A		Diurnal	2
	Pteragogus sp.†	Mac	A		Diurnal	20
	Stethojulis spp.†	Mic	A		Diurnal	20
	Stethojulis bandanensis	Mic	A	Obligate	Diurnal	2, 6, 26

(Continued)

Family	Species	TL	Life stage	Feeding type	Activity	References
	Stethojulis interrupta	Mic	A		Diurnal	2, 26
	Stethojulis strigiventer	Mic	A	Obligate	Diurnal	2, 6, 19
	Stethojulis trilineata	Mic	A		Diurnal	2
	Thalassoma spp.†	Mac	A		Diurnal	20
	Thalassoma hardwicke	O/Mac	A		Diurnal	6, 26
	Thalassoma jansenii	Mac	A	Obligate	Diurnal	2, 6, 26
	Thalassoma lunare	C/P/ Mic	J/A	Obligate	Diurnal	8, 19, 26
	Thalassoma lutescens	Mac	A		Diurnal	6
	Thalassoma trilobatum	Mac	A	Obligate	Diurnal	2
	Wetmorella sp.†	Mac	A		Diurnal	20
Lethrinidae	*Gnathodentex aureolineatus*	Mac	A		Both**	6
	Gymnocranius microdon	Mac	A		Diurnal	6
	Lethrinus atkinsoni	P/C	A		Diurnal	31, 35
	Lethrinus erythracanthus	Mac	A		Diurnal	31
	Lethrinus harak	P/C	A		Diurnal	31
	Lethrinus lentjan	Mac	A		Diurnal	6
	Lethrinus miniatus	C/Mac	J/A	Obligate	Diurnal	31
	Lethrinus nebulosus	P/C	A	Facultative	Diurnal	17, 31
	Lethrinus obsoletus	Mac	A		Diurnal	6, 31
	Lethrinus ornatus	P/C	A		Diurnal	31
	Lethrinus reticulatus	Mac	A	Facultative	Diurnal	31
	Lethrinus variegatus	Mac	A	Facultative	Diurnal	31
	Monotaxis grandoculis	Mac	A		Both**	6, 26
	Monotaxis heterodon	Mac	A		Both**	6
Lutjanidae	*Lutjanus carponotatus*	C/I	A	Both*	Diurnal	8, 32
		C/I/P		Facultative	Diurnal	
	Lutjanus fulviflamma	P/C	A	Facultative	Nocturnal	32
	Lutjanus kasmira	C/Mac	A		Diurnal	6
	Lutjanus quinquelineatus	C/Mac	A		Diurnal	6
	Lutjanus russellii	C/Mac	A		Diurnal	6
	Lutjanus vitta	C/Mac	A		Diurnal	6
Mullidae	*Mulloidichthys flavolineatus*	Mac	A		Nocturnal	6, 26
	Parupeneus barberinus	Mac	J	Facultative	Diurnal	6, 23, 26
		Mac	A	Obligate	Diurnal	
	Parupeneus ciliatus	Mac	A		Nocturnal	6, 26
	Parupeneus cyclostomus	C/Mac	A		Diurnal	6
	Parupeneus indicus	Mac	A		Nocturnal	6
	Parupeneus multifasciatus	Mac	A		Diurnal	6, 26
	Parupeneus pleurostigma	Mac	A		Diurnal	6
	Parupeneus trifasciatus	Mac	A		Nocturnal	6
Nemipteridae	*Pentapodus aureofasciatus*	C/Mac	A		Diurnal	6
	Pentapodus caninus	C/Mac	A		Diurnal	6
	Pentapodus emeryii	C/Mac	A		Diurnal	6
	Scolopsis bilineata	Mac	R/J		Diurnal	4, 6, 26
		Mac	A		Nocturnal	
	Scolopsis lineata	C/Mac	A		Both**	26
	Scolopsis margaritifera	C/Mac	A		Both**	6, 26
	Scolopsis monogramma	C/Mac	A		Both**	6, 26

(Continued)

Family	Species	TL	Life stage	Feeding type	Activity	References
Plesiopidae	*Assessor macneilli*	O	A	Facultative	Diurnal	9
Scaridae	*Chlorurus sordidus*	C/O	R		Diurnal	1, 7
	Scarus spp.	C/O	J		Diurnal	1
	Scarus schlegeli	C/O	R		Diurnal	7
Serranidae	*Cephalopholis boenak*	P/C	Adult	Facultative	Diurnal	3
	Cephalopholis cyanostigma	P/C	Adult	Facultative	Diurnal	3
	Diploprion bifasciatum	C/Mac	Adult		Diurnal	6
	Epinephelus quoyanus	C	R/J/A	Both*	Diurnal	8, 32
		P/C		Facultative	Diurnal	
	Plectropomus leopardus	C	R	Both*	Diurnal	18, 22, 28–30
		C/P	J/A	Facultative	Diurnal	
	Plectropomus maculatus	C	R	Both*	Diurnal	32, 33
		C	J	Facultative	Diurnal	
Siganidae	*Siganus argenteus*	H/D	A	Facultative	Diurnal	16
	Siganus canaliculatus	H	A	Facultative	Diurnal	16
	Siganus corallinus	H/D	A	Facultative	Diurnal	16
	Siganus doliatus	H/D	A	Facultative	Diurnal	16
	Siganus javus	H	A	Facultative	Diurnal	16
	Siganus lineatus	D	A	Facultative	Diurnal	16
	Siganus puellus	Sp	A	Facultative	Diurnal	16
	Siganus punctatissimus	H/D	A	Facultative	Diurnal	16
	Siganus punctatus	H/D	A	Facultative	Diurnal	16
	Siganus spinus	H	A	Facultative	Diurnal	16
	Siganus vulpinus	H/D	A	Facultative	Diurnal	16
Syngnathidae	*Corythoichthys* sp.	Mic	A		Diurnal	26
Tripterygiidae	*Enneapterygius tutuilae*	Mic	A	Obligate	Diurnal	9

Abbreviations: Nominal trophic levels (TL); H, herbivore; D, detritivore; Mic, micro-invertivore; Mac, macro-invertivore; I=both micro- and macro-invertivore; C, carnivore; O, omnivore; Cor, corallivore; Sp, spongivore; P, piscivore; NA=not available. Life stage refers to the stage at which fishes are reported to be feeding on invertebrates; A=adult; R=recruit; J=juvenile.

Note: Feeding types are derived from direct measures presented in the literature. Fishes were classified as obligate consumers when diets contained >65% invertebrates and were otherwise considered facultative.

* Differences in feeding types between locations and studies.

** Differences in periods of activity reported in the literature.

† Species information only to genus level and may overlap with the species listed in full.

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TIDES, THE MOON AND THE KALEIDOSCOPE OF OCEAN MIXING

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Abstract The tides represent a highly predictable element of the Earth system, with the ebb and flow of the tide first linked to phases of the Moon over a millennium ago. However, it is only in the past 50 years that the key role of the tides in driving ocean mixing has been recognised. Here we review progress made in the identification and parameterisation of the pathways of tidal energy, from generation to dissipation and mixing, in a range of ocean environments. The review highlights the key role of tidal dissipation in driving heat, freshwater and biogeochemical fluxes across a range of scales and environments, highlighting the need for representation of the small-scale mixing processes supported by the tide in both regional and global ocean and climate models. We also consider the variation in tidal dissipation through different stages of the Earth's geological history and its impact on the evolution of the Earth–Moon system. We further present a number of examples of past climate states to demonstrate that present tides and tidal dissipation rates are a poor proxy for past and future levels of tidally driven oceanic mixing.

Introduction

The phenomenon of the tide was first explained by Isaac Newton in his 1687 theory of gravitation: as the Earth and Moon rotate around each other, the net centrifugal force and gravitation attraction balance one another. However, the gravitational force at any one point on the surface of the Earth decreases with increasing distance from the Moon. A consequence is a local force imbalance, which results in two bulges (high waters) on opposite sides of the planet. One bulge corresponds to the minimum Earth–Moon separation and hence strongest gravitational attraction, and the second corresponds to the maximum separation, where the gravitation attraction is weakest, and so the influence of the centrifugal force is greatest. Due to the rotation of the Earth about its axis, these high water bulges appear to move, resulting in two tides a day.

Studies of the paths of totality of ancient eclipses (e.g. Lambeck 1980) and ancient fossilised coral growth (Wells 1963, Runcorn 1966) have revealed a gradual increase in day length, along with a corresponding reduction in the number of days in a year, over the history of the Earth. The rate of day length increase over the past 2700 years has been estimated to be 2.3 milliseconds/century. This change has long been attributed to the drag imposed on the Earth by tidal friction, which acts as a brake and is balanced by a gradual recession of the Moon away from the Earth (Darwin 1898, Bills & Ray 1999).

The scientific endeavours of the Apollo Lunar missions provided two important, yet apparently contradictory, pieces of information. Rock samples from the Moon aged it at 4.5 Gy (Gy = 10^9

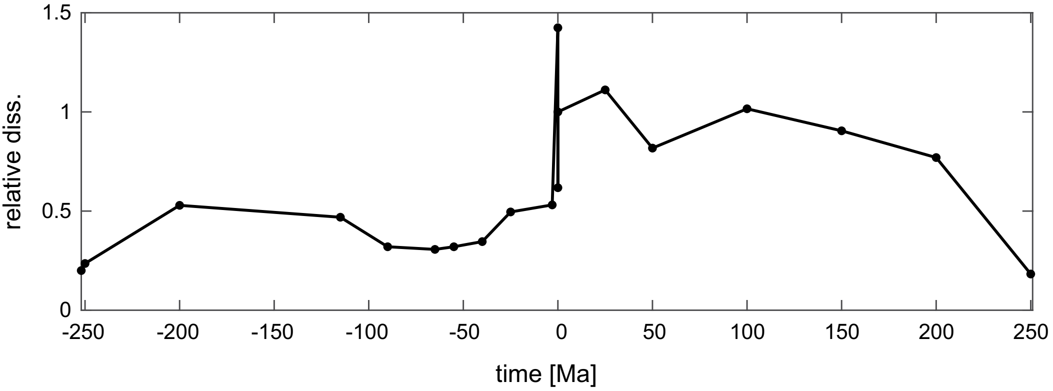

Figure 1 The evolution of tidal dissipation rates, normalised with the present-day value of 2.4 TW, over the past 252 Ma and 250 Ma into the future. Each modelled time slice is indicated by a •. A supercontinent, Pangea, was present from –250 to –180 Ma, and the next supercontinent will form around 200–250 Ma into the future. (Redrawn from Green, J.A.M. et al. 2017. *Earth Planet Science Letters* **461**, 46–53; Green, J.A.M. et al., 2018. *Geophysical Research Letters* **45**, 3568–3576.)

years), whereas laser ranging measurements of the present-day lunar recession rate of 3.8 cm yr^{-1}, facilitated by the lunar reflectors left on the Moon, imply an age of only 1.5 Gy (Gerstenkorn 1967, Canup & Asphaug 2001, Kleine et al. 2005). The implication is that the long-term recession rate must have been significantly smaller than the present day (PD) value. The recession rate of the Moon is set by the tidal drag, which results from the dissipation of tidal energy in the ocean. The implication of this result is that the rate of tidal dissipation has varied through deep time, with the present-day value being relatively high in comparison to those estimated for the past.

The Moon most likely formed near the Roche limit, some 30,000 km from Earth, but has since moved to a position 384,000 km away due to the tidal drag (Bills & Ray 1999). Whilst a series of studies (Munk 1968, Williams 2000, Green et al. 2017) have strongly suggested that tidal drag, and hence the lunar recession rate, have varied through time, details of the evolution of the Earth–Moon system are currently limited to only a few select time slices over the past 430 My (Green et al. 2017, Byrne et al. 2019). Figure 1 shows that the dissipation rate, and hence the lunar recession rate, have indeed on average only been $\sim$40% of present-day values over the past 430 Ma and that the tides today are anomalously energetic. The variability in the dissipation over deep time, coupled with the unusually high present-day dissipation rate, reconciles the 4.5 Gy age of the Moon implied by the lunar rock samples with the present-day recession rate.

The unusually high present-day dissipation is a result of tidal resonance in the present-day ocean basins, where some natural frequencies in the basins, set by basin geometry, are close to the tidal frequencies, which are set by the Earth's orbital factors (Platzman et al. 1981, Müller 2008, Arbic & Garrett 2010, Green 2010). Consequently, the present-day Earth experiences strong tidal currents and large associated energy losses (Egbert & Ray 2003). The strength of this resonance varies through time as a result of eustatic sea-level change (e.g. Green 2010), plate-tectonic reorganisation of the basins (Green et al. 2017, 2018) and decreasing tidal frequencies as Earth's rotation slows (Berger et al. 1992, Green et al. 2019).

Where the tidal energy dissipates

Taylor (1919, 1920) considered the fate of the energy dissipated by the tide in the present-day ocean. In considering the tides in the Irish Sea he expressed the local rate at which tidal energy is dissipated

(D) as the local balance between the rate of working by the tide-generating forces (W) and the tidal energy flux (P; see also Egbert & Ray 2001):

$$D = W - \nabla \cdot P \tag{1}$$

where W and P are defined as:

$$W = g\rho\langle \mathbf{U} \cdot \nabla(\eta_{\mathrm{EQ}} - \eta_{\mathrm{SAL}})\rangle$$

And

$$P = -g\rho\langle \mathbf{U}\eta\rangle$$

where $\langle\ \rangle$ denotes time averages, $\mathbf{U}$ is the tidal transport vector, η is the tidal elevation, η_{EQ} is the tidal equilibrium, η_{SAL} is the self-attraction and loading elevation, g is gravity and ρ is a reference density. The transport, $\mathbf{U}$, is defined as the tidal current, $\mathbf{u}$, times the water depth, h, ($\mathbf{U} = \mathbf{u}h$). Taylor then assumed that the dissipation rate (D) was only due to sea bed friction and hence estimated D using a known formula for skin friction for the wind on the ground and for bed friction on river flows, in which D is proportional to the cube of the tidal current ($\mathbf{u}$) (Equation 2).

$$D = k\rho\left|\mathbf{u}\right|\mathbf{u}^2 \tag{2}$$

where k is a drag coefficient. This was then matched to the tidal energy flux into the Irish Sea ($\nabla \cdot P$) calculated from sea level and tidal current data for the two open ocean connections, the St Georges Channel and the North Channel. A good agreement, $D \approx \nabla \cdot P$, confirmed that the direct contribution of the tidal generating force to the local tidal energy budget in this continental shelf sea was very small.

Jefferys (1920) expanded on this calculation to cover the continental shelf seas globally for which data were available and was able to show that the dissipation of tidal energy through bed friction in the shallow continental shelf seas accounts for about 70% of the then global estimate based on the lunar recession rate. In considering the fate of the ‘missing’ 30%, Jefferys (1920) speculated that it could be dissipated in the Arctic, a then sea ice-locked region for which very limited data were available. Later estimates based on the growing availability of tidal current data globally (Millar 1966) found a similar discrepancy between the astronomically based dissipation estimate and that implied by the bed friction resulting from tidal flow over the seabed. Furthermore, a high-resolution global barotropic tidal model study (LeProvost et al. 1994) essentially confirmed the results of the earlier Jefferies and Millar studies by showing that areas with high dissipation due to bed friction are confined to the continental shelves, whilst tidal dissipation due to bed friction in the abyssal ocean is negligible. These later studies also pointed to the fact that, whilst the Arctic Ocean hosts significant areas of continental shelf seas, the tides are weak and in consequence only account for approximately 1% of the global tidal energy dissipation rate (e.g. LeProvost et al. 1994). The implication is that whilst tidal generation occurs over the large ocean basins, the tidal energy is largely dissipated in the shallow shelf seas.

Shelf seas and tidal mixing fronts

The first quantitative link between irreversible mixing and the dissipation of tidal energy was established through the identification of the processes responsible for the formation of tidal mixing fronts in temperate shelf seas (Simpson & Hunter 1974). In spring and summer, some areas of the temperate shelf seas become thermally stratified as a result of solar heating, whilst neighbouring areas remain completely mixed. Simpson & Hunter (1974) showed that the mixing resulting from turbulence generated by the dissipation of the tides through bed friction competes with the stratifying influence of surface heating to determine water column structure. In regions of strong tidal currents, the rate of buoyancy input due to surface heating is not large enough to establish persistent stratification, and so the water column remains well mixed. However, in regions of weak tidal currents and low levels of turbulence, the heating wins out and seasonal stratification forms, with the warmer surface water overlying a deeper cooler water layer. The two layers are separated by a region of strong vertical gradients, the thermocline, which forms a barrier to vertical exchange of heat, salt and nutrients. Geographical barriers known as shelf-sea or tidal mixing fronts separate the regions of seasonal stratification from the well-mixed regions (Figure 2).

Using energetics arguments, Simpson & Hunter (1974) derived a single parameter to predict the positions of these fronts. By considering only vertical exchange processes and assuming that the surface input of heat (Q) was the only stratifying influence and tides the only source of turbulence (determined as the rate of dissipation of tidal energy from Equation 2), a criterion for the determination of the water column structure in a water depth of h can be derived:

$$\frac{Qh}{u_T^3} = \frac{8ek\rho c_p}{3\pi\alpha g} \tag{3}$$

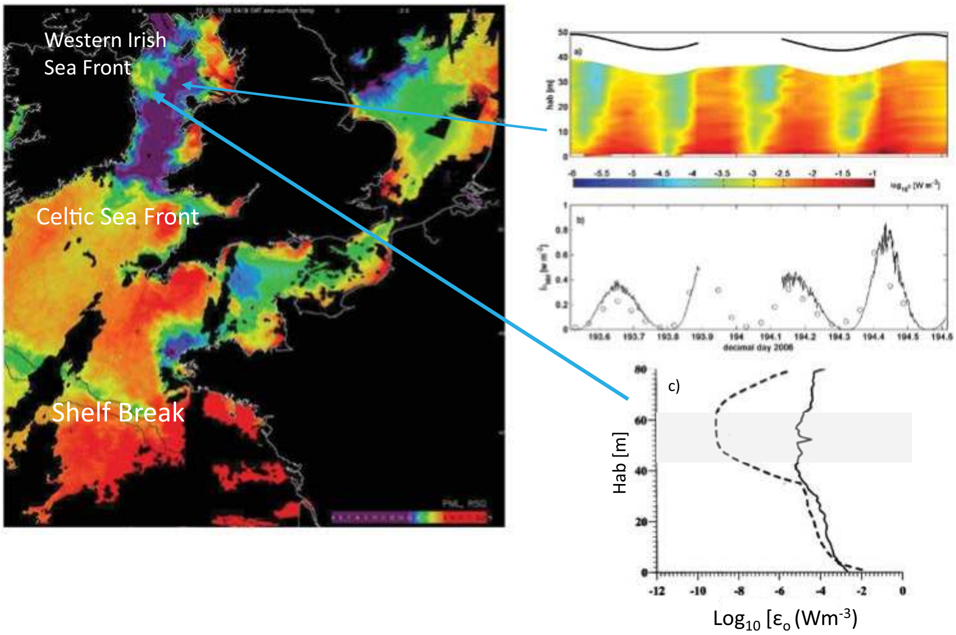

Figure 2 Sea surface temperature of the Celtic and Irish Seas on 13 July 1999 (courtesy Remote Sensing Group, Plymouth Marine Labs). The Celtic Sea and West Irish Sea front are indicated as strong gradients separating the warm seasonally stratified waters from the cooler well mixed zones. (a) The profiles of dissipation are shown for a well-mixed location together with (b) a comparison of the depth-integrated dissipation (o) with that predicted using equation 1 (-) (Reproduced from Stacey, M.T. et al. 2011. *Treatise on Estuarine and Coastal Science* **2**, 9–35) under licence from Elsevier (licence number 4731300300188). (c) Shows the tidal cycle mean dissipation profile (-) for a seasonally stratified Western Irish Sea location, together with a profile predicted using a Mellor-Yamada 2.0 turbulence closure in which a local equilibrium between turbulent production and dissipation is assumed. The grey bar indicates the position of the seasonal thermocline (Redrawn from Rippeth, T.P. 2005. *Philosophical Transactions of the Royal Society A Mathematical Physical and Engineering Sciences* **363**, 2837–2854).

Where in this case u_T represents the depth mean M_2 tidal current amplitude*, α is the volume expansion coefficient, c_p is the specific heat, k the drag coefficient, ρ the density and e a bulk estimate of the efficiency of mixing by the tide (the ratio of the rate of change of water column potential energy due to mixing to the rate of kinetic energy dissipation), which was assumed constant. The equals sign in Equation 3 corresponds to an exact balance between solar heating and stirring by tidally generated bottom boundary layer turbulence (calculated from Equation 2) and defines the location of the transitional front which separates the seasonally stratified and mixed regimes. In temperate regions, Q can be assumed constant, and so the first order control on the water column structure is given by the ratio h/u_T^3. This variable has been mapped using barotropic tidal model simulations of tidal current amplitude (u_T), and through comparison with observations of water column structure, and has been shown to have a critical value of $h/u_T^3 \approx 220\ \mathrm{m^{-2}s^{-1}}$. Areas with higher values ($h/u_T^3 >$ 220) are subject to seasonal stratification whilst those with $h/u_T^3 < 220$ remain mixed throughout the seasonal cycle.

Whilst the critical value for the characterisation of the position of tidal mixing fronts was initially estimated for the Irish Sea (Simpson & Hunter 1974, Simpson & Bowers 1981), consistent values have subsequently been estimated for a range of shelf seas globally [e.g. the Gulf of Maine and Bay of Fundy, Garrett et al. (1978) and Loder & Greenberg (1989); the Yellow Sea, Lie (1989); the Patagonian Shelf, Glorioso & Flather (1995); the northwest European Shelf Seas, Pingree & Griffiths (1978); the Bering Sea, Schumacher et al. (1979)].

The bulk mixing efficiency (the ratio of the rate of change of water column potential energy, through mixing, to the rate of dissipation of kinetic energy) can be estimated empirically for frontal regions from Equation 3 and yields a value of $e \approx 0.004$, implying the turbulence generated by bed shear stresses is relatively inefficient in supporting water column mixing.

Whilst this energetics approach represents a major simplification of the processes which control stratification in shelf sea regimes (e.g. it neglects the stratifying influence of freshwater and wind induced mixing), it provides a good first order determinant of the water column structure in these regimes, thus implying water column structure is controlled by vertical exchange processes. It also provides the first robust quantitative link between the dissipation of tidal energy and mixing in the ocean.

The partition of the shelf into regions of seasonal stratification and mixing provides the first order control on the local ecosystem and biogeochemical fluxes through the regulation of the available of limiting nutrients and light. Tidal mixing fronts, as semi-permanent geographical features, affect the distribution of primary production (Richardson et al. 2000) and have the potential for enhanced biological productivity (e.g. Holligan et al. 1984, Tett et al. 1993, Sharples 2008). However, whilst there is no clear evidence of a direct response of pelagic zooplankton to enhanced productivity at fronts, they are found to accumulate in response to convergent surface currents associated with the front. In consequence, shelf-sea fronts represent important foraging habitats for many marine species, including seabirds (e.g. Cox et al. 2016) and basking sharks (Sims et al. 2000).

As regions of strong physical gradients, fronts also support significant baroclinic flows, which provide an important contribution to the residual flow field in temperate shelf seas in summer (Hill et al. 2005). The mean circulation associated with these frontal jets is key to the survival of a number of fish stocks, as it provides a seasonally reliable conveyor for drifting passive eggs/larvae, linking spawning grounds and adult feeding grounds as, for example, proposed for the *Nephrops* population in the Western Irish Sea (e.g. Hill et al. 1996, Phelps et al. 2015) and the Georges Bank fisheries (e.g. Lough & Manning 2001).

Despite only accounting for 7% of the surface area of the global oceans, continental shelf seas account for approximately 70% of global tidal energy dissipation and about 20% of the global ocean annual primary production (Muller-Karger et al. 2005, Jahnke 2010). Primary production is

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* Different measures of current speed may be used here with the critical value of (h/u^3) changing accordingly.

regulated by the presence of stratification and by mixing, which determine access to light and to nutrients. The major event in the seasonal cycle of primary production is the spring bloom, which is triggered by the onset of stratification (e.g. García-Martín et al. 2017) and which is limited by the availability of nutrients in the surface mixed layer. A direct consequence of the spring bloom is a depression of sea surface CO_2 partial pressure (pCO_2), which in turn leads to the uptake of CO_2 from the atmosphere by the ocean. As a result, the present-day shelf seas are net sinks for atmospheric CO_2 and are thought to account for between 20% and 50% of total oceanic CO_2 uptake through a set of processes known collectively as the *shelf sea pump* (Tsunogai et al. 1999, Thomas et al. 2004a,b, Chen 2010). Seasonally stratified areas act as a sink for CO_2 due to the presence of the seasonal thermocline which separates primary production and respiration, facilitating a depression in sea surface pCO_2. The impact of the disequilibrium of pCO_2 across the sea surface is the drawdown of CO_2 from the atmosphere, which is balanced by an organic carbon flux off-shelf into the deep water (Sharples et al. 2019).

In contrast, in areas with stronger tidal currents, that is, where mixed conditions persist throughout the seasonal cycle, there is no separation of respiration and production, and so any imbalance in pCO_2 resulting from biological activity or changes in solubility will be in direct contact with the atmosphere, which will facilitate equilibration across the air-sea interface. In consequence, the shelf seas represent an important dynamic component of the global carbon cycle (Bauer et al. 2013), linking the atmospheric, terrestrial and oceanic carbon pools (Rippeth 2005). Accordingly, the tides play a key role in mediating the seasonally integrated air-sea CO_2 fluxes through partitioning of the shelf seas in temperate and polar regions (Rippeth et al. 2008, Wilmes et al. 2017).

Turbulence and mixing

In geophysical flows, turbulence can be produced through the interaction of turbulent fluctuations with the vertical shear in the mean flow. This source of the turbulent kinetic energy (TKE) is shear production (P = rate of production of TKE):

$$P = \overline{u'w'}\frac{\partial U}{\partial z} - \overline{v'w'}\frac{\partial V}{\partial z}$$

In the absence of stratification, the energy associated with the turbulence cascades to smaller scales until it reaches a scale whereby molecular viscosity dissipates it to heat (the rate of dissipation of TKE is ε). In steady, unstratified and homogeneous turbulent flow, a local equilibrium exists with the rate of production balancing the rate of dissipation, $P = \varepsilon$. However, if the water column is stratified, the turbulence must do work against buoyancy, creating a vertical buoyancy flux, B:

$$B = -\frac{g}{\rho}\overline{\rho' w'}$$

If the stratification is stable ($\partial\rho/\partial z < 0$), the upward (positive) turbulent velocities ($w' > 0$) carry heavier water upwards, promoting stirring of the gradients, and hence mixing. The net result is the conversion of turbulent kinetic energy to potential energy. Accordingly, the negative buoyancy flux acts as a sink for TKE. In contrast, if the density structure is unstable ($\partial\rho/\partial z < 0$), B is positive and so acts as a source for TKE (manifest as conversion). In assuming a local balance:

$$P + B - \varepsilon = 0 \tag{4}$$

In the case of stable stratification, the local mixing efficiency is then defined as a flux Richardson number, R_f (Turner 1973):

$$R_f = -\frac{B}{P} \tag{5}$$

Modelling and measuring turbulent mixing

Descriptions of the evolution of stratification based on energy arguments, such as Simpson & Hunter (1974), provide a useful first order account of the key processes determining the water column structure. However, such descriptions rely on combining separate analytical solutions for different aspects of the flow and so do not simulate the dynamics or the interactions between the different components. To achieve a more fundamental description, it is necessary to solve the set of dynamical equations with relevant forcing (tides, surface wind stress etc.). The vertical component within these models requires a 'turbulence closure scheme' which enables vertical buoyancy fluxes and water column stratification to interact, with mixing rates sensitive to water column stability. The closure schemes are 1-dimensional (vertically resolving) and have the capacity to predict the evolution of the water column and vertical current structure. This is achieved through the prescription of values of eddy viscosity (N_z), a coefficient which relates the average shear stress to the vertical velocity shear (and is a function of stratification), and eddy diffusivity (K_z), a coefficient which relates the average turbulent diffusion rate to the vertical shear in density. As such, the water column structure evolves with changing vertical current shear and stratification (e.g. Burchard et al. 1998). These types of schemes form the vertical exchange element of the current generation of operational 3-dimensional continental shelf sea models (e.g. Graham et al. 2018).

The development of free-fall and loosely tethered profilers for the measurements of fine-scale velocity shear has facilitated the observation of profiles of the rate at which turbulent kinetic energy is dissipated (ε) (Crawford & Osborn 1980, Moum & Lueck 1985, Dewey et al. 1987, Oakey 1988). This has in turn led to a more fundamental understanding of the distribution of TKE dissipation and mixing within the water column and facilitated the identification of the key processes driving the mixing. The extent of profiler measurements has tended to be limited by the availability of costly ship time. More recently, however, longer time series measurements of turbulence parameters are becoming available through both moored acoustic sensors (reviewed in Simpson et al. 2005, Scannell et al. 2017) and the mounting of microstructure devices on moorings (e.g. Pham et al. 2017) and sea gliders (e.g. Fer et al. 2014, Palmer et al. 2015, Schultze et al. 2017).

Through considering a local balance between production and dissipation of TKE and the work done against buoyancy (mixing) (Equation 4) in a stably stratified water column, Osborn (1980) derived an expression for the estimation of the mixing rate (expressed as an eddy diffusivity, K_z) from the rate of dissipation (ε):

$$K_z = \Gamma \frac{\varepsilon}{N^2} \tag{6}$$

where Γ is the flux dissipation coefficient and is linked to the local mixing efficiency (R_f) by:

$$\Gamma = \frac{R_f}{1 + R_f} \approx 0.2$$

The commonly assumed value of $\Gamma \approx 0.2$ it is generally accepted to hold over a wide range of environmental conditions (e.g. Moum 1996, Smyth et al. 2001, Gregg et al. 2018), including those found in seasonally stratified shelf seas (e.g. Oakey & Greenan 2004, Inall et al. 2000, Palmer et al. 2008, Bluteau et al. 2013). However, the validity of the assumption $\Gamma = 0.2$ has been questioned in regions of weak stratification, such as at depth in the abyssal ocean (e.g. Ijichi & Hibiya 2018, Monismith et al. 2018, Vladoiu et al. 2019).

Time series measurements of profiles of ε have revealed the distribution of turbulence in response to rectilinear tidal flow in well mixed and seasonally stratified water columns (e.g. Simpson et al. 1996), with the largest ε found at maximum tidal flow, close to the sea bed. The quarter diurnal signal in ε is associated with maximum ebb and flood of the tide and is evident throughout the well-mixed water column (Figure 2b). However, it is restricted to the lower part of the water column in the presence of seasonal stratification. It is widely observed that the time of maximum dissipation is increasingly delayed with height above the sea bed (Simpson et al. 1996, Yoshida & Oakey 1996, Peters & Bokhorst 2000, Burgett et al. 2001, Sharples et al. 2001a,b). This phenomenon can be explained theoretically as a result of the systematic delay in the rate of production of turbulence, which is a direct consequence of a phase lag in the horizontal velocity shear with height in both rectilinear (Simpson et al. 2000) and rotating tidal flows (Zhang & Wu 2018).

The measurement of profiles of ε provide a fundamental test of the ability of the closure schemes used to simulate vertical exchange in the water column to model the profile of ε, and by implication vertical mixing, correctly. The first such tests, comparing ε-profile measurements with model predictions, were made for two contrasting locations in the Irish Sea (Simpson et al. 1996). Measurements were made in the seasonally stratified western Irish Sea and in the well-mixed eastern Irish Sea and were then compared to predictions made using a 1-dimensional Mellor Yamada 2.0 closure scheme (in which a local equilibrium is assumed between the rates of production and dissipation of TKE together with the rate working against buoyancy in mixing the water column). The model was forced using time-varying surface slopes to simulate the local tidal flow and initialised with an appropriate density profile. The results showed that the scheme was able to predict profiles of ε similar to those observed in the location with the stronger tides and a well-mixed water column. However, the model failed, by several orders of magnitude, to reproduce the observed levels of ε within the thermocline in the seasonally stratified location (Figure 2c). The deficit in the predicted mid-water ε points to either an incorrect parameterisation of the small-scale physics away from the boundaries or to the absence of representations of key physical processes in the model. In order to rectify this deficit, a number of modified closure-based vertical exchange schemes have been proposed in which vertical diffusion of turbulence is implemented or a 'background' level of mixing is prescribed (e.g. Simpson et al. 1996, Burchard et al. 1998, 2002). Whilst both approaches can be justified by the need to deal with the deficit, the model predictive skills are limited by the assumptions inherent in this approach.

Rippeth (2005) considered the potential for additional physical processes to account for the mid-water column mixing deficit. Coincident fine-scale density and velocity structure measurements across seasonal thermoclines in a variety of tidally swept seasonally stratified shelf seas reveal the thermocline to be in a state of marginal stability (i.e. with an average gradient Richardson number, $R_i \approx 1$) (van Haren et al. 1999, MacKinnon & Gregg 2005, Rippeth et al. 2005, Rippeth 2005, Palmer et al. 2008, Rippeth et al. 2009). This observation implies that the addition of extra shear across the thermocline could reduce $R_i \leq 0.25$, a necessary condition for the development of shear instability and hence the transfer of kinetic energy from the mean flow to turbulence (which will then support vertical fluxes across the thermocline).

Whilst the tides dominate the kinetic energy budget of shelf seas (e.g. Rippeth et al. 2005), inertial oscillations have also been observed to account for a significant proportion of the observed current shear variance in regions of weak tides and seasonal stratification (e.g. Knight et al. 2002, Shearman 2005). Inertial oscillations are the oceans response to abrupt changes in the wind (e.g. Pollard 1980, Itsweire et al. 1989), and estimates of dissipation based on the rate at which the oscillations are dampened suggest they could provide an important source of turbulence in the seasonal thermocline

(Sherwin 1987). Moreover, in stratified shelf seas where coastlines influence the flow, the wind stress triggering the inertial oscillation will also set up an opposing pressure gradient (Craig 1989) which will induce an out-of-phase oscillation in the deep water layer, enhancing the shear across the thermocline (Rippeth et al. 2002, Simpson et al. 2002).

Burchard & Rippeth (2009) developed an analytical model to demonstrate the role of wind–shear alignment, linked to inertial oscillations, in the generation of periods of enhanced shear across the seasonal thermocline in shelf seas. Whilst the model does not predict ε, Burchard & Rippeth (2009) were able to show that periods of enhanced shear, resulting from wind-shear alignment, correlate strongly with periods of enhanced mixing across the seasonal thermocline in a tidally dominated shelf sea. This wind-shear alignment model has subsequently been expanded to explain periods of enhanced mixing observed under sea ice in an Arctic shelf sea (Lenn et al. 2011) and the deepening of the shelf sea thermocline (Lincoln et al. 2016a). It has also been applied to explain periods of enhanced shear at the base of the open ocean seasonal thermocline (Brannigan et al. 2013, Majumder et al. 2015, Johnston et al. 2016), although the other processes may dominate during storms (Lucas et al. 2019).

For the seasonally stratified shelf sea case, it is proposed that the turbulence generated in the bottom boundary layer, as the tidal flow cycles through the springs-neap cycle (e.g. Sharples 2008), acts in concert with wind- and convection-generated turbulence in the surface mixed layer to maintain the state of marginal stability against which the inertial oscillations, through the wind-shear alignment mechanism, drive vertical fluxes across the thermocline (Lincoln et al. 2016a).

Interior mixing and primary production in shelf seas

Whilst the spring phytoplankton bloom dominates the seasonal cycle of primary production in seasonally stratified shelf seas, a persistent and significant level of primary production is sustained throughout the period of seasonal stratification, a conspicuous consequence of which is the subsurface chlorophyll maximum (SCM), a ubiquitous feature of the stratified ocean (Pingree et al. 1982). The persistence of the SCM is determined by light availability in the seasonal pycnocline coupled with a vertical flux of nutrients from the deep nutrient-rich water into the thermocline (Sharples & Tett 1994). In consequence, the processes responsible for mixing across the thermocline are key to delivering the limiting nutrients to the euphotic zone and sustaining the subsurface chlorophyll maximum (Sharples et al. 2001a,b, 2007, Williams et al. 2013a), which plays a vital role in supporting the pelagic food web during summer (Richardson et al. 2000). Estimates based on observations of primary production rates within the SCM suggest that subsurface carbon fixation accounts for up to 50% of annual primary production in the seasonally stratified North Sea (Richardson et al. 2000, Weston et al. 2005). An extrapolation using microstructure-based nitrate flux estimates also gives a figure of approximately 50% (Rippeth et al. 2009). Williams et al. (2013b) report significantly enhanced nutrient fluxes in response to shear spikes generated through the wind-shear alignment mechanism (Burchard & Rippeth 2009). Rippeth et al. (2014) investigated the potential of diapcynal mixing of both carbon and nutrients to contribute to air-sea CO_2 exchange in seasonally stratified shelf seas, showing that the divergence of the ratio of C:N from the Redfield ratio is a control on the impact of the diapcynal mixing on sea surface $p\mathrm{CO}_2$.

Tidally induced mixing processes also play a key role in regulating the lateral flux of freshwater across estuaries and in regions of freshwater influence (e.g. Stacey et al. 2011, MacCready et al. 2018, Burchard et al. 2019). The interaction between the sheared tidal flow and the lateral salinity gradient, coupled with mixing by bed-shear, stress generated turbulence, provides an important mechanism for the offshore transport of freshwater through a process known as tidal straining (e.g. Simpson et al. 1990, Verspecht et al. 2009). This implies the need for numerical models of these regions to resolve subtidal timescale processes in order to predict lateral freshwater dispersion accurately.

Internal tides in fjords

The oscillatory tidal flow of a stratified fluid over sloping topography results in the formation of a depression in the pycnocline downstream of a slope. As the tidal flow slackens, the depression will propagate away as an internal wave, ultimately dissipating energy to turbulence. A depression can form during each tidal cycle, resulting in the generation of an internal tidal wave (internal tide). The formation of the depression exerts a (baroclinic wave) drag on the tidal flow which results in the conversion of kinetic energy associated with the barotropic tidal flow to an internal tide (a process known as tidal conversion).

The semi-enclosed nature and the topography of fjords make a favourable environment for the study of the generation and dissipation of internal tides and the associated irreversible mixing. A fjord is a deep, high-latitude estuary which has been modified by land ice and in consequence tends to have a deep basin with a shallow sill at the mouth. Fjords tend to be stratified as a result of local freshwater run-off (which is augmented by surface heating in the summer). In consequence, a fresher (and in the summer warmer) surface mixed layer overlies deeper saltier (colder) water. The presence of a shallow entrance sill isolates the water in the deep basin from direct communication with the open ocean during periods when the deep water density is greater than that of the inflowing oceanic water. Accordingly, the deep water properties are only altered by local diffusion within the basin or when the across-sill inflow is sufficiently dense to sink into the fjord basin (Stigebrandt & Aure 1989). An impact of vertical mixing is to flux heat and salt between the isolated deep water and the warmer fresher surface layer. The net result is a warming and freshening of the deep water over the period of isolation which results in a reduction in the density; an example from the Clyde Sea, Scotland, is shown in Figure 3. Within the Clyde Sea, the level of stratification varies on a seasonal timescale, with the strongest stratification occurring in the summer, when freshwater stratification is augmented by surface heating. Between June and November, the inflowing Irish Sea water is less dense than the ambient basin water below sill level, and so the basin water is isolated from the across-sill exchange flow. At this time, the warming and freshening of the basin water below sill level is attributed to vertical mixing. However, the level of mixing implied by the observed change in water column structure cannot be explained using the Simpson & Hunter (1974) shelf sea boundary layer mixing model (Simpson & Rippeth 1993, Rippeth and Simpson, 1996), implying the need for an additional source of mixing.

Stigebrandt (1976) proposed that the internal tide was an important source of kinetic energy supporting vertical mixing in fjords. Freeland & Farmer (1980) calculated the net flux of tidal energy into Knight Inlet, a fjord, by considering the progressive nature of the tidal wave at the fjord mouth. They estimated that bottom friction only accounted for 3% of the total tidal energy dissipated within the fjord, implying that an internal tide dominates the dissipation associated with the tidal energy fluxing into the fjord.

The nature of the internal tide in a fjord is determined by the environmental conditions experienced over the sill (Farmer & Freeland 1983), ranging from the generation of a freely propagating linear internal tide to a jet under conditions in which flow is subject to internal hydraulic control. In considering the contribution of the dissipation of the tide to mixing, Stigebrandt & Aure (1989) define two types of fjord basins. In the first, defined as wave basins, progressive linear internal tides are generated at the sill and then propagate into the basin, dissipating and driving mixing. In the second, the currents across the sill are sufficiently strong to separate from the walls, and a jet forms, with the flow subject to internal hydraulic control. For each basin type, they estimated the tidal conversion rate at the sill and then compared it to the change in water column potential energy due to mixing. For wave basins, they estimate a mixing efficiency, $e \approx 5.6\%$, whilst for jet basins, they obtain $e < 1\%$. Similar studies in other fjords globally have supported these results (Freeland & Farmer 1980, Svensson 1980, Lewis & Perkins 1982, de Young & Pond 1989). The robustness of the results across a wide range of fjord shapes and sizes indicates that, whilst the mixing efficiency is sensitive to the

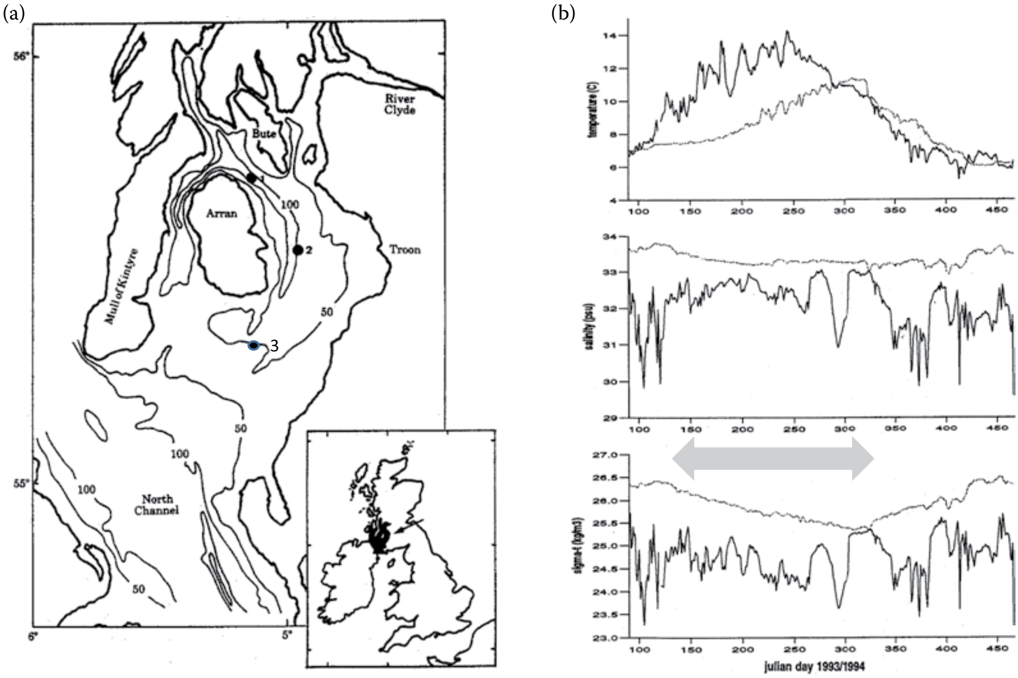

Figure 3 The Clyde Sea, a fjord on the west coast of Scotland [map (a)]. (b) Shows the seasonal cycle (1993/94) of near surface (thick line) and near bed (thin line) temperature, salinity and σ_T for location (2) in Figure (a) (Redrawn from Rippeth et al., 1995). The grey arrow above the σ_T time series indicates the period when the water below sill level is isolated from direct contact with the Irish Sea. The dominant signal in the stratification within this fjord is the seasonal cycle, with water below sill level isolated from Irish Sea in summer and autumn. Over this period, a significant warming and freshening (and hence reduction in density) of the isolated deep water is observed to take place as a result of vertical mixing. The reduction in the density of the isolated deep water enables the inflowing Irish Sea water (which becomes denser than the ambient basin deep water) to sink into the basin, facilitating complete flushing of the basin.

nature of the flow at the sill, it is not particularly sensitive to the fjord geography away from the entrance sill, implying that much of the dissipation must occur locally to the sill.

Stigebrandt & Aure (1989), Stigebrandt (1999) and others demonstrate a clear relationship between the mean rate of work against buoyancy forces, through mixing, in the basin waters of a fjord and the conversion of energy from the surface tide to tidal jets and internal tides at the fjord entrance sill. As such, they identify the key role of the interaction of stratified tidal flow with sloping topography in supporting vertical mixing and hence the overturning circulation in fjords. However, these studies provide little information as to the radiation pathways of the internal tides or the mechanics of the dissipation to turbulence.

In efforts to identify radiation pathways and the processes responsible for the dissipation of tidal energy in fjords, several field campaigns have been carried out which included direct measurements of turbulence parameters. Inall & Rippeth (2002) report observations from the Clyde Sea, a wave basin (Figure 3). Measurements were made at two locations, the first on the basin side of the sill and the second in the fjord interior (stations 1 and 3 in Figure 3a). At the sill station (3 in Figure 3a), the barotropic tidal current amplitude was approximately 20 cms^{-1}. There were jumps evident in the temperature records indicative of hydraulic control of the flow during periods of maximum tidal flow. Liu (2010) and Liu et al. (2012) investigated the stability of the flow at this location and showed that the gradient Richardson number (R_i) was often close to the limit for stable flow (0.25) and that the onset of turbulence due to instability had the effect of stabilising the flow, with periods when turbulence was absent leading to a condition where the flow became unstable. Liu et al. (2012) also note that the occurrence of turbulence may change the state of the flow from subcritical to supercritical.

Inall & Rippeth (2002) also report observations for a location in the basin interior (station 1 in Figure 3a). Here they found that the internal wave field is much less energetic and is dominated by higher internal wave modes. They estimate that ∼80% of the baroclinic energy flux is dissipated between the two stations. Dissipation estimates, based on 25-hour time series of velocity microstructure profiles, are consistent with the estimated decay rate of the internal tide between the two stations. Moreover, they found that the diffusivity, estimated from the dissipation measurements, was able to account for a significant proportion of the basin integrated diffusivity inferred from the warming and freshening of the deep water over the summer period (Figure 3b). However, to fully explain the level of mixing implied by the basin integrated evolution of the deep water properties, an additional source of buoyancy flux was required, which they speculated was due to enhanced mixing near the entrance sill and at the sloping boundaries.

From a study of mixing in the stagnant (wave) basin of Gullmar Fjord, Arneborg et al. (2004) were able to reconcile the total basin-wide dissipation, based on a series of profiles using microstructure profilers, with an estimate of the combined dissipation of the internal tide, internal and barotropic seiches. Furthermore, they show that 77% of the dissipation takes place within the 19% of the basin volume closest to the entrance sill, implying that much of the vertical mass transport is due to mixing which takes place close to the sill.

Inall et al. (2004, 2005) report on a study of Loch Etive, Scotland, a transitional system which is a ‘jet’ basin around springs tides and a ‘wave’ basin close to neaps. They show that for periods with stronger tidal currents, the ratio of energy lost to bottom friction and baroclinic wave drag was approximately 1:4. A further process, barotropic form drag, resulting from horizontal eddy shedding, accounted for a further 15%–20% of the energy loss from the tide. During periods of reduced tidal currents, and the formation of a linear internal tide, the ratio of bottom friction to baroclinic wave drag was again 1:4, whilst they conclude that horizontal aspects of the barotropic form drag such as eddy shedding may be responsible for 30%–40% of the tidal energy loss. Klymak & Gregg (2004) report a similar partitioning of energy in Knight Inlet, British Columbia. The energy pathway from tidal conversion at the sill to dissipation, and hence mixing in these systems, is controlled by the flow conditions at the sill. The evolution of stratification and mixing, flow and the relative roles of shear instability and internal hydraulic control in dissipating energy and driving mixing are therefore intimately linked (see Vlasenko et al. 2005 for a full review).

The vertical mixing in fjords not only supports primary productivity through the driving of vertical nutrients fluxes, as discussed for the shelf sea case above, but can also be important in setting the biogeochemical characteristics of deep water. For example, in the Clyde Sea, the deep water is isolated from renewal in the summer, over which period there is an accumulation of decaying organic matter which depresses dissolved oxygen levels. This water is then flushed out by deep water renewal in the autumn (Rippeth & Jones 1996) raising oxygen levels. However, in some systems, with weaker mixing and less regular deep water renewal, anoxic conditions can persist in the deep water (e.g. Yao & Millero 1995, Pawlowicz et al. 2007), which can be interrupted by intermittent inflows of oxygenated water across the sill with varying consequences (Pakhomova et al. 2014). Deep water inflows can also act to trigger the spring bloom (e.g. Watts et al. 1998).

Internal tides in shelf seas

The upper continental shelf break provides an important region for the conversion of barotropic tidal energy into internal tidal energy (Baines 1982). Internal tidal energy then tends to travel on the shelf as a mode one wave, whilst energy propagating offshore is more varied, initially following lines of characteristic slope (Huthnance 1989). The rate of conversion is influenced by the slope of the topography as well as water column stratification. The internal tides can also be modulated by ambient flows with frequencies less than the local inertial period influencing the stability of the internal tidal wave (e.g. Rippeth & Inall 2002). In regions of strong across-slope tidal flow, such as the Celtic Sea, large amplitude internal tides have been observed (Pingree et al. 1986). Holloway (1987) observed steepening of the leading edge of an internal tide as it propagated across the Australian North West Shelf, with the formation of a 60 m amplitude propagating hydraulic jump (in a water depth of 120 m). The steepening can lead to both dissipative and non-dissipative nonlinear internal waves, sometimes referred to as solitary waves or solitons (when they are weakly dissipative) and solibores (when they are dissipative).

Thorpe (1987) noted that the production of turbulence associated with an internal tide travelling up a slope becomes dominated by internal-wave breaking, rather than bottom stress, whilst Pingree et al. (1986) provide evidence of overturning and interior mixing associated with the breaking of large internal tides. Two classes of internal wave breaking are defined: 'convective overturning' and 'shear instability'. Convectively induced shear instability is driven by the small-scale straining of the density field (Moum et al. 2002, Carr et al. 2008) and can occur at all frequencies but only when the wave is steep (Thorpe 2010). However, shear-induced instability may occur in shallower amplitude waves provided the gradient Richardson number (R_i) is small enough (Thorpe 2010). The occurrence of convection potentially invalidates the applicability of the local TKE balance on which Equation 6 and hence the assumptions on which $\Gamma = 0.2$ are based.

Internal tidal energy fluxes across the shelf can be on the order of 100 Wm^{-2} (e.g. for the Malin shelf; Sherwin 1988). The dissipation (and associated mixing) associated with internal tides propagating across shelf seas tends to vary significantly over relatively short space and time scales (e.g. Pingree & New 1995, Holloway et al. 2001, Rippeth & Inall 2002, Moum et al. 2007, Green et al. 2008, 2010, Stephenson et al. 2016, Wang et al. 2016). Direct measurements of profiles of ε imply that much of the energy associated with the internal tide is dissipated within a few kilometres of the generation zone (Inall et al. 2000, Rippeth & Inall 2002, Stephenson et al. 2016). This leads to an interesting paradox since nonlinear internal tides have been observed hundreds of km from potential generation zones (e.g. Pingree & New 1995, Stanton & Ostrovsky 1998, MacKinnon & Gregg 2003). Furthermore, nonlinear internal waves thought to be of tidal origin have been observed in regions isolated from significant topographic features, such as the seasonally stratified western Irish Sea (Green et al. 2010).

Sandstrom & Oakey (1995) used microstructure measurements to estimate that 20% of the energy dissipated by the internal tide propagating across the Scotian Shelf went into mixing. Inall et al. (2000) show that dissipation is dominated by the nonlinear wave component, with $\approx$70% of dissipation estimated to take place within the bottom boundary layer, implying local coupling between the internal tide and the barotropic tide. Holloway et al. (2001) and Rippeth & Inall (2002) report evidence of internal hydraulic control of the flow and associated enhanced mixing in the thermocline 10s of km from the continental shelf break further, pointing to the evolving nature and widespread influence of the internal tide as a source of mixing as it traverses stratified shelf seas. Palmer et al. (2008, 2013) observed enhanced mixing over a submarine bank in the Celtic Sea associated with the generation of an internal tide. Even relatively small-scale topographic features (on the order of 2 km) are found to act as a significant drag on stratified flow, leading to enhanced dissipation (Moum & Nash 2000) and periods of internal hydraulic control (Nash & Moum 2001). In studying the transit of an internal tide across the South China Sea, Bai et al. (2019) identified the fission of non-linear internal waves into higher-frequency, shorter-wavelength internal waves as a potential pathway to dissipation and mixing.

A consequence of the generation and dissipation of internal tides at the continental shelf break is that it is a region of significantly enhanced primary productivity. The enhanced production is supported by the diapcynal nutrient flux associated with mixing driven by the internal tide (Holligan et al. 1984, Sandstrom & Elliott 1984, Sharples et al. 2001a,b, 2007, Bentson & Richardson 2018). Similarly, the interaction with stratified tidal flow over submarine banks has also been shown to support enhanced localised primary productivity (Tweddle et al. 2013).

The global budget for the dissipation of tidal energy is dominated by the dissipation of tidal energy in the bottom boundary layer of the shelf seas (Munk & Wunsch 1998). Rippeth et al. (2005) showed that for the northwest European shelf seas (which account for 8% of the global figure; Egbert & Ray 2000, 2003), the rate of tidal conversion along the shelf break to an internal tide is 430 MW. This compares to 205 GW dissipated by the barotropic tide via bed shear stresses. However, the dissipation associated with the internal tide is focussed on seasonally stratified regions which have less energetic tides. Furthermore, the internal tides are substantially more efficient at mixing (e.g. Stigebrandt & Aure 1989, Sandstrom & Oakey 1995) and so can have a disproportionally large impact on diapcynal mixing over the stratified outer shelf regions (Sherwin 1988, Rippeth et al. 2005).

The mixing generated by the interaction between the stratified tidal flow and topography at the shelf break significantly enhances primary productivity and also shifts the size structure of the plankton species to favour large cells, to the benefit of fish larvae (Sharples et al. 2007). This link is evident in the relationship between fishing activity and topography in the seasonally stratified Celtic Sea (Sharples et al. 2009). Sharples et al. (2009) also point to the shelf break providing an important region for fish larvae due to the persistence of the plankton supported by the regular supply of nutrient associated with the turbulence generated by the internal tide.

The ocean and abyssal mixing

In considering the fate of the *missing* 30% in the tidal energy budget (Jefferys 1920, Millar 1966), Munk (1966) speculated that the remainder of the tidal dissipation (1 TW) was largely abyssal. Furthermore, he speculated as to the role of tidally generated turbulence in stirring gradients in the stratified water column and consequently driving irreversible mixing in the ocean to balance deep water formation at high latitudes. Munk (1966) estimated that 2 TW of mechanical energy is needed to drive the mixing necessary to support the diapcynal heat flux which balances the formation of cold dense water, due to heat loss to the atmosphere, at high latitudes. This dissipation rate equates to an average diapcynal diffusivity of 10^{-4} m^2s^{-1} (about 700 times the thermal molecular diffusivity). However, this value did not appear to be supported by observations. Microstructure ε-profile measurements in the interior of the abyssal ocean produced estimated $K_z \leq 10^{-5}$ m^2 s^{-1}, an order of magnitude lower than that required to satisfy the Munk model (Gregg 1989, Garrett 1993). This value was independently verified using a purposeful tracer release experiment which provided an integrated diffusion estimate over longer time scales and larger space scales (Ledwell et al. 1993). Sjöberg & Stigebrandt (1992) expanded the fjord parameterisation for mixing by internal tides (Stigebrandt & Aure 1989) to the global ocean to test Munk's speculation. They provided an estimate of the dissipation of tidal energy via the generation of internal tides in the open ocean which suggested that, despite the weak tidal currents in the open ocean, the generation of internal tides over topographic features in the abyssal ocean could account for a significant loss, of about 1 TW of tidal energy, focussed on topographic features*. Munk & Wunsch (1998) expanded the idea in Munk (1966) and computed a dissipation rate from the vertical density structure, arriving at the same conclusion.

