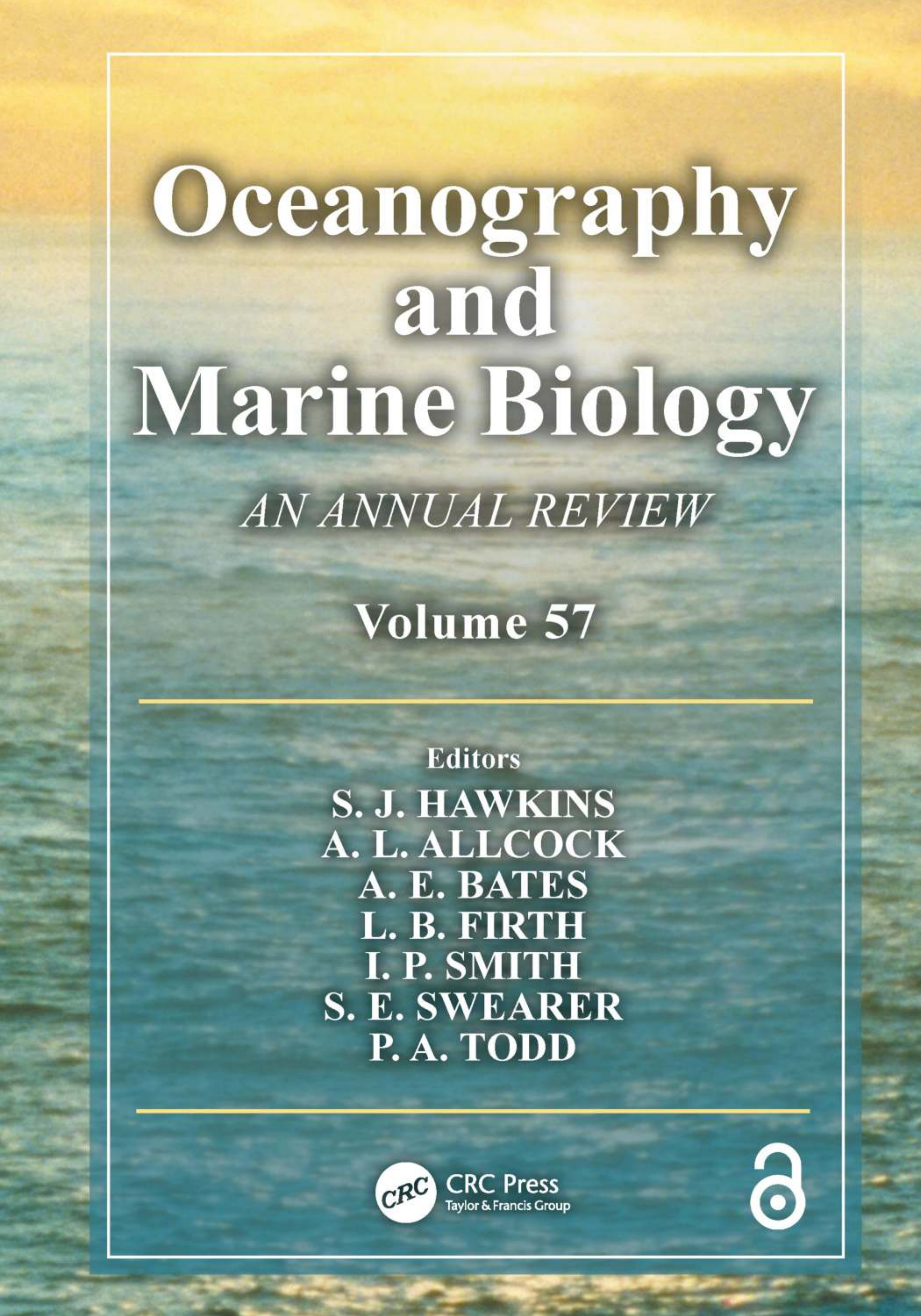

# Oceanography and Marine Biology

## AN ANNUAL REVIEW

## Volume 57

Editors

**S. J. HAWKINS**
**A. L. ALLCOCK**
**A. E. BATES**
**L. B. FIRTH**
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# OCEANOGRAPHY
# and
# MARINE BIOLOGY

## *AN ANNUAL REVIEW*

## Volume 57

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# Contents

# Preface

*Oceanography and Marine Biology: An Annual Review* remains one of the most cited sources in marine science and oceanography. The ever increasing interest in work in oceanography and marine biology and its relevance to global environmental issues, especially global climate change and its impacts, creates a demand for authoritative reviews summarizing the results of recent research. This volume covers topics that include resting cysts from coastal marine plankton, facilitation cascades in marine ecosystems, and the way that human activities are rapidly altering the sensory landscape and behaviour of marine animals.

For more than 50 years, OMBAR has been an essential reference for research workers and students in all fields of marine science. From Volume 57 a new international Editorial Board ensures global relevance, with editors from the UK, Ireland, Canada, Australia and Singapore. The series volumes find a place in the libraries of not only marine laboratories and institutes, but also universities.

The editors wish to acknowledge the help and support of the team at Taylor & Francis (Alice Oven, Jennifer Blaise, Lara Spieker, Damanpreet Kaur and Marsha Hecht) and Nova Techset (Victoria Balque-Burns). In particular we wish to also thank Ms 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.

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# RESTING CYSTS FROM COASTAL MARINE PLANKTON

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## Abstract

Coastal plankton show fluctuations in abundance and species composition. Resting stage (cyst) production is a common strategy adopted by hundreds of plankton species to ensure reproduction and to avoid adverse conditions. During the resting period, these species are normally absent from the water column, and cysts produced in the plankton accumulate in the sediment where they wait for the return of suitable conditions. A portion of the cyst bank does not hatch, instead undergoing a dormancy that may extend for decades. Confined coastal areas accumulate cysts in sediment due to one or more possibilities, including reduced water movement/hydrodynamics, high population density, abundance of cyst-producing species, and the absence or scarcity of possible cyst consumers in the benthos. The pelagic-benthic nexus, which affects both the sediment and the water column (and possibly sea ice) is still poorly understood. In fact, the presence of cysts in the life cycle of organisms is likely to have considerable consequences for the ecology of coastal plankton, as well as the evolution and biogeography of species. This review aims to depict the presence (and even abundance) of resting stages in marine environments and their impact on ecosystem functioning. The review starts with a description of encysted resting stages in all marine planktonic taxa, listing a total of 501 species with known cysts, and methods and tools for their collection and study. The physiology and timing of the rest period is then described for various taxa, followed by a discussion of the evolutionary implications of resting. The presence of encysted stages in different realms and phyla of plankton suggests an ancient origin and a successive diversification of morphologies that, today, roughly characterise each taxa. Ecological and biogeographical implications stem from this general framework and support the hypothesis of seasonal occurrences of planktonic life in ecosystems where productivity is suspended for a long time (e.g. in polar seas). The potential to suspend or resume life has implications for human activities, such as the risk of translocations through ship ballast water and contamination of water and seafood with toxins but also the benefit of cysts for the production of aquaculture feed. The review concludes with perspectives on present knowledge and outstanding questions to address in future studies.

## Introduction

Plankton dynamics are commonly affected by periodicity (seasonality in temperate areas). A holistic approach that is useful for developing and assessing simplified models of pelagic food webs considers plankton as a single entity, with total demographic oscillations that are clearly linked to environmental variability and nutrient availability, particularly in coastal areas (e.g. Ji et al. 2010). It is very important to consider that holoplankton are not a single entity, but rather a community of organisms. By definition, these organisms spend their entire life in the water column. The species structuring such a complex community do not undergo simultaneous demographic variations, but adopt different and competitive life-history strategies (Giangrande et al. 1994). Demographic variations also include the possibility of a species completely disappearing from the water column. Cycles of species' absence or presence (or even abundance) are linked to (or affected by) external and internal factors that also can stimulate or inhibit the demography of other species' populations (Nybakken 1997).

The number of species in plankton communities is so surprisingly high that it led Hutchinson (1961) to write a scientific article in which he urged biologists to think about the reasons for the apparently illogical coexistence of so many species in an apparently isotropic water volume.

Certain species are perennial and always present, albeit with variable abundances. Other species, referred to as *seasonal*, show periods of absence that are sometimes longer than the periods when they are present. The periodicity of species in collected samples can have various causes:

1. *A by-product of the failure to collect species that are rare and/or patchily distributed in the habitat.* In this case, the periodicity of the species is likely a consequence of the sampling methodology.
2. *The result of a species disappearing from the sampled area.* The periodicity of the species is due to its periodical migration, i.e. to its changeable spatial distribution on large geographic scale.
3. *The seasonal presence of a species.* This condition is linked to its rarefaction and/or disappearance from the water column, not in space but in time.

Nevertheless, planktonologists readily admit the weakness of their methodologies; for example, they are not able to collect rare species or they work only on small, unrepresentative portions of the geographic distribution of a species.

Cause 1 is indirectly sustained by the theory of flush and crash (Carson 1975), with species commonly undergoing periods of abundance (flush) and rarity (crash). During the crash period, the species is partitioned into a number of small populations separated in space, a condition that enhances intraspecific variability. Each flush episode, even when affecting a single population, has the effect of reconnecting the isolated populations and sharing any genetic positive novelty, thus giving the species an evolutionary advantage. Such developments are not the rule in the seasonality framework because they are based on random factors and are irregular and unpredictable (unlike the seasons).

Regarding both causes 2 and 3, the disappearance of holoplankton species should be done, more than to the migrating behaviour, with the existence in their life cycles of resting stages that sink to the bottom and wait for the return of suitable pelagic environmental conditions. The existence of such a strategy for many planktonic taxa is well known in both freshwater and marine ecosystems but has not been studied much. The recognition that species can have resting stages in their life cycles is a potentially important contributor to understanding the periodic disappearance of species from the plankton. The ecological role of cysts is still underestimated in marine biology textbooks, up to the point that terms like *cyst, resting*, and *diapause* are absent from the list of arguments at the end of each volume (among the most recent examples of this, see Valiela 1995, Barnes & Hughes 1999, Levington 2001, Kaiser et al. 2005, Speight & Henderson 2010, Mladenov 2013, and Castro & Huber 2016).

While the production of encysted resting stages is typical of unicellular organisms (Protista), it is not the only way to rest. For example, planktonic Metazoa, in addition to resting eggs, can enter a lethargic stage as larvae, juveniles or adults (see Williams-Howze 1997, Baumgartner & Tarrant 2017, for marine copepods). The marine dormant stages of hundreds of species of Protista and

Metazoa, however, are unified in a few typical morphologies (mostly spherical and spiny) and are equally affected by the dynamic processes of sea-bottom sediments, making it possible to develop common methodologies for their study. Nevertheless, resting stages are considered responsible for many of the intermittent occurrences of species and for their abundance/rarity cycles in the coastal marine environment (Boero 1994, Giangrande et al. 1994, Boero et al. 1996).

The germination of active stages from bottom sediment was named "resurrection ecology" by Kerfoot & Weider (2004) and, in contrast to supply-side ecology, where propagules for new populations arrive from adjacent areas (Gaines & Roughgarden 1985, Lewin 1986), it features a great novelty: species subtract themselves from plankton functioning, but their (inactive) cysts remain sympatric with active forms.

In recent years, another element has been added to the plankton ecology picture—the discovery of resting stages that are contained within ice formed in periodically frozen seas (Horner et al. 1992, Brierley & Thomas 2002). When the ice melts, the resting stages may germinate to seed a new plankton population (Rozanska et al. 2008).

In this review, the term *cyst* will be used to refer to all resting stages, according to Belmonte et al. (1995), even though we are conscious that different terminologies are currently in use to refer to some plankton groups that may be related to their functions and modalities of formation. In addition, the world of cysts links marine ecology to other subjects, such as sedimentology, palaeontology and even forest ecology, thus enhancing the presence of different terminologies in the same fields of study. Notwithstanding that cysts from planktonic organisms were recognised as viable resting stages by marine paleosedimentologists more than 50 years ago (Wall & Dale 1966), the approach to marine cyst banks as inactive communities has still more to develop from the work of terrestrial botanists and studies on the ecology of soil seed banks (Leck et al. 1989).

Considering all these aspects, the aims of the present review are:

- To summarise the state of knowledge on the role of encysted stages in the life cycles of marine holoplankton, about 50 years from their recognition (Wall & Dale 1966, for phytoplankton, Sazhina 1968, for zooplankton), in order for them to be correctly considered in models each species population dynamics
- To point out, on the basis of the rich amount of literature available, the ecological role, evolutionary importance and biogeographical implications of the presence of resting stages in marine plankton taxa and communities
- To propose a unifying approach with the presentation of various methodologies and terminologies used to study the world of cysts from marine holoplankton
- To propose a functional role for the bottom sediment cyst bank, in relation to the processes of recruitment, survival/mortality, and export, examined with a focus on the sediment community (although dormant) and not the water column.

## Resting stages in planktonic taxa

Currently, the production of resting stages is known to be a common life-cycle trait for hundreds of coastal plankton organisms belonging to various realms (see Belmonte & Rossi 1998, Lennon & Jones 2011; also see Plate 1). Among the marine Protista, the most studied are Bacillariophyceae and Dinophyceae. As a consequence, these groups comprise the majority of cyst-producing taxa known to date; many are listed by McQuoid & Hobson (1996) and Head (1996), together with dozens of Ciliophora (Reid & John 1983). Marine Metazoa that produce cysts include Rotifera (Gilbert 2004), Cladocera (Onbé 1974) and Copepoda Calanoida (Mauchline 1998). In the published lists, taxa for which the correspondence active/resting stage is not demonstrated are often reported. To address this issue, we have compiled lists for each group, including species where cyst formation and/or theca/cyst correlations have been confirmed by encystment/germination experiments or by observing living

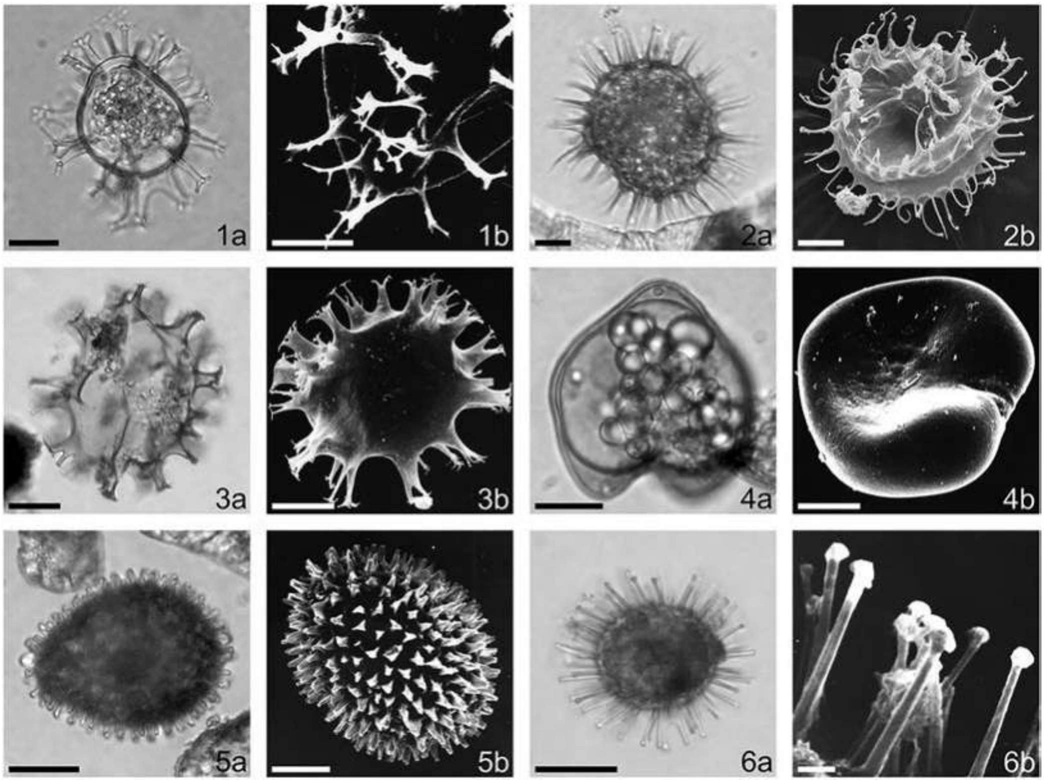

**Plate 1** Photographs of some plankton cysts under (A) light microscopy and (B) SEM. Scale bars = 20 μm unless otherwise specified. Details of the species, the location, year and method of collection (or the publication reference) are as follows: (1) *Gonyaulax* sp. (a) Mar Piccolo of Taranto, Ionian Sea, 2002; sediment trap; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (1b scale bar = 10 μm). (2) *Protoperidinium conicum* (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (3) *P. divaricatum* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (4) *P. oblongum* (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (5) *Scrippsiella acuminata* (a) Mar Piccolo of Taranto, Ionian Sea, 2006; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (6) *S. ramonii* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; sediment trap; (b) North Adriatic Sea. (From Rubio, F. et al. 2000) (6b scale bar = 5 μm). (*Continued*)

cysts within the parental individual. An analysis of the published literature on the topic allowed us to report a total of 501 species among the so-called holoplankters (see Supplementary Material 1–4).

### *Bacillariophyceae*

Bacillariophyceae (best known as diatoms) are photosynthetic eukaryotic organisms that live in marine environments worldwide (Vanormelingen et al. 2008). In spite of the high number of species described, many of their bioecological features, including life-history strategies, remain unknown (Chepurnov et al. 2004).

All diatoms are diplonts (Kaczmarska et al. 2013), spending the majority of their life history undergoing mitotic asexual division. The cell is constrained inside a rigid silicified frustule made up of two valves that resemble a box with a lid, or a Petri dish. Through binary fission, two new cells are formed within the parental theca. Each daughter cell receives one parental cell valve as its epitheca, and the cell division is terminated by the formation of a new hypotheca for each of the new cells.

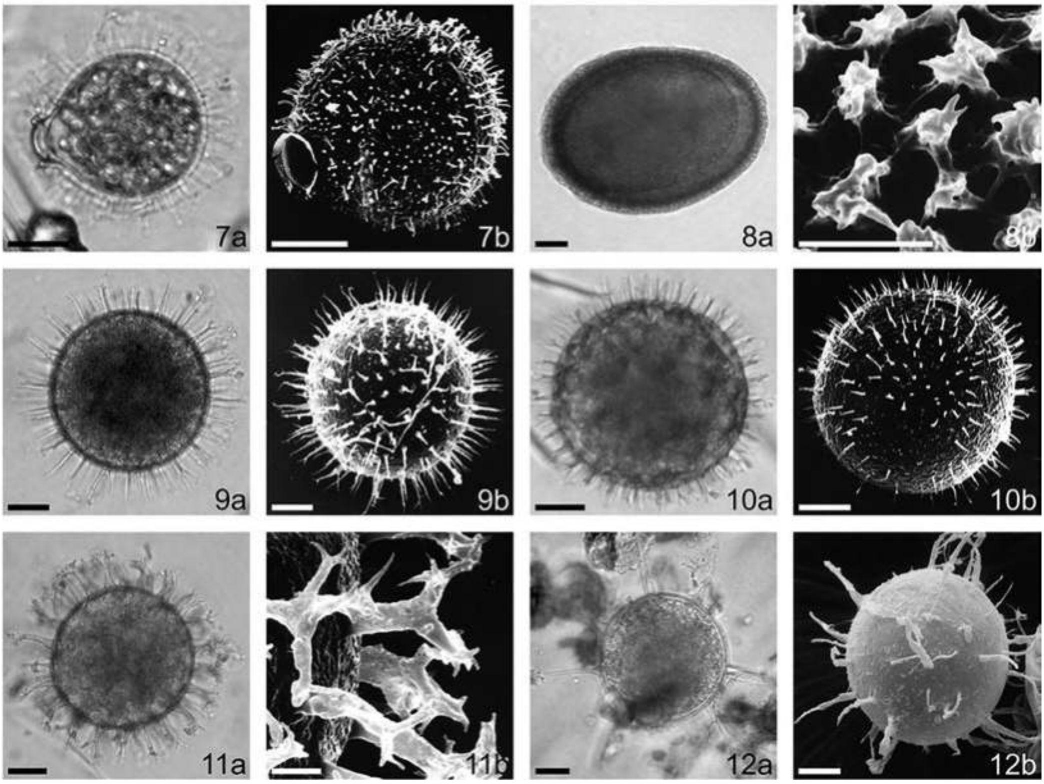

**Plate 1 (Continued)** Photographs of some plankton cysts under (A) light microscopy and (B) SEM. Scale bars = 20 μm unless otherwise specified. Details of the species, the location, year and method of collection (or the publication reference) are as follows: (7) *Laboea strobila* (a) Port of Haifa, Israel, 2011; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (8) *Synchaeta* sp. (a) Port of Ashdod, Turkey, 2004; Surface sediments; (b) North Adriatic Sea (From Rubino, F. et al. 2000.) (8b scale bar = 5 μm). (9) *Paracartia latisetosa* (long spines morphotype) (a) Mar Piccolo of Taranto, Ionian Sea, 2012; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (10) *P. latisetosa* (short spines morphotype) (a) Black Sea, 2013; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (11) *Pteriacartia josephinae* (a) Black Sea, 2013; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (11b scale bar = 5 μm); and (12) *C. typicus* (a) Mar Piccolo of Taranto, Ionian Sea, 2002; surface sediments; (b) North Adriatic Sea. (From Rubino, F. et al. 2000) (12b scale bar = 5 μm).

One daughter cell, which receives the epitheca of the parental cell, has an identical size to the parent, while the other daughter cell, whose epitheca is formed from the hypotheca of the parental cell, is slightly smaller (see Hense & Beckmann 2015 for further details). As an immediate consequence, the mean population cell size decreases. This reduction is accompanied by changes in shape and valve outline complexity (Stoermer & Ladewski 1982) that further complicate classification and identification (Mann 2001). Size restoration is enabled via the auxosporulation phase, which may take place as a vegetative event or, more rarely, as the result of sexual reproduction. This process begins with the shedding of the theca and the formation of a large sphere, the auxospore, in which a new frustule of maximal size is formed, restarting the vegetative cycle (Hense & Beckmann 2015). Thus, in contrast to many other algal groups, sexual reproduction among diatoms is a mechanism for size restoration more than it is a factor in resting stage production or dispersal, as is the case for Dinophyceae (see Edlund & Stoermer 1997, for exceptions). Size reduction is not the only factor that can induce sexual reproduction in diatoms. Environmental conditions such as temperature, light, nutrients, trace metals, organic growth factors and osmolarity might induce gametogenesis and fertilisation (see Schmid 1995, for a review). Sugie & Kuma (2008) showed that nitrogen depletion is responsible for resting spore formation in the whole population of *Thalassiosira nordenskioeldii*.

Three types of resting stages can be observed in diatom life cycles: resting (durable) spores, resting (perhaps temporary) cells and winter cells (McQuoid & Hobson 1996, Kaczmarska et al. 2013). They differ in terms of both morphological and physiological features. Resting spores show thick and heavily silicified frustules and a dense, dark cytoplasm. In some genera (e.g. *Chaetoceros* and *Rhizosolenia*), they are morphologically very different from vegetative cells, so that they can be wrongly described as different species or even new genera, as happened in some of the earlier studies (see Hendey 1964; also see Figure 1).

In contrast, in cysts produced by *Eucampia* or *Thalassiosira* species, for instance, the shapes and valvae patterns are similar to those of the active stages. Generally, resting spores have a thicker and more intensely siliceous frustule than active cells, and this favours their sinking towards the bottom sediment. The thick protection, however, also enables the spore to survive the digestive juices of copepod guts (Kuwata & Tsuda 2005).

Resting spores usually germinate before cell division occurs (Smetacek 1985), although in some species, they can divide to form more cells. This behaviour, unusual for a resting stage, is considered

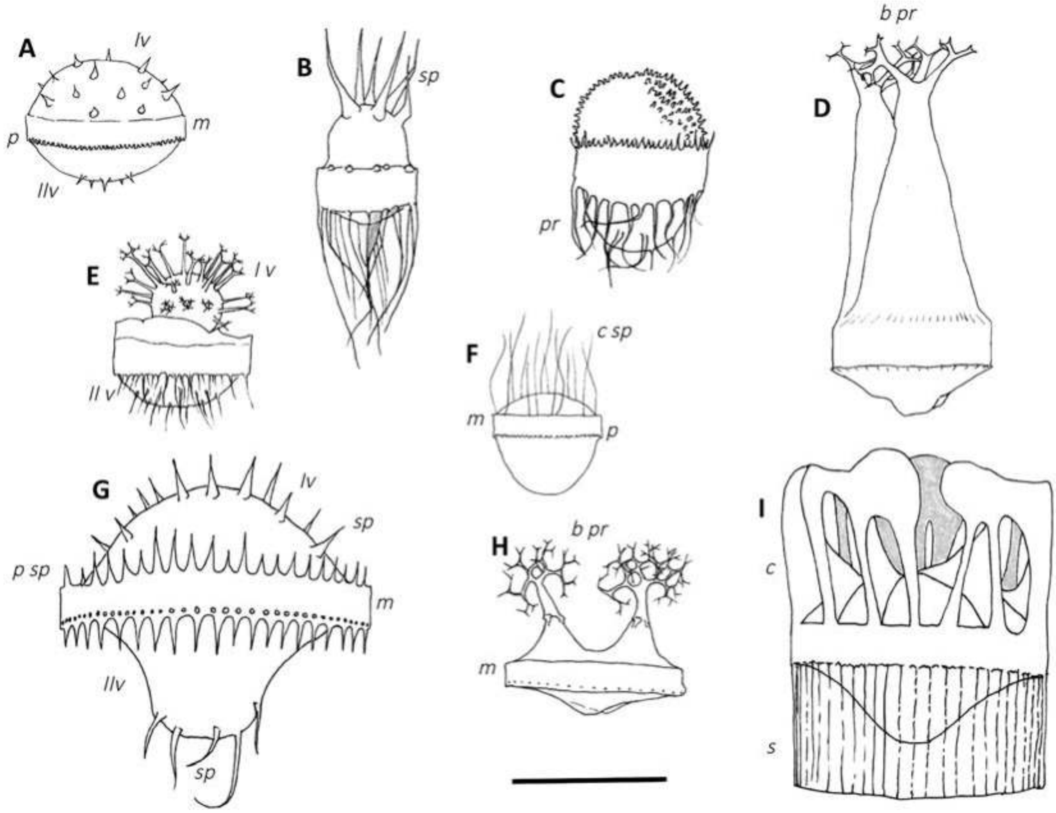

**Figure 1** Sketches of resting spores of the genus *Chaetoceros*, as a representative of the Bacillariophyceae. (A) *Chaetoceros affinis*; (B) *C. lauderi;* (C) *C. brevis;* (D) *C. mitra;* (E) *C. seiracanthus;* (F) *C. diadema;* (G) *C. siamense;* (H) *C. elegans;* (I) *C. coronatus.* Scale bar = 20 µm. (*Abbreviations: Iv*, primary valve; *IIv*, secondary valve; *b pr*, branched processes; *c*, crest; *c sp*, capillate spines; *m*, mantle; *p*, puncta; *p sp*, palisade spines; *s*, sheath; *sp*, spines.) (Modified from Ishii, K.-I. et al. 2011.)

to be evolutionarily advanced (Syvertsen 1979). Moreover, resting spore morphology is a fairly constant feature of the species and has great taxonomic value (Hasle & Syvertsen 1996), particularly for *Chaetoceros* species (Figure 1), where structures such as spines, crests and valve sheaths are highly species-specific (Ishii et al. 2011).

While to the human eye resting cells are generally not distinguishable from vegetative stages in terms of shape and frustule patterns, copepods are able to recognise and selectively prey on the vegetative stage, thus avoiding the resting spores, which contain low levels of nitrogen and are unsuitable for correct copepod growth (Kuwata & Tsuda 2005). Resting cells are characterised by the presence of a very dense cytoplasmic mass, usually in a central position (Sicko-Goad et al. 1989), and they have reduced physiological features, such as respiration rate and photosynthetic activity (Kuwata et al. 1993).

Resting cells are formed mainly by species within the Pennales group, whereas resting spores are common among Centrales species (Round et al. 1990). Some species are able to produce both vegetative and spore resting stages (Kuwata et al. 1993).

Winter cells are very similar to resting spores, as they are heavily silicified and morphologically different from vegetative forms. At the same time, they differ from resting spores because they are metabolically active. In fact, they can divide by binary fission and form colonies (Kaczmarska et al. 2013). Although this kind of resting stage has been observed only in an Antarctic species (namely, *Eucampia antarctica*), they might represent a more general adaptation of phytoplankton species living in polar seas (Fryxell & Prasad 1990).

As suggested previously, diatoms normally form resting stages in a vegetative way. Actually, very few species have been observed to form resting spores as part of the sexual phase (see McQuoid & Hobson 1996 and references therein). Whether reproduction is vegetative or sexual, resting stage formation can occur through three patterns: exogenous types that are completely released from the parent cell, so they are not in contact with it; endogenous types that are wholly enclosed within the parent cell frustules; and semiendogenous types that are attached to one of the two parent valves. The latter case could result from an intermediate pattern of development, with the spore actually being exogenous (Syvertsen 1979).

Not all cells in an active planktonic population produce resting stages. This needs to be taken into account when estimating the number of resting stages that are delivered to bottom sediment during each resting phase. The large number of diatom cells, however, allows the production of a numerically dominant presence of diatoms in bottom-sediment cyst assemblages.

### *Dinophyceae*

Dinophyceae are widely distributed in all aquatic environments in both plankton and benthos. About half of the known species are photosynthetically active, many species are heterotrophic and some are mixotrophic, demonstrating the futility of efforts to class them as plants or animals (Fensome et al. 1996, Dale 2001).

Dinophyceae represent one of the most important groups of microplankton. They show postzygotic meiosis and a haploid life cycle. Reproduction occurs mainly in accordance with vegetative mechanisms (Pfiester & Anderson 1987), leading to high population growth rates. In some cases/species, such a feature leads to dense blooms (red tides) that disturb entire ecosystems (Hallegraeff 2003).

Dale (1983) and Taylor (1987) assumed that 13%–16% of the roughly 2000 species described produce a benthic dormant stage (cyst), which corresponds to the condition of a hypnozygote (sensu Head 1996). Our literature survey produced a list of 182 species for which the production of a resting stage has been demonstrated (Suppl. Mat. 2), but this number is rapidly increasing, thanks to the intensification of studies on this topic. This hypnozygote has no flagella, produces a robust external wall and sinks to the bottom as an inert particle. Due to this wall, cysts of some species can fossilise, and hence they represent an important element in paleoecological investigations (Dale 1996, Pielou 2008).

Although the fossil record indicates that Dinophyceae became common only 245 million years ago (Fensome et al. 1996), a Precambrian origin for the taxon has been proposed on the basis of both comparative morphology and the molecular phylogeny of cysts (Knoll & Walter 1992). Indeed, studies on cysts started with fossils assigned to the *Peridinium* genus that were first observed by Ehrenberg (1838) in siliceous rocks of the Cretaceous period.

The studies by Deflandre (1935), Eisenack (1938) and Evitt (1961), among others, showed the organic nature of the cyst wall and led to the description of new fossil genera of the family Peridineae (Bujak & Davies 1983).

Wall & Dale (1968a,b) established the correspondence between cysts and active stages for a large number of species of the order Peridiniales. These pioneering studies described the most important morphological traits of Dinophyceae cysts, which are still useful today for their identification (Stover 1973, Lentin & Williams 1976):

- General shape
- Tabulation scheme, with indication of the presence/absence of the cingulum
- Archaeopyle position, shape and size
- Wall sculpture (shape and nature of processes)
- Size and position of endocyst in relation with pericyst

Considering the general morphology, the cyst shape shows a narrower range of diversity than the motile forms. This is more evident in living species than in fossil ones (Sarjeant et al. 1987). The general shape of cysts goes from simple spheres or ovoids, with no processes or other structures on the wall, to more complex and distinctive peridinioid (pentagonal) shapes, passing through regular outlines ornamented with columnar processes, crests, septa, horns and spines (Figure 2). Regardless of ornamentation, body shape is considered the most conservative of the cyst features (Dale 1983), generally falling into two distinct categories: either similar to the shape of the motile cells or, more typically, simpler and generally spherical.

Depending on where they are formed inside the planozygote, Dinophyceae cysts are typically classified into three main categories: proximate, chorate and cavate. Starting from the consideration that cysts are always smaller than the motile cells, at least during the zygote stage (because they form inside them), Downie & Sarjeant (1966) proposed that cysts could be grouped according to the degree of difference with respect to the parent cell, which affects their general appearance. Thus, proximate cysts are those that correspond most closely to the morphology of motile forms; about one-half to one-third of the original volume, they also bear signs of cingulum, sulcus and tabulation. Chorate cysts are smaller still (less than one-third of the original) and generally have processes or crests whose height, according to Sarjeant (1982), can exceed 30% of the shortest diameter of the central body. Finally, in cavate cysts, the cellular content is surrounded by two or more walls with spaces between them. For specific terminology and more accurate descriptions, see Williams et al. (2000).

Most Dinophyceae cysts have organic walls that are usually structured with one to three or four layers and are chemically similar to the exine of spores and pollen grains (sporopollenin) of higher plants (Bujak & Davies 1983; Kokinos et al. 1998). This material, which is destroyed only by strong oxidising agents, makes the cysts very resistant over time. In the family Thoracosphaeraceae, the outer layer is of calcium carbonate, imparting a distinctive appearance and colouration to the cyst surfaces. This calcareous outer layer also makes them distinguishable by their birefringence under polarised light down a microscope (Elbrächter et al. 2008). Recent studies have demonstrated that the ultrastructure of this layer is very complex, with the calcite crystals varying in terms of shape and orientation—a characteristic considered to be genetically derived and of high taxonomic value (Elbrächter & Hoppenrath, 2009). In addition to smooth and unornamented walls, as in many *Protoperidinium* species, Dinophyceae cyst coverings are characterised by a great variety of processes and ornamentations, many of them direct consequences of their formation.

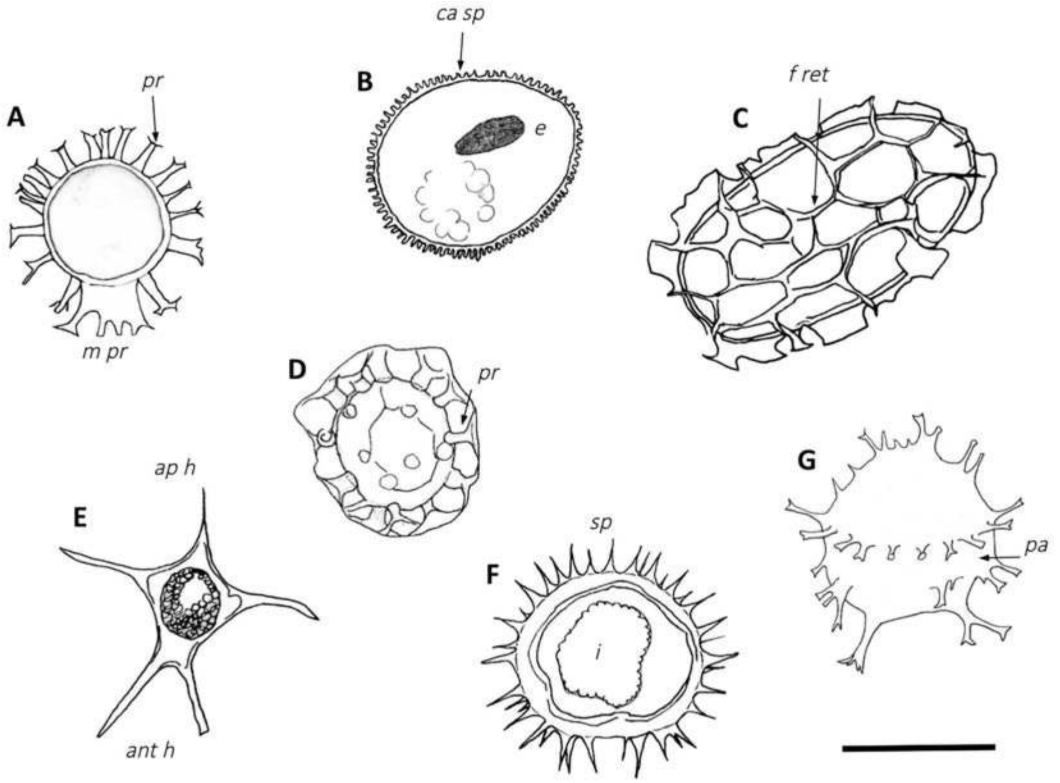

**Figure 2** Sketches of Dinophyceae cysts from the order Peridiniales (original drawings from authors' cysts collection). (A) *Gonyaulax* sp.; (B) *Scrippsiella acuminata*; (C) *Polykrikos schwartzii*; (D) *Pyrophacus steinii*; (E) *Protoperidinium stellatum*; (F) *P. conicum*; (G) *P. divaricatum*. Scale bar = 40 µm. (*Abbreviations: ant h*, antapical horn; *ap h*, apical horn; *ca sp*, calcareous spines; *e*, eyespot; *f ret*, fibrous reticulate layer; *i*, inner protoplasm; *m pr*, membranous process; *pa*, paracingulum; *pr*, processes; *sp*, spines.)

In many cases, the type of wall processes is distinctive in a species and may be considered a taxonomic feature. This notwithstanding, *Lingulodinium polyedrum* and *Protoceratium reticulatum* show great variability in lengths and ultrastructures of processes within the same population, due to the intrinsic variability of the species or the changing environmental conditions affecting their formation (Kokinos & Anderson 1995; Mertens et al. 2011, 2012). The complex species *Gonyaulax spinifera* is reported to produce 16 morphologically different cysts (Head 1996) probably representing several pseudocryptic species (Mertens et al. 2017), even though for 9 of them, the correspondence between theca and cyst has been proven.

Dale (1983) distinguishes ridges from processes. Ridges are often related to the tabulation pattern of the theca, reflecting the position of the sulcus and cingulum or plate boundaries, while processes may or may not be linked to the tabulation (see the discussion that follows for more detail on paratabulation).

Processes are essentially columnar or spinelike, hollow or solid. Distally, they may have pointed, bulbous or capitate endings, or else they may be intricately branched or interconnected.

Following Evitt et al. (1977), all the features of the cysts reflecting those of the theca are indicated by the prefix *para-,* from the Greek παρα- (= near, beside). Thus, paratabulation is, according to Lentin & Williams (1976, p.173), 'the pattern or arrangement of the constituent para-plates in a Dinophyceae cyst'. Just as tabulation is used in the identification of modern motile Dinophyceae taxa, paratabulation is used to distinguish cyst species. Sometimes, even among thecate taxa (i.e. with a well-defined theca), paratabulation is incomplete, with the only evidence of it in cysts being the archaeopyle or the paracingulum, although the presence of these features is sufficient for taxonomic identification. For more details about tabulation, tabulation systems and tabulation formulae in both active cells and cysts, see de Verteuil & Norris (1996).

The archaeopyle is probably the most important feature of the cyst wall, playing a key role in taxonomic identification for both organic and calcareous types (Streng et al. 2004). It was originally defined by Evitt (1961, p. 389) as the 'opening…formed by the release of a single plate or group of plates' and subsequently by Lentin & Williams (1976) as an opening in a Dinophyceae cyst through which the active stage emerges.

Wall & Dale (1968a) observed that the position, shape and number of paraplates involved in the archaeopyle opening are very conservative in the order Peridiniales. This has been shown to be true for other thecate taxa, but not for species lacking thecal plates. Consequently, Matsuoka (1985) proposed a new terminology and new archaeopyle types that also include athecate taxa.

Little information on the structure and chemical composition of the cyst inner protoplasm is available, mainly because the wall is impervious to fixing and staining (Binder & Anderson 1990). As a general rule, the protoplasm undergoes a contraction and a reduction in the number and size of subcellular structures. Typical features of encysted protoplasm include granular starch bodies and lipid droplets, together with one or more orange/red-pigmented bodies (Dale 1983). These latter are often called *red eyes* or *accumulation bodies* due to their possible function as photoreceptors or storage structures. What is known so far is that they are produced by autotrophic species during the cyst formation process and sometimes continue to be present in the active cell for a short time after germination.

A very interesting unresolved issue is the attribution of many cyst morphotypes to a single species (heterospory), as in the case of *Gonyaulax spinifera* (Head 1996). However, it is unclear whether this indicates genuine heterospory or cyst overclassification (Taylor & Gaines 1989, Rochon et al. 2009). This perceived heterospory has stimulated the description of new species, together with the investigation of the correspondence between active and resting stages in other species of the genus *Gonyaulax* (Lewis et al. 2001, Ellegaard et al. 2003, Rochon et al. 2009, Mertens et al. 2015, 2017). In any case, heterospory may simply be an aspect of variability within species and an important strategy (see the section entitled "Evolutionary implications of rest traits") to ensure the persistence of the species in the environment. Experimental evidence comes from recent studies of athecate species such as *Gymnodinium impudicum* (Rubino et al. 2017).

Among Dinophyceae, a distinction exists between temporary, ecdisal and pellicle cysts (see Bravo et al. 2010 for a detailed description of the differences and similarities of these cysts) and resting cysts. These two types mirror the distinction between quiescence and diapause (see the section entitled "Types and physiology of rest" for more details).

Temporary cysts are produced as a consequence of sudden environmental changes (e.g. temperature and salinity variations) and thus represent a rapid response to unpredictable variations. Normally, the theca is shed and the protoplasm of the vegetative cell contracts, becoming rounded or oval within a thin wall. As soon as conditions are favourable again, temporary cysts rapidly germinate a new active stage.

In contrast, resting cysts are normally the result of sexual reproduction, and generally their production is colligated with the arrival of adverse conditions. In some species, a transition from temporary to resting cysts has been observed. If favourable conditions do not return within a given time period, temporary cysts can produce a cyst wall, thereby transforming themselves into resting cysts (Rubino, personal observation).

Practically all planktonic dinoflagellate species are believed to produce temporary cysts. The differing physiological, biological and ecological features of temporary and resting cysts are also reflected in morphological differences.

Dinophyceae cysts can reach high abundances in the sediments of protected bays. Matsuoka et al. (2003) reported values up to about 8000 cysts per gram of dry weight sediment in Tokyo Bay. Godhe et al. (2001) measured a maximum flux of 2.7 million cysts $m^2$/day towards the bottom and a cyst peak in the sediment that did not correspond to the active stage peak in the plankton, but probably to a progressive accumulation with time in the absence of germination.

## *Ciliophora*

Ciliophora of the Tintinnina order and the Strombididae family (order Oligotrichida) are important heterotrophic and/or mixotrophic components of marine microplankton in oligotrophic waters (Stoecker et al. 1996). Most studies on the encystment-germination cycle of Ciliophora focus on soil and/or freshwater species (see Corliss & Esser 1974 and references therein); hence, they may be extended to marine species only with caution.

Encystment is considered as a regular trait of the ciliate life cycle, but of 141 described species of aloricate Oligotrichaea of marine and brackish waters, only a few are known as cyst producers (see Suppl. Mat. 3). Until recently, knowledge of the marine ciliate encystment-germination cycle was limited to only three species: *Strombidium oculatum* (Fauré-Fremiet 1948, Jonsson 1994, Montagnes et al. 2002), *Helicostomella subulata* (Paranjape 1980) and *Cyrtostrombidium boreale* (Kim et al. 2002).

*S. oculatum* lives in rocky pools, and its encystment-germination cycle is correlated with tides (Montagnes et al. 2002). The other two species live in the sea and produce cysts in accordance with a seasonal rhythm. For some other species, such as *S. conicum* (Kim & Taniguchi 1995, 1997), *S. crassulum* (Reid 1987) and some species of *Tintinnopsis* genus (Kamiyama & Aizawa 1990), only one of the two mechanisms (encystment or germination) has been described.

Ciliate cysts are not easily found in plankton samples, probably because of their high sinking speed or the shortness of the period during which they are produced (Reid 1987). In the literature are reported samples characterised episodically by ciliate cysts, as in the case of those collected by Meunier (1910) in the Kara and Barents seas in 1907 (but see also the case presented in Paranjape 1980 for the tintinnid *Helicostomella subulata*).

Tintinnina cysts are typically contained within the lorica of the organism. They are spherical or elliptical in shape. Hypotrichida cysts are spherical. The cysts of Heterotrichida and Oligotrichida are characterised by the presence of an apical bubblelike cap on the apical opening from which the active stages emerge at the end of their dormancy (Figure 3).

The presence of this cap and their flasklike shape (30–140 µm in length) make these cysts unmistakable (Reid & John 1983). These cysts were named Papulifera by Meunier due to the presence of this 'bubble' (= papula, in Latin) on their apex. Meunier's 'bubbled' cysts were grouped according to their shape under the names *Fusopsis* (spindlelike), *Piropsis* (pearlike) and *Sphaeropsis* (spherical or ovoid) (Reid & John 1978). The papula is considered an archaic feature because it is very common among cyst-producing taxa.

However, like Tintinnina cysts, Papulifera cysts can be identified with certainty in many cases only after germination (Kim & Taniguchi 1995). Papulifera cysts often have spines or wrinkles on their outer covering, and the type of ornamentation has been the subject of studies concerning the phylogenesis of these ciliates (Reid & John 1983). Foissner et al. (2007) report that surface ornamentation rarely exists among Ciliophora cysts. When surface ornamentations are present, they can be delicate and tiny, and thus invisible under a compound microscope and/or easily eliminated during treatments applied before observation.

The cysts of the Oligotrichida *S. crassulum* have been described in detail by Reid (1987). The apex closed by the papula narrows into a neck about 14 µm in diameter (the cyst itself has a transversal diameter of about 50 µm). The external membrane is thin and bears tiny spines that make it look like velvet. The underlying layer is the thickest and is composed of calcium carbonate and phosphate, immersed in an organic matrix. This layer is seen to be multistratified when observed

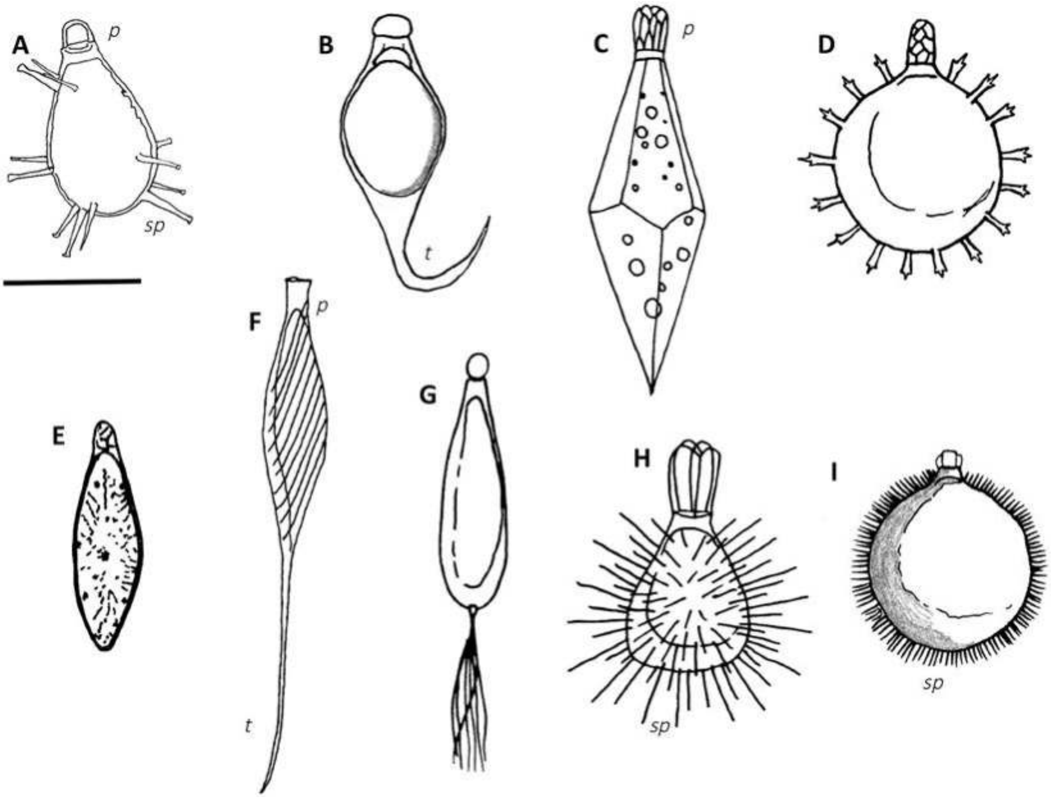

**Figure 3** Sketches of Ciliophora cysts. (A) *Strombidium biarmatum*. (B) *Cyrtostrombidium boreale*. (Redrawn from Moscatello, S. et al. 2004.) Cysts attributed to Ciliophora (Redrawn from Meunier, A. 1910), but waiting to be linked to a motile stage (the terminology of Meunier, A. 1910 is used); (C) *Fusopsis polyedra;* (D) *Sphaeropsis echinata;* (E) *F. pauperata;* (F) *F. spiralis;* (G) *F. flagrifera;* (H) *Piropsis acineta;* (I) *S. brevisetosa*. Scale bar = 40 µm. (Redrawn from Agatha, S. et al. 2005.) (*Abbreviations: p*, papula; *sp*, spines; *t*, tail.)

by transmission electron microscopy (TEM). A thin inner membrane encloses an undifferentiated granular cytoplasm.