Independent confirmation of the key role of the abyssal ocean in the dissipation of tidal energy later came through a series of papers based on emerging satellite altimetry data sets (Egbert & Ray 2000, 2003). They show significant abyssal tidal energy conversion, and by implication dissipation,

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* Note that the reported tidal energy conversion rates estimated using this method were later shown to be sensitive to the model resolution (St. Laurent et al., 2003).

is restricted to topographic features, such as continental shelf breaks and mid-ocean ridge systems (Figure 4). Further confirmation came through field experiments based around profiles of ε, which confirmed enhanced levels of dissipation over the mid-Atlantic Ridge when compared to measurements over the neighbouring Brazil Basin (Polzin et al. 1997). These measurements were linked to the tide through a spring-neap signal evident in the depth-integrated dissipation, as shown in Figure 5 (Ledwell et al. 2000).

In a dedicated experiment at Hawaii, the HOME team estimated the divergence of the internal tidal energy flux observed at the Hawaiian ridge and showed that it agreed with predictions made using tidal conversion parameterisations (Rudnick et al. 2003). The project also showed that the turbulent dissipation rates near the ridge were enhanced by an order of magnitude compared to background values, but that only 15% of the converted energy dissipated within ~60 km of the ridge (Klymak et al. 2006). The remaining 85% of the converted energy propagated away, redistributing the energy over vast distances (e.g. Alford 2003).

Attempts to reconcile the snapshot microstructure mixing estimates with coincident dye release estimates, which provide a spatially and temporally integrated estimates of mixing over larger scales, and with integrated mixing rates suggested by theory, failed due to the high levels of spatial and temporal variability (e.g. Polzin et al. 1997, Watson & Ledwell 2000, Figure 5). The degree of variability is highlighted in a number of studies with higher temporal and spatial resolution measurements. Mead-Silvester et al. (2014) report a series of 12 hourly ε-profiles made at a single location over sloping topography in the Southern Ocean, which reveal a large variation in mid-water dissipation. They report the dissipation to be enhanced by nearly two orders of magnitude during a 3-hour episode of shear instability (characterised by $R_i < 0.25$). Dale & Inall (2015) report measurements made over small-scale topography on the mid-Atlantic Ridge and find dissipation to be highly variable on lateral scales of several hundred metres. Further investigations, based on both theory (e.g. Nycander 2005) and fine structure measurements (Waterhouse et al.

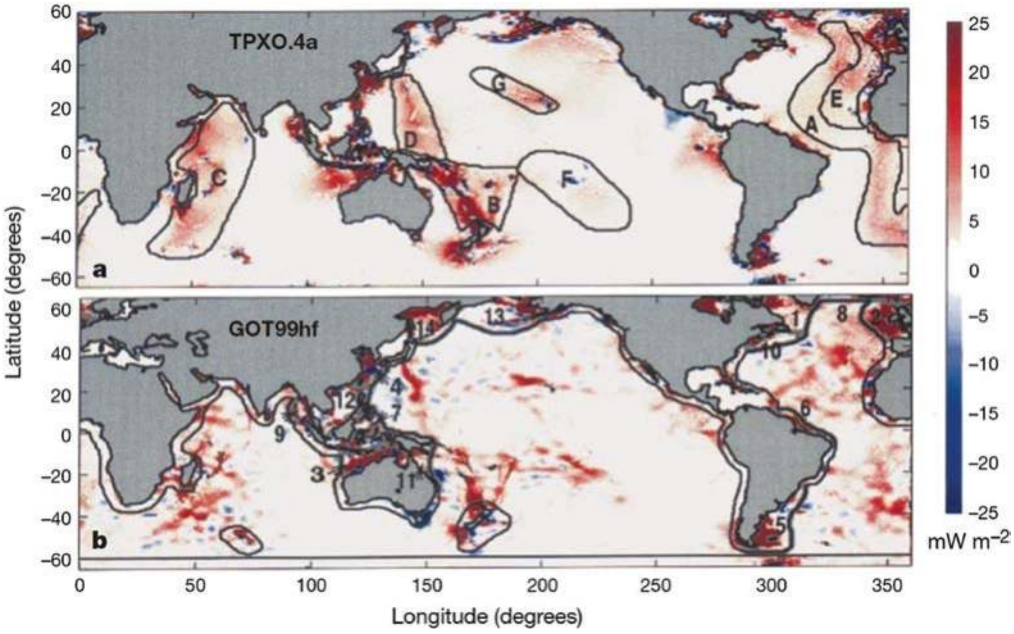

Figure 4 Tidal dissipation rates from altimetry-constrained models, computed using two different methods. (Reproduced from Egbert, G.D. & Ray, R.D. 2000. *Nature* **405**, 775–778 under Creative Commons Licence http://creativecommons.org/licenses/by/4.0/.)

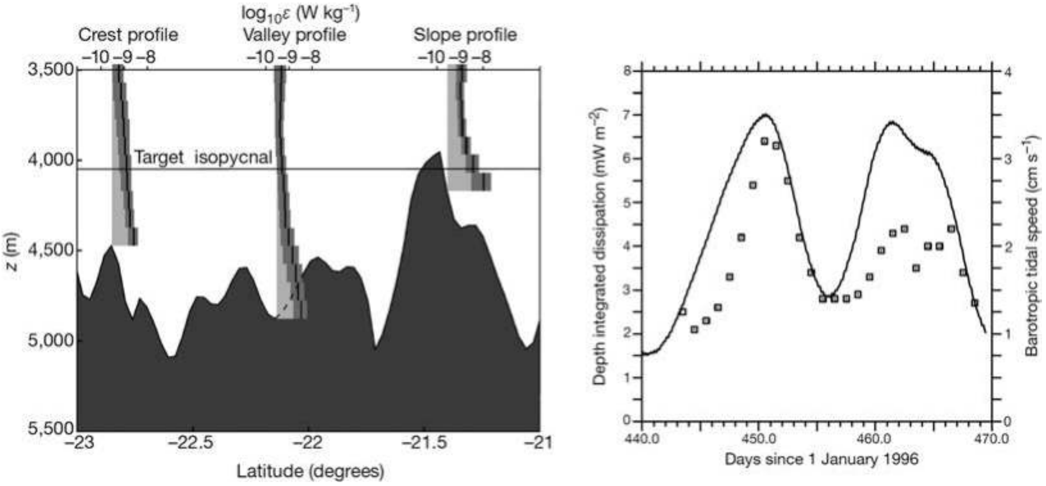

Figure 5 The left panel shows observed dissipation rates from the Brazil basin, highlighting the enhanced dissipation over rough topography (Reproduced from Ledwell, J.R. et al. 2000. *Nature* **403**, 179–182, under Creative Commons Licence http://creativecommons.org/licenses/by/4.0/). The right panel shows a comparison between dissipation rates (markers) and tidal speeds (solid line) from an altimetry constrained tidal model (see Ledwell, J.R. et al. 2000. *Nature* **403**, 179–182, for details). The fortnightly spring-neap variation is evident in both the tidal speeds and the dissipation rates, showing the dissipation is indeed tidally driven.

2014, MacKinnon et al. 2017), confirm the significant temporal and spatial variability of abyssal tidal dissipation.

More recently time-series of measured dissipation rates, coupled with coincident baroclinic energy flux calculations using mooring data, have facilitated the computation of global maps of q, the proportion of the converted baroclinic energy that dissipates locally to the total rate of conversion (Vic et al. 2018, 2019). The results show that the value of $q = 0.3$ based on observations from the HOME experiment (Klymak et al. 2006), whilst valid locally at Hawaii, is an underestimate when compared to the global mean. A revised global mean value of q has recently been estimated as ≈0.6 (Vic et al. 2019, Figure 6). This is a significant result since q is a key parameter in the parameterisation of vertical mixing in state-of-the-art ocean circulation models (e.g. St. Laurent et al. 2002, Schmittner & Egbert 2014). In consequence, the predicted local diffusivity may be underestimated by using a constant value of $q = 0.3$ (although this is usually compensated for in models by adding a constant background diffusivity).

Furthermore, not all energy dissipated in a turbulent flow is used in irreversible mixing, as discussed previously in the shelf sea and fjord sections, and in consequence, the bulk mixing efficiency varies considerably. However, the flux dissipation coefficient tends to be assumed to be $\Gamma = 0.2$ (Osborn 1980) in abyssal ocean mixing parameterisations, despite observations indicating a wide range of mixing efficiencies depending on locality and tidal energy pathway to the turbulence which supports the stirring that drives mixing (e.g. Simpson & Hunter 1974, Stigebrandt & Aure 1989, Arneborg 2001). Recently, Mashayek et al. (2017) used direct numerical simulation (DNS) to show a large variability in Γ in the abyssal ocean, with values surpassing 0.3 in some locations. These variations can significantly influence the strength of the circulation in the lower branch of the meridional overturning circulation (e.g. Mashayek et al. 2017), however, it remains unclear if this impact could be due to changes in q (Cimoli et al. 2019).

Over the past 50 years, Munk's (1966) ideas have been confirmed, with about 30% of the global tidal energy dissipation occurring in the abyssal ocean via conversion into internal tides. The dissipation of these internal tides plays a key role in the Earth system by contributing energy

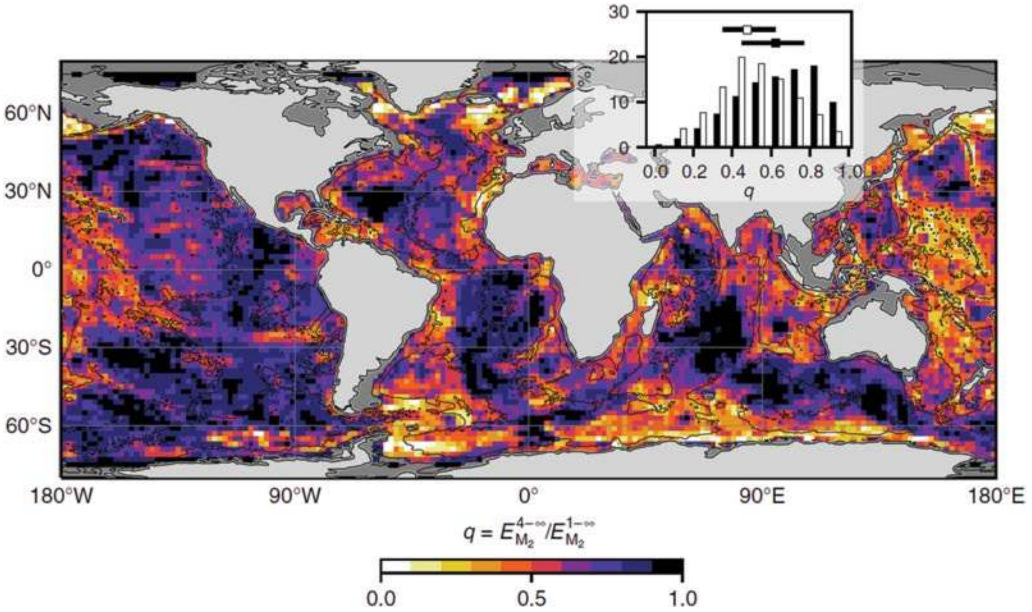

Figure 6 The geographic distribution of *q* – the ratio between local dissipation and total conversion (From Vic , C. et al. 2019. *Nature Communications* **10**, 2099). The bar plot shows histograms of seafloor area (black) and energy conversion (white) as functions of *q* (Reproduced from Vic, C. et al. 2019. *Nature Communications* **10**, 2019 under Creative Commons Licence http://creativecommons.org/licenses/by/4.0/.).

to the irreversible mixing that balances deep water formation at high latitudes and thus sustains the global climate, regulating meridional overturning circulation. It has also been demonstrated that the dissipation of abyssal internal tides plays a key role in redistributing nutrients and thus sustains a subsurface chlorophyll maximum often observed in the oligotrophic oceanic gyres (Stevens et al. 2012, Tuerena et al. 2019).

The Arctic Ocean

The Arctic Ocean is unique in a number of ways. It is characterised by very low levels of mixing when compared to other oceans globally (e.g. Padman & Dillion 1987, Fer 2009, Lenn et al. 2009, Guthrie et al. 2013, Lincoln et al. 2016b), with stratification dominated by changes in salinity with depth. The temperature structure in the upper part of the ocean is inverted due to the presence of relatively fresh cold water overlying a layer of warmer intruding Atlantic water (Polyakov et al. 2011). The intruding Atlantic water provides the largest oceanic heat supply to the Arctic Ocean and contain sufficient heat to melt the Arctic Sea ice several times over. However, it is largely isolated from the sea surface by the layers of colder and fresher water sitting above (i.e., the Halocline). The colder, fresher water overlying warmer, saltier water facilitates double diffusive convection, which in low-turbulence environments is characterised by thermohaline staircases. These staircases support weak vertical heat fluxes (0.05–1 Wm^{-2}) out of the intermediate depth Atlantic water (Padman & Dillion 1987, Timmermans et al. 2008, Lenn et al. 2009, Shibley et al. 2017, Polyakov et al. 2019). The observed persistence of these staircase structures potentially indicates the absence of significant shear induced turbulence (e.g. Lincoln et al. 2016b).

There is speculation that sea ice retreat will result in increasing influence of the wind in mixing the Atlantic water heat towards the surface and so drive a positive feedback of increasing mixing supporting increased ice melt (e.g. Rainville et al. 2011). However, measurements in ice-free conditions in the Canada Basin of the Arctic Ocean, during the 'perfect storm' conditions* of August 2012, show that, whilst there was evidence of increased wind influence in the upper 50 m of the water column, there was no evidence to suggest that the passage of the storm had impacted heat fluxes at the depths of the thermocline which separates the warmer Atlantic water from the halocline above (Lincoln et al. 2016b). Moreover, a recent modelling study has suggested that the increased influence of the wind will not be able to compete with the increasing stratification predicted for the warming Arctic Ocean (Davis et al. 2016).

One notable exception to the widespread low levels of turbulence found in the Arctic Ocean is the continental slope region poleward of Svalbard. Here microstructure measurements reveal significant levels of dissipation supporting heat fluxes of order 10–50 Wm^{-2} towards the sea surface (Padman & Dillion 1991, Steele & Morison 1993, Fer et al. 2010, Rippeth et al. 2015).

Despite early speculation that the Arctic Ocean is an important sink for tidal energy (Jefferys 1920), the tides within the Arctic are now known to be generally weak (Padman & Erofeeva 2005). Moreover, much of the Arctic Ocean is poleward of the critical latitude where the period of the principle lunar semi-diurnal (M_2) tide matches the local inertial period. The linear tidal conversion rate declines rapidly as the critical latitude is approached (Llewellyn Smith & Young 2003), suggesting that the amount of energy extracted from the barotropic tide to a linear internal tide in the Arctic Ocean is small when compared to similar conditions low and mid-latitudes (Llewellyn Smith & Young 2003, Vlasenko et al. 2003, Hughes & Klymak 2019). A further linked dynamical constraint imposed by the location poleward of the critical latitude is that the tidally generated depression in the thermocline cannot freely propagate as a linear internal tide but is a bottom-trapped lee wave (see, e.g., Hughes & Klymak 2019). In consequence, the fraction of converted tidal energy dissipated locally (q) would be expected to be close to 1.

Rippeth et al. (2015) compared altimeter-based tidal conversion estimates with a series of profiles of ε made across much of the accessible shelf break regions in the Arctic Ocean. They found that the variation in dissipation at intermediate depths, and hence implied Atlantic water upward heat flux, is consistent with the longitudinal variation in tidal conversion, implying that, although the tides are weak, they support regionally enhanced turbulent mixing. Potential indirect evidence of the role of the tide in driving significant tidal mixing north of Greenland (an area identified as hosting significant tidal conversion by Rippeth et al. 2015) comes through consideration of finescale measurements (Chanona et al. 2018) and the recent thinning of multiyear sea ice (Lange et al. 2019).

The tidally generated bottom trapped lee waves will contribute to tidal conversion poleward of the critical latitude. In addition, non-linear processes (not normally included in the parameterisations of internal tidal mixing) are also thought to contribute to tidal energy conversion (Bell 1975, Nakamura & Awaji 2000, Nakamura et al. 2000, Musgrave et al. 2016) as the lee wave becomes unsteady (Vlasenko et al. 2003, Rippeth et al. 2017). Rippeth et al. (2017) combined a high-resolution non-hydrostatic, fully non-linear numerical modelling study with observations made over the Spitzbergen Bank, poleward of the critical latitude, to demonstrate the key role of tidally generated lee-waves, and the related internal hydraulic control of the flow, in the transfer of energy from the tide to turbulence, poleward of the critical latitude. They observed barotropic tidal current amplitudes of $\approx 0.3\ \mathrm{ms}^{-1}$ and the midwater R_i estimated to be ≈ 1 (implying the thermocline to be marginally stable), together with periods of enhanced midwater dissipation.

A parallel, non-hydrostatic modelling study predicted the conditions for the internal waves radiating from the bank to be supercritical (internal Froude number, $\mathrm{Fr} > 1$) for much of the time, implying the tidal energy conversion associated with the internal hydraulic control of the flow represents a significant sink for tidal energy, in addition to the energy conversion associated with

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* August 2012 recorded the lowest aerial extent of sea ice for that month since measurements began. It also saw an unusually intense storm which tracked across the Canada basin of the Arctic Ocean during the period of the measurements reported by Lincoln et al. (2016b).

the formation of the lee wave. In comparing the tidal conversion rate predicted by the fully nonlinear model to that predicted using the linear version (i.e. due to the lee wave formation in isolation), Rippeth et al. (2017) show that for the region simulated, the tidal conversion associated with the nonlinear processes accounts for 71% of the total. These nonlinear processes are not currently accounted for in parameterisations of internal tidal mixing poleward of the critical latitude (e.g. Falahat & Nycander 2015), implying that the existing parameterisations will significantly underestimate the contribution of tidal energy to mixing in the Arctic Ocean.

Both the rate of conversion of tidal energy and the dissipation pathways in the Arctic Ocean are sensitive to the levels of stratification and background currents which will interact with the tidal flow. A conspicuous consequence of the warming Arctic is the decline in seasonal sea ice coverage (e.g. Laxon et al. 2013) and, since the formation and melting of sea ice is a key process in determining the upper ocean salinity in much of the Arctic Ocean, declining sea ice volumes will affect the upper ocean salinity and hence upper ocean stratification.

Currently, significant levels of salinity stratification in the upper ocean prevent substantial ice-free conditions in winter by suppressing ventilation of the intermediate depth warmer Atlantic water by vertical mixing and convective overturning. However, the declining sea ice coverage coupled with the warming of the intruding Atlantic water is already weakening stratification in the eastern Eurasian Basin of the Arctic Ocean (Polyakov et al. 2017) and has driven regime shift in winter sea ice cover in the southern Barents Sea over the past decade (Barton et al. 2018). Moreover, the background circulation is increasing in response to reduced sea ice coverage (Giles et al. 2012, Armitage et al. 2017), as is the intensity of upper-ocean near-inertial currents (Dosser & Rainville 2016, Lincoln et al. 2016b). The combination of increasing currents and weakening stratification could conspire to change both the geographical extent of tidal mixing hotspots, over sloping topography, and the rate of tidal energy conversion associated with both the lee wave generation and the temporal extent of the critical and super-critical internal flows. As such, tidal conversion could be a key process in an ice-ocean-mixing feedback loop.

Tides through time

Tides vary over a wide spectrum of time scales (e.g. Haigh et al. 2019) and have been shown to have responded to changes in sea level over the past few decades (e.g. Mawdsley et al. 2015, Schindelegger et al. 2018). However, these recent changes are small when compared to the substantial changes in global tides over Earth history. During the most recent glacial maximum (LGM 22–18 ka), sea level was on average 120–130 m lower than it is today, with global tides $\approx$50% more energetic than today (Egbert et al. 2004, Wilmes & Green 2014). This is a consequence of the present-day North Atlantic being near resonance for the dominating tidal forcing period (Platzman et al. 1981, Green 2010) and because at the low-stand in sea level during the LGM, the shelf seas were largely absent. Since shelf seas are the main energy sink for tidal energy, their absence greatly reduced the damping of the tide, which, coupled with a near-resonant state of the North Atlantic, resulted in an amplification of the tide (see Egbert et al. 2004, Arbic & Garrett 2010, or Green 2010; for a discussion).

As sea level rose during the deglaciation, the shelf seas flooded, gradually transitioning from being permanently well mixed to today's pattern with well-mixed areas separated from seasonally stratified patches by tidal mixing fronts (e.g. Uehara et al. 2006). The predicted timings of the temporal migration of the tidal mixing front positions are independently validated by empirical palaeodata (benthic foraminiferal assemblages, oxygen/carbon foraminiferal stable isotopes) (Scourse et al. 2002). As the positions of tidal mixing fronts can be accurately predicted (from local water depth and tidal current amplitude, using Equation 3), the migration of tidal fronts over the deglacial transition, traced through palaeo records, can provide tidal current amplitude estimates against which tidal models of this period can be validated. The potential impact of the growth of the shelf seas on the global carbon cycle via mediation of the uptake of atmospheric CO_2 via the continental shelf CO_2 pump, over the last deglacial transition, was highlighted by Rippeth et al. (2008).

As sea levels continue to rise in the future, the tides will become less energetic (Green 2010, Wilmes et al. 2017). However, future sea-level rise cannot be assumed to be globally uniform, as large mass losses from the major ice sheets in Greenland and Antarctica introduce spatially heterogeneous changes in sea level, with low stands near the ice sheet and high stands further away (e.g. Gomez et al. 2012). Wilmes et al. (2017) show that even moderate sea level changes can have large regional impacts on shelf sea systems far away from the ice sheets by relocating the positions of tidal mixing fronts.

Over much longer time scales, the tides respond to the movement of the continents through continental drift. Every 400–500 My, the continental plates of the Earth's crust come together to form one large landmass – a supercontinent (e.g. Scotese 2009, Davies et al. 2018). The supercontinent remains in place for a 150–200 My, after which it starts to break up and the tectonic plates scatter (see Scotese 2009 for details). During the supercontinent stage, the tides are weak because there are no major resonant basins (Green et al. 2017). However, as the continents drift apart, basins can go through periods of resonance, in what has been called a supertidal cycle (Green et al. 2018, Figure 1). The large tides on Earth today mark the beginning of a tidal maximum which will last about 20 My before the tides decline. The previous tidal maximum probably occurred about 430 My ago (Byrne et al. 2019), before the formation of the previous supercontinent, Pangea.

The climatic consequences of the associated weak tidally driven mixing in the deep past are largely unexplored, except for the LGM (21 ky) and the Eocene (50 My). The large tides during the LGM helped sustain a relatively vigorous overturning circulation, which would have been suppressed to a larger extent by meltwater inputs, had the enhanced tidal mixing been absent (Green et al. 2009, Schmittner et al. 2015). The Eocene experienced a greenhouse climate, with tropical temperatures in present-day subpolar areas (Huber & Caballero 2011), whilst the equator was only a few degrees warmer than today. For climate models to reproduce this reduced meridional temperature gradient, the level of abyssal mixing had to be greatly enhanced (Huber & Caballero 2011). Green & Huber (2013) have shown that, even though the Eocene tides were weak, the energy that was available was dissipated in the right part of the ocean (the South Pacific) to support the enhanced overturning circulation required to maintain the reduce the meridional temperature gradient.

Summary

The tides play a key role in shaping regional oceanography and global climate through sustaining small-scale mixing processes. These processes determine water column structure and support fluxes of heat, freshwater, carbon and limiting nutrients over a wide range of temporal and spatial scales (e.g. Simpson & Hunter 1974, Stigebrandt & Aure 1989, Simpson et al. 1990, Munk & Wunsch 1998, Wunsch & Ferrari 2004, Rippeth et al. 2015). Consequently an accurate parameterisation of tidally driven mixing processes is a critical component of regional and global numerical ocean and climate models (e.g. Mashayek et al. 2015). Models of the evolution of dissipation associated with tidally generated boundary layers are well developed (e.g. Simpson et al. 1996, Burchard et al. 1998). However, the accurate parameterisation of the key pathways of energy, from the tide to turbulence, associated with the interaction of stratified tidal flow with topography, is still very much work in progress (e.g. Olbers & Eden 2017a,b).

A complication arises in parameterising these processes, as they operate on subgrid scales and vary over relatively short time scales. They are also localised in space, with the conversion of tidal energy taking place close to topography. In consequence, the dissipation and associated mixing supported by tidal conversion can vary by several orders of magnitude over relatively short spatial and temporal scales, as illustrated by the fjord studies presented previously and in open ocean studies (e.g. Mead-Silvester et al. 2014, Dale & Inall 2015). Any uncertainty in Γ must be set against this high degree of spatial and temporal variability in the subgrid scale mixing processes and hence in the calculation of diapcynal fluxes (Thorpe 2005).

Only a fraction of the energy converted, q, generally dissipates near the topography where the conversion takes place; the rest propagates away and dissipates remotely, potentially thousands of km from the conversion zone (e.g. Alford 2003, Vic et al. 2019). In consequence, parameterisations of tidally driven processes away from the bottom boundary layer contain a number of poorly constrained parameters (e.g. St. Laurent et al. 2002), although some progress is being made on improving and better constraining these parameters (e.g. Schmittner & Egbert 2014, Mashayek et al. 2015, 2017, Vic et al. 2019). A major issue in the validation of such parameterisations arises from the expense of collecting abyssal data of sufficiently high resolution. However, emerging technologies for measuring turbulent parameters from moored instrumentation and using sea gliders will help improve the resolution of dissipation on the relevant time and length scales.

The Arctic Ocean represents a special case, as dynamical constraints, imposed by the location of much of the Arctic Ocean poleward of the critical latitude, prevent the generation of a freely propagating linear internal tide (with a dominant M_2 tidal frequency), greatly reducing the efficiency of linear tidal conversion and trapping the lee wave along the slope. However, a recent study by Rippeth et al. (2017) has highlighted the importance of nonlinear processes, in particular demonstrating the potential for the development of critical and super-critical internal control of the flow, to enhance the rate of conversion of tidal energy and mixing. As the conditions of criticality are imposed by the total mean flow (not just the tide), the rate of tidal conversion will not only be influenced by local stratification and topography but also other (non-tidal) currents. Consequently, the influence of these processes must also be included in the parameterisation of tidal conversion and related mixing poleward of the critical latitude.

An examination of global tides and associated mixing at earlier stages of the Earth's history, for example, from the LGM (Egbert et al. 2004, Green et al. 2009, Wilmes & Green 2014, Schmittner et al. 2015) and the Eocene (Green & Huber 2013), has highlighted the importance of specifically including parameterisations for tidally driven mixing which are representative of the tides for the time period of interest in global climate models. These results, and their extension in Green et al. (2017, 2018), show that the present tides and tidal dissipation rates are a poor proxy for past and future levels of tidally driven oceanic mixing and emphasise the need for care in correctly representing the tides and associated mixing when simulating past and future global climates.

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REVIEW: EFFECTS OF MICROPLASTIC ON ZOOPLANKTON SURVIVAL AND SUBLETHAL RESPONSES

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Abstract Microplastics (MPs) are a prolific contaminant in aquatic ecosystems across the globe. Zooplankton (including holoplankton and meroplankton) play vital ecological roles in marine and freshwater ecosystems and have been shown to readily consume MPs. The present review uses 88 pieces of published literature to examine and compare the effects of MPs on survival, growth, development, feeding rate, swimming speed, reproduction, organ damage and gene expression of different groups of zooplankton, including copepods, daphnids, brine shrimp, euphausids, rotifers and the larvae of fishes, sea urchins, molluscs, barnacles, decapods and ascidians. Among the groups studied, daphnids and copepods are the most sensitive to MPs, with their feeding rate and fecundity significantly decreased at environmentally relevant MP concentrations. This might adversely affect daphnid and copepod populations in the long term. In contrast, molluscs, barnacles, brine shrimp and euphausids appear to be more tolerant to MPs. No clear impacts on survival, development time, growth or feeding rate can be observed in these zooplankton groups at any of the MP concentrations tested, suggesting that these groups might become more dominant with prolonged exposure to MP pollution. Leachates derived from MPs can induce severe abnormality in bivalve and sea urchin embryos. MPs have prominent effects on survival and fecundity of F_1 offspring in bivalves, copepods and daphnids, indicating that MPs could incite transgenerational effects and drastically affect sustainability in zooplankton populations.

Introduction

The invention of plastics has had a vast societal and environmental impact (Thompson et al. 2009). Since the material was introduced in 1907, plastic production has increased continuously, rising from 47 million tons in 1975 to 335 million tons in 2016; the plastic industry has now become one of the largest manufacturing sectors in the world (Plastic Europe 2017). However, mismanagement has led to inordinate amounts of plastic waste ending up in the natural environment. Owing to its durability, plastic debris accumulates in the environment, where it poses a threat to a wide range of biota (Thompson et al. 2009).

After entering the natural environment, plastic debris is subjected to fragmentation via UV degradation and physio-chemical and biological processes, eventually breaking down into microscopic pieces, termed microplastics (MPs) (Thompson et al. 2004). The definition of a MP is still under debate, with many different definitions proposed in, for example, Koelmans (2015) and Mendoza et al. (2018). Here, we define a MP as a piece of plastic 0.1 μm–1 mm in diameter in accordance with Hartmann et al. (2019). MPs are a prolific marine contaminant, accounting for more than 90% of all marine plastic debris (Eriksen et al. 2014). Recent studies have shown the presence of MPs in freshwater and marine environments, including the coral reefs (Hall et al. 2015), open oceans (Eriksen et al. 2014), deep oceans (Van Cauwenberghe et al. 2013) and polar regions (Waller et al. 2017, Peeken et al. 2018). Despite their widespread occurrence within the natural environment, the effects of MPs on marine and freshwater ecosystems remain poorly understood (Thompson et al. 2004, Andrady 2011, Law & Thompson 2014, Shim & Thomposon 2015).

Zooplankton encompass both freshwater and marine holoplankton and meroplankton, which exhibit very different life histories. Holoplankton (e.g. copepods and daphnids) spend their entire life as plankton. On the other hand, meroplankton (e.g. bivalve and sea urchin larvae) only spend part of their life as plankton and become either nekton or benthos in later developmental stages. Numerous organisms, including mammals, seabirds, bivalves, fish and zooplankton, have been reported to ingest MPs (Egbeocha et al. 2018). High MP to zooplankton ratios have been documented in the north Pacific gyre and Mediterranean Sea (Moore et al. 2001, Collignon et al. 2012), and both holoplankton and meroplankton have been reported to ingest MPs in the field (Desforges et al. 2015, Sun et al. 2017, Steer et al. 2017) and laboratory studies (e.g. Cole et al. 2013, Setälä et al. 2014). As a primary consumer, zooplankton graze on phytoplankton and transfer energy to higher trophic levels along the food chain and are therefore considered essential sources of prey for numerous marine organisms. They also play a vital role in nutrient cycling by feeding in surface water and packaging the organic matter into dense faeces which facilitate the transport of carbon and nutrients to the deep sea (Turner 2015). Thus, any negative impact MPs have on zooplankton has the potential to subsequently affect different trophic levels and key ecological processes within the marine environment.

One of the controversial issues in MP ecotoxicological studies is the concentration of MP used often far exceed the levels documented in the marine environment (Lenz et al. 2016). Current MP concentrations reported in the field typically range from 1×10^{-3} to 1×10^{-6} mg L^{-1} (Lenz et al. 2016). However, concentrations orders of magnitude higher than field concentrations are often used in laboratory studies to assess the impacts of MPs (Lee et al. 2013, Rehse et al. 2016). As a result, the impacts of MP derived from such high concentrations may never happen in the real environment. It is possible that these laboratory studies are not representative and might overestimate the effects of MPs, although they may still provide important insights into the mechanisms by which MP can cause toxicity.

There is presently no detailed review on the effect different sizes and concentrations of virgin or chemically coated MPs have on survival and sublethal health responses (e.g. growth, development, feeding and swimming behaviours, reproduction, gene expression from transcriptome analysis and organ damages) of individual groups of zooplankton. While a recent detailed review assessed the factors affecting the bioavailability of MPs to marine zooplankton, including size, shape, colour, polymer type, density, age, abundance and aggregation (Botterell et al. 2018), the relative sensitivities of different zooplankton groups to MPs have never been compared before.

The present study reviews and compares the impact of MPs (polymer type, size, concentration and shape) on eight of the most commonly assessed biological endpoints – survival, development, growth, feeding rate, swimming speed, reproduction, organ damage and gene expression – in a range of zooplankton taxa, including holoplankton (copepods, daphnids, brine shrimp, euphausids and rotifers), and meroplankton (larvae of fishes, sea urchins, molluscs, barnacles, decapods and ascidians). We further compared the relative sensitivity among these zooplankton groups for different endpoints. In particular, we reviewed the effects of MPs at concentrations that are relevant to real environments (0–1 mg L^{-1}) and at the high concentrations used under laboratory conditions which are beyond the concentration in the natural environment. This review attempts to give insight into which biological traits and zooplankton groups are more sensitive to MPs (at both environmentally relevant concentrations and high concentrations in laboratory conditions) and could therefore act as a potential indicator for MP pollution in the environment. Finally, we identify the knowledge gaps based on present MP studies on zooplankton.

Abbreviations

Some chemical terms and polymer types are explained subsequently with their abbreviations. The full names of these terms and their abbreviations used in this review are listed in Table 1.

Methods

Published articles evaluating effects of MP on zooplankton were searched for on Science Citation Index (SCI) journals, Google Scholar and the ISI Web of Science using a combination of keywords and Boolean operators (i.e. AND), including microplastic, zooplankton, larvae, fish, copepod, sea urchin, bivalve, gastropod, barnacle, daphnid, brine shrimp, crustacean and rotifer. Eight of the most frequently evaluated endpoints – mortality, development, growth, feeding rate, swimming speed, reproduction, organ damage and gene expression – were extensively reviewed. A total of 88 articles were identified, covering the following zooplankton groups: Holoplankton: copepods, daphnids, brine shrimp, euphausids and rotifers; Meroplankton: the larvae of fishes, sea urchins, bivalves, gastropods, barnacles, decapods and ascidians. In each zooplankton group, the eight endpoints were discussed according to 1) developmental stage (gametal, embryonic, larval or adult stage), 2) transgenerational effects (offspring generation) and 3) the type of MP (virgin MPs or those that had interacted with chemicals).

Microplastic mass calculations

Published literature used a variety of concentration units, such as beads mL^{-1} and mg L^{-1}. For standardisation purposes, studies whose concentration unit was based on the number of particles (beads L^{-1}) were transformed to units of mass (mg L^{-1}). First, the volume (V) of spherical MPs (i.e. beads) was calculated using the formula $V = 4/3\ \pi r^3$, where radius (r) was ascertained from the diameter of the particle. For fibrous MPs, the volume (V) of fibre MPs was calculated using the cylindrical volume formula $V = \pi r^2 h$, where radius (r) and height (h) were ascertained from the diameter and length of the fibre. Literature using fragmented MPs and only reporting the number of particles (beads L^{-1}) cannot be transformed to units of mass (mg L^{-1}). Hence, those studies were described in the context but were excluded from the analysis. Next, the volume of the MP particles was multiplied by the density (ρ) of the specific polymer to obtain the mass (M) of a single MP. Finally, the mass of a single MP was multiplied by the particle concentration (beads mL^{-1}), as reported in the literature, to give the mass of MP per millilitre (g mL^{-1}), with units converted to ascertain the mass per litre (mg L^{-1}).

Table 1 Full names and abbreviations of the terms used in this review

Category	Full names (abbreviations)
Plastics	Microplastic (MP), polyethylene (PE), low-density polyethylene (LDPE), high-density polyethylene (HDPE), polystyrene (PS), polystyrene coated with carboxylic groups (PS-COOH), polystyrene coated with amine groups (PS-NH_2), polyvinylchloride (PVC), polymethyl methacrylate (PMMA), polyamide (PA), polycarbonate (PC), polyethylene terephthalate (PET), polylactide (PLA), acrylonitrile-burtdiene-styrene terpolymer (ABS), polyoxymethylene homopolymer (POM) and styreneacrylonitrile copolymer (SAN)
Additives	Polychlorinated biphenyl (PCB), polycyclic aromatic hydrocarbon (PAH), phenanthrene (Phe), benzo[a]pyrene (BaP), triclosan (TCS), bisphenol A (BPA), 17 α-ethynylestradiol (EE2) and benzophenone-3 (BP-3)
Toxicological terms	Concentration lethal to 50% of a population (LC_{50}), concentration at which an effect is observed in 50% of a population (EC_{50}), lowest observed effect concentration (LOEC) and no effect concentration (NEC)

Calculating percentage change of microplastics

Since all of the studies reviewed here were based on different treatments, there was a need to standardise them all to facilitate comparisons. To compare the percentage change of biological endpoints in the presence of MP, the measured value of animals in the control was subtracted by that in the MP treatment and then divided by the value given in the control and then data multiplied by −1 so adverse effects were shown as negative data:

$$\text{Percentage change}\,(\%) = \frac{X - Y}{X} \times 100 \times -1$$

X = measured value of the control
Y = measured value of MP treatments

For experiments based on virgin MPs, the measured values that were used to calculate the percentage change in each endpoint are as follows: 1) survival: survival rate, hatching rate or fertilisation rate; 2) development: development time; 3) morphological normality or abnormality; 4) growth: body length, width, arm length or weight; 5) feeding rate: ingestion rate (no. of algae/*Artemia* nauplii consumed) or carbon biomass uptake; 6) swimming speed: swimming velocity, maximum swimming velocity or distance travelled in a period; and 7) reproduction: total number of offspring produced, number of offspring produced per brood or egg production rate. Literature that did not use the measured values listed here was excluded from percentage change analysis. Of the 88 articles reviewed, data from 74 papers were included in the percentage change calculation. To compare the effects of size and concentration, MPs were assigned to one of three size classes: 0.1–10, >10–100 and >100 μm; the concentration was categorised into four groups: 0–1, >1–10, >10–100, >100 mg L^{-1}. The mean percentage change with one standard deviation (1SD) was calculated for each size class of MPs at different concentrations. MP concentrations at 0–1 mg L^{-1} are consistent with those documented in the field (Lenz et al. 2016). Thus, the observed effects under this concentration are considered environmentally relevant. For concentrations >1 mg L^{-1}, these are considered higher than have been observed in the natural environment, and therefore the effects potentially exaggerate the impacts of MPs.

When investigating transgenerational effects of MP on zooplankton, measured values used for survival, development, growth, normality, feeding rate, swimming speed and reproduction were the same as previously described. Note that when evaluating transgenerational effects, we combined all the values of different MP sizes and concentrations together, predominantly due to the small number of studies on these effects. Because the interactions between MPs and chemicals are complex, we did not calculate the mean percentage change in interactive effects between MPs and chemicals, but their effects are discussed in context. All literature in the present studies is listed in the supplementary information (Table A1–9).

Survival

Holoplankton

Copepods

Larvae and juveniles MPs (0.1–10 μm) rarely had lethal effects on copepod naupliar larvae. The percentage change in survival was <5% (Figure 1A). Lee et al. (2013) observed that neither acute (96 hours) nor chronic (14 days) exposure to 0.5 and 6 μm polystyrene (PS) MPs (0.125–25 mg L^{-1}) had an observable lethal effect on MP-exposed *Tigriopus japonicus* (Harpacticoida) naupliar larvae. All MP treatments resulted in over 80% survival, including controls (82%) (Figure 1A). Similarly, PS MPs (1–6 μm, 1–10 mg L^{-1}) did not decrease the survival of *Tigriopus fulvus* (LOEC >10 mg L^{-1}). In calanoid copepods, PS (4–6 μm) and polyvinylchloride (PVC) MPs (20 μm) did not affect survival in *Acartia clausi* (LOEC >30 mg L^{-1}) (Beiras et al. 2018, 2019). Because Beiras et al. (2018) only reported LOEC values, data from this study were not included in the percentage change analysis. The lack of impact again indicates that MPs of size 0.1–10 μm rarely had lethal effects on copepods (Figure 1A).

Adults Exposure to virgin 0.1–10 μm and >10–100 μm MPs had no observable impacts on the survival of adult calanoid and harpacticoid copepods that have been studied (Figure 1A,B). In the copepod *T. japonicus*, long-term exposure (14 days) to 0.5 and 6 μm PS MPs did not affect the adult survival rate (up to 80%) at any concentrations tested (0–25 mg L^{-1}) (Lee et al. 2013) (Figure 1A). Similarly, survival rates of calanoid copepods *Calanus helgolandicus* and *Calanus finmarchicus* exposed to 20.0 μm (0.33 mg L^{-1}) and 15 μm (0.095 and 0.95 mg L^{-1}) PS MPs were not significantly different from that of the control (Cole 2014, Cole et al. 2015, Vroom et al. 2017). Both controls (82%) and MP treatments (81%) reached over 80% survival rate (Figure 1B). No study has evaluated the effect of MPs >100 μm on copepods; thus, no data were included in this size class during the percentage change analysis.

Microplastic-chemical interactions Co-exposure to MPs with chemicals might decrease the survival of organisms, but the extent to which it is toxic appears to be chemically dependent. Co-exposure to polyethylene (PE) MPs (43.5 mg L^{-1}) and triclosan (TCS), a synthetic antimicrobial

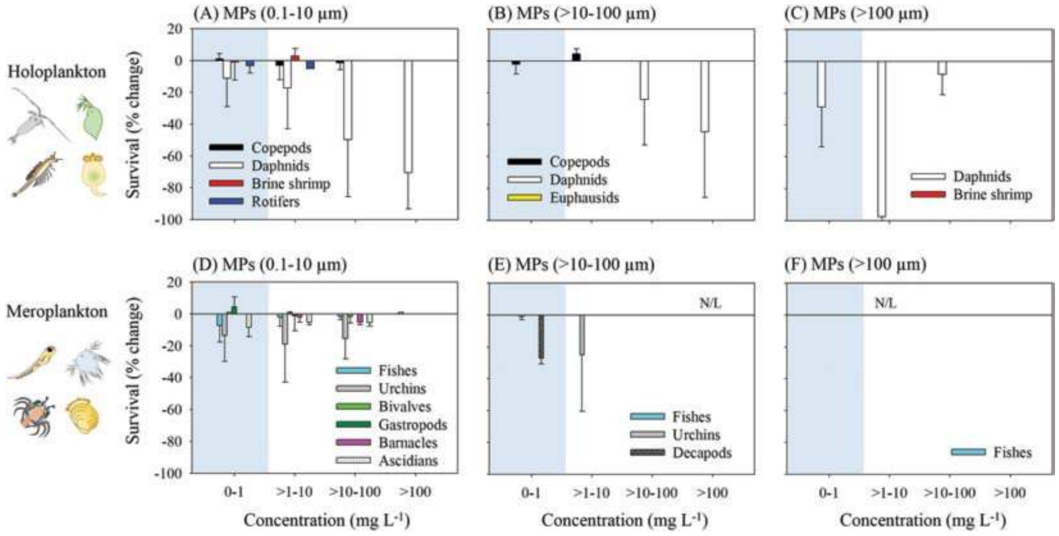

Figure 1 Percentage change in survival (mean + 1SD %) of (A–C) holoplankton and (D–F) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A1. A negative percentage change means a decrease amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available on copepods (>10^2 mg L^{-1}), rotifers (>10 mg L^{-1}) and euphausids (all concentrations). In figure (B), no data are available on brine shrimp and rotifers at all concentrations, except for daphnids (0–1 mg L^{-1}) and euphausids (>10 mg L^{-1}). In figure (C), no data are available for copepods, euphausids and rotifers at all concentrations, except for brine shrimp (0–10, >10^2 mg L^{-1}). In figure (D), no data are available for urchins (>10^2 mg L^{-1}), bivalves (>10^2 mg L^{-1}), gastropods (>10 mg L^{-1}), barnacles (>10^2 mg L^{-1}), ascidians (>10^2 mg L^{-1}) and decapods (all concentrations). In figure (E), no data are available for bivalves, gastropods, barnacles, ascidians at all concentrations, except for fishes (0–1, >10^2 mg L^{-1}), urchins (>10 mg L^{-1}) and decapods (>1 mg L^{-1}). In figure (F), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>1–10 mg L^{-1}). Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear in the environment at the moment. N/L = no data available.

agent, significantly lowered LC_{50} (109.6 ± 0.01 μg L^{-1}) compared to TCS alone (157.9 ± 0.01 μg L^{-1}) in the calanoid copepod *Acartia tonsa* (Syberg et al. 2017). Bejgarn et al. (2015) assessed the toxicity of leachate from plastic products and found that 8 of the 21 plastic materials tested (38%) (<1 mm; 100 g L^{-1}) caused acute toxicity, with PVC and polyurethane (PUR) leachates seeming to have higher toxicities. Exposure to MPs and leachates derived from commercial PVC products significantly reduced the calanoid copepod *A. clausi* survival by 60%–90% (Beiras et al. 2019). In contrast, benzophenone-3 (BP-3) was less toxic: the lowest observed effect concentration (LOEC) was higher than the highest concentration used (10 mg L^{-1} PE MPs [1–6 μm] spiked with 20 μg L^{-1} BP-3), suggesting that BP-3 had no clear impact on the survival of *T. fulvus* and *A. tonsa* (Beiras et al. 2018).

Transgenerational effect The offspring produced by MP-exposed copepods died at a significantly higher rates than the controls, although their MP-exposed parents were not affected (both Calanoida and Harpacticoida). In *T. japonicus*, exposure to 0.5 μm PS MPs (25 mg L^{-1}) significantly decreased the survival of the F_1 generation to 35%, but not the F_0 generation (survival over 80%) (Lee et al. 2013). Hatching success of eggs produced by PS MP-exposed (20 μm; 0.33 mg L^{-1}) *C. helgolandicus* was ~22% lower than that of the control (Cole 2014, Cole et al. 2015). Polyethylene terephthalate (PET) MPs (<11 μm; 14.44 mg L^{-1}) significantly reduced the population size of the copepod *Parvocalanus crassirostris* by around 40% compared to controls after 24 days of exposure (Heindler et al. 2017). These results suggest that MP exposure might have transgenerational effects, reducing the fitness of their offspring. Nevertheless, the size of MPs might affect these results. For example, 6 μm PS MPs (0.125–25 mg L^{-1}) affected neither parental nor offspring survival rates (over 70% survival) (Lee et al. 2013). Thus, the calculated mean percentage change was only ~10% (Figure 2A). However, the study number is still small, and further investigations are highly recommended.

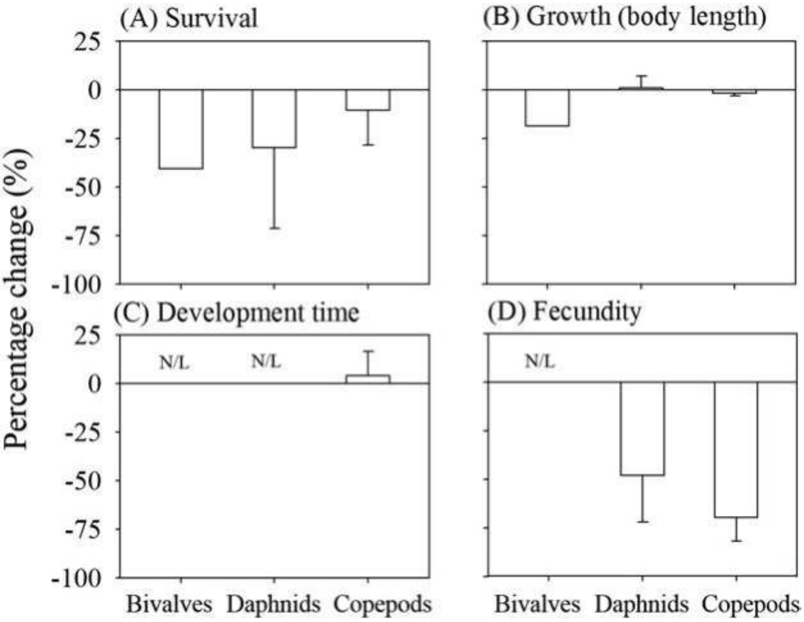

Figure 2 Percentage change in (A) survival, (B) growth (body length), (C) development time and (D) fecundity (mean + 1SD %) of F_1 offspring in MP treatments when compared to controls. N/L = no data available. For literature used for all groups of zooplankton, refer to supplementary Table A2. Note: No data are available for brine shrimp, euphausids, rotifers, fishes, urchins, gastropods, barnacles, decapods and ascidians for transgenerational effects of MPs.

Daphnids

Since daphnids are the most extensively studied organisms for MP toxicity tests, there are plenty of studies evaluating the effects of MP on daphnid survival. This section is divided into three parts: 1) the effect of food particles, 2) MP shape and 3) species.

(1) *Presence of food particles*: The presence of food particles appears to be an important factor in determining MPs' effect on mortality. MPs had no clear effect when food particles were present in the solution. On the other hand, MP significantly increased mortality in the absence of food. In acute toxicity tests, the organisms are usually not fed during the exposure. At the beginning of exposure, MPs had no observable effect on survival if the exposure time was less than 72 hours. For instance, neither PS MPs (1–15 μm) nor polyamide (PA) Ps (15–20 μm; 25–250 mg L^{-1}) were toxic to *Daphnia magna* after 72 hours of exposure (Ma et al. 2016, Puranen Vasilakis 2017, Horton et al. 2018, Rehse et al. 2018). All of the controls and MP treatments reached over 90% survival. One exception was the study by Zhang et al. (2019), who found that *D. magna* survival significantly decreased in a dose-dependent manner after 48 hours of exposure to PS MPs (1 and 10 μm; 0.1–600 mg L^{-1}). However, the toxicity rose with increasing exposure time. Both PET (~5 μm; 0.1–10000 mg L^{-1}) and high-density polyethylene (HDPE) MPs (1 μm; 12.5–400 mg L^{-1}) significantly decreased daphnid (*D. magna*) survival from 20% to 100%, compared to 100% survival in controls, after 96 hours of exposure (Rehse et al. 2016, Gerdes et al. 2018), despite yielding no observed effect at 48 hours. Jaikumar et al. (2018) also compared the toxicity of different exposure times and found a strong time-dependent correlation in which toxicity was higher after 96 hours of exposure. These studies largely contributed to the high percentage decrease in survival observed upon exposure to 0.1–10 μm MPs (Figure 1A).

On the other hand, in chronic-exposure experiments, food particles are added to keep animals alive. If food particles were present in the solution, MPs had minor or negligible effects on daphnid survival. For example, none of the three *D. magna* clones tested had increased mortality after exposure to two mixtures of MPs (PA + polycarbonate [PC] + PET + PVC and acrylonitrile-burtdiene-styrene terpolymer [ABS] + PVC + polyoxymethylene homopolymer ([POM] + styreneacrylonitrile copolymer [SAN]) for 20–22 days (Imhof et al. 2017). No significant effect on survival was found for either PE (63–75 μm; 25–100 mg L^{-1}) or PS (1.25 μm, 2–8 mg L^{-1}; 1–5 μm, 4.5 mg L^{-1}) MP-exposed *D. magna* (Canniff & Hoang 2018, Gorokhova et al. 2018, Tang et al. 2019). Similarly, unknown types of MPs did not cause any clear mortality in *D. magna* (1–5 μm) (0.1 mg L^{-1}; 12.86 mg L^{-1}) (Martins & Guilhermino 2018, Gerdes et al. 2019). All the groups generally attained over 90% survival in these studies (Figure 1A,B). However, some studies found elevated mortality, although these increases were relatively minor. For example, mortality only increased slightly (less than 30%) in unknown plastic type (30%; 1–5 μm; 2 mg L^{-1}) and PS (26%; 1–5 μm; 0.65 mg L^{-1}) exposed *D. magna* (Puranen Vasilakis 2017, Pacheco et al. 2018) (Figure 1A). These results highlight that the presence of food might effectively offset the negative effects of MP. This is further supported by the study of Aljaibachi & Callaghan (2018), who found that low food concentration, not MP ingestion, was the main cause of mortality.

(2) *MP shape*: In contrast to spherical MPs, irregular-shaped MPs (fragments and fibres) significantly reduced the survival of MP-exposed animals. There was, however, variation among studies. Some studies showed that irregular-shaped MPs had higher toxicity than spherical. For example, survival was lower in daphnids (*D. magna*) exposed to irregularly shaped MP (2.6 ± 1.8 μm, 1.19 mg L^{-1}; 0.8 day survival) compared to controls (2.9 day survival) and spherical MP-exposed animals (2.4 day survival) (Ogonowski et al. 2016). Frydkjær et al. (2017) observed only 12%–40% survival (95% in control) after exposure to PE fragmented MPs (*D. magna*; 10–75 μm; 10–5000 mg L^{-1}). Similarly, PET microfibres (60–1400 μm, 12.5–100 mg L^{-1}; 100–400 μm; 0.13–0.24 mg L^{-1}) also decreased survival by 10%–100% in *D. magna* and *Ceriodaphnia dubia* (Jemec et al. 2016, Ziajahromi et al. 2017). The decreased survival observed in these studies led to a high percentage decrease in survival observed in all three size classes of MPs (Figure 1A–C). The

decreased survival could be explained by the formation of aggregates of MP which might cause internal damage during gut passage or interfere with swimming in MP-exposed animals. In contrast, Kokalj et al. (2018) found no clear effect of MP fragments and fibres on daphnids. Neither spherical nor irregular MPs (including fragment and fibre) (PE and PET; 63.05–264 μm; 100 mg L^{-1}) resulted in any mortality (0%) in *D. magna* (Kokalj et al. 2018). Since the size and types of MPs were similar among these studies, the discrepancies might be explained by other factors such as morphological characters which could affect the toxicity of MPs as well.

(3) *Species: C. dubia* appeared to be more sensitive to MP pollution than the model species *D. magna*. Acute exposure (48 hours) to PE MPs (1−4 μm) and PET fibres (100−400 μm) decreased *C. dubia* survival by 10%–100%. No survival (0%) was observed at low MP concentrations, over 0.24 and 8.04 mg L^{-1} for fibres and beads, respectively (Ziajahromi et al. 2017). Similar sizes and concentrations of MPs have never been documented to cause 0% survival in *D. magna*, suggesting that the MPs' toxicity is species specific and that *C. dubia* is more sensitive than *D. magna*. This species-specific sensitivity caused the non-concentration dependent trend in Figure 1C. The data on MPs $>$100 μm at concentrations $\leq$10 mg L^{-1} were calculated from the study by Ziajahromi et al. (2017), which used *C. dubia* as a model species, whereas all data at concentrations $>$10 mg L^{-1} came from studies using *D. magna* (Jemec et al. 2016, Rehse et al. 2016). Thus, the high sensitivity of *C. dubia* peaked the percentage change to nearly 100% at $>$1–10 mg L^{-1}, and then the percentage change decreased afterward because of the high resistance of *D. magna*. However, the number of studies is still small, so further investigations are needed before drawing a strong conclusion.