The three layers (moving from the outside inwards) are named *ectocyst, mesocyst* and *endocyst*.

Foissner et al. (2005, 2007) report that the chemical composition of this multilayer includes various types of carbohydrates, proteins and glycoproteins. The same authors distinguish spines (if formed by the ectocyst) from thorns (if formed by the mesocyst) and lepidosomes or scales (if formed in the cytoplasm and successively transferred to the external surface). In any case, it seems that the strength of the cyst wall in some way requires the cyst to reduce its volume to the minimum. In many freshwater species, this sensible reduction of the final volume to 3%–5% of the active stage volume is probably obtained with a subtraction of water more than a deprivation of cytoplasm and organelles (Verni & Rosati 2011).

Hyperhaline habitats host ciliates (e.g. those of the *Fabrea* genus) with apparently smooth cysts.

The sediments of lagoons and bays sometimes host rich assemblages of such cysts (Moscatello & Belmonte 2004). Their number does not depend on the production rate of the active stages, as in the case of Metazoa. In fact, each active stage produces only one cyst because it simply encysts itself generally after an act of two-cell fusion (sexual reproduction). The number of cysts found in sediments is consequently a simple reflection of the abundance of active stages in the water column just before cyst formation. Nothing can be said about the length of the resting (which could be responsible for the accumulation of ungerminated cysts); in any case, Doherty et al. (2010) established that the cyst bank of sediment may contain only a few ciliate cysts, due not only to the mechanism of production, but also to their relatively short period of rest.

### *Other Protista*

Unicellular organisms of marine plankton, which are different from Bacillariophyceae, Dinophyceae or Ciliophora, are only rarely considered in ecological studies on rest and resting stages, although they are well known in studies of single species. *Chattonella marina* and *Heterosigma hakashiwo* (Raphidophyceae) are probably emblematic examples, being unicellular algae responsible for noxious blooms in coastal areas and whose cysts capture scientists' attention with the hope of understanding their cyclical appearance (Imai 1989, Kim et al. 2015). Never dominant, but sometimes common, are morphotypes such as *Radiosperma corbiculum* and *Hexasterias problematica*, classified as palynomorphs (Price & Pospelova 2011) or as other algae (Candel et al. 2012) (Figure 4).

Very recently, *Hexasterias problematica* (syn. *Polyasterias problematica*) has been recognised as the cyst of a Ciliophora (order Prorodontida), together with *Halodinium verrucatum*, both sharing close relationships with *Radiosperma*, suggesting the latter should be a ciliate and not an alga (Gurdebeke et al. 2018).

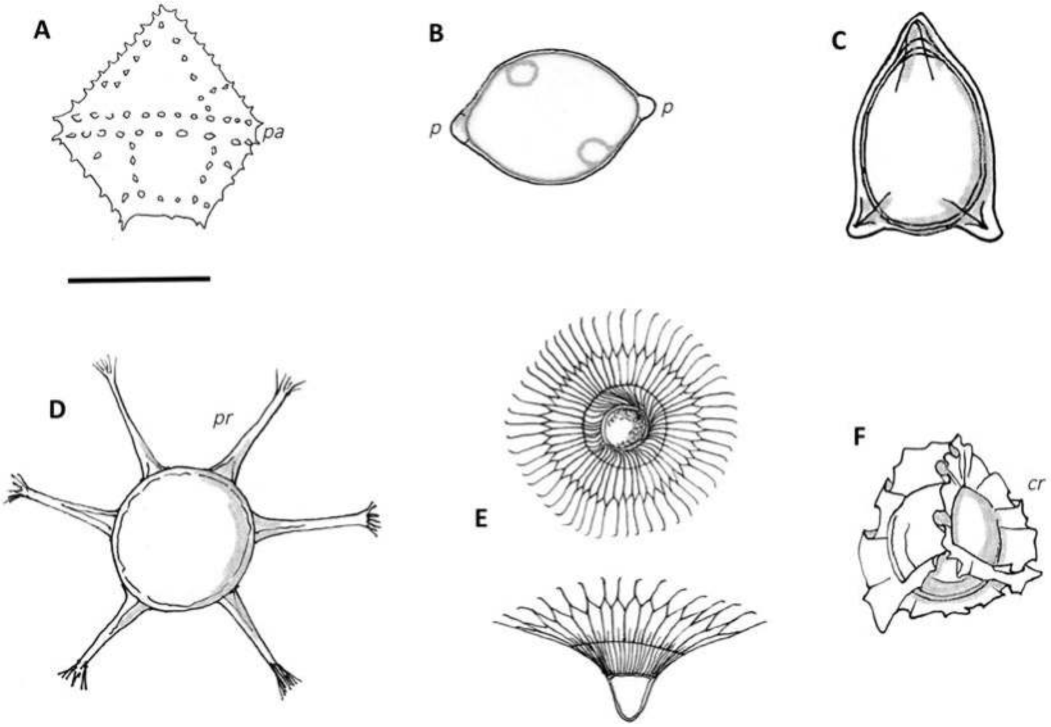

**Figure 4** Cyst morphologies of other Protista, including some palynomorphs of micropalaeontologists. (A) *Protoperidinium* sp. (Dinophyceae) (original drawing from authors' cysts collection). (B) Ciliophora (unidentified) with a double papula. (Drawn from Rubino et al. 2013.) (C) *Favella* sp. (Ciliophora). (Redrawn from Reid & John 1983). (D) *Hexasterias problematica* (Ciliophora) (original drawing from authors' cysts collection). (E) *Radiosperma* in polar and side view. (Redrawn from Meunier 1910.). (F) *Pterosperma*. (Redrawn from Meunier 1910.) Scale bar = 50 µm. (*Abbreviations: cr*, crest; *p*, papula; *pa,* paracingulum; *pr*, processes.)

Other resting stages, of unknown systematics, are commonly reported from coastal or neritic habitats by palaeontologists. The list, continuously updated by micropalaeontologists, includes hundreds of organic-walled microfossils recognised during the last 50 years and generally included under the term palynomorphs. Most of them have been attributed to known taxa on the basis of some distinctive characters (e.g. the paratabulation or the archeopyle for Dinophyceae and the papula for Ciliofora cysts), but many still wait for a final identification in the frame of an intricate network of competences (i.e. palynology, sedimentology, planktonology, and palaeontology).

Generally, open-sea and/or oceanic unicellular organisms show the presence of resting stages in their life cycle, but probably with no interaction with the bottom and no obvious similarities with those of coastal species. Encystment is common in many oceanic Acantharia and involves a complete reorganisation of the architecture of the mineral skeleton, other than a series of mitotic and meiotic divisions (Bernstein et al. 1999). The process, clearly active and efficacious for a rapid sinking, is not reversible, as happens in many planktonic Protista. Being that this is the way to produce thousands of gametes, cysts in Acantharia are not true resting stages, but rather a necessary step for their reproduction (Decelle et al. 2013). The cyst formation in this taxon is thus typical of the open ocean—it does not involve the sediment, there is not a true rest period and it does not show a germination moment.

### *Rotifera*

The Rotifera phylum is not well represented in marine plankton. Its ecological importance grows as it goes from marine to brackish and fresh waters, with some species (e.g. those of the genera *Brachionus*, *Synchaeta* and *Trichocerca*) common in the neritic microzooplankton (de Smeet et al. 2015).

The production of cysts (resting eggs) is documented for all freshwater Rotifera (for a review, see Ricci 2001), and it is generally associated with the sexual phase of the life cycle. Often this occurs only after many parthenogenetic generations. According to Gilbert (2007), this life-cycle trait evolved to achieve the maximum production of resting eggs, which wait for the return of favourable conditions to ensure the persistence of a species. Indeed, when the population deriving from parthenogenesis reaches its maximum density, it induces meiosis in ovogenesis (Gilbert 2004), giving rise to haploid males that are able to fertilise the bulk of available haploid eggs, thus determining the formation of diploid, fertilised eggs destined to become resting stages (the so called male-female encounter hypothesis of Serra et al. 2004). Commonly, the resting eggs of marine Rotifera are ovoid (80–150 µm in length) and easily recognisable in the cyst assemblages of bottom sediment (Marcus 1990, Viitasalo & Katajisto 1994, Belmonte et al. 1995) (Figure 5).

Unlike subitaneous eggs, the surface of resting eggs is often sculptured, rough or both (at least in marine species). However, the surface features never assume the shape of long spines. The cyst is spherical and smooth in species found in continental habitats, even those that are hyperhaline (Ricci 2001).

The internal embryo is often seen to be partially detached from one side of the cyst wall. This forms an empty space accounting for up to 25% of the total cyst volume. In freshwater *Brachionus*, when this space is more than 25%, it means that the embryo is not viable (Garcìa-Roger et al. 2005). In *Synchaeta* and *Brachionus*, birth occurs through a narrow hole that opens like a door in one of the extremities of the cyst wall (Piscia et al. 2016).

Each female produces only one or two resting eggs, and Rotifera account for only a small number of species in the marine plankton. Consequently, the abundance of resting eggs in sediment cyst assemblages is numerically inferior to that of unicellular organisms and comparable with that of other Metazoa (e.g. Rubino et al. 2013).

### *Crustacea, Cladocera*

Although Cladocera, like Rotifera, account for only a few species in the marine zooplankton, in some cases they are reported in such high numbers (as in the north Adriatic and Baltic seas) that

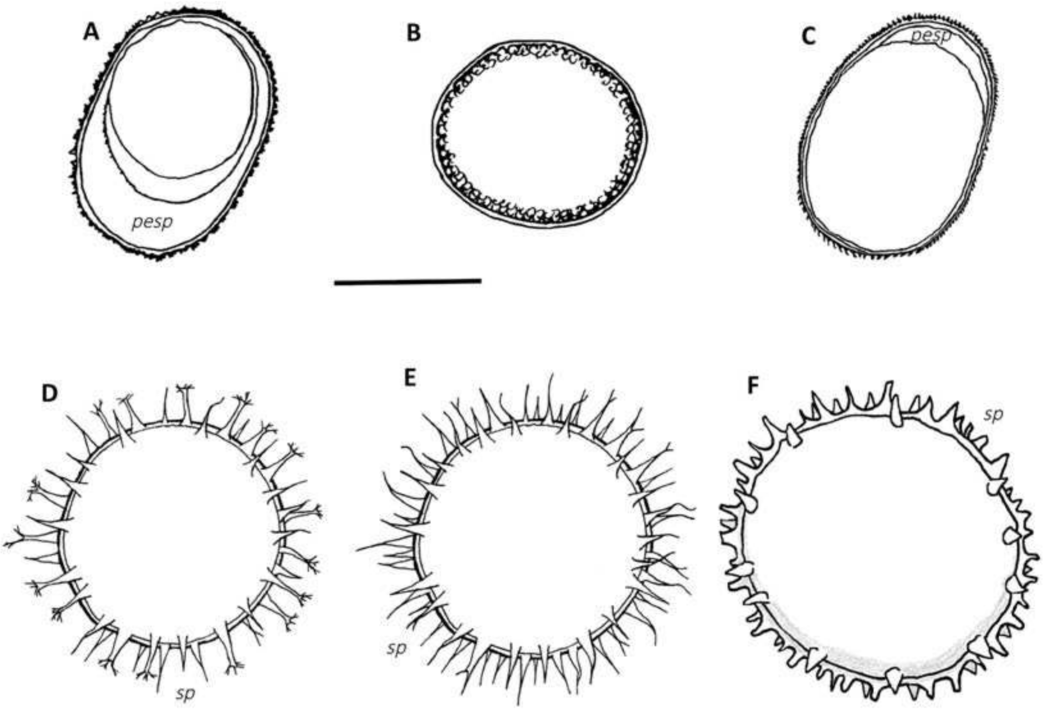

**Figure 5** Sketches of resting eggs of planktonic Metazoa (A, B, C = Rotifera; D, E, F = Copepoda Calanoida); (original drawings from authors' cysts collection). (A) *Brachionus* sp.; (B) *Exarthra* sp.; (C) *Synchaeta* sp.; (D), (E) *Acartiidae* spp.; (F) *Pontellidae* sp. Scale bar = 50 μm. (*Abbreviations: pesp*, periembryonic space; *sp*, spines.)

they characterise local communities (Egloff et al. 1997, Guglielmo et al. 2010, Viitasalo 2012). Reproduction is parthenogenetic during most of the year, and each female produces a relatively high number of parthenogenetic eggs (generally incubated in a dorsal chamber named *ephippium*). The appearance of males in the population follows the same pattern as Rotifera and seems to be directly induced by the numerical growth of populations just before the arrival of the unfavourable season (Alekseev 2007). The fertilised eggs are resting (diapausal) and appear in small numbers (1–2 per female). The appearance of males in the population seems directly connected with the strategy of producing fertilised/diapausal eggs. Indeed, Miyashita et al. (2011) demonstrated that local populations can completely lose their males for years.

In marine Cladocera (8 species in total, belonging to the orders Onychopoda and Ctenopoda), the diapause egg is abandoned in the water column, together with the exuvia of the moulted females or the bodies of the dead ones. Saito & Hattori (2000) described a vertical distribution of the various stages of the marine Cladocera *Podon leuckarti,* with gamogenic females persisting near the bottom, even when the remaining population migrates to subsurface layers during the daytime.

The low number of diapause eggs produced by each female practically corresponds to the egg production rate of Rotifera. However, egg abundance in the sediment assemblages is dependent on the site and the period, with Cladocera being particularly abundant only for short periods and commonly in neritic waters. This leads to a low numerical importance of Cladocera eggs in the sediment of confined environments, although their weight may be important due to their relatively larger size compared to other cyst-producing organisms (average diameter = 150–300 μm).

The diapause eggs of Cladocera are easily distinguishable in the sediment assemblages because they are generally larger than all the other resting eggs (Onbé 1985, 1991). They can be spherical, as in *Evadne* and *Podon*, or ovoid and typically concave on one side, as in *Penilia*. Indeed, such eggs are the largest ones found in sediment cyst assemblages (Marcus 1990, Viitasalo & Katajisto 1994, Belmonte et al. 1995, Madhupratap et al. 1996).

The eggs may also exhibit calcification of the external layer, which results in a higher sinking rate (Braiko 1966). At the same time, this layer enables them to better resist pressure and/or scraping.

Most of the Cladocera resting eggs have a smooth external wall. In addition, they exhibit a multilayered envelope, which is typically thick. The robust external covering is probably a defence against predators. Indeed, the *Mysis* shrimps of the northern Baltic Sea feed selectively on the eggs of *Bosmina longispina maritima* (contained in an ephippium) and ignore the eggs of *Podon polyphemoides* (not ephippiated), which have a thicker external covering (Viitasalo & Viitasalo 2004, Viitasalo 2007).

### *Crustacea, Copepoda*

Copepoda are the most diverse and abundant Metazoa taxon in the marine mesozooplankton. Many orders contribute to species assemblages in the water column, but those belonging to Calanoida are certainly the most representative and the best adapted to a holoplanktonic life in the sea (Huys & Boxshall 1994). In order to overcome adverse periods, species of the superfamily Calanoidea enter a lethargic phase as juveniles (copepodids I–V), while species of the superfamily Diaptomoidea commonly produce resting eggs (see Mauchline 1998 for a review on the rest of the species among Calanoida).

Sazhina (1968) was the first to report the existence of a marine Calanoida resting egg (with delayed hatching) that was morphologically different (it showed a spiny surface) from the subitaneous ones (with a hatching time of 1–2 days), observed in the life cycle of two species (*Pontella mediterranea* and *Centropages ponticus*) from the Black Sea.

Since that time, the list of marine *Calanoida* species that can produce resting eggs has been repeatedly updated (Uye 1985, Williams-Howze 1997, Engel 2005), and today includes at least 54 species (Suppl. Mat. 4). However, the list contains only coastal species, and they are all phylogenetically cognate (belonging to the same superfamily, Diaptomoidea). This suggests that this life cycle trait favoured the adaptation of Diaptomoidea to coastal environments, where abiotic conditions are more variable than in the open sea.

All freshwater Calanoida species belong to this superfamily, and the presence of a resting stage in their life cycle was proposed as being responsible for the adaptation of this marine taxon to freshwater habitats (Lindley 1992, Belmonte 1998c, but see Belmonte 2018 for a more recent interpretation)

The diapause eggs of Calanoida are generally spherical (diameter, 60–200 µm) and commonly show ornamentations on the surface.

Marine Diaptomoidea differ from freshwater species in that they lay eggs in the water column (they have no ovisacs) (Sazhina 1987), and such eggs inevitably sink to the sea bed. In detail, the sinking rate of smooth eggs is higher than that of spiny eggs. According a normal embryo development time (1–2 days), a smooth egg of *Calanus finmarchicus* hatches after a 40-m sink and the spiny egg of *Centropages ponticus* after a 8-m sink from the mother position (Sazhina 1987). The spine length on eggs of *C. typicus* has been found to be inversely correlated with the water temperature and directly with water density, thus suggesting this retarding role (Gaudy 1971). This allows the hypothesis of spines acting as a device for the egg to retard reaching the bottom in coastal areas. At all temperate latitudes (where seasonality is evident), it is common to find that coastal sediments of shallow areas contain Calanoida eggs, and that they are more abundant than on open- and deep-sea beds. In addition, egg abundance in the sediments is often higher than that of active stages in the water column (Uye 1985, Belmonte et al. 1995, Dahms et al. 2006).

Calanoida populations can be very abundant in coastal areas, but it should be noted that only a small portion of the population (adult females) is involved in egg production. Nevertheless, egg production can be high and continuous over many days. Indeed, unlike Rotifera and Cladocera, the number of Calanoida resting eggs in the sediment is higher because it is conditioned by the fact that fertilised females lay eggs throughout their life span (25–45 days), at a rate that can reach 100 eggs per day in *C. typicus* (Ianora 1998). More commonly, the egg production rate of species in coastal-confined habitats ranges from 0 to 78 eggs per female per day (Belmonte & Pati 2007, Drillet et al. 2008b) independent of whether they are subitaneous or resting. This is enough to make the Calanoida eggs (about $10^4$–$10^6$ $m^{-2}$ of bottom area) more abundant than those of Rotifera (about $10^4$ $m^{-2}$) and Cladocera (about $10^3$–$10^5$ $m^{-2}$) in sediment assemblages (Hairston 1996).

Among some marine Calanoida, the eggs that are genetically programmed to rest (diapause eggs) are sometimes indistinguishable from subitaneous ones, as is commonly the case among freshwater species. Grice & Marcus (1981) suggested that in such cases, resting eggs can be identified only by their typical delayed hatching, which they show even if exposed to suitable conditions. Uye (1985) based the identification of egg types in *Acartia clausi* (which does not have resting eggs morphologically different from subitaneous ones) on this approach. However, Belmonte (1998a), Castro-Longoria & Williams (1999) and Castellani & Lucas (2003) detected chorionic structures (tubercules, ridges or both) on apparently smooth resting eggs of neritic Diaptomoidea, albeit only observed by scanning electron microscopy (SEM). In any case, many marine Diaptomoidea produce diapause eggs that are morphologically distinct from the subitaneous ones (e.g. Sazhina 1968, Santella & Ianora 1990, Ianora & Santella 1991, Belmonte 1992, 1997, Belmonte & Puce 1994, Castro-Longoriab & Williams 1999, Onoué et al. 2004).

In these more common cases, diapause eggs show spines and evident processes on the surface (the chorion). Many species also show evident chorionic processes in some subitaneous eggs of their clutches (Hansen et al. 2010), but generally the diapause eggs are never smooth. In one case, smooth diapause eggs of *Paracartia latisetosa* have been reported among the more common spiny ones by Posi & Belmonte (2011), but the authors demonstrated that this was due to a tendency of some diapause eggs, laid as spiny, to lose their external spiny covering in the environment. Morphological processes on the chorion of subitaneous eggs include small tubercles that are invisible under a compound microscope in the case of *Pteriacartia josephinae* and *Acartia adriatica*, short and tiny spines in *Paracartia latisetosa* and *Acartia tonsa,* long and thiny spines in *Acartia italica* and long, thick and branching spines in *Centropages typicus*. In all these species, however, the general rule is that there are more abundant and robust spines on the chorion of diapause eggs than on subitaneous ones (see Belmonte 1997, and Plate 2)

Subitaneous and diapause eggs do not differ in terms of morphology alone. Wang et al. (2005) noted that the dry weight of subitaneous eggs in *Centropages tenuiremis* was substantially less than that of diapause eggs, as was the lipid, protein and carbohydrate content. The levels of aspartic acid, glutamic acid, glycine, methionine, isoleucine, leucine, norleucine, lysine, ammonium chloride and arginine were significantly higher in diapause eggs than in subitaneous ones.

Belmonte et al. (1997) noted that spines are typical of marine species (being absent in freshwater ones) and suggested that this trait could be an adaptation to marine coastal habitats. First, unlike freshwater species, most marine Diaptomoidea have no ovisacs and lay their eggs individually and directly in the water. Spines on the chorion could have evolved to retard the sinking on the bottom (often hypoxic) water layers commonly found in confined coastal environments (Gaudy 1971, Sazhina 1987). This delay favours the early embryonic development, which needs oxygen, before entering the insensible diapause state. The hypoxic conditions recurring in bottom mud and water of confined environments are not suitable for embryonic development or for egg hatching (Lutz et al. 1992). A delayed sink may allow the spiny eggs to complete early embryonic development and to enter diapause before reaching the anoxic bottom. Here, the resting eggs can wait for the seasonal restoration of oxygen concentrations suitable for hatching. In addition, chorionic spines of diapause eggs can protect the egg surface from scraping by mineral particles in the sediment, enlarge the communication surface between the inside and outside of the egg and probably avoid ingestion and wall damage by predatory species (Belmonte et al. 1997).

As already reported for Ciliophora (Foissner et al. 2007) and some Dinophyceae (Kokinos & Anderson 1995, Mertens et al. 2011), the number and length of spines are not constant, even within

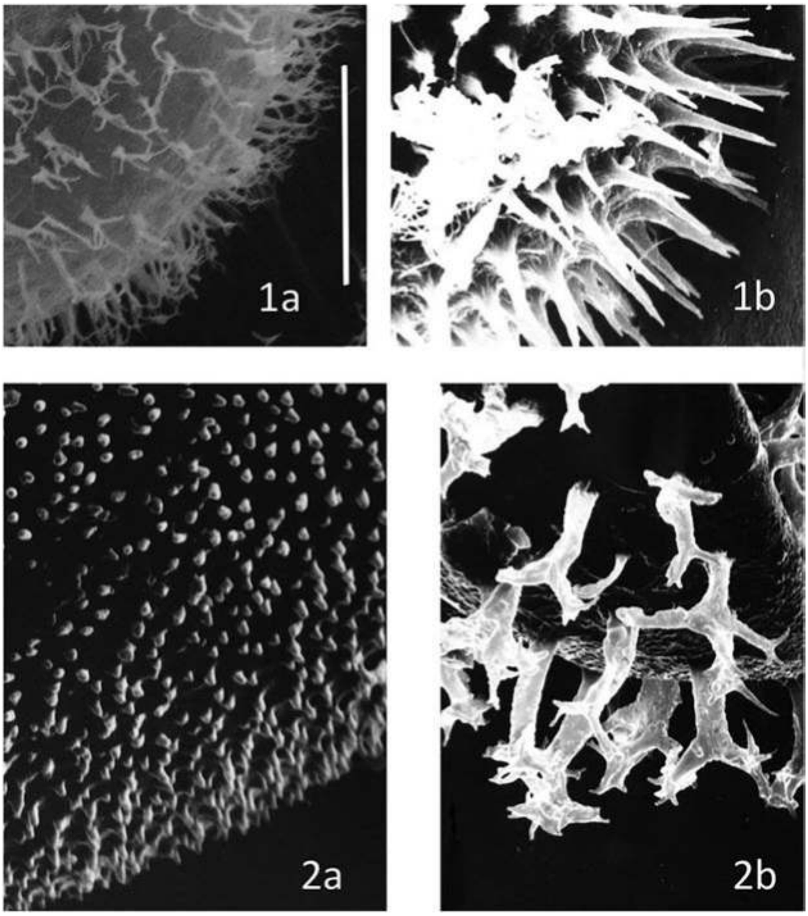

**Plate 2** Surface sculptures of Calanoida resting eggs (original photographs, coastal basin of Acquatina, South Adriatic Sea, 2002). (1) *Centropages ponticus* (a) subitaneous egg; (b) resting egg; (2) *Pteriacartia josephinae* (a) subitaneous egg; (b) resting egg. Scale bar 20 = μm.

the same species. Among Calanoida, there is a continuum of measurements between the minimum and the maximum extremes, which generally correspond to various development destinies (see Belmonte 1992, Hansen et al. 2010).

Due to the spines, Calanoida eggs in recent marine sediment were initially interpreted by micropalaeontologists as fossil cysts of Dinophyceae, and for this reason, they were reported as ‘hystrichospheres’ (West 1961). The birth of Calanoida nauplii from these cysts (McMinn et al. 1992), however, has definitively resolved this puzzle.

On hatching, Calanoida eggs (both subitaneous and diapausal) open along an equatorial fracture line, producing two hemispherical parts. The fracture of the outer envelope happens as a consequence of enhanced internal hydrostatic pressure and is not due to mechanical action by the organism within, because the nauplius is still enveloped in a thin birth membrane when it exits the egg envelope.

Due to intraspecific morphological variability, it is still difficult to identify to what species resting eggs belong. In fact, some spiny patterns are not as typical as proposed (e.g. Belmonte et al. 1997, Belmonte 1998a,b), but rather vary with each species (or even each clutch), as reported also in other taxa (Mura 1986, Foissner et al. 2007), and appearing as adaptive and even inducible by the environment (Dumont et al. 2002). Spines, however, are never rigid, and Santella & Ianora (1992) demonstrated that they elongate themselves on the chorion surface only after laying eggs.

## Methods of collection, identification and investigation

Although plankton cysts were already known from the open ocean (Meunier 1910, Reid 1978), their accumulation in bottom sediments suggests that it is fundamental to consider such a compartment in any study on plankton demographic fluctuations. Reid (1978) reported interesting abundances of cysts in the open sea with the Continuous Plankton Record program, but the low species richness and abundance of specimens allowed him to admit that the large aggregations of cysts in bottom sediments are the result of unknown mechanisms being not explainable by the low number found in the plankton. Among the bottom sediments, those richest are mainly from confined coastal areas, where weak horizontal transport of water masses allows the rapid sedimentation of newly produced resting stages (or the deposition of those transported from elsewhere) towards fine sediment bottoms (see Lindley 1990, Genovesi et al. 2013, as two examples). As a general rule, the finer the sediment, the more abundant the cyst assemblages are. This is because in the water column, cysts behave like the finest sediment particles: they are incapable of active movement and tend to settle towards the bottom in weak hydrodynamic conditions (Anderson et al. 1985b). Sinking cysts replenish the cyst bank, ensuring the persistence of the species in the environment (see section "Ecological implications: resurrection ecology" of the present review, for more information). An effective study of the cyst bank of an area, therefore, must take account of the granulometric features of the sediment, possibly with reference to previously conducted surveys, in order to select the best sites to investigate.

Several tools can be used to collect sediment (Figure 6). The choice depends on the aims of the study. Box-corers, multicorers or gravity-corers must be used for taking quantitative samples, limiting the use of grabs to qualitative sampling and germination experiments. In shallow basins, SCUBA diving can be very effective because it enables direct observation of the sea floor, with the

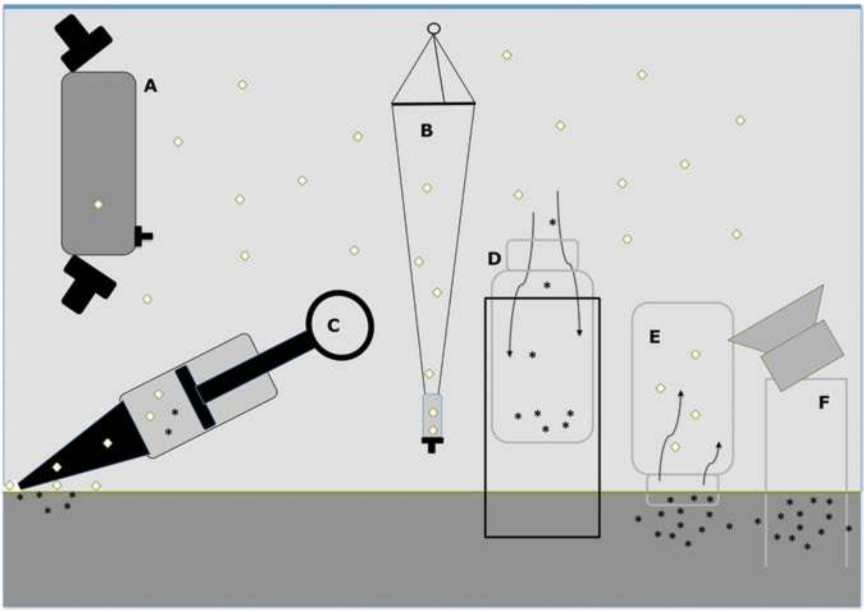

**Figure 6** Sampling devices (exemplified) for collection of marine plankton (white rhombi) and their resting stages (black asterisks). Each device is accompanied by (in brackets) the material collected. Marine plankton: (A) Niskin bottle (Phytoplankton); (B) plankton net (Zooplankton). Resting stages: (C) sucking device for sediment-water interface (hyperbenthos); (D) sediment trap (sinking material); (E) inverted traps (hatchlings and organisms leaving the sediment); (F) sediment corer (sediment with resting stages inside). (A) & (B) also collect resting stages in the water column if the collection is carried out during their production.

only consideration being the need to avoid sediment resuspension (Fleeger et al. 1988). Box-corers, multicorers and gravity-corers are obviously needed in the case of deep basins, and hand-corers in shallow basins, in particular for stratigraphic studies. After collection, sediment must be stored at low temperature in the dark until it can be processed in the laboratory, in order to avoid uncontrolled germinations.

A method that helps to minimise the presence of mineral particles, as well as providing an indication of the flow rate of cysts toward the bottom, is the use of sediment traps. These are positioned well below the water surface in order to collect the production of the overlying water column, but well above the bottom, to avoid collecting resuspended material (for an example, see Price & Pospelova 2011).

Concerning the extraction of cysts from sediment, a great variety of methods have been tested, and again, the choice depends on the aims of the study. For example, when detailed information on the structure of the cyst bank is needed, it is better to adopt simple procedures, such as the use of ultrasound to disrupt sediment particles, followed by fractionated filtration to separate the size classes, roughly corresponding to Protista (20–75-μm) and Metazoa (75–200-μm) cysts (see Rubino et al. 2000).

When the study requires high taxonomical resolution, filtration can be combined with density gradient centrifugation (see Bolch 1997 for dinoflagellates; Onbé 1978 for copepods). Lukic et al. (2016) demonstrated that the sugar flotation method has no effect on the hatching success of Cladocera resting eggs. Notwithstanding, any nonvisual extraction of cysts from sediments always leaves the possibility that the final data on cyst concentration has been modified by this method and does not reflect reality. In some cases, chemicals of varying efficacy are used in order to dissolve sediment particles and obtain a clean assemblage of benthic microorganisms and cysts, at least those with organic walls (Matsuoka & Fukuyo 2000). However, the density gradient centrifugation method probably removes cysts from the final sample portion, which is to be analysed, and the use of chemicals can destroy the wall of many cyst types. Acids especially destroy calcareous cysts, but they may reveal the presence of an inner, organic wall. Yamaguchi et al. (1995) showed that Dinophyceae cysts are best identified under epifluorescence microscopy, without density gradient centrifugation, after fixation of natural sediment samples with glutaraldehyde and methanol and subsequent staining with the fluorochrome primuline. Ichinomiya et al. (2004) found that Ciliophora cysts were clearly distinguished by epifluorescence in natural sediment after simple fixation with glutaraldehyde. However, the fixative makes it impossible to investigate cyst germination and is useful solely for the numerical evaluation of cyst assemblages.

Analyses of encysted communities may also be carried out without extracting cysts from the sediment, but instead waiting for them to germinate from sediment that can be incubated as a slurry after sonification and sieving (Lewis et al. 1999, Persson 2001). This method enables the size of the viable fraction of cysts in the sediment to be determined and rare species to be discovered. Quantitative data on the potential for recolonisation of the pelagic compartment by different species (Rubino et al. 2017) may also be obtained.

Methods used to capture newly produced cysts involve the collection of sinking material from the water column. In this case, sediment traps make it possible to estimate the flow rate of cysts sinking towards the sediment over varying time periods. Ning et al. (2008) proposed a Coconut Fibre Mat (CFM) to capture zooplankton resting stages. According to these authors, the method guarantees clean samples of resting stages that are immediately identifiable under a microscope and ready for rearing and hatching purposes.

Given the interest in the ecology of benthic-pelagic coupling, many researchers have used inverted traps, not to collect particles sinking downwards, but to capture hatchlings derived from sediment cyst assemblages (e.g. see Ishikawa et al. 2007 for microalgae; and Naess 1991, Jiang et al. 2004, Engel 2005, and Sichlau et al. 2011 for Calanoida).

Although they do not seek to establish the actual derivation of the nauplii (nauplius dormancy is never considered, and it is assumed that they result from egg hatching in all cases) these methods give an accurate estimate of the rate of naupliar recruitment per time unit. At present, only Harpacticoida and Cyclopoida (among Copepoda) are thought to enter diapause or dormancy as juveniles or nauplii in the sediments. The possibility of Calanoida nauplii slowing or stopping their development due to unfavourable conditions after hatching has not been demonstrated.

Raw analysis of samples, for both qualitative and quantitative purposes, is carried out under conventional light microscopy (i.e. bright-field, differential interference contrast and phase contrast) but polarised light microscopy also has been proposed as being useful in the identification of dinoflagellates (Reid & Boalch 1987). A 200×–320×–400× magnification is commonly used for Protista cysts, and a 100 × magnification is used for Metazoa resting eggs. Confocal laser scanning microscopy (CLSM) and digital optical microscopy (DOM) have been applied to cyst analysis only recently. They allow researchers to better investigate morphological features and provide high quality and high resolution digital images together with 3-D reconstructions of resting stages. Lastly, SEM and TEM provide far more information, although the equipment and analysis costs are high.

Cyst types can also be identified by molecular tools. In a comparative study of morphological and molecular methods, the diversity of marine Ciliophora was found to be higher when using the latter (Doherty et al. 2010). Montero-Pau et al. (2008) declared as easy and inexpensive the DNA extraction from plankton resting stages, with HotSHOT for polymerase chain reaction (PCR) amplification. Lindeque et al. (2013) defined as easy the recognition of morphologically nondistinguishable eggs of Acartiidae in the sediments of Tau Lagoon (France), if based on the description of the common metazoan DNA barcoding gene mtCOI.

In addition, the presence of resting stages in the life cycle of many toxic Dinophyceae species has led to the development of PCR assays, in order to monitor the presence of cysts in the surface sediments of areas impacted by harmful algal blooms (HABs). Erdner et al. (2010) obtained results with this technique that was comparable to those derived from primuline staining, but only for very recent cysts (those present in the first 1–2 cm of sediment). For deeply buried cysts, PCR gave significantly less information about the cyst assemblage. The method remains encouraging, however, because it can simultaneously identify and count cysts, producing a significant time gain.

It should be considered, however, that molecular methods, at present, give a result relative to the diversity of just one gene (e.g. the mtCOI), and this is unlikely to correspond to the species richness of a community because each taxon is expected to show a different degree of variability for the same gene.

In many cases, identification to the species level is possible only by observing the active stage. Moreover, the direct link between active and resting stages is critical for understanding the life cycle of each species. Germination and encystment experiments are useful in order to demonstrate this link and to confirm the identification, whether this is done by observing the cyst or the active stage. In unicellular organisms, the cyst hatches a motile cell that is generally identifiable without waiting for its development. However, a rearing experiment makes it possible to produce cysts from active stages and thus confirm species identification by completing the full life cycle. In the case of Metazoa, with the exception of Rotifera, the resting egg hatches into a motile stage (juvenile or larva, according to the type of postembryonic development), which is not immediately identifiable at the species level. In such cases, identification may require up to 1 month of rearing in the laboratory (as in the case of Calanoida).

On the other hand, single specimens (females) may be reared independently to obtain resting eggs for descriptive purposes. Suitable females can be obtained in any period of the year. If they are gathered in the prediapause season, resting eggs can be obtained without stimulation (Belmonte 1992, Belmonte & Pati 2007); otherwise, females can be artificially induced to produce resting eggs by varying the photoperiod, the temperature or the quality and quantity of their food.

In many cases, the search for resting stages has revealed the existence of species never before reported for that site. Orlova et al. (2004) added 15 species to the list of Dinophyceae found along the east Russian coast, simply by isolating and waiting for the germination of cysts collected from the sediment of that area.

Whatever approach is used to ascertain the size of cyst assemblages, water column sample collection should not be neglected. Indeed, species producing resting stages represent a variable percentage of the plankton assemblages (depending on the degree of confinement of the coastal system), but never the totality. In addition, although alternative findings of the same species as both active forms (in the water column) and cysts (in the sediment) in successive seasons are possible, they are rare, and an integrated sampling approach to establishing the species richness of each area is recommended (Moscatello et al. 2004, Rubino et al. 2009).

## Rest features

### *Types of rest*

According to Gyllström & Hansson (2004), rest (also known as *dormancy*) encompasses both diapause (stopped development) and quiescence (delayed development). In our opinion, these are the correct terms to use, distinguishing between two aspects of a single phenomenon—that is, dormancy (Figure 7). *Aestivation, hibernation, lethargy* and other similar terms are common; they refer mainly to induced rest, when an unsuitable situation occurs and is adopted in different ways based on the taxa involved. Phytoplanktonologists use the word *dormancy* as a synonym for *diapause* (e.g. Bravo & Figueroa 2014, for Dinophyceae), inheriting it from the terminology used for higher plants (see Baskin & Baskin 1989). The term *diapause*, originally created for insects (Wheeler 1893), could be usefully adopted to refer to all planktonic cyst-producers, including phytoplankters, to indicate a genetically programmed phenomenon, characterised by two periods: insensitive and competent (Mansingh 1971; Grice & Marcus 1981). The former is considered necessary for the completion of physiological maturation (Pfiester & Anderson 1987), and its length is species-specific, varying from hours to months, at least for Dinophyceae. During this time period, the organism does not perceive external stimuli and rests even if external conditions become appropriate for active life. During the second period, the resting organism can awake in the presence of positive external stimuli (Rathaille & Raine 2011).

According to Hallegraeff et al. (1998), there may be two kinds of diapause. A long-term diapause, acting as a true overwintering strategy (dependent on the astronomical date and not on climate) controlled by an endogenous clock, and a short-term rest (not properly diapause), acting as a rapid-response strategy to deal with sudden changes in the environment, allowing the species to shift quickly between pelagic and benthic habitats. The former could be used by species living in deep waters, where cysts must face more constant temperatures and light conditions (Anderson 1998),

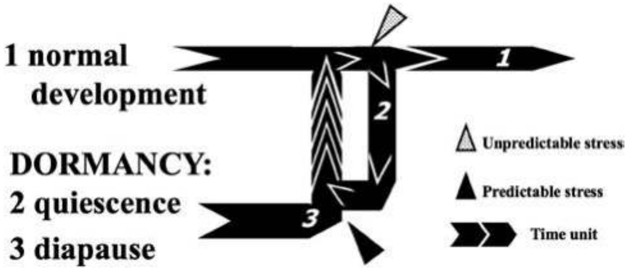

**Figure 7** Graphical comparison between quiescence (path 2) and diapause (path 3). Quiescence is a response to a stress situation. Diapause anticipates the occurrence of a stress situation. (Modified from Giangrande, A. et al. 1994.)

while the latter may be more advantageous for neritic strains that need to be able to perceive stimuli in a more competitive way. This is the case of the Dinophyceae species *Alexandrium catenella,* whose mandatory dormancy period ranges from 24 h to months, depending on the water depth and latitude (Hallegraeff et al. 1998, Figueroa et al. 2005, Tobin & Horner 2011).

In contrast, in the case of quiescence, encystment is triggered by exogenous factors—that is, adverse environmental conditions—and the organism's development or some vital functions slow down. Unlike diapause, this state is immediately reversed by the restoration of suitable conditions (see Giangrande et al. 1994, and Figure 7). In this context, each species can undergo a quiescent stage in any moment of its life cycle, while as a general rule, diapause is associated with precise stages (cysts and spores among Protista, and embryonic early stages among the most common planktonic Metazoa) (Alekseev 1990).

Currently, however, a more complex picture is emerging, at least for Bacillariophyceae and Dinophyceae. Indeed, most Bacillariophyceae resting spores are produced asexually (McQuoid & Hobson 1996) and show high respiration rates and photosynthetic activity when suddenly exposed to light after a period spent in the dark (e.g. in the case of resuspension from the sediment and subsequent resinking) (French & Hargraves 1980). In addition, they do not have a mandatory, insensitive resting period (Hargraves & French 1983). On the other hand, among Dinophyceae, there are species that asexually produce true resting stages (Kremp & Parrow 2006) and species that are capable of sexually forming cysts with a short rest (Figueroa et al. 2006), in response to an increase in temperature and shortage of nutrients.

## *Triggering of rest initiation (encystment)*

Many cues can induce dormancy, depending on the season, but the only one common to all cyst-producing groups seems to be day length (i.e. photoperiod) (see Alekseev 1990, 2007 for Crustacea; Kamiyama et al. 1995 for Ciliophora; McQuoid & Hobson 1996 for Bacillariophyceae; Sgrosso et al. 2001 and references therein for Dinophyceae).

Bacillariophyceae enter dormancy under conditions of nutrient depletion, particularly when this concerns nitrogen. However, *Chaetoceros pseudocurvisetus* can form resting spores only if a large amount of silica is available (Kuwata & Takahashi 1990), because these dormant stages have heavily silicified frustules, otherwise a part of the population forms resting cells (Kuwata & Takahashi 1999). *C. anastomosans* requires high salinity (Oku & Katamani 1997).

In cultures, Dinophyceae show very complex interactions involving at least three factors: temperature (for which there may be a narrow optimal window) (Anderson 1998, Ellegaard et al. 1998), day length and nutrient concentration, of which the latter seems to be by far the most important (Sgrosso et al. 2001, Nagai et al. 2004, Kremp et al. 2009). Indeed, in this group of planktonic Protista encystment is normally a consequence of the induction of sexual reproduction (von Dassow & Montresor 2011) and in most species this is triggered by nutrient shortages, normally at the end of maximum asexual reproduction in the water column. Many studies based on laboratory experiments have shown a species-specific response to nitrogen and/or phosphorus limitation that includes the production of hypnozygotes (Shikata et al. 2008). Figueroa et al. (2006), in a very fascinating study, demonstrated that Dinophyceae life cycles could be considerably more complex than the oversimplified holoplanktonic scheme classically described in textbooks. The sexually produced planozygotes of *Alexandrium taylorii* can evolve into short-term or long-term cysts or undergo direct division depending on the relative concentrations of nitrates and phosphates in the culture media.

Other exogenous factors may play important roles in the encystment of Dinophyceae, most importantly shifts in temperature (Anderson et al. 1985a), but also salinity (Zonneveld & Susek 2007), oxygen, iron (Doucette et al. 1989), bacteria (Adachi et al. 1999, Mayali et al. 2007), overcrowding and chemical pollution as well (Triki et al. 2017; Rubino et al. 2017). Many studies have focussed on the possible concomitant role of these factors, and the picture is further complicated by evidence of contrasting ecotype behaviours in different environments (e.g. in coastal versus deep oceanic waters) and at different latitudes (Bravo & Anderson 1994, Ichimi et al. 2001). In any case, according to Figueroa et al. (2011), the reality emerging from field studies could be even more complex than the virtual situation inferred from laboratory cultures. Recently, the use of sediment traps to catch newly produced cysts has allowed the monitoring of cyst production over time. Evidence of continuous encystment, albeit at low densities, by *Alexandrium minutum* (Garcés et al. 2004) suggests that nutrient dynamics is not a major factor inducing dormancy in this species. Moreover, the results of other studies have demonstrated that encystment is favoured by good growth conditions (Olli & Anderson 2002, Figueroa et al. 2005) and, because it occurs at the end of the population bloom (Rengefors 1998), it suggests that it is caused by life-cycle transitions rather than exogenous factors. Kremp et al. (2009) distinguish between triggers (the proximate causes) and stressors (the ultimate causes) of encystment. The former is a signal of the advent of the latter, such as the increase in temperature which heralds the arrival of spring with low nutrient conditions, which, for a coldwater species, represents the unfavourable season. This topic is directly related to the concept of an endogenous clock—that is, a genetically controlled mechanism capable of activating diapause (Boero, 1994; Anderson, 1998).

Among Rotifera Monogononta, overcrowding (which raises the concentration in the water of chemicals produced by the organisms) seems to be just as important as external cues (Gilbert 1974, 1992, 2007). Indeed, the diapause eggs are only the fertilised ones, and sexually active female Rotifera appear in the population only during periods of high concentrations of parthenogenetic generations. In such cases, the production of diapause eggs is sustained by high food availability and allows the mothers to store high lipid content in the eggs. Due to the extremely reduced metabolism of the diapause eggs, lipid storage is clearly an ideal endowment for the hatchlings. This rule is also valid for Copepoda, at least in the case of *Eurytemora affinis,* whose females produce resting eggs in overcrowded conditions (Ban 1994). In Dinophyceae, only the production of temporary cysts (quiescence) in *Scrippsiella acuminata* is reported as due to allelopathic effects (Fistarol et al. 2004; Tillmann & Hansen 2009), while hypnozygotes (diapausal) are produced by *S. acuminata* and *Gyrodinium instrianum*, and temporary cysts by *Heterocapsa circularisquama* as a response to overcrowding (i.e. cell contacts) (Uchida 2001).

Other than single stimuli, synergistic effects have to be considered. Among Crustacea, photoperiod seems to combine its role with that of temperature and overcrowding (Alekseev 1990).

The start of the diapause can be a clearly identifiable moment during the year (as in *Labidocera aestiva;* see Marcus 1982), or it may be characterised by such a high level of variability that a genetic programme should not be considered responsible. In many species of the copepod family Acartiidae, each single female can produce subitaneous and diapause eggs contemporaneously (Onoué et al. 2004, Pati & Belmonte 2007), and females of the same population show oscillations in the relative abundances of the two types of eggs over a relatively long period (e.g. some months).

Even among Rotifera, the message deriving from the number of asexually produced generations may not be completely obeyed by all parthenogenetic females within the same population, although they perceive the same stimuli. These observations suggest that the genetic character of the phenomenon is subjected to high variability to allow the populations to better adjust physiologically to unpredictable environmental variations.

The hostile period can be either in summer or winter, and it depends on the geographical location (Marcus 1979, Uye 1985). Some species are seasonally present only at certain latitudes and present year round at others. At latitudes where the unfavourable season is completely absent, some of these species maintain the ability to produce resting eggs, while other species lose this trait (Marcus 1979, Ohman et al. 1998).

## *Triggering of germination (excystment)*

Given the presence of a period of obligatory dormancy (the refractory phase), diapause in resting eggs should be considered as part of their unchangeable destiny. However they are able to perceive the moment of their reactivation, which is stimulated by external environmental factors (Kasahara et al. 1974, Uye 1985, Marcus 1987, Alekseev 1990). This sensitivity is activated only after the refractory phase is concluded. From this point of view, there are similarities with quiescence eggs (for terminology differences, see Grice & Marcus 1981), which, in contrast, are not programmed to require a resting period but can rest if unfavourable conditions require it.