Microplastic-chemical interactions Leachates derived from MPs may have toxic chemicals and can be a hazard to biota. However, 100% survival was observed when *D. magna* were exposed to leachates derived from PET fibres (60–1400 μm; 12.5–100 mg L^{-1}) (Jemec et al. 2016). These chemicals may have been at a level too low to cause observable impacts. Moreover, it has been suggested that MPs would concentrate hydrophobic chemicals from the environments and have detrimental effects on biota. However, this hypothesis is currently under debate. Some studies found that MPs and chemicals have synergistic effects. Frydkjær et al. (2017) found that irregular PE MPs (10–75 μm) were a good vector for phenanthrene (Phe) and adding MPs (EC_{50}: 0.14 mg L^{-1}) was more toxic than adding the same concentration of Phe (EC_{50}: 0.47 mg L^{-1}). In contrast, other studies showed that MP did not increase the toxicity of chemicals. Co-exposure to PS MPs and pesticides (dimethoate and deltamethrin) neither increased nor decreased the toxicity of the two pesticides. The probabilities of normal mobility for *D. magna* were similar between treatments with or without MP (0.57 and 0.2 for dimethoate and deltamethrin, respectively) (Horton et al. 2018). Exposure to PS MPs and Phe (5, 10 and 15 μm; 2.5–50 mg L^{-1}) did not decrease *D. magna* survival (Ma et al. 2016). The EC_{50} of Phe (0.59 ± 0.05 mg L^{-1}) did not shift significantly in the presence of MPs (0.66 mg L^{-1}). In some cases, MP presence even lowered the toxicity of contaminants. Treatments with bisphenol A (BPA) and the addition of PA MPs (15–20 μm; 200 mg L^{-1}) reduced immobilisation by 20% compared to daphnids that were treated with BPA alone (Rehse et al. 2018). Adding 1 mg L^{-1} of PS MPs (0.1 μm) increased *D. magna* survival by 45% compared to those that were exposed to the same concentration of polychlorinated biphenyl (PCB)-18 (640 μg L^{-1}) (Lin et al. 2019). The toxicity of nickel (Ni; EC_{50} 3.85 mg L^{-1}) was lower when PS MPs (0.19 μm) were presented in combination with Ni (EC_{50} 17.72 mg L^{-1}) (Kim et al. 2017). These studies suggest that the toxicity of chemicals might decrease when co-exposed with MPs. Since toxicity largely depends on both the type of polymer and the interacting chemicals, more studies are needed to assess the interactive effects on various polymers and chemicals.

Transgenerational effect Although MPs did not affect survival in the *D. magna* F_0 generation, continuous MP exposure to the F_1 generation had transgenerational effects on their offspring (Figure 2A). Decreased survival was observed in F_1 offspring if they were continually exposed to MPs.

No survival (0%) was even found in the first brood of F_1 offspring, with all offspring rapidly dying within 1–4 days of MP exposure (1–5 µm; 0.1 mg L^{-1}). Even the survival rate of the third brood of F_1 offspring decreased by 20% compared to controls (Martins & Guilhermino 2018). Bosker et al. (2019) also found that after 21 days of PS MP exposure (1–5 µm; 4.69 mg L^{-1}), the population size of *D. magna* significantly decreased by 26% compared to that of the control. These studies suggest that long-term exposure to MPs across generations might drastically decrease *D. magna* populations.

If the F_1 offspring were no longer exposed to MPs, however, survival appeared to recover with time, with 100% survival observed in F_1 and the subsequent generations (F_2 and F_3) if they were moved to clean water immediately after birth (*D. magna*) (Martins & Guilhermino 2018). Similarly, offspring survival rates were generally over 90% in all treatments in other studies (Ogonowski et al. 2016, Aljaibachi & Callaghan 2018). These studies suggest that negative transgenerational effects of MPs can be offset with enough recovery time, although some sublethal effects will still last for several generations (see 'Development and growth' and 'Reproduction' in the present review).

Brine shrimp

Larvae Brine shrimp larvae appeared to be highly tolerant to MPs. No significant change in survival was observed in any of the studies, regardless of the size, shape or type of MP used (Figure 1A,C). Short-term exposure to spherical (PS; 1 and 9.9 µm; 0.1 mg L^{-1}), irregular and fibre MPs (PE and PET; 100–300 µm; 100 mg L^{-1}) did not affect survival (100%) in nauplius larvae of *Artemia franciscana* and an unknown *Artemia* sp. (Katzenberger 2015, Kokalj et al. 2018). Similarly, 100% survival was observed in PS MP-exposed *A. franciscana* (0.1 µm; 0.001–10 mg L^{-1}) (Gambardella et al. 2017). Even prolonged exposure to PS MPs (10 µm; 0.00055–5.54 mg L^{-1}) over 10 days had no significant impact on nauplii survival (100%) of *Artemia parthenogenetica* (Wang et al. 2019).

Adults Survival of adult *A. franciscana* was not affected by 1–5 µm MPs (0.4–1.6 mg L^{-1}) at any tested concentrations after 44 days of exposure (Peixoto et al. 2019). The percentage decreases in survival were lower than 5% at all the concentrations tested, suggesting that brine shrimp are quite resistant to MPs (Figure 1A).

Microplastic-chemical interactions Chemical-coated MPs also did not have any observable impact on brine shrimp larvae. PS MPs (1 and 9.9 µm; 0.1 mg L^{-1}) coated with bisphenol A did not affect survival of *Artemia* sp. after 24 hours of exposure (Katzenberger 2015). *Artemia* sp. nauplii take up and store benzo[a]pyrene (BaP) in yolk droplets when being exposed to BaP-spiked PE MPs (1–5 and 10–20 µm), suggesting that MP could function as a vector for transferring BaP (Batel et al. 2016). However, the study did not evaluate the potential toxicological effects of BaPs on *Artemia* sp. nauplii. Sinche (2010) studied the interaction between PS MP and phenol. The LC_{50} values of adult *Artemia* in the PS MP (3 µm; 100–300 mg L^{-1}) addition group (102.9 mg L^{-1}) were greater than those in the group without MPs (90.90 mg L^{-1}), suggesting that phenol toxicity decreased when MPs were present in the solutions. Sinche (2010) suspected that MP could uptake phenol present in the organism's gut, making the phenol less available to the animal and therefore lowering the toxicity.

Euphausids

MPs of size >10–100 µm do not seem to affect adult euphausid survival, with 100% survival observed in both short-term (24 hours) and long-term (10 days) PE MP-exposure (*Euphausia superba*) at all concentrations tested (27–32 µm; 0.042–1.68 mg L^{-1}) (Dawson et al. 2018a,b) (Figure 1B).

Rotifers

MPs (0.1–10 µm) did not have an observable lethal effect on rotifers (Figure 1A). No significant effect was observed on survival in 0.1 µm PS MP-exposed rotifers (*Brachionus plicatilis*) at any concentrations tested (0.01–10 mg L^{-1}) after 24 and 48 hours of exposure (Gambardella et al. 2018);

all treatments had survival >95%. Similarly, exposure to 4–6 μm PE MP did not have any significant effect on *B. plicatilis*, although 1–4 μm PE MP slightly decreased survival of *B. plicatilis* at 1 mg L^{-1} (LOEC = 1) (Beiras et al. 2018). In contrast, the lifespans of *Brachionus koreanus* exposed to high concentrations of 0.5 μm PS MPs (1, 10 and 20 mg L^{-1}) were shorter by ~1.6 days compared to controls. Population size of *B. koreanus* was largely reduced by ~8%–62% after 12 days of exposure (Jeong et al. 2016). However, lifespan was not included in percentage change analysis.

Microplastic-chemical interactions Benzophenone-3–spiked PE MPs proved to have no toxicity in copepod, mussel and sea urchin larvae (Beiras et al. 2018). Similarly, no significant effect was found on survival in BP-3 coated MP-exposed (0.01–10 mg L^{-1}) rotifers (*B. plicatilis*) at any of the BP-3 concentrations tested (0.2 and 20 μg L^{-1}) (LOEC >10 mg L^{-1}) (Beiras et al. 2018).

Meroplankton

Fishes

Embryos The survival rate of fish embryos appeared to be unaffected by virgin MPs (>10–100 μm) (Figure 1E). The hatching success of zebrafish embryos (*Danio rerio*) was not impacted, even when exposed to high concentrations of PE MPs (10–45 μm; 5 and 20 mg L^{-1}). All the treatments and controls reached nearly 100% hatching success after 5 days of MP exposure (LeMoine et al. 2018).

Larvae MPs had no detrimental effect on fish larvae regardless of the species tested. The percentage decrease in survival was <10% in all three size classes of MPs (Figure 1D–F). Exposure to virgin MPs did not reduce survival in the larval stages of zebrafish (*D. rerio*; PS, 45 μm, 1 mg L^{-1}), Japanese rice fish (*Oryzias latipes*; PE, 4–6 μm, 1–10 mg L^{-1}), fathead minnows (*Pimephales promelas*; PE, 212–500 μm, 0.07–140 mg L^{-1}), sheepshead minnows (*Cyprinodon variegatus*; PE, 150–180 μm, 250 mg L^{-1}) or three-spine stickleback (*Gasterosteus aculeatus*; PS, 1 and 9.9 μm, 5.3–530 mg L^{-1}) (Katzenberger 2015, Chen et al. 2017, Beiras et al. 2018, Choi et al. 2018, Malinich et al. 2018). Irregularly shaped MPs did not affect survival of MP-exposed larvae either. The survival rate of zebrafish (*D. rerio*; low-density polyethylene (LDPE) 0–18 μm, 0.500 mg L^{-1}), silver barb (*Barbodes gonionotus*; PVC, 40–300 μm, 1.0 mg L^{-1}) and sheepshead minnow (*Cyprinodon variegatus*; PE, 6–350 μm, 250 mg L^{-1}) larvae were not impacted by fragmented MPs (Karami et al. 2017, Choi et al. 2018, Romano et al. 2018). Both MP-treated and control groups in these studies reached over 70% survival. These results suggest that virgin MPs rarely have lethal impacts on fish larvae, regardless of the MPs' size, shape, polymer type and concentration used (Figure 1D–F).

One exception is larvae of the European sea bass (*Dicentrarchus labrax*), where the survival rate was 13% lower in the PE MP-treated group (<45 μm; 12 mg per gram of diet) than that of the control (Mazurais et al. 2015). The accumulation of MP debris observed in the gastrointestinal tract of dead larvae might be the reason mortality increased, suggesting that European sea bass might be more vulnerable to MP pollution than other species. The concentration unit used in Mazurais et al. (2015) was mass (mg) per gram of diet and cannot be transformed to the unit used in present study (mg L^{-1}); thus, their results were not included in the percentage change analysis.

Microplastic-chemical interactions As for the interaction between MPs and chemicals, the toxicity is largely dependent on the incorporated chemicals. Exposure to PE MPs (4–6 μm; 10 mg L^{-1}) coated with 0.2 and 20 μg L^{-1} BP-3 decreased embryonic survival to 82% and 42%, respectively (compared to 90% in controls), and reduced the hatching rate by 12% and 52% in Japanese rice fish embryos (*Oryzias melastigma*), respectively (Beiras et al. 2018). The decreased survival can be explained by the toxicity of BP-3 and long exposure time (14 days). In addition, three-spine stickleback larvae (*G. aculeatus*) fed with *Artemia* sp. previously exposed to 9.9 μm

PS MPs and a high concentration of bisphenol A (3200 µg L^{-1}) had a 78% survival rate compared to 100% in controls, whereas the same concentration of BPA had no clear effects (Katzenberger 2015). In contrast, exposure to BaP-coated PE MPs (BaP: 10 mM; MP: 1–5 and 10–20 µm) did not result in any lethal effect in zebrafish embryos (*D. rerio*) (Batel et al. 2018), although there was evidence that BaP moved into the fish tissue. It may be that the BaP transferred to embryos was too low to be lethal. Co-exposure to PS MPs (1 mg L^{-1}) and EE2 (2 and 20 µg L^{-1}) did not affect zebrafish (*D. rerio*) survival (Chen et al. 2017). These results suggest that the combined effect of MP and chemical might be more detrimental than either MPs or chemicals alone, but the toxicity level depends on the chemicals incorporated.

Sea urchins

Gametes Virgin MPs of size 0.1–10 µm decreased sea urchin gamete survival (Figure 1D). Decreases in fertilisation success by 42%–30% were observed in PS MP-exposed (6 µm; 0.12–12 mg L^{-1}) sea urchin gametes (*Paracentrotus lividus*), suggesting that MP exposure interfered with the fertilisation process (Martínez-Gómez et al. 2017).

Larvae Sea urchin embryos develop into free-swimming and ciliated larvae called pluteus larvae, which start to feed 36–48 hours post fertilisation (hpf). In *Tripneustes gratilla* larvae, exposure to virgin 10−45 µm PE MPs at 300 beads mL^{-1} (3.46 mg L^{-1}) decreased survival rate by ~40%, although it was not significant (0.012–1.2 mg L^{-1}) (Kaposi et al. 2014) (Figure 1E). In contrast, in *P. lividus*, the survival in both MP and control treatments generally reached 90% at all concentrations tested after exposure to 0.1 µm PS MPs (0.01–10 mg L^{-1}; 24 hours) (Gambardella et al. 2018). Similarly, no significant difference was found in *P. lividus* survival rates between 10 µm PS MPs (0.125–25 mg L^{-1}) and the control treatments after 72 hours of exposure (Messinetti et al. 2018). Moreover, various sizes of PS MPs (4–6, 11–13, 11–15, <40 µm; 1–100 mg L^{-1}) did not induce severe lethality in *P. lividus* (LOEC ≥100 mg L^{-1}) (Beiras et al. 2018), but only LOEC values were reported, so this study was not included in the percentage change analysis. These studies suggest that the larval stage of *T. gratilla* might be relatively more sensitive to MPs than that of *P. lividus*. Due to the variation among studies, the mean percentage decrease in survival did not exceed 20% at any concentration tested (Figure 1D).

Microplastic-chemical interactions All the toxicity studies reviewed here used the sea urchin *P. lividus* as a model organism, with the majority of the studies finding no clear impacts. PE MPs (4–40 µm, 1 and 10 mg L^{-1}) spiked with the toxic chemical benzophenone-3 did not reduce embryo survival, despite the high concentrations of BP-3 used in the study (LOEC higher than 10 mg L^{-1}, MPs coated with 20 µg L^{-1} BP-3) (Beiras et al. 2018). PS MPs did not increase toxicity of 4-n-nonylphenol (NP), either. The EC_{50} of neither starved nor fed *P. lividus* larvae were significantly affected by the addition of MPs (1 and 10 mg L^{-1}; 67.6–83.7, 158.8–171.1 µg L^{-1}) compared to treatments without MPs (64.3, 190.9 µg L^{-1}) (Beiras & Tato 2019). These studies indicate that the chemical-coated MPs tested had no detrimental lethal impacts on the early stages of sea urchin *P. lividus*.

Bivalves

Gametes MPs of size 0.1–10 µm had limited effects on the gametal stage of bivalves (Figure 1D). The fertilisation rates were all over 90% in both 2 µm and 0.5 µm PS MP (0.1–25 mg L^{-1}) treated oyster gametes (*Crassostrea gigas*), except for animals that were treated with 0.5 µm MPs at 25 mg L^{-1} (~86%) (Tallec et al. 2018).

Larvae Exposure to PS MPs (1–4, 4–6, 6–8.5, 11–13, <40 µm; 20–100 mg L^{-1}) did not affect the survival of the mussel *Mytilus galloprovincialis*. The LOEC of these MP sizes was generally higher than 100 mg L^{-1} (Beiras et al. 2018); however, since they only reported LOEC, this study was not included in the percentage change analysis. Although Cole & Galloway (2015) found no effect of MPs on oyster larvae (*C. gigas*) metamorphosis (1 and 10 μm; 0.001–0.06 mg L^{-1}), but they did not report mortality. A high proportion of *C. gigas* larvae still successfully underwent metamorphosis (over 86%) when exposed to high concentrations of PS MPs (2 μm; 0.1–25 mg L^{-1}) (Tallec et al. 2018) (Figure 1D). However, the lack of a clear effect might be related to short exposure time in this study (24 hours). Overall, early stages of bivalves are quite resistant to MPs of size 0.1–10 μm. The percentage change in survival was lower than 5% for all concentrations tested (Figure 1D). No study was found for >10–100 and >100 μm MPs; thus, no data are included for these size classes.

Microplastic-chemical interactions Combined effects of MPs and chemicals seem to be species specific. Neither carboxylic- (COOH) nor amino- (NH_2) coated PS MPs affected the survival of oyster gametes (*C. gigas*). No significant difference was found in the percentage of dead gametes of *C. gigas* (oocytes and spermatozoa) after 5 hours of exposure to 0.1 μm PS-COOH and PS-NH_2 MPs (0.1–10 mg L^{-1}) (González-Fernández et al. 2018). In the mussel *M. galloprovincialis*, BP-3–spiked PE MPs (4–6, 11–13 μm) did not decrease their larval survival. The LOEC was >10 mg L^{-1} in both low and high BP-3–coated MP treatments (0.2 and 20 μg L^{-1}) (Beiras et al. 2018). In contrast, PS-COOH and PS-NH_2 MPs (0.15–0.2 μm; 0.02–2 mg L^{-1}) significantly decreased embryonic hatching rate and larval metamorphosis rate by 5.79%–39.5% and 4.46%–43.2%, respectively, in the clam *Meretrix meretrix* (Luan et al. 2019).

Transgenerational effect MPs have a clear transgenerational effect on the survival of F_1 oyster larvae (Figure 2A). The survival of D-larvae produced by MP-exposed female oysters (*C. gigas*) (29.6 ± 0.3%) was significantly lower compared to that of the control animals (49.8 ± 1.6%). The decrease in larval quality might be explained by the reduction in sperm and oocyte quality observed in parental generation (Sussarellu et al. 2016).

Gastropods

Larvae Like in bivalves, gastropod larval survival was unaffected by 0.1–10 μm MPs (Figure 1D). Exposure to PS MPs (2–5 μm; 0.0002–3.33 mg L^{-1}) did not increase larval mortality in the slipper limpet, *Crepidula onyx*. The mortality rate was similar between controls (~1 individual day^{-1}) and MP treatments (~1.5 individuals day^{-1}) (Lo & Chan 2018), suggesting that MPs have limited lethal effects on mollusc larvae. There were no studies using >10–100 and >100 μm MPs, so no data were present on these size classes.

Barnacles

Nauplius and cypris larvae Both the naupliar and cypris stages of barnacle larvae were resistant to 0.1–10 μm MPs, with a calculated percentage change in survival lower than 10% at all concentrations tested (Figure 1D). The survival of *Amphibalanus amphitrite* stage II naupliar larvae reached over 90% after exposure to 0.1 μm PS and polymethyl methacrylate (PMMA)MPs for 48 and 24 hours (0.001–10 mg L^{-1}; 5–25 ppm) (Gambardella et al. 2017, Bhargava et al. 2018). Moreover, metamorphosis of *A. amphitrite* cypris larvae appeared to be unaffected by the presence of PMMA MPs (0.18 μm; 1–25 ppm) either (Bhargava et al. 2018), but percentage of metamorphosis was not quantified in this study. Overall, these studies suggest that barnacle larvae are quite resistant to MPs (0.1–10 μm).

Decapods

Larvae Larvae of the grass shrimp *Palaemonetes pugio* tended to be relatively sensitive to PE MPs. Exposure to 38 and 59 μm PE MPs (1–0.01 mg L^{-1}; 0.05–0.0005 mg L^{-1}) decreased survival by ~30%, while 100% survival was observed in the control (Weinstein 2015). The higher sensitivity of grass shrimp larvae resulted in decreased percentage change at 0–1 mg L^{-1} observed in Figure 1E.

Ascidians

Embryos Survival of early developmental stages of ascidians were unaffected by MPs. The survival of 1 and 10 μm PS MP-exposed (0.125–25 mg L^{-1}) ascidian embryos (*Ciona robusta*) reached over 80% in all MP treatments and the control after 18 hours of exposure (from two cells to larval stage) (Messinetti et al. 2018, 2019) (Figure 1D).

Larvae The survival from larval stage to stage four juveniles also did not significantly differ between 1 and 10 μm PS MP treatments (0.125–25 mg L^{-1}) and the control in ascidian larvae (*C. robusta*). Survival was generally higher than 90% in all treatment groups (Messinetti et al. 2018, Messinetti et al. 2019) (Figure 1D).

Comparing the effect of microplastic on survival among zooplankton groups under environmentally relevant and high laboratory concentrations

MPs of size 0.1–10 μm have been the most studied in relation to survival of zooplankton. The mean percentage decrease in survival for all zooplankton groups is <20% upon exposure to 0.1–10 μm MPs at 0–1 mg L^{-1} (environmentally relevant concentration) (Figure 1A,D). Comparing all the zooplankton groups examined, sea urchins and daphnids are more susceptible to mortality, suggesting that these organisms might be the more sensitive to 0.1–10 μm MPs. Especially daphnids suffered over 50% decrease in survival at concentrations >10 mg L^{-1} (Figure 1A). However, these detrimental effects are only observed at very high concentrations (>1 mg L^{-1}). In contrast, the percentage decrease in survival for bivalves, gastropod, barnacles, brine shrimp, euphausid, fishes, rotifers and ascidians is generally <10% at both environmental and laboratory concentrations (Figure 1A,D), suggesting that these groups are relatively tolerant to MPs. Similarly, for MPs of size >10–100 μm, there is a trend that sea urchins and daphnids are more sensitive than others at laboratory concentrations (>1 mg L^{-1}) but not at environmental concentrations (0–1 mg L^{-1}) (Figure 1B,E). Decapod larvae show high sensitivity as well, although this again appears to be species specific (Figure 1E). As for MPs >100 μm, daphnids are the most susceptible group, with decreases in survival observed at both environmental and laboratory concentrations (Figure 1C,F). But the number of studies on this size class is relatively small for zooplankton, presumably given these are on the upper size spectra of what can be consumed by organisms of this size. Overall, MPs did not induce severe mortality to all the zooplankton groups at environmentally relevant concentrations (0–1 mg L^{-1}), suggesting that lethal effects would rarely occur under natural conditions. Of all the groups examined, sea urchins, daphnids and shrimp larvae are the most affected groups in zooplankton, while molluscs and other crustaceans – including copepods, barnacles, brine shrimp and euphausids – show high survival when exposed to MPs regardless of size.

The combined effects of MPs and chemicals could either enhance or decrease toxicity. We observed that interactive effects are complex and depend on both polymer type and the chemicals' properties. Due to the small number of studies, it is difficult to compare which zooplankton groups are more tolerant at this stage. In addition, decreases in survival were observed in the offspring produced by MP-exposed copepods, bivalves and daphnids, suggesting that MPs might have transgenerational effects and potentially affect zooplankton populations in the long term (Figure 2A). This may be the case because of the additives and monomers leached from virgin MPs. Cole et al. (2019) detected several additive chemicals such as stabilisers, lubricants and by-products incorporated in virgin nylon MPs used in MP toxicity studies. Long-term exposure to small quantities of the additives and monomers leached from virgin MPs might cause health impacts such as disrupting endocrine chemicals on exposed zooplankton (Cole et al. 2019). Their study suggests that observed health effects not only stem from the physical properties of MPs but also the chemicals present in the polymer matrix.

Development and growth

Holoplankton

Copepods

MPs of size 0.1–10 μm did not severely delay the development time from nauplii to matured adults in copepods (Figure 3A). Neither the Calanoida nor Harpacticoida studied suffered developmental impacts. Development time of *Tigriopus japonicus* (Harpacticoida) from nauplius to matured adult (~15.2 days) was not significantly different to controls (~15 days) after exposure to a very high concentration (25 mg L^{-1}) of 0.5 and 6 μm PS MPs (Lee et al. 2013). Similarly, a calanoid copepod's (*Paracyclopina nana*) development time (~10.8 days) did not differ from those of controls (~11.8 days) after being exposed to the same size of PS MPs (0.5 and 6 μm; 20 mg L^{-1}) (Jeong et al. 2017). In contrast, Cole et al. (2019) found that juvenile copepod (*Calanus helgolandicus*) exposed to nylon fibres (10 × 30 μm, 0.14 mg L^{-1}) and granules (10–30 μm, 0.24 mg L^{-1}) moulted significantly earlier

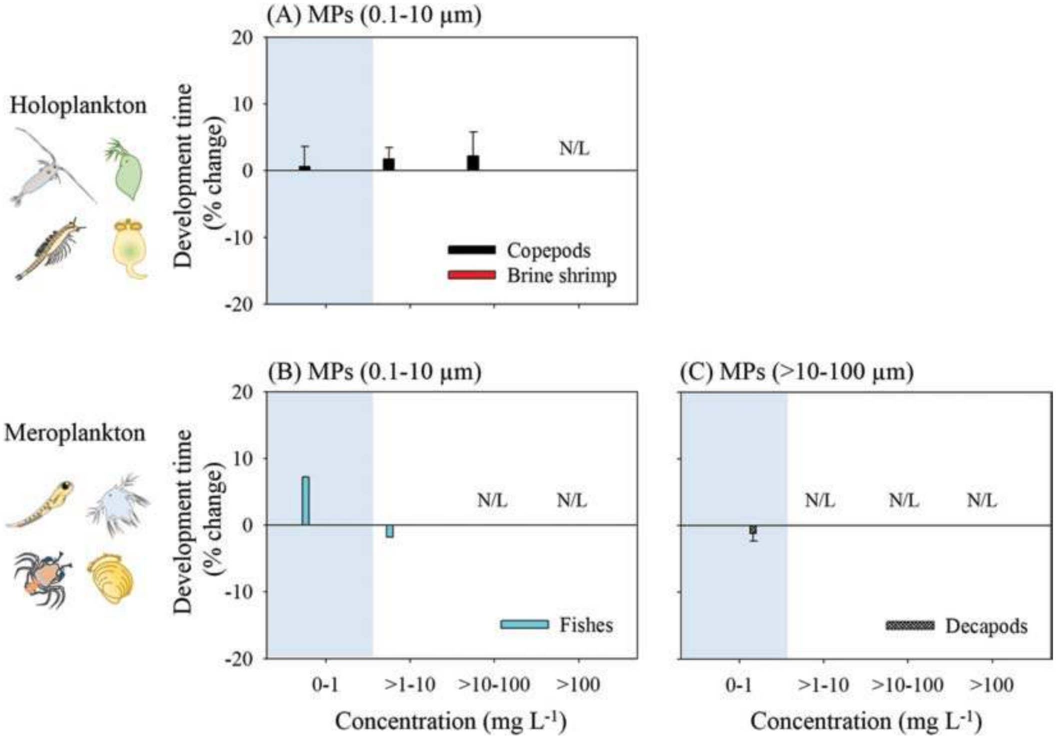

Figure 3 Percentage change in development time (mean + 1SD %) of (A) holoplankton and (B, C) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A3. A negative percentage change means a decrease amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for daphnids, euphausids and rotifers at all concentrations, except for copepods (>10^2 mg L^{-1}) and brine shrimp (>10 mg L^{-1}). No data are available for holoplankton for MPs of size >10–100 μm and >100 μm. In figure (B), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>10 mg L^{-1}). In figure (C), no data are available for fishes, urchins, bivalves, gastropods, barnacles and ascidians at all concentrations, except for decapods (>1 mg L^{-1}). No data are available for meroplankton for MPs >100 μm. Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear in the environment at the moment. N/L = no data available.

than copepods in the control treatment. The premature moulting might relate to compounds detected in nylon MPs which could cause endocrine disruption (Cole et al. 2019). This study did not, however, mention the exact development time of copepods and was thus was not included in percentage change analysis. For MPs' effects on growth, prosome length of *Calanus finmarchicus* juveniles, adult males and females was not significantly affected after being exposed to nylon granules (10–30 μm, 0.24 mg L^{-1}) and fibres (10 × 30 μm, 0.14 mg L^{-1}) (Cole et al. 2019) (Figure 4B).

Transgenerational effect MPs have transgenerational effects on growth as well (Figure 2B). Cole et al. (2015) found that PS MP-exposed (20 μm; 0.33 mg L^{-1}) *C. helgolandicus* produced significantly smaller eggs than those of the control after four (MP: 180.4 μm; control: 185.1 μm) and six days (MP: 179.5 μm; control: 183.4 μm) of exposure, but the effect was relatively mild, and thus the calculated percentage decrease was low (Figure 2B).

Even though there was no apparent impact observed in the F_0 generation, a significant developmental delay in the F_1 generation was found in 0.5 μm PS MP-treated copepods, although this only occurred at high MP concentrations (Figure 2C). Development time of 25 mg L^{-1} MP-treated copepods was ∼17.5 days, compared to only ∼14.5 days in controls, suggesting that MPs could affect

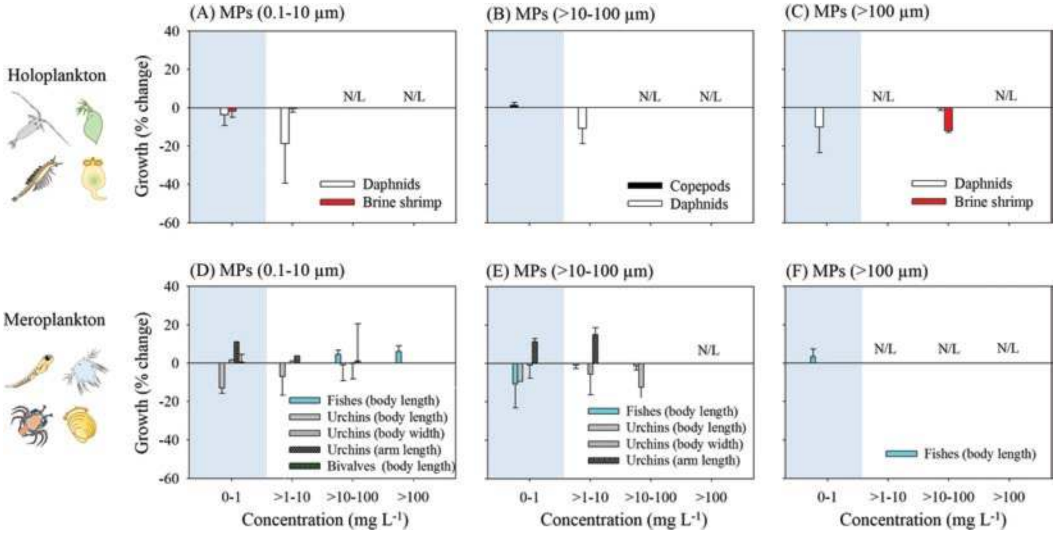

Figure 4 Percentage change in growth (body length, body width, arm length) (mean + 1SD %) of (A–C) holoplankton and (D–F) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A4. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for copepods, rotifers and euphausids at all concentrations, except for daphnids (>10 mg L^{-1}) and brine shrimp (>10 mg L^{-1}). In figure (B), no data are available for brine shrimp, euphausids and rotifers at all concentrations, except for daphnids (0–1, >10 mg L^{-1}) and copepods (>1 mg L^{-1}). In figure (C), no data are available for copepods, euphausids and rotifers at all concentrations, except for daphnids (>1–10, >10^2 mg L^{-1}) and brine shrimp (0–10, >10^2 mg L^{-1}). In figure (D), no data are available for fishes (0–10 mg L^{-1}), urchins (body length, body width and arm length) (>10^2 mg L^{-1}), bivalves (>1 mg L^{-1}) and gastropods, barnacles, decapods and ascidians at all concentrations. In figure (E), no data are available for fishes (>10^2 mg L^{-1}), urchins (body length) (>1–10, >10^2 mg L^{-1}), urchins (body width and arm length) (>10 mg L^{-1}) and bivalves, gastropods, barnacles, decapods and ascidians at all concentrations. In figure (F), no data are available for urchins (body length, body width and arm length), bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>1 mg L^{-1}). Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear in the environment at the moment. N/L = no data available.

naupliar development time across generations (Lee et al. 2013). However, no clear transgenerational effect was observed in copepods exposed to 6 μm PS MPs in the same study (Lee et al. 2013). Due to the variation between sizes, the mean percentage increase was lower than 10% (Figure 2C). This result highlights that the adverse impacts of MP exposure could extend to the offspring of MP-exposed parents and could potentially last for several generations.

Daphnids

Most of the studies showed that MPs of size 0.1–100 μm had no significant impact on *Daphnia magna* body length. For instance, polymers including PE (1–10 μm), PS (1–5 μm; 0.0046–4.6 mg L^{-1}; 19.8 μm, 2.1–9.2 mg L^{-1}), PLA (1–4 μm), unknown type of MPs (1–5 μm, 0.2–2.0 mg L^{-1}; 12.86 mg L^{-1}; 0.001–1 mg L^{-1}) and plastic mixture (PA + PC + PET + PVC, ABS + fPVC + POM + SAN) did not affect body length of *D. magna* and *D. pulex* (Imhof et al. 2017, Puranen Vasilakis 2017, Aljaibachi & Callaghan 2018, Pacheco et al. 2018, Martins & Guilhermino 2018, Bosker et al. 2019, Colomer et al. 2019, Gerdes et al. 2019, Jaikumar et al. 2019) (Figure 4A,B). Similarly, large-sized fragmented (PE, 102.9–264 μm, 100 mg L^{-1}) and fibre MPs (PET, 60–1400 μm, 12.5–100 mg L^{-1}) had no clear effect on *D. magna* body length (Jemec et al. 2016, Kokalj et al. 2018) (Figure 4C). Body length in these studies was generally reduced by less than 10% compared to the controls, suggesting that none of the three size classes of MPs have a severe impact on *D. magna* body length. However, *Ceriodaphnia dubia* suffered from growth retardation by ~11%–33% after exposure to unknown (1–5 μm; 1 mg L^{-1}), PE MPs (1−4 μm; 0.06–2 mg L^{-1}) and PET fibres (100−400 μm; 0.03–1 mg L^{-1}) (Ziajahromi et al. 2017, Jaikumar et al. 2019). Apart from reduced growth, several abnormalities such as deformed carapaces and abnormal-shape seta were also observed in *C. dubia* (Ziajahromi et al. 2017). The higher sensitivity of *C. dubia* largely contributed to the percentage decreases in body length observed in our analyses (Figure 4A,C). In contrast, body weight appears to be relatively sensitive to MPs (Figure 5A). Studies by Ogonowski et al. (2016) and Tang et al. (2019) found that *D. magna* exposed to unknown type (1–5 μm; 0.0018–1.8 mg L^{-1}) and PS MPs (1.25 μm; 4–8 mg L^{-1}) suffered from growth retardation by ~4%–44% compared to controls. The low percentage change in body weight at >10–100 mg L^{-1} (Figure 5A) is predominantly due to the small number of studies at high concentrations.

As for development time, exposure to both 0.1 and 2 μm PS MPs (0.1–1 mg L^{-1}) did not affect the number of moults (eight) compared to the control (eight) (Rist et al. 2017), suggesting that the development time of *D. magna* was not impacted by MPs. Since the exact development time was not evaluated in this study (Rist et al. 2017), their data were not included in percentage change analysis.

Microplastic-chemical interactions Adding MPs (1–5 μm) to PCB-contaminated *D. magna* (MP + PCB: 0.31 mg; PCB: 0.305 mg) did not significantly affect the organism's dry weight (Gerdes et al. 2019). However, the toxicity level tested in these studies might not have been high enough to induce observable growth effects.

Transgenerational effect MPs have relatively mild transgenerational effects on the growth of the daphnid F_1 generation (Figure 2B). No significant impact on the body length of *D. magna* offspring was observed after exposure to spherical (unknown type, 1–5 μm; PE, 1–4 μm) and irregular-shaped MPs (unknown type, 2.6 ± 1.8 μm; PET, 100–400 μm) (Ogonowski et al. 2016, Ziajahromi et al. 2017). In contrast, Martins & Guilhermino (2018) found that the F_1 generation of *D. magna* suffered from reduced body length by ~7% and even the F_2 and F_3 were still 4% less than the control. Imhof et al. (2017) also found some subtle effects such as reduced body width and increased tail spine length in offspring produced by MP-exposed adults (*D. magna*). These effects are relatively subtle, however, with a mean percentage decrease of less than 5% (Figure 2B). Changes in body size and alterations in tail length of offspring are common anti-predation responses in daphnids. Such defence often occurred when predators were present but was expressed after exposure to MPs (Imhof et al.

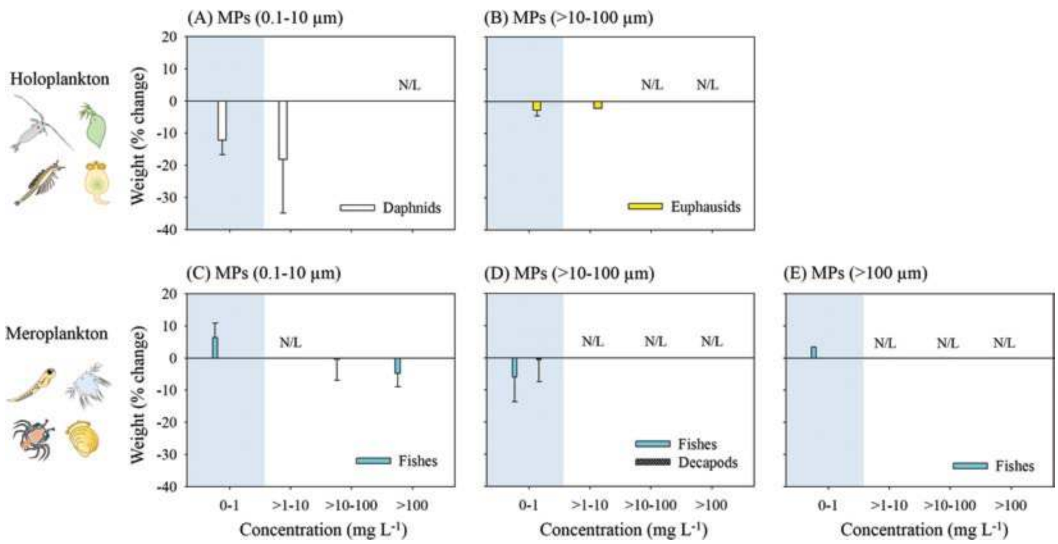

Figure 5 Percentage change in growth (body weight) (mean + 1SD %) of (A, B) holoplankton and (C–E) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A5. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for copepods, brine shrimp, euphausids and rotifers at all concentrations, except for daphnids ($>10^2$ mg L^{-1}). In figure (B), no data are available for copepods, daphnids, brine shrimp and rotifers at all concentrations, except for euphausids (>10 mg L^{-1}). No data are available for holoplankton for >10–100 μm MPs. In figure (C), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>1–10 mg L^{-1}). In figure (D), no data are available for urchins, bivalves, gastropods, barnacles and ascidians at all concentrations, except for fishes (>1 mg L^{-1}) and decapods (>1 mg L^{-1}). In figure (E), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>1 mg L^{-1}). Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear in the environment at the moment. N/L = no data available.

2017). This suggests that MPs might have some signals resembling those of predators and thus induce anti-predation responses in daphnids. Nevertheless, it is also possible that these subtle effects are just a natural variation, so further investigation is needed.

Brine shrimp

Larvae Brine shrimp growth was not severely affected by 0.1–10 μm or >100 μm MPs (Figure 4A, C). *Artemia parthenogenetica* body length was not significantly different from the control group after exposure to 10 μm PS MPs (0.00055–5.5 mg L^{-1}) (Wang et al. 2019) (Figure 4A). On the other hand, a small reduction in body length (∼12%) was observed in naupliar larvae of *Artemia franciscana* after exposure to MPs >100 μm (PE and PET; 22.8–264 μm; 100 mg L^{-1}) (Kokalj et al. 2018) (Figure 4C). The reduction in growth might relate to the adhesion of MPs on the carapace of naupliar larvae rather than direct ingestion (Kokalj et al. 2018). The development time of brine shrimp larvae was also not impacted by 0.1–10 μm MPs (Figure 3A). The instar development time of PS MPs (10 μm; 0.00055–5.5 mg L^{-1}) treated *A. parthenogenetica* (10 days) did not significantly differ from that of the control (10 days) (Wang et al. 2019).

Adults Similarly, body length of adult *A. franciscana* was not significantly affected by 1–5 μm MPs (0.4–1.6 mg L^{-1}) after 26 days of exposure (Peixoto et al. 2019) (Figure 4A).

Euphausids

Euphausids (*Euphausia superba*) did not suffer from growth retardation after 10 days of exposure to 27–32 μm MPs (PE; 0.2–1.6 mg L^{-1}). Weight loss was less than 10% for all MP treatments and controls (Dawson et al. 2018a), suggesting that PE MPs have no clear effect on *E. superba*'s growth rate (Figure 5B).

Meroplankton

Fishes

Embryos The development time of Japanese rice fish *Oryzias melastigma* embryos was not affected by 4–6 μm PE MPs (1 and 10 mg L^{-1}). No significant difference was observed in mean hatching time between MP treatments (~11–12 days) and the control (~11 days) (Beiras et al. 2018) (Figure 3B).

Larvae Neither body length nor weight of most of the studied fish species were affected by MPs, regardless of the MP's size, polymer type or concentration tested (Figures 4 & 5). Exposure to virgin MPs did not alter growth rate (both body length and weight) in the larvae of zebrafish (*Danio rerio*; PE, <17.6 μm, 0.005–0.5 mg L^{-1}; PS, 45 μm, 1 mg L^{-1}; PE, 10–45 μm, 5 and 20 mg L^{-1}), fathead minnows (*Pimephales promelas*; PE, 180–212 μm, 0.14 and 0.27 mg L^{-1}) and three-spine stickleback (*Gasterosteus aculeatus*; PS, 1 and 9.9 μm, 10.6–1060 mg L^{-1}) (Katzenberger 2015, Chen et al. 2017, Karami et al. 2017, LeMoine et al. 2018, Malinich et al. 2018). The percentage change was generally <10% in these studies, suggesting that MPs do not substantially affect fish larval growth (Figures 4 & 5). As for normal development, all of the sheepshead minnow larvae (*Cyprinodon variegatus*) exposed to 6–350 μm MPs (PE, 50 and 250 mg L^{-1}) still exhibited normal morphology to the control, suggesting that MPs >100 μm did not affect sheepshead minnow larvae development (Choi et al. 2018).

Microplastic-chemical interactions Some studies have reported growth alterations in fish larvae, while others found no significant impacts when MPs and chemicals were co-exposed. For instance, exposure to field-collected HDPE, LDPE and PS MPs (>2 mm; 1 and 10 mg L^{-1}) led to significant increases in pericardial sack size in zebrafish larvae (*D. rerio*) by around 4–6 μm^2 compared to the control, which might be explained by the toxic chemicals associated with the MPs (Ravit et al. 2017). The length of zebrafish larvae exposed to EE2 (17 α-ethynylestradiol) spiked PS MPs (45 μm, 1 mg L^{-1}) shortened by 4.7% and 6.1% after 120 hours of exposure (Chen et al. 2017). The retarded growth was probably related to the synergistic effects of EE2 and MPs. In contrast, ingestion of food (*Artemia* sp.) previously exposed to BPA-spiked MPs (0.5 and 9.9 μm) did not significantly affect length and weight of stickleback larvae (*G. aculeatus*) (Katzenberger 2015). We suggest that the reason there was no effect of growth might be because BPA was not in direct contact with exposed fish larvae but was instead incorporated into the food (*Artemia* sp.) and thus needed to be digested before the BPA was released. As for development time, exposure to BP-3 (20 μg L^{-1}) spiked PE MPs (10 mg L^{-1}) significantly reduced hatching time in *O. melastigma* embryos (Beiras et al. 2018). Moreover, exposure to BaP-loaded PE MPs (1–5 and 10–20 μm; 1 and 4 mg L^{-1}) did not induce any abnormality in zebrafish (*D. rerio*) embryos, despite a prominent BaP signal detected in the embryos (Batel et al. 2018). Similarly, co-exposure to EE2 and PS MPs (45 μm, 1 mg L^{-1}) did not affect the development of zebrafish (Chen et al. 2017). The level of chemicals transferred to fish larvae in these studies might have been too low to induce observable impacts.

Sea urchins

Embryos Both MPs of size 0.1–10 and >10–100 μm induced malformations in sea urchin embryos such as undeveloped and collapsed embryos or abnormal proliferation of the ectodermal membrane

(Figure 6A,B). The percentage of abnormal embryos significantly increased by 8%–15% after exposure to virgin HDPE (0.1–80 μm; 5–5000 mg L^{-1}) and PS MPs (6 μm, 0.12–12 mg L^{-1}) in *Paracentrotus lividus* (Martínez-Gómez et al. 2017).

Larvae MPs (0.1–100 μm) induce several growth alterations in sea urchin larvae, including reduced body length and width and increased arm length (Figure 4D,E). Both 0.1–10 μm PS MPs (10 and 6 μm) and >10–100 μm HDPE MPs (0.1–80 μm) decreased body length by 2%–15% compared to the control in *P. lividus* larvae (Martínez-Gómez et al. 2017, Messinetti et al. 2018). In contrast, arm length significantly increased by 4%–18% upon exposure to 10 μm (PS, 1.25–25 mg L^{-1}) and 10−45 μm MPs (PE, 0.01–3.46 mg L^{-1}) in *P. lividus* and *Tripneustes gratilla* (Kaposi et al. 2014, Messinetti et al. 2018) (note the positive value in Figure 4D,E indicates increased growth). MPs' effects on body width appear to be relatively mild – the percentage changes were generally lower than 10% at all concentrations tested (Figure 4D,E). Exposure to 10 μm PS MPs (1.25–25 mg L^{-1}) and 10−45 μm PE MPs (0.01–3.46 mg L^{-1}) did not affect body width in *P. lividus* or *T. gratilla*, although body width was significantly reduced by ~13% at 300 beads mL^{-1} (Kaposi et al. 2014, Messinetti et al. 2018). Moreover, the larval volume of *P. lividus* decreased by 8%–30% after exposure to PE MPs (5.5 μm; 1 and 10 mg L^{-1}) (Beiras & Tato 2019), but larval volume was not included in the percentage change analysis. Growth may have been altered because MPs limited the amount of food in the environment. Many sea urchin species exhibited phenotypic plasticity, such as increased ciliary band and post-oral arm lengths, to enhance particle capture efficiency under food-limited conditions (Soars et al. 2009). However, there is currently no direct evidence to suggest that MPs affect the feeding capacity of pluteus larvae. Thus, we suggest that future studies evaluate the effects of MPs on filter feeding in urchin larvae to elucidate its underlying mechanisms.

Microplastic-chemical interactions Growth alterations were also observed when MPs and chemicals are co-exposed to sea urchin larvae. Larval volume often changed when *P. lividus* larvae were exposed to 4-n-nonylphenol and PS MPs (0.1 μm; 1 and 10 mg L^{-1}) (Beiras & Tato 2019). Leachates of virgin PS (6 μm; 0.12–12 mg L^{-1}) and HDPE MPs (0.1–80 μm; 5–5000 mg L^{-1})

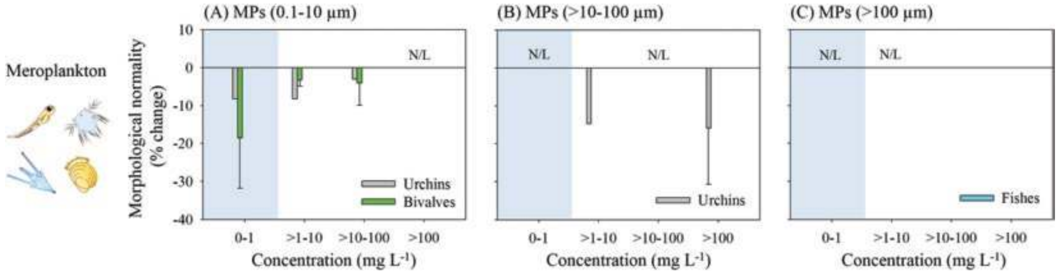

Figure 6 Percentage change in morphological normality (mean + 1SD %) of (a–c) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A6. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for fishes, gastropods, barnacles, decapods and ascidians at all concentrations, except for urchins (>10^2 mg L^{-1}) and bivalves (>10^2 mg L^{-1}). In figure (B), no data are available for fishes, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for urchins (0–1, >10–10^2 mg L^{-1}). In figure (C), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (0–10 mg L^{-1}). No data are available for all groups of holoplankton. Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear at the environment at present. N/L = no data available.

reduced *P. lividus* body length by ~6%–73%, although the effects were not concentration dependent (Martínez-Gómez et al. 2017). There was, however, a trend towards the toxicity of leachate increasing as MP size decreased (Beiras et al. 2019).

Compared to the relatively slight impacts of virgin MPs, exposure to leachates derived from MPs had relatively large detrimental effects on development of sea urchin embryos. Leachates from both PS and HDPE MPs (6 μm, 0.12–12 mg L^{-1}; 80 μm, 5–5000 mg L^{-1}) significantly decreased the percentage of normal larvae by 8% to 92% in *P. lividus* (Martínez-Gómez et al. 2017). In *Lytechinus variegatus* embryos, the proportion of normal larvae in treatments exposed to leachates of virgin PE MPs (58.1%) and beach-collected pellets (34.6%) were significantly lower than controls (88%) (Nobre et al. 2015). The toxicity of virgin MPs could be explained by plastic additives applied when the MPs are manufactured (Cole et al. 2019). On the other hand, the toxicity of field-collected pellets is based on chemicals adsorbed in the environment and thus largely depends on the chemicals present at the collection site. In a heavily contaminated collection site, beach-collected MPs might be more toxic than virgin MPs.

Bivalves

Larvae MPs (0.1–10 μm) affect the normal development of the bivalve embryos tested, although there was variation (Figure 6A). Neither mussel (*Mytilus galloprovincialis*) nor oyster (*Crassostrea gigas*) embryos exposed to PS (0.5 and 2 mg L^{-1}, 0.1–25 mg L^{-1}; 3 μm, 0.00075–0.15 mg L^{-1}) and PE MPs (4–6 μm; 20–100 mg L^{-1}) decreased the percentage of normal larvae in embryo-larval development (Beiras et al. 2018, Capolupo et al. 2018, Tallec et al. 2018). The proportion of normal larvae in both MP and control groups generally reached over 80% in these studies. In contrast, PS MPs (0.1 and 2 μm; 0.03–0.3 mg L^{-1}) significantly increased the malformation rate of blue mussel larvae (*Mytilus edulis*) by 27%–42% after 11–15 days of exposure (Rist et al. 2019), which might be because of the longer exposure time used in the study. As for growth rate, a study by Cole & Galloway (2015) found no clear effect on oyster larvae (*C. gigas*) exposed to PS MP (1 and 10 μm; 100 beads mL^{-1}). Likewise, exposure to 2 and 0.1 μm PS MPs did not affect growth rate of blue mussel larvae (*M. edulis*) at any concentrations tested (0.0004–0.28 mg L^{-1}) (Rist et al. 2019) (Figure 4D). The lack of influence on growth rate could be explained by the conclusion that MP exposure at these concentrations had no effect on filter feeding of oyster larvae, and thus their growth was not impacted (see ‘Feeding rate’ in the present review).

Microplastic-chemical interactions Leachate derived from MPs had high toxicity and severely impaired mussel embryo development. The proportion of normal embryos was significantly lower when mussel embryos (*Perna perna*) were exposed to leachate either from beached (0%) or virgin PP MPs (76.5%) compared to the control (90%) (e Silva et al. 2016). Leachate toxicity could derive from chemicals adsorbed onto beached pellets and monomers released from virgin MPs. Similarly, PS-COOH and PS-NH_2 MPs (0.15–0.2 μm; 0.02–2 mg L^{-1}) significantly increased larval malformation rate and decreased developmental rate and growth rate by 220%–449%, 4.78%–7.86% and 0.65%–4.34% in clam *Meretrix meretrix,* respectively (Luan et al. 2019). These studies suggest that early development of bivalve larvae are sensitive to combined effects of MPs and chemicals.

Transgenerational effect A transgenerational effect of MPs on growth was also observed in offspring produced by MP-exposed bivalves (Figure 2B). The offspring larvae produced by PS MP-exposed (2 and 6 μm; 0.023 mg L^{-1}) oysters (*C. gigas*) suffered from an 18.6% growth reduction (shell length) compared to the control oysters (Sussarellu et al. 2016). This growth retardation could be explained by the reduced quality of gametes observed in MP-exposed adults (Sussarellu et al. 2016). This again highlights that MP exposure could have transgenerational impacts and negatively influence the fitness of their offspring.

Gastropods

Larvae Limpet larvae (*Crepidula onyx*) exposed to 2–5 µm PS MPs at concentrations higher than 1.43 mg L^{-1} grew significantly slower [0.12~ 0.13 mm log ($lday^{-1}$)] than the control [0.16 ± 0.016 mm log ($lday^{-1}$)]. Even though the animals were no longer fed with MPs after the adult stage, the growth rate of juveniles exposed to MPs [~18 and 17.5 mm log ($lday^{-1}$)] during the larval stage still could not catch up with the control group [20.8 mm log ($lday^{-1}$)] (Lo & Chan 2018). Since their algae consumption did not decrease upon MP exposure (See 'Feeding rate' in the present review), the reduced growth rate could be related to the energy depletion induced by MP ingestion and the toxic chemicals leached from polymers. Because they only reported growth rate, their data were not included in the percentage change analysis.

Decapods

Larvae The weight of grass shrimp larvae (*Palaemonetes pugio*) was not affected by medium-sized PE MPs (38 and 59 µm) (Weinstein 2015) (Figure 5D). The percentage change in weight was lower than 10%. Similarly, larval development time of grass shrimp larvae was not affected by PE MPs (38 and 59 µm), except for those exposed to 38 µm MPs at 1.0 mg L^{-1}, which had a significantly faster development time (20.2 days) than control shrimp (20.8 days) (Weinstein 2015) (Figure 3C).

Ascidians

Embryos Exposure to MPs did not affect the normal development of ascidian embryos (*Ciona robusta*). PS MP-exposed embryos (1 and 10 µm; 0.125–25 mg L^{-1}) still showed the same phenotype as those in the controls (Messinetti et al. 2018, 2019). This study did not, however, quantify the effect of MPs, so no data were included here.

Larvae MPs (0.1–10 µm) severely delay the development time of ascidian larvae. The percentage of ascidian larvae that successfully metamorphosed to stage 4 juvenile was significantly reduced by 30%–40% after 4 days of 1 and 10 µm PS MPs exposure (0.125–25 mg L^{-1}). Moreover, the percentage of stage 3 larvae was higher in the 12.5 and 25 mg L^{-1} treatment groups (~23%–45%) than the control (~5%–12%) (Messinetti et al. 2018, 2019). The delayed juvenile development was probably due to the lower amount of food intake caused by MP-induced false satiation. These studies indicate that the development of ascidian larvae is quite sensitive to small-sized MPs (0.1–10 µm). But they did not evaluate the exact development time, so their data were not included in the percentage change analysis.

Comparing the effect of microplastic on growth and development among zooplankton groups under environmentally relevant and high laboratory concentrations

All three sizes of virgin MPs induce growth alterations in most of the zooplankton species examined by either reducing or increasing growth, although no clear concentration trend was observed. However, the percentage change is generally lower than 20% at both environmental (0–1 mg L^{-1}) and high laboratory concentrations (>1 mg L^{-1}) (Figures 4 & 5). Among all the zooplankton groups examined, bivalve larvae and crustaceans, including euphausids, brine shrimp and decapod larvae, appeared to be the most resistant to MPs. In general, the percentage change did not exceed 5% at any of the concentrations tested upon exposure to 0.1–10 µm and >10–100 µm MPs (Figures 4 & 5). Similarly, development (development time and percentage of normal larvae) of most of the zooplankton groups tested is not severely affected by virgin MPs (Figures 3 & 6), except for sea urchins and bivalves, which seemed to be sensitive to the smaller size class of MPs (0.1–10 µm) (Figure 6a). No clear trend can be observed for MPs of size >10–100 µm and >100 µm, predominantly due to the small number of studies (Figures 3C & 6B). Overall, the mean percentage change in growth and development for all the zooplankton groups examined is lower than 20% either at environmental or laboratory concentrations (Figures 3–5). These results suggest that the alterations in growth and development caused by MPs are relatively minor and would not induce detrimental impacts at natural concentrations.

As for the interaction between MPs and chemicals, exposure to leachates derived from MPs reduced the percentage of normal larvae in sea urchins and bivalves. This might be explained by the life stage of the organisms studied. Early developmental stages such as gamete and embryo were used as models in these studies. Thus, the high sensitivity of early stages might contribute to the high percentage decrease observed (Fernández & Beiras 2001), but the underlying mechanisms still needs further investigation. On the other hand, both growth and development of copepods, daphnids and larvae of fishes, sea urchins and molluscs, are not severely affected by co-exposure to chemicals and MPs, but the toxicity depends on properties of chemicals and MPs. In addition, MPs might reduce growth and delay development of the offspring produced by MP-exposed bivalves, copepods and daphnids (Figure 2B,C). But the transgenerational effects are still poorly studied and further investigation are certainly needed to draw a comprehensive conclusion.

Feeding rate

Holoplankton

Copepods

Juveniles and adults MPs of size 0.1–10 μm have detrimental impacts on the feeding rate of copepods. There was a clear trend between increased concentration and decreased feeding rate; the percentage decrease reached over 75% at >1–10 mg L^{-1} for smaller-sized MPs (0.1–10 μm) (Figure 7A). The effects of MPs on feeding rate were mainly studied in calanoid copepods – including *Centropages typicus*, *Calanus helgolandicus, Calanus finmarchicus* and *Acartia tonsa* – all of which showed reduced feeding rates after being exposed to MPs. In *C. typicus*, exposure to natural assemblages of algae and 7.3 μm PS MPs (0.86–5.39 mg L^{-1}) for 24 hours significantly reduced algal consumption by 45%–88% compared to copepods that did not eat MPs (Cole et al. 2013). In *C. finmarchicus*, the average algae removal decreased by 32% and 27% after being exposed to 10 μm PS MPs for 24 and 48 hours, respectively, although these results were not significant (Halland 2017). MPs of size >10–100 μm impaired copepod feeding rate as well (Figure 7B). *C. helgolandicus*'s filter feeding rate decreased by 11% after exposure to 20.0 μm PS MPs (0.33 mg L^{-1}) for 6 days (Cole et al. 2015). Carbon uptake decreased by 54 and 43.5%, respectively, in *A. tonsa* and *C. helgolandicus* exposed to a mixture of 10 and 20 μm PS MPs (0.25 mg L^{-1}) (Dedman 2014). Exposure to nylon fibres (10 × 30 μm, 0.14 mg L^{-1}; 10 × 40 μm, 0.36 mg L^{-1}) caused an overall decrease in total algal ingestion rates and clearance rates in *C. finmarchicus* and *C. helgolandicus*. Exposure to nylon fragments (20 μm, 0.48 mg L^{-1}) significantly decreased the ingestion of algae that had similar size and shape to the fragments in *C. helgolandicus*, although it did not significantly alter the total algal consumption (Coppock et al. 2019).

The impaired feeding rate could be explained by prey selection widely reported in calanoid copepods (Frost 1972, Irigoien et al. 2000, Dedman 2014). Chemoreceptors on the mouthparts of copepods can sense particles and actively capture or reject them (Friedman & Strickler 1975). Previous studies have documented that calanoid copepods shift their preference to avoid ingestion of algae that have similar size to MPs. For example, Cole et al. (2015) found that copepods selectively fed on smaller-sized algal prey (11.6–14.8 μm) to avoid ingesting larger 20 μm MPs, thus decreasing their filtering rate. Cole et al. (2019) and Coppock et al. (2019) observed that copepods avoided food of a similar size or shape to the microfibres. This mechanism might avoid directly ingesting non-nutritious MPs, but at the same time, it impairs their algae consumption rate, reducing the carbon biomass acquired and causing energy depletion. Moreover, the Calanoida are an important food source for many marine organisms. Therefore, energy depletion in copepods might adversely impact the energy transfer from lower to higher trophic levels.

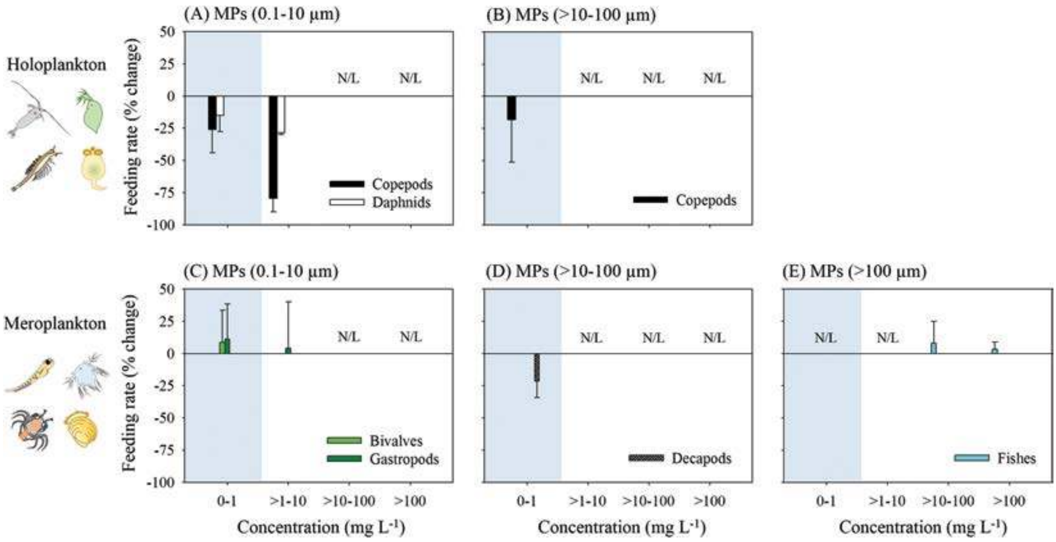

Figure 7 Percentage change in feeding rate (mean + 1SD %) of (a, b) holoplankton and (c–e) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A7. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for brine shrimp, euphausids and rotifers at all concentrations, except for copepods (>10 mg L^{-1}) and daphnids (>10 mg L^{-1}). In figure (B), no data are available for daphnids, brine shrimp, euphausids and rotifers at all concentrations, except for copepod (>1 mg L^{-1}). No data are available for holoplankton for MPs >100 μm. In figure (C), no data are available for fishes, urchins, gastropods, barnacles, decapods and ascidians at all concentrations, except for bivalves (>1 mg L^{-1}) and gastropods (>10 mg L^{-1}). In figure (D), no data are available for fishes, urchins, gastropods, barnacles and ascidians, except for decapods (>1 mg L^{-1}). In figure (E), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (0–10 mg L^{-1}). Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear at the environment at present. N/L = no data available.

In contrast, exposure to 20 μm PS MPs (0.33 mg L^{-1}) had no significant effect on algae consumption in the cyclopoid copepod *Oithona similis* (Dedman 2014). The carbon uptake of MP-exposed animals (1.72 μg C cop^{-1} d^{-1}) did not significantly differ from controls (1.1 μg C cop^{-1} d^{-1}). This is probably because *O. similis* possesses a different feeding mode from calanoid copepods. *O. similis* is an ambush feeder that relies on detecting disturbance in the water column to capture motile prey such as ciliates. The species is unlikely to detect non-motile particles such as MPs, and thus no significant impacts on total ingestion rate and carbon biomass uptake can be observed (Dedman 2014). This suggests that cyclopoid copepods might be more tolerant to MP pollution than calanoid copepods.

Daphnids

MPs (0.1–10 μm) reduce the feeding rate of daphnids in a concentration-dependent manner (Figure 7A), although there is variation among studies. Both adverse impact and no clear effect have been documented in daphnids. Reduction in total algae consumption by 29% and 28% were observed in both spherical (1–5 μm; 4.13 mg L^{-1}) and irregular-shaped (2.6 ± 1.8 μm; 2.69 mg L^{-1}) MP-exposed *Daphnia magna*, respectively (Ogonowski et al. 2016). *D. magna*'s feeding rate also decreased by 30% and 21% after exposure to 1–5 μm (0.65 mg L^{-1}) and 0.1 μm (1 mg L^{-1}) PS MPs, respectively (Puranen Vasilakis 2017, Rist et al. 2017). In contrast, no significant effect was found on the feeding rate in PLA (1–4 µm; 0.93 mg L^{-1}) and PS MPs (2 µm; 1 mg L^{-1}) exposed *D. magna* (Puranen Vasilakis 2017, Rist et al. 2017). The percentage decreases in these studies were lower than 10%. Since the size and concentration of MPs used in these studies were similar, the underlying mechanism is still unclear.

Transgenerational effect No significant effect on the filter feeding rate was observed in the F_1 offspring produced by both spherical (1–5 µm) and irregular-shaped MP (2.6 ± 1.8 µm) exposed animals (*D. magna*) (Ogonowski et al. 2016), although the feeding rate was reduced by 29% and 28% in the F_0 generation, respectively. This result suggests that MP has no adverse transgenerational effect on feeding rate, but the raw data were not reported in this study, and thus the percentage change cannot be calculated.

Meroplankton

Fishes

Larvae The percentage change in the feeding rate of fish larvae was generally lower than 10% upon exposure to MPs >100 µm at any concentrations tested (Figure 7E). The presence of PE MPs (mixture of 425–500 µm and 180–212 µm) did not affect the number of *Artemia* nauplii consumed by fathead minnow larvae (*Pimephales promelas*). No significant difference was found between MP treatments (7.4–9.21) and the control (6.9–8.69) (Malinich et al. 2018). A possible explanation is that the larvae were able to distinguish between MPs and *Artemia* nauplii and actively avoid ingesting MPs during feeding. Similarly, foraging activity (number of bites) of the surgeon fish *Acanthurus triostegus* was not significantly affected after exposure to PS MPs (90 µm; 2.02 mg L^{-1}) (Jacob et al. 2019).

Bivalves

Larvae In general, bivalve larvae do not suffer from reduced feeding rate upon exposure to 0.1–10 µm MPs (Figure 7C), although there is some variation among studies. Exposure to MPs smaller than 1 µm at 1000 beads mL^{-1} (0.00055 mg L^{-1}) significantly reduced carbon uptake by 75% compared to control larvae of oysters (*Crassostrea gigas*) (Cole & Galloway 2015). In contrast, presence of PS MPs >2 µm did not affect the filter feeding rates of the mussels *Mytilus galloprovincialis* (3 µm; 0.03 mg L^{-1}) and *M. edulis* (2 µm; 0.003 mg L^{-1}) or the oyster *C. gigas* (10 µm; 0.00055–0.55 mg L^{-1}) at any concentrations tested (Cole & Galloway 2015, Capolupo et al. 2018, Rist et al. 2019). The percentage decrease in these sizes of MPs were generally lower than 10%. It has been shown that mussel D-veligers express food preferences by actively selecting relatively high nutritional particles with the cilia of the velum (Sprung 1984). These results suggest that the ability of bivalve larvae to select food particles might be influenced by MP size. MPs smaller than 1 µm significantly reduced the filter feeding rate of oyster larvae, but MPs >2 µm did not. The causal mechanisms require further investigation. Due to the variation between studies, the mean percentage decrease on feeding rate of bivalve larvae is lower than 10% (Figure 7C).

Gastropods

Larvae The feeding rate of gastropod larvae is not severely affected by 0.1–10 µm MPs (Figure 7C). The algal consumption rate of *Crepidula onyx* larvae was not significantly affected after 14 days of exposure to high concentrations of MPs (2–5 µm; 0.00024–3.33 mg L^{-1}). All MP-exposed and control individuals had similar algal consumption rates. Although an increased total clearance rate (algae + MP) was observed in the larvae fed with MPs, their algal consumption did not increase (Lo & Chan 2018). This result suggests that *C. onyx* larvae do not selectively feed on algal particles, even though MP exposure increases their clearance rate. It is possible that the absence of effects also related to the size of MP, but the mechanisms are still unclear.

Decapods

Larvae A reduced feeding rate was documented in decapod larvae exposed to >10–100 μm MPs (Figure 7D). Porcellanid larvae suffered from a decreased feeding rate after exposure to PS MPs (10 + 20 μm; 0.25 mg L^{-1}). The ingestion rate and carbon uptake of MP-exposed larvae were approximately 30% and 23% lower, respectively, than those of the control group, although these results were not significant (Dedman 2014).

Comparing the effect of microplastic on feeding rates among zooplankton groups under environmentally relevant and high laboratory concentrations

Reduction in feeding rate is widely documented in copepods, daphnids and decapod larvae (Figure 7). Among all zooplankton groups tested, crustacean zooplankton – including copepods, daphnids and decapod larvae – seem to be the most vulnerable to MPs. Copepods are the most sensitive group; their mean percentage decrease in feeding rate reached 26% at environmental concentrations (0–1 mg L^{-1}) and exceeded 75% at >1–10 mg L^{-1} upon exposure to 0.1–10 μm MPs (Figure 7A). MPs of size >10–100 μm also influence copepods' feeding rates (Figure 7B). Daphnids and decapod larvae are quite sensitive to MPs as well, decreasing feeding rate by 15%–22% at environmental concentrations (0–1 mg L^{-1}) (Figure 7A,D); the least sensitive groups are molluscs (including bivalves and gastropods) and fishes. An increase in feeding rate was reported in these groups upon MP exposure at all the concentrations tested (Figure 7C,E). These results indicate that the feeding rate of crustacean zooplankton would be adversely affected by MPs at environmental concentrations, and the effects would be exacerbated further at sites heavily contaminated by MPs.

Drastic decreases in feeding rate might be explained by the strong selectivity observed in crustacean zooplankton. They selectively feed on phytoplankton and are able to avoid MPs; thus, they might be less efficient at feeding when MPs are present. Nevertheless, this does not mean that unselective feeders will be the 'winners' under MP pollution. If the MPs were heavily contaminated with chemicals, undiscriminating ingestion might have detrimental impacts due to the transfer of toxic chemicals absorbed from MPs after ingestion, while selective feeding might help prevent animals from ingesting toxic MPs, even if it reduces their feeding efficiency.

Swimming speed

Holoplankton

Brine shrimp

MPs (0.1–10 μm) reduce swimming speed in brine shrimp naupliar larvae (*Artemia franciscana*) by 10% after 24 hours of exposure to PS MP (0.1 μm) at 10 mg L^{-1}. However, the speed was significantly accelerated by 10%–18% at high MP concentrations (1 and 10 mg L^{-1}) after 48 hours of exposure (Gambardella et al. 2017) (Figure 8A).

Rotifers

MP (0.1–10 μm) exposure significantly impairs adult rotifer swimming speed (Figure 8A). At a low concentration (0.001 mg L^{-1}), *Brachionus plicatilis* swimming speed first accelerated and then gradually decreased (18%–30%) from 0.1 mg L^{-1} upwards (Gambardella et al. 2018).

Meroplankton

Fishes

Larvae PS MPs (45 μm, 1 mg L^{-1}) do not significantly affect zebrafish (*Danio rerio*) locomotion (Figure 8C). The total swimming distance of the MP-exposed larvae (~950 cm/10 min) was similar

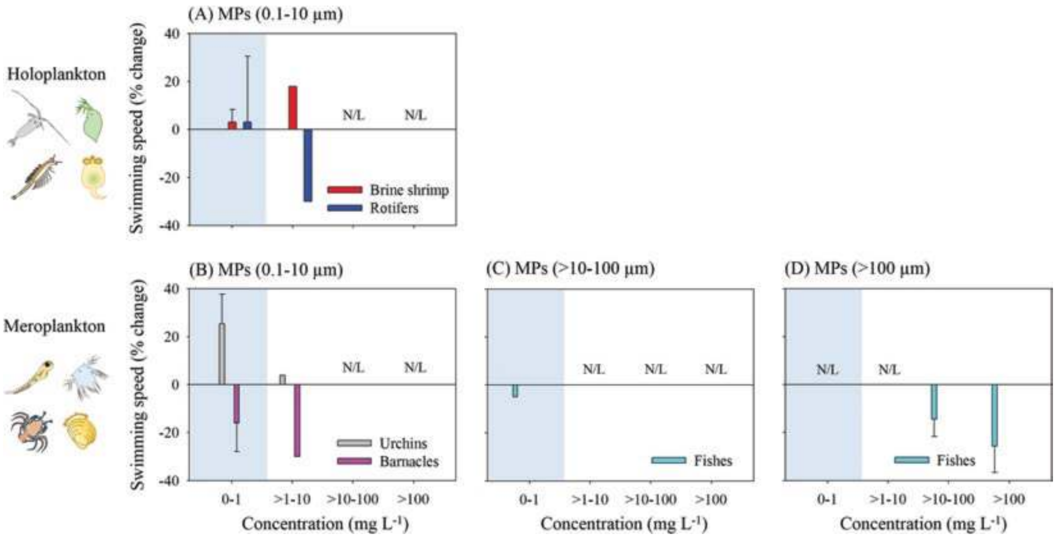

Figure 8 Percentage change in swimming speed (mean + 1SD %) of (a) holoplankton and (b, c) meroplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A8. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for copepods, daphnids and euphausids at all concentrations, except for brine shrimp (>10 mg L^{-1}) and rotifers (>10 mg L^{-1}). No data are available for holoplankton for MPs of size >10–100 μm and >100 μm. In figure (B), no data are available for fishes, bivalves, gastropods, decapods and ascidians at all concentrations, except for sea urchins (>10 mg L^{-1}) and barnacles (>10 mg L^{-1}). In figure (C), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (>1 mg L^{-1}). In figure (D), no data are available for urchins, bivalves, gastropods, barnacles, decapods and ascidians at all concentrations, except for fishes (0–10 mg L^{-1}). Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear at the environment at present. N/L = no data available.

to that of the control ($\sim$1000 cm/10 min) after 120 hours of exposure (Chen et al. 2017). In contrast, exposure to 6–350 μm PE MPs (250 mg L^{-1}) for 96 hours decreased distance travelled and swimming velocity by 17%–25% and 14%–46%, respectively, in minnow larvae (*Cyprinodon variegatus*) (Choi et al. 2018) (Figure 8D).

Microplastic-chemical interactions A mixture of PS MPs (45 μm; 1 mg L^{-1}) and 2 μg L^{-1} EE2 did not have a clear effect on the swimming activity of zebrafish larvae (*D. rerio*). This might be because the MP absorbs EE2 and thus reduces the amount of dissolved EE2 in solution. In contrast, co-exposure to higher-concentration EE2 (20 μg L^{-1}) and PS MPs (45 μm; 1 mg L^{-1}) significantly suppressed locomotion of fish larvae by 23%–34% (Chen et al. 2017). Swimming activity of fish larvae is closely related to energy requirements and predator avoidance. An inhibited ability to swim might largely affect fish larvae's ability to avoid predators and thus reduce their fitness when exposed to MP.

Sea urchins

Larvae The swimming ability of sea urchin larvae is significantly altered by PS MPs. Larval swimming speed of *Paracentrotus lividus* significantly increased by 22%–38% at low MP concentrations (0.001–0.1 mg L^{-1}), although no significant effect was found on those exposed to higher concentrations (1–10 mg L^{-1}) (Gambardella et al. 2018) (Figure 8B). This might be related to an overcompensation response, which indicates apparent stimulations at low levels of toxicity. Such responses have been observed in marine organisms exposed to pesticides and other environmental toxins at low-dose concentrations (Costa et al. 2016).

Bivalves

Gametes Spermatozoa motility (velocity) of the oyster *Crassostrea gigas* was not affected by five-hour exposure to PS-COOH or PS-NH_2 MPs exposure (0.1 µm; 0.1–10 mg L^{-1}). The absence of effect might be because of the short exposure time used in this study (González-Fernández et al. 2018). Because the measured values were not reported, the percentage change was not calculated.

Barnacles

Larvae Exposure to virgin PS MPs (0.1 µm) caused mechanical disturbance and significantly inhibited the swimming speed of barnacle nauplius larvae (*Amphibalanus amphitrite*) by ~30% compared to the control at concentrations of 1 and 10 mg L^{-1} (Gambardella et al. 2017) (Figure 8B). These results indicate that barnacle larval locomotion might be altered when MPs are present in the seawater.

Comparing the effect of microplastic on swimming speed among zooplankton groups under environmentally relevant and high laboratory concentrations

Small-sized MPs (0.1–10 µm) significantly alter the swimming speed of several zooplankton groups, including brine shrimp, rotifers and larvae of sea urchins and barnacles at both environmentally relevant (0–1 mg L^{-1}) and high laboratory concentrations (>1 mg L^{-1}) (Figure 8A,B). In addition, MPs of size >10–100 µm and >100 µm reduced swimming speed of fishes as well (Figure 8C,D). However, due to the relatively small number of studies, it is currently difficult to identify which zooplankton group may be more sensitive to MP exposure. These results suggest that swimming speed is a sensitive endpoint which might be useful for detecting MPs at non-lethal concentration levels. Moreover, co-exposure to MPs and chemicals can potentially enhance the inhibition effects of toxic chemicals, but further investigation is needed to draw a comprehensive conclusion. Nevertheless, these results suggest that MPs cause some mechanical disturbance and change the swimming speed of the exposed organisms.

Reproduction

The reproduction traits mentioned here include egg production rate, number of aborted eggs, number of total offspring produced, number of offspring per brood, number of mobile/immobile juveniles, number of broods, time it takes to produce the first brood of offspring and time between broods. To facilitate comparisons, only reproductive traits related to fecundity – egg production rate, number of total offspring produced and number of offspring per brood – were used to calculate percentage change.

Holoplankton

Copepods

MPs (0.1–10 µm) significantly reduce the number of offspring produced in calanoid and harpacticoid copepods (Figure 9A). For instance, *Paracyclopina nana* (Calanoida) exposed to doses of 0.5 µm PS MPs (0.1–20 mg L^{-1}) showed a 12%–24% decrease in nauplii offspring produced, while 6 µm MPs had no significant effect (Jeong et al. 2017). The harpacticoid copepod *Tigriopus japonicus* produced significantly fewer nauplii (56%–72% compared to the control) when exposed to PS MPs (0.5 and 6 µm; 0.1–25 mg L^{-1}) (Lee et al. 2013). *Parvocalanus crassirostris* exposed to PS MPs (<11 µm;

57.78 mg L^{-1}) decreased egg production by 88% (Heindler et al. 2017). The percentage decrease reached nearly 50% at concentrations of >10–100 mg L^{-1} (Figure 9A), suggesting that MPs of size 0.1–10 μm can severely reduce copepod fitness. In contrast, >10–100 μm MPs did not severely affect egg production and hatching success in *Calanus helgolandicus* after exposure to PS MPs (20.0 μm; 0.33 mg L^{-1}). Even a slight increase in egg production was observed, but this was not significant, predominantly due to the high variation (Cole et al. 2015) (Figure 9B).

Transgenerational effect The adverse impact of MPs on fitness can affect the next generation's reproduction. The number of offspring produced by *T. japonicus* was significantly reduced by 49%–87% after exposure to PS MPs (0.5 and 6 μm; 0.1–25 mg L^{-1}) (Lee et al. 2013) (Figure 2D). If fecundity was negatively impacted by MP exposure, then long-term exposure could have a detrimental influence on both calanoid and harpacticoid copepod populations, as supported by Heindler et al. (2017), who found that exposure to PET MPs (<11 μm; 14.44 mg L^{-1}) for 24 days significantly depleted population size by 40% in the calanoid copepod *P. crassirostris*.

Daphnids

Several studies have evaluated the effects of MP toxicity on daphnid reproductive traits (e.g. number of offspring produced, number of broods and the time to first offspring). This section will be subdivided into three parts discussing the effects of MPs on different reproductive traits:

1. *Number of offspring*: The number of offspring produced by daphnids is significantly reduced upon exposure to 0.1–10 μm MPs (Figure 9A). *Daphnia magna, D. pulex* and *Ceriodaphnia dubia* suffer decreased offspring numbers when exposure to spherical and irregular MPs. Some studies found that the offspring number produced by MP-exposed females was significantly decreased by 9%–94%, 26%–46% and 24%–65% in *D. magna, D. pulex* and *C. dubia*, respectively (Pacheco et al. 2018) (1–5 μm; 0.02 and 0.2 mg L^{-1}), Martins & Guilhermino (2018) (1–5 μm; 0.1 mg L^{-1}), Puranen Vasilakis (2017) (PS and PLA, 1–5 μm; 0.65–0.93 mg L^{-1}), Ziajahromi et al. (2017) (PE and PET, 1–100 μm; 0.03–5 mg L^{-1}),

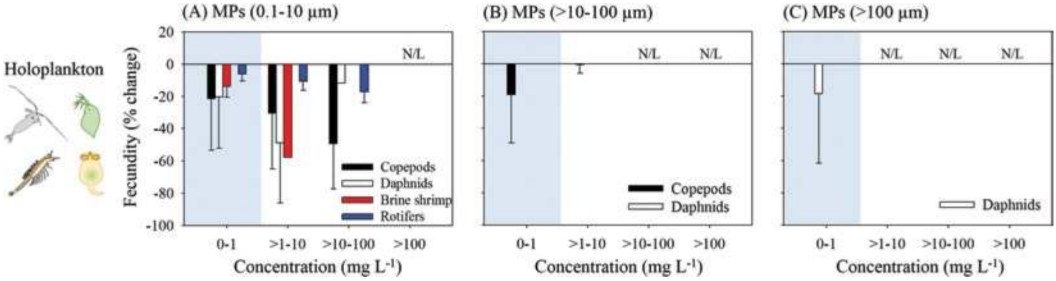

Figure 9 Percentage change in fecundity (mean + 1SD %) of (a–c) holoplankton in MP treatments when compared to controls. For literature used for all groups of zooplankton, refer to supplementary Table A9. A negative percentage change means a decreased amount of the value in MP treatment compared to that of the control and vice versa. Note: In figure (A), no data are available for copepods (>10^2 mg L^{-1}), daphnids (>10^2 mg L^{-1}), brine shrimp (>10 mg L^{-1}), euphausids (all concentrations) and rotifers (>10^2 mg L^{-1}). In figure (B), no data are available for brine shrimp, euphausids and rotifers at all concentrations, except for copepods (>1 mg L^{-1}) and daphnids (0–1, >10 mg L^{-1}). In figure (C), no data are available for copepods, brine shrimp, euphausids and rotifers at all concentrations, except for daphnids (>1 mg L^{-1}). No data are included in meroplankton, since adults of fishes, urchins, bivalves, gastropods, barnacles, decapods and ascidians are not zooplankton. Note: light blue background indicates the concentration where environmentally relevant, and white background indicates high laboratory concentration, which does not appear at the environment at present. N/L = no data available.

Jaikumar et al. (2019) (PE, 1–10 μm). Similarly, exposure to fragmented MPs (2.6 ± 1.8 μm) significantly decreased the number of total offspring released by 76% (*D. magna*) (Ogonowski et al. 2016). However, a small number of studies reported no clear effects on fecundity in *D. magna* after exposure to MPs (Ogonowski et al. 2016) (1–5 μm, 0.0018–1.8 mg L^{-1}), Rist et al. (2017) (PS, 0.1 and 2 μm, 0.1–1 mg L^{-1}), Aljaibachi & Callaghan (2018) (PS, 2 μm, 1.39×10^{-3}–1.11×10^{-2} mg L^{-1}) and Gerdes et al. (2019) (1–5 μm, 12.86 mg L^{-1}). Overall, MPs of 0.1–10 μm decreased daphnid fecundity over 40% at >1–10 mg L^{-1}. But the percentage decrease reduced after this concentration, predominantly because only a small number of studies investigated high concentrations (Figure 9A).

Similarly, 100−400 μm PET MPs significantly decreased the number of offspring produced by 20%–80% in *C. dubia* (Ziajahromi et al. 2017) (Figure 9C). In contrast, offspring number was not significantly affected after exposure to 40 μm MPs (PA + PC + PET + PVC, ABS + PVC + POM + SAN, 3.24–4.89 mg L^{-1}) in *D. magna* (Imhof et al. 2017) (Figure 9B). But the effects of these size classes of MPs are still poorly studied, and thus further investigations are needed.

2. *Number of broods and time to first offspring*: The number of broods produced and the time to first offspring were not affected by MPs in most studies. *D. magna* exposed to PS (2 μm; 0.1–1 mg L^{-1}), PE (1–10 μm) and unknown type MPs (1–5 μm; 0.1 mg L^{-1}) did not significantly change number of broods and their time to first brood (Ogonowski et al. 2016, Rist et al. 2017, Martins & Guilhermino 2018, Jaikumar et al. 2019). No significant difference was found in PE bead (10^{-1} μm) or PET fibre (100–400 μm) exposed *C. dubia*, except at high concentration (1 mg L^{-1}) (Ziajahromi et al. 2017, Jaikumar et al. 2019). However, a study by Pacheco et al. (2018) showed that MP-exposed *D. magna* (1–5 μm; 0.2 mg L^{-1}) decreased brood numbers produced and delayed their reproduction time by 71% and 49% compared to those of the controls. Both MP size and concentration are similar in these studies, and thus further investigations are needed to explain the discrepancies.
3. *Production of dead juveniles and time between broods*: As for other reproductive traits, MP-exposed *D. magna* (1–5 μm, 0.02–0.2 mg L^{-1}) produced dead juveniles (~6–15 animals) (Martins & Guilhermino 2018, Pacheco et al. 2018); MPs (1–5 μm, 0.0018–1.8 mg L^{-1}) did not, however, impact their time between broods (Ogonowski et al. 2016). These reproductive traits are not intensively studied, and thus further research is needed.

Microplastic-chemical interactions It has been commonly reported that MP can be a vector for pollutants. However, it is also possible that the reverse transport of pollutants from biota to MPs can occur if the organisms have higher concentrations of contaminants than that on the ingested MPs. For example, Gerdes et al. (2019) found that clean MPs (1–5 μm; 12.86 mg L^{-1}) eliminated some PCB in heavily contaminated *D. magna*, resulting in the PCB209 body burden of the MP-treated group (0.13 μg g *Daphnia*$^{-1}$) being lower than that of the non-treated group (0.37 μg g *Daphnia*$^{-1}$). Adding MPs even increased fecundity (the number of eggs) by ~35%, suggesting that ingesting MPs might have the positive effects of eliminating toxicity and increasing fitness in exposed organisms.

Transgenerational effect The number of offspring that F_1 neonates yielded also significantly decreased upon exposure to MPs, suggesting that there is a transgenerational effect on daphnid fecundity (Figure 2D). The number of offspring produced by the F_1 generation was 29%–75% less than the control after exposure to PS (2 μm, 1.11×10^{-2} mg L^{-1}) and unknown type MPs (1–5 μm, 0.1 mg L^{-1}) (Aljaibachi & Callaghan 2018, Martins & Guilhermino 2018). In addition, a transgenerational effect was also observed in other reproductive traits. The number of broods and living juveniles released were still ~16%–40% less than the control in F_1 offspring and the following generations (*D. magna*) (unknown type, 1–5 μm, 0.1 mg L^{-1}), although some reproductive traits such as time to first brood had already recovered (Martins & Guilhermino 2018).

Brine shrimp

Adults The total number of offspring significantly decreased by 9%–58% in *Artemia franciscana* after being exposed to 1–5 μm MPs (0.4–1.6 mg L^{-1}) (Figure 9A), suggesting that MPs can negatively affect brine shrimp population size in the long term (Peixoto et al. 2019).

Rotifers

Exposure to 0.5 μm PS MPs (20 mg L^{-1}) significantly reduced the number of offspring produced by 7%–21% in the rotifer *Brachionus koreanus*. On the other hand, 6 μm MPs (0.1–20 mg L^{-1}; 12 days) had relatively mild impacts, with the number of offspring being only 0%–12% less than the control (Jeong et al. 2016) (Figure 9A). However, other reproductive traits in rotifers have different responses toward MPs. The time needed from hatching to maturation did not significantly differ from the control (25.41 hours) after exposure to both 0.5 and 6 μm PS MPs (10 mg L^{-1}) (26.15 and 25.13 hours, respectively) (*B. koreanus*) (Jeong et al. 2016).

Comparing the effect of microplastic on reproduction among zooplankton groups under environmentally relevant and high laboratory concentrations

MP significantly reduces the number of offspring in copepods, daphnids, brine shrimp and rotifers (Figure 9). At environmentally relevant concentrations (0–1 mg L^{-1}), fecundity of zooplankton decreased by 6%–21% upon exposure to 0.1–10 μm MPs (Figure 9A). The percentage change decreased with increasing MP concentrations. At high laboratory concentrations (>1 mg L^{-1}), the percentage decrease can reach 30%–57% for crustacean zooplankton (daphnids, copepods and brine shrimp) (Figure 9A). One exception was in daphnids, for which the percentage decrease markedly lowered at >10–100 mg L^{-1}, probably due to the small number of studies (Figure 9A). Of all the zooplankton groups analysed, daphnids, copepods and brine shrimp appear to be most susceptible to MPs, followed by rotifers (Figure 9A). Moreover, MPs of size >10–100 μm and >100 μm also affect fecundity of copepods and daphnids (Figure 9B,C); however, these size classes are still poorly studied, and further investigations are still needed. These results suggest that MP exposure decreases zooplankton fecundity at environmentally relevant concentrations (0–1 mg L^{-1}). The negative effects might be more prominent under extreme conditions where high MP concentrations occur (>1 mg L^{-1}). Of note is that crustacean zooplankton are most sensitive to MPs than others. One possible reason is that a reduction in feeding rate observed in crustacean zooplankton (See 'Feeding rate' in the present review) leads to less energy available for reproduction. But further investigations are needed to elucidate the underlying mechanisms.

The current studies reviewed here show that the combined MPs and chemicals tested do not enhance the toxicity of chemicals on zooplankton reproduction. But the study numbers are still small, so future research on chemicals is strongly suggested. In addition, MPs have prominent transgenerational effects on copepod and daphnid reproduction, which drastically decrease the fecundity of the F_1 offspring (Figure 2D). This suggests that zooplankton population size is likely to significantly decrease across generations upon continuous MP exposure.

Organ damage

Holoplankton

Brine shrimp

Larvae Several ultrastructural changes have been found in the epithelial cells of the digestive tract in PS MP-exposed brine shrimp larvae (*Artemia parthenogenetica*). The number of microvilli decreased, the number of mitochondrion increased and the autophagosome was present in epithelial cells after 24 hours of MP exposure (10 μm; 0.00055–5.54 mg L^{-1}; 24 hours)

(Wang et al. 2019). These damages to cells in the digestive gut might have negative effects like accelerating energy consumption and disrupting nutrient absorption which could lead to starvation in the long term.

Meroplankton

Fishes

Larvae Most studies suggest that MP causes only negligible damage to fish organs at the larval stage. No cellular structure damages or inflammatory changes to gills, liver, brain, kidneys or intestine were observed in either MP-treated (LDPE, 0.5 mg L^{-1}) or control zebrafish larval groups (*Danio rerio*) (Karami et al. 2017). In silver barbs (*Barbodes gonionotus*), no damage was found to internal organs or gills after exposure to PVC fragments (40–300 μm; 0.2–1.0 mg L^{-1}), although the intestinal lining thickened by 29%–73% (Romano et al. 2018). One exception was minnow larvae (*Cyprinodon variegatus*), which showed intestinal distention, probably due to the excessive ingestion of bead and fragmented MPs (PE, 6–350 μm; 250 mg L^{-1}) (Choi et al. 2018). One reason these conditions were found to be harmless may be that the zooplankton are highly efficient at eliminating MPs. Polyethylene MPs (45 μm) were totally egested out of the European sea bass after 48 hours (Mazurais et al. 2015). This high potential for MP egestion may explain why there was no intestinal damage in fish larvae.

Gene expression

Biomarkers are sensitive to environmental stimulus and thus could reflect the real-time stresses that animals face under MP exposure. Several alterations in gene expression have been widely reported in MP-exposed zooplankton groups. Table 2 lists some commonly used biomarkers and their functions.

Holoplankton

Copepods

Production of cellular reactive oxygen species (ROS) in the calanoid copepod *Paracyclopina nana* increased and its antioxidant enzymatic activities – including GPx, GST and SOD – changed when exposed to PS MPs (0.5 and 6 μm; 20 mg L^{-1}) (Jeong et al. 2017), suggesting that oxidative stress was induced after exposure to MPs. In contrast, no stress response was observed in PET MP (14.44 mg L^{-1}) exposed *Parvocalanus crassirostris* (Calanoida), as indicated by no alteration

Table 2 Common gene biomarkers and their functions

Gene	Process
Cyp1a1	Detoxification
IL-1β, LYS, MYTC, MYTLB, Cxcr5	Immune response
Casp3, tp53	Apoptosis
Sod1, GPx, CAT, GST, GSH, Sod3, CAT, Dm-TRxR	Oxidative stress
AChE, GFAP, α1-tubulin, PChE	Neurotoxicity
HEX, GUSB, CTSL	Inflammatory response
CA, EP, CS, MT10, MT20	Shell biogenesis
HSP60, HSP70	General stress
AK	Energy production
Permeases, p-gp, MRP	Membrane transportation
SERCA	Anti-predation response

in *Hsp70*-like expression after 6 days of exposure. Although expression of the Histone 3 (*H3*) protein, which is related to tumourigenesis in humans (Zhao et al. 2002), was first downregulated after 6 days of exposure, it was not different from the control after 18 days of recovery (Heindler et al. 2017).

Daphnids

PS MPs (1–10 μm; 0.1–8 mg L^{-1}) induced oxidative stress in *Daphnia magna*, as indicated by alterations in CAT, GPx, MDA, GST and Dm-TRxR transcript levels (Tang et al. 2019, Zhang et al. 2019). Enzymes related to energy production and extracellular transportation, AK and permeases, were upregulated in the presence of PS MPs (1.25 μm; 2–8 mg L^{-1}) as well (Tang et al. 2019). Moreover, a batch of genes, including HSP 60, HSP 70 (general stress genes), GST and housekeeping genes (GAPDH, Stx16, aTub, Act and SERCA), were differentially expressed in *D. magna* exposed to plastic mixtures, suggesting that MPs interfered with oxidative pathways and activated protection mechanisms (Imhof et al. 2017). The different expression levels of the gene SERCA upon exposure indicated that there was an interference in the signalling pathway of anti-predation responses. However, it is noteworthy that there was variation between clones. Genetic alterations were only found in clones BL2.2 and Max4, but not clone K34J, suggesting that interclonal variation was high. Since *Daphnia* have the ability to rapidly evolve, potentially acquiring resistance to toxicants, the observed variation between clones might stem from their adaptation to MPs in their collection sites.

Microplastic-chemical interactions Adding PS MPs (1 and 10 μm; 0.1 mg L^{-1}) to roxithromycin (0.01 mg L^{-1}) exposed *D. magna* significantly decreased the responses of MDA, GPx and GST than roxithromycin alone. Moreover, integrated biomarker response analysis revealed that combined effect of PS MPs and roxithromycin induce more serious oxidative damages in *D. magna* than roxithromycin alone, suggesting that MPs enhanced the toxicity of roxithromycin (Zhang et al. 2019).

Brine shrimp

Larvae PS MP (0.1 μm) significantly affected biochemical responses in brine shrimp larvae (*Artemia franciscana*). Inhibition of AChE activity was observed in MP-exposed larvae at 0.001 and 0.01 mg L^{-1}, while PChE activity significantly increased at 0.01 and 0.1 mg L^{-1}, although not in a dose-dependent manner. Catalase activity also increased in MP-exposed larvae at all the tested concentrations (0.001–1 mg L^{-1}) (Gambardella et al. 2017). Cholinesterases (AChE and PChE) and catalase are biomarkers for neurotoxicity and oxidative stress in marine invertebrates. The significant inhibition of cholinesterases, and increase in catalase activity, indicate that neurotoxicity and oxidative stress were induced in brine shrimp larvae after MP exposure.

Rotifers

Several alterations in gene expression were observed in MP-exposed rotifers. Intracellular ROS levels in rotifers (*Brachionus koreanus*) increased significantly after exposure to both 0.5 and 6 μm PS MPs (10 mg L^{-1}). The activity of antioxidant-related enzymes including SOD, GST, GR and GPx increased significantly in MP-exposed rotifers compared to the control (Jeong et al. 2016). The induction of ROS and activation of antioxidant-related enzymes suggest that MPs induce oxidative stress in exposed rotifers. Furthermore, P-gp and MRP activities decreased in a size-dependent manner after exposure to PS MPs (0.5 and 6 μm). P-glycoprotein (P-gp) and multidrug resistance protein (MRP) played an important role in aquatic invertebrates' defence systems that pump many xenobiotics out of cells. They were the first line of defence against xenobiotic pollutants (Jeong et al. 2018). P-gp and MRP inhibition suggests that MP might affect rotifer defence mechanisms by making them more vulnerable to toxicants when MPs are presented in the environment.

Meroplankton

Fishes

Embryos Strong genetic responses have been observed in MP-exposed fish embryos. A transcriptome analysis showed that injecting PS MPs (0.7 μm) into embryos causes significant changes in zebrafish (*Danio rerio*) transcriptomic profiles, with 26 genes differentially expressed when MPs were injected into the yolk of the embryos compared to the non-injected controls. These differentially expressed genes were related to various functions, including lipid metabolism, oxidative stress, complement system and immune responses, suggesting that MP-exposed embryos had a broad response to MPs (Veneman et al. 2017).

Larvae Signs of oxidative stress, chemical toxicity, immune response and apoptosis have been observed in many fish species under MP exposure. In the European sea bass (*Dicentrarchus labrax*), exposure to PE MPs (45 μm) significantly increased cytochrome-P450-1A1 (*cyp1a1*) expression levels (12 mg per gram of diet), suggesting that MP exposure induced chemical toxicity (Mazurais et al. 2015). Exposure to both microbeads and fragmented PE MPs altered gene expressions of *Casp3*, *tp53* and *Cxcr5* in sheepshead minnow larvae (*Cyprinodon variegatus*), indicating apoptosis and immune response were elicited in exposed larvae (Choi et al. 2018). The transcriptions of a visual gene (*zfrho*) significantly increased by 6.4-fold compared to the control in MP-exposed zebrafish larvae (*D. rerio*) (45 μm, 1 mg L^{-1}), indicating an enhanced sensitivity to the light (Chen et al. 2017). AChE activity was inhibited in MP-exposed zebrafish larvae (45 μm, 1 mg L^{-1}), indicating that something was interfering with how the nervous system was functioning (Chen et al. 2017). An upregulation in CYP1A expression suggested that the detoxification processes was upregulated in three-spined stickleback larvae (*Gasterosteus aculeatus*) after seven days of exposure to PS MPs (1 μm, 10.6–1060 mg L^{-1}) (Katzenberger 2015). Furthermore, oxidative stress was induced in PE microfragment (6–350 μm) exposed minnow larvae (Choi et al. 2018) and PS MPs (5 and 50 μm) exposed zebrafish larvae (Wan et al. 2019). On a broader scale, whole animal transcriptomics and gene transcription analysis in zebrafish larvae show a transient and extensive change in gene expression. The majority of the differentially expressed genes were related to the nervous system, immune response and energy metabolism, suggesting that MPs are recognised by the immune system and impair neurodevelopment and metabolic pathways in zebrafish larvae (Veneman et al. 2017) (PS, 0.7 μm, 5 mg mL^{-1}), LeMoine et al. (2018) (PE, 10–45 μm, 5 and 20 mg L^{-1}), Wan et al. (2019) (PS, 5 and 50 μm, 0.1 and 1 mg L^{-1}).

In contrast, zebrafish larvae exposed to LDPE MPs (0–18 μm; 0.5 mg L^{-1}) displayed no change in anti-apoptotic, oxidative and neurotoxic genes (Karami et al. 2017). Similarly, expression of nervous-related genes (*gfap* and *α1-tubulin*) and CAT and GPx levels were both unchanged compared to those of the control after MP exposure (45 μm, 1 mg L^{-1}) (Chen et al. 2017). Moreover, vitellogenin B (VTG B) expression did not change after exposure to PS MPs (1 μm, 10.6–1060 mg L^{-1}) in three-spined stickleback larvae, suggesting that no oestrogenic chemicals were released from MPs (Katzenberger 2015). These discrepancies could be explained by the difference in genetic markers and polymer types used.

Microplastic-chemical interactions Co-exposure to MPs and chemicals might have an even higher impact than each individually. The combined effects of PS MPs (45 μm, 1 mg L^{-1}) and EE2 (2 and 20 μg L^{-1}) upregulated a batch of biomarkers, including nervous-related genes (*gfap* and *α1-tubulin*), visual-related genes (*zfrho* and *zfblue*) and the activities of GPx, CAT, GST (oxidative damage) and AChE (related to neurodevelopment) enzymes in zebrafish larvae, suggesting that the co-exposure induced neurotoxicity and oxidative stress (Chen et al. 2017). Moreover, BaP-spiked PE MPs (1–5 μm, 10–20 μm, 1 and 4 mg L^{-1}) induced chemical toxicity in zebrafish, as indicated by CYP 1A induction (Batel et al. 2018).

Bivalves

Embryos Significant alterations in gene expression have been found in virgin MP-exposed mussel embryos. Down-regulation of lysosomal enzyme activities – including hexosaminidase (*HEX*), b-glucorinidase (*GUSB*) and cathepsin-L (*CTSL*) – were observed in PS MP (3 μm; 0.0007–0.007 mg L^{-1}) exposed embryos, as indicated by inflammatory responses in mussels (*Mytilus galloprovincialis*). Exposure to MP also significantly impacted the expression of immune-related genes (*LYS*, *MYTC* and *MYTLB*), shell biogenesis genes (carbonic anhydrase [*CA*], extrapallial protein [*EP*] and chitin synthase [*CS*]) and methallotionein genes (*MT10* and *MT20*) (Capolupo et al. 2018). Total multixenobiotic resistance (MXR)efflux activity was reduced and Mrp and P-gp transcripts were down-regulated in PS MP-exposed (3 μm; 0.0007 and 0.007 mg L^{-1}) embryos (*M. galloprovincialis*), suggesting that cytoprotective mechanism was impaired (Franzellitti et al. 2019). These studies suggest that MP can induce a range of responses in MP-exposed embryos, including oxidative stress, immune response and neuroendocrine interference, and impaired their defence system toward environmental stresses.

Microplastic-chemical interactions PS-COOH MPs (0.1 μm; 10 and 100 mg L^{-1}) significantly increased ROS production by 30%–70% in oyster spermatozoa (*Crassostrea gigas*) after five hours of exposure. In contrast, PS-NH_2 MPs (0.1 μm; 0.1–100 mg L^{-1}) did not affect ROS production in spermatozoa or oocytes (González-Fernández et al. 2018). The differential effects of MPs could be explained by the surface functionalisation coated on MPs or membrane characteristics of the exposed cells.

Barnacles

Larvae Oxidative stress and neurotoxicity have been observed in MP-exposed *Amphibalanus amphitrite* larvae. The activity of the oxidative stress related enzyme catalase was inhibited at low concentrations of PS MPs (0.1 μm; 0.001–0.1 mg L^{-1}), indicating that oxidative stress was induced upon MP exposure. Significant increases in cholinesterases expression (both AChE and PChE activity) were also observed in MP-exposed larvae (stage II nauplii) (Gambardella et al. 2017), suggesting that PS MPs impair neurofunction in exposed nauplius larvae (*A. amphitrite*).

Comparing the effect of microplastic on gene expression among zooplankton groups under environmentally relevant and high laboratory concentrations

MPs elicit various genetic alterations at the molecular level in all the zooplankton groups tested at both environmentally relevant and high laboratory concentrations. Oxidative stress, immune response and neurotoxicity are the most commonly reported responses to MPs. Besides, alterations in genes related to inflammatory response, chemical toxicity and membrane transportation are also widely documented. Due to the variation in biomarkers used in different studies, it is difficult to compare which zooplankton group is more sensitive to MPs at the present stage. But the genes whose expressions are influenced are usually related to important life functions. Hence, these studies emphasise that MPs might disrupt normal cell functions and damage many zooplankton organisms in the long term.

Knowledge gaps and recommendations for future studies

1. There is a growing number of studies exploring the effects of MPs on zooplankton. However, the effects of MPs on early stages such as gametes and embryos are still under-represented. With a well-developed *in vitro* fertilisation technique, gametes and embryos of sea urchins and bivalves might be suitable models for evaluating the impacts of MPs on early developmental stages. More studies evaluating the effects of MPs on early developmental stages are needed.

2. Several sublethal impacts of MPs, including alteration in growth, decreases in feeding rate and fecundity, are being extensively studied in zooplankton groups. Where adverse effects have been observed, the causal mechanisms are often poorly elucidated. For example, MP-induced changes to growth in sea urchins might relate to decreased food intake; however, no study has evaluated the impact of MPs on sea urchin feeding rate. Further investigations to elucidate the underlying causes of the observed effects are needed.
3. The impacts of MPs on swimming speed of zooplankton mainly focus on smaller-sized MPs (0.1–10 μm). However, MPs of larger size classes (>10 μm) can cause a physical disturbance to zooplankton, although they might not be directly ingested. Hence, we recommend future studies use high-speed high-resolution cameras to record how the MPs interfere with the appendage movements and swimming patterns of zooplankton (see Chan et al. 2013). Moreover, the underlying cause of altered swimming speed (and indeed behaviour) requires further study, particularly for zooplankton other than fish larvae.
4. MP can have prominent impacts on zooplankton fecundity and affect the quality of their offspring. Recent studies have suggested that MP can even reduce the number of offspring produced by their F_1 generation, suggesting a transgenerational effect. This can have long-term detrimental effects on zooplankton populations. However, current studies assessing MPs' effects largely focus on the organismal or suborganismal level. To evaluate the potential effects of MPs on zooplankton populations, studies on higher organisational levels such as population or community are strongly recommended.
5. Organ damage caused by MPs is not well studied in zooplankton groups, except for fish larvae and brine shrimp. Moreover, irregular MPs appear to cause more severe damage to internal organs than spherical particles, but their effects are still poorly studied. More histopathological analyses on effects of the microfibres and fragmented MPs are suggested in future studies.
6. Transcriptomic studies on gene expression in the presence of MP largely focus on fish larvae, whereas only a few genetic markers have been studied in other zooplankton groups. In addition, compared to the studies on the larval and adult stages, transcriptomic studies on the embryonic stage are relatively rare and should receive further attention.
7. Different feeding types might affect the amount of MP ingested and hence affect the impacts of MPs (Setälä et al. 2016, Scherer et al. 2017). Salps are a particularly interesting group, as they exhibit a different feeding mode from other zooplanktons. They feed by secreting mucus to form a net and unselectively filter particles (Harbison & McAlister 1979). MP ingestion has been documented in several salp species (Chan & Witting 2012, Wieczorek et al. 2019), but there are currently no MP toxicity studies. Zooplankton are a diverse group of organisms. To assess MP impacts on zooplankton communities more fully, toxicity studies on zooplankton groups exhibiting different feeding strategies such as salps (holoplankton) and larvae of polychaete and cnidarian species (meroplankton) are strongly recommended.
8. The interactions between MPs and chemicals are still rarely studied in zooplankton. Polycyclic aromatic hydrocarbons (PAHs), phenanthrene (Phe), pyrene, 17 α-ethynylestradiol (EE2), Benzo[a]pyrene and Bisphenol A are commonly reported pollutants that adhere to MPs in aquatic environments (Teuten et al. 2007). Despite the presence of chemicals on MPs, their interactive effects with different sizes and types MPs are still poorly investigated. Further studies should evaluate the combined effects of MPs and chemicals on biological endpoints including feeding rate, swimming speed and reproduction.
9. The characteristics of MP (e.g. size, shape and polymer type) might affect its impacts on organisms. Spherical MPs are currently the most commonly studied shape in MP toxicity studies because they are commercially available and often used in experiments. But fibres and fragments are the most commonly detected types of MPs in aquatic environments. The

use of spherical MP might not be a good representative of all shapes of MPs present in real environments. Thus, more research using irregular-shaped MPs are needed. In addition, current MP toxicity studies mainly focus on the effects of single-sized or single type and shaped MPs. In natural environments, however, zooplankton would encounter mixed MPs from various sizes, shapes and types. We recommend that future studies include a range of sizes, shapes and polymer types of MPs to identify the variety of effects on zooplankton.

10. We note that the MP concentrations used in most of the MP toxicity studies exceed those currently documented in the aquatic environments. These unrealistically high concentrations could potentially overestimate the impacts of MPs. Instead of acute toxicity assessment using high MP concentrations under laboratory conditions, experiments with environmentally relevant concentrations and longer exposure times are recommended. Further, signs of transgenerational MP effects have been observed in some studies. Hence, experiments over several generations are strongly recommended.
11. Compared to marine zooplankton, the effect of MP on freshwater zooplankton is poorly studied. Daphnids and fish larvae are the only freshwater zooplankton that have been investigated to date. Other common zooplankton groups such as freshwater copepods, rotifers and decapod larvae are still understudied and need more attention.
12. The relative impacts between natural microparticles such as silt and clay and MPs have been less studied so far. Small, naturally occurring microparticles are commonly found in aquatic environments. These particles are similar to MPs in that both of them are non-digestible and non-nutritious and are potential vectors for hydrophobic organic contaminants (HOCs) (Teuten et al. 2007). Ingestion of all these microparticles may be detrimental to zooplankton. Future studies should consider the relative abundance of MPs compared to natural microparticles in the natural environment and make an attempt to study the combined effects of MP and natural microparticles in laboratory assays.
13. There is a lack of studies on MPs with different surface characteristics and the impact that this has on zooplankton. MPs present in the environment are usually soaked in seawater for a long periods and are often coated with biofilm made up of microbes or carry compounds produced by phytoplankton (e.g. dimethyl sulphide [DMS]). It has been shown that DMS infused MPs increase grazing rates of calanoid copepod *Calanus helgolandicus* (Procter et al. 2019), suggesting that this compound could be an olfactory stimuli to enhance MP foraging response. Presences of these coatings might affect the fate and bioavailability of MPs, potentially enhancing ingestion of MPs by zooplankton. Thus, the surface characteristics of MPs should be considered in future studies.
14. The interactive effects of MPs and other anthropogenic stressors are still poorly studied. Temperature rise, acidification and hypoxia are likely to occur simultaneously with MP pollution, especially in estuaries and coastal ecosystems which are highly anthropogenic impacted regions. The combined effects of these stresses may be synergistic or antagonistic due to the complex interaction among these stresses (Wen et al. 2018). For example, elevated temperature can possibly enhance the food consumption and feeding activities of fish. Presences of MP in such conditions can at the same time reduce fish feeding activities. Digestive enzyme activities and energy metabolism of fish can be affected by elevated temperature of lowered environmental pH. MP can also affect the enzyme activities and energy metabolism of fish when ingested. Therefore, the synergistic effect of MPs with other anthropogenic stressors should be a direction for further studies.

Conclusion

MPs rarely cause direct mortality but can induce sublethal effects on zooplankton which may alter individual- to population-level dynamics. Feeding rate, swimming speed, reproduction and gene expression are affected at both environmentally relevant and unrealistically high laboratory MP concentrations, suggesting that these endpoints are sensitive and potentially can act as a bioindicator to detect MP levels in environments. Survival, growth, development and organ damage are less sensitive endpoints. Survival and organ damage are not influenced at environmental concentrations, but negative effects can be observed at high laboratory concentrations, while no severe impacts on growth and development were found at any concentrations tested. Among the zooplankton groups studied, daphnids are the most sensitive; their survival, feeding rate and fecundity significantly decreased after being exposed to virgin MPs. Moreover, daphnid survival is heavily affected by feeding condition of the animal and exposure time, with unfed daphnids and longer exposure time inducing the most severe impacts. Copepods suffered from reduced feeding rate and fecundity upon MP exposure, which might adversely affect copepod populations in the long term. In contrast to daphnids and copepods, larvae of molluscs and barnacles, brine shrimp and euphausids appear to be relatively tolerant to MPs, suggesting that these groups would be more dominant when faced with prolonged MP pollution.

Leachates derived from MPs have severe impacts on zooplankton, including abnormal development in bivalve and sea urchin embryos. However, their effect on other zooplankton groups are still not well understood owing to the small number of studies. More studies are needed before any conclusion can be drawn. In addition, MPs have been shown to cause prominent effects on the survival and fecundity of F_1 offspring in bivalves, copepods and daphnids, indicating that MP might have transgenerational effects and can drastically affect zooplankton populations in the long term. This is probably owing to the chronic exposure to small amounts of additives and monomers leached from virgin MPs, suggesting that the effects of virgin MPs are not just related to the physical characteristics of the particle itself. We have noted that the causal mechanisms are often poorly demonstrated within MP studies, and the elucidation of the physio-chemical triggers for stress and adverse health in zooplankton and other biota should be considered a key priority for future research.