In Dinophyceae, the exit from diapause and consequent germination are controlled or regulated by both exogenous and endogenous factors (Tobin & Horner 2011). The latter includes a mandatory dormancy period and the presence of a biological clock (Castell-Perez et al. 1998, Rengefors & Anderson 1998), which is incapable of triggering germination but capable of preventing it during untimely periods (Matrai et al. 2005). Both exogenous and endogenous factors may be related to variables such as their belonging to a particular geographical strain and the depth of the water where the cysts germinate.

Among the exogenous factors acting on germination, temperature and photoperiod seem to be the most important (Itakura & Yamaguchi 2001, Kim et al. 2002), but some uncertainty exists as to the exact nature of their action. Notwithstanding some studies showing contradictory results, many data generally indicate temperature as having the greater impact on germination rate, and temperature and photoperiod as enhancing development once germination succeeds (Kirm et al. 2005, Rathaille & Raine 2011). In polar and subpolar areas, due to low light conditions and sea-bottom temperature, *in situ* cyst beds could represent situations without a future, i.e. cysts have not the possibility to germinate. Richlen et al. (2016) hypothesised that in this case, blooms may be derived from advected populations, originating from nearby fjords and bays.

Raphidophyta and Bacillariophyceae appear to differ from Dinophyceae in this regard, although few field studies are available, and thus any attempt to define a general rule may be premature. Cyst germination in the Raphidophyta *Heterosigma ahashiwo* is strongly controlled by temperature (Shikata et al. 2007), while a photoperiod plays a role in controlling the fate of the inoculum once germinated. Indeed, cysts can germinate in the dark, but the survival of the new active cells greatly decreases. For resting cells of the Bacyllariophyceae *Skeletonema costatum* and *Leptocylindrus danicus*, the pattern seems to be the opposite; a photoperiod is the trigger of germination (Hollibaugh et al. 1981, Shikata et al. 2008), while temperature influences the survival of the new planktonic cells (von Stosch & Fecher 1979, Shikata et al. 2008).

Salinity (Kim et al. 2002, McQuoid 2005), oxygen (Keafer et al. 1992, Kirm et al. 2005), nutrients (Binder & Anderson 1987, Figueroa et al. 2005), turbulence (Kremp 2001, Kirm et al. 2005) and bacteria (Adachi et al. 1999) can also play a role in germination in Dinophyceae, but, as seen with encystment, they interact, creating many scenarios for the various species. This picture is similar for the other main plankton groups.

Engel (2005) discussed the role of temperature, photoperiod and dissolved oxygen on the hatching of Calanoida eggs. He found inhibition of hatching in many cases but was never convinced of an effective triggering action, which appeared to be relatively independent of external conditions. Kamiyama et al. (1995) showed a rare example of irradiance being responsible for the germination of Tintinnina cysts. However, this observation needs to consider the not-infrequent case of cysts sinking to a dark bottom or being covered by sediment particles, which makes useless this sensitivity and suggests, as for Calanoida, the existence of an internal trigger independent from external stimuli.

## *Timing and duration of rest*

Given the passivity of diapause eggs, the duration of rest is likely to be determined by the cyst-producing organism (the grandmother among Rotifera and Cladocera, the mother among Copepoda, and the active stage among Protista). Among Metazoa, the maternal role in reactivation automatically derives from the programming of the refractory phase duration. In such cases, external stimuli merely play an interfering role (e.g. as reactivation inhibitors), which affects but not determines an already-programmed reactivation time (Marcus 1987; Ban 1992; Belmonte & Pati 2007). Marcus (1987) found different diapause durations in eggs produced by co-specific females in different seasons. Ban (1992) was the first to clearly speak of a 'mother effect' in *Eurytemora affinis*, finding that ovogenesis of potentially fertile females were affected by temperature and photoperiod when they were still at the nauplius stage.

In *Paracartia latisetosa*, Belmonte & Pati (2007) demonstrated that the mother sets the clock for the duration of diapause in each egg. Diapause eggs obtained in the laboratory from mature females were maintained under constant conditions until hatching. Hence, no temperature or photoperiod variation could affect their diapause termination. Eggs produced in August and December both hatched on average in the same period, thus suggesting that diapause interruption and synchronous hatching could not have been induced by environmental conditions. The environment role is one possibility to prohibit egg hatching at the end of diapause, but the hatching moment remains genetically programmed and independent from external conditions.

Regardless of the season (mainly photoperiod and temperature) or overcrowding that determines the start and duration of diapause, resting eggs hatch at the end of their refractory phase in the presence of adequate oxygen concentration. Calanoida diapause eggs do not hatch in hypoxic environments even if the refractory period has terminated. Furthermore, oxygen seems to be absolutely essential for the complete development of embryos (Lutz et al. 1992, Engel 2005).

Cysts and resting eggs may accumulate on the bottom of water basins where the photoperiod cannot be perceived and where temperature variations may be insignificant. Such sea beds, especially in deep and confined coastal sites, may be periodically hypoxic or anoxic due to the absence of water mixing and photosynthesis (oxygen-producing), at least in some periods of the year. This, as a consequence, can inhibit the resumption of the oxidative metabolism of embryos that are awaking from diapause but have not hatched yet. In this framework, the spiny surface of resting eggs has been considered as useful for the entrance into diapause. Indeed, by delaying egg sinking, the parachute effect determined by the presence of spines could allow each egg to reach the bottom only after the embryo initial development, which needs high oxygen levels. This hypothesis is suggested by a study on Calanoida, where Lutz et al. (1992) demonstrated that low oxygen concentrations (typical of bottom mud in confined areas) during initial embryonic development impede correct entrance into diapause.

In addition to low oxygen concentration, egg hatching can be inhibited by temperature (the case of Cladocera in the Onagawa Bay is described by Komazawa & Endo 2002). However, synchronous hatching can be triggered by external stimuli, as in the case of Cladocera eggs in the Guanabara Bay (Mugrabe et al. 2007), but it can be delayed or staggered (nonsynchronous), also for endogenous reasons (Marcus et al. 1994). This might even be the result of a deliberate strategy by the species, which engineers non-synchronous hatching of the cysts so as to distribute the risk of unsuccessful hatching over time.

Notwithstanding the rest period, the metabolism of Rotifera cysts is not completely depressed, and embryo cells profit from the resting period by repairing damaged portions of DNA, thus obtaining hatchlings with greater fitness than that of the generation they derive from (Ricci & Fontaneto 2009). Tunnacliffe et al. (2005) found that these freshwater Rotifera undergo dehydration/vitrifying by producing small hydrophilic proteins. This type of metabolic vitrifying, however, has not been ascertained in the diapause of marine species, which never leave the water.

Among Crustacea, the metabolism of cysts in the refractory phase is at undetectable levels. This is obtained by deep dehydration of the embryo and/or substitution of water molecules with trealose. Clegg (1997) attributed the phenomenon in *Artemia* to the presence of endocellular chaperon proteins that vitrify the entire molecular apparatus with reversible alterations.

In both Rotifera and Crustacea, the molecules involved are simple, they are not exclusive to particular taxa, and chaperon proteins are a common molecular tool in living organisms.

### *Passive defence*

Generally, the cyst wall is thicker and more resistant than the covering of the corresponding active stage. This is considered sufficient to protect the diapause subject, although Stabili et al. (1999) found lysozimelike and trypsinlike activity on the cyst wall of *Artemia franciscana*, highlighting the existence of passive immunity, as well as mechanical defence, in that particular resting stage. In addition to the physical barrier and the possible immunological defence, the environment could contribute to the preservation of resting stages. A chemically reducing and anoxic environment (such as the muddy bottoms of confined coastal areas) is hostile to the majority of living organisms, thus preventing other species from damaging or preying on cyst assemblages (Persson, 2000), while the chemical aggression of such an environment does not in itself damage cysts.

The resistance capability of resting stages (and the duration of their rest period) has been ascertained in many cases. Pati & Belmonte (2003, 2007) showed that the most common disinfectants (such as those typically used in aquaculture) have only a partial effect on cyst germination in certain species of Dinophyceae, Ciliophora, Rotifera and Crustacea. Raikow et al. (2006) found SEACLEAN® (menadione) to be effective in impeding cyst germination, but the sensitivity of the product to light and its ineffectiveness on cysts buried in the sediment mean that it is still far from being a comprehensive threat.

Due to their generalised resistance, cysts can pass throughout the gut of Metazoa with no consequences for their viability. Cysts and resting eggs have been hatched in the laboratory after passage through the gut of birds (Figuerola & Green 2002), polychaetes (Marcus 1984, Kremp et al. 2003), fishes (Redden & Daborn 1991) and small crustaceans (Montresor et al. 2003, Kuwata & Tsuda 2005).

The survival capacity of cysts in bottom sediment has been evaluated as decades in Copepoda (Marcus et al. 1994, Jiang et al. 2004, Dahms et al. 2006), with some Protista cysts able to hatch after 100 years (Belmonte et al. 1999, Härnström et al. 2011, Ribeiro et al. 2011, Ellegaard et al. 2016) and some freshwater Calanoida eggs after 300 years (Hairston et al. 1995).

## Evolutionary implications of rest

As a life-history trait, reproductive plasticity is fundamental for survival in variable environments. The shift from the production of normal to diapause eggs can be considered an indicator of phenotypic plasticity (Giangrande et al. 1994). In a study of 167 Crustacea, Hairston & Càceres (1996) proposed that diapause is more common among species inhabiting variable or temporary environments (such as inland waters) than among species in stable, large environments. Inland, temporary waters have been conquered by primitive Crustacea, whilst more recently evolved ones remain in the open sea. Hairston & Bohonack (1998) considered the production of resting eggs among Calanoida as a key tool in the conquest of inland freshwater. This claim, however, is not consistent with the fact that all the other freshwater Copepoda (Harpacticoida and Cyclopoida) do not appear to have resting eggs but are able to rest during other life-cycle stages (i.e. larva, juvenile, adult). Thus, the resting cyst/egg is not the solution, but the rest capacity per se. Marine Calanoida, also have a rest capacity in a copepodite or adult condition (Baumgartner & Tarrant 2017). In freshwater Crustacea (that have incubating devices as egg sacs and ephippia), the resting capacity may be coupled with a form of parental care as a successful adaptation to freshwater. This character may also be responsible for the general absence of spiny surfaces on freshwater eggs. In fact, resting eggs of Centropagoidea are free laid and spiny in marine and smooth in freshwater (Belmonte, 2018).

Cohen et al. (2009) suggested interpreting the organic walled spiny resting stages of early marine Metazoa—the large ornamented Ediacaran microfossils (LOEM) of about 600 million years ago—as spiny resting stages in their life cycle. They also suggest that this feature is truly primitive and would have been indispensable for survival in the shallow hypoxic seas of the Pre-Cambrian era.

Thus, the fact that many phyla show resting stages with spiny surfaces (Belmonte et al. 1997) may be the result not of evolutionary convergence, but of plesiomorphy, if this feature was widely present and common in early Metazoa. The loss of spines, conversely, might be considered a consequence of the evolution of parental care. In fact, it seems that spiny surfaces are particularly common among the cysts or eggs laid free in the water, and they are not common if cysts are contained in specially developed structures (egg sacs in Calanoida, ephyppia in Cladocera or lorica in Tintinnina), carried by the mother (as in Rotifera) or both. However, this is just a suggestive interpretation that needs confirming opinions of many researchers of different taxa.

Undoubtedly, the loss of spines (or their shortening) could also be due to a general size diminution. Oxygen ($\delta^{18}O$) enrichment, as well as the climate in general, were suggested by Finkel et al. (2007) to be responsible for an observed reduction in size of fossil phytoplankton and their cysts from the Cenozoic to the present day. The largest median size corresponds to the warm and highly $\delta^{18}O$-rich Eocene period, and the smallest sizes to the glacial Pleistocene. In addition to a hypothetical anti-sinking role, the morphological differences detectable among the surface features of modern resting eggs may represent the result of the evolutionary divergence of taxa.

The cyst banks in sediment contain cysts derived from overlapping generations of free-swimming organisms. For this reason, at any one time, cyst banks host a wider genetic diversity than is found in water column communities (Gyllström & Hansson 2004). Cyst banks actually produce a generation overlap which, together with environmental fluctuations, can maintain species coexistence in a different interpretation of the so-called Storage Effect of Chesson & Warner (1981).

Rich cyst banks, together with the existence of an extralong diapause (ELD), increase the resilience of each population and enhance the community variability. ELD opens up genetic flows between generations living at distant times. For this reason, it has been described as a delaying factor in the species' evolutionary process (Hairston & De Stasio 1988). When cysts germinate, they introduce genetic variability comparable to immigration from an external source (the 'evolutionary information from the past' of Templeton & Levin 1979, p. 246). Bohonack et al. (2006) confirmed the idea of delayed evolution and suggested that this could result in higher genetic uniformity across populations in each region.

An ELD of phytoplankton cysts can be a powerful strategy for the permanent residence of a population of a species in a region. Estimated as more than 100 years by Ribeiro et al. (2011), an ELD has been proposed as a possible way that photosynthetic marine communities recovered after the asteroid impact at Chixculub-Yucatan and the resulting period of prolonged darkness that occurred about 65.5 million years ago at the Cretaceous-Tertiary transition.

An ELD is the consequence of both environmental conditions and genetic programming. In basins with variable water volumes (mainly freshwater), Ellner et al. (1999) found that the timing of diapause and success of germination from the cyst bank more strongly affects the plankton population than any selective factor acting directly on the active stages. Càceres & Tessier (2003), studying freshwater species, reported that only a portion of cysts produced every year (from 6% to 50% in *Daphnia*) germinate at the first suitable opportunity. The remaining cysts are dormant for varying lengths of time, allowing the population to take advantage of future scenarios. Even smaller percentages of germination (3.5%) were found by Glippa et al. (2014) in the egg bank of three copepods in the Seine estuary (France). This bet-hedging strategy of variable timing of hatching pays off in habitats where conditions occasionally are so bad that recruitment totally fails from the dormant stage pool (Cohen 1966, Seger & Brockmann 1987, Philippi & Sen 1989). Tarazona et al. (2017) demonstrated empirically the existence of the bet-hedging strategy in resting egg production and hatching of the rotifer *Brachionus plicatilis*. In this recent study, populations experiencing unpredictable environmental variations showed an earlier start to resting egg production and a smaller fraction hatched, in comparison to populations reared under predictable variations.

In this framework, diapause duration may simply represent the average value of a distribution (wide or narrow) of many time values, some of them potentially very far apart. ELD is probably responsible for decadal survival (Marcus et al. 1994, Dahms et al. 2006, Sichlau et al. 2011), or multicentennial (Hairston et al. 1995) in the case of Calanoida. In any case, the existence of cyst banks and possible successive injections of propagules of the same population is responsible for the adaptive success of ELD (Hairston 1996). The most adapted genotypes (the ones that produce the most cysts) are repeatedly proposed, even in the absence of suitable conditions, as a means of ensuring the survival of active stages and results in the coexistence of many potentially competitive species (Hairston & Fox 2010).

According to Warner and Chesson (1985) the Storage Effect based on resting stages offers a possible explanation for the coexistence of many species in a single aquatic environment, the need for which had already been highlighted by Hutchinson (1961). Interestingly, both the Hutchinson hypothesis (proximity of bottom and sinuosity of lake shorelines) and the random injection of propagules cited by Hairston & Fox (2010) indicate a need to extend the research field to the benthos, to solve the paradoxical coexistence of many species in the plankton.

Any understanding of the mechanisms of adaptation to variable environments (such as confined coastal waters), as well as the correct interpretation of plankton community dynamics, must take account all the biological aspects of benthic-pelagic coupling. For this to be achieved, the traditional compartments separating scientists of plankton from those of the benthos has to be overcome (Boero et al. 1996, 2004).

## Ecological implications: resurrection ecology

The presence of plankton species in a resting form in ecological compartments different from the water column and yet sympatric with their own active stages, is fundamental to understanding the dynamics of single populations and that of the whole plankton community.

Bottom sediments seem to be the obvious site for accumulation of cysts from the overlying water column, but in cold seas, cysts could also be trapped in a sympagic habitat of the surface ice. Both the benthic and the sympagic compartments are the object of studies due to the existence of complex autochthonous communities (meiobenthos within sediments, sympagic biota within ice), although the nonactive biological components have been disregarded in the past. Dormant biotic pools should instead represent an essential link between activity seasons and are responsible for biomass and energy transfer between ecological compartments.

In both the meiobenthos and sympagic biota, the attention of researchers in the past has mostly focussed on exclusive or typical taxa (i.e. those that are perfectly adapted to local conditions). Pati et al. (1999), however, found that the abundance of cysts in sediment may be even greater than the active components of the meiofauna and proposed the term *Inactive Temporary Meiobenthos* to refer to this fraction. Such abundant, yet disregarded, organisms allowed Marcus & Boero (1998) to propose the term *Supply-Vertical-Ecology* to refer to the processes and implications of recruitment and biomass transfer, mediated by plankton cysts, between the water column and sediments. Such a term was inspired by the supply-side ecology of Lewin (1986) (see also Underwood & Fairweather 1989). That term was successively replaced with the more impactful *resurrection ecology,* proposed by Kerfoot & Weider (2004) (Figure 8).

Confined coastal areas are able to capture and accumulate large numbers of resting stages in their sediment (Belmonte et al. 1995). Cyst production and accumulation are particularly evident during the abundance peaks of plankton populations. Cyst production is likely a consequence of nutrient subtraction from the water during periods of rapid phytoplankton growth. Peak abundances in the water and sediment, however, are always separated by a time lapse, with cyst peaks delayed by 1–2 months with respect to the active stage (Chen et al. 2009).

It is not entirely clear whether the richness of confined coastal areas derives from the abundance of cyst producers that bloom in these areas, or to an accumulation effect of small particles due to the low hydrodynamism, or even to the lack of benthic predators. In open neritic habitats,

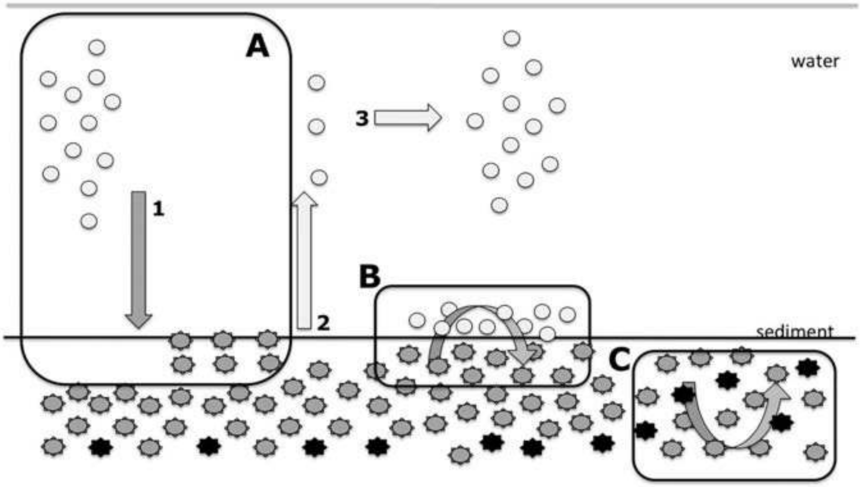

**Figure 8** A schematic diagram of the dynamic interactions of resting stages between the water column and sediment cyst bank. (A) possibly long-lasting exchange; (1) supply from the water column (production by plankton); (2) subtraction in favor of water column (germination); (3) multiplication of active stages (potentially producers of resting stages). (B) Tight and fast exchange; supply-removal (encystment-germination) from/to hyperbenthos. (C) Mixing within the bottom cyst bank.

cyst-producing species are present, but this sediment tends to be coarser (i.e. the area is subjected to high hydrodynamism) and have numerically poorer cyst assemblages. In contrast, confined coastal areas, although with a shallower water column and less oxygenated sediments (due to their limited hydrodynamism), show high concentrations of cysts in sediment. This links the cyst abundance to the size of sediment particles.

According to Cohen et al. (2009), the abundance of cysts in confined environments also could be enhanced by the absence of potential predators, which are poorly adapted to hypoxic sediments. Scheef & Marcus (2010, 2011) found an abundance of resting stages in bottom seagrass beds. In such habitats, the low oxygen content, high summer temperature (which enhances the decomposition of organic matter) and low hydrodynamism (the vegetation acts as a drag on water movements) greatly favour cyst accumulation. It should be pointed out that some spatial situations, not properly identifiable as confined (and thus not typically hypoxic), such as the German Bight and Kiel Bay, show rich assemblages of cysts in sediment (Madhupratap et al. 1996, Engel 2005). Moreover, even in sediment that is hypoxic, cyst assemblages are not necessarily abundant.

Modig & Òlafsson (2001) demonstrated that the amphipod *Monoporeia affinis* can rework sulphide sediment and thus reoxygenate them to a depth of 10 mm, thereby playing an indirect role (through oxygenation and bioreworking) in the germination of cysts. *M. affinis* was cited by Albertsson & Leonardsson (2000) as possibly affecting the recruitment of active stages to the water column because its burrowing activity can drive resting eggs deeper into the sediment. More recently, Viitasalo & Viitasalo (2004) and Viitasalo (2007) demonstrated that Mysida feed selectively only on certain cyst types, thus possibly affecting plankton composition by differentiated subtraction of propagules. Interestingly, the indicated Mysida are planktivorous and probably exploit cyst banks when active stages of their prey are absent from the water column.

In many cases, however, cysts pass through the gut of deposit feeders without consequences for their viability. Marcus (1984) showed that both subitaneous and diapause eggs produced by the copepod *Labidocera aestiva* were capable of surviving passage through the gut of two benthic Polychaeta. Redden & Daborn (1991) even proposed that being preyed upon (with a consequent passage through the gut) could be a strategy for egg-carrying copepods to enhance their reproductive success at the population level because embryos contained in the egg sac of *Eurytemora herdmanni* are not digested by the fish *Menidia menidia*. Finally, the selective predation of egg-carrying females enhances the likelihood that nonmature females will survive and produce their own clutch of eggs.

Bacillariophyceae resting spores have been found undamaged, and even viable, in faecal pellets of Calanoida (Hargraves & French 1983). It is likely that their highly silicified frustules are indigestible to copepods, which may even avoid them during their filter feeding, selectively preferring active cells (Kuwata & Takahashi 1999, Kuwata & Tsuda 2005). Dinophyceae cysts have repeatedly been found in faecal pellets from Polychaeta and Bivalvia (Ichimi & Montani 2001, Tsujino et al. 2002). Kremp et al. (2003) found that gut passage and pelletisation do not substantially reduce the germination rates of Dinophyceae cysts, and may even enhance them. Montresor et al. (2003) even found that passage through the gut of a copepod functioned as a trigger for hatching of Dinophyceae cysts.

Limicole Polychaeta rework sediment, with substantial implications for the overlying water column, similar to the impact of soil reworkers on seed banks in terrestrial forests (Meysman et al. 2006). For example, Giangrande et al. (2002) found that such Polychaeta rework sediment particles (and Dinophyceae cysts that these authors used in the experiments) down to 7 cm below the sediment surface. This reworking leads to rapid burial of newly arrived cysts, but at the same time allows the uplift of deeply buried cysts to the surface.

This reworking of the sediment can also be produced by human activities. Although this field has not been extensively studied, some data (Giannakourou et al. 2005, Siokou-Frangou et al. 2005) suggest that trawling causes the resuspension (and consequently germination) of cysts in the Gulf of Thermaikos. This aspect of the interaction between fishery and cyst banks not only involves resuspension and possible germination of cysts, but also their damage (e.g. the reduction of their germination rate), as demonstrated by Drillet et al. (2014).

Whatever the destiny of cysts in the superficial sediment layer (whether or not they are digested by a cyst consumer), the mechanisms of their subtraction (e.g. germination) are responsible for the characteristic vertical profile of their abundance in the sediment column. Indeed, abundance peaks are typically found just below the most superficial layer (Hairston & Fox 2010, Sichlau et al. 2011). Some findings of abundance peaks at the sediment surface, on the contrary (Dahms et al. 2006), can easily be attributed to a proxy period/episode of massive production from the plankton. In any case, the top layer of sediment is what is most relevant to encystment/germination dynamics, showing strong fluctuations in cyst abundance according to the season (Rubino et al. 2016).

Resurrection ecology is at the basis of the functioning of confined environments (sensu Guelorget & Perthuisot 1992). Although such environments are known to be the most productive on the planet (Odum 1971), for a long time they were believed to depend on marine vivification (sensu Sacchi 1985) for the restoration of biological communities seasonally suppressed by environmental stress. The marine vivification hypothesis assumed the colonisation of a highly productive, although stressed, area from a less productive one, whose biota is not biologically adapted to habitats with such high availability of resources, although periodically stressed.

Today, Resurrection Ecology may explain the reappearance of species in accordance with the seasons; that for many species, they do not depend on neighboring environments (supply-side ecology) but mainly on the bottom sediments of a confined area where they spent the adverse season. Resurrection ecology in confined areas is a typical example of ecological resilience. The plankton of confined environments appear to be autochthonous, and the presence of similar species in neighboring neritic areas is now believed to be the consequence of the export of a species from the assemblages of a confined area, the exact opposite of what was thought some time ago (Figure 9).

The export of cysts from production areas involves other marine habitats as well. In fact, cysts have been detected in deep-sea sediment (Dale & Dale 1992) or captured by deep sediment traps (Rynearson et al. 2013), and studies have even proposed a role for cysts via coastal-deep sea connections. Della Tommasa et al. (2004) showed that cysts, mainly produced by coastal species,

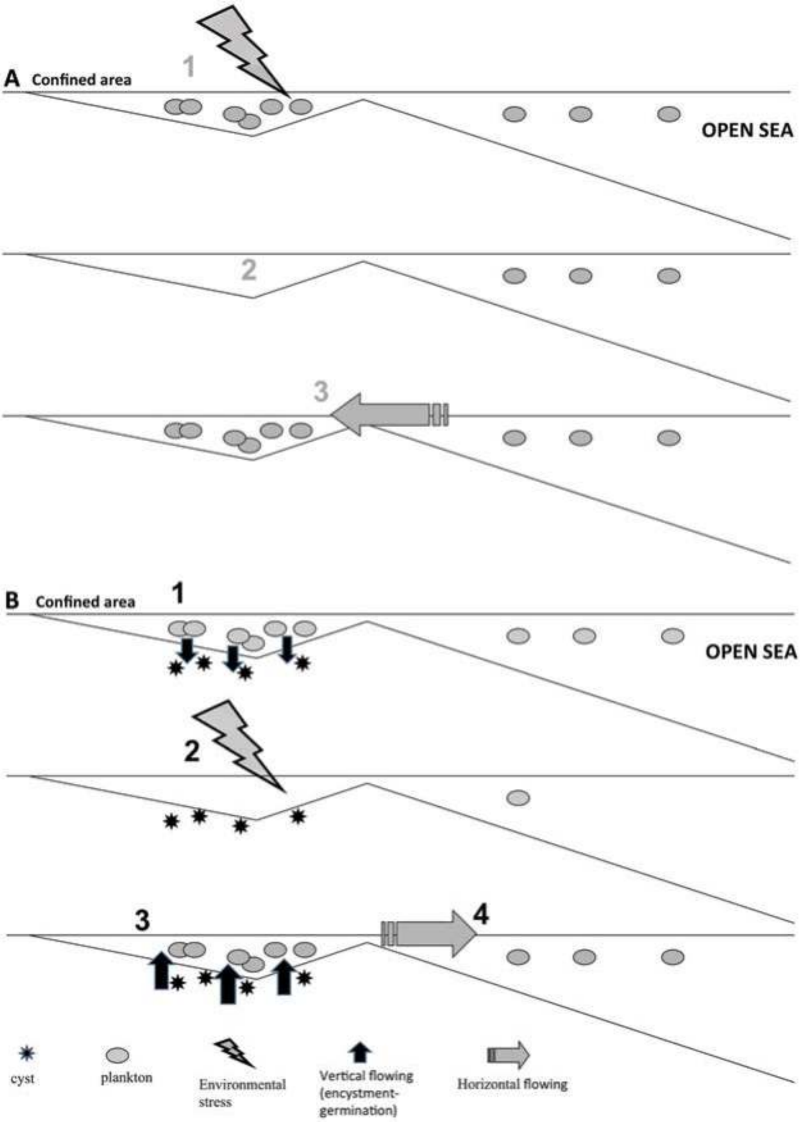

**Figure 9** (A) The marine vivification theory elaborated for coastal confined environments: for the restarting of confined plankton communities. (1) occurrence of harsh environmental conditions; (2) disappearance of a confined plankton community; (3) restoration of the confined plankton community by recruitment from the adjacent sea. (B) The resurrection ecology theory for the restarting of confined plankton communities. (1) production of cysts before the occurrence of harsh environmental conditions; (2) occurrence of harsh conditions after the disappearing of confined plankton community from the water column; (3) restoration of the confined community by the sediment cyst bank; (4) spillover and export of propagules and biomass in the adjacent open sea.

accumulate in deep-sea sediment off the mouth of the Foix canyon (Spain), and suggested that such bottom morphologies play a role in the ecology of coastal areas. In fact, during the periodical upwelling of deep-sea waters which at times occurs in such canyons, cysts deposited in the deep sea may be redistributed to the marine neritic areas from which they originally came.

In the last 20 years, scientists have suggested that ice habitats also provide a biological reservoir for the plankton community in cold seas (Gradinger 1999, Brierley & Thomas 2002). The trapped plankton organisms, both as a planktonic stage and cysts, may remain dormant in the ice during the adverse season and repopulate the water column when the ice melts. Although scientists admit the data need confirmation, they consider the biodiversity found as sufficient to hypothesise that cysts provide an injection to initiate plankton blooms at the start of each ice-melting season. Gradinger (1999) also reported: ‘In some cores (e.g. Station 204 of ARK 10/1) cysts of unknown origin, which were not attributed to either diatoms or flagellates, contributed a high proportion of the algal abundance’.

The overwintering of plankton species within ice is an admitted possibility (see Horner 1985, for a review of sea-ice communities) and Heikkilä et al. (2016) propose the rich number of cysts collected by their sediment traps as coming (at least partly) from the melt-mediated release of sea ice-dweller cysts to the water column in Hudson Bay. Further research is needed to clarify where the rich assemblages of sympagic benthic species originate, when the sympagic assemblages appear in the ice formation and where the organisms go when the ice melts.

Taxa potentially able to produce cysts are well represented in the sea-ice biota, and together with taxa found in that habitat, some papers (Buck et al. 1992, Ikavalko & Thomsen 1997, Gradinger 1999, Ikavalko 2001) list unspecified cysts. Other studies (Garrison & Buck 1989, Schnack-Schiel et al. 2001, Meiers et al. 2002, Ikavalko et al. 2004) have recognised planktonic taxa in the sea ice biota, and Friedrich & De Smet (2000) have reported the production of cysts, but before the melting period, by species commonly active in the ice during the winter. The extreme conditions present within the ice during the long-lasting polar winters (low temperature, low light or complete darkness and high salt concentration in liquid water segregated in ice crevices) suggest the suitability of a resting strategy for at least generalist species (Thomas & Dieckmann 2002, Werner et al. 2007). However, again, little attention has yet been paid to this particular aspect of polar sea ecology.

The sea-ice biota is a peculiar compartment where planktonic species, trapped during the autumn in the forming ice, may have evolved the possibility of producing cysts to survive the extreme winter conditions. Conversely, it may be that specialised ice species survive in the sympagic biota and produce cysts after the ice melts to wait for the formation of a new ice cover (Ratkova & Wassmann 2005). In any case, the presence of cysts could allow the immediate restoration of planktonic communities when favourable conditions return (Figure 10).

As with terrestrial forest seed banks, in order to make a decisive contribution to our understanding of plankton functioning in coastal areas, the ecology of marine cyst banks must evaluate input

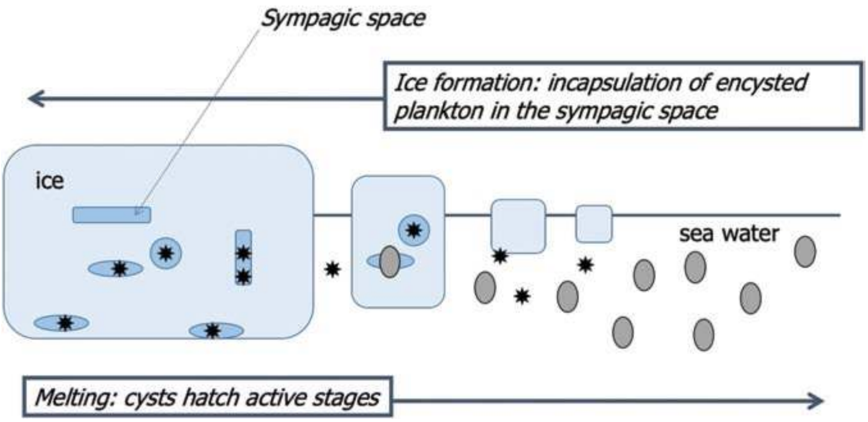

**Figure 10** Resurrection ecology applied to sea ice. At the beginning of winter, plankton produce cysts that do not sink to the bottom, but rather are entrapped in sympagic spaces within the ice as it forms. As the season warms from spring, melting of the ice frees resting stages that germinate, restarting the plankton community.

(fecundity/fertility, import), storage (short and long term) and subtraction (death, predation, recruitment, export) for each of the species involved. Persson & Rosenberg (2003) demonstrated that the relative abundance of a cyst type is affected by the composition of the predator community that feeds on cysts in sediment. If the whole community is considered, such grazing mortality is likely to affect the size and viability of a seeded plankton community (Persson 2000). Kamiyama (2013) suggested that the existence of short resting periods (e.g. in Tintinnina) might be responsible for reduced numbers of cysts in sediment of species that are abundant in the plankton. Broman et al. (2015) called for a consideration of cyst germination within the context of the carbon biological pump, which until now has been focussed on pelagic-benthic fluxes and does not take into account any back flow from sediment to the water column.

Viitasalo (2007) examined the complex network of interactions which could play a role in the population dynamics of the cladoceran *Bosmina longispina maritima* in Baltic Sea plankton. The polychaete *Marenzelleria* sp. is believed to be responsible for the upward transfer of deeply buried ephippia in the sediments. In contrast, the amphipod *Monoporeia affinis* and the bivalve *Macoma baltica* may be responsible for their transfer downwards in the sediment. Upward transfer (carried out by the polychaete) exposes the ephippia to predation by the mysidacean *Mysis mixta* (which cannot prey on ephippia buried under 1 cm of sediment). The bivalve probably ingests part of the ephippia that it moves. Hence, the bivalve and the amphipod subtract recruits from the plankton and/or preys for the mysidacean. This framework (even when based on only four actors) clearly demonstrates the complexity of interactions in the sediment cyst assemblage, which represents a real challenge for marine plankton ecologists.

## Biogeographic implications

According to Fenchel (1993, p. 375), ‘smaller organisms tend to have wider or even cosmopolitan distributions, a higher efficiency of dispersal, a lower rate of allopatric speciation, and lower rates of local and global extinction than do larger organisms’. Wilkinson (2001) confirmed that organisms smaller than 150 µm are generally cosmopolitan because their low body mass facilitates aerial dispersal. Finlay (2002) attributed this lack of biogeographical separation to the large number of individuals. A high percentage of microorganisms in a natural system are inactive (from 20% to 80%, according to Lennon & Jones 2011), and dispersal of dormant stages may contribute to the apparent cosmopolitan distributions of taxa. Among freshwater Protista and small Metazoa at least, the capability to produce resting stages facilitates dispersal by air, dust and migrating animals (but see the critical review of Foissner 2006). However, the low species richness that should derive from this situation contradicts May’s (1986) rule, which posits the existence of a higher number of small species than large ones.

Modern methodological approaches such as molecular biology and genetics have shown that the number of ubiquitous species is smaller than usually thought, even among smaller species (see Ricci & Fontaneto 2009, for Rotifera). This, however, cannot exclude the large dispersal potential that resting stages give to species. Although endemics have been recorded among marine Protista (see Taylor & Pollingher 1987, for Dinophyceae), it is presumed as obvious that while biogeographical limits generally affect large organisms, they do not apply to microorganisms.

Although sceptical of the cosmopolitism of microorganisms, Foissner (2006) admits that the geographical distribution of Protista species is in any case broader than that of multicellular organisms. The presence of cysts, in this framework, both enables and enhances the dispersal capacity of species.

The ability to avoid being affected by adverse conditions automatically allows cysts to pass barriers that are both geographical and ecological for the active stages. The composition of the cyst wall and the physiology of the encysted organisms, still poorly understood, may be closely connected to the species’ geographical distribution (Foissner 1997, Foissner et al. 2002).

The possibility of seed transfers between separate water bodies by passive transport in the gut of fishes swallowed by migrating water birds was proposed by Darwin (in Reznick 2011, p. 334) to explain the wide distribution of freshwater organisms. More recently, Figuerola & Green (2002) reported the possibility that cysts could also be exchanged between different environments in birds' guts. Indeed, the digestive enzymes of birds were found to affect neither the viability nor the hatching of cysts.

This framework has yet to be verified for marine environments, where birds cannot play the same role as in brackish waters or flooded plains. However, as already mentioned, benthic detritivores as well as fishes can be vectors of plankton species whose cysts are resistant to digestion and can survive in the gut of a fish for days before being expelled in faeces.

Flinkman et al. (1994) found similar hatching success for *Eurytemora* eggs taken from the faeces of Baltic herring. Indeed, the vulnerability of ovisac-bearing females probably reduces the chances of immature females being preyed upon and, as already reported, Kremp et al. (2003) demonstrated that passage through a polychaete gut actually ameliorates the hatching rate of resting eggs.

All these cases demonstrate that cysts can be transported long distances from their deposition site in the gut of vagile, or even swimming organisms. The shape of the resulting dispersal kernel depends on the mobility of the swallowing animal, its behaviour (migratory or sedentary), the time spent by cysts in its gut and its own trophic destiny—that is, whether it becomes the prey of other species. Consequently, cyst distributions in space are the result of a complex set of linked processes.

Being inactive, cysts simply sink to the bottom sediment when produced. Once there, they may be transferred up and down within the sediment as a consequence of the actions of limivorous organisms, leading either to their subtraction from or their injection into bottom water currents (Meysman et al. 2006).

The sculptures on the surface of the majority of marine cysts have been interpreted as being useful for many purposes (Belmonte et al. 1997). One of these is possibly to favour their attachment to floating or moving objects. This form of dispersal may account for the geographic distribution of species, including their appearance in previously unreported sites. If an extra long diapause (ELD) is added to the framework of geographic distribution, it is not obvious that a new record in an area corresponds to a nonindigenous species (NIS). In fact, the newly appearing species might derive from the germination of ELD cysts, thereby introducing a species from a different time (the past), but from the same site. In any case, although the possibility cannot be excluded, the majority of NISs in the world today are attributed to dispersion via human vectors, such as in the ballast waters of ships navigating between continents. The latter mechanism is believed to have been responsible for about 400 NISs present today along the marine coasts of the United States (Ruiz et al. 1997), and about 4000 NISs (most of them planktonic) have been dispersed throughout the world in this way (Carlton & Geller 1993; Ruiz et al. 2000).

As cysts, the majority of these stowaways survive the adversity of a long period in the ballast tanks, where they accumulate in the bottom sediments and rest for long periods (Bailey et al. 2003; Wonham et al. 2005). Although a true ecological community of active stages has been described as functioning in such tanks during the period of navigation (Galil & Hulsemann 1997), cysts represent the best way to travel. Ballast waters are the most extensively studied and verified of these vectors, partly due to the fear that toxic organisms may be transferred this way (e.g. Lacasse et al. 2013) and the ecological risks connected to the new arrivals (e.g. Seebens et al. 2013).

The dispersal of mesozooplankton species in accordance with the abovementioned mechanisms is still limited in comparison to the huge knowledge that is available for freshwater habitats. According to Bollens et al. (2002), (relative to coastal brackish waters), current knowledge about marine mesozooplankton dispersal is based on about 100 papers, referring to 32 species worldwide.

Data from Hallegraeff and Bolch (1992) suggested that such worldwide circulation might damage local biodiversity, in addition to distributing species that contain toxins. Hallegraeff (1998) advised aquaculture farmers to avoid establishing their farms near the ballast water charge-discharge sites of oceanic ships. Only recently have attempts been made to conduct research on biocides that can be applied to resting stages contained in ballast waters or their residue (Raikow et al. 2006, Fahnenstiel et al. 2009). Considering that ballast waters are responsible even for transcontinental transfer, they represent for marine biogeography what birds represent for wetlands biogeography.

When new species are recorded in ports, it is highly likely that they arrived with ships. The calanoid *Paracartia grani,* well known from the North Atlantic, was first reported in the Mediterranean in the port of Malaga in the late twentieth century (Rodrigues & Vives 1984). Subsequent reports of the species (Lakkis & Zeidane 1990), in other Mediterranean ports, were associated with its capacity to produce resting eggs (Guerrero & Rodrigues 1998), supporting the hypothesis of dispersal via ships (Belmonte & Potenza 2001).

Navigation also seems to be the cause of dispersal for species living in apparently isolated habitats. The cladoceran *Podon polyphemoides* and the calanoid *Acartia clausi* have been reported in the Caspian Sea (an enclosed sea) since 1957 and 1984, respectively. Their arrival in that sea has been attributed to its navigable connection, via the Volga-Don canal, with the Azov-Black Sea system (Zaitsev & Ozturk 2001).

Navigation via the Volga–Don-Neva has also been definitively accepted as responsible for the transfer of fauna from the Ponto-Caspian system (Black, Azov and Caspian Seas) to the Baltic Sea along a “trans-Sarmatian route”, now believed to be an important channel of geographic dispersal. Although some species that have recently invaded the Baltic Sea from the Caspian (such as the cladoceran *Cercopagis pengoi,* first reported in the Baltic by Leppäkoski & Olenin 2000) are known to be highly tolerant of the fresh waters of rivers, they appear to have crossed the Sarmatian plain and invaded the Baltic Sea only recently. The construction of canals and the beginning of their navigation provides the best explanation for the recent northward dispersal of many species.

The trans-Sarmatian route is not only a conduit for northward dispersal. In the case of the calanoid *Acartia tonsa,* southward dispersal has been recorded, apparently bucking the current climate change trend, which is expected to drive species poleward. *A. tonsa* was first reported in the Baltic Sea by Smirnov (1935), just a few years after it was first recorded in European Atlantic waters (Remy 1927 in Brylinski 1981). The species was reported in the Mediterranean basin more than 50 years later (Gaudy & Viñas 1985, Farabegoli et al. 1989), and in the Black Sea later still (Belmonte et al. 1994), allowing Belmonte & Potenza (2001) to hypothesise penetration through the Gibraltar Strait. Recently, however, it was ascertained that samples from the Black Sea studied by Belmonte et al. (1994) were taken in 1976 (see Zaitsev & Ozturk 2001, p. 89–94); hence, the species was already in the Black Sea before its appearance in the Mediterranean Sea. Although its arrival in the Bay of Sevastopol (the Crimea and Black Sea) could be attributed to any incoming ship, the trans-Sarmatian route, direct from the Baltic, is also a possibility.

Hence, the river connection over the Sarmatian plain carries species in both directions, towards either the Baltic or the Black-Caspian basins. Although noncyst producing organisms (such as the ctenophoran *Mnemiopsis leydi*) also use this route, the resting eggs of *C. pengoi* and *A. tonsa* better enable them to survive the adverse conditions that they face along this 1000-km river journey.

## Plankton cysts and humans

Resting stages are used as feed in aquaculture, partly because they lend themselves to transport and storage. Both *Artemia* (Anostraca) and *Brachionus* (Rotifera) cysts are widely used by specialised rearing enterprises, although the hatchlings of the former are too large and those of the latter are too small for some specific developmental stages of fish. Thus, Calanoida nauplii have been proposed as a living food of intermediate size (Støttrup 2000), and the use of potentially storable resting eggs has been explored (Marcus & Murray 2001), including attempts to obtain them on an industrial scale (Murray & Marcus 2002, Jo & Marcus 2004, Sedlaceck & Marcus 2005). At the same time, there also have been attempts to harvest and store eggs laid spontaneously by copepods in nature. Calanoida nauplii have the advantage of having high nutritional content, in addition to their intermediate size (between that of Rotifera and Anostraca hatchlings). Drillet et al. (2006) demonstrated that the subitaneous eggs of *A. tonsa* can remain quiescent if stored cold (2°–3°C), without severe effects on the viability of hatchlings even after 11 months. Cold storage, however, is not useful for all geographical populations of the species and can be ameliorated with chemicals such as antibiotics (Drillet et al. 2007, 2008a).

In addition, the generally high tolerance of cysts to chemicals (as demonstrated by Pati & Belmonte 2003, 2007) allows the use of disinfectants that both ameliorate cyst-hatching success and prevent the transfer of pathogens to rearing pools by means of the living food supply. *Brachionus* cysts maintain their hatchability even after lyophilisation (i.e. freeze-drying) and canning at various atmospheric pressures, a procedure that has been considered as effectively guarding against microbial attack (Balompapueng et al. 1997).

The same resistance of cysts to disinfectants must also be taken into account in treatments of aquaculture tanks or ponds after algal blooms. The disinfectant concentrations, exposure times used or both may not succeed in eliminating undesirable or toxic microalgae, with an impact on production in terms of both quality and quantity.

The attention received by cysts from the aquaculture community is probably the maximum level of voluntary human interaction with plankton resting stages. A review by Drillet et al. (2011) lists a series of aspects (production methodology upgrading, conservation and shipping and commercialisation strategy) to be taken into account, which insert the cysts problem into a human economic dimension.

The toxicity of some cyst-producing species poses a contamination risk not only for aquaculture species, but also for water and food used by humans. Indeed, many toxic organisms can be reactivated by resuspension processes (e.g. port-dredging activities), potentially contaminating the trophic chain up to the final human consumers. In this respect, the trawl fishery has already been shown to actively resuspend cysts from the sea bed (Siokou-Frangou et al. 2005), and infrequent nonroutine dredging of ports (i.e. carried out after many years) may be responsible for a large resuspension of cysts (Belmonte et al. 1995). It has been demonstrated that aquaculture farms set up in bays may negatively affect the survival of sediment cyst banks (Wang et al. 2016). This study suggested that fish and shellfish mariculture may be responsible for a reduction in the numbers and hatching success of resting eggs.

Among the involuntary consequences of human activities, ballast water release from shipping in geographically distant ports has been recognised as a major factor in the transport of NISs around the world. Such introductions lead to ecological imbalances, and potentially to the introduction of harmful algae and the development of toxic planktonic blooms.

Sanitary aspects of mariculture represent an important element in the frame of resting stage–human interactions.

HABs are produced by many species that can produce cysts (Bacillariophyceae, Dinophyceae, Haptophyta and Raphidophyta), inhabiting coastal areas where they cause harm to humans and other organisms (Faust & Gulledge 2002, Hallegraeff et al. 2003). HABs have a direct impact on human health, with negative influences on human wellbeing and the economy (with consequences to fisheries, tourism and recreation) (Falconer 1993). Anthropogenic pressures in coastal areas possibly favour HABs, and their impacts on human life is becoming a more pressing public health issue (Berdalet et al. 2015, and references therein). Humans may be influencing algal blooms by increasing nutrient availability via runoff, sewage, fertilisers, microclimate change, remixing of coastal sediments or merely by infecting new areas by transferring new species (as resting stages) from infected areas by a ship's ballast waters. Marine biotoxins produced by HABs can accumulate in marine animals (molluscs and fish) that can enter into the human diet. HAB toxins are distinguished in water- and fat-soluble molecules, all showing acute toxicity, but still little knowledge is available about the consequences of chronical exposition. Symptoms for humans may vary from minor to severe gastrointestinal intoxication to neurological disorders. Monitoring of HAB species should be regulary implemented and include assessments of the viability and size of cyst banks, in order to obtain more reliable estimates of potential impacts from HAB (Visciano et al. 2016, and references therein).

## Perspectives and challenges

Not all plankton groups, even in highly variable environments, produce encysted and/or recognisable resting stages, and hence this trait cannot be considered as the only mechanism that protects species against environmental change. Consequently, a cyst-based strategy to survive unfavourable periods is part of a general framework of species and community dynamics, with different strategies for each site or species.

The strategy used by many seasonal species or groups is still not known, although this may simply mean that resting stages have yet to be discovered, as suggested by the recent impressive increase of knowledge registered for dinoflagellate life cycles. On the other hand, species that are dormant as larvae or juveniles deserve to be considered in this framework. Notwithstanding the growing interest in resting stages in coastal habitats, there is little understanding of the rest in species that do not produce specialised cysts or resting eggs. Not all recorded resting stages are easily assignable to a taxon, and much effort is still required to resolve this simple descriptive question of who is who.