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Supplementary Tables are provided online at https://www.routledge.com/9780367367947

Supplementary Table A1 References used in percentage change calculation for survival in Figure 1

	Holoplankton				
	Copepods	Daphnids	Brine shrimps	Krills	Rotifers
(A) MPs (0.1–10 μm)	Lee et al. (2013) (0–1, 1–10, 10–10^2 mg L^{-1})	Ma et al. (2016) (1–10, 10–10^2 mg L^{-1}) Puranen Vasilakis (2017) (0–1 mg L^{-1}) Horton et al. (2018) (0–1 mg L^{-1}) Rehse et al. (2016) (1–10, 10–10^2, $>10^2$ mg L^{-1}) Tang et al. (2019) (1–10 mg L^{-1}) Martins & Guilhermino (2018) (0–1 mg L^{-1}) Pacheco et al. (2018) (0–1, 1–10 mg L^{-1}) Ziajahromi et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1}) Ogonowski et al. (2016) (0–1, 1–10 mg L^{-1}) Rist et al. (2017) (0–1 mg L^{-1}) Gorokhova et al. (2018) (0–1 mg L^{-1}) Lin et al. (2019) (0–1, 1–10, 10–10^2 mg L^{-1}) Kim et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1}) Gerdes et al. (2018) (0–1, 1–10, 10–10^2, $>10^2$ mg L^{-1}) Zhang et al. (2019) (0–1, 1–10, 10–10^2, $>10^2$ mg L^{-1}) Aljaibachi & Callaghan (2018) (0–1 mg L^{-1})	Gambardella et al. (2017) (0–1, 1–10 mg L^{-1}) Wang et al. (2019) (0–1, 1–10, 10–10^2, $>10^2$ mg L^{-1}) Peixoto et al. (2019) (0–1, 1–10 mg L^{-1})		Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})
(B) MPs (10–100 μm)	Cole et al. (2015) (0–1 mg L^{-1}) Syberg et al. (2017) (0–1, 1–10, 10–10^2, $>10^2$ mg L^{-1}) Vroom et al. (2017) (0–1 mg L^{-1}) Beiras et al. (2019) (0–1, 1–10 mg L^{-1})	Ma et al. (2016) (1–10, 10–10^2 mg L^{-1}) Rehse et al. (2018) ($>10^2$ mg L^{-1}) Frydkjær et al. (2017) (1–10, 10–10^2, $>10^2$ mg L^{-1}) Imhof et al. (2017) (1–10 mg L^{-1})		Dawson et al. (2018a) (0–1, 1–10 mg L^{-1}) Dawson et al. (2018b) (0–1, 1–10 mg L^{-1})	
(C) MPs (>100 μm)		Rehse et al. (2016) (10–10^2, $>10^2$ mg L^{-1}) Jemec et al. (2016) (10–10^2 mg L^{-1}) Ziajahromi et al. (2017) (0–1, 1–10 mg L^{-1}) Kokalj et al. (2018) (10–10^2 mg L^{-1})	Kokalj et al. (2018) (10–10^2 mg L^{-1})		

(*Continued*)

Table A1 (*Continued*) References used in percentage change calculation for survival in Figure 1

	Meroplankton						
	Fishes	Urchins	Bivalves	Gastropods	Barnacles	Decapods	Ascidians
(D) MPs (0.1–10 μm)	Beiras et al. (2018) (0–1, 1–10 mg L^{-1}) Katzenberger (2015) (1–10, 10–10^2, $>10^2$ mg L^{-1}) Batel et al. (2018) (0–1 mg L^{-1})	Martínez-Gómez et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1}) Messinetti et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1}) Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})	Tallec et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1})	Lo & Chan (2018) (0–1, 1–10 mg L^{-1})	Gambardella et al. (2017) (0–1, 1–10 mg L^{-1}) Bhargava et al. (2018) (1–10, 10–10^2 mg L^{-1})		Messinetti et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1}) Messinetti et al. (2019) (0–1, 1–10, 10–10^2 mg L^{-1})
(E) MPs (10–100 μm)	LeMoine et al. (2018) (10–10^2 mg L^{-1}) Batel et al. (2018) (1–10 mg L^{-1})	Kaposi et al. (2014) (0–1, 1–10 mg L^{-1})				Weinstein (2015) (0–1 mg L^{-1})	
(F) MPs (>100 μm)	Romano et al. (2018) (0–1 mg L^{-1}) Choi et al. (2018) (10–10^2, $>10^2$ mg L^{-1})						

Table A2 References used in percentage change calculation for transgenerational effects in Figure 2

	Bivalves	Daphnids	Copepods
(A) Survival	Sussarellu et al. (2016)	Aljaibachi & Callaghan (2018) Martins & Guilhermino (2018)	Lee et al. (2013) Cole et al. (2015)
(B) Growth (body length)	Sussarellu et al. (2016)	Martins & Guilhermino (2018) Imhof et al. (2017) Ziajahromi et al. (2017)	Cole et al. (2015)
(C) Development time			Lee et al. (2013)
(D) Fecundity		Aljaibachi & Callaghan (2018) Martins & Guilhermino (2018)	Lee et al. (2013)

Table A3 References used in percentage change calculation for development time Figure 3

Holoplankton			Meroplankton		
	Copepods	Brine shrimps		Decapods	Fishes
(A) MPs (0.1–10 μm)	Lee et al. (2013) (0–1, 1–10, 10–10^2 mg L^{-1}) Jeong et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1})	Wang et al. (2019) (0–1, 1–10 mg L^{-1})	(B) MPs (0.1–10 μm)		Beiras et al. (2018) (0–1, 1–10 mg L^{-1})
			(C) MPs (10–100 μm)	Weinstein (2015) (0–1 mg L^{-1})	

Table A4 References used in percentage change calculation for body length, body width and arm length in Figure 4

Holoplankton			
	Copepod (body length)	Daphnids (body length)	Brine shrimps (body length)
(A) MPs (0.1–10 μm)		Puranen Vasilakis (2017) (0–1 mg L^{-1}) Pacheco et al. (2018) (0–1, 1–10 mg L^{-1}) Martins & Guilhermino (2018) (0–1 mg L^{-1}) Ziajahromi et al. (2017) (0–1, 1–10 mg L^{-1}) Rist et al. (2017) (0–1 mg L^{-1}) Jaikumar et al. (2019) (0–1 mg L^{-1}) Bosker et al. (2019) (0–1, 1–10 mg L^{-1}) Aljaibachi & Callaghan (2018) (0–1 mg L^{-1})	Wang et al. (2019) (0–1, 1–10 mg L^{-1})
(B) MPs (10–100 μm)	Cole et al. (2019) (0–1 mg L^{-1})	Imhof et al. (2017) (1–10 mg L^{-1}) Colomer et al. (2019) (1–10 mg L^{-1})	
(C) MPs (>100 μm)		Ziajahromi et al. (2017) (0–1 mg L^{-1}) Kokalj et al. (2018) (10–10^2 mg L^{-1}) Jemec et al. (2016) (10–10^2 mg L^{-1})	Kokalj et al. (2018) (10–10^2 mg L^{-1})

(*Continued*)

Table A4 (*Continued*) References used in percentage change calculation for body length, body width and arm length in Figure 4

	Meroplankton				
	Fishes (body length)	Sea urchins (body length)	Sea urchins (body width)	Sea urchins (arm length)	Bivalves (body length)
(D) MPs (0.1–10 μm)	Katzenberger (2015) (10–10^2, >10^2 mg L^{-1})	Martínez-Gómez et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1})	Messinetti et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1})	Messinetti et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1})	Cole & Galloway (2015) (0–1 mg L^{-1}) Rist et al. (2019) (0–1 mg L^{-1})
(E) MPs (10–100 μm)	Karami et al. (2017) (0–1 mg L^{-1}) LeMoine et al. (2018) (1–10, 10–10^2 mg L^{-1})	Martínez-Gómez et al. (2017) 1–10, >10^2 mg L^{-1})	Kaposi et al. (2014) (0–1, 1–10 mg L^{-1})	Kaposi et al. (2014) (0–1, 1–10 mg L^{-1})	
(F) MPs (>100 μm)	Malinich et al. (2018) (0–1 mg L^{-1})				

Table A5 References used in percentage change calculation for body weight in Figure 5

	Holoplankton			Meroplankton	
	Daphnids (body weight)	Krills (body weight)		Fishes (body weight)	Decapods (body weight)
(A) MPs (0.1–10 μm)	Gerdes et al. (2019) (10–10^2 mg L^{-1}) Tang et al. (2019) (1–10 mg L^{-1}) Ogonowski et al. (2016) (0–1, 1–10 mg L^{-1})		(C) MPs (0.1–10 μm)	Katzenberger (2015) (0–1, 10–10^2, >10^2 mg L^{-1})	
(B) MPs (10–100 μm)		Dawson et al. (2018a) (0–1, 1–10 mg L^{-1})	(D) MPs (10–100 μm)	Karami et al. (2017) (0–1 mg L^{-1})	Weinstein (2015) (0–1 mg L^{-1})
			(E) MPs (>100 μm)	Malinich et al. (2018) (0–1 mg L^{-1})	

Table A6 References used in percentage change calculation for morphological normality in Figure 6

	Meroplankton		
	Fishes	Urchins	Bivalves
(A) MPs (0.1–10 μm)		Martínez-Gómez et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1})	Capolupo et al. (2018) (0–1 mg L^{-1}) Tallec et al. (2018) (0–1, 1–10, 10–10^2 mg L^{-1}) Beiras et al. (2018) (10–10^2 mg L^{-1}) Rist et al. (2019) (0–1 mg L^{-1})
(B) MPs (10–100 μm)		Martínez-Gómez et al. (2017) (1–10, >10^2 mg L^{-1})	
(C) MPs (>100 μm)	Choi et al. (2018) (1–10, 10–10^2 mg L^{-1})		

Table A7 References used in percentage change calculation for feeding rate in Figure 7

	Holoplankton			Meroplankton			
	Copepods	Daphnids		Fishes	Bivalves	Gastropods	Decapods
(A) MPs (0.1–10 μm)	Cole et al. (2013) (0–1, 1–10 mg L^{-1}) Halland (2017) (0–1 mg L^{-1})	Ogonowski et al. (2016) (1–10 mg L^{-1}) Puranen Vasilakis (2017) (0–1 mg L^{-1}) Rist et al. (2017) (0–1 mg L^{-1})	(C) MPs (0.1–10 μm)		Capolupo et al. (2018) (0–1 mg L^{-1}) Cole & Galloway (2015) (0–1 mg L^{-1}) Rist et al. (2019) (0–1 mg L^{-1})	Lo & Chan (2018) (0–1, 1–10 mg L^{-1})	
(B) MPs (10–100 μm)	Cole et al. (2015) (0–1 mg L^{-1}) Cole et al. (2019) (0–1 mg L^{-1}) Coppock et al. (2019) (0–1 mg L^{-1})		(D) MPs (10–100 μm)				Dedman (2014) (0–1 mg L^{-1})
			(E) MPs (>100 μm)	Malinich et al. (2018) (10–10^2, >10^2 mg L^{-1})			

Table A8 References used in percentage change calculation for swimming speed in Figure 8

Holoplankton			Meroplankton			
	Brine shrimps	Rotifers		Fishes	Sea urchins	Barnacles
(A) MPs (0.1–10 μm)	Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})	Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})	(B) MPs (0.1–10 μm)		Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})	Gambardella et al. (2018) (0–1, 1–10 mg L^{-1})
			(C) MPs (10–100 μm)	Chen et al. (2017) (0–1 mg L^{-1})		
			(D) MPs (>100 μm)	Choi et al. (2018) (10–10^2, >10^2 mg L^{-1})		

Table A9 References used in percentage change calculation for fecundity in Figure 9

Holoplankton				
	Copepods	Daphnids	Brine shrimps	Rotifers
(A) MPs (0.1–10 μm)	Heindler et al. (2017) (1–10, 10–10^2 mg L^{-1}) Jeong et al. (2017) (0–1, 1–10, 10–10^2 mg L^{-1}) Lee et al. (2013) (0–1, 1–10, 10–10^2 mg L^{-1})	Pacheco et al. (2018) (0–1, 1–10 mg L^{-1}) Puranen Vasilakis (2017) (0–1 mg L^{-1}) Ziajahromi et al. (2017) (0–1, 1–10 mg L^{-1}) Rist et al. (2017) (0 − 1 mg L^{-1}) Ogonowski et al. (2016) (0–1, 1–10 mg L^{-1}) Gerdes et al. (2019) (10–10^2 mg L^{-1}) Martins & Guilhermino (2018) (0–1 mg L^{-1}) Jaikumar et al. (2019) (0–1 mg L^{-1}) Aljaibachi & Callaghan (2018) (0–1 mg L^{-1})	Peixoto et al. (2019) (0–1, 1–10 mg L^{-1})	Jeong et al. (2016) (0–1, 1–10, 10–10^2 mg L^{-1})
(B) MPs (10–100 μm)	Cole et al. (2015) (0–1 mg L^{-1})	Imhof et al. (2017) (1–10 mg L^{-1})		
(C) MPs (>100 μm)		Ziajahromi et al. (2017) (0–1 mg L^{-1})		

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COMPARATIVE BIOGEOGRAPHY OF MARINE INVADERS ACROSS THEIR NATIVE AND INTRODUCED RANGES

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Abstract Biological invasions continue to exert extensive environmental and economic impacts. Understanding why some introduced species become invasive is critical to their management. Determining the mechanisms underpinning invasion success has focussed on aspects of the ecology and physiology of the species in the introduced range. Through the application of biogeographic approaches, however, a growing body of research highlights insights that stem from studying invasion success as a biogeographic issue. In particular, a comparison of both biogeographic regions (i.e. the native and introduced ranges) allows exclusive insight into seven different major biogeographic hypotheses that we identified to explain invader success. These include the enemy release hypothesis, niche shifts, trait differences, the evolution of invasiveness, native allies, environmental matching and genetic diversity. All imply a difference or gradient between the ranges that may mechanistically explain an invader's differential performance. This review summarizes the support for these seven different theories underpinning the biogeography of marine invasions and also provides case studies for different theories addressing the comparative biogeography of marine invasions. Additionally, we catalogue the geographic regions of the invasive species used in biogeographic comparisons and the diversity of species, habitats and climate zones examined. Finally, we highlight critical knowledge gaps and suggest future research directions for improving our understanding of the processes driving invasion success.

Introduction

Invasive species are a major source of economic and biodiversity loss globally – costing $100 billion annually in the United States alone (Pimentel et al. 2005, Meyerson et al. 2019). In the most extreme cases, invasive species can alter native environments, upsetting the balance of native ecosystems by displacing native biota and destabilizing microenvironments (Wright & Gribben 2008, Simberloff et al. 2013, Gribben et al. 2017, 2018). However, not all introduced species are successful, let alone problematic or invasive. Many species fail upon introduction; others form only small, localised populations. Williamson & Fitter (1996) proposed the tens rule, which stipulated that, on average, about 10% of introduced species go on to become invasive, and about 10% of those reach pest (i.e. problematic) status, although there is no quantitative rationale underpinning this rule. A recent quantitative meta-analysis suggests that the percentage of introduced species that can transition along the invasion pathway may, in fact, be much higher than this, specifically about 25%

of non-native plants and invertebrates and about 50% of non-native vertebrates (Jeschke & Pysĕk 2018). Regardless, a major interest in the field of biological invasions has been to determine which species would be successful and in what places.

The field of comparative biogeography was recognised by invasion biologists as a useful tool to examine whether there were ways to predict which species perform better in their invasive range (Crawley 1987, Lonsdale & Segura 1987, Van Kleunen et al. 2010, Parker et al. 2013). Differences in species performance that were uncovered might suggest insight into the processes that enable the establishment and spread of species once introduced to a new location. Comparative biogeography also offered a means to test mechanistic theories that had been developed to explain the differential success of invasive species over natives. The gist of these biogeographical comparisons was to ask whether there were environmental or biotic differences in the native versus introduced range that might suggest a context dependency to the success of the invasive species. Such biological differences that depend on context might include a species entering an environment with fewer predators, parasites or competitors. Absent such differences, the success seemingly stemmed from innate taxonomic or physiological characteristics of the species itself, suggesting its invasion had only been hindered by a previous lack of necessary dispersal capabilities (Byers 2009).

Several mechanistic theories have been developed and tested to explain the establishment and spread of invasive species and their differential success over native species (Table 1). Some of these, like propagule pressure or quality (Marshall et al. 2003, 2006, Hollebone & Hay 2007b, Warren et al. 2012, Uyà et al. 2018), disturbance (Hobbs & Huenneke 1992, Burke & Grime 1996, Byers 2002a, Uyà et al. 2017, 2020) and their interaction (Thomsen et al. 2006, Clark & Johnston 2009, Bulleri et al. 2020), require no biogeographic comparisons and simply ask whether the presence/absence or degree of these factors in the introduced range enhances invasion. In the invasion literature, to explore successful invasion, there are three main types of comparative studies. Two of these look exclusively within the introduced ranges and compare invasive introduced species to closely related native species or non-invasive introduced species (Reichard & Hamilton 1997), examining how much relatively better performing they are. The third is the one that we focus on here, which is biogeographical comparisons of an invasive species in its native vs introduced range to ask whether an invasive species' success is related to a change in its performance between ranges and to what factors such a change might be attributed. It is common for invasive species to be non-problematic in their native range (Williamson & Fitter 1996), so determining what has released a species and is causing it to perform differently is of key interest.

To be clear, both introduced range studies and those that involve native and introduced range comparisons often investigate common processes (see Table 1). For example, changes in competition and/or predation can underpin both the escape from natural enemies (studied across both ranges) and biotic resistance (studied in the introduced range only) hypotheses, and a change in positive interactions with native species is central to both the acquisition of native allies (studied across both ranges) and biotic assistance (studied in the introduced range only) hypotheses. One could then ask, 'What is to be gained by having separate hypotheses addressing similar processes?' A key gain may be in the perspective inherent to each. Introduced range studies often emphasise how the invader compares *interspecifically* to the native species around it and also how these interactions might regulate an invader's success or impacts in its introduced range. In contrast, comparative biogeographic approaches (i.e. native-introduced range studies) often compare an invader *intraspecifically* across its two ranges to examine what traits, processes or interaction strengths may explain invasive range success. Thus, the study approach employed will be specific to the question that is being addressed. Essentially, both types of studies ask very different questions, which often do not necessarily inform each other, nor do they need to. Introduced range only studies can demonstrate why an invader is successful and impactful. But without a biogeographic context, those studies cannot speak to the specific mechanism from which such an advantage to the invader stems – for example, inherently advantageous traits, a sufficiently different biotic or abiotic environment that enables success or

Table 1 Hypotheses for the success of invasive species and whether addressing these hypotheses requires assessment in both the native and introduced range (grey rows) or the introduced range (blue rows) only. Thus, the former category represents the true biogeographic comparisons.

Hypothesis	Definition	Ranges required	Key studies
Enemy release	Loss of natural enemies that control population growth	Both	(Keogh et al. 2017)
Acquisition of native allies	The number or strength of positive interactions with native species differs in the introduced compared with native range	Both	(Reinhart & Callaway 2006, Stout & Tiedeken 2017; Gribben et al., 2020)
Evolution of invasive success	Invaders experience rapid genetic and/or phenotypic changes to new selection pressures (biotic and abiotic) in the introduced range that enhance invasion success (e.g. via increasing competitive ability or acquisition of resources)	Both	(Blossey & Notzold, 1995, Daehler & Strong 1997, Howard et al. 2018)
Founder effects	Degree of reduction in genetic diversity in invasive population	Both	(Roman & Darling 2007, Lejeusne et al. 2014)
Traits	A shift in traits that likely reflects a change in invader fitness in the invasive range	Both	(Grosholz & Ruiz 2003, Gribben et al. 2013)
Environmental matching	Suitability of invasive range to meet the abiotic requirements of the invasive species	Both	(Iacarella et al. 2015, Cope et al. 2019)
Niche shift	Invasive species undergoes changes in environmental (abiotic and/or biotic) niche use or tolerance	Both	(Tepolt & Somero 2014, Sotka et al. 2018, Gewing et al. 2019)
Biotic resistance	The strength of negative interaction (predation and competition) by native species on invading species that slow or preclude establishment and spread of invader	Introduced	(Kimbro et al. 2013, Gribben et al. 2017, Gribben et al. 2018)
Biotic assistance	The strength of positive interaction (facilitation) by native species on invading species that aids establishment and spread of invader	Introduced	(Thomsen & McGlathery 2005, Altieri et al. 2010, Byers et al. 2012, Wright et al. 2016, Wright et al. 2018)
Superior competitive ability	Invader outcompetes native analogues to accrue niche space	Introduced	(Byers 2000, Britton-Simmons 2006, Byers 2009)
Empty niche	Invasive species utilise resources unused by native species	Introduced	(Elton 1958, Levine & D'Antonio 1999, Mack et al. 2000)
Disturbance	Invasive species are better adapted to disturbance	Introduced	(Byers 2002a, Bando 2006, Bulleri et al. 2016, Uyà et al. 2017, 2018)
Species richness	Species-rich communities are more resistant to invasion than species-poor communities	Introduced	(Stachowicz et al. 1999, Clark & Johnston 2011)
Habitat availability	Invasive population size is affected by suitable habitat	Introduced	(Byers 2002b, Gribben et al. 2015, Wright et al. 2016, Wright et al. 2018)
Propagule pressure/ quality	A metric of the intensity of introduction that is often highly positively correlated with establishment and spread of invaders	Introduced	(Clark & Johnston, 2009, Uyà et al. 2018)

Source: Adapted from Hierro et al., 2005. *Journal of Ecology* 93, 5–15.

evolutionary change that has occurred in the invader during or after introduction. Biogeographic comparisons seek such larger mechanistic understanding, and reviews of biogeographic comparisons seek common trends as a step toward predicting invasion success.

Biogeographically relevant hypotheses to explain invader success implicate favourable, and sometimes superior, aspects in the introduced versus the native range. These aspects pertain to one of three areas – 1) the abiotic environment, 2) the biological community or 3) traits of the invasive species itself. First and foremost, the abiotic environment of the invasive range must be suitable (i.e. similar) to the native range. Usually these conditions will match the native range conditions since those are the ones to which the species has adapted for thousands of years. Some studies invoke a compatible, or possibly a more favourable, abiotic environment in the introduced range as a reason for success. Habitat or niche modelling, often approached through joint probability distribution modelling like maximum entropy (maxent), has become a popular approach to determine whether a species can thrive in a new region (Kumar & Stohlgren 2009, Byers et al. 2013, McDowell et al. 2014, Jarnevich & Young 2015). Essentially, these studies examine whether an introduced region matches the native region in the fundamental niche. Data fed into these models are often mostly, if not exclusively, abiotic. Often these models are run only in the introduced range (provided the invader has spread sufficiently to supply the model with enough data for training). But effective approaches have used environmental data and presence/absence locations for a species in its native range to train a niche model and then predicted the species distribution in the introduced range (Verbruggen et al. 2013, Crafton 2015, Robinson et al. 2017).

Second, assuming the abiotic environment in the introduced range provides the proper fundamental niche, differences in the biological community may be considered next to help explain changes in the realised niche that could contribute to invasive success. Most commonly invoked in the area of biological community is the hypothesis of enemy release (Mitchell & Power 2003, Callaway et al. 2004), which refers to the fitness advantage caused by a reduction in predators, parasites, pathogens or competitors in the invasive range compared with the native range.

Often within the introduced range alone, native species richness has been examined as an important mediator of invasion success, with less diverse communities considered to offer more unexploited niche opportunities for invasive species (Stachowicz et al. 1999, Byers & Noonburg 2003, Clark 2013). Similarly, reductions in the density, cover or biomass of spatially dominant species such as foundation species (*sensu* Dayton 1972) can promote the establishment of non-native species by increasing access to limiting resources such as space and light (Valentine & Johnson 2003, Uyà et al. 2018) and by altering below-ground processes, often under microbial control, to the benefit of invasive species (Gribben et al. 2017, 2018; Bulleri et al., 2020). Many mechanisms of invasive success can be addressed without a biogeographical approach (Table 1). In fact, those studies, perhaps due to their relative ease, are far more common. To be clear, the success of an invasive species can often be shown with only evidence gathered in the invasive range. But knowing whether a species is succeeding because of inherently superior traits or because of conditions that are more favourable in the introduced range helps predict future range expansions of that species and the invasion success of other species emanating from the same region or of similar phylogeny. However, studies are rare that quantify differences in the biological community between the native and invasive ranges. Torchin et al. (2003) and Mitchell & Power (2003) compared parasite prevalence and richness patterns in animals and plants, respectively, between the native and introduced range and found substantial support for lower parasite richness in the introduced range. Fewer still are studies that document whether fitness advantages result from the observed reductions in enemies (but see Keogh et al. 2017). Addressing the question of whether invasion success is, in fact, underpinned by higher abundances and/or changes in life-history traits in the introduced compared with native ranges, and the mechanisms that may drive any such shifts, requires biogeographic approaches that incorporate biological and ecological information from both ranges. Thus, biogeographic approaches to invasion success can yield important insights that invasive range-only studies cannot resolve.

Third, the invasive species itself may have traits that help it operate well or better in the introduced range. The rapid spread and impacts of invasive species may be underpinned by changes in key life-history traits (e.g. larger body size) allowing higher abundances in their introduced compared with their native range (Grosholz & Ruiz 2003, Levine et al. 2003, Gribben et al. 2013). However, broad analysis has provided only mixed evidence for enhanced traits in invasive species related to reproduction, size and abundance (Parker et al. 2013). Sometimes the performance of traits is due to a fortuitous matching of the invasive species with an environment where its traits prosper; other times, heightened performance is hypothesised to be due to changes to a species that occur in the introduced range after the introduction process. Such evolution of invasiveness may give invaders enhanced resource acquisition in the introduced compared with the native range. For example, changes in traits may give invasive predators enhanced ability to capture prey. Alternatively, trait shifts may lead to an increase in competitive ability (Blossey & Notzold 1995). For invasive terrestrial plants, a relaxation of natural enemies in the introduced range can enable them to reallocate resources from defence mechanisms into growth and development, thereby evolving to grow taller, produce more biomass and yield more offspring than their native counterparts (Blossey & Notzold 1995, Daehler & Strong 1997). Sotka et al. (2018) showed that invasive species can evolve rapidly in their new environments. Specifically, with a genetically informed climatic niche shift analysis, they demonstrated that native source populations of the red seaweed *Agarophyton vermiculophyllum* occur in colder and highly seasonal habitats, while most invasive populations occur in warmer, less seasonal habitats. This climatic niche expansion predicts that invasive populations evolved greater tolerance for elevated heat conditions relative to native source populations.

As this last example demonstrates, traits may be under genetic control. Thus, many studies directly compare the difference in a species' genetic diversity between the native and introduced range. Authors do not typically link genes to traits; rather, they often infer that reduced genetic diversity compromises a species' ability to adapt well. Although theoretically, genetic bottlenecks are supposed to occur during the introduction process and decrease species' genetic potential to adapt to new environments, genetic bottlenecks in invasive species may not be as frequent as thought (Roman & Darling 2007).

Traditionally, evidence for life-history or abundance shifts of invasive species between introduced and native ranges has come from terrestrial ecosystems (Hierro et al. 2005, Parker et al. 2013). However, for marine invasive species, over the past 15 years or so, evidence for biogeographic changes in their introduced compared with native range has also been steadily increasing for numerous species. An early multispecies review of the published literature by Grosholz & Ruiz (2003) showed that 12 of 19 invertebrate species had higher body size in their introduced range. Providing additional support are the numerous intraspecific biogeographic comparative studies. Such studies clearly show differences in genetic diversity for many taxa, reduced enemies (e.g. parasites) for several invertebrates (Torchin et al. 2001, 2003), increased chemical differences in algae (Hammann et al. 2013), higher abundances and trait increases (e.g. body size; Gribben et al. 2013) of invasive species in their introduced compared with native ranges. Trait increases can also enhance the acquisition of resources. For example, higher attack rates and lower feeding times for the European green crab, *Carcinus maenas,* were related to larger claw size in crabs from some introduced compared with native populations (Howard et al. 2018). Whether larger claw size gives *C. maenas* enhanced competitive ability over native consumers of the same prey is unknown. In addition, recent studies highlight the positive effects native species can have on invader abundance in the introduced range (Rodriguez 2006, Bulleri et al. 2008, Northfield et al. 2018). As an example, Gribben et al. (2020) showed that the abundance of the porcelain crab *Petrolisthes elongatus* in its introduced range was facilitated by the presence of a habitat-forming tubeworm under boulders that was largely absent from its native range. This suggests the acquisition of native allies may also be an important process in determining shifts in the abundance of invasive species (see Reinhart & Callaway 2006, Stout & Tiedeken 2017 for terrestrial examples).

Support for these biogeographic shifts comes from an increasing number of species from a diverse range of marine taxa, including, but not restricted to, ascidians (Gewing et al. 2019), crustaceans (Torchin et al. 2001, Gribben et al. 2013), molluscs (Blakeslee et al. 2012, Riquet et al. 2013), algae (Krueger-Hadfield et al. 2016, Wang et al. 2017), plants (Allen et al. 2015, Guo et al. 2016), cnidarians (Bolton & Graham 2004, Govindarajan et al. 2017) and fish (Cure et al. 2012, Evangelista et al. 2016).

Given the burgeoning interest and increasing number of studies conducting biogeographic comparisons, it is timely to review the current state of knowledge of the evidence for demographic and population changes across native and introduced ranges. In doing so, we also investigate the support for different biogeographic theories underpinning these patterns. In the following sections, we review the current understanding of the biogeography of marine invasions by: 1) providing an overview of published studies of comparative biogeography of marine invasions (e.g. including a synthesis of the locations and habitat in which they have been described, and the species they involve); 2) summarising evidence for various mechanisms underpinning changes in life-history and population characteristics; 3) providing case studies for different mechanisms of a few well-studied examples and 4) discussing key research gaps and providing recommendations for future research into how these studies may improve our understanding of species distributions at biogeographic scales.

Overview of published introduced and native range comparisons

Literature search

We explored the evidence for the key hypotheses (e.g. the enemy release hypothesis, acquisition of native allies, shifts in resource acquisition and/or increased competitive ability, changes in traits, niche shifts, founder effects) that have been the focus of introduced/native range biogeographic comparative studies. We also determined what species were the focus of this research and explored the geographic regions across which biogeographic comparisons were made. For the search of each individual hypothesis, we included terms for native and introduced range because we wanted to capture the literature that specifically addressed hypotheses that required native-introduced range comparisons. *Thus, from our search, only papers that report both introduced and native comparisons in their abstracts were considered further.* For each search, we also included search terms to capture both marine and estuarine studies and those that used different methodologies (e.g. experimental or comparative surveys). Full search terms, and the number of papers returned under the searchers, for each of our hypotheses investigated are shown in Supplementary Table 1. All searches were conducted using the Web of Science database by searching the terms in the 'All Fields' category between January 28 and February 4, 2019. Initially we captured 3647 papers, many of which were conducted in the introduced range only and were immediately excluded.

We created two separate databases for papers: one for those that measured shifts in individual, population, and trait metrics (hereafter referred to as 'IPT' papers) and one that measured shifts in genetic diversity between native and introduced ranges. We kept these two categories separate because the metric for genetic studies (genetic diversity) is distinctly different from the trait and population metrics used in the IPT papers. Also, the number of genetics papers was large, and we did not want them to overwhelm interesting physiological and ecological patterns in a combined database. For all papers, we only retained papers that used first-hand collected data from both ranges. We did not consider papers that made comparisons using previously published data. That excluded many studies in this category where, for many, the focus was largely on the introduced range, with only brief ad hoc comparisons with published data from the native range (e.g. Hollebone & Hay 2007a). For the genetics papers, we additionally excluded all those whose primary objective was to determine source populations or range expansions and did not provide easily extractable tests for shifts in genetic diversity between native and introduced ranges. That is, it was beyond our scope to distil more sophisticated tests that compare genetic structure (e.g. discriminant analysis of principal components relationships among microsatellite genotypes).

For all papers retained, we extracted the following information: date of publication, phylum (e.g. crustacean, mollusc, plant, alga etc.), species identity, regions studied in both ranges (based on oceanographic boundaries as defined by the International Maritime Organisation) and climate zones (binned into traditional zones; Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°) in which populations were sampled in both ranges. We also extracted information on the habitat occupied (hard substrata, sedimentary or pelagic) and tidal height (intertidal, subtidal or pelagic). Hard substrata included both natural (e.g. rocky shores) and artificial substrata, and sedimentary habitats included unvegetated sediments and habitats associated with sediments (e.g. seagrass). We also noted the theory addressed. Often the theory was not explicitly stated, so we assigned theory, where possible, based on the variables measured. Finally, we also noted study type (e.g. comparative surveys, experimental or both) and whether the theory predictions were supported. Often, within papers, there were multiple measures which presented opposing evidence. In these instances, we determined whether there was overall support for the theory addressed based on all the evidence presented. We also provide case studies for individual species that have been a particular focus of biogeographic work and thus provide extended evaluation of various hypotheses.

Results

Of the 3647 papers our searches initially returned, we retained 56 IPT and 29 genetics papers (Tables 2 and 3). Most of the papers only examined species in their introduced range and therefore did not meet our criterion of a biogeographical comparison. The numbers of studies recorded for both IPT and genetics followed similar patterns, steadily increasing for the past 15 years (Figure 1).

In total, both IPT and genetics papers recorded similar numbers of native (25 and 28, respectively) and introduced (28 and 26, respectively) regions studied. For the IPT studies, the Sea of Japan (7 papers), Northwest Pacific (8 papers) and Northeast Atlantic (6 papers) and for the genetics papers the Northwest Atlantic (4 papers) were the most recorded native regions studied (Figure 2A,B; Tables

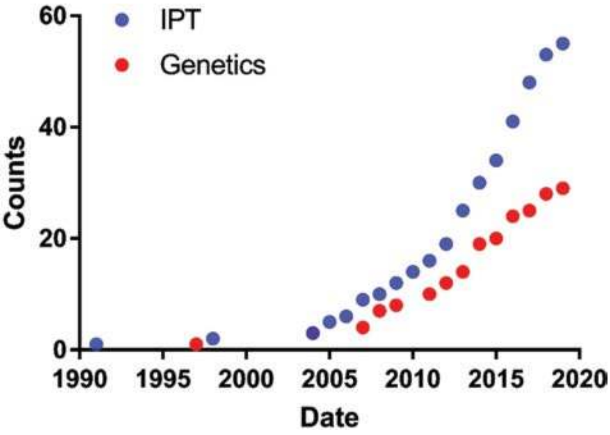

Figure 1 Cumulative list of publications over time of biogeographical comparisons meeting our criteria for inclusion in this review. The publications are categorised into two groups – those that examine individual, population and trait (IPT) metrics and genetic diversity.

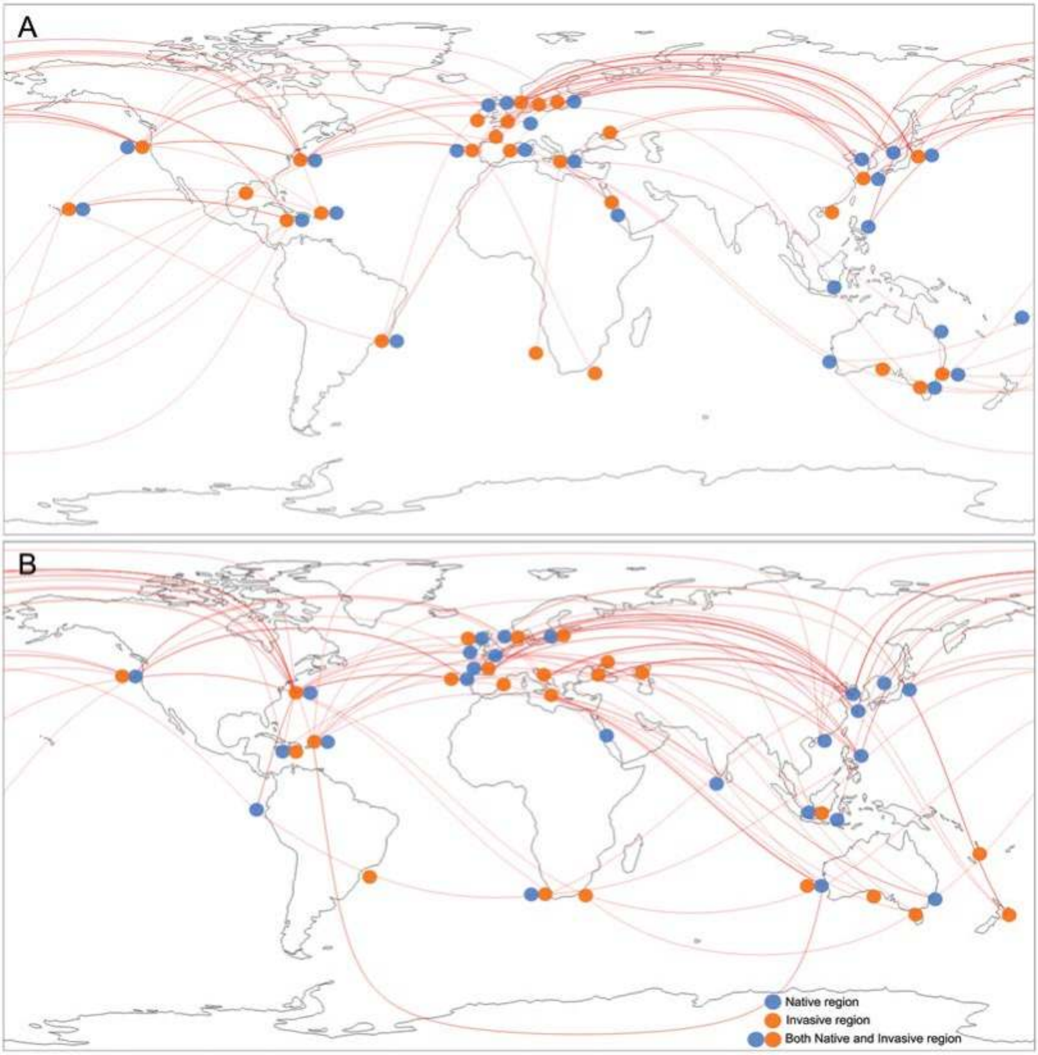

Figure 2 Maps showing native and invasive regions studied for individual population and trait papers (A) and genetics papers (B) retained in our review. For each paper, regions were counted only once if multiple populations were sampled within a region. Solitary dots highlight regions that were only found to be native species regions (blue) or invaded regions (orange) within studies. Regions with both blue and orange dots are both suppliers and receivers of introduced species. Lines always connect blue to orange dots. If it appears otherwise, it is because of a resolution issue in a region that serves as both native and introduced region. Darker lines indicating increased numbers of studies connect the native and recipient regions.

2,3). For both IPT and genetics studies, the Northeast Pacific (13 and 9, respectively), the Northwest Atlantic (13 and 8, respectively) and the Mediterranean Sea (7 and 4, respectively) were the most recorded introduced regions (Figure 2A,B; Tables 2,3).

For the IPT papers and genetics papers, algae and molluscs were the most studied taxonomic groups, respectively, accounting for ~37% of papers in each group (Figure 3A,B). For both IPT and genetics papers, crustaceans and fishes were the next most common taxonomic groups studied (Figure 3A,B). Patterns of species richness within each taxonomic group recorded (Figure 3C,D) were similar to those for number of studies on each taxonomic group.

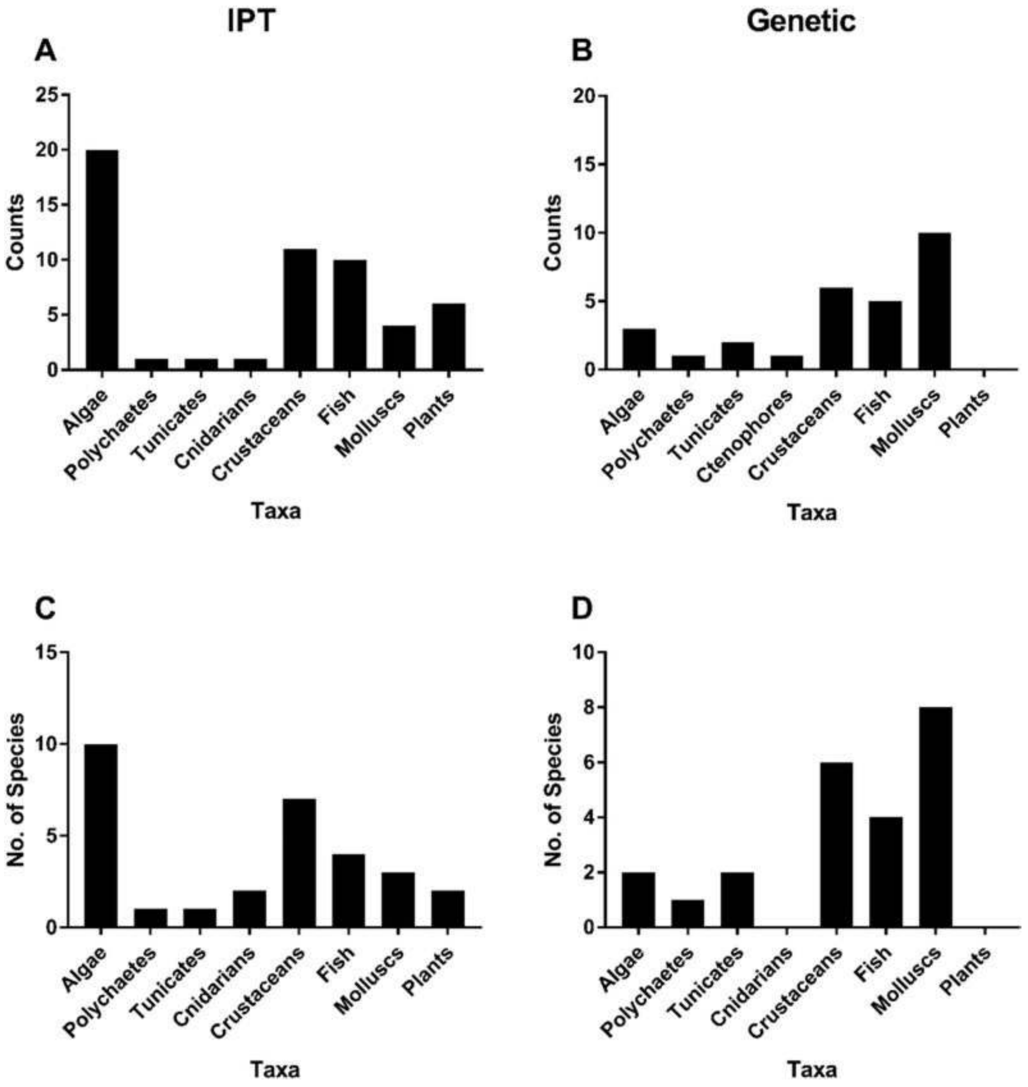

Figure 3 Number of individual population and trait (IPT) and genetic studies within taxonomic group (A,B, respectively) and diversity of species studied within each taxonomic group (C,D, respectively) investigating changes in invasive species across their native and introduced ranges.

For both IPT and genetics papers, across both ranges, most studies (~50%) were conducted in the temperate zone, followed by subtropical and tropical zones (Figure 4A,B). No studies were recorded from either range in polar regions. Within individual studies, the majority recorded similar climate regions for both the native and introduced ranges. Across all studies, there were only three instances where the climate in the native range of study was noted as temperate and in the introduced range as tropical (see Kappas et al. 2004, Riquet et al. 2013, Zanolla et al. 2015, Tables 2,3).

Most studies were conducted on hard substrata (61% and 76% for IPT and genetics studies, respectively), although there was a higher proportion of studies conducted in sedimentary environments for IPT compared with genetic studies (29% and 13%, respectively; Figure 5A,B). Studies conducted in pelagic environments were uncommon. Studies were relatively common at both intertidal and subtidal elevations and rare in pelagic environments (Figure 5C,D).

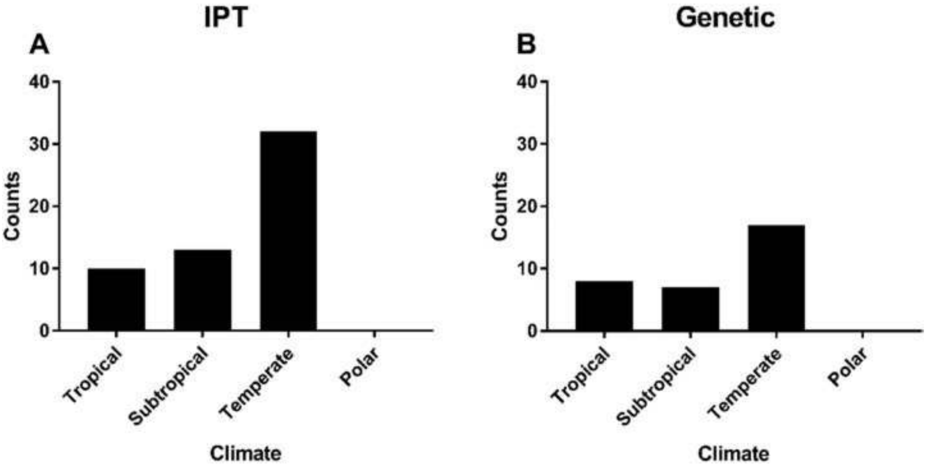

Figure 4 Number of individual, population and trait (IPT) and genetic studies according to the climatic regions of the focal species' introduced range.

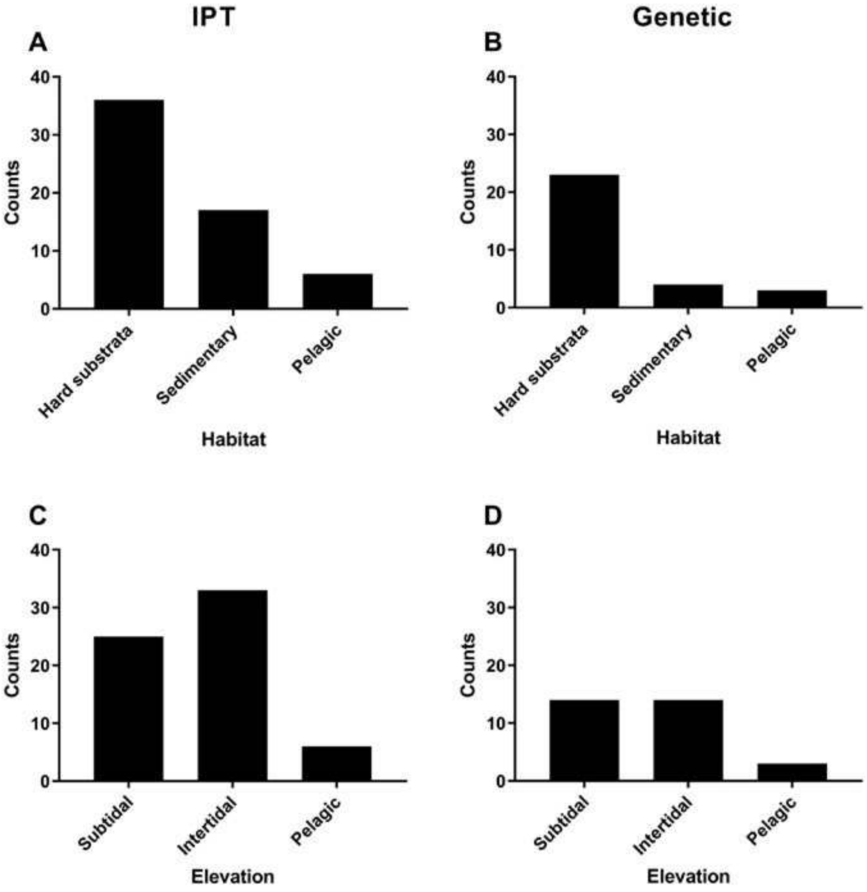

Figure 5 Habitats (A,B) and elevations (C,D) recorded for individual population and trait (IPT) and genetic studies, respectively. Hard substrata, sedimentary, subtidal and intertidal categories were used for species associated with the benthos, while species more closely associated with the water column were termed pelagic.

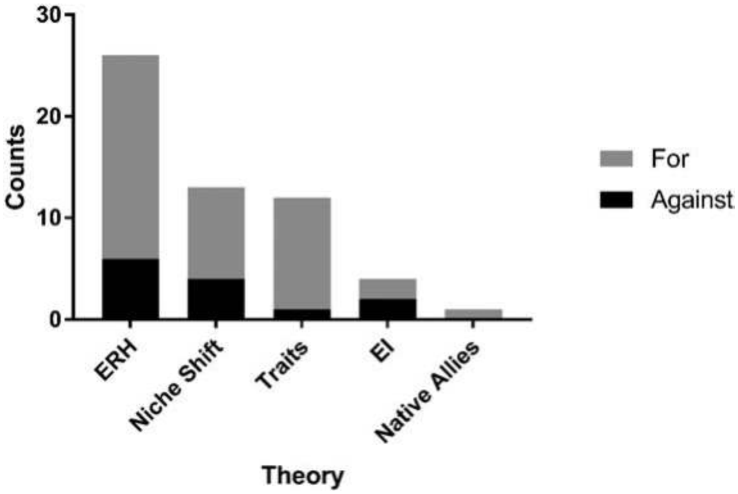

Figure 6 The number of individual population and trait (IPT) papers retained in this review investigating different comparative biogeographic theories to explain invader success (e.g. enemy release [ERH], niche shifts, traits, evolution of invasiveness [EI], and native allies). Grey and black bars indicate number of papers showing support for or against each theory, respectively.

For IPT, the enemy release hypothesis (ERH; 46% of studies) was the most common theory tested, followed by niche shifts (23% of studies) and traits (22% of studies; Figure 6). Overall, there was strong support for the ERH, niche shift and trait theories (Figure 6, Table 2). Support for evolution of invasibility was evident in two out of the four studies that addressed this theory. For the genetics studies, genetic diversity was lower (e.g. in support of founder effects) in 75% studies (Table 3). IPT studies generally employed either mensurative (29 studies) or experimental approaches (21 studies), and only in a few instances did they employ both (6 studies; Table 2). All genetics papers except one were mensurative (Table 3).

For the ERH, because of the higher number of studies recorded (Figure 6), we further explored patterns within this hypothesis. No taxonomic group was particularly over-represented across all ERH studies; however, algae (4 species across 11 studies) and fish (3 species across 8 studies) were the most common taxa studied. *Agarophyton vermiculophyllum* was the most studied alga (6 studies), whereas *Pterois volitans* and *Planiliza haematocheilus* (3 studies each) were the most studied fish species. The most common home ranges studied were the Sea of Japan (7 studies), Northeast Atlantic (5 studies) and Northwest Pacific (5 studies). The introduced ranges featuring in the highest number of studies were the North Sea (8 studies), Northwest Atlantic (6 studies), Northeast Pacific and Baltic Sea (5 studies each). Hard substrata/intertidal habitats (11 studies) were the most common habitat combination studied, followed by hard substrata/subtidal (7 studies), sedimentary/intertidal habitats (5 studies), and pelagic habitats (4 studies). Sedimentary/subtidal habitats were not recorded for any study of the ERH.

Evidence for different hypotheses explaining biogeographic shifts in invasive species

Enemy release hypothesis

The enemy release hypothesis is the most addressed biogeographic theory (Box A; *Littorina littorea*) and one of the hypotheses which received the strongest support, approximately 83%. Much evidence supports the pattern that fewer enemies are present in the introduced range, including predators,

Table 2 List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Allen et al. 2015. *Biological Invasions* 17: 3419–3432	*Phragmites australis*	Grass	NE Atlantic	Temperate	NW Atlantic Gulf of Mexico	Subtropical temperate	Sedimentary	Intertidal	Mensurative	Lipara infestation	Higher and Lower	ERH	Mixed
Allen et al. 2015. *Biological Invasions* 17: 3419–3432	*Lipara* spp.	Grass	NE Atlantic	Temperate	NW Atlantic Gulf of Mexico	Subtropical temperate	Sedimentary	Intertidal	Mensurative	Abundance	Higher	ERH	Yes
Aires et al. 2013. *PLOS ONE* 8: 11	*Caulerpa cylindracea*	Alga	SE Indian Ocean	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Bacterial communities	Higher	Native allies	Yes
Arias et al. 2013. *Estuarine, Coastal and Shelf Science* 131: 117–128	*Perinereis linea*	Worm	Yellow Sea	Subtropical	Mediterranean	Temperate	Sedimentary	Intertidal Subtidal	Mensurative	Variation taxonomic characteristics Reproductive plasticity	Lower Higher	Trait	Yes
Bippus et al. 2018. *Marine Biology* 165: 39	*Agarophyton vermiculophyllum*	Alga	East China Sea Sea of Japan	Subtropical Temperate	NE Pacific NW Atlantic North Sea Kattegat NE Atlantic	Temperate	Sedimentary	Intertidal	Experimental	Palatability	Equal	ERH	No
Blakeslee et al. 2012. *Journal of Biogeography* 39: 609–622	*Littorina saxatilis*	Snail	NW Atlantic	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Parasite load Parasite richness	Lower Lower	ERH	Yes
Calvo-Ugarteburu & McQuaid. 1998. *Journal of Experimental Marine Biology* 220: 47–65	*Mytilus galloprovincialis*	Mussel	Mediterranean	Temperate	SE Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Parasite prevalence	Equal	ERH	No

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Table 2 (*Continued*) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Cure et al. 2012. *Marine Ecology Progress Series* 467: 181–192	*Pterois volitans*	Fish	Philippines Sea N Pacific	Tropical	W Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Foraging time Prey size Foraging behaviour	Equal Higher Lower	Trait	Yes
Davidson et al. 2008. *Biological Invasions* 10: 399–410	*Sphaeroma quoianum*	Isopod	Bass Strait	Temperate	NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal	Mensurative	Population density Habitat use Salinity Range	Higher Similar Similar	Niche shift	No
Davis 2005. *Evolutionary Ecology* 19: 255–274	*Spartina alterniflora*	Grass	NW Atlantic	Subtropical	NE Pacific	Temperate	Sedimentary	Intertidal	Experimental	Reproductive effort Size at reproduction Death rate	Higher Lower Higher	Traits	Yes
Forslund et al. 2010. *Oecologia* 164: 833–840	*Fucus evanescens*	Alga	NE Atlantic	Temperate	Kattegat	Temperate	Hard substrata	Intertidal	Experimental	Palatability	Lower	ERH	Yes
Gewing et al. 2019. *Biological Invasions* 21: 349–361	*Herdmania momus*	Ascidian	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Experimental	Temperature tolerance	Higher	Niche shift	Yes
Glasby. 2007. *Marine Biology* 152: 255–263	*Caulerpa taxifolia*	Alga	Coral Sea	Tropical Subtropical	Tasman Sea	Subtropical	Hard substrata Sedimentary	Subtidal	Experimental	Growth response to temperature	Lower or Equal	Niche shift	No
Gribben et al. 2013. *Biological Invasions* 5: 1877–1885	*Petrolisthes elongatus*	Crab	SW Pacific	Temperate	Tasman Sea Bass Strait	Temperate	Hard substrata	Intertidal	Mensurative	Abundance Male biomass Female biomass Sex ratio	Higher Higher Equal Equal	Traits	Yes
Guiry & Dawes 1992. *JEMBE* 158: 197–217	*Asparagopsis armata*	Alga	Bass Strait	Temperate	Celtic Sea Mediterranean	Temperate	Hard substrata	Subtidal	Experimental	Reproductive success	Higher	Trait	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Guo et al. 2016. *Biological Invasions* 18: 2555–2561	*Phragmites australis*	Grass	Mediterranean	Subtropical	NW Atlantic	Subtropical	Sedimentary	Intertidal	Experimental	Chlorophyll concentrations Photosynthetic assimilation Shoot number Shoot height	Lower Lower Higher Higher	Niche shift	Yes
Guo et al. 2014. *Ecology and Evolution* 4: 4567–4577.	*Phragmites australis*	Grass	North Sea Baltic Sea Adriatic Sea	Temperate	NW Atlantic	Temperate	Sedimentary	Intertidal	Experimental	Biomass allocation Stem diameter Nitrogen use efficiency Construction costs	Higher Higher Higher Higher	Trait	Yes
Hammann et al. 2013 *Marine Ecology Progress Series* 486: 93–101	*Agarophyton vermiculophyllum*	Alga	East China Sea Yellow Sea	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate Subtropical	Hard substrata	Intertidal Subtidal	Experimental	Biomass consumption C:N ratios	Lower Higher	ERH	Yes
Hammann et al. 2016. *Harmful Algae* 51: 81–88	*Agarophyton vermiculophyllum*	Alga	Sea of Japan Yellow Sea	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate subtropical	Sedimentary	Intertidal	Experimental	Chemical compounds	Higher	ERH	Yes
Hammann et al. 2016. *Marine Biology* 163: 104	*Agarophyton vermiculophyllum*	Alga	Sea of Japan	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate subtropical	Sedimentary	Intertidal	Experimental	Heat stress survival HSP70 expression	Higher Higher	Niche shift	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Henkel et al. 2009. *Marine Ecology Progress Series* 386: 1–13	*Undaria pinnatifida*	Alga	Sea of Japan	Temperate	NW Pacific	Subtropical	Hard substrata	Intertidal Subtidal	Experimental	HSP70 expression	Equal	Niche shift	No
Howard et al. 2018. *PeerJ* 6: 22	*Carcinus maenas*	Crab	Inner Seas	Temperate	SW Atlantic NE Pacific NW Atlantic	Subtropical temperate	Hard substrata	Intertidal	Both	Foraging behaviour Morphology Prey handling time Feeding rates	Higher Higher Lower Higher	Evolution of invasibility	Yes
Kappas et al. 2004. *Marine Biology* 146: 103–117	*Artemia franciscana*	Shrimp	NE Pacific	Temperate	South China Sea	Tropical	Pelagic	Pelagic	Both	Reproductive output at high temperatures	Higher	Niche shift	Yes
Keogh et al. 2017. *Ecology*. 98: 2241–2247	*Hemigrapsus sanguineus*	Crab	NW Pacific Sea of Japan	Temperate	NW Atlantic	Temperate	Hard substrata	Intertidal	Both	Parasite load Infection rate O_2 consumption	Lower Higher Lower	ERH	Yes
Krueger-Hadfield et al. 2016. *Molecular Ecology*. 25: 3801–3816	*Agarophyton vermiculophyllum*	Alga	NW Pacific	Temperate	NW Atlantic NE Atlantic NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal Subtidal	Mensurative	Life cycle complexity	Lower	Niche shift	Yes
Marquet et al. 2013. *Biological Invasions* 15: 1253–1272	*Mytilus galloprovincialis*	Mussel	NE Atlantic	Temperate	SW Indian Ocean	Temperate	Hard substrata	Intertidal	Mensurative	Endolithic infestation Mortality	Higher Higher	ERH	No
McGaw et al. 2011. *Marine Ecology Progress Series* 430: 235–240	*Carcinus maenas*	Crab	Irish Sea	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Body size	Higher	Trait	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Meyer & Dierking 2011. *Marine Ecology Progress Series* 439: 203–212	*Cephalopholis argus*	Fish	S Pacific	Tropical	N Pacific	Tropical	Pelagic	Pelagic	Mensurative	Length Biomass Growth Body condition Stomach vacuity rate Diet breadth	Higher Higher Higher Higher Lower Higher	ERH	Yes
Pascual et al. 2015. *Marine Ecology-an Evolutionary Perspective* 36: 994–1002.	*Aurelia aurita*	Jellyfish	Balearic Sea	Temperate	Red Sea (Gulf of Eilat) Baltic Sea	Subtropical temperate	Pelagic	Pelagic	Experimental	Survival Asexual reproduction rate Offspring	Lower or Equal Higher or Equal Higher or Lower	Niche shift	Mixed
Pechenik et al. 2017. *Invertebrate Biology* 136: 394–402.	*Crepidula fornicata*	Snail	NW Atlantic	Temperate	North Sea	Temperate	Hard substrata	Intertidal	Mensurative	Egg capsule size Egg density Egg capsules per brood	Higher Higher Equal	Niche shift	Yes
Pickholtz et al. 2018. *Biological Invasions* 20: 3499–3512.	*Siganus rivulatus*	Fish	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Home range movement Site fidelity	Higher Lower	Trait	Yes
Pusack et al. 2016. *Environmental Biology of Fishes* 99: 571–579.	*Pterois volitans*	Fish	SW Pacific	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Total length	Higher Higher	ERH	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Qing et al. 2012. *Journal of Experimental Marine Biology and Ecology* 416: 230–236	*Spartina alterniflora*	Grass	NW Atlantic	Subtropical	East China Sea	Subtropical	Sedimentary	Intertidal	Experimental	Herbivory tolerance	Higher	ERH	Yes
Ros et al. 2014. *Estuarine Coastal and Shelf Science* 139: 88–98	*Caprella scaura*	Amphipod	SW Atlantic	Subtropical	Balearic Sea	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Diet composition	Equal	Evolution of invasibility	No
Ros et al. 2014. *Estuarine Coastal and Shelf Science* 139: 88–98	*Paracaprella pusilla*	Amphipod	SW Atlantic	Subtropical	Balearic Sea	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Diet composition	Equal	Evolution of invasibility	No
Roth-Schulze et al. 2018. *Limnology and Oceanography* 63: 459–471	*Caulerpa taxifolia*	Alga	SW Pacific	Tropical Subtropical	Great Australian Bight	Subtropical	Sedimentary	Subtidal	Experimental	Growth rate	Equal	Niche shift	No
Saha et al. 2016 *Journal of Ecology* 104: 969–978	*Agarophyton vermiculophyllum*	Alga	East China Sea Yellow Sea	Temperate	Baltic Sea North Sea NE Pacific	Temperate Subtropical	Hard substrata	Intertidal Subtidal	Experimental	Chemical defence against fouling	Higher	ERH	Yes
Sarabeev. 2015. *Parasitology International* 64: 6–17	*Planiliza haematochella*	Fish	Sea of Japan	Temperate	Mediterranean	Subtropical	Pelagic	Pelagic	Mensurative	Parasite richness Parasite assemblage size	Lower Higher	ERH	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Sarabeev et al. 2018. *International Journal for Parasitology* 48: 793–803	*Planiliza haematochella*	Fish	Sea of Japan	Temperate	Sea of Azov	Temperate	Pelagic	Pelagic	Mensurative	Monogenean prevalence Monogenean abundance Diogenean prevalence Diogenean abundance	Equal Higher Higher Higher	ERH	Yes
Sarabeev et al. 2017. *International Journal for Parasitology* 47: 687–696	*Planiliza haematochella*	Fish	Sea of Japan	Temperate	Sea of Azov	Temperate	Pelagic	Pelagic	Mensurative	Total mean parasite abundance	Lower	ERH	Yes
Schaefer & Zimmer. 2013. *Marine Ecology Progress Series* 483: 221–229	*Carcinus maenas*	Crab	Baltic Sea	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Both	Claw size Body size Handling time Handling success	Higher Higher Equal or Lower Equal or Higher	Evolution of invasibility	Yes
Schwartz et al. 2017. *PLOS ONE* 12: e0189761	*Sargassum muticum*	Alga	NW Pacific	Subtropical	North Sea	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Defence chemicals	Lower	ERH	No
Schwartz. et al. 2016. *Marine Biology* 163: 13	*Sargassum muticum*	Alga	NW Pacific	Subtropical	North Sea	Temperate	Hard substrata	Intertidal	Both	Palatability Nutritional value Herbivore preference	Higher Lower Higher	ERH	No

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Shenkar & Loya. 2008. *Biological Invasions* 10: 1431–1439	*Herdmania momus*	Ascidian	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Habitat depth Length Total weight Gonad weight Egg diameter Occurrence of symbionts Reproductive season	Higher Higher Higher Lower Lower Equal Lower	Trait	Yes
Sikkel et al. 2014. *PLOS ONE* 9: 8.	*Pterois volitans*	Fish	Philippines Sea	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Experimental	Parasite susceptibility	Equal	ERH	No
Sotka et al. 2018 *Evolutionary Applications* 11: 781–793	*Agarophyton vermiculophyllum*	Alga	NW Pacific	Temperate	NE Atlantic English Channel North Sea NE Pacific NW Atlantic	Temperate	Sedimentary	Subtidal	Mensurative	Thermal tolerance Salinity tolerance	Higher Higher	Niche shift	Yes
Tepolt & Somera. 2014. *Journal of Experimental Biology* 217: 1129–1138	*Carcinus maenas*	Crab	North Sea NE Atlantic	Temperate	NW Atlantic NE Pacific	Temperate	Hard substrata	Intertidal	Experimental	Gradients in thermal tolerance Acclimation plasticity	Unclear	Niche shift	Yes
Tuttle et al. 2017. *Biological Invasions* 19: 563–575	*Pterois volitans*	Fish	Philippines Sea	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Parasite prevalence	Lower	ERH	Yes
Vermeij et al. 2009. *Biological Invasions* 11: 1463–1474	*Acanthophora spicifera*	Alga	Caribbean	Tropical	N Pacific	Tropical	Hard substrata	Intertidal	Experimental	Herbivory pressure Growth	Lower Higher	ERH	Yes

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Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Vignon et al. 2009. *Parasitology Research* 104: 775	*Cephalopholis argus*	Fish	SW Pacific	Tropical	N Pacific	Tropical	Hard substrata	Subtidal	Mensurative	Parasite prevalence Parasite diversity	Lower Lower	ERH	Yes
Wang et al. 2017. *Journal of Ecology* 105: 445–457	*Agarophyton vermiculophyllum*	Alga	NW Pacific Yellow Sea	Temperate	Baltic Sea North Sea Bay of Biscay	Temperate	Sedimentary	Intertidal	Experimental	Chemical defence against biofouling	Higher	ERH	Yes
Wang et al. 2017. *Marine Biology* 164: 193	*Agarophyton vermiculophyllum*	Alga	NW Pacific	Temperate	Baltic Sea North Sea	Temperate	Sedimentary	Subtidal	Experimental	Biofouling pressure	Lower	ERH	Yes
Wikström et al. 2006. *Oecologia* 148: 593–601	*Fucus evanescens*	Alga	NE Atlantic	Temperate	Kattegat	Temperate	Hard substrata	Intertidal	Both	Herbivore assemblage Herbivore preference Palatability	Lower Lower Lower	ERH	Yes
Wright 2005. *Marine Biology* 147: 559–569.	*Caulerpa taxifolia*	Alga	Coral Sea	Subtropical	Tasman Sea	Subtropical	Sedimentary	Subtidal	Mensurative	Thallus size Thallus density Asexual reproduction Total biomass	Lower Higher Higher Higher	Trait	Yes
Zabin et al. 2007. *Biological Invasions* 9: 523–544.	*Chthamalus proteus*	Barnacle	Caribbean SW Atlantic	Tropical	N Pacific	Tropical	Hard substrata	Intertidal	Mensurative	Habitat use Body size Fecundity	All Equal	Trait	No
Zanolla et al. 2015. *Biological Invasions* 17: 1341–1353.	*Asparagopsis taxiformis*	Alga	Coral Sea	Tropical	Mediterranean	Temperate	Hard substrata	Inter-tidal/ subtidal	Experimental	Photosynthetic plasticity	Higher	Trait	Yes

Table 3 List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Anderson et al. 2017. *Journal of Fish Biology* 91: 558–573	*Chromis limbata*	Fish	SE Atlantic	Tropical	SW Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity – number of haplotypes	Invasion dynamics	Lower	Yes
Andrew & Ward. 1997. *Marine Ecology Progress Series* 152: 131–143	*Sabella spallanzanii*	Worm	Mediterranean English Channel	Temperate	East Indian Ocean Great Australian Bight	Subtropical	Hard substrata sedimentary	Subtidal	Mensurative	Allozyme	Invasion dynamics	Lower	Yes
Blakeslee et al. 2008. *Mol. Ecol.* 17: 3684	*Littorina littorea*	Snail	Skagerrak NE-Atlantic Gulf of Biscay Celtic Sea Irish Sea North Sea English Channel	Temperate	NW Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Cahill and Viard. 2014. *Marine Biology* 161: 2433–2443	*Crepidula convexa*	Snail	NW-Atlantic	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No
Chandler et al. 2008. *Molecular Ecology* 17: 4079–4091	*Rapana venosa*	Snail	Bohai Sea Yellow Sea East China Sea Philippines Sea	Temperate	Black Sea Adriatic Sea Gulf of Biscay English Channel NW Atlantic	Temperate	Sedimentary	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

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Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Cohen et al. 2014. *Biological Invasions* 16: 1743–1756	*Megabalanus coccopoma*	Barnacle	Eastern Pac	Tropical	NW Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No
Coleman et al. 2014. *Molecular Ecology* 23: 5552–5565	*Abudefduf vaigiensis*	Fish	Indo-Pacific	Tropical	Pacific	Tropical	Hard substrata	Subtidal	Mensurative	Genetic diversity – haplotype diversity	Invasion dynamics	Higher	Yes
Dias et al. 2018. *Biological Invasions* 20: 1749–1770	*Perna viridis*	Bivalve	Laccadive Sea South China Sea Java Sea Flores Sea	Tropical	W Atlantic	Tropical	Hard substrata	Intertidal	Mensurative	Genetic diversity – number of haplotypes	Invasion dynamics	Lower	Yes
Ghabooli et al. 2011. *Biological Invasions* 13: 679–690	*Mnemiopsis leidyi*	Ctenophore	Western Atlantic	Temperate Subtropical	Black Sea Azov Sea Caspian Sea Baltic Sea	Subtropical Temperate	Pelagic	Pelagic	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Gilg et al. 2013. *Biological Invasions* 15: 459–472	*Perna viridis*	Mussel	South China Sea Laccadive Sea	Tropical	NW Atlantic Caribbean Sea	Tropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Gillis et al. 2009. *Diversity and Distributions* 15: 784–795	*Mytella charruana*	Mussel	Eastern Pac Caribbean Sea	Tropical	NW Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Gislason et al. 2013. *Marine Ecology Progress Series* 494: 219–230	*Cancer irroratus*	Crab	NW-Atlantic	Temperate	N Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No

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Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Hamner 2007. *Journal of Fish Biology* 71: 214–222	*Pterois volitans*	Fish	Indian Ocean	Tropical	W Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hamner 2007. *Journal of Fish Biology* 71: 214–222	*Pterois miles*	Fish	Indian Ocean	Tropical	W Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hanyuda et al. 2016. *Phycological Research* 64: 102–109	*Ulva australis*	Alga	Western N Pac	Temperate	NE Pacific Baltic Sea NE Atlantic SE Pacific SW Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hasselman et al. 2018. *Biological Invasions* 20: 3123–3143	*Alosa sapidissima*	Fish	Western N Atlantic	Subtropical	NE Pacific	Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Kappas et al. 2004. *Marine Biology* 146: 103–117	*Artemia franciscana*	Shrimp	Eastern N Pac	Temperate	Indo-Pacific	Tropical	Pelagic	Pelagic	Both	Haplotype diversity	Invasion dynamics	Lower	Yes
Krueger-Hadfield et al. 2016. *Molecular Ecology*. 25:3801–3816	*Agarophyton vermiculo-phyllum*	Alga	NW Pacific	Temperate	NW Atlantic NE Atlantic NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Martel et al. 2004. *Marine Ecology Progress Series* 273: 163–172	*Ocinebrellus inornatus*	Snail	East China Sea	Temperate	Gulf of Biscay NE Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No

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Table 3 (*Continued*) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Munoz et al. 2014 *Hydrobiologia* 726: 25–41	*Artemia franciscana*	Shrimp	Eastern N Pac	Temperate	NE Atlantic Balearic Sea Mediterranean Adriatic Sea	Subtropical	Pelagic	Pelagic	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Riquet et al. 2013. *Molecular Ecology* 22: 1003–1018	*Crepidula fornicata*	Limpet	Western N Atlantic	Temperate	NE Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Rius et al. 2008. *Diversity and Distributions* 14: 818–828	*Microcosmus squamiger*	Ascidian	SE Indian Ocean Southern Ocean Tasman Sea	Temperate	NE Pacific SW Indian Ocean NE Atlantic Mediterranean	Tropical Subtropical Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Shabtay et al. 2014. *Marine Biology Research* 10: 407–415	*Spondylus spinosus*	Oyster	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Shan et al. 2019. *European Journal of Phycology* 52: 154–161	*Undaria pinnatifida*	Alga	Yellow Sea East China Sea	Subtropical	North Sea English Channel	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Smith et al. 2012. *PLOS ONE* 7: e30473	*Didemnum vexillum*	Ascidian	Western N Pac	Temperate	SW Pacific	Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

(Continued)

Table 3 (*Continued*) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Tepolt and Palumbi 2015. *Molecular Ecology* 24: 4145–4158	*Carcinus maenas*	Crab	North Sea NE Atlantic	Temperate Subtropical	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Xue et al. 2018. *Biological Invasions* 20: 3297–3314	*Rapana venosa*	Snail	Philippines Sea Yellow Sea	Subtropical Temperate	Adriatic Sea Black Sea Bay of Biscay English Channel NW Atlantic SW Atlantic	Subtropical Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Wong et al. 2016. *Marine Biology* 164: 133	*Charybdis japonica*	Crab	East China Sea Yellow Sea	Subtropical	SW Pacific	Temperate	Sedimentary	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

BOX A *LITTORINA LITTOREA*. – CASE STUDY: USING THE BIOGEOGRAPHIC PATTERN OF ENEMY ESCAPE FROM PARASITES TO HELP DISCERN THE INVASIVE STATUS OF A PREVIOUSLY CRYPTOGENIC SPECIES

Because of extensive, consistent support for decreased parasite richness in introduced populations (e.g. Torchin et al. 2003), Blakeslee & Byers (2008) explored whether patterns of enemy release could be used in reverse, that is, to use parasite signatures to inform the ecological origin of a given cryptogenic host. Specifically, they tested the predictions for parasite release among three North Atlantic marine congeneric snails that were believed to have very different invasion and colonization histories in their established populations. Two species (*Littorina saxatilis* and *L. obtusata*) were thought to be naturally cosmopolitan on both sides of the Atlantic Ocean, while a third (*L. littorea*) had originally been thought to be an introduced species in North America; however, its ecological history there had recently been called into question, giving it a cryptogenic status (Wares et al. 2002). All three snail species serve as first intermediate hosts to host-specific digenean trematode (flatworm) parasites. Although the enemy release hypothesis had been used to explain heightened invasion success and ecological impact, this study represented the first endeavour to use the hypothesis's predictions to determine the status of a cryptogenic species as either native or introduced.

Through an extensive literature review and supplemental field sampling, Blakeslee & Byers (2008) identified total trematode species richness that was 55% lower for *Littorina littorea* in North America vs Europe. Mean site-level richness was also significantly lower in North America compared with Europe, and the decline (47%) was nearly equivalent to the decline based on the total species richness (55%). This greatly reduced parasite richness in the invasive range is consistent with the expectation for enemy escape. In contrast, for the two known native species – *L. saxatilis* and *L. obtusata* – smaller, non-significant reductions in trematode species richness in North America vs Europe were demonstrated (33% and 24%, respectively). Mean site-level richness for *L. saxatilis* and *L. obtusata* also exhibited much smaller differences between North America and Europe compared with *L. littorea*. Thus, lower parasite richness in *L. littorea* compared with the other definitively native congeners (which functioned as positive controls in this study) strongly implicated *L. littorea* as an invasive species that demonstrated sizable enemy escape in its invasive North American range.

This conclusion was later corroborated with direct genetic evidence from both the *L. littorea* host snail and its parasites, which demonstrated signatures of introduction (i.e. a reduced subset of genetic diversity in the putative invasive range; Blakeslee et al. 2008). Also, Brawley et al. (2009) supported *L. littorea* as an invasive species in North America using historical records (and more genetic analyses) that furthermore documented the snail's source region within its native range to be Great Britain and Ireland.

competitors and parasites (Torchin et al. 2001, 2003). Torchin et al. (2001) sampled the crab *Carcinus maenas* around the world in its native and introduced locations and reported on parasite loads. Relative to the native European range, parasite diversity was reduced in every invasive range examined, often by large amounts, including South Africa, where *C. maenas* was parasite free. Although the pattern of ERH is well documented, the effects of having lower exposure to enemies to the fitness and establishment of invasive species is seldom examined. A positive influence of fewer enemies is often assumed, even though the enemy that is reduced in number may not necessarily have been a limiting factor on the invasive species' population abundance.

Keogh et al. (2017) document one of the only experimental approaches to ERH in marine systems. The authors surveyed the Asian shorecrab, *Hemigrapsus sanguineus,* in its native and introduced range, finding the crab in the invasive range to be parasite free. They then employed a common garden experiment in the native range in Japan using crabs from the native and introduced range and exposed them to infective stages of a castrating rhizocephalan barnacle parasite. The crabs from the introduced range were between 1.8 and 6 times more susceptible. This shows that the crabs in the introduced range were escaping their parasites ecologically but not physiologically. Furthermore, their findings imply that the cost of maintaining immune defences against infection was high, such that the crabs lost resistance to the parasite once they were not exposed to it for several generations in the invasive range. Thus, Keogh et al. (2017) provide experimental evidence of ERH and suggest a double fitness benefit from escaping the parasite – not only lower infections but also physiological savings from less investment in immunity.

Trait and niche shifts across native and introduced ranges

Trait and niche shifts are the second and third most examined biogeographic hypotheses, and support for them was high: 92% and 77%, respectively. These two are somewhat related because shifting traits can often be related to a species changing its niche. Our literature search found that all of the papers that explicitly use the term 'niche shift' refer to temperature shifts. Although niche shifts were not apparent in all studies (e.g. Glasby 2007, Davidson et al. 2008, Henkel et al. 2009), several species did have an increased tolerance to high and low temperature stress in their introduced compared with native ranges (e.g. Kappas et al. 2004, Sotka et al. 2018), and for the red alga *A. vermiculophyllum*, high temperature tolerance was associated with increased levels of heat-shock proteins (Hammann et al. 2016). Interestingly, the invasive ascidian *Herdmania momus* also had lower tolerance to cooler temperatures (Gewing et al. 2019). Gewing et al. (2019) suggested that the tropical origin of *H. momus* may limit its dispersal into cooler waters but facilitate its spread into warmer waters in introduced Mediterranean populations.

Trait and niche shift theories often employ circular logic, assuming that an observed shift in traits and niches must be positively affecting an invader. These positive shifts could happen because of a genetic bottleneck in the small, inoculating population (also possibly coupled with genetic drift), rapid selection in the introduced range or character displacement of a species expanding to fill a vacant or less crowded niche. However, trait and niche shifts need to be tested to know whether they causally affect invader fitness and advantage over natives. For example, a crab with bigger claws in the invasive range may be assumed to have a fitness advantage stemming from that trait shift. However, if untested, it might be just as likely that small claws are advantageous. Niche shift as it pertains to temperature may be more objective because a species' temperature optimum can be objectively defined and thus readily evaluated to determine whether a temperature shift has moved a species to be more aligned with the local climate. Likewise, certain traits like increased chemical defences might also allow more objective assessment of whether the direction of a shift has provided mechanistic advantage. For example, the red alga *Agarophyton vermiculophyllum* has become better defended against epiphytes and bacterial epibionts in its introduced European range compared with native populations in Asia (Saha et al. 2016, Wang et al. 2017). Indeed, constituent chemical related changes may be generally important in explaining the invasion success of many invasive macrophytes (Wikström et al. 2006, Vermeij et al. 2009, Forslund et al. 2010, Qing et al. 2012, Hammann et al. 2013, 2016), although not all macrophytes experience palatability shifts between their native and introduced ranges (Bippus et al. 2018).

Evolution of invasiveness and acquisition of native allies

In marine ecosystems, the evolution of increased competitive ability, and evolution of invasiveness more broadly, as well as the acquisition of native allies, have been theorised about, but empirical examinations are lacking. Although most of the biogeographic comparisons on these metrics affirm their operation, there are too few studies to draw conclusions about the commonality of these mechanisms in invasion success. Facilitation is certainly a mechanism of growing interest in ecology in general (Stachowicz 2001, Kollars et al. 2016, Thomsen et al. 2018, Gribben et al. 2019); however, native allies had only a single study using a biogeographic comparison (Aires et al. 2013). Another more recent example, outside of the dates of our literature search, is Gribben et al. (2020) who demonstrated that higher abundances of the porcelain crab, *Petrolisthes elongatus,* on intertidal boulder shorelines in its introduced range of Tasmania, Australia, is due to the presence of the calcareous matrix provided by the tube-worm *Galeolaria caespitosa* on the underside of boulders, which is rare under boulders in its native range of New Zealand (see Box D for expanded *P. elongatus* case study). Positive interactions, such as facilitation, may be important drivers of changes in invader abundance across ranges, particularly when their abundance is strongly tied to habitat availability.

Three studies addressed the evolution of invasiveness, and all three examined changes in resource acquisition, with two of these studies showing that, compared with its native range, *C. maenas* has undergone behavioural and morphological (e.g. body size and claw size) adaptations that increase prey capture (Schaefer & Zimmer 2013, Howard et al. 2018). An improved amount, rate, or efficiency of resource acquisition can imply better competitive strength. However, none of these papers actually measured relative competitive abilities in the native and introduced ranges. Thus, the evolution of increased competitive ability – and evolution of invasiveness more broadly – remains a popular theory in invasion biology, but support for it here is only partial.

Environmental matching

We did not find any studies that investigated environmental matching as a mechanism behind invasion success. From a coarse perspective, we know that matching must occur to some degree, as all but three studies examined invasive species in the same climate zone in the introduced and native range. However, formal examination of environmental matching typically investigates much more finely resolved environmental attributes and also multidimensional aspects of niche apart from just temperature.

Genetic shifts

Finally, genetic change is examined a lot, and most species in our database exhibit reduced diversity in the introduced range (Box B). This reduction is parsimoniously explained by founder effects and associated genetic bottlenecks from small inoculation size. However, this finding is far from universal. Roman & Darling (2007) found an equal or even increased diversity in the introduced range of marine and freshwater species which they attributed to high propagule vectors, such as ballast water and shellfish transplantations, and multiple introductions that can infuse more heterogeneity into the introduced range and eliminate founder effects in the majority of successful aquatic invasions. What remains unclear is, even if genetic reduction occurs, whether there is a disadvantage to the invader, for example, for fitness, establishment success, or spread. Roman & Darling (2007) suggest even when diversity is low that it likely does not matter because even low-diversity introductions

BOX B *AGAROPHYTON VERMICULOPHYLLUM*. – CASE STUDY: GENETICS OF AN INVASIVE SEAWEED IDENTIFY ITS SOURCE OF INTRODUCTION AND EVIDENCE AN ENVIRONMENTALLY FORCED SHIFT TO ASEXUAL REPRODUCTION

Krueger-Hadfield et al. (2017) thoroughly examined the genetics of the invasive Asian seaweed *Agarophyton vermiculophyllum* in its native and invasive range using microsatellite and mitochondrial cox1 amplification and genotyping. The size of their sampling was impressive, with more than 2000 thalli sampled from more than 30 native sites in Asia and 35 non-native sites along the coastlines of western and eastern North America and Europe (Krueger-Hadfield et al. 2016). In doing so, they uncovered the source of the introduced populations in Europe and North America as being from the Pacific shorelines of northeastern Japan (Krueger-Hadfield et al. 2017). Based on ecological, genetic and historical evidence, they further suggested that *A. vermiculophyllum* hitchhiked with the exports of the Japanese oyster *Magallana gigas* from Japan during the 20th century, which abounded from this exact region at the same time that *A. vermiculophyllum* was introduced.

Of equal interest was their exploration of the degree of reduction in genetic diversity that often accompanies species that have founder effects, like invasive species that are introduced in small numbers. In many dimensions, invasive populations were significantly lower in genetic diversity. For example, there were significantly more unique genotypes (i.e. genotypic richness) within native sites (91%) than introduced sites (61%). But the most noteworthy aspect of the genetic diversity shift was that the native populations were 58% diploid, while the introduced populations were 81% diploid. Non-native sites were dominated by diploid tetrasporophytes as a result of asexual fragmentation. Because hard substratum is required for algal spore recruitment, the authors determined that an ecological shift from hard to soft substratum during the invasion of North American and European estuaries by *A. vermiculophyllum* resulted in a shift from sexual to asexual reproduction (Krueger-Hadfield et al. 2016). Thus, an initial colonization of a soft-sediment estuary in the non-native range by a diploid thallus meant the species was trapped in that stage, able to reproduce only asexually without a hard substratum to promote sexual reproduction. Since non-native sites were presumably the sources of inoculation for many other sites in the invasive range, it is not surprising that the predominant diploids were the stage introduced to the new secondary sites, thus perpetuating diploids as the life stage trapped in asexual reproduction throughout much of the invasive range.

have many means of avoiding the negative impact of diversity reduction. Genetic signatures that are distinctive to various parts of the native range can be used to track multiple introductions from the native range and monitor spatial and temporal changes including the mechanisms and speed of spread (Darling et al. 2008, Box C).

BOX C *CARCINUS MAENAS*. CASE STUDY: DISTINCT AND REDUCED GENETIC DIVERSITY OF AN INVASIVE CRAB IDENTIFIES ITS INVASION HISTORY AND ASYMMETRIC SPREAD WITHIN THE INVASIVE RANGE

The European green crab, *Carcinus maenas*, first appeared on the mid-Atlantic coast of the eastern United States in 1817. Over the decades, it spread northward against the mean current throughout northeastern North America until it reached Halifax, Nova Scotia, Canada, in 1964 where its upstream spread seemingly stopped (Figure C1). Byers & Pringle (2006) have demonstrated that even planktonically dispersed species like crabs can spread in an upstream direction as long as the variation in currents their larvae experience is large enough to counteract the movement in the mean current, which is by definition in the downstream direction. Methods to increase the variation in currents experienced by larvae, and thereby boost retention and upstream spread, include spawning copious larvae over long periods and decreasing larval exposure to the mean current by minimizing larval development times (and thus time spent in plankton), which are exponentially lower in warmer temperatures.

In the 1990s, *C. maenas* populations in northern Nova Scotia north of Halifax exploded (Figure C1). Roman (2006) determined that the genetic composition of the previously existing *C. maenas* populations in the United States and southern Nova Scotia were all of a single haplotype. The populations in northern Nova Scotia represented a new introduction which was composed of a suite of distinct haplotypes,

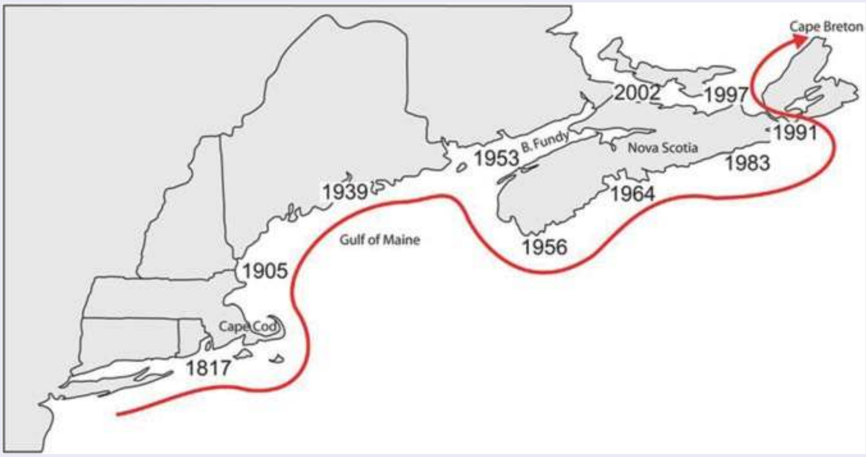

Figure C1 Dates of *Carcinus maenas* expansion northward up the coast of northeastern North America. Dates depict first record of the crab at various locations. The direction of travel is in the upstream direction throughout this domain. Red line depicts a simple proposed scenario for the crab's expansion if it had spread upstream on its own power. Adapted with permission from Roman (2006), © the Royal Society 2006, and based on a figure originally adapted from Audet et al. (2003).

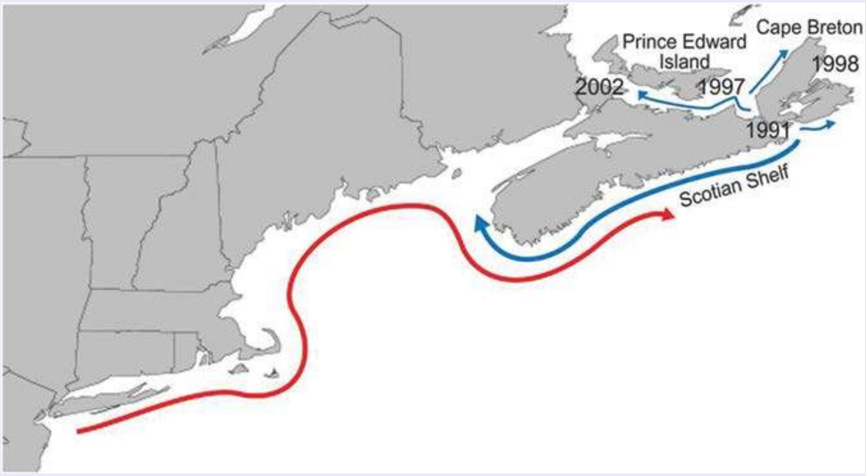

Figure C2 Hypothesised spread of the crab according to the theory of Byers & Pringle (2006). Hypothesis was tested using baseline genetic data from Roman (2006) and Pringle et al. (2011). Red represents historical invasion of *Carcinus maenas* upstream from south to north ending in Halifax, Nova Scotia. Blue represents a second introduction of *C. maenas* from a different portion of the native range to northern Nova Scotia that spread readily in the downstream direction.

most likely from the Baltic region of the crab's native European range. It was hypothesized that the northern Baltic strains were cold water adapted and therefore thriving in northern Nova Scotia. However, the theory of Byers & Pringle (2006) predicted a simpler, testable explanation – namely that *C. maenas* in North America historically had spread on its own in the upstream direction as far as it could on its own power and ceased spreading in Halifax, where the cold water temperatures meant it could no longer overcome mean advection and spread further upstream. Under this hypothesis, the new introductions were not necessarily better adapted to temperature but simply anchored in place in retention zones in northern Nova Scotia, such as the Straight of Canso and the Bras d'Or Lakes, that were not subject to the mean advective currents that sweep larvae downstream and hinder upstream establishment. However, with populations anchored in place, the crabs could easily supply larvae into coastal currents to move in the downstream direction and backfill in the portions of the range above Halifax that they could not fill on their own power (Figure C2). This prediction appears to be supported by the genetic signature of spread (Pringle et al. 2011). In fact, not only have the northern Baltic haplotypes filled in that previously unpopulated region north of Halifax, but they have continued spreading in the downstream direction, mixing with the previously homogenous single haplotype of the historical southern invasion (Figure C3). In fact, in seven years (about two crab generations), the upstream haplotypes became 20% more common throughout the entire *C. maenas* invasive range. Such downstream asymmetrical dispersal was readily observable in the genetic signature (though now introgression of haplotypes makes using the haplotypes as a tracer much harder).

Comparison with the native range indicated an originally bottlenecked North American population of *C. maenas* whose genetic homogeneity persisted for >100 years. The homogeneity was disrupted by the introduction of a novel set of haplotypes from a different part of the native range that also allowed observation of spread and subsequent mixing of genetically distinct populations within the invasive range.

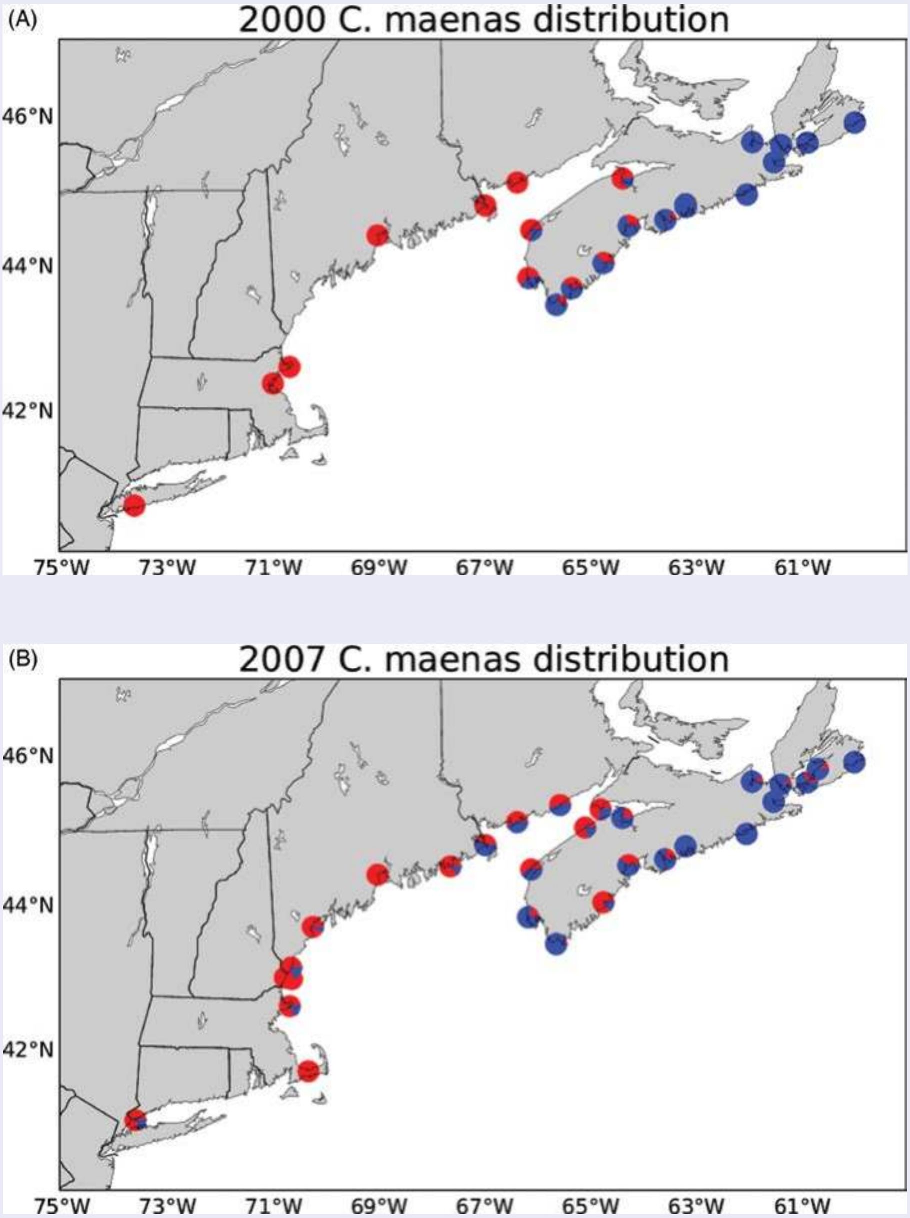

Figure C3 (A) Original haplotype distribution of *Carcinus maenas* in 2000 from Roman (2006). Red represents the haplotype of the older historical invasion to the US that spread north to Halifax. Blue is the haplotype suite that was introduced in the 1990s to northern Nova Scotia. Note these data were collected almost a decade after the introduction(s) of *C. maenas* to northern Nova Scotia, and spread away from the point of introduction has already occurred. (B) Within seven years, the upstream (blue) haplotype suite has begun to displace the red haplotype downstream and was 20% more abundant throughout the domain. The northern haplotypes have even passed to the south of major biogeographic boundaries like Cape Cod (Pringle et al. 2011). Adapted from Pringle et al. (2011).

Knowledge gaps

What role for increased competitive ability?

The evolution of increased competitive ability (EICA, Blossey & Notzold 1995) predicts that enemy release should result in introduced species losing costly traits that confer resistance to native enemies, with a subsequent reallocation of resources to other traits (e.g. body size or reproduction) that may be under greater selection in the introduced range (Hierro et al. 2005). While tests are equivocal (e.g. Blossey & Notzold 1995, Maron et al. 2004, Felker-Quinn et al. 2013), in terrestrial ecosystems, invasive plants can undergo evolutionary changes through the invasion pathway which can give them increased competitive ability in their introduced compared with native ranges (Blossey & Notzold 1995). We could find no studies that have addressed this hypothesis for marine ecosystems. However, there are several reasons the EICA may play an important, yet underappreciated, role in invasion success in marine ecosystems. First, competition has strong effects on the structure of marine ecosystems, particularly rocky intertidal ones. Because of this, it has been a focal process of study in marine environments (Branch 1984, Byers 2009). Second, studies show that invasive marine species can undergo phenotypic (morphological and behavioural) changes and that those changes, in some instances, increase their acquisition of resources in their introduced compared with native range (Schaefer & Zimmer 2013). Moreover, separate studies show that invasive species can be better at acquiring resources than native competitors (Byers 2000, Hendrickx et al. 2015). However, no study has approached this using a biogeographic framework to test the importance of EICA in explaining the success of marine invasive species.

What role for associated microbes in controlling the biogeography of marine invasions?

In terrestrial ecosystems, plant-soil-feedbacks (PSFs; Bever 1994) play an important role in regulating community succession, coexistence and invasiveness (Van der Putten et al. 1993, Klironomos 2002, Bever 2003, Callaway et al. 2004, Kulmatiski et al. 2008). There is mounting evidence that different PSFs experienced by invasive plants in their introduced compared with native range are also critical to their invasion success. Invasive success of plants can be enhanced by leaving behind below-ground enemies or by encountering stronger soil mutualists or having enhanced competitive ability through stronger allelopathic effects in the introduced compared with native range (Callaway 1995, Callaway & Aschehoug 2000, Reinhart et al. 2003, Vivanco et al. 2004, Reinhart & Callaway 2006, Callaway et al. 2008). Despite invasive marine plants and algae that colonise soft sediments constituting some of the most damaging invaders globally, the role of changes in PSFs across their native and introduced range in contributing to their success remains relatively unexplored. However, by manipulating microbial communities from native seagrass sediments, Gribben et al. (2017) demonstrated that the presence or absence of a sediment microbial community from the native seagrass *Zostera muelleri* inhibited and promoted success, respectively, of the invasive alga *Caulerpa taxifolia*. Manipulation of the sediments occupied by *C. taxifolia* had the opposite effect. Moreover, field experiments show, compared to disturbed sediments, intact sediments from native seagrasses have similar strong negative effects on the growth of reducing fragment growth of invasive *Caulerpa* spp. fragments in the Mediterranean and Australia (Gribben et al., 2018; Bulleri et al. 2020). Success (or not) of both *Caulerpa* spp. was linked to microbial control of sediment sulphur cycles. In another example, Chen et al. (2020) found that soil properties of native *Spartina* marshes depressed freeze tolerance of range-expanding tropical mangrove competitors. These studies demonstrate an emergent role for PSFs in controlling the success of invasive soft-sediment macrophytes, similar to that demonstrated for terrestrial plants.

Changes in surface-associated ‘epibacteria’ on invasive macrophytes between native and introduced ranges may also influence invasion success. The results may be positive or negative depending on how the host benefits from the microbial community it acquires in the introduced range. For example, some epibacteria can be virulent or promote the settlement of fouling organisms, or they contribute to anti-fouling defence or provide essential nutrients (Egan et al. 2001, Dobretsov et al. 2009, Goecke et al. 2010, Fernandes et al. 2011, 2012, Egan et al. 2014, Wichard 2015). We suggest that understanding changes in microbial communities, and the processes they control, across native and introduced ranges of macrophytes will be a critical avenue of future research for fully explicating the mechanisms behind their success.

Integrating hypotheses to determine mechanisms

Many of the comparative biogeographic theories to explain invader success overlap. Also, multiple theories likely operate at once, especially due to the correlation of ecological processes and traits. For example, a niche shift in the introduced range could easily involve a shift in traits. The evolution of invasiveness might involve traits that shift in the absence of certain enemies in the introduced range. Traits shifts in particular are very likely to be operating with other processes, since trait changes in and of themselves do not always imply a mechanism of success. For example, changes in macrophyte traits (e.g. chemistry) are potentially neutral but could indirectly enhance invasion success if shown to reduce herbivore pressure (Wikström et al. 2006). Thus, splitting hairs regarding which hypothesis fits a study or species could rapidly become futile. Instead, the overlap among various potential mechanisms should be viewed in a positive light since it lends itself to integrated theory and approaches. For example, an integrated theory of biogeographic success by an invader might invoke advantages from the evolution of invasiveness and enemy release, despite lower genetic diversity.

Towards a mechanistic understanding using experimental approaches

Somewhat surprisingly, our review indicated that experimental approaches were almost as frequent as mensurative surveys when investigating biogeographic shifts in the biology and ecology of invasive species between their native and introduced ranges (Table 2). Studies using experimental approaches mostly use common-garden experiments where the experimenter brings introduced and native-range individuals together in a common setting, usually in the lab. Such experiments provided robust tests for niche shifts via, for example, changes in temperature tolerances (Krueger-Hadfield et al. 2016, Gewing et al. 2019) or a reduction in natural enemies via reduced palatability or parasites (Vermeij et al. 2009, Keogh et al. 2017), benefitting invasive species in their introduced ranges.

In addition to common-garden experiments, another approach to experiments is through *in situ* experiments conducted in both the introduced and native range. Although this approach is theoretically possible, no such papers appeared in our database. Likely this is influenced by ethical considerations that place strict limits on where invasive species can be moved. This is part of the reason common-garden experiments have been so useful – native and invasive species can be transported between ranges under controlled conditions. Comparative biogeographic experimental approaches whereby equivalent experiments in an invader's native and introduced range provide a useful alternative for elucidating shifts in the net strength of species interactions (e.g. predation, competition) or tolerances across ranges (Hierro et al. 2005), although they are confounded by different species pools and/or environmental conditions in the native and introduced ranges.

However, there are creative ways to employ unconfounded *in situ* experiments of factors testing the biogeography of invader success. Gribben et al. (2020) provide one such example (Box D). In this case, surveys indicated that higher abundances of *Petrolisthes elongatus* in its introduced range were due to the presence of a habitat-forming tube worm that forms a calcareous matrix underneath rocks that was largely absent from its native range, and this was confirmed in replicated biogeographic experiments with habitat mimics in both ranges (see Box D for more detail). Where invasion success

BOX D *PETROLISTHES ELONGATUS* – BIOGEOGRAPHIC CASE STUDY: THE ROLE OF POSITIVE INTERACTIONS IN PROMOTING HIGHER ABUNDANCES OF AN INVASIVE CRAB

Native to New Zealand, the porcelain crab *Petrolisthes elongatus* was introduced into Tasmania, Australia, in the early 1900s via ballast rock or the live oyster trade between the two countries (Dartnall 1969, King 1997). Following its introduction, *P. elongatus* spread rapidly and is now widespread and a dominant member of intertidal rocky shore communities, where it reaches high abundances (up to 2000/m^2) under boulders (Gribben et al. 2015, Wright & Gribben 2017). Throughout Tasmania, high abundances of *P. elongatus* are associated with strong shifts in community structure (Gribben et al. 2015, Wright et al. 2016). Higher overall abundances of *P. elongatus* in the introduced compared with native range were shown in two separate studies which surveyed crab abundances throughout the invasive range in Tasmania (Gribben et al. 2013, 2020). In the introduced range, the abundance of *P. elongatus* is positively correlated to habitat availability (i.e. the amount of boulder material available for colonisation; Gribben et al. 2015, Wright et al. 2018). However, higher abundances of *P. elongatus* in the introduced range are not simply explained by greater habitat availability because surveys of habitat characteristics (amount of boulder material, boulder sizes) indicated no difference among the two ranges (Gribben et al. 2020). Instead, these surveys showed a high presence of habitat-forming tube worm *Galeolaria caespitosa* under rocks in Tasmania – where it is known to enhance recruitment of *Petrolisthes elongatus* compared with rocks without the tube worm – compared with New Zealand, where it was virtually absent (Wright et al. 2016). Deploying mimics of rocks with and without worms at three sites in both the native and invasive range, Gribben et al. (2020) experimentally demonstrated that rocks with worm structure facilitated crab by at least 50% in both the native and introduced ranges. This study was novel for two main reasons. First, it is an unconfounded *in situ* experimental test of the mechanism explaining higher abundances of invasive species in their introduced range, and second, it shows that positive interactions are an important mechanism explaining differences in the abundance of an invasive species between its native and introduced ranges. In this example, the higher cover of a native habitat-forming species facilitates higher abundances of an invader in its introduced range, possibly because the presence of this habitat-former reduces temperature stress (Wright & Gribben 2017).

is linked to changes in the physical environment, such as changes in habitat structure, structural mimics may provide a particularly powerful tool for conducting unconfounded *in situ* experiments at biogeographic scales.

Comparative studies that do not involve experiments can still be valuable. Two aspects that will boost their value are enhanced replication and proper spatial spread of sampling points. Often studies only examine a few sites in the native and introduced range to make comparisons. But, especially for species with wide ranges, capturing the effect of within-region heterogeneity is important for a fair comparison. That is, to know that there is a real difference between regions, you need adequate replication in both ranges. Alternatively, if the exact region of the native range from which the inoculating invasive individuals were drawn is known, as it is for several prominent invasive species (Brawley et al. 2009, Krueger-Hadfield et al. 2017), then that area of the native region should be sampled exclusively for comparisons since variation in other parts of the native range is moot. Diversity studies need equal sample sizes in both ranges (or rarefaction techniques to control for unequal sample size) (e.g. Blakeslee & Byers 2008) since species richness scales with sampling effort.

Another goal for future studies is to diversify our taxonomic exploration. We know, for example, that many species traits vary with phylogeny, for example, larval duration and temperature tolerance. As most reviews of invasive species have found (e.g. Ruiz et al. 2000, Byers 2009), our database is biased toward molluscs, crustaceans and seaweed. Getting taxonomic balance will help us learn whether certain levels of taxonomic organisation show biases in biogeographic comparisons. Also, as most invasion reviews have reported, various regions around the globe are understudied, for example, the tropics (Figure 4). Moreover, Asia, Africa and South America are highly underrepresented (Figure 2). This underrepresentation likely affects biogeographic comparisons heavily because one needs data from two regions of the world to make comparative studies. When half the world is highly understudied (in many cases even with no baseline inventories of what is native vs introduced), that makes these comparisons rare. In particular, many invaders originate from Asia, often where there are no data from the native range. This was a problem that heavily affected Parker et al. (2013), who sought to compare the world's 100 worst invasive species that formed their target list of species in their native and introduced ranges. Many of those 100 species were native to Asia and had to be dropped from the meta-analysis for lack of native range data. Some studies are starting to obtain their own native range data from Asia (Keogh et al. 2017, Krueger-Hadfield et al. 2017, Sotka et al. 2018).

Cross-ecosystem evidence for different hypotheses

Working towards a general biogeographic theory of invasion, one of the key questions is whether the different hypotheses identified in this review receive similar or different support across ecosystems. Except for the ERH, there are too few studies to test for the strength of different hypotheses across ecosystems. Jeschke et al. (2012) showed approximately 75% support for the ERH in marine ecosystems from a small number of papers (13). The level of support was not statistically different from that observed in terrestrial and freshwater ecosystems, suggesting relatively equal support for this hypothesis across ecosystems. With the addition of further studies, we will ideally be able to ascertain the underlying strength of the different hypotheses reviewed here, including their differences across ecosystems.

Conclusions/summary

Biogeographic study of invasions is more than a one-way street. Throughout this article, we have stressed how biogeography may inform invasive species biology through comparative analysis. It is also the case that invasive species may inform biogeography. After all, invasive species are a unique opportunity to inform biogeography because without invasion, you cannot study species in similar climatic regions where they do not already exist. However, through species invasions, one can test biogeographic regions for interchangeability and similarities in biological suitability using the receptivity of the region and the subsequent fitness of the invasive species as proxies for the similarity and substitutability of multiple biogeographic regions.

Despite the huge size of the biological invasion literature, given the difficulties of working at continental scales, it is perhaps understandable that biogeographic comparative studies, especially experimental ones, are lacking. However, as we have shown here, the growing number of comparative studies provides interesting insight and much-needed empirical evidence to address the theoretical biogeographic hypotheses for the success of invasive species. The evidence for and against these hypotheses should improve over time as researchers plug many of the knowledge gaps we have exposed.

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Supplementary Tables are provided online at https://www.routledge.com/9780367367947

Supplementary Table 1 Search terms used to extract papers and the number of initial papers extracted from the Web of Science. Searches were performed for various metrics used in comparative studies of invasive species between their native and invasive range.

Metrics	Number of papers	Search terms
Enemies	479	(parasit* or enemy or herbivor* or predat* or pathogen* or consumpt*) and (population* or rang*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Competition and facilitation	392	(competit* or facilitat*) and (population* or rang*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Genetics	324	(Allel* or Haplotyp* or Genet* or Heterozygosit*) and (rang* or population*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Population abundance	829	(abundance or densit* or biomass or recruitment or mortality or survivorship or growth) and (population* or rang*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Life-history traits	638	(size or trait* or height or length or morpho* or "life history") and (population* or rang*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Reproduction	427	(reproduct* or gamet* or propagul* or egg or offspring or fecundit* or gonad or seed or larva*) and (population* or rang*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Chemical defense	74	(‘Secondary compound*’ or metabolite* or shock or defense or weapon and (rang* or population*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)
Resource utilisation	484	(Resource* or diet* or prey) and (rang* or population*) and native and (invas* or introduc* or exotic) and (marine* or estuarine) and (compar* or experiment* or relativ* or biogeograph* or survey*)

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HUMAN PRESSURES AND THE EMERGENCE OF NOVEL MARINE ECOSYSTEMS

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Abstract The progressive expansion of human activities is causing unprecedented changes to marine ecosystems. In some cases, the extent of these changes may be so large as to generate ecosystems in which structure and functioning have no historical analogs (i.e. novel ecosystems). Here, we review the main abiotic and biotic drivers of change in the marine realm and provide a critical assessment of ecosystems for which there is empirical evidence of human-induced shifts into novel states. Our review indicates that there is evidence for human agency of changes, no-analog species composition and threshold crossing for a variety of marine ecosystems, including intertidal rocky shores, temperate and tropical reefs, estuaries and pelagic systems, while there is no definitive proof of irreversibility of changes. We discuss how a more thorough recognition of the novel ecosystem concept may help initiate conservation and restoration efforts in each of these systems.

Background

Human domination of the Earth is causing unprecedented changes to natural systems (Vitousek et al. 1997). Intensive land and ocean use, alteration of climate and biogeochemical cycles, along with species loss and introductions, have resulted in profound changes in terrestrial and aquatic ecosystems (Vitousek et al. 1997, Crutzen 2002, Doney 2010, Steffen et al. 2011). The magnitude of these changes can be so large that modern ecosystems can be characterised by species composition and functioning that have not existed in the past. These ecosystems have been referred to as emerging (Milton 2003), no-analog (Williams & Jackson 2007) or, more often, novel (Hobbs et al. 2006).

The novel ecosystem concept has attracted the attention of terrestrial and freshwater ecologists but is less often applied to the marine realm. In their seminal paper, Hobbs et al. (2006) pose the question, "How does the concept of novel ecosystems relate to the marine environment?" An initial scan of the Web of Science (WoS) database in December 2018 returned just a handful of papers on the marine environment that have delved into this concept (Box 1). As pointed out by Schläppy & Hobbs (2019), this suggests that, after more than one decade, this question remains

BOX 1 NOVEL MARINE ECOSYSTEMS IN THE SCIENTIFIC LITERATURE

An initial scan of the literature for papers explicitly touching upon the concept of novel ecosystems (i.e. referring to an ecosystem as novel, emergent or no-analog) in marine environments was performed through the ISI Web of Science on 5 December 2018. Worth stressing is that our intention was not that of conducting a systematic review of the literature. The following strings of search terms were used:

> 'novel ecosystem*' or 'emerg* ecosystem*' or 'no-analog ecosystem*' or 'no analog ecosystem*'
> AND marine or intertidal or subtidal or pelagic or coastal or benthic or demersal

A total of 504 papers were retrieved from the search (Supplementary Material). Assessment of references obtained through the search was performed through a three-step process: 1) scanning of article titles (to exclude articles dealing with completely unrelated topics), 2) reading of the abstract and 3) reading of full text.

A total of 14 papers were retained at the end of the selection process. Out of these, six papers dealt with novel ecosystem establishment in estuaries, five in coral reefs and one on sandy beaches. Two papers were broader in scope and did not focus on a specific marine ecosystem. On purpose, the search did not include human-built, artificial habitats, which, as described in the text, are *per se* novel and do not display some of the attributes that define the emergence of novel ecosystems as a result of human-driven alterations of natural ecosystems (i.e. threshold crossing).

largely unaddressed. Of course, this does not reflect a smaller effort towards the assessment and management of human perturbations in the marine realm but rather a perceived reduced relevance of the novel ecosystem concept in marine environments or its limited dissemination and application amongst the global marine ecology community. Thus, this paper aims to: 1) provide a critical review of empirical evidence of human-induced shifts into novel states for marine ecosystems, 2) explore the drivers underpinning these shifts, 3) discuss how a more thorough recognition of this concept may help initiate conservation and restoration efforts in each of these systems and 4) identify major knowledge gaps and present a future outlook. As a first step, we provide an operational definition of novel and hybrid ecosystems and some hints on the major abiotic and biotic drivers of change in marine environments in order to facilitate the reader navigating across the subsequent sections.