Cyst production and settling involves conspicuous biomass transfer from the water column to the benthos, and yet the potential consumers of this resource are still largely unknown. *Mysis relicta,* in the Baltic Sea, has been identified as one such consumer, but whether a species guild based mainly on this energy supply exists in the benthos—or indeed, whether such a guild is even possible—is unknown. The research is made more difficult by the proven ability of cysts to pass through the gut of animals without consequence. Hence, it is insufficient to identify who eats the cysts; who actually uses them as an energy source for their own metabolism must be found as well. This is of paramount importance for the ecology of coastal environments because the population dynamics of plankton may depend partially or totally on such benthic predators.

A suggestion that has emerged from the studies conducted over the last 25 years (still awaiting definitive confirmation) is that the abundance of cyst bank assemblages is directly correlated with the instability of the environment. Indeed, in such environments, the investment of species in the future may be higher. In stressed situations, species could be induced to invest more in the long-term future by means of diapause and a bet-hedging strategy (as in seed banks) than in creating the next generation. In temporary waters, species that produce cysts to rest and not to hatch immediately are common. Such species (including Anostraca, Cladocera and Calanoida) produce just one generation per year. The difficulty of obtaining larvae from eggs of the previous generation is responsible in part (if at all) for the population in the following year.

Most cysts are designed to ‘travel in time’, each clutch hatching in small percentages every year for many years. This is consistent with the general impression of the numerical predominance of cysts over active stages in the species of very temporary environments, but studies explicitly concerned with this topic are still rare.

One of the most interesting issues that deserve attention is sediment dating. Although some work has already been done, it is evident that dating of layered sediments, coupled with a knowledge of species that produce cysts and their biology, is a powerful tool in the reconstruction of the history of plankton communities. In the present period of global climate change, this has importance to what constitutes change, and what is the effect of long-term resilience.

Sediments are not the only place where cysts may be found. Sea ice may also act as an important cyst reservoir, which plays a fundamental role in the reappearance of polar plankton at the return of sunlight to polar areas. It is still to be ascertained if cysts can be trapped in the surface film in the open sea, from which currents and wind may disperse them in any direction, not only within polar latitudes.

Finally, there is a pressing need for a unification of the terminology used to describe and measure various cysts and eggs. Methods need to be shared, and an integrated approach adopted for the study of dormant resting cysts and eggs that is relevant to studies of the plankton and benthos, but also sedimentology, palaeontology, microbiology, environmental chemistry and marine coastal management.

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# Supplementary Material 1

List of modern species of planktonic marine Bacillariophyceae producing resting stages.

| Modern taxon | Type | References |
|---|---|---|
| *Actinocyclus curvatulus* Janisch 1878 | RS | Piredda et al. (2017) |
| *Actinoptychus senarius* (Ehrenberg 1838) Ehrenberg 1843 | RC | Ishii et al. (2012) |
| *Amphora coffeaeformis* (Agardh) Kützing | RC | Anderson (1975, 1976); McQuoid & Hobson (1996) |
| *Arcocellulus mammifer* Hasle, von Stosch & Syvertsen 1983 | RS | Piredda et al. (2017) |
| *Asterionellopsis glacialis* (Castracane 1886) Round 1990 | RS | Montresor et al. (2013) |
| *Bacteriastrum delicatulum* Cleve 1897 | RS | Hargraves (1976); McQuoid & Hobson (1996) |
| *Bacteriastrum furcatum* Shadbolt 1854 | RS | Karsten (1905); McQuoid & Hobson (1996) |
| *Bacteriastrum hyalinum* Lauder 1864 | RS | von Stosch & Fecher (1979); McQuoid & Hobson (1996); Bosak et al. (2015a) |
| *Bacteriosira bathyomphala* (Cleve 1883) Syvertsen & Hasle 1993 | RS | McQuoid & Hobson (1996); Hasle & Syvertsen (1996) |
| *Biddulphia alternans* (Bailey 1851) Van Heurck 1985 | RC | Ishii et al. (2012) |
| *Biddulphia tridens* (Ehrenberg 1838) Ehrenberg 1841 | RS | Piredda et al. (2017) |
| *Cerataulus smithii* Ralfs 1861 | RS | Piredda et al. (2017) |
| *Chaetoceros aculeatus* Makarova 1962 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros affinis* Lauder 1864 | RS | Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996) |
| *Chaetoceros anastomosans* Grunow 1882 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Oku & Kamatani (1997) |
| *Chaetoceros approximatus* Gran & Angst 1931 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros brevis* Schütt 1895 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros ceratosporus* Ostenfeld 1910 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Ferrario et al. (1998) |
| *Chaetoceros chinchae* Mereschkowsky 1899 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Suto (2005) (As *Vallodiscus chinchae*) |
| *Chaetoceros chunii* Karsten 1905 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros cinctus* Gran 1897 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Gaonkar et al. (2017) |
| *Chaetoceros compressus* Lauder 1864 | RS | Pitcher (1990); McQuoid & Hobson (1996); Rines (1999); Chamnansinp et al. (2015) |
| *Chaetoceros constrictus* Gran 1897 | RS | Pitcher (1990); Rines & Hargraves (1988); McQuoid & Hobson (1996) |
| *Chaetoceros contortus* Schütt 1895 | RS | McQuoid & Hobson (1996); Chamnansinp et al. (2015) |
| *Chaetoceros contortus* Schütt 1895 var. *ornatus* Chamnansip, Moestrup & Lundholm 2015 | RS | Chamnansinp et al. (2015) |
| *Chaetoceros coronatus* Gran 1897 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros costatus* Pavillard 1911 | RS | Garrison (1981); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros crinitus* Schütt 1895 | RS | Stockwell & Hargraves (1986) |
| *Chaetoceros criophilus* Castracane 1886 | RC | Fryxell (1989); McQuoid & Hobson (1996) |

(*Continued*)

| Modern taxon | Type | References |
|---|---|---|
| *Chaetoceros crucifer* Gran 1931 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros curiosus* Makarova 1962 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros curvisetus* Cleve 1889 | RS | Hargraves (1979); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros cylindrosporus* Makarova 1962 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros dayanensis* Li & Zhu 2015 | RS | Li et al. (2015) |
| *Chaetoceros debilis* Cleve 1894 | RS | Garrison (1981); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros diadema* (Ehrenberg 1854) Gran 1897 | RS | Hargraves (1972); Garrison (1981); French & Hargraves (1985); Pitcher (1990); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros dichatoensis* Gaonkar, Montresor & Sarno 2017 | RS | Gaonkar et al. (2017) |
| *Chaetoceros didymus* Ehrenberg 1845 | RS | Garrison (1981); Pitcher (1990); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros difficilis* Cleve 1900 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros dipyrenops* Meunier 1913 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros distans* Cleve 1873 | RS | Stockwell & Hargraves (1986), McQuoid & Hobson (1996) |
| *Chaetoceros diversus* Cleve 1873 | RC | McQuoid & Hobson (1996) |
| *Chaetoceros dubius* Proschinka-Lavrenko 1955 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros eibenii* Grunow 1882 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros elegans* Li, Boonprakob, Moestrup & Lundholm 2017 | RS | Li et al. (2017) |
| *Chaetoceros elmorei* Boyer 1914 | RS | Rushforth & Johansen (1986); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros exospermus* Meunier 1913 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros externus* Gran 1897 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros furcellatus* Yendo 1911 | RS | Stockwell & Hargraves (1986); Eilertsen et al. (1995); McQuoid & Hobson (1996) |
| *Chaetoceros gelidus* Chamnansinp, Li, Lundholm & Moestrup 2013 | RS | Degerlund et al. (2012) (as *Chaetoceros socialis*, northern strains); Chamnansinp et al. (2013) |
| *Chaetoceros heterovalvatus* Proschinka-Lavrenko 1953 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros hirtisetus* (Rines & Hargraves 1990) Chamnansinp, Moestrup & Lundholm 2015 | RS | Chamnansinp et al. (2015) |
| *Chaetoceros hispidus* (Ehrenberg 1844) Brightwell 1856 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros holsaticus* Schütt 1895 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros horridus* Krasske 1941 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros incertus* Makarova 1962 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros ingolfianus* Ostenfeld 1902 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros laciniosus* Schütt 1895 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros laevisporus* Li, Boonprakob, Moestrup & Lundholm 2017 | RS | Li et al. (2017) |
| *Chaetoceros lauderi* Ralfs 1864 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Ishii et al. (2011) |
| *Chaetoceros longicornis* Makarova 1962 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros lorenzianus* Grunow 1863 | RS | Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996); Li et al. (2017) |

(*Continued*)

| Modern taxon | Type | References |
|---|---|---|
| *Chaetoceros melchersianus* Margalef 1967 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros millipedarius* Xu, Li & Lundholm 2019 | RS | Xu et al. (2019) |
| *Chaetoceros minimus* (Levander 1904) Marino, Giuffré, Montresor & Zingone 1991 | RS | Marino et al. (1991); McQuoid & Hobson (1996) |
| *Chaetoceros mitra* (Bailey 1856) Cleve 1896 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Li et al. (2017) |
| *Chaetoceros muelleri* Lemmermann 1898 | RS | Reinke (1984); Rushforth & Johansen (1986); Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros neglectus* Karsten 1905 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros neogracilis* van Landingham 1968 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros nipponica* Ikari 1928 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros paradoxus* Cleve 1873 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros paulsenii* Ostenfeld 1902 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros pavillardii* Ikari 1928 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros protuberans* Lauder 1864 | RS | Montresor et al. (2013) |
| *Chaetoceros pseudocrinitus* Ostenfeld 1901 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros pseudocurvisetus* Mangin 1910 | RS<br>RC | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Oku & Kamatani (1995); Kuwata & Takahashi (1999) |
| *Chaetoceros radicans* Schütt 1895 | RS | Syvertsen (1979); Garrison (1981); Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996) |
| *Chaetoceros rigidus* Ostenfeld 1902 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros robustus* Makarova 1961 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros rotosporus* Li, Lundholm & Moestrup 2013 | RS | Li et al. (2013) |
| *Chaetoceros scabrosus* Proschinka-Lavrenko 1955 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros secundus* Cleve 1873 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros seiracanthus* Gran 1897 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros siamense* Cleve 1902 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros similis* Cleve 1896 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros simplex* Ostenfeld 1902 | RS | Rushforth & Johansen (1986); Stockwell & Hargraves (1986) |
| *Chaetoceros socialis* Lauder 1864 | RS | Garrison (1981); Pitcher (1990); Stockwell & Hargraves (1986); Eilertsen et al. (1995) |
| *Chaetoceros sporotruncatus* Gaonkar, Kooistra & Lange 2017 | RS | Gaonkar et al. (2017) |
| *Chaetoceros subcoronatus* Krasske 1941 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros subtilis* Cleve 1896 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros subtortilis* Proschinka-Lavrenko 1961 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) |
| *Chaetoceros tenuissimus* Meunier 1913 | RS | Montresor et al. (2013) |
| *Chaetoceros teres* Cleve 1896 | RS | Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996) |
| *Chaetoceros throndsenii* Marino, Montresor & Zingone 1991 | RS | Marino et al. (1991); McQuoid & Hobson (1996) |
| *Chaetoceros vanheurckii* Gran 1897 | RS | Garrison (1981); Hollibaugh et al. (1981); Stockwell & Hargraves (1986); Pitcher (1990); McQuoid & Hobson (1996) |

(*Continued*)

| Modern taxon | Type | References |
|---|---|---|
| *Chaetoceros vixvisibilis* Schiller 1930 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996); Hernández-Becerril et al. (2010) |
| *Chaetoceros wighamii* Brightwell 1856 | RS | Stockwell & Hargraves (1986); McQuoid & Hobson (1996) (as *Chaetoceros amanita*); Bosak et al. (2015b) |
| *Cylindrotheca closterium* (Ehrenberg 1839) Reimann & Lewin 1964 | RS | Montresor et al. (2013) |
| *Dactyliosolen blavyanus* (Peragallo 1892) Hasle 1975 | RS | McQuoid & Hobson (1996) |
| *Detonula confervacea* (Cleve 1896) Gran 1897 | RS | Hargraves (1976); Durbin (1978); McQuoid & Hobson (1996) |
| *Detonula pumila* (Castracane 1886) Gran 1900 | RS | Ishii et al. (2012) |
| *Ditylum brightwellii* (West 1860) Grunow 1883 | RS | Hargraves (1976); McQuoid & Hobson (1996); Riaux-Gobin (1996); Koester et al. (2007) |
| *Ditylum buchananii* von Stosch 1987 | RS | McQuoid & Hobson (1996) |
| *Eucampia antarctica* (Castracane 1886) Mangin 1915 | WS | Fryxell (1989) |
| | RS | Hoban et al. (1980) as *Eucampia balaustium* Castracane (1886) |
| *Eucampia antarctica* (Mangin 1915) var. *recta* Fryxell & Prasad 1990 | RS | Fryxell & Prasad (1990) |
| *Fragilariopsis cylindrus* (Grunow 1883) Krieger 1954 | RS | McQuoid & Hobson (1996); Ferrario et al. (1998) |
| *Fragilariopsis oceanica* (Cleve) Hasle 1965 | RS | McQuoid & Hobson (1996); Hasle & Syvertsen (1996) |
| *Leptocylindrus danicus* Cleve 1889 | RS | Hargraves (1976); French & Hargraves (1985) (1986); Ishizaka et al. (1987); McQuoid & Hobson (1996) |
| *Leptocylindrus minimus* Gran 1915 | RS | Hargraves (1990); McQuoid & Hobson (1996) |
| *Lithodesmium variabile* Takano 1979 | RC | Ishii et al. (2012) |
| *Melosira arctica* Dickie 1852 | RS | McQuoid & Hobson (1996) |
| *Melosira moniliformis* (Müller 1783) Agardh 1824 | RS | McQuoid & Hobson (1996) |
| *Minutocellus* cf. *polymorphus* (Hargraves & Guillard 1974) Hasle, Stosch & Syvertsen 1983 | RS | Montresor et al. (2013) |
| *Odontella aurita* (Lyngbye 1819) Agardh 1832 | RC | McQuoid & Hobson (1996) |
| *Odontella litigiosa* (van Heurck 1909) Hoban 1909 | RS | Hoban et al. (1980); McQuoid & Hobson (1996) |
| *Odontella longicruris* (Greville 1859) Hoban 1983 | RC | Ishii et al. (2012) |
| *Odontella mobiliensis* (Bailey 1851) Grunow 1884 | RC | Ishii et al. (2012) |
| *Odontella weissflogii* (Grunow 1882) Grunow 1884 | RS | Hoban et al. (1980); McQuoid & Hobson (1996) |
| *Papiliocellulus simplex* Gardner & Crawford 1992 | RS | Piredda et al. (2017) |
| *Paralia sulcata* (Ehrenberg 1838) Cleve 1873 | RS | McQuoid & Hobson (1996) |
| *Pauliella taeniata* (Grunow 1880) Round & Basson 1997 | RS | Hasle & Syvertsen (1996) (as *Achnanthes taeniata* Grunow 1880) |
| *Porosira glacialis* (Grunow 1884) Jørgensen 1905 | RS | Villareal & Fryxell (1990); McQuoid & Hobson (1996) |
| *Proboscia alata* (Brightwell 1858) Sundström 1896 | RS | McQuoid & Hobson (1996) |
| *Rhizosolenia braunii* Hustedt 1952 | RS | McQuoid & Hobson (1996) |

(*Continued*)

| Modern taxon | Type | References |
|---|---|---|
| *Rhizosolenia formosa* Peragallo 1888 | RS | McQuoid & Hobson (1996) |
| *Rhizisolenia longiseta* Zacharias 1893 | RS | McQuoid & Hobson (1996) |
| *Rhizisolenia polydactyla* Castracane 1886 | RS | McQuoid & Hobson (1996); Hasle & Syvertsen (1996) |
| *Rhizisolenia setigera* Brightwell 1858 | RS | Hargraves (1976); McQuoid & Hobson (1996) |
| *Rhizisolenia sima* Castracane 1886 | RS | McQuoid & Hobson (1996) |
| *Sellaphora pupula* (Kützing 1844) Mereschkovsky 1902 | RS | Piredda et al. (2017) |
| *Skeletonema costatum* (Greville 1866) Cleve 1873 | RC | Sakshaug & Andresen (1986); McQuoid & Hobson (1996) |
| *Skeletonema dohrnii* Sarno & Kooistra 2015 | RS | Piredda et al. (2017) |
| *Skeletonema menzelii* Guillard, Carpenter & Reimann 1974 | RS | Montresor et al. (2013) |
| *Skeletonema pseudocostatum* (Medlin 1991) Sarno & Zingone 2005 | RS | Piredda et al. (2017) |
| *Skeletonema tropicum* Cleve 1900 | RS | Montresor et al. (2013) |
| *Stellarima microtrias* (Ehrenberg 1884) Hasle & Sims 1986 | RS | Syvertsen (1985) (as *Coscinodiscus furcatus* Karsten 1905); Fryxell (1989); McQuoid & Hobson (1996) |
| *Stephanopyxis nipponica* Gran & Yendo 1914 | RS | Haga (1997); Ferrario et al. (2013) |
| *Stephanopyxis palmeriana* (Greville 1865) Grunow 1884 | RS | Drebes (1966); McQuoid & Hobson (1996) |
| *Stephanopyxis turris* (Greville & Arnott) Ralfs 1861 | RS | Hargraves (1976) |
| *Syringidium bicorne* Ehrenberg 1845 | RS | Hasle & Sims (1985); McQuoid & Hobson (1996) |
| *Syringidium simplex* Bailey 1861 | RS | Hasle & Sims (1985) |
| *Thalassionema nitzschioides* (Grunow1862) Mereschkowsky 1902 | RS | Montresor et al. (2013) |
| *Thalassiosira allenii* Takano 1965 | RS | Piredda et al. (2017) |
| *Thalassiosira antarctica* Comber 1896 | RS | Doucette & Fryxell (1985); McQuoid & Hobson (1996) |
| *Thalassiosira antarctica* var. *borealis* Fryxell, Doucette & Hubbard 1981 | RS | Krawczyk et al. (2012) |
| *Thalassiosira australis* Peragallo 1921 | RS | Syvertsen (1985); McQuoid & Hobson (1996) |
| *Thalassiosira constricta* Gaarder 1938 | RS | Heimdal (1974); McQuoid & Hobson (1996) |
| *Thalassiosira* cf. *eccentrica* (Ehrenberg 1840) Cleve 1904 | RS | Piredda et al. (2017) |
| *Thalassiosira gravida* Cleve 1896 | RS | Krawiec (1982) (as *Thalassiosira rotula* Meunier 1910); McQuoid & Hobson (1996) |
| *Thalassiosira kushirensis* Takano 1985 | RS | Krawczyk et al. (2012) |
| *Thalassiosira mediterranea* (Schröder 1911) Hasle 1972 | RS | Montresor et al. (2013) |
| *Thalassiosira nordenskioeldii* Cleve 1873 | RS | Durbin (1978); Hollibaugh et al. (1981); McQuoid & Hobson (1996) |
| *Thalassiosira pseudonana* Hasle & Heimdal 1970 | RS | Piredda et al. (2017) |
| *Thalassiosira scotia* Fryxell & Hoban 1979 | RS | Fryxell et al. (1979); McQuoid & Hobson (1996) |
| *Trieres mobiliensis* 2013 | RS | Piredda et al. (2017) |

*Abbreviations:* RS = resting spore; RC = resting cell; WS = winter stage.

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## Supplementary Material 2

List of modern species of planktonic marine Dinophyceae producing resting stages.

| Modern taxon | Paleontological taxon | References |
|---|---|---|
| Order **Prorocentrales** Lemmermann 1910 | | |
| *Prorocentrum gracile* Schütt 1895 | | Cannon (1993)* |
| *Prorocentrum leve* Faust, Kibler, Vandersea, Tester & Litaker 2008 | | Mertens et al. (2017a)* |
| *Prorocentrum lima* (Ehrenberg 1873) Dodge 1975 | | Faust (1993)* |
| *Prorocentrum micans* Ehrenberg 1833 | | Cannon (1993)* |
| Order **Dinophysiales** Lindemann 1928 | | |
| *Dinophysis acuminata* Claparède & Lachmann 1859 | | Bardouil et al. (1991)<br>Hajdu & Larsson (2006) |
| *Dinophysis acuta* Ehrenberg 1839 | | Moita & Sampayo (1993)<br>Reguera et al. (1995) |
| *Dinophysis ovum* Schütt 1895 | | Cannon (1993)* |
| *Dinophysis* cf. *tripos* Gourret 1883 | | Moita & Sampayo (1993) |
| Order **Gymnodiniales** Lemmermann 1910 | | |
| *Akashiwo sanguinea* (K. Hirasaka 1922) Hansen & Moestrup 2000 | | Tang & Gobler (2015)* |
| *Amphidinium carterae* Hulburt 1957 | | Cao Vien (1967)*; (1968)*<br>Sampayo (1985)* |
| *Amphidinium operculatum* Claparède & Lachmann 1859 | | Barlow & Triemer (1988)* as *A. klebsii* (division cysts) |
| *Barrufeta bravensis* Sampedro & Fraga 2011 | | Sampedro et al. (2011)* |
| *Barrufeta resplendens* (Hulburt 1957) Gu et al. 2015 | | Gu et al. (2015b)* |
| *Grammatodinium tongyeonginum* Li & Shin 2017 | | Li et al. (2017)* |
| *Gymnodinium aureolum* (Hulburt 1957) Hansen 2000 | | Tang et al. (2008)* |
| *Gymnodinium catenatum* Graham 1943 | | Anderson et al. (1988)*<br>Ellegaard et al. (1994)*<br>Gu et al. (2013b)* |
| *Gymnodinium corollarium* Sundström et al. 2009 | | Sundström et al. (2009)* |
| *Gymnodinium impudicum* (Fraga & Bravo 1995) G. Hansen & Moestrup 2000 | | Sonneman & Hill (1997)* as *Gyrodinium impudicum*<br>Kobayashi et al. (2001)* as *Gyrodinium impudicum*<br>Rubino et al. (2010)* as *Gymnodinium impudicum* cyst type a |

(*Continued*)

| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Gymnodinium inusitatum* Gu 2013 | | Gu et al. (2013b)* |
| *Gymnodinium litoralis* A. Reñé et al. 2011 | | Reñé et al. (2011)* |
| *Gymnodinium microreticulatum* Bolch & Hallegraeff 1999 | | Bolch et al. (1999)*<br>Gu et al. (2013b)* |
| *Gymnodinium nolleri* Ellegaard & Moestrup 1999 | | Ellegaard & Moestrup (1999)*<br>Figueroa & Bravo (2005a)*<br>Rubino et al. (2010)* |
| *Gymnodinium trapeziforme* Attaran-Fariman & Bolch 2007 | | Attaran-Fariman et al. (2007)* |
| *Gyrodinium undulans* (Hulburt 1957) | | Sonneman & Hill (1997)* |
| *Karenia brevis* (Davis 1948) G. Hansen & Moestrup 2000 | | Walker (1982)* as *Ptychodiscus brevis*<br>Persson et al. (2013)* |
| *Katodinium fungiforme* (Anissimova 1926) Fott 1957 | | Spero & Morée (1981)* |
| *Katodinium rotundatum* (Lohmann 1908) Loeblich III 1965 | | Hamer et al. (2001) |
| *Levanderina fissa* (Levander 1894) Moestrup et al. 2014 | | Kojima & Kobayashi (1992)*; Uchida et al. (1996)*; Shikata et al. (2008)*as *Gyrodinium instriatum*<br>Moestrup et al. (2014)* |
| *Margalefidinium polykrikoides* (Margalef 1961) Gómez, Richlen & Anderson 2017 | | Li et al. (2015a)*; Thoha et al. (2019)* |
| *Nematodinium armatum* (Dogiel 1906) Kofoid & Swezy 1921 | | Bolch (2001)* possible germination inferred from PCR amplification<br>Rubino et al. (2017)* germination from incubation experiments |
| *Polykrikos hartmannii* Zimmerman 1930 | | Matsuoka & Fukuyo (1986)* |
| *Polykrikos kofoidii* Chatton 1914 | | Matsuoka et al. (2009)* |
| *Polykrikos schwartzii* Bütschli 1873 | | Matsuoka et al. (2009)* |
| *Wangodinium sinense* (Z. Luo et al. 2018), Y. Tang & H.F. Gu 2018 | | Luo et al. (2018)* |
| *Warnovia* cf. *rosea* (Pouchet 1897) Kofoid & Swezy 1921 | | Ellegaard et al. (2002)* |
| Order **Suessiales** (Fensome & al. 1993) | | |
| *Biecheleria baltica* Moestrupb, Lindberg & Daugbjerg 2009 | | Moestrup et al. (2009)* |
| *Biecheleria cincta* (Siano, Montresor & Zingone 2009) Siano 2012 | | Siano et al. (2009)* |
| *Biecheleria halophila* (Biecheler 1952) Moestrup, Lindberg & Daugbjerg 2009 | | Kremp et al. (2005)* as *Woloszynskia halophila*<br>Moestrup et al. (2009)* |
| *Biecheleriopsis adriatica* Moestrup, Lindberg & Daugbjerg 2009 | | Kang & Wang (2018) |
| *Dactylodinium pterobelotum* Takahashi, Moestrup & Iwataki 2017 | | Takahashi et al. (2017)* |

(*Continued*)

| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Polarella glacialis* Montresor, Procaccini & Stoecker 1999 | | Montresor et al. (1999)* |
| *Woloszynskia* sp. | | Bolch & Hallegraeff (1990)* |
| Order **Gonyaulacales** F.J.R. Taylor 1980 | | |
| *Alexandrium affine* (Inoue & Fukuyo 1985) Balech 1995 | | Fukuyo et al. (1985)*; Band-Schmidt et al. (2003)* |
| *Alexandrium andersonii* Balech 1990 | | Montresor et al. (1998)*; Ciminiello et al. (2000)* |
| *Alexandrium catenella* (Whedon & Kofoid 1936) Balech 1985 | | Meksumpun et al. (1994)*<br>Sonneman & Hill (1997)*<br>Bravo et al. (2006)* |
| *Alexandrium compressum* (Fukuyo, Yoshida & Inoue 1985) Balech 1995 | | Matsuoka (1992) |
| *Alexandrium fraterculus* (Balech 1964) Balech 1985 | | Nagai et al. (2009)* |
| *Alexandrium fundyense* Balech 1985 | | Anderson et al. (2014)<br>Anglés et al. (2012a)* |
| *Alexandrium hiranoi* Kita & Fukuyo 1988 | | Kita et al. (1985)* as *Goniodoma pseudogonyaulax*<br>Kita & Fukuyo (1988)<br>Kita et al. (1993)* |
| *Alexandrium kutnerae* (Balech 1979) Balech 1985 | | Bravo et al. (2006)* |
| *Alexandrium leei* Balech 1985 | | Fukuyo & Pholpunthin (1990b)* |
| *Alexandrium lusitanicum* Balech 1985 | | Blanco (1989a)*<br>Bolch et al. (1991)* |
| *Alexandrium margalefii* Balech 1985 | | Bravo et al. (2006)* |
| *Alexandrium minutum* Halim 1960 | | Bolch et al. (1991)*<br>Bravo et al. (2006)*; Anglés et al. (2012b)* |
| *Alexandrium monilatum* (Howell 1953) Balech 1995 | | Walker & Steidinger (1979)* as *Gonyaulax monilata* |
| *Alexandrium ostenfeldii* (Paulsen 1904) Balech & Tangen 1985 | | Mackenzie et al. (1996)*<br>Jensen & Moestrup (1997)* temporary cysts |
| *Alexandrium pacificum* Litaker 2014 | | Fertouna-Bellakhal et al. (2015) |
| *Alexandrium peruvianum* (Balech & Mendiola 1977) Balech & Tangen 1985 | | Bravo et al. (2006)*<br>Figueroa et al. (2008)* |
| *Alexandrium pseudogonyaulax* (Biecheler 1952 Horiguchi, Yuki & Fukuyo 1992 | | Kita et al. (1985) formation of temporary cysts<br>Montresor (1995a)*; Zmerli Triki et al. (2015)* |
| *Alexandrium tamarense* (Lebour 1925) Balech 1995 | | Anderson & Wall (1978)* as *Gonyaulax tamarensis*<br>Blanco (1989a)*; Person et al. (2000)*<br>Genovesi et al. (2011)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Alexandrium tamiyavanichi* Balech 1994 | | Fukuyo & Pholpunthin (1990a)*as *A. cohorticula*<br>Godhe et al. (2000) |
| *Alexandrium tamutum* Montresor, Beran & John 2004 | | Montresor et al. (2004)*<br>Figueroa et al. (2007)* |
| *Alexandrium taylorii* Balech 1994 | | Garcés et al. (1998)*; Giacobbe et al. (1999)*; Figueroa et al. (2006)* |
| *Fragilidium heterolobum* Balech ex Loeblich III 1965 | | Steidinger (1975) in Head (1996) |
| *Fragilidium mexicanum* Balech 1988 | | Orlova et al. (2004)*<br>Selina & Orlova (2009)* |
| *Fragilidium subglobosum* (von Stosch 1969) Loeblich III 1965 | | Sonneman & Hill (1997)* |
| *Gonyaulax* cf. *alaskensis* Kofoid 1911 | *Spiniferites* sp. | Dobell & Taylor (1981)* |
| *Gonyaulax baltica* Ellegaard, Lewis & Harding 2002 | *Spiniferites bulloideus* Deflandre & Cookson 1955 | Ellegaard et al. (2002)* |
| | *Impagidinium caspienense* Marret 2004 | Marret et al. (2004);<br>Mertens et al. (2017a,b)* |
| *Gonyaulax digitalis* (Pouchet 1883) Kofoid 1911 | *Spiniferites bentorii* (Rossignol 1962) Wall & Dale 1970 | Matsuoka (1985a); Wall & Dale (1968)*<br>Orlova et al. (2004) |
| | *Spiniferites nodosus* (Wall 1967) Sarjeant 1970 | Wall & Dale (1968)* |
| | *Bitectatodinium tepikiense* Wilson 1973 | Lewis et al. (2001)*<br>Marret & Zonneveld (2003) |
| *Gonyaulax ellegardiae* Mertens et al. 2015 | *Spiniferites pachydermus* (Rossignol 1964) Reid 1974 | Zonneveld et al. (2013)<br>Mertens et al. (2015)* |
| *Gonyaulax elongata* Reid 1974 Ellegaard, Daugbjerg, Rochon, J.Lewis & Harding 2003 | *Spiniferites elongatus* Reid 1974 | Ellegaard et al. (2003)*; Van Nieuwenhove et al. (2018) |
| | *Spiniferites frigidus* Harland & Reid 1980 | Marret & Zonneveld (2003) |
| *Gonyaulax membranacea* (Rossignol 1964) Ellegaard, Daugbjerg, Rochon, J.Lewis & Harding 2003 | *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 | Ellegaard et al. (2003)* |
| *Gonyaulax scrippsae* Kofoid 1911 | *Spiniferites bulloideus* (Deflandre & Cookson 1955) Sarjeant 1970 | Wall & Dale (1968)*<br>Matsuoka (1985a)* |
| | *Spiniferites belerius* Reid 1974 | Marret & Zonneveld (2003) |
| *Gonyaulax* cf. *scrippsae* Kofoid 1911 | *Spiniferites* sp. cf. *S. delicatus* Reid | Matsuoka (1987)* |
| *Gonyaulax spinifera* (Claparède & Lachmann 1859) Diesing 1866 | *Ataxiodinium choane* Reid 1974 | Rochon et al. (2009)<br>Marret & Zonneveld (2003)<br>Price et al. (2017) |
| | *Bitectatodinium tepikiense* Wilson 1973 | Rochon et al. (2009)<br>Price et al. (2017) |
| | *Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid 1974 | Wall & Dale (1968)*<br>Rochon et al. (2009)<br>Price et al. (2017) |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| | *Nematosphaeropsis lemniscata* Bujak 1984 | Wall & Dale (1968)* as *N.balcombiana* Deflandre & Cookson (1955) |
| | *Spiniferites hyperacanthus* Deflandre & Cookson 1955 Cookson & Eisenack 1974 | Rochon et al. (2009)<br>Price et al. (2017) |
| | *Spiniferites mirabilis* (Rossignol 1967) Sarjeant 1970 | Wall & Dale (1968)*<br>Rochon et al. (2009); Price et al. (2017) |
| | *Spiniferites ramosus* (Ehrenberg 1838) Mantell 1854 | Wall & Dale (1970)*<br>Lewis et al. (1999)*<br>Rochon et al. (2009) |
| | *Spiniferites scabratus* (Wall 1967) Sarjeant 1970 | Wall & Dale (1968)* as *Hystricosphaera scabrata*<br>Lewis et al. (1999)* |
| | *Tectatodinium pellitum* Wall 1967 | Wall & Dale (1968)*<br>Marret & Zonneveld (2003)<br>Rochon et al. (2009) |
| *Gonyaulax verior* Sournia 1973 | | Matsuoka et al. (1988)*<br>Zonneveld & Dale (1994)*<br>Ellegaard et al. (1994)* |
| *Lingulodinium polyedrum* (Stein 1883) Dodge 1989 | *Lingulodinium machaerophorum* (Deflandre & Cookson 1955) Wall 1967 | Kokinos & Anderson (1995)*<br>Lewis & Hallett (1997)*<br>Figueroa & Bravo (2005b)* |
| *Pentaplacodinium saltonense* Mertens, Carbonell-Moore, Pospelova & Head 2018 | | Mertens *et al.* (2018)* |
| *Peridiniella catenata* (Levander 1894) Balech 1977 | | Kremp (2000)* |
| *Protoceratium globosum* Kofoid & J.R. Michener 1911 | | Morquecho et al. (2009)* |
| *Protoceratium reticulatum* (Claparède & Lachmann 1859) Bütschli 1855 | *Operculodinium centrocarpum* (Deflandre & Cookson 1955) Wall 1967 | Sonneman & Hill (1997)*<br>Rubino et al. (2017)* |
| | *Operculodinium israelianum* (Rossignol 1962) Wall 1967 | Morquecho et al. (2009) |
| | *Operculodinium psilatum* Wall 1967 | Morquecho et al. (2009) |
| *Pyrodinium bahamense* Plate 1906 | *Polysphaeridium zoharyi* (Rossignol 1962) Davey & Williams 1966 | Wall & Dale (1969)*<br>Usup et al. (2012) |
| *Pyrodinium bahamense* var. *compressum* (Böhm 1931) Steidinger, Tester & Taylor 1980 | *Polysphaeridium zoharyi* (Rossignol 1962) Davey & Williams 1966 | Matsuoka (1989)*<br>Azanza (1997)*<br>Onda et al. (2014) temporary cysts |
| *Pyrophacus horologium* Stein 1883 | | Steidinger & Davis (1967)*<br>Wall & Dale (1971)* |
| *Pyrophacus steinii* (Schiller 1935) Wall & Dale 1971 | *Tuberculodinium vancampoae* (Rossignol 1962) Wall 1967 | Wall & Dale (1971)*; Matsuoka (1985b)*<br>Faust (1998)*; Pholpuntin et al. (1999)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| Order **Peridiniales** Haeckel 1894 | | |
| *Archaeperidinium bailongense* Liu et al. 2015a | | Liu et al. (2015b)* |
| *Archaeperidinium constrictum* (Abé 1936) Liu, Mertens, Matsuoka & Gu 2015 | | Liu et al. (2015b)* |
| *Archaeperidinium minutum* (Kofoid 1907) Yamaguchi et al. 2011 | | Wall & Dale (1968)*; Ribeiro et al. (2010)*<br>Mertens et al. (2012)*; Liu et al. (2015b)* |
| *Archaeperidinium saanichi* Mertens et al. 2012 | | Mertens et al. (2012)* |
| *Bysmatrum subsalsum* (Ostenfeld 1908) Faust & Steidinger 1998 | | Gottschling et al. (2012)<br>Anglès et al. (2017)* |
| *Boreadinium breve* (Abé 1981) Sournia 1984 | | Liu et al. (2015a)* |
| *Calciodinellum albatrosianum* (Kamptner 1963) Janofske & Karwath 2000 | *Thoracosphaera albatrosiana* Kamptner 1963 | Janofske & Karwath (2000)* |
| *Calciodinellum elongatum* (Hildebrand-Habel, Willems & Versteegh 1999) Meier, Janofske & Willems 2002 | | Meier et al. (2002)* |
| *Calciodinellum levantinum* Meier, Janofske & Willems 2002 | | Meier et al. (2002)* |
| *Diplopelta globula* (Abé 1941) Balech 1979 | | Liu et al. (2015a)* |
| *Diplopelta symmetrica* Pavillard 1913 | | Dale et al. (1993)*<br>Zonneveld & Pospelova (2015) |
| *Diplopsalis lenticula* Bergh 1881 | | Matsuoka (1988)*; Lewis (1990)*<br>Liu et al. (2015a)* |
| *Diplopsalopsis latipeltata* Balech & Borgese 1990 | | Dale et al. (1993)* |
| *Diplopsalopsis orbicularis* (Paulsen 1907) Meunier 1910 | | Wall & Dale (1968)*<br>Matsuoka (1988)* |
| *Diplopsalopsis ovata* (Abé 1941) Dodge & Toriumi 1993 | | Liu et al. (2015a)* |
| *Ensiculifera carinata* Matsuoka et al. 1990 | | Matsuoka et al. (1990)* |
| *Ensiculifera imariense* Kobayashi & Matsuoka 1995 | | Kobayashi & Matsuoka (1995)* |
| *Ensiculifera mexicana* Balech 1967 | *Pentadinellum oblatum* Keupp 1991 | Zonneveld et al. (2005) |
| *Glenodinium foliaceum* Stein 1883 | | De Sousa & Silva (1962)<br>Head (1996) |
| *Glenodinium hallii* Freudenthal & Lee 1963 | | Head (1996) |
| *Gotoius abei* Matsuoka 1988 | | Matsuoka (1988)* |
| *Heterocapsa triquetra* (Ehrenberg 1840) Stein 1883 | | Olli (2004) |
| *Islandinium minutum* (Harland & Reid 1980) Head, Harland & Matthiessen 2001 | *Islandinium minutum* (Harland & Reid 1980) Head, Harland & Matthiessen 2001 | Potvin et al. (2013)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Kryptoperidinium foliaceum* (Stein 1883) Lindemann 1924 | | Figueroa et al. (2009)* |
| *Lebouraia pusilla* (Balech & Akselman 1988) Dodge & Toriumi 1993 | | Liu et al. (2015a)* |
| *Leonella granifera* (Fütterer 1977) Janofske & Karwath 2000 | *Thoracosphaera granifera* Fütterer 1977 | Janofske & Karwath (2000)* |
| *Niea acanthocysta* (Kawami, Iwataki & Matsuoka 2006) Liu et al. 2015a | | Matsuoka (1988)* as *Diplopelta parva*<br>Kawami et al. (2006)* as *Oblea acanthocysta*<br>Liu et al. (2015a)* |
| *Niea chinensis* Liu et al. 2015 | | Liu et al. (2015a)* |
| *Niea torta* (Abé 1941) Liu et al. 2015a | | Liu et al. (2015a)* |
| *Oblea rotunda* (Lebour 1922) Balech ex Sournia 1973 | | Lewis (1990)*<br>Liu et al. (2015a)* |
| *Pentapharsodinium dalei* Indelicato & Loeblich III 1986 | | Lewis (1991)*<br>Zonneveld & Pospelova (2013) |
| *Pentapharsodinium dalei* var. *aciculiferum* Gu 2013 | | Gu et al. (2013d)* |
| *Pentapharsodinium jinhaense* Li, Han & Shin 2015 | | Li et al. (2015c)* |
| *Pentapharsodinium tyrrhenicum* (Balech 1990) Montresor, Zingone & Marino 1993 | *Calcicarpinum bivalvum* Versteegh 1993 | Montresor et al. (1993)* |
| *Pernambugia tuberosa* (Kamptner 1963) Janofske & Karwath 2000 | *Thoracosphaera tuberosa* Kamptner 1963 | Janofske & Karwath (2000)* |
| *Posoniella tricarinelloides* (Versteegh 1993) Streng, Banasová, Reháková & Willems 2009 | | Streng et al. (2009); Gu et al. (2013a)* |
| *Preperidinium meunieri* (Pavillard 1912) Elbrächter 1993 | *Dubridinium caperatum* Reid 1977 | Matsuoka (1988)*; Lewis (1990)*<br>Liu et al. (2015a)* |
| *Protoperidinium abei* (Paulsen 1931) Balech 1974 var. *rotunda* (Abé 1936) Taylor 1967 | | Liu et al. (2015b)* |
| *Protoperidinium achromaticum* (Levander 1902) Balech 1974 | | Bolch & Hallegraeff (1990)* as *Protoperidinium* sp.2 Head (1996) |
| *Protoperidinium americanum* (Gran & Baarud 1935) Balech 1974 | | Lewis & Dodge (1987)*; Zonneveld et al. (2013)<br>Liu et al. (2014)* |
| *Protoperidinium avellana* (Meunier 1919) Balech 1974 | *Brigantedinium cariacoense* (Wall 1967) Reid 1977 | Wall & Dale (1968)*; Reid (1977)<br>Matsuoka (1984)*; Liu et al. (2015b)* |
| *Protoperidinium biconicum* (P. Dangeard 1927) Balech 1974 | | Gu et al. (2015a,b)* |
| *Protoperidinium brochii* (Kofoid & Swezy 1921) Balech 1974 | | Blanco (1989b)* |
| *Protoperidinium claudicans* (Paulsen 1907) Balech 1974 | *Votadinium spinosum* Reid 1977 | Wall & Dale (1968)*; Matsuoka (1985a)*; Bolch & Hallegraeff (1990)* |
| *Protoperidinium conicoides* (Paulsen 1905) Balech 1974 | *Brigantedinium simplex* (Wall 1965) Reid 1977 | Lewis et al. (1984)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Protoperidinium conicum* (Gran 1900) Balech 1974 | *Selenopemphix quanta* (Bradford 1975) Matsuoka 1985 | Wall & Dale (1968)*; Marret & Zonneveld (2003); Gu et al. (2015a,b)* |
| *Protoperidinium* cf. *curvipes* (Ostenfeld 1906) Balech 1974 | | Head (1996) |
| *Protoperidinium denticulatum* (Gran & Braarud 1953) Balech 1974 | *Brigantedinium irregulare* Matsuoka 1987 | Matsuoka (1987)* |
| *Protoperidinium divaricatum* (Meunier 1919) Balech 1974 | *Xandarodinium xanthum* Reid 1977 | Zonneveld et al. (2013)<br>Gu et al. (2015a,b)* |
| *Protoperidinium* cf. *divergens* (Ehrenberg 1841) Balech 1974 | *Peridinium ponticum* Wall & Dale 1973 | Wall & Dale (1973)<br>Dale (1983)*; Matsuoka & Head (2013) |
| *Protoperidinium excentricum* (Paulsen 1907) Balech 1974 | | Lewis et al. (1984)*<br>Liu et al. (2015b)* |
| *Protoperidinium* cf. *expansum* Abé 1981 | | Hallegraeff & Bolch (1992)* |
| *Protoperidinium fukuyoi* Mertens, Head, Pospelova & Matsuoka 2013 | | Mertens et al. (2013)* |
| *Protoperidinium fuzhouense* Liu et al. 2015 | | Liu et al. (2015b)* |
| *Protoperidinium haizhouense* Liu, Gu & Mertens 2013 | *Islandinium brevispinosum* Pospelova & Head 2002 | Liu et al. (2014)* |
| *Protoperidinium humile* (Schiller 1937) Balech 1974 | | Gu et al. (2015a,b)* |
| *Protoperidinium latidorsale* (Balech 1951) Balech 1974 | *Votadinium calvum* Reid 1977 | Sarai et al. (2013)* |
| *Protoperidinium latissimum* (Kofoid 1907) Balech 1974 | | Wall & Dale (1968)*<br>Wall & Dale (1968)*; Sonneman & Hill (1997)*<br>Gu et al. (2015a,b)* |
| *Protoperidinium leonis* (Pavillard 1916) Balech 1974 | *Quinquecuspis concretum* (Reid 1977) Harland 1977 | Lewis et al. (1984)* |
| *Protoperidinium lousianensis* Mertens, Gu, Price & Matsuoka 2016 | *Trinovantedinium pallidifulvum* Matsuoka 1987 | Mertens et al. (2016)* |
| *Protoperidinium monospinum* (Gran & Maarud 1930) Balech 1974 | | Zonneveld & Dale (1994)* |
| *Protoperidinium nudum* (Meunier 1919) Balech 1974 | *Selenopemphix quanta* (Bradford 1975) Matsuoka 1985 | Wall & Dale (1968)*; Matsuoka (1985a,b)* |
| *Protoperidinium obtusum* (Karsten 1906) Parke & Dodge 1976 | | Aydin et al. (2011); Uzar et al. (2010) |
| *Protoperidinium paraoblongum* Sarai et al. 2013 | *Votadinium pontifossatum* Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwye 2019 | Sarai et al. (2013)*; Gurdebeke et al. (2019) |
| *Protoperidinium parthenopes* Zingone & Montresor 1988 | | Moscatello et al. (2004); Kawami & Matsuoka (2009)*; Ferraro et al. (2016); Liu et al. (2014)* Rubino et al. (2017)* |
| *Protoperidinium pentagonum* (Gran 1902) Balech 1974 | *Brigantedinium majusculum* Reid 1977 | Nehring (1994)*<br>Gu et al. (2015a,b)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Protoperidinium punctulatum* (Paulsen 1907) Balech 1974 | *Brigantedinium cariacoense* (Wall 1967) Reid 1977 | Wall & Dale (1968)* |
| *Protoperidinium quadrioblongum* Sarai et al. 2013 | *Votadinium rhomboideum* Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwye 2019 | Sarai et al. (2013)*; Gurdebeke et al. (2019) |
| *Protoperidinium shanghaiense* Gu et al. 2015 | *Trinovantedinium applanatum* (Bradford 1977) Bujak & Davies 1983 | Zonneveld et al. (2013)<br>Gu et al. (2015a)* |
| *Protoperidinium sinuosum* Lemmermann 1905 | *Brigantedinium majusculum* Reid 1977 | Li et al. (2015b)* |
| *Protoperidinium steidingerae* Balech 1979 | *Votadinium reidii* Gurdebeke, Mertens, Pospelova, Matsuoka, Li & Louwye 2019 | Wall & Dale (1968)*<br>Gribble et al. (2009)*; Sarai et al. (2013)*<br>Gurdebeke et al. (2019) |
| *Protoperidinium stellatum* (Wall 1968) Head 1999 | *Stelladinium stellatum* (Wall 1968) Reid 1977 | Wall & Dale (1968)*; Rochon et al. (1999)<br>Liu et al. (2015b)* |
| *Protoperidinium subinerme* (Paulsen 1904) Loeblich III 1969 | *Selenopemphix nephroides* (Benedek 1972) Benedek & Sarjeant 1981 | Wall & Dale (1968)*<br>Lewis et al. (1984)* |
| *Protoperidinium thorianum* (Paulsen 1905) Balech 1974 | | Lewis et al. (1984)* |
| *Protoperidinium thulesense* (Balech 1958) Balech 1973 | | Matsuoka et al. (2006)* |
| *Protoperidinium tricingulatum* Kawami, van Wezel, Koeman & Matsuoka 2009 | | Kawami et al. (2009)*<br>Liu et al. (2014)* |
| *Qia lebouriae* (Nie 1943) Liu et al. 2015 | | Matsuoka (1988)* as *Diplopsalis lebouriae*<br>Liu et al. (2015a)* |
| *Scrippsiella acuminata* (Ehrenb 1836) Kretschmann et al. 2015 | | Wall & Dale (1968)*; Montresor et al. (1994)* Janofske (2000)*; Kretschmann et al. (2015) |
| *Scrippsiella bicarinata* Zinssmeister, Soehner, Meier & Gottschling 2012 | | Zinssmeister et al. (2012)* |
| *Scrippsiella crystallina* Lewis 1991 | | Lewis (1991)* |
| *Scrippsiella donghaienis* Gu 2008 | | Gu et al. (2008)* |
| *Scrippsiella enormis* Gu 2013 | | Gu et al. (2013c)* |
| *Scrippsiella erinaceus* (Kamptner 1937) Kretschmann et al. 2014 | | Kretschmann et al. (2014)<br>Ferraro et al. (2016)* |
| *Scrippsiella hangoei* (Schiller 1937) Larsen 1995 | | Lewis et al. (1984)* as *Protoperidinium hangoei*<br>Rintala et al. (2007)* temporary cyst<br>Kremp & Parrow (2006)* |
| *Scrippsiella infula* (Deflandre 1948) Montresor 2003 | *Calcigonellum infula* Deflandre 1948 | D'Onofrio et al. (1999)*<br>Montresor et al. (2003)* |
| *Scrippsiella kirschiae* Zinssmeister, Soehner, Meier & Gottschling 2012 | | Zinssmeister et al. (2012)*<br>Satta et al. (2014); Rubino et al. (2017)* |
| *Scrippsiella lachrymosa* Lewis 1991 | | Lewis (1991)* |

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| Modern taxon | Paleontological taxon | References |
|---|---|---|
| *Scrippsiella minima* Gao & Dodge 1991 | | Gao & Dodge (1991)* |
| *Scrippsiella operosa* (Deflandre 1947) Montresor 2003 | | Montresor et al. (1997)* as *Calciodinellum operosum*<br>Montresor et al. (2003) |
| *Scrippsiella patagonica* Akselman & Keupp 1990 | *Obliquipithonella irregularis* Akselman & Keupp 1990 | Akselman & Keupp (1990)* |
| *Scrippsiella plana* Luo, Mertens, Bagheri & Gu 2015 | | Luo et al. (2015)* |
| *Scrippsiella precaria* Montresor & Zingone 1988 | | Montresor & Zingone (1988)*; Montresor et al. (1994) |
| *Scrippsiella ramonii* Montresor 1995 | | Montresor (1995b)* |
| *Scrippsiella regalis* (Gaarder 1954) Janofske 2000 | | Janofske (2000)* |
| *Scrippsiella rotunda* Lewis 1991 | | Lewis (1991)*; Gu et al. (2008)* |
| *Scrippsiella spinifera* Honsell & Cabrini 1991 | | Kobayashi (1995)*<br>Gu et al. (2013c)*<br>Luo et al. (2015)* |
| *Scrippsiella trifida* Lewis 1991 | | Lewis (1991)* |
| *Vulcanodinium rugosum* Nézan & Chomérat 2011 | | Zeng et al. (2012)* division cysts |
| Order **Pyrocystales** Apstein 1909 | | |
| *Dissodinium pseudolunula* Swift ex Elbrächter & Drebes 1978 | | Gomez & Artigas (2013)* |

*Note:* * = cyst formation and/or theca/cyst correlation confirmed by encystment/excystment experiments or by observing living cysts within the theca.

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# Supplementary Material 3

List of species of planktonic marine Ciliophora producing resting stages.

| Taxon | Cyst name | References |
|---|---|---|
| *Acanthostomella norvegica* (Daday 1887) Jörgensen 1927 | | Yu et al. (2012) |
| *Acanthostomella* sp. | | Kamiyama (2013) |
| *Amphorides amphora* (Claparede & Lachmann 1858) Strand 1928 | | Yu et al. (2012) |
| *Chaetospira mulleri* Lachmann 1856 | | Reid & John (1983) |
| *Codonella aspera* Kofoid & Campbell 1929 | | Rubino et al. (2013) |
| *Codonella orthoceras* (Haeckel 1873) Jorgensen 1924 | | Rubino et al. (2013) |
| *Codonellopsis monacensis* (Rampi 1950) Balech 1950 | | Rubino et al. (2013) |
| *Codonellopsis schabii* (Brandt 1906) Kofoid & Campbell 1929 | | Rubino et al. (2013) |
| *Coxliella helix* Claparede & Lachmann 1858 | | Yu et al. (2012) |
| *Cyrtostrombidium boreale* Kim, Suzuki & Taniguchi 2002 | | Kim, Suzuki & Taniguchi (2002) |
| *Cyttarocylis cassis* Haeckel 1837 | | Yu et al. (2012) |
| *Diophrys oligothrix* Borror 1965 | | Gong et al. (2018) |
| *Diophrys scutum* (Dujardin, 1841) Kahl 1932 | | Reid & John (1983) |
| *Epiplocylis undella* (Ostenfeld & Schmidt 1901) Jörgensen 1924 | | Rubino et al. (2013) |
| *Eutintinnus apertus* Kofoid & Campbell 1929 | | Yu et al. (2012) |
| *Eutintinnus fraknoi* (Daday 1887) Kofoid & Campbell 1929 | | Yu et al. (2012) |
| *Eutintinnus ludus-undae* Entz 1885 | | Yu et al. (2012) |
| *Eutintinnus tubulosus* (Ostenfeld 1899) Kofoid & Campbell 1939 | | Kamiyama (2013) |
| *Fabrea salina* Henneguy 1890 | | Moscatello et al. (2004) |
| *Favella ehrenbergii* (Claparede & Lachmann 1858) Jörgensen 1924 | | Yu et al. (2012) |
| *Gastrostyla steinii* Engelmann 1862 | | Reid & John (1983) |
| *Halteria grandinella* (Muller 1773) Dujardin 1840 | | Kamiyama (2013) |
| *Helicostomella longa* Brandt 1906 | | Kamiyama (2013) |
| *Helicostomella subulata* (Ehrenberg 1833) Jörgensen 1924 | | Reid & John (1983) |
| *Helicostomella* sp. | | Ichinomiya et al. (2004) |
| *Laboea strobila* Lohmann 1908 | | Rubino et al. (2009) |
| *Laurentiella strenua* (Dingfelder 1962) Berger & Foissner 1989 | | Kamiyama (2013) |
| *Leprotintinnus bottnicus* Jörgensen 1900 | | Yu et al. (2012) |
| *Leprotintinnus pellucidus* Cleve 1899 | | Yu et al. (2012) |
| *Leprotintinnus* sp. | | Kamiyama (2013) |
| *Limnostrombidium viride* (Stein 1867) Krainer 1995 | *Sphaeropsis* sp. | Agatha et al. (2005) |
| *Meseres corlissi* Petz & Foissner 1992 | *Sphaeropsis* type | Foissner et al. (2005) |
| *Metacylis* sp. | | Kamiyama (2013) |
| *Nyctotherus ovalis* Leidy 1850 | *Nyctotherus* type | Reid & John (1983); Rubino et al. (2009) |
| *Oxytricha bifaria* Stokes 1887 | | Verni & Rosati (2011) |
| *Oxytricha fallax* Stein 1859 | | Reid & John (1983) |
| *Oxytricha granulifera* Foissner & Adam 1983 | | Kamiyama (2013) |
| *Parafavella denticulata* (Ehrenberg 1840) | | Yu et al. (2012) |
| *Parafavella edentata* Brandt 1896 | | Yu et al. (2012) |
| *Parafavella gigantea* Brandt 1896 | | Yu et al. (2012) |
| *Parundella caudata* (Ostenfeld 1899) Jörgensen 1924 | | Yu et al. (2012) |
| *Parundella* sp. | | Kamiyama (2013) |
| *Pelagostrombidium fallax* (Zacharias 1896) Krainer 1991 | *Sphaeropsis* sp. | Kamiyama (2013) |
| *Pleurotricha lanceolata* (Ehrenberg 1835) Stein 1859 | | Reid & John (1983) |

(*Continued*)

| Taxon | Cyst name | References |
|---|---|---|
| *Rhabdonella spiralis* Fol 1881 | | Rubino et al. (2013) |
| *Salpingella acuminata* (Claparede & Lachmann 1858) Jörgensen 1924 | | Yu et al. (2012) |
| *Schmidingerella serrata* (Mobius 1987) Agatha & Struder-Kypke 2012 | | Reid & John (1983) |
| *Schmidingerella taraikaensis* (Hada 1932) Agatha & Strüder-Kypke 2012 | | Kamiyama (2013) |
| *Steinia sphagnicola* Foissner 1989 | | Kamiyama (2013) |
| *Stenosemella oliva* Meunier 1910 | | Yu et al. (2012) |
| *Stenosemella ventricosa* (Claparède & Lachmann 1858) Jörgensen 1924 | | Rubino et al. (2013) |
| *Stentor* sp. | *Stentor* type | Moscatello et al. (2004) |
| *Strombidium acutum* Claparède & Lachmann 1859 | *Sphaeropsis* sp., elongate | Rubino et al. (2009) |
| *Strombidium biarmatum* Agatha, Struder-Kypte, Beran & Lynn 2005 | *Sphaeropsis* sp. | Agatha et al. (2005) |
| *Strombidium capitatum* (Leegaard 1915) Kahl 1932 | *Sphaeropsis* sp. | Ichinomiya et al. (2004) |
| *Strombidium conicum* (Lohmann 1908) Wulff 1919 | *Sphaeropsis* sp. | Kim & Taniguchi (1995) |
| *Strombidium crassulum* (Leegaard 1915) Kahl 1932 | *Sphaeropsis* sp. | Reid (1987) |
| *Strombidium rassoulzadegani* MacManus, Xu, Costas & Katz 2010 | *Sphaeropsis* sp. | McManus et al. (2010) |
| *Strombidium stylifer* Levander 1894 | *Sphaeropsis* sp. | Katz et al. (2005) |
| *Strombidium tintinnodes* Entz 1884 | *Sphaeropsis* sp. | Jonsson (1994) |
| *Strombidinopsis* sp. | *Sphaeropsis* sp. | Ichinomiya et al. (2004) |
| *Stylonethes sterkii* Garnjobst 1937 | | Reid & John (1983) |
| *Tintinnidium mucicula* (Claparède & Lachmann 1858) Daday 1997 | | Yu et al. (2012) |
| *Tintinnopsis baltica* Brandt 1896 | | Yu et al. (2012) |
| *Tintinnopsis beroidea* Stein 1867 | | Rubino et al. (2013) |
| *Tintinnopsis buetschlii* Daday 1887 | | Rubino et al. (2013) |
| *Tintinnopsis campanula* Ehrenberg 1840 | | Yu et al. (2012) |
| *Tintinnopsis corniger* Hada 1964 | | Kamiyama (2013) |
| *Tintinnopsis cylindrica* Daday 1887 | | Yu et al. (2012) |
| *Tintinnopsis directa* Hada 1932 | | Kamiyama (2013) |
| *Tintinnopsis fracta* Brandt, 1906 | | Yu et al. (2012) |
| *Tintinnopsis karajacensis* Brandt 1896 | | Yu et al. (2012) |
| *Tintinnopsis kofoidi* Hada 1932 | | Yu et al. (2012) |
| *Tintinnopsis lohmanni* Laackmann 1906 | | Yu et al. (2012) |
| *Tintinnopsis meunieri* Kofoid & Campbell 1929 | | Yu et al. (2012) |
| *Tintinnopsis nucula* Fol 1884 | | Yu et al. (2012) |
| *Tintinnopsis radix* Imhof 1886 | | Yu et al. (2012) |
| *Tintinnopsis rapa* Meunier 1910 | | Yu et al. (2012) |
| *Tintinnopsis subacuta* Jörgensen 1899 | | Yu et al. (2012) |
| *Tintinnopsis tocantinensis* Kofoid & Campbell 1929 | | Yu et al. (2012) |
| *Tintinnopsis tubulosa* Levander 1900 | | Yu et al. (2012) |
| *Tintinnopsis urnula* Meunier 1910 | | Yu et al. (2012) |
| *Tintinnopsis* sp. | | Kamiyama (2013) |
| *Undella claparedei* (Entz 1885) Daday 1887 | | Rubino et al. (2013) |
| *Urocryptum tortum* Maupas 1883 | | Perez-Uz & Guinea (2001) |
| *Uronema marinum* Dujardin 1841 | | Fenchel (1990) |

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## Supplementary Material 4

List of species of planktonic marine Metazoa producing resting stages.

| Taxon | References |
|---|---|
| **Rotifera** | |
| *Asplanchna pryodonta* Gosse 1850 | Viitasalo & Katajisto (1994) |
| *Brachionus* sp. | Marcus et al. (1994) |
| *Hexarthra fennica* Levander 1892 | Moscatello & Belmonte (2004) |
| *Keratella* sp. | Viitasalo & Katajisto (1994) |
| *Ptygura* sp. | Moscatello & Belmonte (2004) |
| *Synchaeta* sp. | Viitasalo & Katajisto (1994) |
| **Cladocera** | |
| *Bosmina maritima* P.E. Muller 1868 | Purasjoki (1958) |
| *Daphnia cucullata* G.O. Sars 1862 | Viitasalo & Katajisto (1994) |
| *Evadne nordmanni* Lovén 1836 | Onbé (1985) |
| *Evadne tergestina* Claus 1864 | Onbé (1973) |
| *Moina* sp. | Moscatello & Belmonte (2004) |
| *Penilia avirostris* Dana 1849 | Onbé (1972) |
| *Podon intermedius* Lilljeborg 1853 | Onbé (1991) |
| *Podon leuckarti* Sars G.O. 1862 | Onbé (1985) |
| *Podon polyphemoides* Leuckart 1859 | Onbé et al. (1977) |
| **Copepoda Calanoida** | |
| *Acartia adriatica* Steuer 1910 | Belmonte (1997) |
| *Acartia bifilosa* Giesbrecht 1881 | Castro-Longoria and Williams (1999) |
| *Acartia bilobata* Abraham 1970 | Beyrend-Dur et al. (2014) |
| *Acartia californiensis* Trinast 1976 | Johnson (1980) |
| *Acartia clausi* Giesbrecht 1889 | Kasahara et al. (1974) |
| *Acartia erythraea* Giesbrecht 1889 | Kasahara et al. (1974) |
| *Acartia discadudata* Giesbrecht 1882 | Lindeque et al. (2013) |
| *Acartia hudsonica* Pinhey 1926 | Sullivan & McManus (1986) |
| *Acartia italica* Steuer 1910 | Belmonte (1997) |
| *Acartia lilljeborgi* Giesbrecht 1889 | Ara (2001) |
| *Acartia longiremis* Lilljeborg 1853 | Marcus (1990) |
| *Acartia pacifica* Steuer 1915 | Uye (1985) |
| *Acartia omori* Bradford 1976 | Itoh and Aoki (2010) |
| *Acartia sinjiensis* Mori 1940 | Uye (1985) |
| *Acartia spinicauda* Giesbrecht 1889 | Marcus (1996) |
| *Acartia steueri* Smirnov 1936 | Uye (1980) |
| *Acartia teclae* Bradford 1976 | Naess (1996) |
| *Acartia tonsa* Dana 1849 | Zillioux & Gonzalez (1972) |
| *Acartia tsuensis* Ito 1956 | Uye (1985) |
| *Anomalocera ornata* Sutcliffe 1949 | Marcus (1996) |
| *Anomalocera patersoni* Templeton 1837 | Ianora & Santella (1991) |
| *Boeckella hamata* Brehm 1928 | Hall & Burns (2001) |
| *Boeckella poppei* Mrazec 1901 | Jiang et al. (2012) |
| *Calanopia americana* Dahl F. 1894 | Marcus (1996) |
| *Calanopia thompsoni* Scott A. 1909 | Kasahara et al. (1974) |

(*Continued*)

| Taxon | References |
|---|---|
| *Centropages abdominalis* Sato 1913 | Kasahara et al. (1974) |
| *Centropages furcatus* Dana 1849 | Marcus (1989) |
| *Centropages hamatus* Lilljeborg 1853 | Mauchline (1998) |
| *Centropages ponticus* Karavaev 1895 | Sazhina (1968) |
| *Centropages typicus* Krøyer 1849 | Lindley (1990) |
| *Centropages velificatus* Oliveira 1947 | Chen & Marcus (1997) |
| *Centropages yamadai* Mori 1934 | Kasahara et al. (1974); Marcus (1996) |
| *Epilabidocera amphitrites* Mc Murrich 1916 | Marcus (1990); Johnson (1980) |
| *Eurytemora affinis* Poppe 1880 | Johnson (1980) |
| *Eurytemora americana* Williams 1906 | Marcus (1984) |
| *Eurytemora pacifica* Sato 1913 | Uye (1985) |
| *Eurytemora velox* Lilljeborg 1853 | Gaudy & Pagano (1987) |
| *Gippslandia estuarina* Bayly & Arnott 1969 | Newton & Mitchell (1999) |
| *Gladioferens pectinatus* Brady 1899 | Hall and Burns (2001) |
| *Labidocera aestiva* Wheeler 1900 | Grice and Lawson (1976) |
| *Labidocera bipinnata* Tanaka 1936 | Uye et al. (1979) |
| *Labidocera mirabilis* Fleminger 1957 | Chen & Marcus (1997) |
| *Labidocera rotunda* Mori 1929 | Itoh and Aoki (2010) |
| *Labidocera scotti* Giesbrecht 1897 | Marcus (1989) |
| *Labidocera trispinosa* Esterly 1905 | Uye (1985) |
| *Labidocera wollastoni* Lubbock 1857 | Grice & Gibson (1982) |
| *Paracartia grani* Sars G.O. 1904 | Guerrero & Rodrigues (1998) |
| *Paracartia latisetosa* Krizcaguin 1893 | Belmonte (1992) |
| *Pontella meadi* Wheeler 1900 | Grice & Gibson (1977) |
| *Pontella mediterranea* Claus 1863 | Sazhina (1968) |
| *Pteriacartia josephinae* Crisafi 1974 | Belmonte & Puce (1994) |
| *Sinocalanus tenellus* Kikuchi 1928 | Hada et al. (1986) |
| *Sulcanus conflictus* Nicholls 1945 | Newton & Mitchell (1999) |
| *Temora longicornis* Müller O.F. 1785 | Marcus (1996) |
| *Tortanus derjugini* Smirnov 1935 | Chen & Li (1991) |
| *Tortanus dextrilobatus* Chen & Zhang 1965 | Chen & Li (1991) |
| *Tortanus discaudatus* Thompson I.C. & Scott A. 1903 | Marcus (1990) |
| *Tortanus forcipatus* Giesbrecht 1889 | Kasahara et al. (1974) |

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# ESTABLISHED AND EMERGING TECHNIQUES FOR CHARACTERISING THE FORMATION, STRUCTURE AND PERFORMANCE OF CALCIFIED STRUCTURES UNDER OCEAN ACIDIFICATION

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## Abstract

Ocean acidification (OA) is the decline in seawater pH and saturation levels of calcium carbonate ($CaCO_3$) minerals that has led to concerns for calcifying organisms such as corals, oysters and mussels because of the adverse effects of OA on their biomineralisation, shells and skeletons. A range of cellular biology, geochemistry and materials science approaches have been used to explore biomineralisation. These techniques have revealed that responses to seawater acidification can be highly variable among species, yet the underlying mechanisms remain largely unresolved. To assess the impacts of global OA, researchers will need to apply a range of tools developed across disciplines, many of which are emerging and have not yet been used in this context. This review outlines techniques that could be applied to study OA-induced alterations in the mechanisms of biomineralisation and their ultimate effects on shells and skeletons. We illustrate how to characterise, quantify and monitor the process of biomineralisation in the context of global climate change and OA. We highlight the basic principles, as well as the advantages and disadvantages, of established, emerging and future techniques for OA researchers. A combination of these techniques will enable a holistic approach and better understanding of the potential impact of OA on biomineralisation and its consequences for marine calcifiers and associated ecosystems.

## Introduction

The precipitation of minerals such as $CaCO_3$ for shells and skeletons using dissolved carbonate and calcium ions is commonly called *biomineralisation* (Doney et al. 2009). Marine organisms have been producing $CaCO_3$ biominerals since the Precambrian, and the resultant rich fossil record provides insight into the evolution of intricate, orderly and often beautiful structures (Wilkinson 1979). The composition of biominerals varies among taxa and, as the production of shell materials is dependent on the availability of mineral ion resources and on physiological conditions at the site of calcification (Wilbur 1964), mineral composition can reveal how organisms have interacted with environmental conditions over geological time to the present day.

Atmospheric $CO_2$ levels have increased at a faster rate during the Anthropocene than in any previous time in Earth's history, causing a rapid decline in seawater pH and lowering the amount of $CaCO_3$ minerals (Orr et al. 2005). Since concerns about ocean acidification (OA) were first highlighted (Feely et al. 2004, Raven et al. 2005) there has been a concerted international effort to understand its implications for marine life. It has become apparent that $CO_2$-driven acidification can lead to skeletal abnormalities and slower growth in many marine calcifiers (Hofmann et al. 2008, Vézina & Hoegh-Guldberg 2008, Wittmann & Pörtner 2013). Aragonite, calcite, vaterite (Wehrmeister et al. 2011) and amorphous $CaCO_3$, which is an important precursor of crystalline carbonate minerals (Addadi et al. 2003), are phases of $CaCO_3$ whose production may be modified by OA. Organisms can be affected by OA, as they need to maintain conditions that are chemically suitable for the process of calcification (supersaturated with calcium [$Ca^{2+}$] and carbonate [$CO_3^{2-}$]) or for preventing dissolution (saturation state $\Omega < 1$). Calcite is less susceptible to dissolution at lower pH values than aragonite unless it contains high levels of magnesium (Ries et al. 2009, Chan et al. 2012). Production of any form of $CaCO_3$ can be energetically expensive (Comeau et al. 2017a) and so the impact of OA on the production and maintenance of $CaCO_3$ structures are modulated by energy acquisition (Melzner et al. 2011) and may be due to $CO_2$-driven organism hypercapnia (Byrne et al. 2013).

To capture fully the impact of OA on biomineralisation, several key questions should be addressed. These include questions regarding the direct impact of OA on the process of biomineralisation itself, and also about the functional consequences of these changes on shells and skeletons. Resolving these issues requires multidisciplinary research ranging from omics to cell culture, from physiological mechanisms to ecology, and from materials science to crystallography. The complexity of the task is reflected in the plethora of techniques that have been used to investigate biomineralisation under OA conditions, including buoyant weight, total alkalinity anomality, total calcium content, annual estension, calcein labelling and the use of radio isotopes (Table 1). This diversity of approaches allows investigators to tackle different questions related to the impact of OA on the process of biomineralisation, although there is a need to understand how techniques compare when measuring similar processes (Schoepf et al. 2017). The selection and refinement of a technique depend upon scientific question and practical aspects related to the study question, experimental design and biological models (Figure 1).

Here, we review an array of techniques used to explore the consequences of rising global $CO_2$ levels on biomineralisation in marine organisms. We organise the techniques by the biological or mineralogical parameters of interest. We evaluate their advantages and disadvantages so that future work can more effectively measure the effects of OA on biomineralisation. We also highlight recent advances in the study of the effects of OA on biomineralisation and how interdisciplinary collaboration can advance the field.

**Table 1** Summary of established techniques on growth and development to measure calcification and morphology under OA conditions

| Technique | Measurements | Advantages | Disadvantages |
|---|---|---|---|
| Dyes— alizarin red and calcein | • Alizarin red stains; calcium-rich structures; a red/light purple colour<br>• Calcein stains; calcium-rich structures; a fluorescent green colour | • Low cost, noninvasive<br>• Track shell growth of living organisms during exposure to an experiment<br>• Data comparable to published work<br>• Dye location can be analysed with advanced characterisation methods | • Alizarin red also binds free Ca<br>• Calcein also binds $Ca^{2+}$, $Mg^{2+}$ and $Zn^{2+}$<br>• Is not compatible with other fluorescence techniques, such as internal pH measurement<br>• No mineral phase information |
| SEM | • High-resolution characterisation<br>• Ultrastructures of minerals | • Low cost<br>• Data are comparable<br>• Provide structural information | • No mineral phase information |
| Buoyant weight | • Mineral content determined from the submerged weight of the organism | • Low cost<br>• Noninvasive<br>• More accurate than length or area measurements<br>• Mineral density changes are reflected in measurement | • Seawater density varies when temperature and salinity change<br>• Purpose-made setup needed |
| Radioactive isotopes | • $^{45}Ca$ incorporation rate<br>• $^{14}C$ incorporation<br>• Represents mineralisation process during an experiment | • More accurate than length or area measurements<br>• Synthetic isotopes are specific to the study | • Invasive acid digestion of mineral samples are needed for scintillation measurement<br>• Requires handling of radioactive substances |
| Total alkalinity anomaly technique | • Alkalinity reduction surrounding an organism | • Low cost<br>• Accurate | • Incubation in individual organism required<br>• Not suitable for long-term studies |

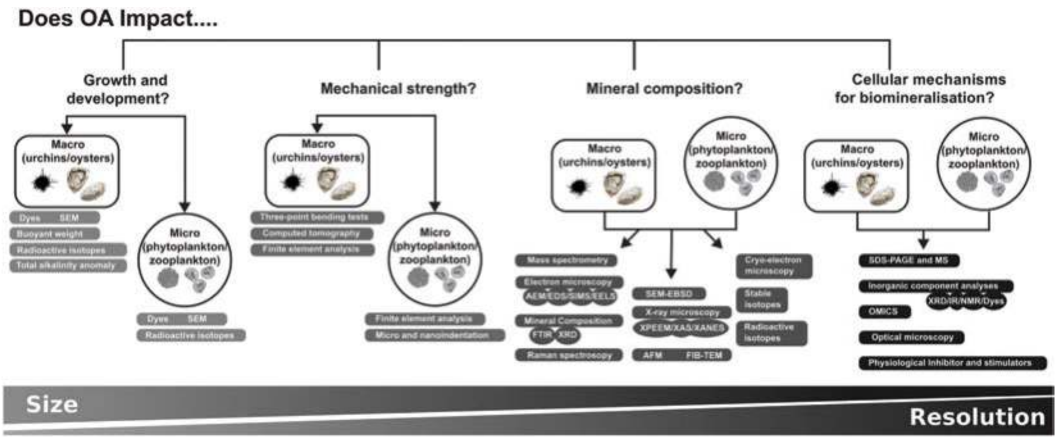

**Figure 1** A schematic representation of analytical methods studying whole-animal growth and development, mechanical strength, mineral composition and cellular mechanisms of biomineralisation, which enables the answering of various levels of questions. These techniques can be strategically applied to macrobiota (e.g. urchin or oysters) or microbiota (e.g. phytoplankton or zooplankton). From left to right, the figure shows the techniques applicable to smaller-scale samples with increasing resolution. At a lower resolution, macrobiota can be measured in terms of various shell growth and development parameters and mechanical properties, while some approach has more limitations with microbiota. At a high resolution, microbiota and macrobiota can be studied for their shell structure and cellular mechanisms for biomineralisation.

## *Growth and development*

When evaluating the impact of OA on biomineralisation, it is important to discriminate among methods measuring gross and net calcareous shell growth as the product of biomineralisation (Figure 2). The term *gross calcification* refers to the biologically controlled process of $CaCO_3$ production through the formation of $CaCO_3$ minerals from a supersaturated solution ($CaCO_3$ precipitation). In contrast, the term *net calcification* is the net effect of gross calcification and dissolution (Cyronak et al. 2016). $CaCO_3$ dissolution or decalcification is the dissolution of $CaCO_3$ minerals in an undersaturated solution. These processes combine to influence net calcification; for example, the upregulation in gross calcification rates of the limpet *Patella caerulea* helps to counteract faster shell dissolution rates (Rodolfo-Metalpa et al. 2011).

### *Dyes*

A range of chemical dyes (e.g. alizarin red, calcein) are used to mark shells or exoskeletons to assess growth over time and have been used in OA studies to determine the impact on calcification in corals, coralline algae and bivalves (Rodolfo-Metalpa et al. 2011, Dickinson et al. 2012, Tambutté et al. 2012, Bradassi et al. 2013, Venn et al. 2013, Fitzer et al. 2014b, 2015b). Calcein labelling is often preferable because calcein was found to be better incorporated into foraminiferan calcite and emitted fluorescence more strongly than the other markers such as alizarin complexone, oxytetracycline and xylenol orange (Bernhard et al. 2004). Calcein has been applied in OA research to assess coralline algal, coral and mollusc growth during experiments (Dickinson et al. 2012, Bradassi et al. 2013, Venn et al. 2013, Fitzer et al. 2014b, 2015b). The techniques are low cost and less invasive than sacrificial shell sampling and the results are readily comparable.

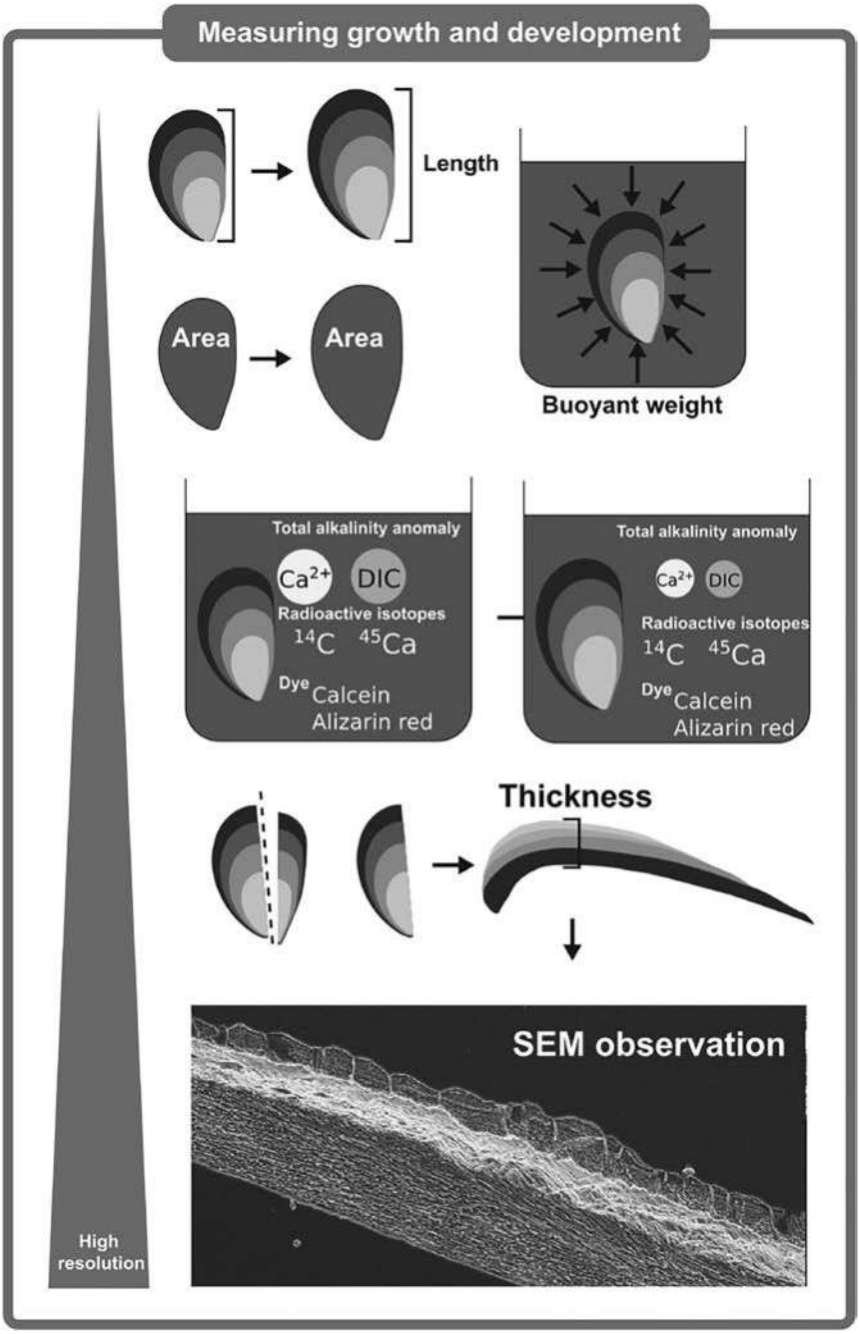

**Figure 2** Schematic representation of techniques for measuring growth and development in biomineralising organisms. The tapering bar on the left indicates the changing level of resolution for each technique. From top to bottom, growth and development can be measured on whole shells and skeletons using techniques such as length and buoyant weight measurements. More sensitive techniques are represented in the middle for the use of dyes, radioactive isotopes and a total alkalinity anomaly technique. At the bottom, sectional surface of a shell at higher resolution can be visualised, and thickness can be measured using techniques such as SEM.

### *SEM*

Abnormalities and morphology can be assessed by optical microscopy. However, scanning electron microscopy (SEM) is required for high-resolution characterisation of biomaterial microstructures and has been used to show modified skeletal phenotypes in a range of species grown under OA conditions (Riebesell et al. 2000, Orr et al. 2005, Iglesias-Rodriguez et al. 2008, Lombardi et al. 2015). The advantage of this approach includes the ability to assess shape and malformation in net growth, while the disadvantages include higher costs and an extended preparation time.

When evaluating net shell growth as the overall product of biomineralisation, one of the simplest and most widely used methods to approximate net calcification is shell and exoskeleton length, as it is both noninvasive and low cost. However, this approach can fail to reveal impacts on gross and net calcification that are not expressed in the overall structure of the skeleton. For example, OA can cause skeletal malformations that can be identified only by microscopy (Langdon et al. 2000, Reynaud et al. 2003, Langdon & Atkinson 2005, Gazeau et al. 2007, Cooper et al. 2008, Jokiel et al. 2008, Ries et al. 2009). This can be partly addressed by including morphometric parameters to resolve shapes, and thickness, for example using 3-dimensional measurements generated from computed tomography (Rühl et al. 2017). It is, therefore, important to consider the net growth of the whole shell or skeleton.

Skeletal growth assessed as annual extension rate ($cm^2/yr$) is commonly used to determine growth rates of calcareous red algae and corals (Marsh 1970), with recent research applying photogrammetric methods based on digital photography and advanced image-processing techniques for nondestructive measurements of area and volume (Mackenzie et al. 2014, Norzagaray-López et al. 2017). Densitometry using X-rays (Table 2) assesses the density of calcified structures (Carricart-Ganivet & Barnes 2007) and has been used to identify growth bands and to calculate growth rates of individuals or colonies (Cooper et al. 2008).

### *Buoyant weight*

To monitor changes in mineral content, buoyant weight determined by immersion is frequently used (Davies 1989, Herler & Dirnwöber 2011). Correction for seawater salinity and temperature variation between measurements is necessary (Fang et al. 2013). The buoyant weight technique is noninvasive (Molina et al. 2005) and remains one of the most common techniques to determine net calcification rate in OA studies, especially in corals (Herler & Dirnwöber 2011). Such an approach has shown that an array of temperate corals (*Oculina arbuscular*), pencil urchins (*Eucidaris tribuloides*), hard clams (*Mercenaria mercenaria*), conchs (*Strombus alatus*), serpulid worms (*Hydroides crucigera*), periwinkles (*Littorina littorea*), bay scallops (*Argopecten irradians*), oysters (*Crassostrea virginica*), whelks (*Urosalpinx cinerea*) and soft clams (*Mya arenaria*) show mixed responses to $CO_2$-induced acidification, highlighting the complexity of biomineralisation responses (Ries et al. 2009).

### *Radioactive isotopes*

Naturally occurring radioactive isotopes can be used to measure growth by spiking organisms with a radiotracer (Sabatier et al. 2012). Liquid scintillation counting is used to amplify the signal and quantify the amount or rate of $^{45}Ca$ being incorporated into the biomineral structure (Rodolfo-Metalpa et al. 2011, 2015). $^{45}C$ is a nonnatural radioactive isotope, so any changes in $^{45}Ca$ quantity represents shell material accretion or loss by the calcification process that occurs during the experiment, and prior calcification is not taken into account (Furla et al. 2000). Similarly, synthetic radioactive $^{14}C$ isotopes enable the measurement of carbon flux related to photosynthesis and calcification (Guo et al. 2009, Li et al. 2015). The $^{45}Ca$ technique has been used in OA research to determine the impact of increasing $pCO_2$ levels on cold-water corals, suggesting that calcification is not disrupted under OA (Rodolfo-Metalpa et al. 2015). Gross calcification rates have been quantified using $^{45}Ca$ in corals,

**Table 2** Summary of emerging techniques on mechanical tests to investigate mechanical properties under OA conditions

| Technique | Measurements | Advantages | Disadvantages |
|---|---|---|---|
| Three-point bending tests | • Elastic modulus<br>• Fracture toughness | • Mimicking predatory attack<br>• Simple operation<br>• Low cost | • Requires a tailor-made device<br>• Test samples are cut into a standard size for testing |
| CT | • Shell thickness<br>• Shell volume<br>• Shell density | • 3-dimensional visualisation of shell shape for morphometric analysis | • Hard to detect planktonic and larval samples (15–1000 μm per pixel)<br>• Standard density calibrated with bone mineral density (BMD, in g/cm$^3$) |
| FEA | • Visualise structural weakness of a material<br>• Provide a numerical model for material properties | • Links nanoindentation data to whole sample measurements<br>• Takes shell shape changes into account<br>• Data can be verified by mechanical tests | • Requires computational skills<br>• Shape information requires simplified experimental data<br>• FEA models need experimental verification |
| Microindentation | • Compressive force using 4-Vickers tip<br>• Hardness<br>• Elasticity modulus | • Broader Vickers tip is less localised than nanoindentation<br>• Lower cost than nanoindentation<br>• Provides microscale spatial resolution | • Localised measurement<br>• Does not represent the shape and mechanical behaviour of the whole structure<br>• Destructive to the sampling area of the specimen |
| Nanoindentation | • Compressive force using Berkovich tip<br>• Hardness<br>• Elasticity modulus | • Sharper Berkovich tip enables higher spatial refinement of measurements<br>• Provides both hardness and elasticity data in one measurement | • Localised measurement<br>• Does not represent the shape and mechanical behaviour of the whole structure<br>• Destructive to the sampling area of the specimen |

limpets, mussels, foraminifera, coccolithophores and oyster larvae (McEnery & Lee 1970, Erez 1978, Satoh et al. 2009, Rodolfo-Metalpa et al. 2011, 2015, Frieder et al. 2016). In contrast, $^{14}C$ has mainly been applied in unicellular organisms such as coccolithophores (Paasche 1963, Nimer & Merrett 1993, Gao et al. 2009), foraminifera (ter Kuile et al. 1989) and diatoms (Li et al. 2015). Advantages include the improved spatial resolution, taking into account material accretion during the incubation period. However, a major disadvantage of this technique is the destructive nature of sampling, unlike other techniques such as buoyant weight that are used to determine calcification rates.

### *Total alkalinity anomaly technique*

Net calcification rate can be measured by determining the amount of $CaCO_3$ taken up by an organism (Gazeau et al. 2007). When an organism precipitates 1 mole of $CaCO_3$ it takes up 2 moles of $HCO_3^-$, thereby reducing the alkalinity of the surrounding seawater over the incubation period (Langdon et al. 2000, Langdon & Atkinson 2005, Gazeau et al. 2007). The total alkalinity anomaly technique has been used as an alternative to the buoyant weight method to determine net calcification rates in a range of calcifying organisms, including corals, mussels and oysters (Langdon et al. 2000, Langdon & Atkinson 2005, Gazeau et al. 2007). A recent study recommends that the technique is more suitable for shorter-term (e.g. day/night) incubations, whereas the buoyant weight method is suitable for longer-term studies when resources are limited (Schoepf et al. 2017). Less frequently, calcium content has been determined directly using mass spectrometry as a proxy for calcification (Wood et al. 2008). Both the total alkalinity anomaly and the buoyant weight techniques are low cost and take into account skeleton malformations; however, there is variability between incubation methods. Promisingly, there is agreement in the results obtained from the various methods, with the major trend of a reduction in net biomineralisation under OA being shown by both techniques (Langdon et al. 2000, Langdon & Atkinson 2005, Gazeau et al. 2007).

## Mechanical tests: Protective function or ability to survive

OA affects the gross and net calcification in many marine calcifiers, and therefore, it would be expected that OA would similarly affect the function of the shell or skeleton. Mechanical properties of shells/skeletons can be quantified by two parameters: (1) hardness (resistance to irreversible deformation) and (2) compressive strength (the force needed to induce cracking). These parameters can be used to evaluate the functional impacts of changes in biomineralisation under OA. For example, changes in these parameters have implications for the vulnerability of reef-forming species and associated ecosystems, as well as consequences for predator-prey interactions (Fu et al. 2016).

### *Three-point bending tests*

As a classical, simplistic and low-cost approach to examine the mechanical features of brittle biomineral structures, three-point bending tests measure the flexural strength and modulus and commonly are used to define material properties in its ability to resist bending. Three-point bending tests have been applied to measure the stiffness of the ambital plates in sea urchins grown in OA, and it was found that there was no significant impact on the protective function of the exoskeleton (Collard et al. 2016). Devices made for the purpose of applying crushing tests, consisting of two supportive beams with appropriate span lengths and a loading beam, can be built according to the specific morphology of the biomineral sample (Guidetti & Mori 2005, Asnaghi et al. 2013). These tests provide relevant information to the protective function of the shell or exoskeleton. The flexural response to a three-point bending test device mimics the deformation response to predatory attack by fish (Guidetti & Mori 2005). This exoskeleton robustness test was applied in the OA study of a sea urchin and revealed increased $p\mathrm{CO}_2$ reduced the defence of a sea urchin to the predator (Asnaghi et al. 2013). If samples are to be directly compared, it is essential to standardise the thickness and sectional area of the test material, which requires additional preparation time to ensure that the biomineral samples are cut to a standard size. The three-point bending tests have the advantage of being able to measure the whole structure mechanical response; their disadvantages are that it can be time consuming, as purpose-made devices may be required for unusually shaped shell structures.

### *Computed tomography*

Computed tomography (CT) and micro-computed tomography (Micro-CT) are powerful, nondestructive techniques to evaluate biomineralised structures. Micro-CT allows 3D visualisation of X-ray image series generated by scanning with axial rotation in small steps. This method enables examination of internal structural features at fine spatial resolution (Li et al. 2016). A micro-CT data set allows a variety of quantifiable measurements, including thickness in terms of pixel distance, volume in terms of voxel counts and density in terms of brightness of each pixel at higher resolutions compared to CT (Fantazzini et al. 2015, Tambutté et al. 2015, Chatzinikolaou et al. 2017).

With these 3D geometric morphometrics and measurements, the growth rate, density and morphological changes due to OA can be investigated. Micro-CT has been applied in OA studies on gastropods (Chatzinikolaou et al. 2017), tubeworms (Li et al. 2014, 2016) and shrimp (deVries et al. 2016) to infer changes in the protective function of the exoskeletons. 3D-model visualisation also enables the analysis of density distribution to understand the engineering of calcareous structures.

Consequently, the presence of structurally vulnerable regions can be identified. Micro-CT analysis has been used in OA to determine the survival of coral through protective exoskeleton function (Tambutté et al. 2015). Exoskeleton porosity often represents shell protective function. In particular, the intertidal gastropods *Nassarius nitidus* and *Columbella rustica* exhibited density reduction in acidified conditions (Chatzinikolaou et al. 2017), while coral skeletons also showed an increased porosity at lower pH values through micro-CT (Fantazzini et al. 2015, Tambutté et al. 2015).

The spatial resolution of most medical micro-CT is sufficient to provide a good measurement for large calcifiers and typically have a resolution of 15–1000 μm per pixel. As a consequence, however, observation of marine plankton and larvae remains as a challenge. Another limitation of micro-CT is the detection sensitivity, which can generate false negatives through thin minerals where regions may appear as empty space in the 3D reconstruction. Therefore, it is important to verify the representative morphology by combining micro-CT with an SEM approach. All density measurements should be calibrated with a standard material that has a known bone mineral density (BMD, g/cm$^3$) in terms of calcium hydroxyapatite and its corresponding pixel intensity for each scan (Li et al. 2014). Because there are no commercially available standards for $CaCO_3$ calibration, density measurements are relative and has limited comparability with other studies.

## *Finite element analysis*

The field of engineering and computational simulation can be applied creatively to understand structural impacts to biominerals caused by OA. In a simulation, any weakness in the architecture is highlighted and the loading capacity can be calculated from the shape and empirical data (Li et al. 2016). Therefore, the application of structural analysis can be performed when shapes and mechanical properties of the biological mineral are both known, providing a holistic picture of how well each calcified material functions as the protective or supportive structure.

The most widely applied numerical tool for computational simulation is finite element analysis (FEA) (Li et al. 2014, 2016). To solve a problem using FEA, the problem is divided into smaller and simpler parts, which are called *finite elements*. By assembling the solution of all finite elements mathematically, a total approximate solution of the large problem can be obtained. FEA enables the mechanical behaviours of complex biomineralised structures to be investigated accurately. The FEA can include the various experimental mechanical properties, such as elasticities of components of the shell structure, as well as simulate the effects of loading, such as the crushing forces associated with a predator attack.

With the diverse calcareous structures being produced by marine organisms, FEA can be applied to assess changes in mechanical performances due to morphological changes. For example, FEA has been applied to understand the mechanical response of a tubeworm under OA, combined with low salinity and warming treatments. This enabled the identification of the most vulnerable region of the tube and the highest risk of fracture failure under predatory attack (Li et al. 2014, 2016). This demonstrates that FEA can be developed as a biologically accurate model to determine the impact of OA on the protective function of calcareous shells and exoskeletons. However, a FEA model, especially when it is 2-dimensionally simplified (Ragazzola et al. 2012), often fails to account for heterogeneity, malformation and shape changes. Alternatively, 3-dimensional models are complex and require advanced computational efforts (Melbourne et al. 2015).

## *Microindentation and nanoindentation*

Biominerals are composed of mineral crystals and an organic matrix framework. As a result, biogenic calcite has been reported to be 50%–70% harder than geological calcite (Kunitake et al. 2012, 2013). Due to the high heterogeneity in the morphology, structure and composition of mineralised shells and exoskeletons, hardness has been widely used as a comparable evaluation of mechanical properties (Beniash et al. 2010, Dickinson et al. 2012, Fitzer et al. 2015b) (Table 2).

The strength of biomineralised structures can be characterised by a crushing or compressive test in which a machine applies and reads compressive force versus displacement. The entire structure of specimens can be used to mimic a predatory attack (Byrne et al. 2014). However, biomineralised structures are typically not homogenous, and using a single point allows a better mechanical understanding of the shell property.

Two main methods can be used to understand the impact of OA on shell mechanical properties (Figure3): (1) microhardness tests can measure Vickers hardness, determined by the ratio of the force applied by the indenter and the surface area of the final indent (Beniash et al. 2010, Dickinson et al. 2012); and (2) nanoindentation, which can measure the hardness and elasticity in a single indent. With the development of a depth-sensing indenter, the hardness and elastic modulus (a measure of stiffness)

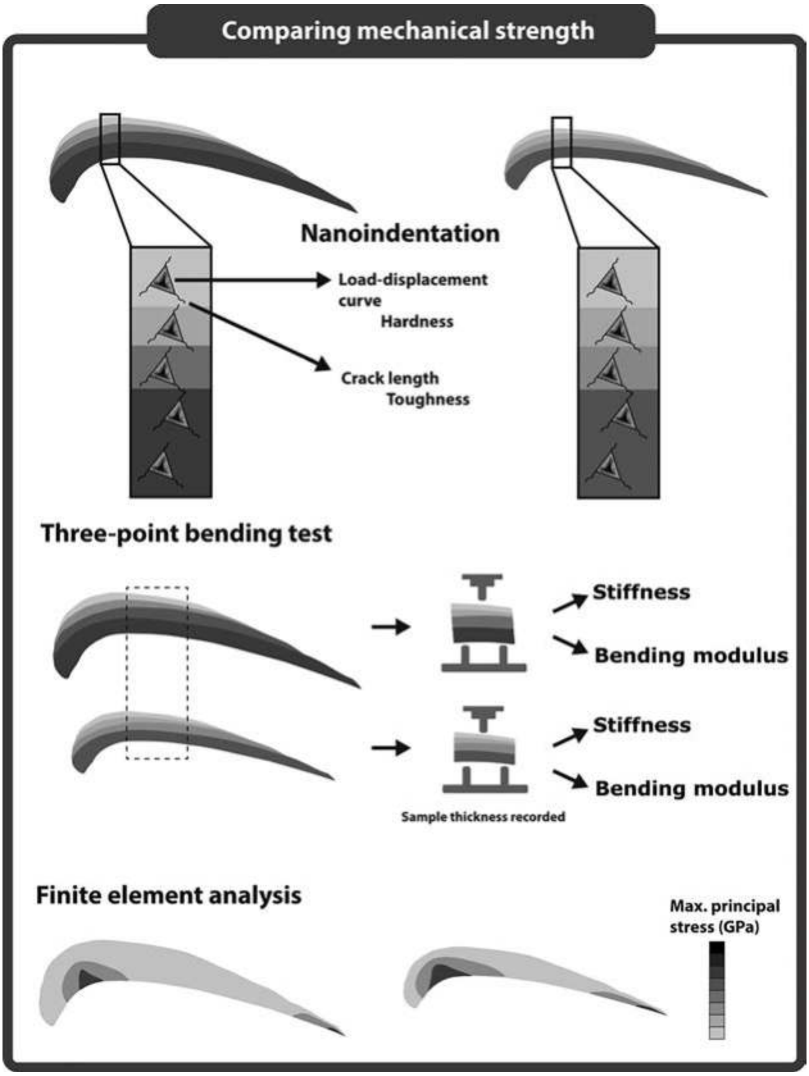

**Figure 3** Schematic representation of techniques to compare the mechanical properties of biomineralising organisms. Nanoindentation and three-point bending are two highlighted techniques for assessing mechanical properties, including hardness, elasticity, fracture toughness and stiffness of biominerals. Microindentation and nanoindentation in the combination of CT and FEA project the impact of OA on the mechanical properties of shells and skeletons during predatory attacks.

measured in pascals (Pa) from each indentation can be obtained from the loading-unloading curve by using the Oliver–Pharr model (Oliver & Pharr 1992). This method enables the measurement of shell hardness and has been used to address how the protective function of several mollusc species grown under experimental OA might be affected (Beniash et al. 2010, Dickinson et al. 2012, Fitzer et al. 2015b). The results indicate no significant impact on microhardness in clams (Beniash et al. 2010) and oysters (Dickinson et al. 2012), but the microhardness in mussels increases (Fitzer et al. 2015b).