Novel and hybrid ecosystems: A definition and implications for natural system management

The novel ecosystem concept has spurred substantial debate over its definition, the type of data necessary for its identification and the implications it can have for the management of natural systems (Hobbs et al. 2014, Morse et al. 2014, Murcia et al. 2014, Truitt et al. 2015). Several definitions have been proposed (Truitt et al. 2015) and it is not our intention to formulate a new one here. Thus, for the remainder of the paper, we adopt the operative definition proposed by Morse et al. (2014): "A novel ecosystem is a unique assemblage of biota and environmental conditions that is the direct result of intentional or unintentional alteration by humans, i.e. human agency, sufficient to cross an ecological threshold that facilitates a new ecosystem trajectory and inhibits its return to a previous trajectory regardless of additional human intervention. The resulting ecosystem must also be self-sustaining in terms of species composition, structure, biogeochemistry, and ecosystem services. A defining characteristic of a novel ecosystem is a change in species composition relative to ecosystems present in the same biome prior to crossing a threshold."

Following Morse et al. (2014), novel habitats are defined by four main characteristics: human agency, the crossing of thresholds, novel species composition and the ability to self-sustain. Although fossil and geologic records indicate that novel ecosystems have appeared naturally in the past, there is substantial consensus over a key role of direct (deliberate or inadvertent) or indirect anthropogenic stressors in their onset (Hobbs et al. 2006). Alternative stable state theory (Holling 1973, May 1977, Petraitis & Dudgeon 2016) is central to the definition of the novel ecosystem concept. State changes of an ecological system, because of the modification of external conditions, can occur either gradually or abruptly once conditions approach a critical threshold (Scheffer et al. 2001). In some systems, forward and backward state shifts occur at different thresholds or tipping points (i.e. hysteresis), which implies the existence of alternative domains of stability (Scheffer et al. 2001). This is the case for novel and hybrid ecosystems, where a human perturbation would, either directly or indirectly, cause the system to cross a critical threshold and enter the basin of attraction of an alternative stable state, characterised by unprecedented species configuration and functioning. Once established, the novel state would be very difficult, or indeed impossible, to reverse because of the intervention of stabilising feedback mechanisms. The nature of drivers causing threshold crossing can be biotic, abiotic or both (Hobbs et al. 2006). For instance, invasive species can trigger novel feedback mechanisms and lock the system into an alternative state that persists even when the invader is eradicated (Gaertner et al. 2017). Likewise, changes in climatic conditions, nutrient loading or altered regimes of disturbance can cause the system to shift into an alternative, self-sustaining state (van der Heide et al. 2007, Gorman et al. 2009, Vergés et al. 2014a, Hughes et al. 2018b, Schmitt et al. 2019).

The possibility of a shift back to the historical state underpins the distinction between hybrid and novel ecosystems (Hobbs et al. 2009). Hybrid ecosystems retain some of the historical characteristics along with some novel elements and can, either with time or human intervention, return to the original state. By contrast, the severity of the alterations suffered makes the shift irreversible in the case of novel ecosystems. Thus, a shift to an alternative state is necessary, but not sufficient, to generate a novel ecosystem. In other words, shift-back thresholds can be seen as 'soft' and 'hard' in the case of hybrid and novel ecosystems, respectively (Hobbs et al. 2009).

Most of the debate around the novel ecosystem concept concerns the way it challenges, at least at first glance, traditional conservation and restoration strategies aiming to preserve or restore biotic and abiotic conditions matching historical benchmarks (i.e. in the absence of humans) or, more often, displayed by contemporary reference systems putatively unaffected by human activities (Kopf et al. 2015). Many terrestrial systems (e.g. cities, open-pit mines, pastures, agricultural fields) have undoubtedly undergone changes that are difficult, if not impossible, to reverse. Under these circumstances, traditional management goals appear unrealistic and should be abandoned to embrace change (Hobbs et al. 2006, Hobbs et al. 2009). Recognition that the historical state cannot be recovered fundamentally changes the principles underpinning management goals, re-directing efforts towards sustaining species, functions and services that do not necessarily resemble those found in the past but that are deemed ecologically, socially or economically valuable (i.e. rehabilitation, remediation or reallocation, rather than restoration).

Criticism of the novel ecosystem concept articulates along three major axes. First, establishing whether a given species configuration has not existed in the past requires long time-series of data, which are seldom available (Murcia et al. 2014). Second, determining the magnitude of differences from the historical state to define an ecosystem as novel remains somewhat subjective (Aronson et al. 2014, Murcia et al. 2014). Third, empirical demonstration of irreversibility after a threshold has been crossed, although representing a quantifiable benchmark, is difficult to obtain. In some cases, such as that of species extinctions, changes can be irreversible; for instance, large marine carnivores and herbivores and some habitat-forming species are ecologically extinct at many temperate and tropical sites (Jackson et al. 2001, Pandolfi et al. 2003). On the other hand, there are examples of surprising recoveries of functionally extinct species: sea otters were extirpated along the coast of the Olympic Peninsula of Washington state, United States, in the early 1900s, but reintroduction of 59 individuals in 1969–1970 was effective in reinstating the local population after two decades (Shelton et al. 2018). In other cases, irreversibility is not ecological, but it is a consequence of the amount of effort needed to promote the shift-back and, hence, limited by economic and social constraints. Whilst most barriers preventing an ecosystem returning to its historical state may be removed (although there is no remedy against species extinction), the associated costs would be, in many cases, too high to be deemed worthwhile (Hobbs et al. 2014). Practical difficulties in determining whether shifts are reversible blurs the distinction between novel and hybrid systems. For these reasons, unwarranted labelling of an ecosystem as novel may undermine initiatives to protect natural ecosystems (Aronson et al. 2014, Murcia et al. 2014).

The aim of this paper is not to further delve into this ongoing debate. There is evidence suggesting that some coastal environments, such as those in urban areas, have been modified by human activities to such an extent that their return to a historical state is extremely unlikely, if not impossible (Firth et al. 2016). For example, the destruction and fragmentation of natural habitats due to building seawards through land reclamation or construction of artificial islands is irreversible (Chee et al. 2017). Although urban environments were not included in earlier formulation of the novel ecosystem concept, they are generally composed of a mix of systems that vary in their degree of novelty, from entirely novel to hybrid (Perring et al. 2013). In some cases, these systems might be returned to the original state, although economic, social and cultural constraints impose practical limits. This is, however, impossible when novel ecosystems are founded upon artificial substrates. Likewise, aquaculture ponds or comparably built facilities (e.g. enclosed docks) replacing coastal habitats, such as rocky and sandy shores, mangrove forests or salt marshes, are intensively managed, artificial systems that can be considered novel.

At the same time, human perturbations have facilitated the shift of some ecosystems into alternative states that, due to hysteresis, can be difficult to reverse. Concerns over the loss of ecosystem services following state shifts has produced a large body of research on multiple stable states, tipping points and early warning signals, using marine systems (e.g. temperate and tropical reefs) as study models (Benedetti-Cecchi et al. 2015, Ling et al. 2015, Schmitt et al. 2019). These studies have brought evidence of catastrophic shifts and bi-stability for some marine ecosystems, but, to the best of our knowledge, little empirical proof of threshold irreversibility (i.e. backward shift). In addition, shifted systems, although characterised by altered species configurations and biogeochemistry, generally retain some historical characteristics. Thus, there are reasons, including a precautionary principle, to categorise these ecosystems as hybrid rather than novel. In this regard, we disagree with Schläppy & Hobbs (2019), who argue that the lack of historical baselines to be pursued by restoration plans marks, by default, an ecosystem as novel. Of course, this does not negate the possibility for these systems to become novel (i.e. irreversibility of changes) without human interventions aiming to reduce global and regional drivers of change.

Drivers of change in marine environments

Physical drivers

Human activities are altering physical and chemical conditions of marine systems at a hierarchy of spatial scales, from local to global. Pathways of introduction, accumulation and persistence of a great variety of organic and inorganic pollutants, heavy metals, oil and nutrients in coastal waters and sediments, from both land- and sea-based human activities, as well as their effects on plants and animals, have long attracted the attention of marine biologists and ecologists (Gray 1997). Contaminants and nutrient subsidies can affect a limited water body when introduced via point sources, such as domestic or industrial effluents, but scale up to entire regions when contamination occurs at the catchment scale (Gorman et al. 2009). Likewise, pollutant and nutrient inputs can be constant or occur as pulses according to complex regimes varying in number, intensity, duration and temporal clustering of discrete release events.

The relevance of other sources of pollution, such as noise, artificial light and plastic litter, has been increasingly recognised in the last two decades (Davies et al. 2014, Peng et al. 2015, Yan et al. 2019). Expansion of a variety of sea-based human activities, including maritime traffic from oil tankers, cargo ships, ferry boats, recreational and fishing vessels, renewable energy installations (tidal and wind turbines), use of sonar, seismic testing, drilling, dredging and pile-driving, have increased background levels of underwater noise, generating unprecedented soundscapes in vast expanses of coastal and oceanic waters (Peng et al. 2015). Similarly, intertidal and shallow-water seascapes are lit by artificial light at night (ALAN), an escalating phenomenon linked with the development of shorelines (Bolton et al. 2017). Lights associated with offshore installations also alter natural light-dark regimes in open waters. Commercial and fishing vessels are also an important, though variable, source of ALAN (Davies et al. 2014). Thus, light pollution is not limited to coastal habitats but extends to the high seas.

Urban waters and river deltas receiving input from heavily populated areas are often hotspots of macro- and microplastic pollution (Fok & Cheung 2015, Yan et al. 2019). Plastic debris can range in size from metres to microns and, due to its buoyancy and long degradation time, can be dispersed by winds and currents at great distances out to sea. Plastic debris has been documented in the deep sea (Chiba et al. 2018), on remote oceanic islands (Lavers & Bond 2017) and accumulating in oceanic gyres (Lebreton et al. 2018). Thus, virtually every marine ecosystem on the planet is affected by plastic pollution.

Human-driven alterations of environmental conditions at local to regional scales are framed within scenarios of global climate change, caused by anthropogenic emissions of greenhouse gases, mainly CO_2, in the atmosphere. The oceans absorb almost 80% of the atmospheric heat and 50% of CO_2, resulting, as direct effects, in ocean warming and acidification. Recent analyses indicate that the ocean heat anomaly in 2018, relative to a 1981–2010 baseline, was the greatest on record and that the warmest years since 1958 were those within the period 2014–2018 (Cheng et al. 2019). Ocean warming rates are not homogeneous in space, but some areas appear to heat up more rapidly than others (Burrows et al. 2011). For example, the south-eastern parts of the Mediterranean and Australia, the Gulf of Alaska and the Galapagos Archipelago, just to name a few, are considered ocean warming hotspots (Frölicher & Laufkötter 2018).

Along with a mean increase in seawater temperatures, extreme atmospheric events are increasing in intensity and frequency (Oliver et al. 2017). For example, in the period 1925–2016, heatwaves have increased by 34% in frequency and by 17% in duration, with devastating consequences for marine life (Frölicher & Laufkötter 2018, Oliver et al. 2018). Some positive anomalies in ocean temperature, such as 'The Blob' that developed in the Gulf of Alaska and spread over the coast of north-west America, lasted almost three years, disrupting entire ecosystems and trophic webs and causing the collapse of local fisheries (Cornwall 2019). Likewise, 2016 and 2017 were characterised by coral bleaching over thousands of kilometres of the Great Barrier Reef on the north-east coast of Australia, a consequence of elevated seawater temperatures during summer months (Hughes et al.

2019). A recent meta-analysis found strong negative effects of marine heatwaves across biological processes and taxa (Smale et al. 2019).

Other indirect effects of warming include sea-level rise and increased intensity and frequency of extreme atmospheric events, such as floods, hurricanes, storms and hypoxia (IPCC 2014). Heat accumulation by the oceans is melting marine-terminating ice sheets, causing global sea level to rise at a rate of ~3–4 mm/yr (Watson et al. 2015). Importantly, feedbacks (e.g. increasing ocean stratification, slowing deep-water formation) triggered by meltwater may amplify ice melting, producing, under some scenarios, a multimetre rise of sea level within a 50–150 year timeframe (Hansen et al. 2016). In addition, storms and precipitation events are expected to become more intense and frequent as a consequence of increased atmospheric energy and alterations to ocean circulation (Fischer & Knutti 2015, Hansen et al. 2016). More frequent flooding due to sea-level rise, in combination with strong storm surge and large waves, will expose coastal areas to novel regimes of disturbance (Nicholls & Cazenave 2010, Cazenave & Le Cozannet 2013, Wong et al. 2014). Finally, elevated temperatures reduce oxygen levels in seawater, potentially culminating in climate-driven hypoxia, a phenomenon underpinning marine mass mortalities in the past (Kump 2018).

Ocean acidification (OA) is a global phenomenon, consisting of the ongoing increase of pCO_2 and consequent decrease of seawater pH levels, caused by the increasing uptake of atmospheric CO_2. Ocean pH has decreased by 0.08 units on average since the preindustrial period, and projections indicate a further 0.15–0.50 drop by the year 2100 (IPCC RCP2.6 and RCP8.5 projections). At low pH levels, calcium carbonate deposition for skeleton formation in marine organisms is impaired, putting at risk the long-term viability of key bio-constructor organisms such as corals, bivalves and encrusting coralline algae and of mobile, shell-forming invertebrates such as coccolithophores, molluscs and echinoderms (Doney et al. 2009).

Anthropogenic release of chlorofluorocarbons and other active compounds into the atmosphere has caused the thinning of the stratospheric ozone layer, increasing the fluxes of ultraviolet-B (UVB) transmitted to Earth's surface, in particular at high latitudes (Hegglin & Shepherd 2009). Although the ozone layer is predicted to recover in following years, reduced ultraviolet radiation shielding has been shown to have negative effects on a variety of aquatic organisms (Hader et al. 2015).

In addition to altering physical and chemical conditions, human activities have destroyed marine habitats. For instance, coastal land reclamation for urban and industrial expansion or aquaculture is causing substantial loss of key habitats, such as mangrove forests, salt marshes, seagrass meadows and macroalgal beds (Primavera 2006, Firth et al. 2016, Chee et al. 2017). Likewise, some fishing practices, such as bottom trawling and dynamite fishing, have devastated sensitive bottom habitats. The intensity and spatial extent of trawling can be astounding. For example, in 2017, the trawling effort in European seas exceeded one million hours (Dureuil et al. 2018). Human activities can also cause habitat destruction indirectly, via climate-driven rise of sea level and increased frequency of extreme events (i.e. hurricanes, storms, floodings).

Biotic drivers

Along with alterations in environmental conditions, human activities modify the structure of trophic webs through species harvesting and introduction. More than half of the world's oceans are exposed to industrial-scale harvesting, including long-lines, bottom trawling and purse-seining (Kroodsma et al. 2018). Estimates of global catches from industrial, artisanal, subsistence and recreational fisheries exceed 100 million tonnes, including discarded bycatch (Watson 2017). The biomass extracted from the oceans is not even across trophic levels, as species at higher trophic levels, such as apex predators, are more intensively targeted by fisheries (Parsons 1992, Pauly et al. 1998). Loss of predators can trigger far-reaching trophic cascades, with the effects propagating down to lower trophic levels (Parsons 1992, Estes et al. 2011). Loss of apex predators can release mesopredators, with dramatic consequences for their prey populations. Off the coast of North Carolina, the decline of large sharks released the cownose ray from predation control, which, in turn, increased pressure on their prey, the bay scallop, to the point of population collapse (Myers et al. 2007). Worth stressing is that fisheries have often responded to the over-exploitation of high trophic populations (i.e. piscivores) by targeting lower trophic levels (herbivores, planktivores and invertebrates), a phenomenon termed 'fishing down the food web' (Pauly et al. 1998).

In response to a stagnation in catches from wild fisheries, aquaculture production has increased steadily since the 1970s. In 2014, global marine and coastal aquaculture produced 26.7 million tonnes of finfish, molluscs, crustaceans and other animals (FAO 2016). However, aquaculture is still dependent on wild fisheries, since a relatively large proportion of global fish catch, about 13% in 2014 (equivalent to 8–15 million tonnes), is used for producing fish feeds and oil (FAO 2016). Forage fish targeted for such use include pelagic, low trophic-level species (e.g. anchovy, sardine, herring, menhaden) whose populations are on the brink of collapse due to over-exploitation and climate change (Pinsky et al. 2011, Cao et al. 2015). For instance, China, the world-leading country in aquaculture production, has bought fishing quotas in the Peruvian anchovy fisheries to guarantee high-quality feeds for farmed fish, contributing to the development of a global fishmeal market (Cao et al. 2015). In addition, use of non-targeted species (i.e. trash fish) for fishmeal may depress attempts to reduce by-catch.

In an era of globalisation, unrestricted movement of people and goods has accelerated species introduction rates, reshuffling the biogeography of marine species. Marine species can be transported, deliberately or accidentally, across a geographical barrier by a variety of vectors, including ballast waters, hull fouling, aquaculture, aquariology and marine debris. Invasion is a complex process, characterised by at least three stages (transport, establishment and spread; Williamson & Fitter 1996) and regulated by environmental factors, resource availability, regimes of disturbance, features of the recipient community, invader life traits, propagule pressure and quality (Lockwood et al. 2013, Gribben & Byers 2020). Once a species has gone through the establishment stage, a population can undergo expansion, becoming invasive and, hence, likely to alter the structure and the functioning of the invaded community. In marine environments, notable examples are the invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi*, whose predation intensity caused the collapse of local fisheries (Shiganova & Bulgakova 2000), and of the Mediterranean and temperate Australia by the seaweed *Caulerpa taxifolia*, which altered native biodiversity at different trophic levels (Williams & Smith 2007).

Combined pressure of species harvesting and introduction can fundamentally alter the trophic structure and, hence, the functioning of marine ecosystems. Many of the species whose populations have been driven to the point of collapse by human over-exploitation are at higher trophic levels (e.g. consumers; Jackson et al. 2001, Pandolfi et al. 2003, Stachowicz et al. 2007). By contrast, a large proportion of introductions, about 70%, involve lower trophic-level species, such as macroplanktivores, herbivores, detritivores and deposit-feeders (Stachowicz et al. 2007). Thus, whilst the two processes may have caused minor changes in total species diversity, they have caused a skew towards lower trophic levels (Stachowicz et al. 2007).

Multiple stressors and ecosystem state shifts

The interactive nature of human stressors in marine environments is widely acknowledged (Lotze et al. 2006, Crain et al. 2008, Halpern et al. 2008, Moore et al. 2018). The cumulative effect of interacting stressors can be additive or multiplicative (Crain et al. 2008). For example, in acidified waters, reduced ability to develop a carbonate exoskeleton enhances susceptibility to UVB radiation damage in organisms such as phytoplankton, calcified macroalgae and corals (Hader et al. 2015). Likewise, at CO_2 vents, negative effects of low pH on shell formation by the mussel *Mytilus galloprovincialis* are exacerbated by elevated seawater temperature (Rodolfo-Metalpa et al. 2011). In other cases, one stressor can mitigate the effects of other stressors. For example, algal ability to repair UVB ray damage is dampened by reduced nutrient availability, a side effect of the stratification of water masses, but it is fostered by seawater warming (Beardall et al. 2014).

There is growing evidence that simultaneous exposure to multiple stressors often underpins ecosystem state shifts. For example, Vasilakopoulos & Marshall (2015) identified a state shift in the Barents Sea cod population (*Gadus morhua*) in 1981, constituting the transition from large and slow-maturing to small and fast-maturing fish, and demonstrated that it was the result of combined effects of overfishing and climate change. At one sand flat on the west coast of New Zealand, decreased organic loading during a prolonged El Niño–Southern Oscillation (ENSO) event resulted in a shift from dominance by the tube-dwelling polychaete *Boccardia syrtis* to destabilised sediments lacking protruding hard substrata and, hence, in a major trophic and functional change (Hewitt & Thrush 2010). Likewise, using dynamic models, the combination of fishing, nutrient loading and sedimentation was shown to underpin the shift from coral to algal dominance in coral reefs (Fung et al. 2011). Although evidence of state irreversibility following shifts is lacking, these examples suggest that the emergence of novel marine ecosystems is more likely under multiple stressor scenarios.

Novel and hybrid marine systems

Coastal and offshore artificial habitats

Modification of coastlines to provide shelter to vessels and facilitate military and commercial activities dates back to millennia BC (de Graauw 2017) and represents one of the most ancient forms of human-driven alterations of abiotic conditions in the marine environment. The demand for infrastructure to sustain modern commercial, industrial, recreational and tourism activities has resulted in the proliferation of artificial structures, such as seawalls, pilings, breakwaters and floating pontoons (Figure 1). Likewise, renewable energy devices (e.g. windfarms), oil and gas platforms are flourishing in offshore waters (Firth et al. 2016). The presence of these habitats is ubiquitous and is set to escalate in the coming years in response to the progressive development of coastal areas, increasing need to protect shorelines from extreme atmospheric events and sea-level rise and energy demand (Bulleri & Chapman 2010, Firth et al. 2016). These built environments do not fit the definition of novel ecosystems by Hobbs et al. (2006) or later descriptions (e.g. Morse et al. 2014), since they do not result from the crossing of critical thresholds and are actively managed. Nonetheless, we sense that defining their degree of novelty can inform management strategies.

Urban marine ecosystems are generally exposed to severely altered chemical and physical conditions generated by the variety of land- and sea-based activities that take place in large human aggregations. In the last two decades, emergent sources of pollution, including enhanced rates of sedimentation, plastic litter, noise and artificial light, have been particularly severe in urban coastal settings. Habitat provided by offshore installations can instead be exposed to more pristine environmental conditions, although light pollution can have strong consequences. For example, in the northern Gulf of Mexico, gas flare and floodlights associated with oil platforms increased underwater light irradiance between 10 and 1000 times in comparison with natural open-water control sites at distances of up to 250 m and depths exceeding 20 m (Keenan et al. 2007).

Less attention has been given to climate-related stressors in marine urban environments. Nonetheless, the intensity of climate-driven stress, such as increasing seawater temperature and acidification, should differ between urban and 'pristine' areas. Alterations of temperature have long been at the core of urban ecology and the functioning of cities as islands of heat has become a paradigm (Mills 2014). Recent measurements along the coasts of the north-west Mediterranean suggest a similar effect in marine environments since surface seawater temperatures inside marinas were generally warmer than adjacent open waters, with deltas exceeding 3°C (Figure 2). These data, although preliminary, suggest that confined waters warm up more than open waters, reaching higher summer mean and peak temperatures. Under future scenarios of warming, these environments may become inhospitable for many native species due to excessive thermal stress.

Figure 1 Examples of common coastal artificial structures: (A) seawall; (B) pier pilings; (C) floating pontoons; (D) breakwater. [Photo credits: Fabio Bulleri (A-C) and Michele Magri (D).]

In coastal areas, pH levels and fluctuations are influenced by inputs of nutrients, organic and inorganic carbon, acids, carbonate alkalinity and freshwater, as well as the life traits of benthic communities (Duarte et al. 2013, Carstensen & Duarte 2019). Elevated inputs of these compounds in the proximity of densely populated areas can lower seawater pH levels, potentially exacerbating the effects of future ocean acidification.

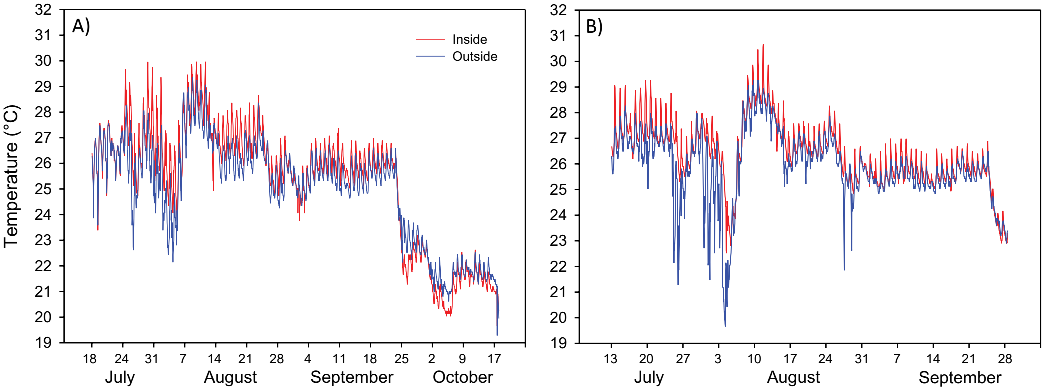

Figure 2 Records of (A) surficial and (B) 1-m-depth temperatures inside and outside a marina along the coast of Tuscany (north-west Mediterranean) during summer–autumn 2018. Note the variation in the temporal extent of temperature recordings between (A) and (B).

Regimes of mechanical disturbance can be altered in different ways. Breakwaters, ports and marinas dampen hydrodynamic forces from waves and surge and can, thus, provide wave-sheltered hard substrata along exposed coasts. Altered hydrodynamics also influence depositional processes, ultimately increasing the proportion of finer particles in superficial sediment layers (Martin et al. 2005). By contrast, in highly populated harbours, intertidal infrastructure can be exposed to continuous washing by boat-generated waves (Blockley & Chapman 2008). Regular maintenance and renovation works further alter the regimes of disturbance at which artificial structures are exposed (Airoldi & Bulleri 2011).

Beyond the altered biotic and abiotic conditions to which they are exposed, it is their artificial origin that makes marine infrastructures intrinsically different from natural hard substrata. Construction materials used to build infrastructure are often human-made (e.g. concrete, metal). Thus, they provide novel environmental conditions for benthic organisms, such as substrate composition, texture and pH. In addition, some artificial structures, such as floating docks, pontoons and equipment used in aquaculture facilities (floating rafts, buoys and lines), are moving, providing novel hydrodynamic conditions (Kirk et al. 2007, Dafforn et al. 2009). In some cases, natural materials, such as rock or wood, are used; for example, breakwaters and ripraps for shoreline protection are commonly made of quarried blocks of different types of rock (e.g. limestone, granite, dolomite). However, these natural materials can be extraneous to the local marine environment or can differ in orientation, exposure, size, shape and slope from nearby rocky shores or boulder fields (Bulleri et al. 2005). For example, the construction of breakwaters along sandy shores, independently from the composition of the blocks of which they are made, attracts a novel suite of rock-dwelling species through the provision of otherwise absent rocky habitat (Bacchiocchi & Airoldi 2003, Vaselli et al. 2008). In other cases, materials used to build coastal infrastructure do not differ from natural hard substrata. For example, in Sydney Harbour, retaining seawalls are made from sandstone blocks extracted from local natural cliffs and shores (Chapman & Bulleri 2003). Nonetheless, the surface of quarried blocks is unnaturally smooth since it lacks elements of topographic complexity, such as pits, ridges and crevices, that characterise nearby vertical rocky shores (Bulleri et al. 2005).

Plant and animal communities in urban settings are generally different from those occurring in 'pristine' or less impacted areas (Tamburello et al. 2012). Often, the severity of environmental conditions and increased intensity and frequency of disturbance limits the number of species able to maintain viable populations in these areas and favours the blooming of ephemeral, more stress-tolerant forms (Tamburello et al. 2012, Stuart-Smith et al. 2015, Portugal et al. 2016, Doubleday & Connell 2018).

Benthic assemblages on marine artificial structures are often characterised by low species diversity and by the dominance of a small set of opportunistic species, a very common pattern on structures deployed on sandy bottoms (Bacchiocchi & Airoldi 2003, Mayer-Pinto et al. 2018). For example, along sedimentary shores of the north-east Adriatic Sea, frequent disturbance due to sand scour and maintenance work maintains assemblages at an early successional stage, dominated by fast-growing species, such as the ephemeral filamentous algae that compose turfs (Airoldi & Bulleri 2011).

When marine artificial structures are introduced on hard bottoms, they often support a suite of macroalgae, invertebrates and fish resembling those on natural habitats (Bulleri & Chapman 2010). However, a large proportion of species or functional groups often display different relative abundances in comparison to natural rocky habitats (Bulleri & Chapman 2004, Bulleri et al. 2005). Although communities on artificial habitats can converge on those on nearby natural hard substrata with increasing time since construction, they generally remain distinct after long periods of time (>30 years; Burt et al. 2011), suggesting altered ecological processes (Bulleri & Chapman 2004, Bulleri et al. 2005, Ivesa et al. 2010, Mayer-Pinto et al. 2018). For example, in Sydney Harbour, altered recruitment, likely due to variations in topographic complexity, underpins the establishment of different benthic assemblages between sandstone seawalls and adjacent vertical rocky shores (Bulleri 2005). Other studies demonstrate variations in other key processes, including competition, grazing, predation and animal behaviour between natural and artificial habitats (Rodemann &

Brandl 2017). In addition, variation in species relative abundance can be associated to variations in key life traits. For example, in Sydney Harbour, oysters growing on pilings are smaller than on rocky shores (Mayer-Pinto et al. 2018). Similarly, limpets can be smaller and with fewer and smaller egg masses on seawalls than rocky shores (Moreira et al. 2006).

Ports and marinas function as gateways and are primary sites of non-native species establishment (Ojaveer et al. 2014). Not surprisingly, non-native species often make up a large proportion of benthic communities supported by built habitats (Bulleri & Airoldi 2005, Glasby et al. 2007, Tyrrell & Byers 2007, Dafforn et al. 2009). High propagule pressure is undoubtedly at the core of invader success in these habitats. However, intrinsic features of artificial structures can facilitate their establishment and spread. For example, artificial structures made of concrete provide highly suitable habitat for recruits of non-native epibiota (Glasby et al. 2007). Increased water flow would facilitate the dominance of non-native epifauna on floating and moving structures, likely by enhancing recruitment and food supply (Glasby et al. 2007, Dafforn et al. 2009). Intense disturbance, removing mussels, facilitates dominance of the invasive seaweed *Codium fragile* ssp. *tomentosoides* and of some non-native ascidians on breakwaters in the north-west Adriatic Sea (Bulleri & Airoldi 2005, Airoldi et al. 2015). Such high rates of species introduction combine with intense commercial and recreational harvesting of fin-, cray- and shellfish (Pflugh et al. 1999, Hunt et al. 2011, Mayer-Pinto et al. 2015). For example, recreational harvesting of mussels contributes to the proliferation of ephemeral macroalgae on breakwaters, including invasive species (Bulleri & Airoldi 2005). Few studies have compared the functioning between artificial and natural habitats; nonetheless, as a consequence of altered environmental conditions, species diversity, relative abundances and life traits, the functioning of intertidal and shallow communities supported by artificial structures can be expected to differ from natural hard substrata (Firth et al. 2016, Mayer-Pinto et al. 2018).

In addition to urban infrastructure, disused docks, artificial enclosed habitats often actively maintained by de-stratification and biofiltration, are totally novel ecosystems, akin to freshwater canals and reservoirs (Hawkins et al. 1992a,b, 1999, Allen & Hawkins 1993). These brackish water bodies can host a diverse flora and fauna (Allen et al. 1992). Other artificial coastal ecosystems include farming ponds, wetlands and salt marshes. Although few studies have assessed how species composition and functioning of artificial farming ponds compare to natural ones, intensive management for maximising yields (e.g. input of antibiotics, probiotics, antifungals and formulated feeds; Sapkota et al. 2008) is likely to enhance their novelty.

Implications for conservation and management

Marine life in urban settings such as ports, smaller harbours, docks, marinas, and along city waterfronts has traditionally been given little ecological value – hence, has been little studied (Bulleri 2006). Progressive recognition of the potential of urban marine ecosystems to sustain declining species and functions has challenged this view. Artificial habitats, due to their origin and to being exposed to altered regimes of disturbance, often support novel species compositions and, likely, functions. While reverting these systems to the historical state is impossible, reducing their degree of novelty and/or enhancing their ecological value appears pursuable.

Since artificial structures are truly novel systems, an interventionist approach appears justified. Indeed, earlier attempts to recover some ecological functions in artificial marine systems date back to the 1980s and were performed in disused docks of the macrotidal estuary of Liverpool (Russell et al. 1983, Wilkinson et al. 1996). Direct (dredging and artificial mixing) and indirect (enhancement of mussel and brown algae populations) improvement of water quality produced a marked increase of flora and fauna in these semi-enclosed, brackish water bodies, enhancing their heritage, educational and economic value, as well as their potential to function as sites for the conservation of lagoonal species (Allen et al. 1992, 1995). The collaboration among ecologists, engineers, environmental scientists, managers and stakeholders has given birth to the vibrant field of ecological engineering, which aims to improve the design of marine infrastructure to accommodate ecological restoration, rehabilitation or reallocation (Firth et al. 2016). Restoration, intended as the return of the system to a prehuman condition, is impossible. However, these structures can be used to enhance degraded habitats (i.e. without the aim of recovery to a predefined historical state). For instance, addition of elements of complexity to vertical seawalls (e.g. pits, ridges, overhangs, crevices, pools) can provide habitat for species that generally occur on more heterogeneous horizontal rocky shores, reducing the ecological footprint of the construction (Browne & Chapman 2014, Firth et al. 2016). Likewise, transplants on subtidal breakwaters can sustain endangered populations of canopy-forming macroalgae that function as nursery habitat (Perkol-Finkel et al. 2012). These artificial habitats can also be used to sustain a new set of species or functions with ecological, social or economic value (i.e. reallocation). For instance, greater support of filter-feeders can reduce water turbidity (Allen et al. 1992, Wilkinson et al. 1996), possibly facilitating macrophytes (McCay et al. 2003), while the application of shell-made refuges can enhance the survival of juveniles of fish species subjected to intense harvesting pressure (Bouchoucha et al. 2016). As a prologue, we would like to stress that overestimating – or, more often, overemphasising – the success of interventions aiming to increase the ecological value of artificial structures may promote their proliferation (Firth et al. 2020). Thus, any action taken for accommodating ecological principles into the design of artificial structures should be viewed as a form of mitigation of their impacts. Ecological engineering is very unlikely to generate a complete offset of the alterations caused by the introduction of new infrastructure and even less an improvement of nature.

Intertidal rocky shores

Addressing the question of whether novel ecosystems can emerge in rocky intertidal environments requires consideration of how global change will modify the prevailing environmental conditions on rocky shores and how organisms will respond to these changes. A novel ecosystem will emerge if extant organisms become unable to cope with the new environment because of unsuitable abiotic conditions, emergence of new enemies or a combination of both (Williams & Jackson 2007, Hobbs et al. 2009). Rocky intertidal environments are characterised by the prevalence of directional environmental gradients. Tidal fluctuations generate gradients of environmental stress at scales ranging from a few centimetres to metres, whereas gradients of wave exposure take place on scales of tens of metres to kilometres, and latitudinal gradients – reflecting mostly variation in temperature regimes – occur at scales of hundreds to thousands of kilometres. Many studies have documented how species and assemblages sort along these gradients and how processes such as recruitment, predation and competition may change in relation to the prevailing environmental conditions (Benedetti-Cecchi & Trussell 2014).

Although powerful ecological drivers, directional environmental gradients provide only a coarse view of how species and assemblages are distributed on rocky shores, reflecting differences between the extremes of an otherwise continuous spectrum of variation. Indeed, seamless variation occurs within the boundaries of prevailing abiotic discontinuities, such as within tidal levels and wave exposure conditions. For example, Denny et al. (2004) have documented continuous patterns of variation of temperature and wave force along transects tens to hundreds of metres in length within the same tidal level. Using mussel mimics, Helmuth et al. (2006a) demonstrated how body temperature in model intertidal invertebrates is best described as a mosaic of thermal patches that vary in relation to regional patterns of tidal regimes and local patterns of wave splash. This thermal patchiness can override the latitudinal gradient of thermal variability along the west coast of the United States. Given the patchy nature of the physical environment, it is not surprising that small-scale variation in species abundances can be large, even larger within than across the prevailing abiotic discontinuities on rocky shores (Benedetti-Cecchi 2001).

Intensifying extreme events such as storms and heatwaves can exacerbate directional gradients and reduce the availability of thermal refuges on rocky shores. Poleward range shifts in rocky intertidal species provide evidence of ecological responses to climate change along a directional (latitudinal) gradient (Helmuth et al. 2006a). Several species of gastropods, barnacles and algae have extended their leading edges toward northern latitudes in the last decades and, in some cases, contractions have been observed at the trailing edges (Hawkins et al. 2009, Nicastro et al. 2013). The pace of range shifts is faster in marine than terrestrial environments, and many intertidal species have moved up to 50 kilometres per decade (Helmuth et al. 2006b, Sorte et al. 2010). Empirical evidence and modelling studies indicate that species' range shifts are reshuffling rocky intertidal assemblages, originating novel species combinations with no historical analog (Williams & Jackson 2007, Wilson et al. 2019).

Migrating organisms may alter key interactions on rocky shores. Foundation species such as canopy algae and mussels provide shelter and maintain thermal mosaics in intertidal environments, buffering less tolerant organisms from harsh physical conditions (Jurgens & Gaylord 2018). Foundation species are already declining in some regions in response to intensifying wave action and rising temperatures, with cascading effects on associated assemblages (Sorte et al. 2017). The occurrence of new competitors and consumers in no-analog assemblages may further contribute to the decline of foundation species, reducing habitat availability and thermal refuges. However, range expansions may also result in the replacement of foundation species by other organisms performing the same or similar functions; thus, species' range shifts may not necessarily have an impact on the recipient assemblages (Bulleri et al. 2018). The balance between positive and negative effects of species' range shifts is hard to predict and will probably be context dependent in future climates (Lima et al. 2007, Poloczanska et al. 2011).

Evidence of threshold crossing and irreversibility

To what extent no-analog rocky shore assemblages will translate into novel ecosystems remains an open question. Several factors make the simple prediction that new climates and new species combinations will generate novel ecosystems uncertain for rocky intertidal environments. First, species can acclimatise or become genetically adapted to changing climates, and even the most threatened species may be rescued through natural selection (Somero 2010, Bell 2013, Chirgwin et al. 2015). Second, we lack quantitative and well-justified criteria to make the novel ecosystem concept operative in rocky intertidal systems. What is the relevant spatial scale of change that needs to be observed to declare a novel ecosystem? Even in the most dramatic examples where new habitat-forming species have replaced existing assemblages, as in the case of the tunicate *Pyura praeputialis* in Chile, changes have occurred at spatial scales that hardly correspond to those of an ecosystem (Castilla et al. 2004). Similarly, how much change in species composition and abundance should be observed, compared to historical conditions, to claim that a novel ecosystem has emerged? One may argue that observing differences in community dissimilarity will not be enough, as significant differences in multivariate space can also be observed within the same ecosystem.

Finally, the requirement that novel ecosystems cannot be reversed is difficult to assess and, again, we lack an operative criterion to gauge the relevant temporal scale at which stability should be observed (Table 1). Growing evidence suggests that rocky intertidal assemblages are resilient to perturbations. For example, models and experiments indicate that a transition from macroalgal forests to turf-dominated assemblages requires the loss of more than 75% of canopy cover; otherwise, the system has hysteresis and can recover from perturbations (Benedetti-Cecchi et al. 2015, Rindi et al. 2017) (Table 1). Alternative stable states have repeatedly been documented in rocky intertidal assemblages, suggesting that transitions and switches are common in these environments (Paine & Trimble 2004, Petraitis & Dudgeon 2016). However, resistance to change has also been documented (Bertness et al. 2002, Menge et al. 2017). Whatever view one adopts, resilience or resistance implies that strong reinforcing feedback mechanisms are at work to maintain structure in rocky intertidal assemblages, making the onset of novel ecosystems unlikely.

Rocky intertidal assemblages are organised as mosaics of patches at different successional stages, ignited by spatially and temporally asynchronous disturbances (Sousa 1984). So far, there

Table 1 Summary of the evidence from the marine literature in support of each of the four criteria that define a novel ecosystem (human agency, no-analog species composition, threshold crossing and threshold irreversibility) for each of the marine ecosystems encompassed by this review: intertidal rocky shores, subtidal rocky reefs, coral reefs, estuaries/mangrove forests/seagrasses/oyster reefs/salt marshes/mud flats, and pelagic.

ECOSYSTEM	Human agency	No-analog species composition	Threshold crossing	Threshold irreversibility	References
Intertidal rocky shores	✓ [1–6]	✓ [7]	✓ [8,9]	✗	1. Castilla (1999) 2. Castilla (2000) 3. Crowe et al. (2000) 4. Thompson et al. (2002) 5. Halpern et al. (2007) 6. Halpern et al. (2008) 7. Harley et al. (2012) 8. Benedetti-Cecchi et al. (2015) 9. Rindi et al. (2017)
Subtidal rocky reefs	✓ [1–4]	✓ [5,6]	✓ [1,7]	✗	1. Ling et al. (2015) 2. Krumhansl et al. (2016) 3. Filbee-Dexter & Wernberg (2018) 4. Smale et al. (2019) 5. Wernberg et al. (2013) 6. Filbee-Dexter et al. (2016) 7. Boada et al. (2017)
Coral reefs	✓ [1–11]	✓ [2,7]	✗	✗	1. Adjeroud et al. (2018) 2. Aronson et al. (2014) 3. Cleary et al. (2008) 4. Darling et al. (2013) 5. Green et al. (2008) 6. Guest et al. (2016) 7. Hughes et al. (2018a) 8. Loya et al. (2001) 9. McClanahan (2014) 10. van Woesik et al. (2011) 11. Yamano et al. (2011)
Estuaries, mangrove forests, seagrasses, oyster reefs, salt marshes and mud flats	✓ [1–6]	✓ [7–10]	✓ [11,12,13]	✗	1. Cloern et al. (2016) 2. Gonzalez et al. (2019) 3. Lotze et al. (2006) 4. Ruiz & Carlton (2003) 5. Valiela et al. (2001) 6. Waycott et al. (2009) 7. Gribben et al. (2013) 8. Naylor et al. (2000) 9. Mayer-Pinto et al. (2015) 10. Worm et al. (2006) 11. Connell et al. (2017) 12. McGlathery et al. (2013) 13. Thrush et al. (2004)

(*Continued*)

Table 1 (*Continued*) Summary of the evidence from the marine literature in support of each of the four criteria that define a novel ecosystem (human agency, no-analog species composition, threshold crossing and threshold irreversibility) for each of the marine ecosystems encompassed by this review: intertidal rocky shores, subtidal rocky reefs, coral reefs, estuaries/mangrove forests/seagrasses/oyster reefs/salt marshes/mud flats and pelagic.

ECOSYSTEM	Human agency	No-analog species composition	Threshold crossing	Threshold irreversibility	References
Pelagic	✓ [1–4]	✓[5,6,7]	✓[8]	✗	1. Beaugrand et al. (2008) 2. Fauchald et al. (2011) 3. Oguz & Gilbert (2007) 4. Polovina et al. (2011) 5. Beaugrand et al. (2008) 6. Lynam et al. (2006) 7. Roux et al. (2013) 8. Casini et al. (2009)

Note: Green ticks indicate the presence of relevant scientific evidence in support of a criterion, with their size representing relative confidence levels. Red crosses indicate lack of scientific evidence in support of a criterion. For each criterion and ecosystem, key references are reported.

is no evidence that species' range expansions and anthropogenic climate change have modified this structure substantially. Although successional convergence and biological homogenisation can occur in response to disturbance and invasion (Castilla et al. 2004, Martins et al. 2018), effects can vary greatly in relation to species life histories and disturbance regimes (Bertocci et al. 2017, Dal Bello et al. 2017, 2019). Most changes occur at small spatial scales, and strong feedback mechanisms prevent ecosystem-level cascades in rocky intertidal environments. The balance between winners and losers results in new species combinations and no-analog assemblages, which are better described as hybrid ecosystems (Williams & Jackson 2007, Hobbs et al. 2009).

Implications for conservation and management

As with other marine ecosystems, the goal of preserving 'natural' environments has proved unrealistic in rocky intertidal habitats, due to the difficulties of gauging historical reference states and of managing global stressors (Pauly 1995, Dayton et al. 1998, Lotze et al. 2006). Nevertheless, alternative management options can be implemented on rocky shores, including management of keystone species (*sensu* Paine 1966), managing for ecosystem functions and services and enforcing conservation through Marine Protected Areas (MPAs) (Thompson et al. 2002, Branch et al. 2008). Keystone species provide targets for conservation because, by definition, they play a disproportionate role for the maintenance of species diversity (Paine 1966). Therefore, protecting such influential species should guarantee the maintenance of the structure of an entire assemblage (Mills et al. 1993). An underlying assumption of this approach is that a keystone species should play its fundamental role consistently over broad spatial and temporal scales, justifying managerial actions at regional and national levels. This assumption is, however, questionable, as species interactions are often context dependent, so that protecting a supposed\ keystone species may not always produce the expected effects (Chamberlain et al. 2014).

The way in which a lack of understanding of species interactions may jeopardise management options based on the conservation of keystone species is illustrated by the recent decline of the predatory seastar *Pisaster ochraceus*, the iconic species that inspired the formulation of the keystone species concept (Paine 1966). Starting in 2011, many populations of *P. ochraceus* have been decimated by a wasting syndrome outbreak along the west coasts of the United States (Gravem & Morgan 2017, Schiebelhut et al. 2018). These mass mortality events provided an opportunity to test the prediction that the disappearance of the keystone predator would lead to the proliferation of its preferred prey, the competitive dominant mussel *Mytilus californianus*, with consequent cascading effects on other rocky intertidal species. After eight years since the onset of the epidemic disease, evidence of such strong responses is lacking. Although predation pressure on mussels re-established quickly at some sites due to unprecedented recruitment of *Pisaster ochraceus*, research has shown that trophic compensation by other predators, variable recruitment of mussels, unfavourable environmental conditions or a combination of these factors challenge the simple prediction that loss of the keystone predator generates large-scale, spatially consistent responses in assemblages (Menge et al. 2016, Moritsch & Raimondi 2018, Kay et al. 2019). Protecting keystone species under the assumption that their disappearance will cause deterministic ecological changes is at odds with the view that natural assemblages are functionally redundant and that compensatory mechanisms are common in webs of species interactions (Connell & Ghedini 2015). A better understanding of the processes that overwhelm keystone interactions would help in deciding when and where management strategies based on keystone species will be appropriate.

The goal of managing for ecosystem functions and services through restoration of biogenic habitat is gaining momentum in rocky intertidal systems. A focus on functions and services is attractive, especially in urban areas where managing to preserve natural assemblages may be exceedingly costly or impossible to achieve. Shifts in species composition and the appearance of novel assemblages is common in urban areas, but these assemblages may still be managed to promote specific functions. For example, restoration of filter-feeders to improve water clarity and generate habitat for other species, a practice already implemented on artificial substrata (discussed in the previous section) and in estuaries (see next section), is also an option for natural rocky shores (McAfee et al. 2018). Restoration of canopy-forming algae is also a growing practice, with the goal of restoring the biodiversity and functions that these habitat-formers typically promote (Bellgrove et al. 2010, De La Fuente et al. 2019). However, despite numerous attempts, convincing evidence that large-scale restoration of canopy-forming algae is feasible in rocky intertidal habitats is not yet available.

Planning for conservation also depends on environmental context. Management goals and approaches differ between remnant stretches of shore in urban environments and remote shores far from direct sources of anthropogenic disturbance. Conservation of remote rocky shores through MPAs offers a valid option to preserve biodiversity, to provide natural barriers against the spread of invasive species and, ultimately, to maintain functions and services (Gallardo et al. 2017, Mellin et al. 2019). However, by providing hotspots of biodiversity, effective MPAs can become the foci of the most severe impacts of global change to marine coastal environments. Marine heatwaves and other oceanographic events frequently cross the boundaries of MPAs with the potential to cause disproportionate impacts to marine biodiversity, originating what has been termed the ‘protection paradox’ (Bates et al. 2019). Increasing resilience against large-scale perturbations requires the implementation of networks of MPAs, but a clear understanding of the relation between network topology and resilience has remained elusive and is one of the most pressing conservation challenges for the decades to come.

Subtidal rocky reefs

Constant change characterises the ecology of subtidal rocky reefs and forests over decadal scales, increasingly reflecting the imprint of human activity. Whilst extreme events, such as heatwaves, create novel communities over short timescales (i.e. sudden loss of canopies and arrival of tropical herbivores), over the long term, adjustments in species interactions may either facilitate recovery to original community states or hasten the formation of novel states (Table 1). Research at the warmer limits of kelp distribution tends to emphasise the direct effects of temperature on creation of novel communities through habitat replacement and tropicalisation. Researchers at the cooler range of kelp distribution tend to emphasise indirect effects, particularly how herbivores mediate the effects of fish or climate to either sustain communities in their original state or to drive them to a novel state. The following sections summarise these effects, particularly those that could force hybrid or novel states in shallow subtidal rocky reef environments.

Overfishing of predators that control herbivore populations has long been considered a leading cause of kelp and fucoid loss from rocky reefs (Steneck et al. 2002, Guidetti 2006). While we now accept there are other mechanisms of loss (discussed subsequently), overfishing remains a pervasive impact, and large predators are functionally extinct along the coasts of most developed countries. The key issue associated with overfishing of vertebrate predators at the top of the food chain is their effect on herbivore populations, leading to widespread deforestation of rocky reef habitats (i.e. a classic trophic cascade). This loss of canopy-formers normally results from sea urchin grazing, which is controlled by predation where fishing is minimal; overgrazing can, however, occur when herbivores are released from predation (Steneck et al. 2002).

Fishing is predicted to interact with new stressors associated with climate change. For example, the expansion of the sea urchin *Centrostephanus rodgersii* into Tasmania, due to the intensification of the East Australian Current, has resulted in substantial loss of kelp forests from subtidal rocky reefs (Ling et al. 2009). This loss of kelp may be reversed by allowing recovery of predators within marine reserves. Yet, climate change may counter the loss of predators and facilitate the recovery of kelp. Benthic dinoflagellates bloom during warm periods and have been found to reduce sea urchin foraging in northern New Zealand (Shears & Ross 2010), allowing the recovery of kelp in urchin barrens. Similar urchin mass mortalities have been recorded along the rapidly warming coasts of the eastern Mediterranean (Yeruham et al. 2015). The capacity for such novel conditions to interact with trophic interactions, therefore, poses challenges for understanding and managing these systems.

Tropicalisation of temperate coastlines occurs where warm-water species disperse to warm-water latitudes, whilst cool-water species recede towards the poles (Vergés et al. 2014a,b). Tropicalisation has caused the replacement of canopy-forming macroalgae on subtidal rocky reefs with either urchin barrens or turfs and shifts in community composition towards species characteristic of warm-temperate, subtropical and tropical reefs (Johnson et al. 2011, Wernberg et al. 2013, Bennett et al. 2015, Vergés et al. 2016). At warmer latitudes, ocean warming drives two notable effects. It tends to be physiologically stressful to canopy-formers (kelp and fucoid species) that are most resilient at cooler temperatures (Wernberg et al. 2010) and drives the range expansion of warm-water herbivores. This expansion has been particularly noticeable in the Mediterranean (Vergés et al. 2014b) and where poleward-flowing boundary currents have intensified around Australia (Vergés et al. 2014a) and Japan (Tanaka et al. 2012).

Novel rocky reef communities can emerge after marine heatwaves. One of the clearest examples was a 100 km contraction of canopy-forming algae in Western Australia, which experienced anomalies of 2–4°C for ten weeks along over 2000 km of coastline (Wernberg et al. 2013). Community-wide tropicalisation emerged after this event, altering community composition and species interactions, particularly herbivory. The biomass and diversity of herbivorous fish from the tropics increased so that grazing rates intensified to the extraordinarily high rates of coral reef herbivory (Bennett et al. 2015, Zarco-Perello et al. 2017). This rate of herbivory contributed to a shift from reefs supporting canopy-forming forests to turf-dominated reefs (Bennett et al. 2015). As a result, kelps have been replaced by novel communities of invertebrates, corals and fishes characteristic of subtropical and tropical waters (Wernberg et al. 2013, 2016).

The shift from canopy-forming to algal turf dominance due to tropicalisation by fish communities (Vergés et al. 2014a,b, Bennett et al. 2015) demonstrates that climatic extremes can drive wholesale changes in biodiversity on subtidal rocky reefs (Oliver et al. 2017). The increasing frequency and intensity of such episodes suggests that such novel communities will become increasingly common at the warmer latitudes of temperate coasts.

The anticipated effects of warming-induced invasions are thought to be enhanced by the duality of increasing propagule dispersal of invasive species and decreasing biotic resistance of native species

(Walther et al. 2009, Sorte et al. 2010). Their combined influence hastens change to biodiversity both directly, through invasion, and indirectly, by reducing community resistance and resilience. Invasive seaweeds, which often thrive in disturbed locations, also reduce the diversity and biomass of native macroalgal assemblages and prevent or dampen their recovery after disturbance (Maggi et al. 2015, Bulleri et al. 2017). For example, invasion of disturbed patches of reef within stands of the canopy-forming macroalga *Cystoseira brachycarpa* by the clonal seaweed *Caulerpa cylindracea* hinders canopy recovery, even at sparse densities (Bulleri et al. 2017). These observations suggest that invaders can trigger novel positive feedback mechanisms that lock a system into a degraded state.

Two of the most limiting resources in the sea are carbon and nitrogen, and their release to coastal waters is unprecedented (Vitousek et al. 1997). Societal aspirations for improving quality of life are dependent on the intensification of food production (nitrogen fertilisers), removal of human waste (nitrogen effluent) and supply of energy and goods to cities (carbon emissions). Both the release of nitrogen (eutrophication; Gorman et al. 2009) and carbon propagate through marine food webs (Ghedini & Connell 2017, Goldenberg et al. 2017), bringing the potential for community change. Resource liberation increases the potential for the competitive displacement of kelps and fucoids on rocky reefs (Russell et al. 2009, Piazzi & Ceccherelli 2017). Enrichment of resources (carbon or nitrogen) supercharges the growth of ephemeral algal species (turfs) whilst having minor effects on perennial canopy-formers (Connell et al. 2018). Kelps do not benefit from resource enrichment (carbon and nitrogen) nearly as much as turfs (Falkenberg et al. 2013b), so that the competitive advantage is conferred to turfs (Connell et al. 2008, Gorman & Connell 2009). Thus, rather than killing kelp directly, resource enrichment drives their loss by altering this competitive hierarchy (Gorman & Connell 2009). On oligotrophic coasts, minor increases in nutrients may foster the recovery of canopy-forming species (Tamburello et al. 2019), but such effects appear to depend on the severity of nutrient limitation (natural levels) relative to nutrient enhancement (pollution levels) (Gorman et al. 2009).

Replacement of kelp by turfs via carbon or nitrogen pollution reflects a combination of direct and indirect effects (Connell et al. 2018). The life history and physiology of turfs not only directly benefit from resource enrichment (Falkenberg et al. 2013b), but they also benefit indirectly from conditions that reduce their consumption by herbivores (Mertens et al. 2015) – essentially allowing them to expand unchecked. Hence, the likelihood of kelp forest collapse is heightened when the increased production of turfs is exacerbated by reduction in its consumption by herbivores (Ghedini et al. 2015). Put simply, collapse occurs when resource enrichment reverses the competitive dominance of producers, but consumers then fail to compensate by neutralising the competitor. What this means is that small cumulative increases in enrichment drive a much greater consequence than would be predicted from linear effects measured between competitors (e.g. kelps vs turfs), because these interactions are embedded within a broader network of change that propagates collapse.

Evidence of threshold crossing and irreversibility

Globally, the switch from kelp to urchin barrens or turf-forming landscapes has been difficult to reverse. The widespread collapse of kelp-dominated forests to sea urchin-dominated barrens provides the clearest and most intensely studied example of regime shifts (Table 1). A global synthesis by Ling et al. (2015) recognised this transition as a non-linear regime shift, whereby a critical threshold of increasing urchin biomass triggers overgrazing of subtidal forests. As urchin biomass exceeds a critical threshold, the loss of canopy-forming macroalgae is typically sudden. Importantly, the threshold of herbivore biomass that triggers canopy loss is substantially greater than the threshold density that allows canopies to recover (Figure 3).