The advantage of nanoindentation is its precision at the nanometre scale. Nanoindentation enables spatial refinement, where the mechanical properties profile can be examined (Li et al. 2014). At finer spatial resolution, mechanical features can be associated with the different textures of the mineral (Goffredo et al. 2014). The influence of OA can be reflected in various mineralised layers or structures of the marine invertebrate shell. Nanoindentation enables substantial refinement, such as the hardness and modulus of the tubeworm from the exterior to the interior were mapped by nanoindentation to address questions about the protective function of the structure (Li et al. 2014, Fitzer et al. 2015b). The mechanical properties of the exterior to the interior portion of the tube were shown to decrease under OA compared to the middle portion of a tubeworm (Li et al. 2014). Researchers can analyse the same polished sample using SEM, allowing correlation between structural alteration and mechanical performance. This has been done for mussels (Fitzer et al. 2015b) and tubeworms (Chan et al. 2012, Li et al. 2014) grown in OA for extended periods of time, showing that OA-induced structural alteration may lead to deteriorations in mechanical performance. Both hardness tests have the disadvantage of requiring a highly polished sample surface (Perez-Huerta & Cusack 2009), and sample preparation can be both time-consuming and challenging (Milano et al. 2016).

In addition to hardness, the dimensions of the cracks generated around the indent can be used to determine the fracture toughness combined with the elasticity of the material as shown for bivalves grown under OA conditions (Beniash et al. 2010, Dickinson et al. 2012, Fitzer et al. 2015b). By measuring the lengths of cracks, the plane-strain fracture toughness can be calculated, applying the stress intensity factor (K) for a know compaction IC denoted as KIC. (Lawn et al. 1980, Anstis et al. 1981). However, it is difficult to define the local and bulk fracture behaviours by this technique, which makes it problematical to determine the accuracy of the fracture toughness values given by indentation (Kruzic et al. 2009). This technique has enabled the determination of the impact of OA on shell protective function. The fracture toughness of oyster shells and mussel shells was reduced (as measured by microhardness tests), which confirmed that the calcite shell became more brittle in OA conditions (Beniash et al. 2010, Dickinson et al. 2012, Fitzer et al. 2015b).

## Mineral composition: Biomineralisation mechanisms to enable shell growth

Trace elements present in seawater are incorporated within the shell structure of calcifying organisms and several empirical relationships have been observed between the trace element-to-calcium ratio and environmental parameters of the surrounding water. For example, the Mg-to-Ca ratio of a shell is positively correlated with the temperature of the surrounding water (Nürnberg et al. 1996, Dwyer et al. 2013, Pérez-Huerta et al. 2008, Kamenos et al. 2013). Based on empirical and experimental calibration, several trace element-to-calcium ratios have been observed to reflect the environmental conditions. Trace element-to-calcium ratios, particularly Mg/Ca and Sr/Ca, have been widely used to examine the biomineralisation process (but note that biological activity can influence the elemental composition in the mineral, rather than recording the environmental conditions; see Weiner & Dove 2003). For example, OA has been shown to affect the trace element-to-calcium ratios in corals (Sinclair 2005), foraminifera (Elderfield et al. 1996, Keul et al. 2013, Not et al. 2018), ostracods (Dwyer et al. 2013) and tubeworms (Chan et al. 2015b), but not sea urchins (Byrne et al. 2014) (Table 3). For sea urchins grown under OA and warming from the juvenile to the adult stage, the Mg-Ca ratio was not affected by OA, but as expected, it was altered

**Table 3** Summary of emerging techniques on mineral composition to investigate mechanical properties under OA conditions

| Technique | Measurements | Advantages | Disadvantages |
|---|---|---|---|
| **Elemental analysis** | | | |
| ICP spectrometry | • Trace element-to-calcium ratios (e.g. Mg-Ca, Sr-Ca)<br>• Analyse acid digested samples | • Quantitative<br>• Data are comparable<br>• Coupling with OES, MS or AES provides different sensitivity at various costs | • Destructive sample preparation<br>• Requires elemental standards<br>• More sensitive instruments are more expensive |
| LA | • Element-to-calcium ratios (e.g. Mg/Ca, Sr/Ca)<br>• Analyse solid samples | • Spatial resolution<br>• Less destructive than ICP approach<br>• Data are comparable | • Spatial resolution of >5 μm, which is less than SIMS<br>• Less sensitive than the ICP approach |
| AEM with EDS | • Element-to-calcium ratios (e.g. Mg-Ca, Sr-Ca)<br>• Microanalysis provides a compositional map with spatial resolution | • Low cost and accessible<br>• Spatial resolution<br>• Nondestructive to specimen surface, so it can be followed by EBSD, LA-ICP-MS or nanoindentation | • Requires elemental standards<br>• Detection level at 1000 ppm |
| AEM with WDS | | • Moderate cost<br>• Nanometre-scale resolution | • More expensive than AEM-EDS |
| Structured illumination microscopy | | • Spatial resolution of SEM<br>• Detection sensitivity of 1 ppm | • High cost<br>• Destructive to the sampling area of the specimen |
| EELS | | • 10 ppm detection limit<br>• High-resolution compositional map | • High-cost<br>• Require 10-nm-thick samples<br>• Small region of interest |
| **Mineral composition analyses** | | | |
| FTIR | • Intensity ratio ($I_{max}\nu_2/I_{max}\nu_4$) between the absorption bands<br>• Identifies the presence of aragonite or calcite | • Low cost<br>• Provides a comparable measurement of ACC<br>• Requires ~1 mg of mineral sample | • Semi-quantitative<br>• No spatial resolution<br>• Destructive |

(*Continued*)

**Table 3 (Continued)** Summary of emerging techniques on mineral composition to investigate mechanical properties under OA conditions

| Technique | Measurements | Advantages | Disadvantages |
|---|---|---|---|
| XRD | • Identifies the presence of aragonite or calcite | • Allows for quantification of calcite and aragonite ratios<br>• Peak position suggests Mg content<br>• Powdered sample can be acid-digested to provide elemental data | • Requires more powdered samples than FTIR<br>• No spatial resolution<br>• Destructive<br>• Quantitative measurement requires the addition of $CaF_2$ as an internal standard |
| Raman spectroscopy | • Identifies the distribution of aragonite or calcite | • Spatial resolution<br>• Area of calcite and aragonite is quantifiable<br>• Specimen surface can be analysed by SEM and AEM methods for ultrastructure and elemental contents | • Requires sectional surfaces<br>• Bleaching is necessary to remove organic contaminants<br>• Limited spatial resolution |
| SEM-EBSD | • Identifies the distribution of calcite and aragonite<br>• High-resolution crystallographic orientation data | • Allows visual comparison of mineral crystals<br>• Provides quantifiable data on thickness of polymorphs<br>• Spatial resolution | • Requires fine polishing<br>• Sectional axis and plane of observation must be standardised<br>• Moderate cost |
| XPEEM<br>XAS<br>XANES | • High-spatial resolution composition map<br>• Localises and characterises ACC<br>• Identify mineral phases | • High spatial resolution<br>• Sample preparation enables SEM observation and SEM-EBSD characterisation | • High-cost<br>• Requires fine polishing<br>• Time-consuming |
| AFM | • Records force-distance curve<br>• Visualises fine topographical features | • Nanometre resolution<br>• Simple sample preparation<br>• Possible to measure hydrated samples in electrolyte solution | • High-cost<br>• Small area of interest<br>• Time-consuming |
| FIB-TEM | • Fine spatial resolution<br>• FIB prepares TEM sections | • Selective region of interest<br>• High spatial resolution<br>• Suitable for small samples | • High cost<br>• Time-consuming<br>• Small area of interest |
| Cryo-electron microscopy | • High-resolution study of biological sample after rapid freezing | • High resolution<br>• Provides information on composition and crystallography | • High cost<br>• Requires stabilising detergents for structure |
| Stable isotopes | • Detection of stable isotopes (e.g. δ13C, δ18O, 10B and δ11B) | • Data are comparable<br>• Measures changes in metabolic activity in biomineralisation | • Destructive<br>• Some proxies are not well established |
| Radioactive isotopes | • Calcification rate<br>• Labelling with radioactive isotopes (e.g. $^{45}Ca$ and $^{14}C$) | • Sensitive technique<br>• Specific to experimental exposure | • Continual spiking of radiotracer required during incubation<br>• Destructive |

by temperature (Byrne et al. 2014). When exposed to OA, the Mg-Ca ratio increased in vermetid shells, suggesting a dissolution of aragonite and increase in calcite (Chan et al. 2012, Milazzo et al. 2014). Milazzo et al. (2014) applied inductively coupled plasma (ICP) optical emission spectrometry (ICP-OES) techniques to understand the impacts of OA on calcification as growth, and they suggested that under OA, shell dissolution will occur, with the potential to affect survival through weakened shell protection.

### *Mass spectrometry*

A variety of methods are available to measure the elemental ratios of a biological mineral (Table 3). Basically, calcifying organisms can be measured in a solid phase using techniques such as X-ray fluorescence (XRF) or laser ablation (LA) or in dissolved phase after digestion using a range of ICP spectrometry. Because trace elements are measured within the mineral, several cleaning steps are required to remove organic matter and potential lithogenic contaminations (Martin & Lea 2002). Typically, analysis of a dissolved sample by ICP spectrometry requires the preparation of the shell or skeleton sample by acid digestion, fusion, or ash drying. Techniques for solution analyses include, ICP–optical emission spectrometry (OES), ICP–atomic emission spectroscopy (AES), ICP–mass spectrometry (MS) and multiple collector (MC) ICP-MS. The differences between these ICP spectrometry techniques are the increase in precision of the analyses, the higher resolution (and therefore lower detection limits) of elements up to isotopic measurement with MC-ICP-MS, whereas the disadvantages are the cost and maintenance of the equipment.

### *Electron microscopy AEM/EDS/SIMS/EELS*

Spatial information of elemental distribution in the mineral provides valuable information to predict mechanical properties. Solid-sampling methods have been developed for ICP analysis for this purpose. Electrothermal-vaporisation (ETV) and LA are applied to generate vapour for characterisation. In combination with ICP-OES or ICP-MS, these techniques are suitable for analysis of a solid sample (Limbeck et al. 2017). However, LA-ICP-MS provides resolution of only >5 µm, while secondary ion mass spectrometry (SIMS) distinguishes submicrometre resolution (Becker et al. 2010). Although SIMS has a sensitive detection level of 1 ppm, the technique is not directly quantitative due to its dependence on a solid-state chemical standard, as well as the nonlinear and highly variable nature of the ionisation process of elements in SIMS (Williams 1985). In addition, secondary-ion mass spectrometry (SIMS) can be used to obtain depth profiles of mineral composition of shells (Jeffree et al. 1995). All these methods have an advantage of giving spatial information on the elemental distribution; the differences lie in the resolutions of ICP-MS, ICP-OES and SIMS. ICP-OES is already applied using acid digestion of collected individuals for determination of elemental ratios (Milazzo et al. 2014). The application of SIMS to OA research would enable the analysis of much smaller samples and to examine the response of individual calcifying organisms in terms of growth and survival (Eichner et al. 2017).

The spatial detection of trace elements on a bulk material surface can be achieved through electron microscopy (Müller et al. 2011). Analytical electron microscopy (AEM) with energy-dispersive X-ray spectrometry (EDS) and wavelength-dispersive X-ray spectroscopy (WDS) provides data at the nanometre scale (Newbury 1998). EDS offers an advantage of greater specimen area than the high-resolution method of electron energy loss spectrometry (EELS), which also requires a 10-nm-thick specimen to be prepared. Therefore, EDS is a more efficient and accessible AEM approach for OA research.

Notably, detection levels of AEM-EDS are around 1000 ppm, EELS 10 ppm and structured illumination microscopy 1 ppm. EDS and WDS both enable the microanalysis of biominerals and provide additional spatial information of the elemental profile. The cost of EDS is considerably lower than WDS and has a high acquisition speed. In comparison, the spectral resolution of WDS is superior to that of EDS. These techniques have been applied to address the question of whether OA would have an impact on the calcification of shrimp and tubeworm skeletons, in order to understand the impact on exoskeleton critical function including protective defence against predators (Chan et al. 2012, Taylor et al. 2015). EDS was employed to determine magnesium content in the exoskeleton of shrimps grown under OA with the finding that increased calcium content with lowered pH resulted in a greater Mg/Ca ratio (Taylor et al. 2015). Mg/Ca as an environmental indicator of calcite has been suggested to increase as aragonite saturation decreases (Chan et al. 2012).

Taken together, there has been significant growth in a number of techniques available for quantifying elements present in liquid and solid materials. Some of the surface techniques, such as LA-ICP-MS, and other AEM techniques, such as SIMS, AEM-EDS and AEM-EELS, have different resolutions and sample preparation requirements, which should be considered in the context of experimental objectives. The recent development of MS analytic methods for bioimaging opens opportunities to investigate mineralising tissues at the biomolecule level (Becker et al. 2010). Complementing optical and electron microscopy techniques, as discussed in the following section, these tools will enable a better understanding of the mechanism of OA impacts on the processes involved in the production of biominerals. However, these techniques currently have the disadvantages of requiring sample specific standards for calibration, time-consuming sample preparation, observation confined to a tiny area of interest and the destructive nature of sample analysis.

## *Mineral composition analyses by FTIR and XRD*

Mineral composition characterisation techniques target the comparison of mineral phases, elemental ratios and amorphous $CaCO_3$ to clarify the intricate process of biomineralisation (Figure 4). In the context of OA, it is important to understand the process of biomineralisation mechanisms to appreciate how continued growth will be possible under future environmental change.

Fourier-transform infrared (FTIR) spectra can be used to determine the relative quantity of amorphous $CaCO_3$ from an intensity ratio ($I_{max}\nu_2/I_{max}\nu_4$) between the absorption bands. The major disadvantage of the FTIR approach is its semi-quantitative nature; results can only be compared within the same experimental data set. This method has been adopted in OA research on a marine tube worm, where amorphous $CaCO_3$ content was found to be higher at low pH values (Chan et al. 2012, Leung et al. 2017). Chan et al. (2012) suggest that this result indicates the presence of an active shell repair mechanism when animals are counteracting shell weakening by OA. The advantage of FTIR is that it takes as little as 1 mg of mineral sample and thus may be applied to larval specimens.

The ratio of calcite and aragonite content, that has implications for the vulnerability of shells and skeletons to OA, can be quantified by X-ray diffraction (XRD). This is an advantage over FTIR, but XRD has its own drawback—namely, loss of spatial resolution due to the need for powdered samples. The XRD approach has been used to assess shell or exoskeleton growth under OA. Unless it contains large amounts of Mg, calcite is considered to be less susceptible to dissolution at lower pH values than aragonite (Ries et al. 2009, Chan et al. 2012). OA relevant changes in the thickness of the calcite and aragonite layers were first noted in mussels transplanted into low-pH environments (Hahn et al. 2012). Calcite-aragonite ratios have been shown to change under OA, leading to a thinner and more vulnerable aragonite layer in mussel shells (Fitzer et al. 2015a). The shell thickness index in comparison to the measured thickness of the aragonite or calcite layers uses the thickness, length, height and dry mass of the shell and is considered to produce a lower measurement error compared to direct measurement (Freeman & Byers 2006, Naddafi & Rudstam 2014, Fitzer et al. 2015a). The shell thickness index, in comparison to XRD, has the advantage of being nondestructuive to the sample, but it also has a disadvantage: a loss in spatial resolution.

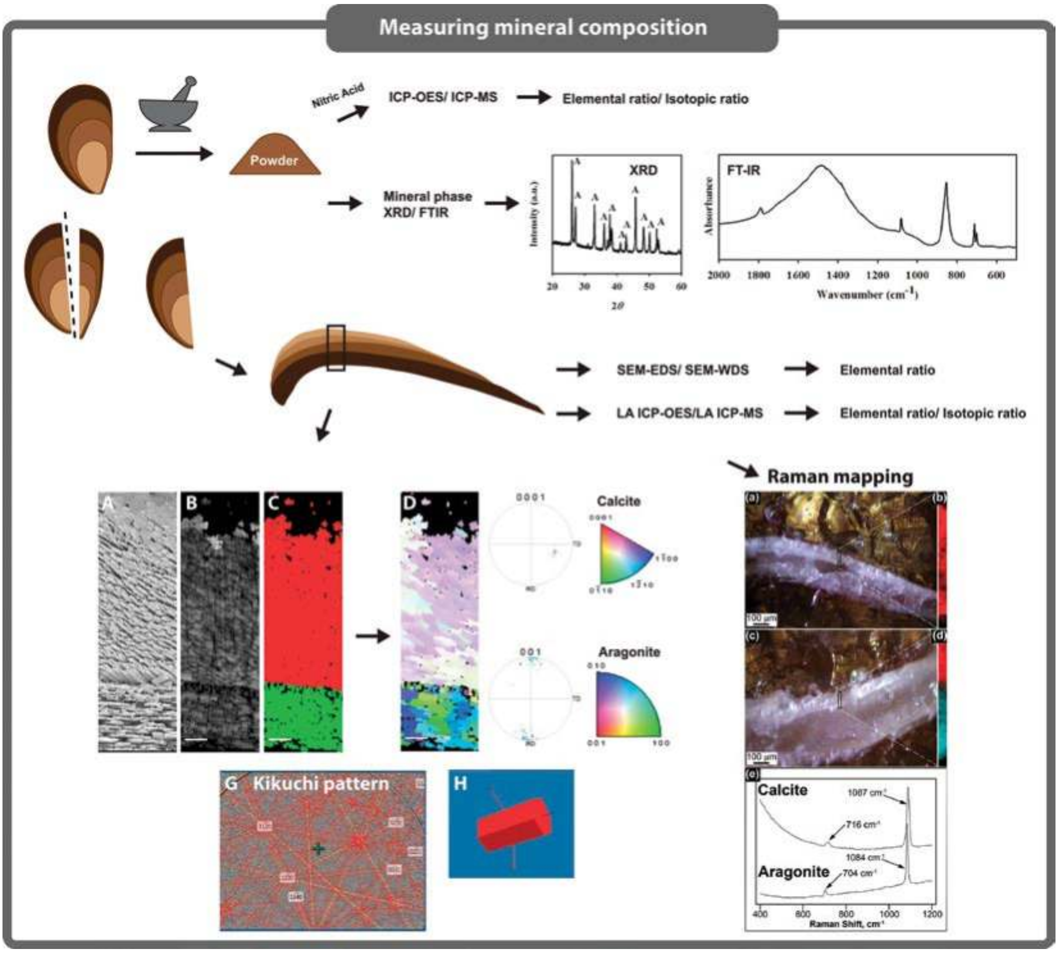

**Figure 4** Schematic representation of highlighted techniques for characterising mineral composition in biomineralising organisms. Shell powder samples are digested prior to mass spectrometry characterisation (e.g. ICR-OES/ICP-MS) for determining elemental ratio or isotopic ratio. Sectional surface of the shell are inspected for elemental ratio mapping using electron microscopy techniques such as SEM-EDS or SEM-WDS; or using mass-spectrometry approaches by LA-ICP-MS or LA-ICP-OES. Additionally, a sample of shell powder provides mineral phase indentification using FTIR or XRD [figures modified from Chan et al. (2012)]. SEM-EBSD, SEM-WDS and Raman spectroscopy are highlighted as techniques to determine the mineral composition and crystallographic orientation in a mussel shell to determine the impacts on shell growth under OA as an alternative to techniques such as ICP-OES or ICP-MS to determine elemental or isotope ratios in biominerals. SEM-EBSD figure data taken from Fitzer et al. (2014a). Secondary electron images of the crystal structure from an etched (A) and polished (B) sample, the mineral composition can be seen in the phase map where calcite is shown in red and aragonite in green (C). The crystallographic orientation map (D), corresponding pole figures (E) and colour keys (F) are indicated for calcite and aragonite. EBSD uses Kikuchi patterns to identify the mineral phase (G) and the crystallographic orientation (H). Raman mapping figure modified from Chan et al. (2015b). Raman microscopy has been used to provide photomicrographs of younger (a) and older regions (c), of a juvenile tubeworm, phase maps indicate regions of aragonite only (b) and aragonite and calcite (d) in the tube. A Raman spectra (e) of aragonite and calcite has been measured in the same specimen (c).

## *Raman spectroscopy*

Raman spectroscopy is a nondestructive technique that enables molecular bonds and mineralogical information to be precisely characterised at a submicron resolution. By illuminating a sample with a monochromatic laser beam, a Raman spectrum is generated that contains unique peaks that are diagnostic of mineral polymorphs due to their characteristic Raman shifts (Eisenstein et al. 2016). Structural components, such as calcite, aragonite and collagen, have been identified and mapped with resolution as fine as 1 μm (Eisenstein et al. 2016, Taylor et al. 2016). Advantages of Raman spectroscopy over other spectroscopic methods, such as FTIR, include the improved spatial resolution and the direct relevance of this method for biomineralisation, as well as the potential to examine samples in their native state (Eisenstein et al. 2016, Von Euw et al. 2017). This technique is considered a complementary method to FTIR, and is perhaps more suitable for OA studies. Raman microscope imaging has been applied to OA research to identify the mineral composition and polymorphic forms to assess rates of calcification under increasing $p\mathrm{CO}_2$ in coralline algae and limpets (Kamenos et al. 2013, Langer et al. 2014). For instance, Raman mapping of the shells of limpets from a $CO_2$ vent demonstrated that the polymorph distribution pattern is maintained despite living at low pH (Langer et al. 2014). In coralline algae, although calcification continues under OA, Raman has identified disorder in the molecular position of the carbonate ions, which suggests a weakened skeletal structure (Kamenos et al. 2013). These applications were used to assess exoskeleton structural weaknesses, which can affect the protective function of the calcified structures under OA.

## *SEM-EBSD*

Electron backscatter diffraction (EBSD) is widely used to determine the crystallographic orientation of biogenic minerals. EBSD provides additional information to precursory SEM imaging of shell dissolution or exoskeletal microstructure, as it allows for the examination of microstructure at the individual crystal level. The technique identifies Kikuchi patterns (Kikuchi 1928, Nishikawa & Kikuchi 1928) as scattered electrons are reflected as per Bragg's law from the crystal lattice onto a phosphorus screen. It was first used to observe the impact of OA on the shell ultrastructure of the mussel (*Mytilus galloprovincialis;* Hahn et al. 2012) and was further applied across a broad range of species, including argonauts (Wolfe et al. 2013) and corals (Hennige et al. 2015). The effects on crystalline structure identified using this technique in OA research have been used to address the question of how changes in seawater environment can affect the orderly arrangement of shell or exoskeleton structures, which has an implication for the animal's ability to survive.

## *X-ray microscopy XPEEM: XAS and XANES*

An alternative emerging technique for determining the mineral composition of marine skeletons is high-spatial resolution synchrotron X-ray photo emission electron microscopy (XPEEM) combined with X-ray absorption spectroscopy (XAS) (Fitzer et al. 2016). The benefits of the XPEEM and XAS over SEM is the high level of spatial resolution, as well as the fact that it can detect without the need for an energy filter by measuring the secondary electrons yield as a function of photon energy. This technique can be applied alongside EBSD to identify mineral phases throughout the shell structure (Fitzer et al. 2016). X-ray absorption near edge structure (XANES) and XPEEM techniques use the principles of X-ray absorption fine structure (XAFS), which interpret the scattering of photoelectrons emitted from an absorbing atom in a structure when excited by high-energy photons (Politi et al. 2008, Fitzer et al. 2016). XANES has been used as a tool to examine the phase transformation mechanisms of amorphous $CaCO_3$ into calcite, particularly in sea urchin larval spicules (Politi et al. 2006, 2008, Gong et al. 2012). Recently, XPEEM combined with XAS has been used as a tool to examine amorphous $CaCO_3$ in mussels reared under OA conditions (Fitzer et al. 2016) showing more induced amorphous $CaCO_3$ with less crystallographic control over shell formation. This technique was applied to address the question of OA impact on biomineralisation and shell repair to determine the protective function of the shell under changing environments (Fitzer et al. 2016). The technique requires the embedding and fine-polishing of samples, similar to SEM-EBSD preparation (Politi et al. 2008, Perez-Huerta & Cusack 2009, Fitzer et al. 2016). XANES and XPEEM have the advantage of providing high spatial resolution to locate amorphous $CaCO_3$ embedded within the shell structure when applied in combination with SEM techniques (Politi et al. 2008). Disadvantages include the high instrumentation cost and lengthy sample preparation time.

## *AFM*

Atomic force microscopy (AFM) provides atomic resolution analysis of material properties. As a type of scanning probe microscopy, AFM scans and interacts with a sample directly using a tip that is connected to a cantilever spring. The vertical deflection and the force-distance curve are recorded by a piezoelectric translator (Butt et al. 2005). In tapping mode, AFM generates fine topographical images with nanometre resolution. The time-dependent relationship between applied pressure (stress) and deformation (strain) represents viscoelastic properties (Butt et al. 1995) that enable the measurement of local mechanical properties.

Easy sample preparation and high resolution are the major advantages of using AFM over conventional microscopy methods (Butt et al. 1995). The typically small interacting surface for AFM must be smooth and homogeneous, requiring polished and etched surfaces similar to EBSD sample preparation (Dalbeck et al. 2011). Therefore, AFM complements the observations of SEM-EBSD analysis, which can provide high-resolution textural data for OA studies (Dalbeck et al. 2011). AFM performed in the presence of an electrolyte solution is possible (Butt et al. 1995), and therefore enabling better biological relevance. In order to obtain comparable regions of interest, correlative SEM or light microscopy data are often helpful to effectively navigate at AFM resolution (Sikes et al. 2000). AFM has yet to be applied to determine the impact of OA on biomineralisation. Once applied, this technique will provide a correlation with EBSD data to address the question of biomineralisation mechanisms in shell growth (and hence survival).

## *FIB-TEM*

The finest biological observations have been achieved via transmission electron microscopy (TEM), providing resolutions of nanometres down to below 1 angstrom (Nellist et al. 2004), exceeding superresolution microscopy. In addition, TEM is an important characterisation tool that collects XRD with a micrograph, enabling the subcellular features and location of crystals to be analysed together. A nanofabrication technique using the focussed ion beam (FIB) system has emerged as a powerful tool for precise TEM specimen preparation, where milling and cutting of a sample is performed inside an SEM or scanning ion microscopy (SIM) (Titze & Genoud 2016). This preparation approach overcomes the technical challenges of manual preparation of ultrathin TEM sections, with the localisation of the region of interest, and reduces the risks of sample loss (Chan et al. 2017).

Suzuki et al. (2011) revealed the details of five microstructures in the limpet shell using FIB-TEM. The FIB technique was used to separate each microstructure in cross section to determine crystal morphology and orientation. The FIB technique is powerful in handling tiny larval or juvenile shells (Yokoo et al. 2011, Chan et al. 2015a, 2017), and reduces costs of analysis time for TEM on samples with poor orientation or an unfocussed area of interest. FIB-TEM ensures a consistent cutting angle at the nanoscale, so providing comparable observation of a larger number of experimental samples.

Depending on institutional resources, fine spatial resolution, long-hour procedures performed using FIB-TEM can be costly in a centralised facility. In summary, FIB-TEM is currently a qualitative observational method, but it has the potential to be applied in a more quantitative setting.

## *Cryo-electron microscopy*

In cryo-electron microscopy, biological samples can be visualised by a freeze fracture process that is achieved by rapid freezing of fixed tissue samples by vitrification (Alfredsson 2005). A hydrated sample that is close to the native state can be observed in high resolution without the requirement of destructive conventional preparation procedures for SEM and TEM (Levi-Kalisman et al. 2001, Khalifa et al. 2016, Thompson et al. 2016). Electron microscopy also enables XRD characterisation essential for identification of minerals. Ice from humidity in the environment can contaminate the sample; therefore, samples must be prepared after vitrification (Thompson et al. 2016). Technical disadvantages associated with cryomethods include the need for stabilising detergents for structure (Singh & Sigworth 2015) which, in addition to its high cost, will make the application of this technique challenging for large-scale OA experiments.

## *Stable isotopes*

Biogenic stable isotopes have been used extensively to reconstruct the paleaoclimates in terms of temperature, pH and salinity (Lear et al. 2000, Parkinson et al. 2005, Ghosh et al. 2006, McConnaughey & Gillikin 2008, Martin et al. 2016, Stewart et al. 2016). They can also be used to understand biomineralisation mechanisms of ion transport at the site of calcification (Furla et al. 2000, Rae et al. 2011, Allen et al. 2012, Allison et al. 2014). The detection of Mg, Sr and Ca, the detection of the isotopes, $\delta^{13}$C, $\delta^{18}$O, $^{10}$B and $\delta^{11}$B requires acid digestion prior to mass spectrometry analyses (Krief et al. 2010). Here, we list some of the target isotopes that have promise for OA research.

Quantification of isotopic elements can be applied to detect the consequence of stress on calcification pathways (Rae et al. 2011, Allison et al. 2014, Stewart et al. 2016). Brachiopods, in particular, form their exoskeletons in good isotopic equilibrium with the seawater (Parkinson et al. 2005). Because pH is dependent on two boron species: boric acid ($B(OH)_3$) and the borate ion ($B(OH)_4^-$) (Hemming & Hanson 1992, Stewart et al. 2016, Zhang et al. 2017), the species of boron isotopes found in shells represents the dissolved inorganic carbon (DIC) chemistry of the calcification fluid (Allison et al. 2014). Stable isotope techniques have been applied in OA research to understand the mechanisms of biomineralisation—specifically, whether material is laid down under control by the organism, irrespective of the seawater isotopes (Krief et al. 2010). For example, seawater pH affects the skeletal $\delta\ ^{13}$C and $\delta\ ^{18}$O in corals, but there is an offset in the $\delta\ ^{11}$B between the calcified material and that of seawater, suggesting control of biomineralisation by ion-transport enzymes (Krief et al. 2010). This technique addresses the question of calcification mechanism change under OA and whether there is a reduced metabolic incorporation of isotopes through enzyme control (hence reduced growth and survival under OA). The influence of carbonate ion concentration on $\delta\ ^{13}$C and $\delta\ ^{18}$O is still being explored, particularly in foraminifera (Spero et al. 1997).

Isotopic approaches have the disadvantage of requiring a relatively large amount (~2 mg) of biogenic $CaCO_3$ powder. Sample preparation with micromilling is time consuming and can be technically challenging, especially when investigating different polymorphs and seasonal growth bands in smaller specimens (Stewart et al. 2016). Advances in stable isotope techniques will consist of improved ways of separating organics from biominerals, micromilling samples for biomineral powder, and LA methods that increase spatial resolution of measurements (Fietzke et al. 2010, Wall et al. 2016).

## *Radioactive isotopes*

In addition to using $^{45}$Ca for estimation of calcification, radioactive isotopes can contribute to a mechanistic understanding of the calcification process. Furla et al. (2000) used a double radioactive isotope experimental design ($H^{14}CO_3$ and $^{45}$Ca) to show inorganic carbon transport. Comprehensive measurement of both the DIC species and Ca for calcification was accomplished in terms of net radioactivity by $^{14}$Ca and $^{45}$Ca (Furla et al. 2000). These data also unraveled the carbonate-concentrating mechanisms within coral cells (Furla et al. 2000).

The use of radioactive isotopes ($^{45}$Ca, $^{14}$C) is specific and sensitive to experimental conditions. Moreover, the maintenance of radioactive substances can be challenging. Before adopting the use of radioactive isotopes within an experimental culture, a protocol must be optimised to label specimens adequately and avoid contamination. Therefore, even though the approach is quite well established in environmental geochemistry (Parkinson et al. 2005, Ghosh et al. 2006, McConnaughey & Gillikin 2008), the disadvantages of requiring continual radioactive tracer application and the destructive nature of the sample digestion by acid mean that it has yet to be applied more widely in OA studies (Furla et al. 2000).

## Cellular biomineralisation mechanisms

The processes by which organisms control the substrate for calcification are complex and can occur internally within tissues, or outside the organism, but both need to modify the seawater chemistry for calcification to take place (Roleda et al. 2012). It is thought that $HCO_3^-$ is the choice of substrate for biomineralisation, which can be taken directly from seawater or metabolised from $CO_2$ (Roleda et al. 2012). The mechanisms revolve around producing an abundance of ions and the right conditions to favour the precipitation of $CaCO_3$ from available $Ca^{2+}$ and $CO_3^{2-}$ (Roleda et al. 2012). An understanding of biomineralisation mechanisms under forecasted OA conditions will require the use of a wide range of techniques (Figure 5), but it also works at different levels, from genes to organisms and ecosystems. This can be achieved by taking advantage of established techniques from other disciplines. For example, methods to culture larval sea urchin primary mesenchyme cells facilitate the study of the calcification process *in vitro* (Basse et al. 2015). Identifying and evaluating the roles of organic molecules in shells is a major topic in biomineralisation as the mechanical properties of shells are highly influenced by their 1% content of organic components. In the context of OA impacts on marine calcifiers, the response of organic molecules provides insight into cellular mechanisms for the ability to reproduce and develop and can be applied to all marine organisms, irrespective of size (Figure 1, schematic of question versus scale). Mechanisms of biomineralisation are largely unresolved and vary from species to species.

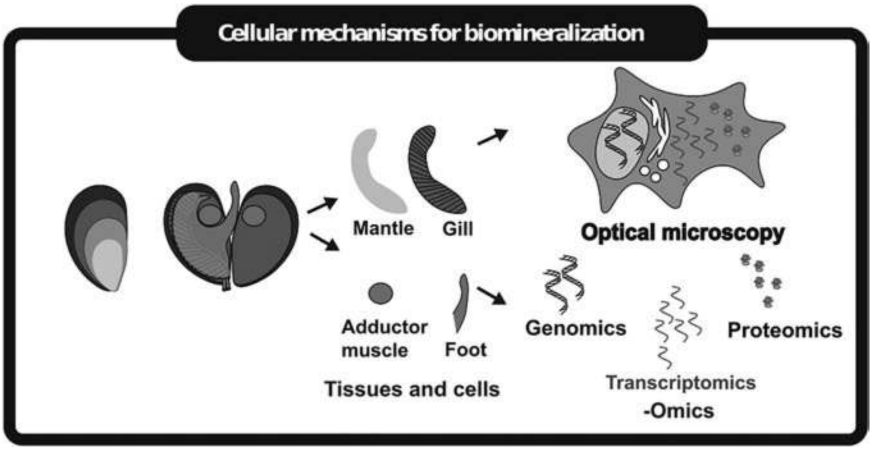

**Figure 5** Schematic representation of techniques to examine the cellular mechanism of biomineralisation. Techniques with omics and optical microscopy are established techniques that could be applied to various tissues and cells to determine the impact of OA on molecular biomineralisation.

## *SDS-PAGE and MS*

Shell protein extraction is achieved by recovering the protein from decalcified shell. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE), or 2-dimensional gel electrophoresis enables a comparison of protein profiles. In addition, mass spectrometry (MS) enables the identification of proteins from available databases. As marine organisms studied in OA research are usually not model-organisms, protein identification is challenging. Protein purification, protein sequencing and protein digestion may be required in the identification process (Marxen et al. 2003, Suzuki et al. 2004). When a large protein (more than 30 kDa) needs to be identified, cloning methods can be used to recover the nucleotide sequence for deduction of the protein sequence (Miyamoto et al. 1996, Samata et al. 1999, Suzuki et al. 2009, 2011). Many genome and transcriptome databases of calcifying invertebrates generated by next generation sequencing are also available as open resources (Takeuchi et al. 2012, Zhang et al. 2012).

MS is also a promising technique to understand shell proteins (Table 4). The MS/MS spectra of peptides allow the determination of amino acid sequence without a need for a protein sequencer, and MS/MS has become a low-cost and high-throughput technique. The combination of MS/MS and databases from next-generation sequencing is dramatically increasing the efficiency of protein identification (Joubert et al. 2010, Marie et al. 2010, 2011). The potential disadvantage of generating big data from the high-throughput process is covered in more detail in the next section. These techniques have been applied to show the proteome responses of invertebrates grown in OA conditions. For example, the shell matrix proteins of the larval pacific oyster (*Magallana gigas*) were observed to decrease under OA (Harney et al. 2016).

SDS-PAGE and MS offer advantages of low-cost and (in the case of MS) high-throughput protein identification to understand why physiological responses may be influenced by OA. The disadvantages of these techniques include time-consuming sample preparation to extract and purify proteins for analysis and production of big data, which can be difficult to interpret.

## *Insoluble organic component analyses using XRD, IR and pyrolysis NMR, and dyes*

Insoluble organic components in the shell, such as chitin, are an essential polysaccharide that connects organic matrices and the initial deposition of the mineral (Nakayama et al. 2013); it serves as a scaffold for organic materials during the deposition of minerals. For example, the molluscan periostracum is made of chitin and it serves as a waterproof layer of a calcification compartment. Chitin is commonly found in the forms of $\alpha$ and $\beta$-chitin. Crustaceans use $\alpha$-chitin in their exoskeletons and molluscs use $\beta$-chitin in their shells, as such, chitin is an essential additive to greatly improve the mechanical properties of biomaterials. Due to the insoluble and organic nature of chitin, the impact of OA on chitin content is currently unknown. There are many techniques to identify chitin, including XRD (Weiner & Traub 1980, Levi-Kalisman et al. 2001, Falini et al. 2003), infrared (IR) spectroscopy in the fingerprinting region (700–1800 $cm^{-1}$) (Pearson et al. 1960) and nuclear magnetic resonance (NMR) or MS detection of the glucosamine hydrochloride after hydrolysis (Nakayama et al. 2013). The analysis of pyrolysis (thermal decomposition of materials in a vacuum) gas chromatography–mass spectrometry (GC-MS) is able to identify characteristic chitin decomposition markers (Furuhashi et al. 2009). However, many other contaminants (such as proteins) produce a complex of unknown peaks that make the identification of chitin in biominerals difficult and, in the case of insufficient crystallinity, a clear diffraction pattern may be hard to obtain. Recently, a colorimetric assay of chitin has been developed to quantify chitin (Katano et al. 2016). The workers found that upon complete hydrolysis of chitin in strong acid (5M HCl), characterisation of depolymerised glucosamine is possible using colorimetry at the absorbance maximum at 750 nm. The method

**Table 4** Summary of emerging techniques on cellular biomineralisation mechanisms to investigate mechanical properties under OA conditions

| Technique | References | Measurements | Advantages | Disadvantages |
|---|---|---|---|---|
| SDS-PAGE and MS | Miyamoto et al. (1996), Samata et al. (1999), Marxen et al. (2003), Suzuki et al. (2004), (2009), (2011) | • Characterises shell proteins | • Established protocol for protein identification<br>• Low cost and high throughput of samples | • Sensitivity insufficient to detect shell proteins occurring at low quantity<br>• Protein extraction and purification is time consuming<br>• Difficult to interpret sequences from nonmodel marine organisms |
| Insoluble organic component analysis using XRD | Weiner and Traub (1980), Levi-Kalisman et al. (2001), Falini et al. (2003) | • Characteristic spectroscopy correlated to chitin | • Provides evidence on the presence of chitin<br>• Analyses insoluble solid samples | • Destructive<br>• Sufficient sample is hard to obtain<br>• Information has poor relevance to the cells and tissue associate with chitin |
| Insoluble organic component analysis using IR spectroscopy | Pearson et al. (1960), Suzuki et al. (2007) | | | |
| Pyrolysis NMR GC-MS | Furuhashi et al. (2009), Nakayama et al. (2013) | • Detects decomposition product of chitin after chitinase action | • Analyses the digested products<br>• Digested product peaks can be quantified and compared | • Requires chemical standards of digested products<br>• Protocol optimisation can be time-consuming |
| Colorimetric assay for acid hydrolysate of chitin | Katano et al. (2016) | • Detects decomposition product of chitin after acid hydrolysis | • Low cost<br>• Quantitative<br>• Simple protocol | • Destructive<br>• Cannot distinguish forms of chitin<br>• Spatial information is lost |
| Calcofluor-white | Shillito et al. (1995) | • Visualises chitin in relation to cells and tissues | • Nondestructive to tissues and cells<br>• Low cost<br>• Commercially available | • Also binds to cellulose<br>• Also binds to N-acetyl-D-glucosamine and sialic acid |
| Wheat-germ agglutinin (WGA) | | | | |
| CBD-GFP | Weiss and Schönitzer (2006), Nudelman (2007), Chan et al. (2018) | | • Nondestructive to tissues and cells<br>• Specific to chitin | • Requires a time-consuming bioengineering approach to express and purify CBD-GFP |

(*Continued*)

**Table 4 (Continued)** Summary of emerging techniques on cellular biomineralisation mechanisms to investigate mechanical properties under OA conditions

| Technique | References | Measurements | Advantages | Disadvantages |
|---|---|---|---|---|
| OMICS – transcriptomics | Takeuchi et al. (2012), Zhang et al. (2012) | • mRNA of expressed genes | • Assesses the molecular pathways of the organism from expressed genes or proteins<br>• Provides a whole physiological picture | • mRNA presence may not represent protein activities<br>• Tissue-specific response<br>• Costly<br>• Identification of transcripts in a nonmodel marine species is difficult |
| OMICS – proteomics | Dineshram et al. (2015) | • Total protein profile | | • Shell proteins occurring at low quantity of 5%<br>• A high-sensitivity method like iTRAQ is very costly<br>• Identification of protein in a nonmodel marine species is difficult |
| Cellular pH imaging | Venn et al. (2011), Stumpp et al. (2012), Tambutté et al. (2015), Chan et al. (2017), Toyofuku et al. (2017) | • Intracellular pH indicated by a pH sensitive ratiometric probe<br>• Visualises the sites of biomineralisation | • Examines living organisms<br>• High swpatial resolution | • Not well established and requires optimisation and customisation<br>• Ratiometric pH probes require calibration |
| Physiological inhibitors and stimulators | Toyofuku et al. (2017) | • Enables examination of the physiological response of a nonmodel organism<br>• The importance of a biological pathway is evaluated by a specific inhibitor | • Applies to nonmodel organisms | • Some inhibitors are not specific to a single pathway<br>• Action of inhibitors should be verified by a known physiological measurement |

requires small amount of sample (10 mg), it is low cost, simple and quantitative. However, the detection is robust and cannot distinguish polymorphs and spatial distribution of chitin.

Chitin can be visualised microscopically by calcofluor white, which binds strongly to cellulose and chitin, and wheat-germ agglutinin (WGA), which binds to N-acetyl-D-glucosamine and sialic acid (Suzuki et al. 2007). Due to the nonspecific nature of calcofluor-white and WGA (Shillito et al. 1995), more specific detection is accomplished by using chitin-binding domain fused with green fluorescent protein (CBD-GFP), as shown in the larval shell of *Mytilus galloprovincialis* (Weiss & Schönitzer 2006) and the prismatic layer of *Atrina rigida* (Nudelman et al. 2007). Quantifying the expression of the chitin synthase gene is an alternative approach to measure chitin production (Cummings et al. 2011).

While the role of chitin may be essential in providing a waterproof cover and biomineralisation framework to the shell formation process, the plasticity of chitin synthesis under OA environmental stress has not yet been investigated. Chitin has many important biological roles in a diverse taxonomic group of animal models (Lee et al. 2011); therefore, the detection of chitin could provide valuable information on both the structural and functional responses to OA. The disadvantages of XRD, IR and pyrolysis NMR or GC-MS techniques for chitin analysis, such as the low abundance of organic materials in calcareous structures (and therefore time-consuming sample preparation), may limit the application of this approach to future OA studies. On the other hand, visualising chitin with dyes such as calcofluor white and WGA are prone to nonspecific reactivity to other molecules than chitin. The more specific CBD-GFP labeling requires a bioengineering protocol to express and purify the chitin probe.

## *Omics*

Omics studies are generating ‘big data’. However, these data cannot be simply used as proxies of fitness (Feder & Walser 2005). As a consequence, little information can be extracted from purely exploratory studies (e.g. comparisons between two OA scenarios). A more powerful approach involves the analysis of the data to test a hypothesis based on physiological or ecological experiments. For example, De Wit et al. (2016) filtered a large-scale transcriptomic database to select genes following the same pattern identified at the physiological level in copepods exposed to OA (Thor & Dupont 2015, De Wit et al. 2016). The future use of omics to investigate the effects of OA on biomineralisation is promising, especially using the integration of an omics technique with other physiological end points.

The three main omics approaches to consider are transcriptomics, proteomics and metabolomics. Transcriptomics is a study of messenger ribonucleic acid (mRNA) and actively expressed genes, while proteomics investigates the total protein profile and metabolomics capture the biochemical status of an organism.

Transcriptomic changes can provide insights into genetic pathways involved in calcification by comparison of gene expression (e.g. at different stages of calcification or under different environmental conditions). That is, when applied in a time series, changes in transcriptomes of developing larvae provide useful information relevant to the onset of biomineralisation (Zhang et al. 2012). De Wit et al. (2018) used OA as a tool to delay calcification in an early stage of oyster development and using a time series were able to identify genes involved in larval shell calcification (De Wit et al. 2018). Under OA, transcriptomic studies are used to assess the physiological capacity of organisms by studying not just the biomineralisation molecular pathways but also the other related pathways giving a complete picture in understanding the consequences of living in a high-$CO_2$ ocean (Todgham & Hofmann 2009).

Proteomics investigates the total protein profile. Because proteins are the active functional units of an expressed gene, these data are closer to the organism at the functional level and phenotype. Proteomes can be altered by OA, as shown by different calcification protein expressions in oysters (Dineshram et al. 2015). The organic matrix proteins that are associated with shell deposition have been profiled in corals (Drake et al. 2013), oysters (Suzuki & Nagasawa 2013) and blue mussels (Suzuki et al. 2011), although this information has not been profiled in the OA context.

As with the transcriptome, some precautions should be taken during the interpretation of a proteome. The quantity of a protein commonly cannot be directly linked to the fitness of an organism as regulatory posttranslational modifications play a key role (Mann & Jensen 2003). This is an essential consideration for the study of shell proteins, which are often heavily glycosylated, phosphorylated or tyrosine-sulfated as required for calcium binding (Zhang & Zhang 2006).

A major disadvantage of applying omics to the study of biomineralisation is the low abundance of about 5% organic content in calcareous structures (Zhang & Zhang 2006). In order to isolate sufficient protein or polysaccharide for analysis, a large amount of shell must be used. In addition, the extraction and purification of the organic content is greatly influenced by decalcification, and the shell can often contain organic impurities (Watabe 1965). Researchers should be aware of technical limitations using different characterisation techniques; for example 2-dimensional gels have a lower sensitivity than isobaric tags for relative and absolute quantitation (iTRAQ) analysis (Wiese et al. 2007). In addition, the interpretation of omics data is highly dependent on genomic information; therefore, it remains as a challenging method for nonmodel organisms.

## *Cellular pH imaging*

When live imaging is conducted, inverted microscopy enables living marine organisms to be fully submersed in seawater during observation (Venn et al. 2011, Stumpp et al. 2012, Tambutté et al. 2015, Chan et al. 2017). In some imaging methods, synthetic ratiometric images are generated by sequential images of the same region of interest. Mobile organisms can be immobilised (e.g. 2%–4% agarose seawater or using micropipettes) to enable image acquisition of the region of interest. For longer periods of observation, a perfusion chamber is necessary to remove metabolic waste and allow exchange of aerated experimental seawater with enriched $CO_2$.

Fluorescent microscopy has been applied to visualise the calcification compartment during mineralisation at a low seawater pH using markers including calcein, alizarin and calcofuor white for *in situ* analysis of calcification and tracking of calcification, as shown for coralline algae (Lewis & Diaz-Pulido 2017). Newly deposited minerals can be quantified from their fluorescent appearance at their respective excitation (Exλ) and emission wavelengths (Emλ) (e.g. alizarin: Exλ = 530–560 nm, Emλ = 580 nm; calcein: Exλ = 494 nm, Emλ = 517 nm; calcofluor white: Exλ = 365 nm, Emλ = 435 nm). Calcein is a preferable marker because of its high efficiency, noninvasiveness (Lewis & Diaz-Pulido 2017) and relatively low cost. In addition, the fluorescent region can be isolated and characterised using the techniques described for measuring growth and development in the earlier sections of this review.

The heterogenous distribution of carbon sources (e.g. $CO_3^{2-}$ ions at the calcification site) can be monitored by measuring intracellular pH (de Nooijer et al. 2008, Venn et al. 2011, Venn et al. 2013, Tambutté et al. 2015). Similar to the carbonate dynamics in the ocean, a shift in pH influences the DIC abundance in the biomineralisation compartment, in terms of $CO_3^{2-}$ and $HCO_3^-$. As shown in foraminifera, pH of the site of calcification increases during calcification, while the surrounding ambient pH decreases probably through active proton pumping (Toyofuku et al. 2017). A higher pH value facilitates the conversion of $CO_2$ and $HCO_3^-$ to $CO_3^{2-}$ (Toyofuku et al. 2017), and both the $CO_3^{2-}$ concentration and $CaCO_3$ saturation state can then be calculated (Venn et al. 2011, 2013, Tambutté et al. 2015). Furthermore, it is possible to estimate the number of emitted protons by image processing of pH-sensitive ratiometric microsopy. Ratiometric fluorescent dyes enable the monitoring of intracellular and extracellular pH (Chan et al. 2015a, Comeau et al. 2017b, Toyofuku et al. 2017). Several pH-sensitive dyes are available depending on the tested pH range. When the cell-permeable dye SNARF-1 acetoxymethyl ester is excited at a wavelength of 543 nm, the ratio of fluorescence captured at emission wavelengths of 585 ± 10 and 640 ± 10 nm shows a linear relationship to intracellular pH (Venn et al. 2013). Similarly, cell impermeable SNARF-1 can be used to measure pH in the calcifying fluid in corals; 2′-7′-bis(carboxyethyl)-5(6)-carboxyfluorescein (BCECF) for intracellular pH of echinoderm larvae (Stumpp et al. 2012) and pyranine for foraminifera (Toyofuku et al. 2017). This technique has been applied to OA to investigate how growth and calcification rates are affected by increasing $p\text{CO}_2$ (Stumpp et al. 2012), where extracellular pH was actively compensated.

More recently, measurement of intracellular pH employs the use of microelectrodes between 10- and 15-µm tip diameter for direct in-tissue measurement (Cai et al. 2016), using pH polymeric membrane microelectrodes (Zhao & Cai 1999) and $\text{CO}_3^{2-}$ electrodes (Cai et al. 2016). Using this approach, pH and $\text{CO}_3^{2-}$ were observed to sharply increase in the calcifying fluid of various coral species, confirming the presence of $\text{H}^+$ pump (Cai et al. 2016). In addition to intracellular pH determination, microelectrodes can be designed to monitor dissolved oxygen and calcium concentrations to enable analysis of a wider range of parameters (Glas et al. 2012a,b). The cellular pH-imaging techniques have an advantage of high spatial resolution for direct in-tissue measurement; however, the disadvantages include time-consuming sample preparation. This includes the challenge that organism immobilisation strategies vary and the protocol requires optimisation to ensure that the organism is capable of generating biominerals. Ratiometric pH probe also requires calibration before the ratios can be converted to pH values.

### *Physiological inhibitors and stimulators*

The use of physiological inhibitors or stimulators is a useful approach to investigate the biochemical pathways and pumps involved with biomineralisation (Basse et al. 2015). How biological pathways may be influenced by specific inhibitors can explain the mechanism of shell formation under OA conditions. For example, treatment with adenylyl cyclase inhibitors alleviates the negative effects of OA in Pacific oysters, suggesting the potential mechanism change under OA (Wang et al. 2017). This result confirmed the role of adenosine triphosphate (ATP) generation is essential to support shell production (Pan et al. 2015). Not requiring complete genetic information is the greatest advantage of using inhibitors and stimulators to evaluate the mechanisms of biomineralisation in a reductionist approach (Toyofuku et al. 2017). However, the choice of inhibitors may be nonspecific to a single pathway, and its action requires verification by a known physiological end point.

## Combining techniques

The techniques described in this review can be employed individually to answer specific scientific questions to determine the impact of OA on marine biomineralisation. However, it is important to consider combining techniques to address complex scientific questions.

### *Combining x-ray microscopy techniques*

Due to the development of optimum sample preparation for the analysis of a flat surface (Perez-Huerta & Cusack 2009), the output of XPEEM with XAS (Fitzer et al. 2016) and SEM-EBSD (Hahn et al. 2012, Wolfe et al. 2013, Fitzer et al. 2014a,b) can be readily compared. This has allowed the influence of OA on both the biomineral structure and composition to be determined for corals (Rodolfo-Metalpa et al. 2011), sea urchins (Bray et al. 2014) and mussels (Melzner et al. 2011). Likewise, the simple mapping of calcite and aragonite is applicable across a wide variety of species, including mussels and limpets (Hahn et al. 2012, Langer et al. 2014, Fitzer et al. 2015a). In contrast, the comparison of mineral composition between high-resolution microscopy with spectral techniques such as XRD, FT-IR and XPEEM with XAS is more complex. The use of SEM imaging, as well as calcite and aragonite thickness by EBSD or species-specific visual inspection using compound microscopy (Fitzer et al. 2014b), have their merits when it comes to examining larger areas of shell erosion. However, to examine the intricate details of biomineralisation and potential changes under OA conditions, these methods should be used in conjunction with XRD, FT-IR, XPEEM with XAS and SEM-EBSD.

### *Multiomics data integration*

Several omics approaches can be integrated [i.e. multiomics (Huang et al. 2017)]. For example, the mantle transcriptome and shell proteomes were integrated to study the shell formation of the pearl oyster (Joubert et al. 2010, Berland et al. 2011), enabling proteomics data to be analysed without a complete genome. Similarly, proteomics and metabolomics were studied together in oysters (Wei et al. 2015). A more complex multiomics study examined the genome, transcriptome and proteome in the Pacific oyster (Zhang et al. 2012). Such a multiomics approach also provided insights into the phosphate biomineralisation in brachiopods (Luo et al. 2015). This is a promising approach in the context of OA to understand the fitness or survival of organisms.

## Conclusions: What now for OA research on biomineralisation?

A range of tools to help researchers determine the impact of OA on biomineralisation mechanisms at physiological and molecular levels, and thus on shell or skeleton structural mechanics, have been discussed in this review, the purpose of which is to explore commonly available biomineralisation tools for understanding this single physiological response to OA. However, organisms have complex physiological profiles, and it is important to note that biomineralisation is not an isolated process, nor is it the only physiological process that needs to be considered in this context. Given the nature of biomineralisation mechanisms and their complex responses to OA, a variety of physiological, materials science and crystallography tools are needed to thoroughly understand the biomineralisation process and its vulnerability to OA.

This discussion outlines techniques that can be used to characterise, quantify and monitor the process of biomineralisation in a variety of calcifying marine organisms, especially when they are cultured under OA experimental conditions. It also highlights basic principles and the advantages and disadvantages of established, emerging and future techniques for OA researchers. The key to developing a strategy aimed at better understanding the potential consequences of OA is to define clear questions and hypotheses for testing. This would naturally lead to constraints (e.g. tested species, quantity of material available, size) that, when combined with practicalities (e.g. budget, equipment), will lead to selection of the appropriate experimental approach.

Recently, more attention has been paid to the underlying biological and physiological mechanisms of biomineralisation. For example, tissues and external organic layers can protect the shell from corrosion in undersaturated waters (Rodolfo-Metalpa et al. 2011). To address the underlying mechanisms affected by the impacts by OA, various methods need to be combined. For instance, determination of amorphous $CaCO_3$ is important to characterise mineral choice and relate phase transitions at the earliest stage of biomineral formation. Mechanisms of cellular involvement and specific biomolecules for biomineralisation can be examined using fluorescent microscopy and omics. The interactions of proteins in the extrapallial fluid and shell interface can be understood by applying techniques in isotope labelling and microscopy. It is also crucial to consider the fitness consequences of observed changes. For example, in a prey species, shell strength should be considered in relation to predator behaviour. The combination of established, emerging and future techniques will enable a holistic approach and better understanding of the potential impact of OA on biomineralisation by marine species and consequences for marine calcifiers and associated ecosystems.

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# FACILITATION CASCADES IN MARINE ECOSYSTEMS: A SYNTHESIS AND FUTURE DIRECTIONS

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## Abstract

Facilitation cascades occur when a habitat-forming species facilitates another habitat-forming species with synergistic effects on biodiversity. This review summarizes the current state of knowledge of facilitation cascades in marine environments, describing (1) the geographic distribution of studies documenting facilitation cascades; (2) the range of habitats and organisms involved; (3) the mechanisms underpinning their establishment; and (4) the sources of their spatial and temporal patterns and variability. We synthesize this knowledge to identify ways in which facilitation cascades could be integrated with other ecological theories regarding community assembly and function, and also to explore how they may be integrated into conservation and management strategies. Finally, we identify critical knowledge gaps and future research directions for improving our understanding of the mechanisms regulating the establishment and persistence of facilitation cascades in marine environments.

## Introduction

Historically, the processes structuring ecological communities have been viewed through the lens of negative species interactions such as competition and predation (Connell 1961, Paine 1966, Menge & Sutherland 1976). However, the importance of positive interactions in driving community structure has clearly emerged in the last three decades (Connell & Slatyer 1977, Bertness & Callaway 1994, Stachowicz 2001, Reise 2002, Bruno et al. 2003, Silliman et al. 2011). For example, it is now broadly recognized that spatially dominant foundation species (*sensu* Dayton 1972), such as algae, salt-marsh plants, oysters and corals, support biodiversity by defining the physical architecture of many ecosystems. Similarly, the physical structure of autogenic ecosystem engineers (Jones et al. 1994), which may or may not be space-dominant, shapes biodiversity by creating and maintaining habitats. Together, these two groups, collectively referred to here as *habitat-forming species,* are a key focus of research on positive species interactions. The notion that a suite of organisms create or modify habitat for others has been recognized for over 150 years (Darwin 1859, Hatton 1938). In the late nineteenth century, Karl Möbius, then a professor of zoology at the University of Kiel, coined the term *biocoenosis* to describe biota living together on an oyster bed (Möbius 1877). This term explicitly acknowledged the interconnectedness among taxa from different trophic levels (Keller & Golley 2000)—in this instance, within a habitat-former. A more formal and quantitative understanding of the roles of habitat-formers has developed only recently, however (Jones et al. 1994, Bertness & Leonard 1997, Bruno & Bertness 2001, Hastings et al. 2007, van der Zee et al. 2016).

The majority of studies on positive interactions have considered the effects of habitat-formers independent of one another (Wright & Jones 2006), but habitat-forming species often co-occur in time, space or both, in spatially overlapping or adjacent configurations (Angelini et al. 2011). Multiple habitat-formers may have additive or interactive effects on biodiversity, where they vary functionally, or they cumulatively enhance the availability of a limiting resource (Thomsen et al. 2010, 2018, Angelini et al. 2011). A subset of interactions between habitat-formers, referred to as *facilitation cascades* (a term first coined by Altieri et al. 2007), are hierarchical, whereby a basal habitat-former promotes a secondary habitat-former, which in turn supports an inhabitant community. The species in such hierarchical relationships may spatially overlap (e.g. cordgrass promotes habitat-forming mussel beds between its shoots through shading and substrate stabilization; Altieri et al. 2007) or operate across landscapes (e.g. a mussel bed modifies hydrodynamic and sediment conditions to facilitate a habitat-forming cockle bed hundreds of meters away; van de Koppel et al. 2015) (Figure 1A–C). Although most examples of facilitation cascades include two levels of habitat-formers, up to five levels of co-occurring habitat-formers have been documented (Thomsen et al. 2013, 2016a, Yakovis & Artemieva 2017).

Facilitation cascades arise through three major pathways: (1) the basal habitat-former provides resources (e.g. attachment substrate) to the secondary habitat-former (Boström & Mattila 1999, Bishop et al. 2013, Thomsen et al. 2016a); (2) the basal habitat-former facilitates the secondary habitat-former by reducing environmental stress (Altieri et al. 2007, Gribben et al. 2009a); and (3) the basal habitat-former reduces consumer or competition pressure on the secondary habitat-former (Levenbach 2008, Bulleri et al. 2011, Clements & Hay 2015, Kayal & Kayal 2017, Figures 1 and 2). In many cases, the secondary habitat-former derives two or more of these benefits from the basal habitat-former. As facilitation cascades organize communities hierarchically, the presence of a basal habitat-former is a precondition for the recruitment and persistence of additional habitat-formers (Bruno & Bertness 2001, Altieri et al. 2007, Angelini et al. 2011), with subsequent positive effects on biodiversity.

Facilitation cascades have been documented in a range of terrestrial (Callaway et al. 2001, Ellwood & Foster 2004), freshwater (Blanco et al. 2008, Mormul et al. 2010, Furey et al. 2012) and marine ecosystems (Thomsen et al. 2010, Angelini et al. 2011, Gribben et al. 2017a). For example, epiphytes growing on trees and freshwater plants or drifting algae entrapped by mangrove pneumatophores enhance biodiversity relative to habitat provided by only a single or no habitat-former (Mormul et al. 2010, Bishop et al. 2012, Watson & Herring 2012). Critically, facilitation cascades can have the same or greater importance in shaping community structure than more widely recognized trophic cascades (Estes & Duggins 1995, Schmitz et al. 2000, Shurin et al. 2002), which are another form of sequential interactions (Thomsen et al. 2018). The best-documented facilitation cascades are in marine ecosystems and, more specifically, in intertidal habitats (Thomsen et al. 2018). This may partly reflect a long history of studies of habitat-formers that have focused intensively on their role in alleviating stressors, such as water flow (Fonseca et al. 1982), desiccation (Leonard 1999) and predation pressure (Heck & Orth 1980, Crowder & Cooper 1982). Moreover, interest in

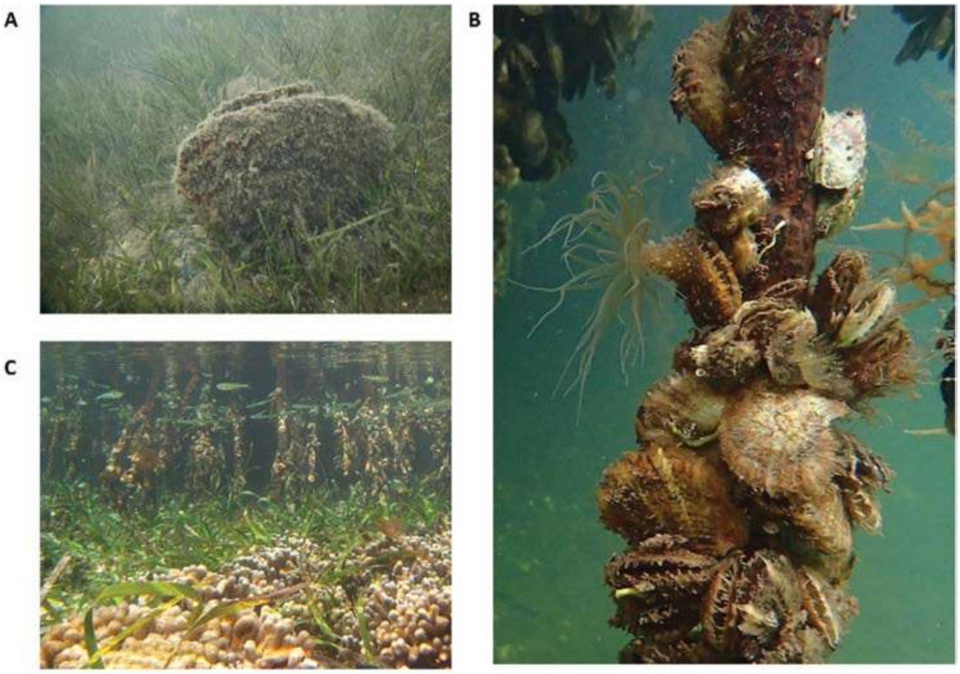

**Figure 1** Examples of documented facilitation cascades. (A) Seagrass (basal habitat-former) promotes recruitment of razor clams (secondary habitat-former), possibly by reducing biotic stress (e.g. predation pressure), which in turn provide a surface for attached epibionts (inhabitants); (B) a mangrove pneumatophore (basal habitat-former) provides a surface from colonization by oysters (secondary habitat-former), which in turn provide a surface for an anemone (inhabitant) to colonize; (C) coral reefs buffer seagrass and mangroves from offshore wave energy, allowing them to establish in relative calm areas, whereas mangroves and seagrass trap terrestrial sediment and nutrients that would otherwise lead to smothering of reefs. (A) and (B) are examples of embedded facilitation cascades, whereas in (C), corals, seagrass and mangroves form zones that facilitate one another in a tropical coastal ecosystem. (Photo credits (A) Paul Gribben; (B, C) Andrew Altieri.)

the conservation and restoration of biodiversity in these environments has further motivated research on habitat-formers (Bertness & Hacker 1994, Bertness et al. 1999, Halpern et al. 2007, Wright & Gribben 2017). Among the habitat-formers that play a critical role in shaping marine biodiversity are seagrasses, salt-marsh grasses, algae and kelp, oysters, mussels, polychaete worms, mangroves and deep-sea hydrothermal vent tubeworms and bivalves (Bruno & Bertness 2001, Dubois et al. 2006, Govenar 2010, Portail et al. 2015). Each of these basal habitat-formers, except deep-sea tubeworms and bivalves, which warrant further study, have been observed in facilitation cascades (Altieri et al. 2007, Gribben et al. 2009a, 2017a, Bishop et al. 2012, 2013, Bell et al. 2014, Thomsen et al. 2016a). Nevertheless, the literature on these habitat-formers has largely focused on their aggregate effects, rather than considering interactions among the habitat-formers. One of the most obvious and common examples of this occurs in studies of coral reefs in which investigators often attribute the positive effects of multiple, structurally distinct reef-building corals on fish and invertebrate diversity to the effects of the reef as a whole (Angelini et al. 2011). The growing documentation of marine facilitation cascades suggests that the processes by which habitat-formers control biodiversity have been oversimplified and warrant further attention to inform marine ecosystem management and biodiversity conservation.

Given the burgeoning interest and increasing number of studies documenting facilitation cascades, it is appropriate at this time to review the current state of knowledge of their ecological impacts

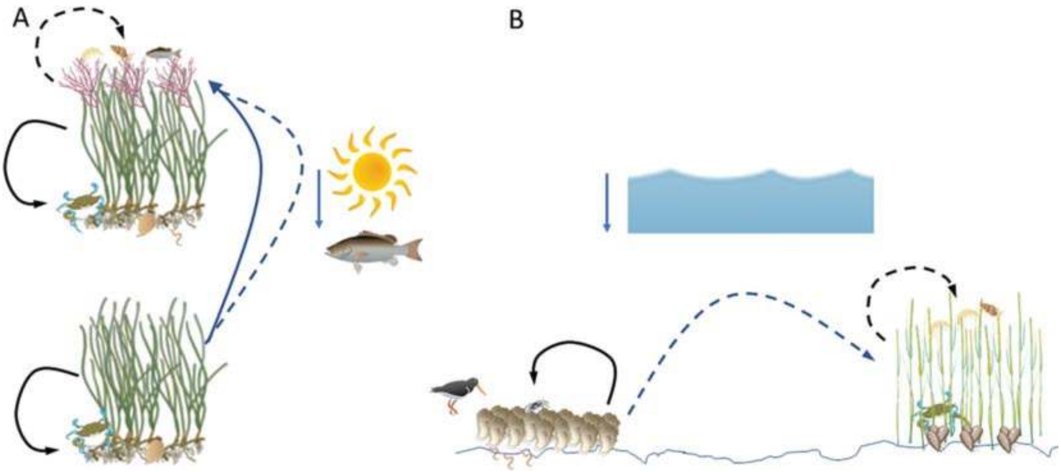

**Figure 2** Examples of mechanisms underpinning (A) embedded and (B) adjacent (or landscape) facilitation cascades. For embedded facilitation cascades, basal habitat-formers directly (via substrate provisioning or propagule entrapment; solid blue line) or indirectly (via amelioration of biotic and abiotic stress; dashed blue line) facilitate secondary habitat-formers with synergistic effects on biodiversity; (A) depicts seagrass facilitation of epiphytes. These types of cascades are predicted to have strong positive effects on biodiversity at the patch or local scale. For adjacent facilitation cascades, basal habitat-formers will indirectly (via amelioration of abiotic stress) facilitate secondary habitat-formers outside the basal habitat-former. These types of cascades are predicted to have strong positive effects on biodiversity at the scale of landscapes; (B) indicates facilitation of salt marsh by oysters through buffering wave action. Inhabitants associated with basal and secondary habitat-formers are indicated with solid and dotted black lines, respectively. Pictures courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

and the mechanisms by which they influence biodiversity. In doing so, we identify how facilitation cascades can be integrated with other ecological theories such as the Stress Gradient Hypothesis (SGH; Bertness & Callaway 1994) and be applied to the management of marine ecosystems. In the following sections, we review the current understanding of facilitation cascades in marine ecosystems by (1) providing an overview of published studies on marine facilitation cascades (e.g. including a synthesis of the locations and habitat in which they have been described, and the species they involve); (2) summarizing known mechanisms by which facilitation cascades establish and promote biodiversity; (3) discussing how facilitation cascades may function across multiple spatial scales and environmental contexts; and (4) highlighting how the integration of facilitation cascades into ecological theory is essential for conserving biodiversity, restoring ecological communities and ecosystem functions and managing biodiversity. Finally, we discuss key research gaps and provide recommendations for future research.

## Overview of published studies on marine facilitation cascades

### *Literature search*

We explored trends in the geographic regions and marine ecosystem types where facilitation cascades have been documented and summarized the identity of habitat-formers involved in facilitation cascades, as well as the communities they facilitated. To do this, we searched for studies that compared the abundance or taxonomic richness of inhabitants associated with only a basal habitat-former to those associated with co-occurring basal and secondary habitat-formers. We used the methodological definition of a facilitation cascade outlined in Thomsen et al. (2018) in which they compared and reported the abundance or taxonomic richness of inhabitants associated with only a primary foundation species to those associated with co-occurring primary and secondary foundation species based on field-data collection criteria that allow researchers to evaluate facilitation cascades quantitatively with effect sizes. Relevant studies were identified from literature searches identifying papers up to November 2017.

First, we conducted a standardized Web of Science search, with terms related to fauna, epiphytes and epibionts (because epiphytes and epibionts are typical secondary habitat-formers; Thomsen et al. 2010). Second, we searched for terms related to facilitation and habitat cascades because these processes specifically describe the effects of secondary habitat-formers on inhabitants (Thomsen et al. 2010). This was a two-tiered search, in which we next located references cited in our previous publications on facilitation and habitat cascades, or that cited those works (e.g. Altieri et al. 2007, Thomsen et al. 2010, Thomsen & Wernberg 2014). We then examined papers in which the title, abstract or keywords indicated that relevant data were collected for faunal inhabitants, such as birds, fish or invertebrates associated with a facilitation cascade.

From these searches, we identified 62 relevant papers. Based on personal research expertize and a less-structured search of the literature, we identified another 38 relevant papers that also could be classified as facilitation cascade studies but were not found in the two systematic searches (see Table 1). For each publication in the resulting database, we extracted information about the geographic study location (i.e. the geocoordinates of field data collection sites) and year of publication; latitude, which we binned into traditional climate zones (Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°); overall ecosystem type where the study was conducted (e.g. in a salt-marsh or a mangrove forest); substrate type (rock or soft-sediment substrata); and tidal elevation (subtidal versus intertidal). Additionally, we recorded the taxonomic identity of the habitat-formers (e.g. alga, bivalve, and barnacle), habitat-former type (e.g. studied as a single algal species or as a group of algal species, such as epiphytes) and structural dependencies (i.e. attached to, embedded within or entangled around habitat-formers) of the studied basal and secondary habitat-formers, as well as the type of inhabitants (e.g. invertebrates, fish) that they supported.

## *Results*

To date, facilitation cascades have been studied in 29 countries covering all continents except Antarctica, with more than half (55%) of the cascades being in either the United States or Australia (Figures 3 and 4A). Although the term *facilitation cascade* was first coined in 2007 (Altieri et al. 2007), the first study we identified that described something that seemed to be a facilitation cascade was published in 1980. It documented the positive relationships between red drift algae entangled within seagrass beds and the abundance of banded blennies (*Paraclinus fasciatus*; Stoner & Livingston 1980). Since this publication, at least 99 more studies have documented additional facilitation cascades (Figure 4B, Table 1). Most marine facilitation cascade studies were conducted in subtropical (49%) and temperate regions (35%), with relatively few studies in tropical (10%) or polar (6%) regions (Figure 5A). Importantly, all identified studies occurred in coastal benthic habitats, with no known examples from pelagic or deep-sea benthic ecosystems (Figure 5B). Finally, we found more studies in soft- than hard-bottomed systems (Figure 5C), and in the subtidal zone than in the intertidal zone (Figure 5D).

A total of 37 species have been identified as basal habitat-formers in facilitation cascades (Table 1); most of these are seagrass species, followed by macroalgae, mangrove trees, reef-forming bivalves and salt-marsh plants (but with *Spartina alterniflora* as the only studied salt-marsh species) (Figure 6A). Interestingly, only two studies showed indirect facilitation arising from a mobile basal habitat-former: the snails, *Batillaria australis* and *Littorina littorea* (Thieltges & Buschbaum 2007, Thomsen et al. 2010). Most studies included a single basal habitat-former, although in a few instances, the basal habitat-former consisted of a mixture of species, such as when two or three co-occurring seagrass

**Table 1** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| Adams et al. 2004. *Journal of Experimental Marine Biology and Ecology* 299: 17–33 | Seagrass | Alga | Fish | Soft sediments/Subtidal |
| Albrecht & Reise. 1994. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 48: 243–256 | Bivalve | Alga | Invertebrates | Soft sediments/Intertidal |
| Altieri et al. 2007. *American Naturalist* 169: 195–206 | Salt marsh | Bivalve | Invertebrates, Alga | Rocky shores/Intertidal |
| Altieri et al. 2010. *Ecology* 91: 1269–1275 | Salt marsh | Bivalve | Invertebrates | Rocky shores/Intertidal |
| Altieri & Irving 2017. *PeerJ* 5:e2848. | Salt marsh | Bivalve | Invertebrates | Rocky shores/Intertidal |
| Angelini et al. 2015. *Proceedings of the Royal Society B* 282: 1811 | Salt marsh | Bivalve | Invertebrates | Rocky shores/Intertidal |
| Armitage & Sjoetun 2016. *Hydrobiologia* 776: 35–49 | Alga | Alga | Invertebrates | Rocky shores/Intertidal |
| Armitage & Sjoetun 2016. *Hydrobiologia* 776: 35–49 | Alga | Alga | Invertebrates | Rocky shores/Intertidal |
| Arroyo et al. 2013. *Marine Ecology* 34: 345–362 | Seagrass | Alga | Invertebrates | Soft sediments/Subtidal |
| Barros & Rocha-Barreira. 2013. *Annals of the Brazilian Academy of Sciences* 85: 1397–1410 | Seagrass | Alga | Invertebrates | Soft sediments/Intertidal |
| Bell & Westoby. 1987. *Australian Journal of Ecology* 12: 333–337 | Seagrass | Alga | Invertebrates, Fish | Soft sediment/Subtidal |
| Bell et al. 2014. *Marine Ecology Progress Series* 501: 1–10 | Alga | Urchin | Invertebrates | Rocky shores/Subtidal |
| Bishop et al. 2009. *Marine Ecology Progress Series* 392: 111–122 | Mangrove pneumatophores | Alga | Invertebrates | Soft sediments/Intertidal |
| Bishop et al. 2012. *Ecology* 93: 1388–1401 | Mangrove pneumatophores | Alga | Invertebrates | Soft sediments/Intertidal |
| Bishop et al. 2013. *Ecology* 94:1927–1936 | Mangrove pneumatophores | Alga | Invertebrates | Soft sediments/Intertidal |
| Bologna & Heck 1999. *Journal of Experimental Marine Biology and Ecology* 242: 21–39 | Seagrass | Alga | Invertebrates, Alga | Soft sediments/Subtidal |
| Bologna & Heck. 1999. *Journal of Experimental Marine Biology and Ecology* 242: 21–39 | Seagrass | Alga | Invertebrates, Alga | Soft sediments/Subtidal |
| Bologna & Heck. 2000. *Estuaries* 23: 449–457 | Seagrass | Alga | Invertebrates | Soft sediments/Subtidal |
| Borg et al. 2010. *Marine Ecology Progress Series* 406: 91–104 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Bostroem & Mattila. 1999. *Oecologia* 120: 162–170 | Seagrass | Alga, diatoms | Invertebrates | Soft sediment/Subtidal |
| Bostroem & Mattila. 1999. *Oecologia* 120: 162–170 | Seagrass | Alga, diatoms | Invertebrates | Soft sediment/Subtidal |
| Bryars & Wear. 2008. *Transaction of the Royal Society of South Australia* 132: 81–94 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Buzá-Jacobucci & Pereira-Leite. 2014. *Latin American Journal of Aquatic Research* 42: 353–363 | Alga | Alga | Invertebrates | Rocky Shores/Subtidal |

(*Continued*)

**Table 1 (Continued)** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| Buzá-Jacobucci & Pereira-Leite. 2014. *Latin American Journal of Aquatic Research* 42: 353–363 | Alga | Alga | Invertebrates | Rocky Shores/Subtidal |
| Cardoso et al. 2004. *Journal of Experimental Marine Biology and Ecology* 308: 207–220 | Seagrass | Alga | Invertebrates | Soft sediment/Intertidal |
| Cardoso et al. 2004. *Journal of Experimental Marine Biology and Ecology* 308: 207–220 | Seagrass | Alga | Invertebrates | Soft sediment/Intertidal |
| Castejon-Silvo et al. 2012. *Estuarine, Coastal and Shelf Science* 112: 225–235 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Chapman et al. 2005. *Journal of the Marine Biological Association of the United Kingdom* 85: 1481–1488 | Mangrove | Alga | Invertebrates | Soft sediment/Intertidal |
| Christie et al. 2003. *Journal of the Marine Biological Association of the United Kingdom* 83: 687–699 | Alga | Alga | Invertebrates | Rocky Shores/Subtidal |
| Dijkstra et al. 2012. *Oikos* 121: 646–654 | Salt marsh | Alga | Invertebrates | Soft sediment/Intertidal |
| Dijkstra et al. 2012. *Oikos* 121: 646–654 | Salt marsh | Alga | Invertebrates | Soft sediment/Intertidal |
| Drouin et al. 2011. *Marine Ecology Progress Series* 424: 105–117 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646 | Reef-forming tubeworm | Alga | Invertebrates | Rocky shore/Intertidal |
| Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646 | Reef-forming tubeworm | Alga with bivalve | Invertebrates | Rocky shore/Intertidal |
| Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646 | Reef-forming tubeworm | Bivalve | Invertebrates | Rocky shore/Intertidal |
| Dubois et al. 2006. *Estuarine, Coastal and Shelf Science* 68: 635–646 | Reef-forming tubeworm | Bivalve with Alga | Invertebrates | Rocky shore/Intertidal |
| Edgar & Robertson. 1992. *Journal of Experimental Marine Biology and Ecology* 160: 13–31 | Seagrass | Alga | Invertebrates, Alga | Rocky shore/Subtidal |
| Ekloef et al. 2006. *Marine Ecology Progress Series* 325: 73–84 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Escapa et al. 2004. *Journal of Shellfish Research* 23: 765–772 | Salt marsh | Bivalve | Invertebrates | Soft sediment/Intertidal |
| Gartner et al. 2013. *Journal of Experimental Marine Biology and Ecology* 143–151 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Gartner et al. 2013. *Journal of Experimental Marine Biology and Ecology* 143–151 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Green & Crowe. 2014. *Biological Invasions* 16: 1145–1165 | Bivalve | Bivalve | Invertebrates | Soft sediment/Intertidal |
| Gribben et al. 2009. *Ecology Letters* 12: 1127–1136 | Alga | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Gribben et al. 2017. *Ecosphere* 8: 1–14 | Seagrass | Bivalve | Invertebrates, Fish | Soft sediment/Subtidal |
| Grutter & Irwin. 2007. In *Marine Ecology* Oxford University Press (eds: Connell & Gillanders) p 110–137 | Seagrass | Epibionts | Invertebrates | Soft sediment/Subtidal |

(*Continued*)

**Table 1 (Continued)** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| Gutierrez & Palomo. 2016. *Journal of Sea Research* 112: 49–54 | Bivalve | Barnacle | Alga | Rocky Shore/Intertidal |
| Hall & Bell. 1988. *Journal of Marine Research* 46: 613–630 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Hall & Bell. 1993. *Marine Biology* 116: 137–146 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Hamamoto & Mukai. 1999. *Marine Ecology* 20: 521–272 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Holmquist. 1997. *Marine Ecology Progress Series* 158: 121–130 | Seagrass | Alga | Invertebrates, Alga | Soft sediment/Subtidal |
| Hughes et al. 2014. *Marine Ecology Progress Series* 508: 129–138 | Mangrove pneumatophores | Alga | Invertebrates | Soft sediment/Subtidal |
| Hughes et al. 2014. *Marine Ecology Progress Series* 508: 129–138 | Mangrove pneumatophores | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Inglis. 1994. *Oecologia* 99: 352–365 | Seagrass | Bivalve | Alga | Soft sediment/Subtidal |
| Ingólfsson & Olafsson. 1997. *Journal of Plankton Research* 19: 15–24 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Irving et al. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 40–49 | Seagrass | Epibionts | Invertebrates | Soft sediment/Subtidal |
| Jaxion & Speight. 2012. *Journal of Experimental Marine Biology and Ecology* 414: 19–27 | Mangrove | Alga | Invertebrates | Soft sediment/Intertidal |
| Jones & Thornber. 2010. *Marine Ecology Progress Series* 400: 87–100 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Kelaher et al. 2001. *Journal of the Marine Biological Association of the United Kingdom* 81: 917–930 | Coralline turf | Alga | Invertebrates | Rocky shore/Intertidal |
| Kelaher et al. 2005. *Estuarine, Coastal and Shelf Science* 63: 155–165 | Coralline turf | Alga | Invertebrates | Rocky shore/Intertidal |
| Kelaher et al. 2007. *Journal of Molluscan Study* 73: 139–146 | Coralline turf | Alga | Invertebrates | Rocky shore/Intertidal |
| Kochmann et al. 2008. *Journal of Experimental Marine Biology and Ecology* 364: 1–10 | Bivalve | Bivalve | Invertebrates | Soft sediment/Intertidal |
| Koivisto & Westerbom. 2010. *Marine Biology* 157: 1463–1474 | Bivalve | Alga | Invertebrates | Rocky shore/Subtidal |
| Koivisto & Westerbom. 2010. *Marine Biology* 157: 1463–1474 | Bivalve | Alga | Invertebrates | Rocky shore/Subtidal |
| Koivisto et al. 2011. *Aqautic Biology* 12: 261–270 | Bivalve | Alga | Invertebrates | Rocky shore/Subtidal |
| Kulczycki et al. 1981. *Estuarine, Coastal and Shelf Science* 12: 341–347 | Seagrass | Alga | Fish | Soft sediment/Subtidal |
| Laegdsgaard & Johnson. 2001. *Journal of Experimental Marine Biology and Ecology* 257: 229–253 | Mangrove | Alga | Fish | Soft sediment/Intertidal |
| Leber. 1985. *Ecology* 66: 1951–1964 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| MacDonald et al. 2008. *Estuaries & Coasts* 31: 981–993 | Mangrove | Sponge | Fish | Soft sediment/Subtidal |
| MacDonald et al. 2008. *Estuaries & Coasts* 31: 981–993 | Mangrove | Tunicate | Fish | Soft sediment/Subtidal |

(*Continued*)

**Table 1 (Continued)** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| MacDonald et al. 2013. *Journal of Experimental Marine Biology and Ecology* 441: 90–98 | Mangrove | Epibionts (alga, sponges, tunicates, molluscs) | Fish | Soft sediment/Subtidal |
| Macreadie et al. 2014. *Journal of Molluscan Study* 80: 102–106 | Seagrass | Bivalve | Invertebrates, Fish | Soft sediment/Subtidal |
| Martin-Smith. 1993. *Journal of Experimental Marine Biology and Ecology* 174: 243–260 | Alga | Alga | Invertebrates | Rocky shore/Subtidal |
| McAfee et al. 2016. *Ecology* 97: 929–939 | Mangrove pneumatophores | Bivalve | Invertebrates | Soft sediment/Intertidal |
| Mendez et al. 2015. *Aquatic Ecology* 49: 441–452 | Salt marsh | Barnacle | Invertebrates | Soft sediment/Intertidal |
| Mendez et al. 2015. *Aquatic Ecology* 49: 441–452 | Bivalve | Barnacle | Invertebrates | Soft sediment/Intertidal |
| Mukai & Ijima. 1995. *Ecological Research* 10: 243–257 | Seagrass | Cyanobacteria | Invertebrates | Soft sediment/Subtidal |
| Munguia & Miller. 2008. *Journal of Animal Ecology* 77: 1175–1182 | Seagrass | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Munguia. 2007. *Marine Biology* 152: 149–156 | Seagrass | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Munguia. 2014. *Oecologia* 174: 1335–1344 | Seagrass | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Newell et al. 1991. *Journal of World Aquaculture Society* 22: 134–152 | Seagrass | Alga | Invertebrates | Soft sediment/Intertidal |
| Norling & Kautsky. 2007. *Marine Ecology Progress Series* 351: 163–175 | Bivalve | Alga | Invertebrates | Soft sediment/Intertidal |
| Norton & Benson. 1983. *Marine Biology* 75: 169–177 | Alga | Diatoms | Invertebrates | Rocky shore/Subtidal |
| Pavia et al. 1999. *Journal of Experimental Marine Biology and Ecology* 236: 15–32 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Poore et al. 2000. *Marine Ecology Progress Series* 208: 183–196 | Alga | Alga | Invertebrates | Rocky shore/Subtidal |
| Poore et al. 2000. *Marine Ecology Progress Series* 208: 183–196 | Alga | Alga | Invertebrates | Rocky shore/Subtidal |
| Proches & Marshall. 2002. *Journal of the Marine Biological Association of the United Kingdom* 85: 937–942 | Mangrove | Alga | Invertebrates | Soft sediment/Intertidal |
| Ray et al. 2014. *PLOS ONE* 9: e107751 | Seagrass | Alga | Invertebrates, Fish | Soft sediment/Subtidal |
| Rohr et al. 2011. *Aquatic Ecology* 45: 213–219 | Alga | Alga | Invertebrates | Rocky shore/Subtidal |
| Ross. 2006. *Wetlands Ecology & Management* 14: 167–184 | Mangrove | Alga | Invertebrates | Soft sediment/Intertidal |
| Rutledge & Fleeger. 1993. *Estuaries* 16: 760–768 | Salt marsh | Alga | Invertebrates | Soft sediment/Intertidal |
| Saunders & Connell. 2001. *Austral ecology* 26: 109–115 | Mangrove | Seagrass | Invertebrates | Soft sediment/Intertidal |

(*Continued*)

**Table 1 (Continued)** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139 | Alga | Alga | Invertebrates | Soft sediment/Subtidal |
| Schneider & Mann. 1991. *Journal of Experimental Marine Biology and Ecology* 145: 119–139 | Alga | Alga | Invertebrates | Soft sediment/Subtidal |
| Skilleter & Warren. 2000. *Journal of Experimental Marine Biology and Ecology* 244: 107–129 | Mangrove | Alga | Invertebrates | Soft sediment/Intertidal |
| Stoner & Lewis. 1985. *Journal of Experimental Marine Biology and Ecology* 94: 19–40 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Stoner & Livingston. 1980. *Marine Biology* 56: 239–246 | Seagrass | Alga | Fish | Soft sediment/Subtidal |
| Thieltges & Buschbaum. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 90–95 | Gastropod | Barnacle | Invertebrates | Rocky shore/Intertidal |
| Thieltges & Buschbaum. 2007. *Journal of Experimental Marine Biology and Ecology* 340: 90–95 | Gastropod | Worm (burrowing) | Invertebrates | Rocky shore/Intertidal |
| Thomsen. 2010. *Aquatic Invasions* 5: 341–346 | Seagrass | Alga | Invertebrates | Soft sediment/Intertidal |
| Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175 | Tube worm | Alga | Invertebrates | Soft sediment/Intertidal |
| Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175 | Gastropod | Alga | Invertebrates | Soft sediment/Subtidal |
| Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175 | Bivalve | Alga | Invertebrates | Soft sediment/Intertidal |
| Thomsen et al. 2010. *Integrative and Comparative Biology* 50: 158–175 | Bivalve | Alga | Invertebrates | Soft sediment/Intertidal |
| Thomsen et al. 2012. *Harmful Alga* 16:74–80 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145 | Bivalve | Alga | Invertebrates | Soft sediment/Subtidal |
| Thomsen et al. 2013. *Aquatic Invasions* 8: 133–145 | Seagrass | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303 | Seagrass | Alga | Invertebrates, Alga | Soft sediment/Intertidal |
| Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303 | Seagrass | Alga | Invertebrates, Alga | Soft sediment/Intertidal |
| Thomsen et al. 2016. *Ecology and Evolution* 6: 8291–8303 | Bivalve | Alga | Invertebrates, Alga | Soft sediment/Intertidal |

(*Continued*)

**Table 1 (Continued)** List of 100 reviewed studies of marine facilitation cascades

| References | Basal habitat-former | Secondary habitat-former | Inhabitants | Substratum/elevation |
|---|---|---|---|---|
| Thomsen et al. 2016. *Marine and Freshwater Research* 67: 144–152 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Trowbridge. 1993. *Marine Ecology Progress Series* 101: 263–272 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Tyrrell et al. 2012. *Estuaries & Coasts* 35: 754–762 | Salt marsh | Alga | Invertebrates | Soft sediment/Intertidal |
| Valentine & Heck. 1993. *Marine Ecology Progress Series* 96: 63–74 | Seagrass | Bivalve | Invertebrates | Soft sediment/Subtidal |
| Verweij et al. 2006. *Marine Ecology Progress Series* 306: 257–268 | Mangrove | Alga | Fish | Soft sediment/Subtidal |
| Viejo & Aaberg. 2003. *Marine Biology* 142: 1229–1241 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Viejo & Aaberg. 2003. *Marine Biology* 142: 1229–1241 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Wikstroem & Kautsky. 2004. *Biological Invasions* 6: 141–150 | Alga | Alga | Invertebrates | Rocky shore/Intertidal |
| Williams & Hughes. 2002. *Biological Bulletin* 203: 248–249 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Worm & Sommer. 2000. *Marine Ecology Progress Series* 202: 283–288 | Alga | Alga | Invertebrates | Rocky Shore/Subtidal |
| Worthington et al. 1991. *Australian Journal of Ecology* 16: 289–293 | Seagrass | Alga | Fish | Soft sediment/Subtidal |
| Yakovis & Artemieva. 2017. *Scientific Report* 7: 1–11 | Bivalve | Barnacle | Invertebrates | Soft sediment/Subtidal |
| Yakovis & Artemieva. 2017. *Scientific Report* 7: 1–11 | Bivalve | Barnacle | Invertebrates | Soft sediment/Subtidal |
| Yamada & Kumagai. 2012. *Hydrobiologia* 680: 125–133 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |
| Zakhama-Sraieb et al. 2011. *Helgoland Marine Research* 65: 203–209 | Seagrass | Alga | Invertebrates | Soft sediment/Subtidal |

**Figure 3** Location of 100 publications documenting marine facilitation cascades. See Table 1 for details about each of these publications.

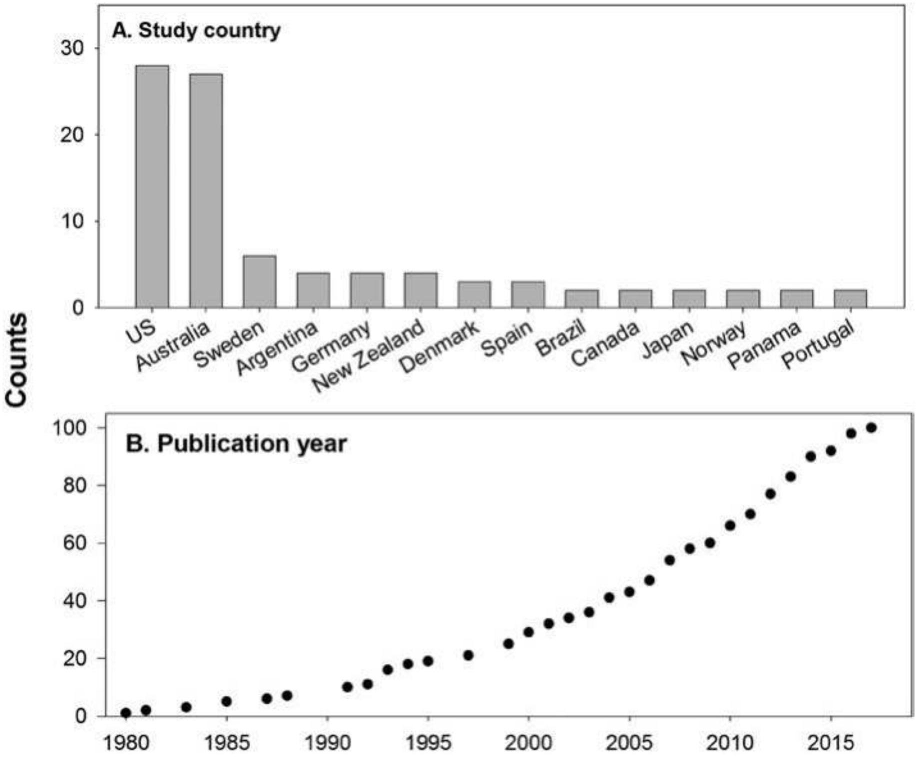

**Figure 4** Study attributes of 100 marine facilitation cascade studies. (A) Countries where studies were carried out (to simplify this plot, countries with a single study were excluded—that is, Chile, Fiji, Finland, France, Honduras, Iceland, Ireland, Malta, Antilles, Russia, South Africa, Tanzania, Tunisia, the United Kingdom and Venezuela). Note that a single publication could include multiple counts, such as if it examined the incidence of facilitation cascades in several countries. (B) Cumulative list of publication from 1980 (first publication) to 2017 (100 publications).