Empirical research into urchin-dominated systems generally demonstrates that the densities of herbivores that drive kelp loss (i.e. barren formation) are not only greater than that required to maintain a barren, but that recovery of kelp requires removal of nearly all urchins. This difference in thresholds for loss (high threshold) and recovery (low threshold) demonstrates a discontinuous

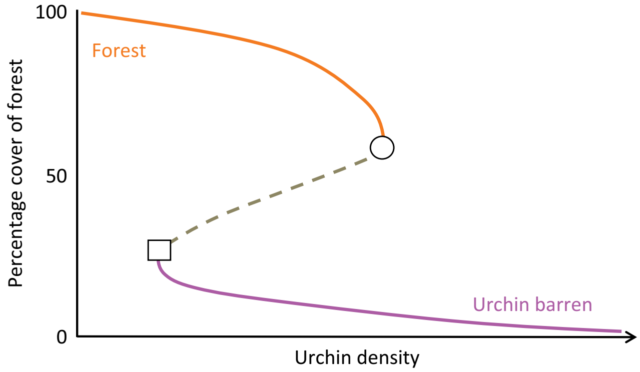

Figure 3 Conceptual diagram of the relationship between the density of urchins and the cover of subtidal forests. After barrens are created (pink trajectory), reversing to canopy-dominated reefs (orange trajectory) is more difficult (i.e. hysteresis), because the density at which urchins need to be thinned is substantially less (□) than the density that created barrens (○). Grey line shows unstable equilibrium between forest and barren-dominated systems. (Redrawn from Ling, S.D. et al. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B-Biological Sciences* 370, 20130269.)

regime-shift with hysteresis (Ling et al. 2015). Under these circumstances, the shift to either encrusting-coralline barrens or turf-forming algae cannot be regarded as novel ecosystems (*sensu* Morse et al. 2014).

Implications for conservation and management

Where the persistence of forests is the focus of management for subtidal rocky reefs, the potential solutions centre on maintaining the biomass of herbivores below the threshold for barrens formation or reducing water pollution to stop turf-domination. Often, this involves focus on the role of increasing stocks of predators that control the abundance of sea urchins and barrens formation (Estes et al. 2011) or policies that reduce urban discharge to control turf formation (McAfee et al. 2020). In trophically structured systems, where management focuses on reducing fishing pressure to enable the recovery of urchin predators (e.g. MPAS) (Babcock et al. 2010), the hysteresis effect needs to be recognised in the system. The capacity of sea urchin predators to reduce sea urchin abundance and trigger the trophic cascade that restores kelp forests places attention on the feedbacks and hysteresis in these systems. It is notable that the hysteresis in kelp systems are substantial. The urchin biomass needed to be consumed by predators to restore kelp is about one order of magnitude greater than that required to maintain the kelp-dominated state (i.e. by keeping urchin density below the critical threshold for barrens-formation). In systems susceptible to turf-domination, the focus of management tends to centre on managing water quality (Filbee-Dexter & Wernberg 2018), for which there is increasing interest in understanding nitrogen thresholds of collapse (Connell et al. 2017).

For kelp- or fucoid-supporting reef systems with discontinuous regime-shift dynamics, investment into bolstering the processes of resilience before a shift occurs is more effective than the investment needed to erode the resilience of unwanted ecosystem states (e.g. barrens or turfs, which have their own self-reinforcing regimes). Indeed, investment in prevention is substantially more effective and less costly than investment in restoration. Whilst the idea of prevention being easier than the cure may seem overly simple, demonstration of the difficulty and predictability of reversals is timely given the increasing intensity and diversity of human-driven change. Many of these stressors combine across local to global scales to increase the vulnerability of algal forests (Russell et al. 2009), but not all of them are under the control of local managers. Yet, local managers that reduce local stressors (e.g. fishing and nutrient pollution) can reduce the effects of global stressors not under their governance (e.g. ocean warming and acidification) (Falkenberg et al. 2013a).

Coral reefs

Coral reefs provide valuable ecosystem services to coastal and island populations throughout the tropical world, including the support of fisheries, tourism, coastal defence from hurricanes, generation of sand and building materials, pharmacological products and the highest marine biodiversity on Earth (Moberg & Folke 1999). Despite their relatively stable community on the scale of millennia (Jackson 1992), they have experienced an unprecedented decline over the past 50 years due to escalating anthropogenic impacts (Hughes et al. 2010). Numerous coral reefs have transitioned to alternative non-coral states (e.g. from hard corals to seaweed or other non-coral organisms) (Norstrom et al. 2009, de Bakker et al. 2017). However, less exposed or more resilient reefs have turned into novel coral-dominated ecosystems by forming new species configurations through divergent species responses to climate change and other disturbances, but also through a rapid expansion of the geographic range of corals into higher latitudes (Graham et al. 2014). In the context of rapid climate change and unprecedented human pressure on coastal resources, it is very unlikely that these altered coral ecosystems will return to pristine conditions. However, their emergence provides hope that coral reefs, albeit in a modified form, may persist in the future if conservation and management efforts are re-evaluated (Graham et al. 2014). In this review, we follow the definition proposed by Graham et al. (2014) in that novel coral ecosystems remain within the parameter space of calcifying coral-dominated reefs. We thus exclude the ecosystems that have undergone a regime shift to non-coral organisms (e.g. from hard corals to seaweed) and that are no longer in a calcifying condition.

The first example of state shift in a coral ecosystem came from the Caribbean region where global warming, disease and overfishing combined to cause a decline in large and complex *Acropora* and *Orbicella* species (Figure 4A). While this decline reinforced pathways to non-coral states, some coral reefs shaped into coral-dominated assemblages composed of simpler and small weedy *Porites* and *Agaricia* species, which, in some cases, have persisted over decadal timescales (Figure 4B) (Aronson et al. 2004, Green et al. 2008). Similar shifts in the functional composition of coral communities occurred elsewhere in the tropics, mainly as the result of coral bleaching, storms, crown-of-thorns starfish predation, overfishing, sedimentation and land-based pollution (Loya et al. 2001, Cleary et al. 2008, van Woesik et al. 2011, Darling et al. 2013, McClanahan 2014, Denis et al. 2017, Adjeroud et al. 2018).

More recently, the mass coral bleaching events of 2016 and 2017 caused significant damage to Australia's Great Barrier Reef and to reefs in the Pacific, with a replacement of fast-growing, 3-dimensional, tabular and staghorn corals by more heat-tolerant massive corals (Figure 4C,D) (Hughes et al. 2018b, Moritz et al. 2018). To date, there is no evidence that ocean acidification is leading to novel coral ecosystems. While most of these studies indicate a synergistic or additive impact between disturbances, some stressors can interact antagonistically with other disturbances. For example, high turbidity allows the persistence of coral dominance at chronically disturbed shallow reefs off Singapore by reducing the impact of thermal stress and limiting algal overgrowth (Guest et al. 2016). Assuming species co-tolerance between local and climate change-related stressors, local stressors can also reduce the abundance of disturbance-sensitive coral taxa and lead to a less diverse community of stress-tolerant and/or opportunistic taxa that is resilient to climate change (Côté & Darling 2010).

Because of environmental stress, communities from degraded coral-dominated assemblages are typically depauperate compared to 'pristine' areas or historic states. The predominance of simple and small corals reduces structural complexity, which in turn lessens the abundance, diversity and trophic structure of the associated fish community (Rogers et al. 2014). Introduced species have reinforced transitions towards non-coral states, and it is yet to be seen whether they could contribute to the emergence of novel coral ecosystems (Graham et al. 2014). As global temperatures rise, a major driver of potentially novel coral ecosystems is the expansion of many taxa towards higher latitudes.

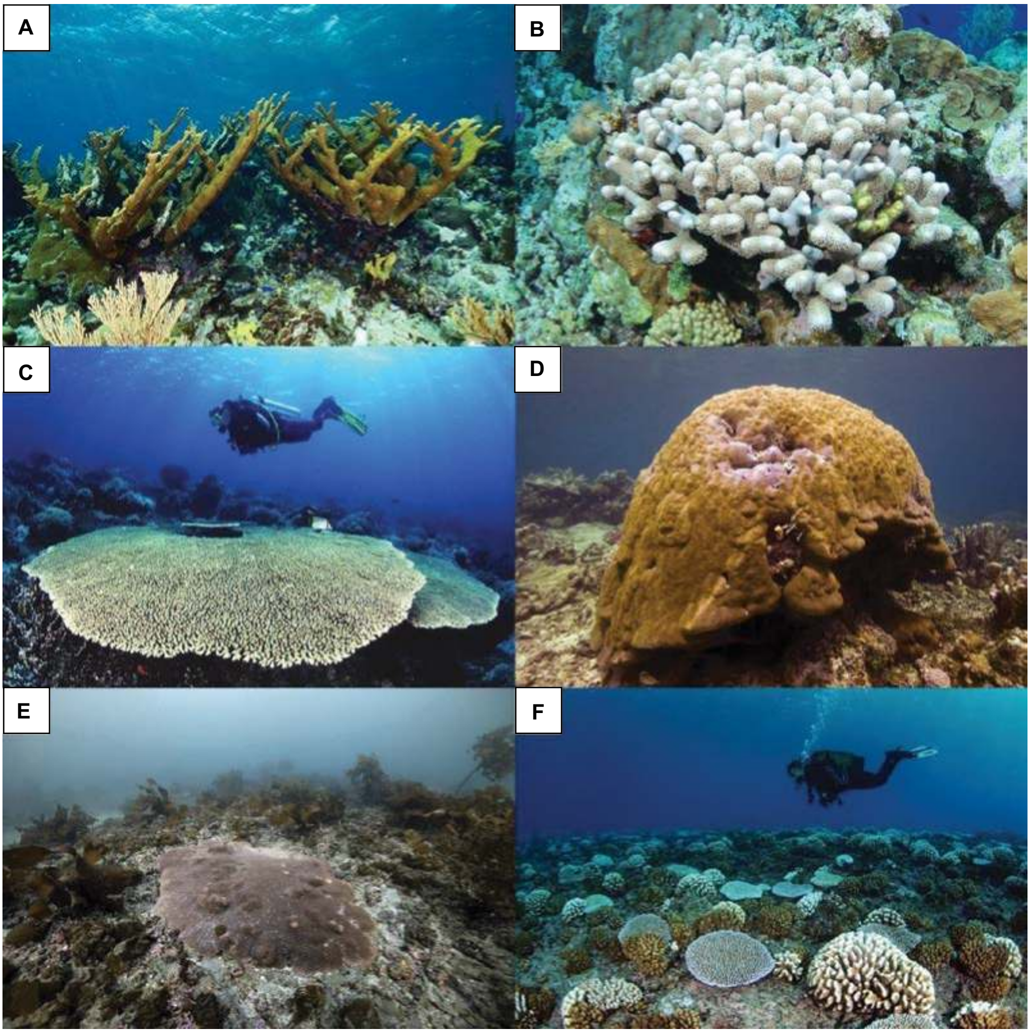

Figure 4 (A) Elkhorn corals (*Acropora palmata*) and (B) *Porites* sp. coral colony on the reef flat in Curaçao, southern Caribbean. (C) Tabular and (D) massive coral colonies at Derawan Island, East Kalimantan, Indonesia. (E) Mixed kelp and coral communities at the entrance of Tokyo Bay, Japan. (F) Coral colonies exhibiting contrasting bleaching tolerance on the reef slope of Moorea, French Polynesia. [Photo credits: Maggy Nugues (A–D, F) and Nicolas Floc'h (E).]

For example, reef corals in Japan have been extending their range northward at rates of up to 14 kilometres per year, generating new reef structures along these coastlines with cascading effects on other associated organisms (Yamano et al. 2011, 2012). Similar development has been documented in the Australian Great Barrier Reef (Baird et al. 2012) and in the Caribbean (Precht & Aronson 2004).

Evidence of threshold crossing and irreversibility

There is little definitive evidence for truly novel ecosystems in coral reef environments (Table 1). Tropicalised systems where corals have established dominance represent largely novel ecosystem configurations. However, they are often cohabitations between tropical and temperate organisms (Figure 4E). Thus, they retain some original characteristics as well as novel elements, fitting the definition of 'hybrid' systems. For example, tropical fish species are mixing with temperate fish species down the coast beyond Sydney (Figueira & Booth 2010). Similarly, resilient reefs that have switched to alternative coral species assemblages commonly retain an abundance of original species. For example, after two thermal stress events in Sesoko Island, Japan, coral assemblages were composed of three groups: 1) thermally tolerant, locally persistent colonies; 2) remnant survivors that rapidly regrew; and 3) regionally persistent colonies that recruited (van Woesik et al. 2011). At a small number of Indo-Pacific reefs, local coral species increased their bleaching tolerance following successive bleaching events, suggesting that adaptation or acclimatisation of native coral species to changing climates can occur naturally under certain circumstances (Maynard et al. 2008, Guest et al. 2012, Penin et al. 2013).

The existence and stability of regime shifts in coral reef ecosystems have been the subject of intense debate but have mostly focused on shifts towards non-calcifying macroalgae. The assumption that coral-macroalgae shifts are a common phenomenon has been challenged by meta-analyses and modelling work (Bruno et al. 2009, Zychaluk et al. 2012). Using benthic cover data from 1851 reefs worldwide, Bruno et al. (2009) found that most reefs were in neither a coral-dominated state (more than 50% coral cover) nor a macroalgae-dominated state (more than 50% macroalgal cover). However, these studies were contested for their statistical assumptions with regard to the constancy of environmental variables and the resolution of field data and disturbance dynamics, as well as the 50% cut-off as few reefs display such abundances of dominating benthic taxa (Hughes et al. 2010, Mumby et al. 2013). Using a novel approach for detecting, visualising and defining potential multiple ecosystem regimes, distinct reef regimes dominated by hard corals, turf algae or macroalgae were identified in the Hawaiian archipelago (Jouffray et al. 2015). In Moorea, French Polynesia, macroalgae have recently been demonstrated to be alternative attractors in the lagoon but not on the fore reef, where ambient herbivory fell outside the experimentally delineated region of hysteresis (Schmitt et al. 2019). Moorea's fore reefs have undergone gradual changes in the structure of their coral communities in response to major stress rather than collapsing abruptly and irreversibly (Adjeroud et al. 2018). Contrasting with the abundant research on coral-macroalgae regime shifts, there is hardly any evidence of threshold crossing and irreversibility within the parameter space of calcifying coral-dominated reefs. Hence, this subject is clearly in need of further research.

Implications for conservation and management

Initially, novel or hybrid coral ecosystems were given little ecological value. Coral reef research and management were oriented towards preserving 'natural' ecosystem states, functions and services (Jackson et al. 2001, Pitcher 2001), and how these changes in coral species composition affect the ability of reefs to provide ecosystem services and resources remained poorly studied for some time. However, in the context of severe, global-scale stressors and mounting evidence for reduced recovery rates and return times between disturbances, restoring reefs to baseline targets became questionable. The number of years between recurrent severe bleaching events has diminished 5-fold in the last four decades and is now only approximately six years (Hughes et al. 2018a). Climate models predict that, by the middle of the century, most of the world's coral reefs will suffer long-term degradation from the impacts of climate change and over 75% of reefs will experience annual severe bleaching before 2070 (Frieler et al. 2012, van Hooidonk et al. 2016). In comparison, coral communities need at best 10–15 years to recover to mature assemblages. Hence, in the longer term, reef health will depend on curbing global carbon emissions and local stressors (van Hooidonk et al. 2016). However, in the more immediate future, it is acknowledged that novel or hybrid coral reef ecosystems can still provide valuable goods and services and that science, management and governance need to embrace these unavoidable changes (Graham et al. 2014, Norstrom et al. 2016, Hughes et al. 2017).

Coral reef management needs to turn towards maintaining the delivery of key ecosystem services in novel or hybrid ecosystems. Marine reserves have been widely used as a management tool, particularly to replenish fish populations. However, their benefits are predicted to be limited for reefs with low structural complexity (Rogers et al. 2015) and for preserving sensitive and specialised species that cannot persist in disturbed or altered environments (Côté & Darling 2010). Indeed, coral richness does not necessarily imply higher resilience to disturbances (Zhang et al. 2014). In contrast, tools such as artificial complexity, fish aggregation devices, coral restoration and herbivore management could be more effective, and it is likely that achieving high ecosystem service provision in these ecosystems will require a diversity of complementary management approaches, with important technological innovation, capacity building and policy-making.

Climate resilience of corals can be increased through assisted evolution, which aims to accelerate natural evolutionary processes to enhance certain desired traits (van Oppen et al. 2015, 2017). These processes incorporate genetic, epigenetic and microbiome modifications. Several techniques can be included in coral reef restoration initiatives, including the exposure of adult corals to environmental stressors to induce heritable stress tolerance in their offspring, manipulation of the composition of the coral microbiome (e.g. algal symbionts, prokaryotes), inoculation of stress-resistant symbionts in the coral hosts and selective breeding of adult coral colonies showing bleaching tolerance (Figure 4F) (van Oppen et al. 2017). Heavily degraded coral reef ecosystems are unlikely to be considered in such initiatives. However, van Oppen et al. (2017) argued that restoration goals could be based on the desired attributes of the historical or hybrid ecosystems and proposed a decision tree for incorporating assisted evolution into restoration initiatives where 'local' options have priorities over non-native ones.

Estuaries, mangrove forests, seagrasses, oyster reefs, salt marshes and mud flats

Globally, estuarine ecosystems and the key habitat-forming species they contain, such as tidal marsh/mangroves, seagrass and oysters, deliver ecosystem services valued around US$30 trillion/yr (Costanza et al. 2014). Estuaries provide critical nutrient cycling services, support high biodiversity and important commercial and recreational fisheries. Habitat-forming species within estuaries also provide important infrastructure, stabilising sediments, attenuating wave action and reducing storm surge, which can buffer coastlines and coastal structures from erosion (Hemminga & Duarte 2000, Orth et al. 2006). They are also important for improving water quality and structuring food webs, providing both food and habitat for fauna and flora, including acting as nursery grounds that support fisheries production (Beck et al. 2001, Heck Jnr et al. 2003, Moore 2004).

As for coastlines described previously, estuaries have been a focal point of colonisation and resource use throughout human history (Lotze et al. 2006). Their sheltered nature and originally abundant resources, including fish and shellfish (e.g. clams, oysters), made them ideal ecosystems for colonisation and subsequent industrialisation. Centuries of environmental degradation, fisheries exploitation and habitat loss have led to estuarine ecosystems becoming one of the most threatened natural systems globally (Lotze et al. 2006, Worm et al. 2006, Halpern et al. 2008, Cloern et al. 2016) (Table 1). Estuaries in many parts of the world initially exhibited long periods of slow degradation; however, this has accelerated in the last 150–300 years (Lotze et al. 2006) and is predicted to continue to do so (Cloern et al. 2016). Whether the cumulative effects of many different sources of abiotic and biotic stress on estuaries has degraded them to the point where they now represent novel or, at best, hybrid ecosystems is an intriguing question.

Increases in sediment, nutrient and contaminant loadings are the key drivers of the degradation of estuaries (Lotze et al. 2006, Cloern et al. 2016). Deforestation and coastal farming have increased sediment and nutrient (e.g. nitrogen and phosphorous) flows, and urbanisation has increased the amount of impervious surfaces facilitating runoff into estuaries. Industrial discharge, storm drains and sewage overflow also contribute substantially to the pollution inputs (Birch & Taylor 1999, Sun et al. 2012).

Increased sediment loading can lead to negative effects on submerged macrophytes such as seagrass via burial or reducing light levels (Onuf 1994, Terrados et al. 1998, Cabaço et al. 2008). High nutrient and contaminant inputs have, in many instances, led to eutrophication, anoxia in both the overlying water column and sediments and the build-up of toxic compounds in sediments (Diaz & Rosenberg 1995, Chapman & Wang 2001, Rabalais et al. 2001, Kennish 2002). Chemical pollutants can be particularly problematic because they can bioaccumulate and be transferred through food chains to higher trophic levels. Accumulation of contaminants (heavy metals) in sediments can also have legacy effects even if management strategies have eliminated or reduced inputs. For example, whilst undisturbed sediments may 'lock away' contaminants, physical disturbance (e.g. via dredging) of sediments can resuspend polluted sediments, increasing their bioavailability (Hedge et al. 2009).

Estuaries have also undergone major physical changes. To buffer wave action and prevent shoreline erosion, estuaries have undergone significant shoreline hardening. The resultant effects on water flow and sedimentation are similar to that described previously for coastal ecosystems, so they are not described again in detail here. Importantly, the loss of habitat-forming species, the natural buffers of coastal ecosystems, has also increased the impacts of typhoon and storm events (Cochard et al. 2008, Barbier et al. 2011).

In addition, because of their benign environmental conditions and high primary productivity, estuaries are a focal ecosystem for aquaculture development. The rapid expansion of coastal aquaculture has been supported through conversion of large areas of fringing habitat. For example, shrimp culture is the major human activity accounting for 35% of the global decline in mangrove forests (Valiela et al. 2001). Aquaculture farms can also alter physico-chemical properties of sediments beneath them. Biodeposition of organic-rich fine particles can lead to anoxic sediments and changes in benthic community structure (Forrest & Creese 2006, Forrest et al. 2009). Off-bottom culture can also affect sediment deposition rates and decrease light availability to the benthos, which can negatively affect the health of nearby seagrass beds (Ferriss et al. 2019).

Human activities have also had a range of direct and indirect effects on biotic communities and the ecosystem services estuaries provide. One of the key consequences of this is to greatly reduce the cover of habitat-forming species: an estimated 25%–50% of salt marshes, 35% of mangroves and 29% of seagrass habitats are either lost or degraded worldwide (Valiela et al. 2001, Barbier et al. 2011, Waycott et al. 2009). Oyster reefs have fared even worse (Figure 5). An estimated 85% of reefs

Figure 5 Remnant reefs of the Sydney Rock Oyster, *Saccostrea glomerata*, at Towra Point, Botany Bay, Australia. (Photo credit: Paul Gribben.)

globally have been lost, with 99% considered functionally extinct in 39% of estuaries (Beck et al. 2009, 2011). Hand-in-hand with the loss of habitat-forming species is the loss of the vast biodiversity of flora and fauna they support.

High contaminant loads have also greatly altered communities in unvegetated sediments, a habitat that occupies much of the benthos in estuarine ecosystems. Contaminants have reduced the abundances of several important functional groups such as bioturbators and filter-feeders. The loss of bioturbators not only reduces biodiversity but has resulted in negative feedbacks on sediment communities and processes through reduced delivery of oxygen into the sediments (required for detoxification), exacerbating the effects of contaminants (Douglas et al. 2017, Gonzalez et al. 2019). The filter-feeding bivalves and other species (e.g. subtidal macrophytes and wetlands) that also provide detoxification services have declined 63% globally (McLeod et al. 2019). High nutrient loads also impact water-column communities, resulting in blooms of toxic algae and red tides (Hallegraeff 1993, Anderson et al. 2002).

Increasing international boat traffic, coupled with the increasing prevalence of artificial structures and estuarine degradation, have all contributed to non-native species becoming prominent members of estuarine ecosystems. Domestic boat traffic, movement of aquaculture infrastructure and other artificial structures also play important roles in the internal spread of non-native species (Floerl & Inglis 2003, Minchin et al. 2006, Coutts & Forrest 2007). Once established, non-native species can have devastating effects on native biota. For example, once it establishes, the green alga *Caulerpa taxifolia* alters microbial community function, degrading sediment conditions by increasing sediment anoxia and toxic sulphide loads (Gribben et al. 2009, McKinnon et al. 2009). These changes severely reduce the abundance of key filter-feeding bivalves as well as completely altering the structure of both invertebrates and fish communities (York et al. 2006, Wright et al. 2007).

Non-native species can also affect commercial fisheries. For example, in south-eastern Australia, the European green crab *Carcinus maenas* consumes large quantities of commercially valuable clam species (Ross et al. 2004). In New Zealand, the invasive ascidian *Didemnum vexillum* colonised mussel culture lines, smothering the mussels; destabilised mussel crops and added weight to infrastructure led to substantial mitigation and control costs (Pannell & Coutts 2007). Aquaculture activities can also impact benthic communities, with adjacent sediments often supporting smaller-bodied organisms (e.g. worms) tolerant to high organic loads and sediments at the expense of large species such as urchins, starfish and bivalves (Christensen et al. 2003, Hartstein & Rowden 2004). Moreover, direct extraction by fisheries and the indirect effects of dredging (increasing sedimentation), habitat loss via hardening coastlines, aquaculture development and pollution on key nursery habitats have seen the number of viable (non-collapsed) fisheries decline by 33% (Barbier et al. 2011).

Evidence of threshold crossing and irreversibility

Formal evidence of threshold crossing, bi-stability and reinforcing feedbacks is available for some estuarine habitats, such as seagrass meadows, salt marshes, oyster reefs and mud flats (Thrush et al. 2004, McGlathery et al. 2013, Maxwell et al. 2017) (Table 1). For example, saltmarsh vegetation and mud flats can represent intertidal alternative stable states, whose transition is regulated by biotic and abiotic drivers of sediment accretion/erosion dynamics (McGlathery et al. 2013). Likewise, light availability, storms and seawater temperature regulate transitions between seagrass and subtidal mud flats (van der Heide et al. 2007), while increases in nutrients and salinity can cause a shift from seagrass to phytoplankton dominance (Webster & Harris 2004). In addition, as a result of eutrophication, mud flat habitats themselves can cross thresholds whereby repeated hypoxic events lead to enhanced vulnerability to additional hypoxia, which may be difficult to reverse (Conley et al. 2009). Importantly, the different systems within an estuary are connected by energy and matter fluxes, and state change in one system can alter state dynamics of adjacent systems (McGlathery et al. 2013). For example, seagrass decline reduces sediment deposition, influencing oyster reef dynamics, which, in turn, influence erosion/accretion dynamics at the marsh edge (McGlathery et al. 2013).

Transitions between alternative estuarine habitats do not necessarily imply the establishment of a novel ecosystem, as each of these habitats (e.g. seagrass, salt marsh and mud flat) is a natural component of estuarine land- and seascapes and, hence, not characterised by an unprecedented species assemblage. Altered proportion among different habitats is rather indicative of a hybrid ecosystem. This is also supported by the lack of evidence of state irreversibility (Table 1). In some instances, major human-driven changes may be reversible, such as the potential reconversion of aquaculture back to mangrove forests. In other instances, they may be irreversible, such as the hardening of shorelines. Long-term monitoring programmes indicate that some estuarine habitats have not fully recovered following the removal of the key drivers of collapse. For example, in Sydney Harbour, oyster reefs have declined due to their over-exploitation for food and lime and have not recovered to predisturbance levels despite the considerable reduction in harvesting pressure (Kirby 2004, Lotze et al. 2006, Alleway & Connell 2015). Clearly, human influences have impacted the different habitats that compose estuaries in different ways and to varying degrees – whether their cumulative effects have resulted in entire estuaries transitioning to novel ecosystems is unclear (Table 1). More likely, many estuaries have transitioned to hybrid ecosystems consisting of different compartments that are now novel or may be rehabilitated with further human intervention.

Implications for conservation and management

Despite the massive impacts human disturbances have had on estuaries, recent studies suggest that there is potential for developing more resilient estuarine ecosystems. Improved estuarine management practices, tighter controls of pollution and removal of many of the historical polluters of estuarine ecosystems have already greatly improved water quality. Moreover, new restoration efforts for habitat-forming species such as oysters, seagrasses and mangroves are seeing some of the vital functions they perform enhanced, if not to predisturbance levels, at least to levels at which they improve estuarine health (e.g. Orth et al. 2012). The explicit acknowledgement that habitats are interconnected, and that restoration needs to acknowledge and incorporate these into estuarine rehabilitation strategies, is also a novel development. For example, establishing oyster beds in front of salt marshes enhances salt marsh recovery and may provide a natural solution of mitigating the effects of predicted increases in wave action and storm events with ongoing climate change (Meyer et al. 1997, Scyphers et al. 2011). There is great potential for building resilience in the face of global change in estuarine ecosystems.

In some instances, utilising novel species in estuarine systems may be important for improving some ecosystem functions. For example, where native oyster populations, and the filter-feeding services they provide, are no longer viable, but invasive oysters are present and could provide the same function. However, rarely, if ever, have invasive species been shown to provide the full range of functions that similar native species previously supported (Wilkie et al. 2012).

The range of human impacts on estuarine systems, the increasing pressure of growing populations around estuaries, the social and economic dependence of communities and industries on the resources that estuaries provide (e.g. fisheries and aquaculture) and the likely permanent integration of invasive species and the ecosystem changes they have elicited suggest that estuaries will remain forever altered ecosystems.

Pelagic systems

The key biological members of pelagic ecosystems are phytoplankton, zooplankton, small pelagic fishes and top predators such as birds, mammals and other fishes. Zooplankton communities are typically dominated by copepods, the most numerous group of multicellular organisms in aquatic systems (Walter & Boxshall 2019), and although they have a diversity of prey, they are, for the most part, supported by the phytoplankton, especially diatoms. Small pelagic fish communities across the globe are dominated by clupeids, which have evolved to forage by particulate- (copepods) and/or filter-feeding (diatoms) (van der Lingen et al. 2006). They can influence the biomass and size composition of plankton communities through a top-down effect (Boldt et al. 2019). Clupeids also act as a very important conduit by which energy is channelled (bottom-up) towards the top of coastal and oceanic food webs, providing food for pelagic seabirds, mammals and tunas, as well as mesopelagic and demersal fishes and cephalopods (Cury et al. 2000). They are a key group of species and effectively create what are known as 'wasp-waist' ecosystems. This guild is, in fact, usually represented by only one or two species and, hence, significantly less diverse than either its consumers or its prey (Cury et al. 2000). Upwelling and some other coastal shelf regions are typically of the wasp-waist type and frequently experience temporary 'regime shifts' as one species (e.g. sardine) is replaced by another (e.g. anchovy) (Lluch-Belda et al. 1992).

Novel ecosystems can arise when climate change stimulates the expansion and reduction of existing 'biogeochemical provinces' through bottom-up control (Table 1). There are several classification systems in use for marine biogeochemical provinces which have defined the pelagic realm in terms of major oceanographic and ecological patterns: 1) the Longhurst Biogeochemical Provinces (BGCP; Longhurst 2007), 2) the Marine Ecoregions of the World (MEOW; Spalding et al. 2007) and 3) the Large Marine Ecosystems (LME for coastal systems; Sherman 2005), which also includes socioeconomic factors in the delineations. A recent classification for the mesopelagic realm that considers the reduced impacts of light and turbulence, when compared to the epipelagic realm taken into account by the previous three systems, is that proposed by Reygondeau et al. (2018). Pelagic ecosystems, like others, are considered to be structured by bottom-up or top-down controlling processes (Moloney et al. 2010). In the former, physical factors influencing the base of the food web are propagated upwards through it, whilst in the latter, any change in the abundance of predators will lead to alterations in their prey, which in turn will trickle down through trophic cascades from top to bottom through the food web (Moloney et al. 2010). Unlike bottom-up control, an ecosystem experiencing positive feedbacks within a food web associated with strong top-down control may exist in one of several alternative stable states or 'regimes' under the same set of external drivers (Fauchald et al. 2011). In this case, "a perturbation [to the system] … may be followed by a reorganisation of the trophic structure resulting in a non-linear ecosystem shift" (Fauchald et al. 2011).

Temperature changes are the most obvious consequence of climate change, with direct and indirect effects on the physical and biogeochemical parameters of the water column and its inhabitants. Temperature-driven alterations at the ecosystem level are the result of individual physiological and/or behavioural responses (Beaugrand & Kirby 2018). Migrations or local extinctions ultimately underpin changes in the structure and dynamics of food webs. Since the majority of pelagic organisms are ectotherms, temperature changes affect an organism's physiology and seasonal timing (phenology). In the North Sea, a mean increase of just 1°C over 40 years (much less than the seasonal temperature changes experienced within a year) was sufficient to shift the once boreal pelagic system into a temperate system through continual small changes in species life cycles (Beaugrand et al. 2008).

Regime shifts appear to have led, more recently, to significant changes in ecosystem structure. Many of the shifts observed are still linked to synchronised climate signals (Beaugrand et al. 2015), augmented by local, bottom-up drivers such as cultural eutrophication (Deyoung et al. 2008, Mollmann & Diekmann 2012, Conversi et al. 2015). However, in most of these ecosystems, resilience has been compromised by changes in top-down controls following fish over-exploitation (Mollmann & Diekmann 2012, Gardmark et al. 2015, Pershing et al. 2015). In addition, because of the unpredictable and non-linear nature in which trophic cascades can be manifested, there is a general lack of cohesion across systems. A modelling paper by Lynam et al. (2017), based on over 40 years of observational data in the North Sea, highlights such complexity, suggesting that bottom-up processes, forced by temperature, regulate changes in the abundance of planktonic groups, whereas top-down effects of fishing underpin changes in the biomass of commercially exploited fish. Some species are directly affected by both fishing and temperature (such as cod and sandeel). Interestingly, sandeel, herring, sprat and haddock are influenced by indirect temperature effects through a cascade of interactions in the plankton, whereas whiting, zooplankton groups and diatoms are indirectly influenced by fishing mortality. Whilst the altered regimes described to date have caused changes in the relative abundance of different species, no region-wide extinctions have been observed. Likewise, in no systems have there been profound alterations in the way energy moves through the system, though there have been changes to fishery production (Schwartzlose et al. 1999).

The ability of clupeids to feed close to the bottom of the food web allows their populations to reach enormous sizes and dominate capture fisheries worldwide (FAO 2016). They are a key and integral part of 'healthy' modern marine ecosystems and provide both a range of regional services (Rocha et al. 2015) and an important livelihood for many coastal communities (Ommer et al. 2009). The onset of novel ecosystems is a significant challenge for fisheries, their dependent communities and governance structures. Polovina et al. (2011) predicts major changes in the boundaries and extent of the subtropical and equatorial upwelling biogeographical regions of the North Pacific by the end of the century, in response to CO_2 emissions. Fish catch is expected to change in each region because of changing primary production, with projected increases in the subtropics and decreases in temperate and equatorial regions. The current legal framework for international fisheries regulation does not consider changing distributions, yet projections suggest that almost all Exclusive Economic Zones (EEZs) will include one or more new fishery stocks by 2100 (Pinsky et al. 2018). As resource species shift across national or other political boundaries, policies will struggle to keep pace as there is likely to be conflict over suddenly shared resources.

Jellyfish and clupeids occupy similar positions within the pelagic food web, as they both prey on crustacean zooplankton, fish eggs and larvae (Szeinfeld 1991, Koster & Mollmann 2000, Tilves et al. 2016) and, likely, ephyrae and juvenile jellyfish (Lamb et al. 2017) (Figure 6).

Medusae and ctenophores (jellyfish) have been present for much longer than clupeids, having evolved several hundred million years before copepods (Cartwright et al. 2007, Dunn et al. 2008, Betancur-R et al. 2017). Both groups of organisms have protein-rich tissues made up of ~96% water (Doyle et al. 2007, Lucas et al. 2011) and are strictly carnivorous, though some medusae may also support photosynthetic symbionts (Arai 1997). While beroid ctenophores engulf their prey (Swanberg 1974), most jellyfish trap or ensnare prey items on the surface of various feeding structures (Costello & Colin 1995, Colin et al. 2003, 2010). Although the bulk of their current diets is made of copepods, jellyfish can feed and survive on microplankton that would not be trapped by the gill-rakers of clupeid fishes (e.g. Kamiyama 2011). Jellyfish are not streamlined and do not use sight to locate prey, but they compensate for these deficiencies by being of large size and moving slowly (Acuna et al. 2011). They can attain the same instantaneous prey clearance and growth rates of pelagic fishes and, indeed, in very dilute food environments, they have the advantage over fishes of being able to shrink (Arai 1997).

Whilst jellyfish may be found in most fish-dominated pelagic marine ecosystems, they are not routinely dominant over pelagic fishes because populations are intrinsically ephemeral. The reason for this is that the majority of scyphozoans have metagenic life cycles (Arai 1997). Medusae (as ephyrae) are liberated following asexual reproduction by sessile polyps in winter, they mature during spring–early summer and reproduce sexually towards the end of summer (e.g. Lucas 2001). The life cycle of metagenic species is tightly linked to environmental productivity cycles. As a consequence, whilst jellyfish populations may be ever present within an ecosystem, they are not always present in the pelagos as medusae (Boero et al. 2008).

Evidence of threshold crossing and irreversibility

There are two regional ecosystems that appear to have undergone profound structural changes: the Black Sea and the northern Benguela. They are described subsequently as examples of state shifts in pelagic ecosystems arising through combined top-down and bottom-up effects.

The Black Sea In the case of the Black Sea, which is arguably the best understood example of pelagic jellification, over-exploitation of large predatory fishes at the end of the 1950s led to

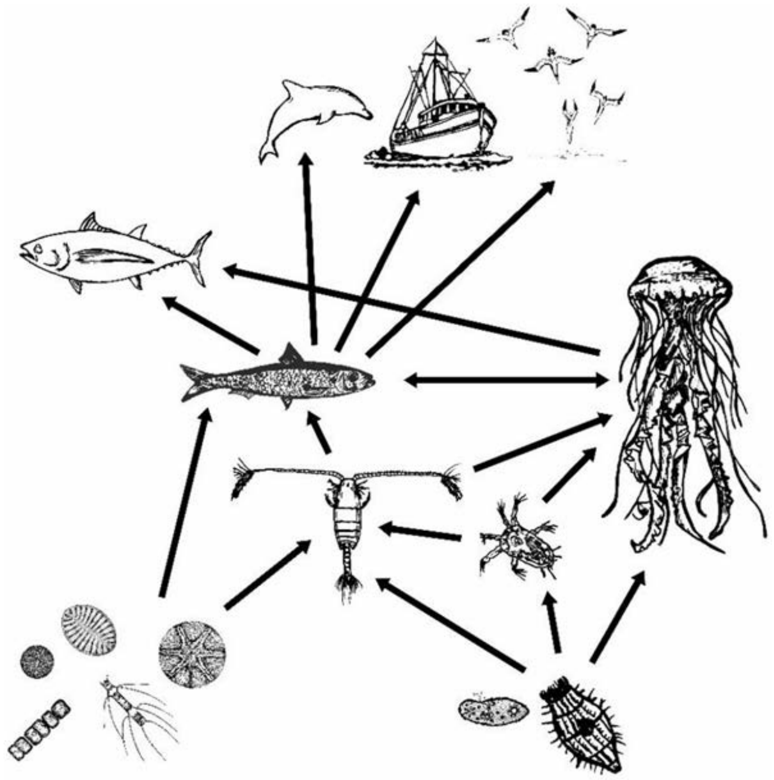

Figure 6 Diagram illustrating simplified trophic flows through a pelagic ecosystem supporting populations of both small pelagic fishes and jellyfish.

an increase in local clupeids, a decrease in zooplankton and an increase in phytoplankton (Llope et al. 2011). This trophic cascade was amplified by cultural eutrophication (principally P) and was accompanied by blooms of the heterotrophic dinoflagellate *Noctiluca* and the scyphozoan *Aurelia* (Oguz 2005). Overfishing of the small pelagic fish stocks occurred towards the end of the 1980s, at approximately the same time as an alien ctenophore *Mnemiopsis leidyi* was introduced (Oguz et al. 2006). The effects of the trophic cascade were thus maintained, though pelagic fishes and *Aurelia* were replaced by the new guild member, assisted by the warm winter conditions observed at that time (Oguz 2005, Oguz & Gilbert 2007). By the mid-1990s, P-inputs had declined and there was insufficient production to support the needs of the massive *Mnemiopsis* population (Oguz & Velikova 2010). This occurred at about the same time as a ctenophore predator (*Beroe*) appeared on the scene (Shiganova 2004) and was coincident with critically cold winters that did not favour the large-scale survival of *Mnemiopsis* (Oguz 2005). Populations of the latter species have not returned to the size witnessed in the early 1990s; neither has the Black Sea returned to its pristine state (Oguz & Velikova 2010). It is characterised by low zooplankton and fish biomasses and interannually variable but moderate quantities of *Aurelia*, *Mnemiopsis* and *Noctiluca* (Oguz & Velikova 2010).

The northern Benguela Less well documented, but equally dramatic, is the situation off the coast of Namibia (Figure 7). This south-west African country lies at the centre of the Benguela upwelling region, which, like other ecosystems dominated by eastern boundary currents, is highly productive (Hutchings et al. 2009). Historically, the biomass of the pelagic ecosystem across the entire region was dominated by small pelagic fishes (sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus*), which alternated in abundance in response to subtle changes in climate forcing (Cury

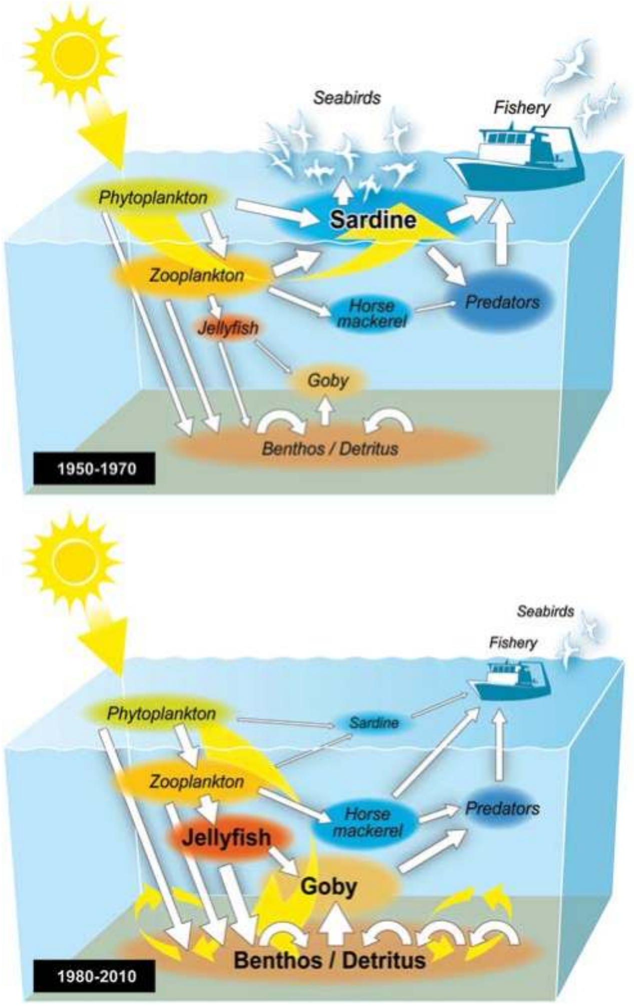

Figure 7 Conceptual sketch of the main energy flows toward fish production and fisheries in the northern Benguela. The sardine was the main link between primary and secondary producers and fish, fisheries and predators in the early period (top); after the sardine collapse in the early 1970s, most of the energy flow (yellow arrows) was diverted away from the pelagos through jellyfish, detritus, benthic recycling and bearded goby (bottom). (From Roux, J.P. et al. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fish: Lessons from the Benguela. *Bulletin of Marine Science* 89, 249–284, with permission.)

& Shannon 2004). As in other upwelling ecosystems, these small pelagic fishes provide a very important food source for top predators, including seals, seabirds and demersal fishes (e.g. Crawford 2007). The Lüderitz upwelling cell at ~26°36′S effectively divides the Benguela system into northern and southern regions (Hutchings et al. 2009), and populations of these small pelagic fishes are still relatively healthy in the southern sector (Roux et al. 2013). Unfortunately, however, first sardine and then anchovy were heavily over-exploited at the end of the 1960s and early 1970s (respectively), to the point that the system today bears little resemblance to that beforehand (Roux et al. 2013). Indeed, catches of sardine off Namibia at the end of the 1960s exceeded 1.5 million tonnes, yet in 2016, the industry could only catch 3400 tonnes of its meagre 14,000-tonne quota (Mereghetti 2017). The ecosystem has effectively transitioned from one with healthy populations of top predators and demersal fisheries to one dominated by gobies (*Sufflogobius bibarbatus*), horse-mackerel (*Trachurus* *capensis*, previously *Trachurus trachurus capensis*) and, yes, jellyfish (Lynam et al. 2006, Roux et al. 2013). Seabird populations have crashed and/or moved south (Crawford 2007, Crawford et al. 2008), whilst fur seal numbers have declined and the population regularly experiences years of mass starvation (Sibeene 2006).

The increase in jellyfish numbers off Namibia first noticed in the 1980s (Venter 1988) has been suggested to reflect an expansion of the resident species (*Aequorea forskalea* and *Chrysaora fulgida*) into the guild space 'vacated' by small pelagic fishes (Bakun & Weeks 2006, Roux et al. 2013). Elsewhere in the world, it has been suggested that jellyfish may be competitors with small pelagic fishes for zooplankton (but see Opdal et al. 2019) and there is certainly evidence to show significant spatial overlap in distribution (Brodeur 1998, Brodeur et al. 2008). Unlike the situation in other temperate shelf ecosystems, however, there is no temporal relaxation of pressure on fish populations, as medusae are present year-round (Flynn et al. 2012). Flynn et al. (2012) have shown that greatest occurrences of jellyfish are coincident with traditional sardine spawning areas (in space and time), suggesting that intraguild predation may contribute to the weak recovery of pelagic fish populations (Bakun & Weeks 2006, Roux et al. 2013). Interestingly, however, jellyfish appear to be less effective predators of zooplankton than pelagic fishes (Opdal et al. 2019), as populations of mesozooplankton have seemingly increased (Verheye et al. 2016).

In addition to jellyfish, the abundance of the bearded goby *Sufflogobius bibarbatus* has increased in the waters off Namibia (Boyer & Hampton 2001). This species cannot be considered to belong to the same guild as jellyfish, sardines or anchovies. Unlike most gobies, *S. bibarbatus* has retained a swim bladder and displays ontogenetic diel vertical migration, though like all gobies, it is a trophic opportunist, feeding on benthic infauna or sedimented diatoms when adult and on demersal and zooplankton when juvenile and pelagic (Cedras et al. 2011, Hundt et al. 2011, van der Bank et al. 2011). The species grows slowly, matures late and exhibits low fecundity (Melo & Le Clus 2005). Large males likely build and defend nests on the seabed (Utne-Palm et al. 2013), though sneaker males are also known (Seivåg et al. 2016). This species is adapted to very low concentrations of oxygen and high concentrations of hydrogen sulphide and takes advantage of hypoxic bottom waters in order to avoid demersal predators (Utne-Palm et al. 2010). At night, animals move up into the water column to reoxygenate their blood and to digest food, but also to prey upon jellyfish (Utne-Palm et al. 2010).

Likely, both bottom-up and top-down forces underpin the expansion of populations of this goby. The loss of sardines could have increased diatom flows to the benthos, leading to increased incidences of local hypoxia, which benefited gobies but not their predators, principally hakes (*Merluccius capensis*, *M. paradoxus*). Salvanes et al. (2015) have documented a decline in the hake population and an increase in that of gobies coincident with the expansion of the shelf area inundated with hypoxic waters. The effects of this trophic cascade are exaggerated by remotely forced bottom-up hypoxia (Monteiro et al. 2016). Further, the reliance of hakes on low-energy prey (Ludynia et al. 2010) could negatively impact their recruitment, leading to positive effects on gobies. The increase in jellyfish, which do not appear to be impacted negatively by hypoxia, additionally benefits gobies through the increased provision of both refugia and food (Salvanes & Gibbons 2018).

Differences between the Black Sea and the northern Benguela As Roux et al. (2013) have suggested, "overfishing of small pelagic fishes …[may have been] the trigger of a chain of events resulting in the rise of jellyfishes and goby and their maintenance in the system for the last four decades" off Namibia. This contrasts with the situation in the Black Sea, where both top-down and bottom-up controls have clearly played a role in restructuring the ecosystem. Aside from the effects of eutrophication, environmental temperatures appear to have had an impact on the size of overwintering populations of *Mnemiopsis* in the Black Sea (Oguz & Gilbert 2007). Therein lies a key difference to the situation off Namibia: planktonic ctenophores are holopelagic and hermaphrodite. This means that individuals can grow fast and that populations can expand in size very quickly, readily exploiting bursts of environmental productivity (Robinson & Graham 2014, Jaspers et al. 2015). On the other hand, it also means that when water column conditions deteriorate, populations will crash, leading to marked oscillations. By contrast, medusozoans are buffered from environmental changes by their ability to enter dormancy as polyps (Boero et al. 2008). So, while there is perhaps some hope for the situation in the Black Sea, this is by no means clear off Namibia.

Implications for conservation and management

In contrast to some benthic systems, the management of pelagic ecosystems is complicated by their generally vast areal extent, global interconnectivity and synchronous dynamics (Beaugrand et al. 2015). Unlike benthic systems, humankind does not add or take away physical habitat to create new habitats, and novel ecosystems will emerge only when the strength of external destabilising forces exceeds internal stabilising feedbacks. Resilience within the present ecosystem to change is being challenged by climate change, but it is also being significantly threatened by exploitation. Whilst Pershing et al. (2015) have suggested that altered trophic cascades may only play an important role in semi- or wholly enclosed systems such as the Black or Baltic Seas, the situation off Namibia is shelfwide. Current closure systems exist off Namibia and it might be viewed as a semi-enclosed system (Hutchings et al. 2009), but similar arguments can probably be made for most shelf ecosystems. As a consequence, the biggest threat to pelagic ecosystem integrity must be associated with the over-exploitation of living marine resources, and it is towards this issue that conservation efforts should be directed.

Key knowledge gaps

A major gap hindering the operational value of the novel ecosystem concept is the poor knowledge of the mechanisms underpinning state shift and their reversibility. Whether our understanding of catastrophic shifts has been advanced conceptually and threshold crossing and bi-stability documented under controlled conditions, experimental evidence from field studies remains rather limited (Table 1) (Ling et al. 2009, 2015, Benedetti-Cecchi et al. 2015, Schmitt et al. 2019). Nonetheless, irreversibility after crossing a threshold has not been documented in real-world settings (Table 1). This could indicate reversibility of shifts or, alternatively, less attention to backward shifts. For example, a relatively large research effort has been devoted to identifying tipping points and early warning signals of impending shift (Carpenter et al. 2011, Dai et al. 2012, Rindi et al. 2017). This research reflects our concerns of losing the goods and services associated with ecosystems shifting towards a degraded state. We now need to move on by assessing whether and under which external circumstances these shifts can be reversed. This implies running experiments reducing the intensity of biotic or abiotic drivers beyond theoretical backward shift thresholds. In other words, studies simulating a relaxation of local to regional stressors, as well as the reversal of current trends of warming and acidification, are urgently needed to provide insights into threshold irreversibility. Logistic constraints represent a major hurdle, as the spatial and temporal scales over which experiments are to be conducted are not trivial. This issue appears particularly relevant in coastal systems that are structured by the presence of long-lived foundation species, such as corals, macroalgae, seagrasses and mangrove trees, and by the interconnectivity among the habitats they form.

Beyond alterations in species distribution and abundance, there is evidence for some human pressures, such as urbanisation and fishing, to act as evolutionary forces (Donihue & Lambert 2015, Heino et al. 2015). Does this add to the novelty of ecosystems? Does it make reverting systems to a less altered state even more difficult? To the best of our knowledge, these questions are yet to be addressed. Nonetheless, these aspects are key for assessing threshold reversibility, since individuals that have been selected under novel conditions might be not able to sustain viable populations were original conditions to be reinstated. For instance, a large research effort has been devoted to assessing species adaptive potential to future climatic conditions, either phenotypically or genetically (Carlson et al. 2014, Sunday et al. 2014). Such research must be complemented by assessments of the adaptive potential of individuals that have been exposed to climatic conditions comparable to those expected under future scenarios – long enough for selective forces to have influenced their genetic makeup – to current conditions. For example, natural subtidal CO_2 vents provide a unique opportunity, as individuals of short-dispersal species likely to have evolved under lower pH levels could be transplanted into areas at ambient pH levels (Doubleday et al. 2017). Likewise, assessing how individuals belonging to equatorward populations perform at higher latitudes would provide an insight into their potential to adapt to cooling climates.

Management of marine hybrid ecosystems: A future outlook

As described in the previous sections, human alteration of biotic and abiotic conditions can result in the onset of novel species configurations in some marine systems. For some systems, there is empirical evidence that these novel states are self reinforcing and, hence, difficult to shift back. Nonetheless, there is no definitive proof of irreversibility, a requisite for labelling an ecosystem novel (Table 1). Under these circumstances, should their management be oriented towards actions that may facilitate their return to a state closer to the historical state (i.e. reduce their degree of novelty) or, embracing change, the gain of goods and services that are valuable to humans?

Evidence from late-glacial terrestrial systems indicates that the onset of non-analogous climates (NACs, i.e. climates without modern analogs on Earth) was correlated with the formation of non-analogous plant assemblages (Williams & Jackson 2007). Predictions of increased prevalence of NACs in future scenarios, in particular in tropical and subtropical regions (Williams & Jackson 2007, Li et al. 2018), could be thus associated with enhanced occurrence of non-analogous communities. Our ability to forecast future patterns of species distribution and abundance, generally based upon niche modelling procedures using current species distributions, remains, however, limited. This is a consequence of intrinsic difficulties in accounting for complex interactions among global and regional physical drivers, species physiological, phenological and evolutionary responses and demographic, economic and cultural features of human societies (Dawson et al. 2011, Ellis 2015). The evidence that many marine ecosystems have drifted, or are progressively drifting, away from a historical state is compelling. Nonetheless, our review has identified the lack of rigorous proof of threshold irreversibility for most marine systems (Table 1) and, following a precautionary principle, we would label most of these shifted systems hybrids. Although a relatively small proportion of declining species have recovered following the implementation of conservation measures (Lotze et al. 2011), there are examples of successful population, community and functioning recovery in marine systems over relatively short timescales, that is, years to decades (Jones & Schmitz 2009). Under these circumstances, efforts spent conserving or restoring species or communities characterising a state more similar to the historical should not be abandoned.

Whether a return to the historical state can be considered unlikely under projections of future climatic conditions and human population growth, reducing the degree of novelty of degraded ecosystems may present a pursuable goal. Acknowledging that baselines of what can be now regarded as pristine have shifted, we sense that ecosystems least impacted by humans can provide realistic reference targets for restoration actions. Procedures for selecting reference sites are well established (Underwood 1991, 1992). The main advantage of using a 'spatial' over the 'temporal' alternative (i.e. using past ecosystems) for selecting reference conditions is that targets to be achieved are established under current climatic conditions and, hence, provide a more robust picture of what are realistic goals to pursue. Reducing the intensity of human stressors operating at local to regional scales can buffer climate change impacts and, hence, be effective to achieve species configurations that are as close as possible to those found at sites regarded as the least impacted. A recent Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) report clearly indicates that, along with climate changes, many other human-borne alterations are contributing to the re-shaping of global biodiversity (Diaz et al. 2019). While writing this review, atmospheric pCO_2 reached another record (415 ppm) (Scripps Institute of Oceanography; https://scripps.ucsd.edu/programs/keelingcurve/2019/06/04/carbon-dioxide-levels-hit-record-peak-in-may/), casting doubts over the likelihood of reversing current climate trends. Under these circumstances, attempts at reducing the intensity of drivers underpinning ecosystem shifts that operate over shorter smaller spatial scales (e.g. overfishing, eutrophication) and, hence, more prone to control might be a profitable short- to mid-term strategy. This does not imply, by any means, that efforts for cutting CO_2 emissions should be relaxed, as controlling drivers of change operating at smaller spatial scales is a sort of time-buying strategy, ultimately aimed to avoiding some systems becoming actually novel. Although human avoidance of cultural traumas (i.e. maintenance of the status quo) may explain the staid attitude towards the ongoing biodiversity crisis (Brulle & Norgaard 2019), increased awareness of what is at stake, mixed with a dose of optimism, might be a recipe for halting or indeed reversing current trends of planetary changes.

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Supplementary Material

List of articles retrieved from the literature search. Articles dealing with novel ecosystem establishment in marine environments are reported in bold.

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