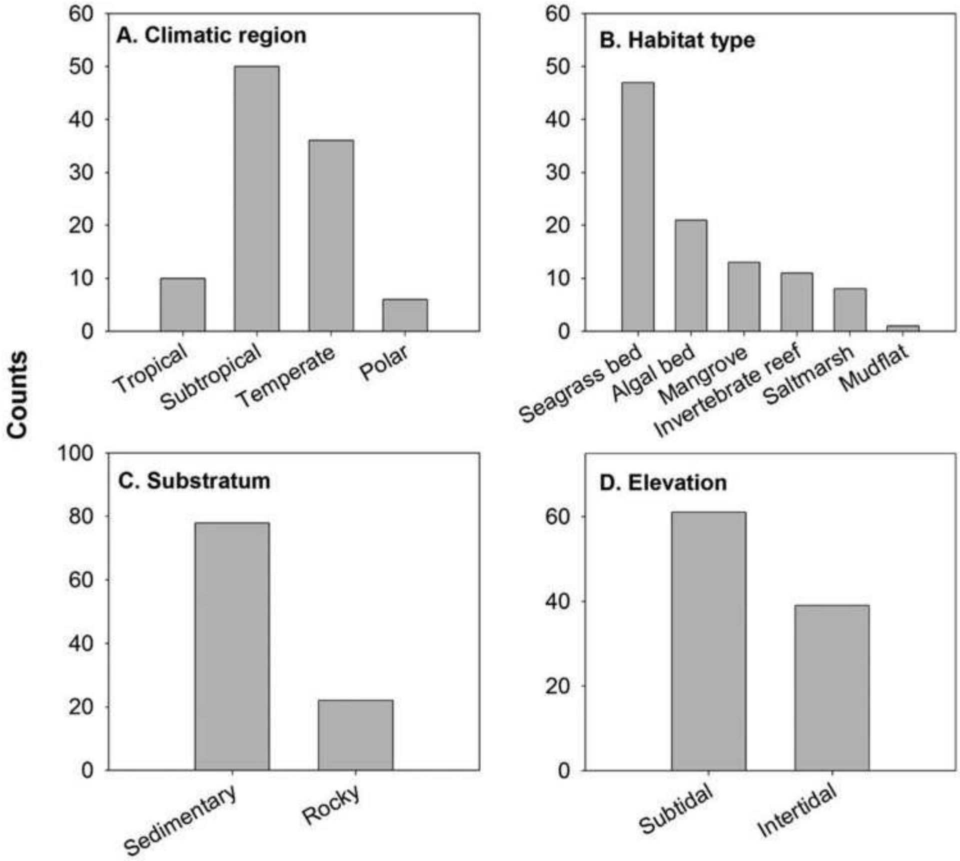

**Figure 5** System attributes of the 100 marine facilitation cascade studies (summarized in Table 1). (A) Studies divided by climatic region (Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°). (B) Studies classified by the type of habitat the study was conducted in. (C) Studies divided by fundamental substratum (soft-sediments or hard) each study was conducted on (note, all studies from seagrass beds were carried out in soft-sediment systems whereas most studies from seaweed beds were carried out on rocky reefs). (D) Studies divided into subtidal or intertidal elevations. A single publication could include multiple counts, such as if a facilitation cascade study was carried out simultaneously in different habitats (e.g. adding seaweed to both a seagrass bed and a mussel reef as a secondary habitat-former).

species provide a mixed habitat for secondary habitat-forming epiphytes (e.g. Stoner & Livingston 1980, Edgar & Robertson 1992; see Figure 6B and Table 1 for details). A few studies used mimics or dead shells/tests of basal habitat-formers to elucidate the relative importance of trophic versus structural mechanisms by which they facilitate secondary habitat-formers (e.g. Bologna & Heck 1999, 2000, MacDonald et al. 2008, Yakovis & Artemieva 2017).

Algae were the most commonly recorded secondary habitat-formers, followed by bivalves (Figure 6C), which together accounted for 92% of all studies. In contrast to basal habitat-formers, a large proportion (41%) of studies on secondary habitat-formers involved multiple coexisting species (Figure 6D), typically because epiphyte assemblages are studied as an entity (Table 1). Only one study documented a facilitation cascade involving a mobile secondary habitat-former, the urchin *Holopneustes purpurascens,* which inhabits the canopy of the kelp *Ecklonia radiata* wrapping the kelp around itself, in doing so, facilitates the gastropod *Phasianotrochus eximius* (Bell et al. 2014). Similar to basal habitat-formers, however, only a few studies used mimics or shells/tests to

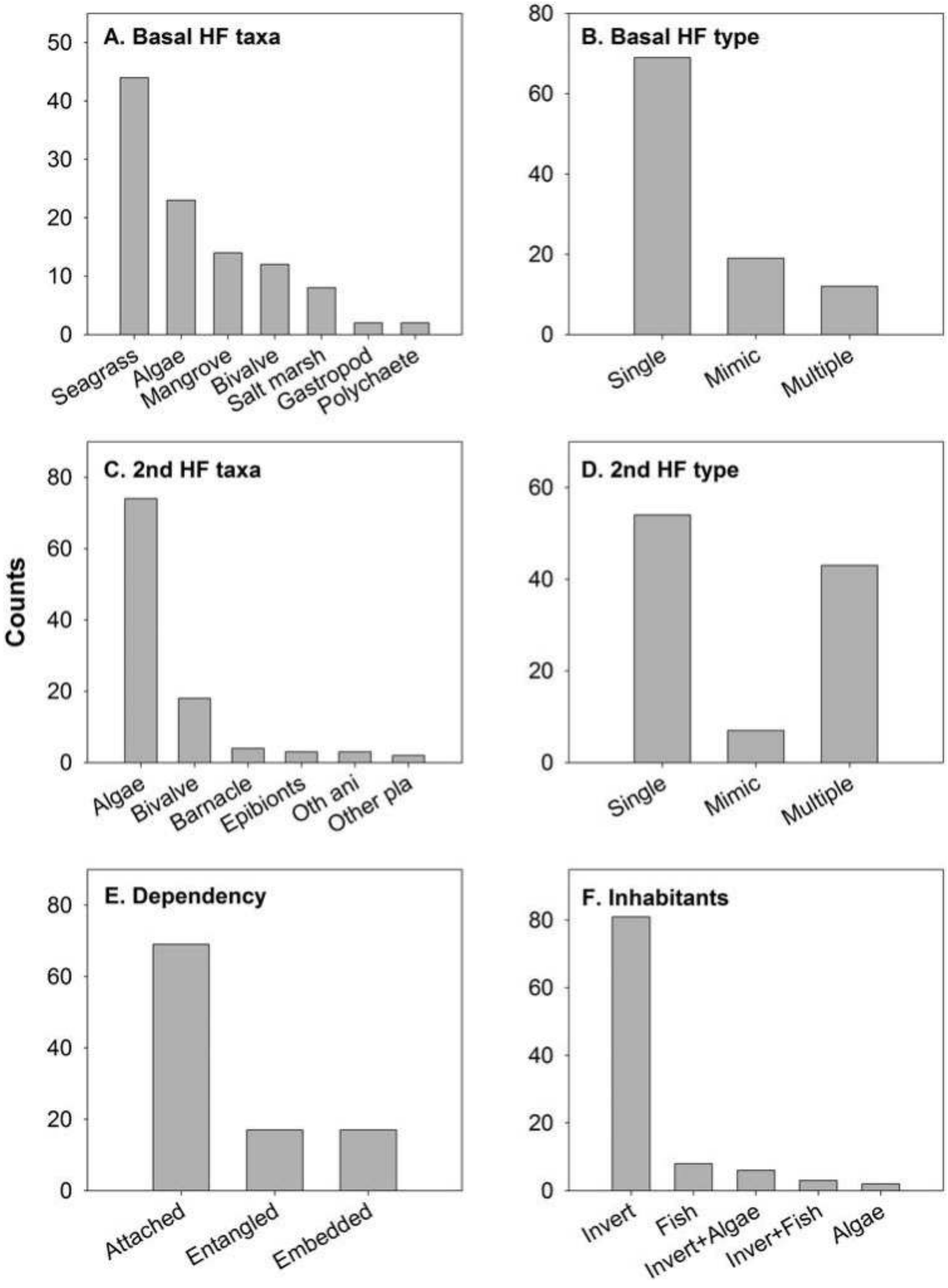

**Figure 6** Organismal attributes of 100 marine facilitation cascade studies. (A) The coarse taxonomic identity habitat of basal habitat-formers. (B) Whether basal habitat-formers were Single (i.e. an individual, living species), Mimic (i.e. a single, nonliving mimic of a species) or Multiple (i.e. a group of species, such as 'seaweed' referring to multiple species). (C) and (D), same as (A) and (B), respectively, but for secondary habitat-formers. (E) The type of physical dependency between the basal and secondary habitat-formers. (F) The identity of the inhabitant species and/or assemblage that was studied. 2nd = secondary, HF = habitat-forming species. Invert = Invertebrate. A single publication could include multiple counts, for example if a facilitation cascade study was carried out simultaneously with different 2nd habitat-formers.

determine how secondary habitat-formers facilitate biodiversity (e.g. MacDonald et al. 2008, Gartner et al. 2013, Yakovis & Artemieva 2017). Most studies focused on secondary habitat-formers that are physically attached to the basal habitat-formers (Figure 6E). Macroinvertebrates were the most common inhabitants recorded, although facilitation of fish communities was demonstrated in several studies (e.g. Stoner & Livingston 1980, MacDonald et al. 2008, MacDonald & Weis 2013, Figure 6F).

## The mechanisms underpinning facilitation cascades

While a growing number of studies demonstrate hierarchical positive interactions among species, the mechanisms by which facilitation cascades are established and maintained have been subject to surprisingly little investigation (Thomsen et al. 2018). The treatments that are necessary to ascertain whether facilitation occurs through resource provisioning or environmental or biotic stressor amelioration, such as structural mimics or manipulations of predators, competitors and/or stressors, are rarely included in experimental designs (Thomsen et al. 2018; but see notable exceptions discussed later in this review). Studies comparing species interactions across environmental gradients provide some insights into mechanisms, as described in the section on facilitation cascades along abiotic and biotic gradients later in this review, although such a comparative approach alone is insufficient to infer causal relationships due to their descriptive nature. Experimental tests of facilitation cascades have largely focused on how biodiversity responds to manipulations of secondary habitat-formers (e.g. Hall & Bell 1988, Koivisto & Westerbom 2010, Gartner et al. 2013). In a few instances, however, the full range of hierarchical interactions underpinning facilitation cascade control of biodiversity has been determined. For example, Gribben et al. (2009a,b) and Altieri et al. (2007) demonstrated, through the use of experimental treatments mimicking the stress-altering effects of habitat-formers, that interactions between the basal and secondary habitat-formers were largely mediated by the modification of abiotic conditions. However, secondary habitat-former effects on the associated community occurred through the provision of physical structure and further reductions in environmental stress. Thus, experiments can reveal how multiple mechanisms operate within a facilitation cascade where basal and secondary foundation species have complementary traits.

Regardless of how species benefit from positive interactions, associations between basal and secondary habitat-formers and between secondary habitat-formers and inhabitant communities may arise via active or passive processes. In some instances, the dependent species may be able to detect the facilitator and actively search for it or remain within or on it once found. In others, the dependent species may not actively choose the facilitator per se, but may suffer enhanced mortality when not associated with it, so that the two become associated. These relationships may be obligate, if survival of the dependent species is impossible in the absence of the habitat-former, or facultative, if the dependent species, although more abundant when found with the basal habitat-former, is able to survive outside the association. In obligate mutualistic associations, host recognition is vital for the survival of the participants involved (Ambrosio & Brooks 2011). In facultative relationships, however, the need for host detection is less critical, and often the proficiency of host recognition is weaker (Ambrosio & Brooks 2011). The relative importance of active and passive processes in maintaining facilitation cascades is little studied. Nevertheless, using a combination of field and laboratory experiments, Bell (2013) found that both reduced mortality and habitat selection contributed to a gastropod's greater abundance on kelp with urchins than without them. In the laboratory, the gastropod, *P. eximius*, used visual cues to locate urchins on kelp.

### *Resource provisioning*

Facilitation commonly results from the provision of limiting resources by habitat-formers (Jones et al. 1994, 1997, Bruno & Bertness 2001, Bruno et al. 2003, Bulleri 2009). For marine organisms, such resources commonly include settlement substrate and food. In many instances, basal habitat-formers appear to facilitate secondary habitat-formers by providing a stable or suitable substrate for colonization via larval/propagule settlement or entrapment (Figures 1A,B and 2A). For example, mollusc shells provide a hard surface for colonization by algae on rocky substrata (Dayton 1973, O'Connor & Crowe 2008, Martins et al. 2014), where consumer pressure and competition for space are great (Connell 1961, Menge 1976, Hawkins 1981, Menge & Lubchenco 1981), and in soft-sediment environments, in which suitable substrata are otherwise absent (Gutierrez et al. 2003, Thomsen et al. 2016a) and mangrove pneumatophores and seagrass shoots trap and retain floating algae (Adams et al. 2004, Bishop et al. 2012, 2013, Hughes et al. 2014). Secondary habitat-formers commonly enhance biodiversity by providing structural resources for colonization (Hall & Bell 1988, Bologna & Heck 2000, Altieri et al. 2007, Gartner et al. 2013, Figures 1A,B and 2A,B). Interestingly, via overgrowth and smothering or increasing the likelihood of dislodgment during storms, colonizing habitat-formers can also reduce the growth, health and survivorship of basal habitat-formers (Dayton 1973, Inglis 1994, O'Connor et al. 2006). Although not considered in a facilitation cascade context, such negative feedbacks have the potential to affect the facilitation of the associated community and the stability of the facilitation cascade itself.

Although not necessarily the primary mechanism by which they support inhabitant communities, basal and secondary habitat-formers may also facilitate biodiversity by enhancing the availability of food resources. First, the habitat-former may trap or retain food resources, such as detritus and other organic matter, that are drifting through a habitat. For example, intertidal ribbed mussels consume detritus that is produced and retained by the basal habitat-forming cordgrass (Kreeger et al. 1988, Altieri et al. 2007). These mussels also filter planktonic algae from the water column during high tide and through their deposition of pseudofeces, which locally alter nutrient and benthic algae composition and quantity (Bertness 1984, Derksen-Hooijberg et al. 2018). Second, inhabitants facilitated by habitat-formers may consume one another. Gribben et al. (2017a) found that predatory fish facilitated by secondary habitat-forming razor clams consumed epibionts that recruited to the surface of the clams. In a few instances, the habitat-formers in the facilitation cascade provide both physical habitat and food resources. Epiphytes on the fucoid alga *Ascophyllum nodosum* provided a physical habitat for several species of amphipod species that also fed on both the epiphytes and the alga (Pavia et al. 1999). Explicit tests that utilize mimics of habitat-formers to resolve whether facilitation occurs via food enhancement versus habitat-provisioning, however, provide mixed results. Communities on habitat mimics can be characterized by different compositions and numbers of taxa compared to a live habitat-former (Hall & Bell 1988, Verweij et al. 2006, Koivisto et al. 2011, Gartner et al. 2013). In addition to mimics, stable isotopes have been used to identify potential trophic linkages among habitat-formers and associated intertidal food webs. For example, cordgrass and mussels on New England cobble beaches and seagrass and pool-excavating crabs in West African seagrass meadows all enhanced food-web complexity, primarily through habitat modification rather than food provisioning (van der Zee et al. 2016). In both systems, the habitat-formers accounted for little to none of the diet of most species they facilitated.

When they consume habitat-forming species, dependent species may have negative effects on their biomass. For example, sea slugs facilitated by a secondary habitat-former, epiphytic algae, increased herbivory on the basal algal habitat-former (Trowbridge 1993). Clearly, for the facilitation cascade to persist, the basal and/or secondary habitat-formers cannot be consumed in quantities that result in the collapse of the facilitation cascade. Competition for space from inhabitants that do not consume the habitat-formers may be one important (but untested) mechanism reducing negative feedbacks on habitat-formers and enabling the persistence of the facilitation cascade. Regardless, consumptive effects may nevertheless result in the realized biodiversity of a facilitation cascade being lower than the potential biodiversity that would occur in the absence of consumption.

### *Environmental stressor amelioration*

Alternatively, the role of basal habitat-formers can be that of buffering environmental stress (Figures 1C and 2A,B), a mechanism widely documented in intertidal environments (Figure 5D). For example, on cobble beaches along the Atlantic coast of the United States, cordgrass fosters the abundance of ribbed mussels, the secondary habitat-formers, by stabilizing the cobble substrates and reducing stress due to waves and desiccation (Altieri et al. 2007). On intertidal rocky shores, reduction of heat and desiccation by intertidal habitat-forming species, such as macroalgal canopies (Bertness et al. 1999, Jenkins et al. 1999), barnacles (Kawai & Tokeshi 2006) and bivalves (Silliman et al. 2011), promotes the colonization of more stress-sensitive macroalgae and invertebrates (see Bulleri 2009 for a review). In at least one instance, the exacerbation rather than the amelioration of an environmental stressor appears to be the driver of a facilitation cascade. Decreases in sediment oxygen by the invasive alga *Caulerpa taxifolia* promote a shallower burial depth of clams, enhancing the recruitment of epibionts to exposed shells (Gribben et al. 2009a, b). Although changes in habitat quality can also decrease the health and survivorship of individual clams, this is somewhat mitigated by clam behaviour (Wright et al. 2007, 2010, Wright & Gribben 2008), and there is a clear net gain in biodiversity across the landscape when this facilitation cascade is present.

### *Biotic stressor amelioration*

The physical structure provided by habitat-formers can also facilitate associated biota by reducing negative biological interactions such as predation or competition (e.g. Orth et al. 1984, Grabowski 2004, Griffen & Byers 2006; also see Figure 2). For example, drift algae entrapped in seagrass (Adams et al. 2004) and algal cover on mangrove prop-roots (Jaxion-Harm & Speight 2012) facilitated post-settlement fish and crab survival by reducing predator foraging. On shallow rocky reefs, anemones and tube-building gastropods can constrain foraging bouts of sea urchins, thus providing a refuge for algal turf (Levenbach 2008, Bulleri et al. 2011). Although positive effects of enhanced macroalgal cover on invertebrates (the inhabitant species) have not been formally assessed in these specific cases, there is a wealth of evidence that they are very likely to occur (Sarda 1991, Kelaher et al. 2001, Teagle et al. 2017). Further, macroalgal canopies often promote understory assemblages of macroalgae and sessile invertebrates which in turn, facilitate a diversity of mobile invertebrates, likely because the canopy-forming macroalgae reduce dominance by competitively superior species, predation pressure or both (Bulleri et al. 2002, Eriksson et al. 2006, Clements & Hay 2015, Cardenas et al. 2016). This was observed where opportunistic, fast-growing macroalgal species (i.e. filamentous algal turf) readily monopolize space under full light, driving the loss of sessile invertebrate and macroalgal habitat-formers (Bulleri et al. 2002, Cardenas et al. 2016).

### *Variation between intertidal and subtidal environments*

Research on individual habitat-formers indicates that the mechanisms underpinning positive species interactions in marine environments vary between intertidal and subtidal environments. For example, Bulleri (2009) showed that positive interactions generated through the amelioration of physical stress were more common in intertidal environments, while those arising from a reduction in consumer pressure—either predation or grazing—are more common in subtidal environments. These patterns might reflect variations in the prevalence of forces (i.e. physical versus biological) that control intertidal and subtidal communities, respectively. Are such variations in the prevalence of biological versus physical mechanisms of facilitation reflected in facilitation cascades?

There are several examples of facilitation cascades triggered by physical stress-buffering in the intertidal, including salt marshes and mangrove forests (Altieri et al. 2007, McAfee et al. 2016).

By contrast, facilitation cascades documented in subtidal environments are generally the result of resource provision (Gribben et al. 2009a, 2017a). To the best of our knowledge, no study has formally documented a subtidal facilitation cascade triggered by reduction of consumer pressure, which is at odds with convincing evidence of the relevance of this facilitation mechanism in subtidal environments (Levenbach 2008, Bulleri et al. 2011, Kayal & Kayal 2017). A likely example would be colonies of the fire coral *Millepora platyphylla* providing refuge to other coral taxa (*Acropora and Pocillopora*) against the predatory sea star, *Acanthaster planci* (Kayal & Kayal 2017). Although not investigated directly, positive effects on coral taxa susceptible to predation are very likely to propagate to a multitude of other species (fish and invertebrates) through habitat provision.

## Sources of spatial and temporal variability in facilitation cascades and their impact

It is increasingly apparent that the direction and magnitude of the species interactions that underpin facilitation cascades vary both spatially and temporally (Thomsen 2010, Angelini & Silliman 2014, McAfee et al. 2016, Thomsen et al. 2016b). Identifying the factors that operate at local to landscape scales to influence these species interactions can provide insight into where facilitation cascades are more likely to be found and how they are influenced by variation in abiotic and biotic conditions.

### *Trait- and density-mediated effects*

Both basal and secondary habitat-forming species can display considerable spatio-temporal variation in individual-level (e.g. morphology) and population-level traits (e.g. density; Bishop et al. 2013; also see Figure 7A and Table 2). Where these traits modify the availability of a limiting resource or stressor amelioration, the existence or strength of facilitation cascades may be affected (Bishop et al. 2013, Table 2). The traits and density of a basal habitat-former may influence facilitation-cascades by (1) determining whether the environment is suitable for the secondary habitat-former to colonize and form habitat, and (2) modifying traits of the secondary habitat-former.

Studies have generally examined the effects of variation in basal and secondary habitat-former traits on the enactment of the cascade independent of one another (but see Bishop et al. 2013). Surveys and experimental manipulations of habitat-formers generally demonstrate positive relationships between increasing habitat-former biomass, cover or density and the associated species' abundance or richness (Mukai & Iijima 1995, Pavia et al. 1999, Gribben et al. 2009a, Thomsen 2010, Drouin et al. 2011, Koivisto et al. 2011, Angelini et al. 2015). However, such relationships are often nonlinear as they start to plateau at higher abundances of the basal habitat-former (Bishop et al. 2013), perhaps indicating a saturation point beyond which structural habitat no longer limits colonization of the secondary habitat-former or the facilitated inhabitants, or a point beyond which increases in density no longer enhance amelioration of abiotic or biotic stress. Indeed, it is conceivable that at very high densities, the relationship between basal and secondary habitat-formers may shift from facilitative to competitive, although this has not yet been observed or tested.

In a few instances, studies have simultaneously manipulated multiple traits of basal and secondary habitat-formers, indicating independent and additive effects of them on biodiversity. For example, in a study investigating the implications of intraspecific trait variations, Bishop et al. (2013) found that both the density and height of pneumatophores of the basal habitat-former, the mangrove *Avicennia marina,* had independent and additive effects on the trapping and retention of the secondary habitat-former, the fucoid alga *Hormosira banksii*. High densities of tall pneumatophores initially served as a physical barrier to algal colonization of pneumatophore plots, but, over the longer term, they enhanced the retention of colonized algae. Increased algal biomass, in turn, facilitated epifaunal colonization. In an interspecific example, the densities of two secondary habitat-formers (*H. banksii* and the oyster *Saccostrea glomerata*), each dependent on pneumatophores, had independent and

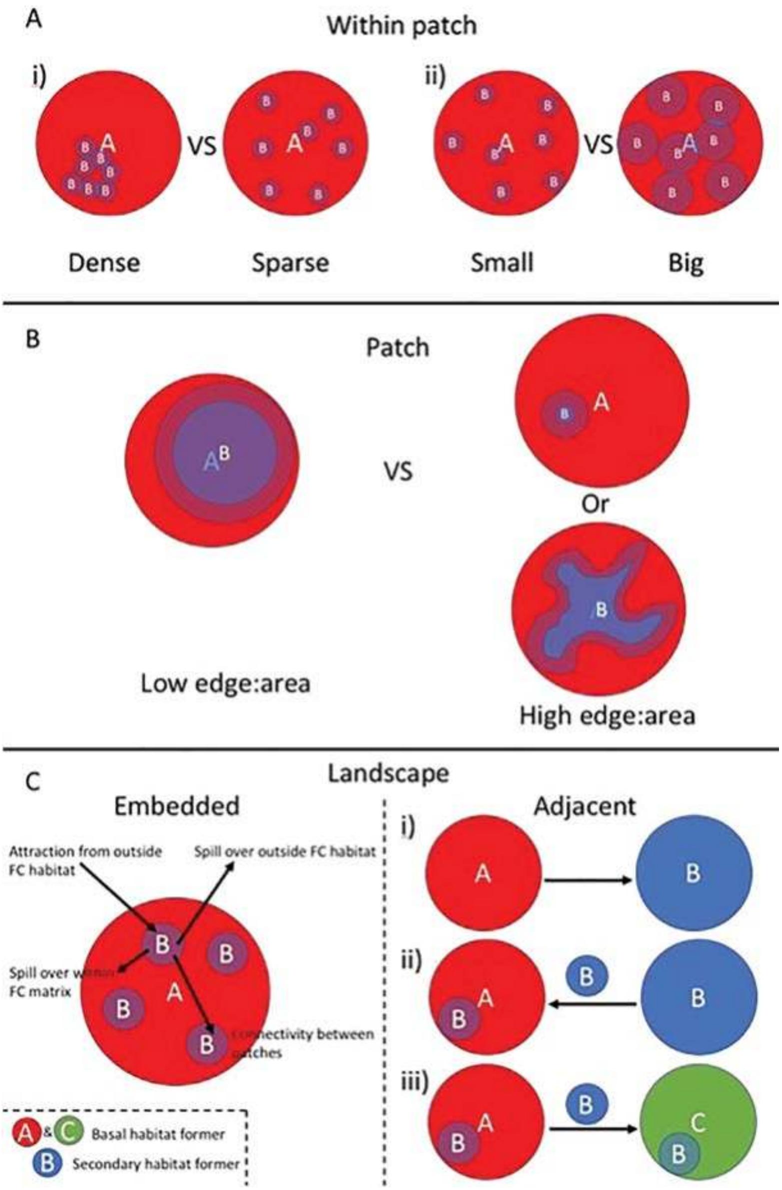

**Figure 7** (A) Traits including (i) gregariousness and (ii) body size of individual habitat formers within a patch can influence facilitative interactions between the basal and secondary habitat former, or between a habitat-former and inhabitants. See Table 2 for additional traits that can influence interactions and outcomes in a facilitation cascade. (B) Characteristics of a habitat-former patch, such as edge to area ratio, can influence the outcome of facilitation cascades because habitat modification is likely to vary with distance from the edge of a patch. The proportion of a patch that is comprised of edge habitat (lighter color) can be influenced by both size and shape as seen in this diagram. See Table 2 for other patch traits that can influence the outcome of facilitation cascades. (C) Habitat-formers in a facilitation cascade interact at the landscape scale with one another, the surrounding habitat, and with inhabitants. This connectivity can take the form of habitat modification or transport of resources and propagules. The nature of the connectivity depends on whether the basal and secondary habitat-formers are in a spatially embedded or adjacent configuration. (*Continued*)

**Figure 7 (Continued)** In the embedded configuration, the effects of a secondary habitat-former (B) may influence other individuals or patches of the secondary habitat-former, the matrix of the basal habitat-former (A), or spill over into the habitat outside the habitat where the basal and secondary habitat reside (including distant patches created by the facilitation cascade). When the basal and secondary habitat-former are found adjacent to one another, they can interact through (i) resource exchange, migration of inhabitants, or habitat amelioration effects that carry over distance; (ii) transport of a secondary habitat-former from a source population into a patch of a basal habitat-former, where it becomes entrained; or (iii) transport of a secondary habitat-former from the patch of one basal habitat-former to another basal habitat-former.

**Table 2** Potential metrics for characterizing habitat-formers at the scale of an individual habitat-former (e.g. a single, mussel, oyster, mangrove root or tree), discrete patches of a habitat-former (e.g. a mussel bed, oyster reef, mangrove island) and arrays of habitat-former patches at the landscape scale and for assessing the effects of these habitat-former characteristics on beneficiary species- and community-level responses

| | Individual traits | Patch | Landscape: embedded habitat-former assemblages | Landscape: adjacent habitat-former assemblages |
|---|---|---|---|---|
| Characteristics of habitat-former | Surface area, volume, fresh and dry weight, structural complexity metrics (e.g. fractal dimension, circularity, lacunarity) | Patch area, patch volume, patch edge-to-area ratio, number and size of individual habitat-formers (e.g. for mussels, oysters), patch age | Distance to nearest patch neighbor, patch cover, patch spatial configuration (e.g. random, clustered, uniform), patch persistence, patch size distribution | Distance and connectivity between habitat-former patches, size of habitat-former patches |
| Beneficiary species and community responses | Body size, species identity, life stage | Species abundance, species richness, food chain length, predator: prey ratios | Population size, population stability, community stability, species-area relationships | Population connectivity, trophic subsidies and feedbacks |

*Embedded and adjacent habitat-former patch arrays are differentiated in separate columns because of the differences in connectivity that can be manifested in these types of facilitation cascades.*

additive effects on inhabitant biodiversity (Hughes et al. 2014). Finally, in an example investigating the interactive effects of traits of a basal (*A. marina* pneumatophore) and secondary (*H. banksii*) habitat-former, both the height of pneumatophores and the thallus length of *H. banksii* independently influenced the biomass of the algae retained by the mangroves (Bishop et al. 2013).

### *Patch size–mediated effects*

Habitat-formers commonly occur in spatially discrete patches that vary in size. Patchy facilitation cascades can occur either because a basal habitat-former occurs in patches, or the secondary habitat-former occurs in patches within a large continuous habitat created by the basal habitat-former (Crotty et al. 2018). An example of each is evident in the cordgrass-ribbed mussel association in various wave exposure contexts. On wave-exposed cobble beach shorelines, where cordgrass grows in discrete beds that are each occupied by a homogenous ribbed mussel reef, patches of the facilitation cascade habitat are defined by the dimensions of the cordgrass beds (Altieri et al. 2007). On sheltered shorelines, cordgrass forms expansive salt marshes and facilitation cascades occur in the relatively small patches of ribbed mussels that dot the marsh landscape (Angelini et al. 2015).

Patch size mediates how habitat-formers influence the physical environment and other species (Figure 7A and Table 2). For example, early work with cobble beach plant communities found that the length of cordgrass beds had a nonlinear relationship with substrate stability and the diversity of forbs in areas sheltered by beds (Bruno & Kennedy 2000). Evidence is also accumulating for nonlinear relationships between the patch size of co-occurring habitat-formers and the strength of facilitation cascades. For example, in salt marshes of the southeastern United States, the functional diversity of invertebrates increased with the number of mussels in a patch following a nonlinear power function—with the greatest increases in diversity occurring with increases at the lower end of the range in patch sizes (Angelini et al. 2016). In contrast, the abundance and total biomass of invertebrates increased linearly with patch size. Nonetheless, both the diversity and biomass *per unit area* were greater in larger patches, suggesting that the function of facilitation cascades differs qualitatively between large and small patches.

There are several explanations for this nonlinear positive relationship between patch size and the strength of a facilitation cascade apparent in the diversity or abundance of inhabitants. First, large patches of co-occurring habitat-formers are likely to incorporate a greater degree of environmental heterogeneity because they are more likely than small patches to span gradients in environmental conditions, incorporate a range of size and age classes of habitat-formers and offer differentiated edge and interior habitats (Angelini et al. 2015; also see Figure 7B). Second, larger patches may support more species because they buffer against population stochasticity, as predicted by classic island biogeography theory (MacArthur & Wilson 1967). Third, larger patches can be more resilient to disturbances due to facilitation between the co-occurring habitat-formers and the increased likelihood of remnant individuals surviving a disturbance event that allows vegetative regrowth (Derksen-Hooijberg et al. 2018). This greater stability and structural continuity of large habitat-former patches may allow the development of more diverse communities, as well as the persistence of those communities once they establish.

## *Landscape-scale considerations*

Much of the early research on facilitation cascades focused on the occurrence of facilitation within patches and on the contrasting patterns of species diversity and abundance inside versus outside these patches (Altieri et al. 2007, Gribben et al. 2009a, Bishop et al. 2013). Recently, it has been recognized that habitat-formers may interact with one another at the landscape scale, resulting in emergent properties and outcomes of facilitation cascades that extend beyond the boundary of a given patch. In particular, patches of co-occurring habitat-formers can influence the surrounding matrix through spillover of organisms (Figure 7C and Table 2). For example, patches of cordgrass and ribbed mussels observed at mid-intertidal elevations on cobble beaches form a nursery habitat for invasive crabs that enhances the number of adult invasive crabs and coexistence with native crabs in adjacent lower intertidal areas outside the patch (Altieri & Irving 2017). In other cases, the habitat-formers themselves can be mobile, with implications for the occurrence of the facilitation cascade and even the transport of associated organisms. For example, habitat-formers that initially establish in different ecosystems may form a facilitation cascade if one species is dislodged and transported over long distances, as when rocky shore algae are dislodged and then trapped among mangrove pneumatophores, facilitating an invertebrate community (Bishop et al. 2009). In another instance, entire communities of invertebrates inhabiting algae, which are facilitated by a gardening polychaete on intertidal mudflats (Byers et al. 2012), are commonly transported to adjacent salt marshes following storms and dislodgment of the algae, thereby extending mudflat cascades into salt-marsh cascades (Thomsen et al. 2009, Byers et al. 2012).

Associated biota can move in reciprocal directions as well, and patches of habitat created by a facilitation cascade also have the potential to attract mobile organisms from the surrounding matrix. An example of this is marsh organisms migrating into the alga *Gracilaria vermiculophylla*, which is facilitated on intertidal mudflats by tubes of the worm *Diopatra* (Figure 7C). This leads to the question of the extent to which the elevated diversity and abundance of associated organisms in patches result from the higher recruitment and survivorship due to the facilitation cascade, or just the aggregation of organisms that would otherwise persist in the surrounding area. Studies demonstrating higher survivorship of juvenile blue crabs and mud crabs in *Gracilaria* algae attached to *Diopatra* worm tubes than in adjacent seagrass or bare mudflats indicate that, in at least some cases, production is increased by facilitation cascades (Johnston & Lipcius 2012, Bishop & Byers 2015). Regardless of the underlying mechanisms of how organisms come to be associated with the facilitation cascade habitat, the elevated abundance and diversity of inhabitants within patches constitute evidence that they are benefitting from conditions created by the co-occurring habitat-formers.

Modification of abiotic conditions by facilitation cascades can also extend into the surrounding areas beyond the patches where habitat-formers co-occur (Figures 2B and 7C, Table 2). Such long-distance interactions are likely to occur where patches can absorb energy such as water currents and wave movement, or intercept materials such as propagules or sediment transported passively across the landscape (Donadi et al. 2013, van de Koppel et al. 2015). For example, coral reefs, which are built through a network of facilitation cascades in which various corals, algae, and sponges facilitate one another and build the reef structure (Wulff & Buss 1979, Adey 1998), can buffer shorelines against wave energy (Gerritsen 1980, Hardy & Young 1996, Ferrario et al. 2014) and thereby allow the development of diverse shoreline communities hundreds of metres inshore of the reef crest.

Linkages of long-distance interactions can also allow habitat-forming species that are adjacent to one another, rather than embedded in the same patch, to form facilitation cascades (Figures 1C, 2B and 7C). This is evident at the edge of marshes where oysters reduce wave energy, which results in shoreline stabilization, sediment accretion and establishment of marsh grass inshore of the oysters—a powerful interaction that can be harnessed for restoration activities (Meyer et al. 1997, Piazza et al. 2005, see section on Restoration, later in this review). A diverse community of marsh occupants, including crabs, snails, fish and birds, in turn benefit from this cascade (Scyphers et al. 2011). The enactment of such long-distance facilitation cascades can be scale-dependent and influence environmental factors such as wave energy (Piazza et al. 2005). On the mudflats of the Wadden Sea, for instance, mussels have a negative competitive effect on cockles (secondary habitat-formers) in their immediate vicinity by reducing substrate stability and depleting food resources, but a positive effect on cockles that are 50–100 m away by reducing wave energy (Donadi et al. 2013). The conclusion to be drawn from these examples is that multiple habitat-formers may facilitate one another with cascading effects on the diversity and abundance of inhabitant species, but these effects may be apparent only when observations are made at appropriately large scales and when considering mechanisms of connectivity among habitat modifying species and their configuration on the landscape.

### *Time scale and the variability of facilitation cascades*

The strength and importance of facilitation cascades are likely to vary with time for several reasons. First, the abundance of one of the habitat-formers in a facilitation cascade may change based on when it occurs, such as habitat-forming algae that are more abundant on oysters and worm tubes in summer than winter (Thomsen et al. 2007). On the time scale of days, the urchin *H. purpurascens,* which wraps itself in the blades of live *E. radiata* kelp to form shelters for the snail *P. eximius*, moves between kelp plants (Bell et al. 2014). This in turn, results in temporally dynamic associations between the snails and kelp (Bell et al. 2014). Second, inhabitants may be dependent on habitat within a facilitation cascade during only a portion of their life, such as shore crabs that associate with cordgrass and mussel habitat as recruits before moving into adjacent habitats as adults (Altieri & Irving 2017). Reciprocally, habitat-formers may have particularly strong facilitative effects during a subset of their life stages, as occurs for pen shells (*Atrina* species, formerly called *Pinna*) that can have a greater facilitative effect on some inhabitants after they have died because their gaping shells provide habitats for nesting fish and burrowing amphipods (Munguia 2007), although a higher abundance of epibionts on live versus dead shells of pen shells has also been documented (Gribben et al. 2017a). Third, the importance of facilitation cascades may vary with time because the stress that the habitat-formers ameliorate becomes limiting for inhabitants only at certain times. For example, year to year variation in temperature resulted in algae that grow on barnacles having a positive effect on associated species by buffering against thermal stress during warmer years, but otherwise having negative effects via smothering in cooler years (Leonard 2000). Given that the strength of facilitation, as well as shifts between positive and negative interactions, are likely to vary over time scales of hours to months, the timing and interpretation of experiments and sampling require knowledge of natural history and environmental regimes.

## *Variation in facilitation cascades along abiotic and biotic gradients*

A large body of theoretical and empirical work, stimulated by the SGH (Bertness & Callaway 1994), has provided compelling evidence that species interactions tend to shift from negative (i.e. competition) to positive (i.e. facilitation) along environmental stress or consumer pressure gradients (Brooker et al. 2008, Maestre et al. 2009, Bulleri et al. 2011, He et al. 2013). Thus, the SGH can provide a useful theoretical background for predicting how the strength and stability of facilitation cascades can change according to external biological and physical conditions. As proposed by Angelini et al. (2011) and discussed in previous sections (i.e. the section entitled "The mechanisms underpinning facilitation cascades," earlier in this review), facilitation between multiple habitat-formers is expected to be the dominant interaction at both ends of gradients of physical stress. In harsh environments, amelioration of physical stress by the basal habitat-formers can foster the persistence of less stress-tolerant habitat-formers (Altieri et al. 2007, McAfee et al. 2016). By contrast, in environmentally benign environments, basal habitat-formers can shelter secondary habitat-formers from consumers and, by enhancing the availability of or access to limiting resources, stronger competitors as well (Bulleri et al. 2002, Eriksson et al. 2006, Clements & Hay 2015, Cardenas et al. 2016). The mechanism through which basal habitat-formers facilitate secondary habitat-formers, and secondary habitat-formers facilitate inhabitants, however, may determine the sensitivity of a cascade to variations in abiotic and biotic factors.

Positive interactions at different hierarchical levels of a cascade can be elicited by either the same or different mechanisms (Figure 8; Altieri et al. 2007). Predicting how the strength of cascades will vary along abiotic and biotic gradients becomes more difficult when they involve different facilitative mechanisms. Cascades including one single mechanism of facilitation (Figures 8A–C) may respond to a restricted set of abiotic and biotic factors. Arguably, the presence of different mechanisms of facilitation broadens the set of factors influencing its strength. For example, the strength of a facilitation cascade in which the basal habitat-former facilitates a secondary habitat-former by ameliorating environmental stress and the secondary habitat-former provides shelter from predation to the focal species, or vice versa (Figures 8B,C), would respond to variations in relevant physical stressors and the density or behaviour of consumers.

Facilitation cascades in which positive effects between species depend on the provision of or enhanced access to limiting resources presumably will display less variation in persistence and strength along gradients of biotic and abiotic stresses, in comparison to facilitation cascades that occur when environmental stress, consumer pressure or both are reduced (Figure 8A). In fact, provision of resources by one habitat-former would benefit another habitat-former or inhabitants, even at increasing levels of biotic or abiotic stress. This does not imply that interactions among species in facilitation cascades based on enhanced resource provision are disconnected from background biotic and abiotic conditions.

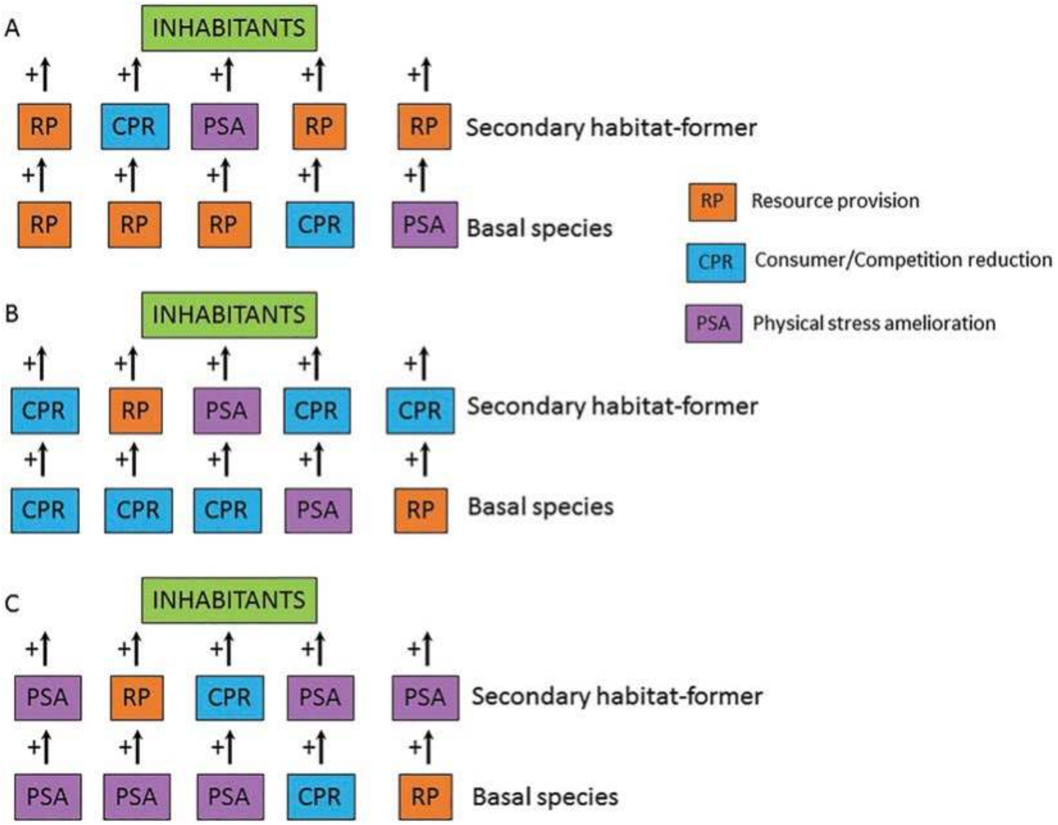

**Figure 8** Diagram showing possible combinations of various facilitation mechanisms (Resource provision, Consumer/Competition reduction and Physical stress amelioration) enacting a three-level facilitation cascade. Each of the mechanisms can operate both at the first (between the basal and the secondary habitat-former) and second (between the secondary habitat-former and the inhabitant community) link. The diagram illustrates cascades in which at least one of the positive interaction is due to (A) Resource provision, (B) Consumer/Competition reduction, (C) Physical stress amelioration.

As previously discussed, there are important mediators of facilitation cascades, such as interacting species traits and density, that may respond to those background conditions. For example, enhanced nutrient loading may cause macroalgal blooms, reducing seagrass shoots' density (Holmer et al. 2011, Höffle et al. 2012) and, ultimately, their functionality as basal habitat-formers. Extreme hydrodynamic forces may dislodge or reduce the size of epiphytic or enmeshed macroalgae, impairing their ability to provide habitats to invertebrates (Bishop et al. 2009), and high herbivore pressure may reduce seagrass leaf length or macroalgal biomass to levels too low for benefits for inhabitants to accrue. In addition, failure or decline of the basal habitat-former because of unsuitable abiotic or biotic conditions may reduce its ability to deliver positive effects to the secondary habitat-former. For example, in soft sediment habitats along the Northwest Atlantic coast, the positive effects of the tube-building polychaete *Diopatra* on macroalgae decreased in strength towards lower latitudes due to the reduced density of tubes (Berke 2012). Although facilitation cascades generated by resource provisioning are known to occur both in stressful and benign environments and be characterized by relatively high stability (van der Zee et al. 2016, Derksen-Hooijberg et al. 2018, Crotty et al. 2018), their strength is still likely to vary as a function of background biotic and abiotic conditions.

When the main mechanism of facilitation between habitat-formers is physical stress amelioration, the strength of the cascade is likely to vary among patches along an environmental gradient, with greater dependence of inhabitants on the facilitation cascade with increasing stress (Angelini et al. 2011). For example, on the east coast of the United States, grasses and forbs dominate in wave-sheltered sites, but they rely upon substrate stabilization by *Spartina alterniflora* at sites moderately exposed to wave action (van Wesenbeeck et al. 2007). The facilitation cascade fails, however, at the most extreme wave-exposed sites, where abrasion by cobbles prevents the establishment of vegetation. Conversely, studies across broad latitudinal gradients have documented little variation in the strength of facilitation cascades generated by physical stress amelioration. For example, in terrestrial environments, Angelini and Silliman (2014) found that positive effects on insect assemblages generated by the oak–*Tillandsia usneoides* (Spanish moss) association did not vary across an 800-km span on the east coast of the United States. Likewise, positive effects of oysters growing on mangrove aerial roots on macroinvertebrate assemblages were consistent across 8° latitude on the east coast of Australia (McAfee et al. 2016). However, direct comparisons of how the strength of facilitation cascades vary across larger latitudinal gradients spanning tropical to temperate environments have received little attention, so it is difficult to draw any meaningful conclusions.

The analysis of pairwise interactions along one single gradient of stress may yield less predictive power of where a facilitation cascade will be found, or under which circumstances it will persist when the habitat-formers involved in a facilitation cascade are characterized by different life history-traits (e.g. size, feeding-behaviour, or trophic level) and sensitivity to different environmental stressors. For example, in the five-level habitat-former facilitation cascade documented by Thomsen et al. (2016a), an increase in suspended organic matter may benefit the basal habitat-former (a filter-feeder, the cockle *Austrovenus stutchburyi*), but be detrimental for higher-level habitat-formers (i.e. the macroalgae *Ulva* and *Sarcothalia* (formerly *Gigartina*) *atropurpurea*) through reduction in light levels. Under these circumstances, analyses of variations in the sign and strength of species interactions along multiple gradients of stress (i.e. those most likely to affect each of the species involved in the cascade) would be necessary to provide an insight into the context dependency and variability of the facilitation cascade.

To the best of our knowledge, no study has formally investigated variations in strength of facilitation cascades triggered by associational defence along gradients of consumer pressure. Facilitation cascades in which reduction of competition and consumer pressure is the predominant facilitation mechanism between pairs of habitat-formers or between a habitat-former and inhabitants will be most sensitive to spatial and temporal variations in these biological forces, which often intensify with decreasing environmental stress (Bertness & Callaway 1994). From the SGH, a decrease in the intensity of negative biotic interactions, either predation or competition, is predicted to modify the trade-off between the benefits and costs of associational defences. For example, corals can suffer lower mortality from predation by the sea star, *Acanthaster planci,* or corallivorous fish when associated with canopy-forming algae, such as *Sargassum polycystum* or *Turbinaria ornata* (Bulleri et al. 2013, Clements & Hay 2015). However, branched corals underneath macroalgal canopies exhibit lower growth rates than corals in open areas when consumer pressure is low (Bulleri et al. 2013). Similarly, the ability of a habitat-former to provide refuge from consumption for another habitat-former or for inhabitants can decrease or collapse when predation pressure exceeds a critical threshold. For example, on subtidal rocky reefs in the Santa Barbara Channel, California, USA, the intensity of positive effects of anemones on macroalgae peaked when sea urchin density was 10 per square metre and decreased thereafter, and all macroalgae were consumed when the highest density was reached (85 individuals per square metre) (Levenbach 2009).

## Length and stability of facilitation cascades

To date, facilitation cascades including from two to five levels of habitat-formers have been described (Thomsen et al. 2016a, Yakovis & Artemieva 2017). Yet, to the best of our knowledge, the relationship between facilitation cascade length and stability remains unexplored. The stability of a cascade might be predicted to decrease with increasing number of facilitation links due to its hierarchical nature (Yakovis & Artemieva 2017). The loss of one intermediate habitat-former could destabilize the whole cascade, with effects becoming greater as the perturbed level is lower in the hierarchy of interactions (i.e. close to the basal habitat-former). By contrast, redundancy of habitat-formers within levels of the hierarchy would add stability to the cascade (Yakovis & Artemieva 2017). For example, in mangrove forests, some species of echinoderms, gastropods and crustaceans are supported by both oysters and macroalgae, which act as secondary habitat-formers (Hughes et al. 2014). These facilitated species are, therefore, less susceptible to decline or local extinction following the disappearance of either of the two secondary habitat-formers compared with those invertebrates that are able to use only one of the two habitats. Similarly, the sharing of habitat-formers across levels of the hierarchy should promote cascade stability. For example, in the shallow subtidal of the White Sea, red algae are common on barnacles, ascidians and mussels, which represent the second, third and fourth levels of the hierarchy of positive interactions, respectively (Yakovis and Artemieva 2017). Similarly, mussels can grow on both cockles (the basal habitat-former) and ascidians. Thus, the decline of some of the species at intermediate levels of the hierarchy should not cause a collapse of the whole cascade.

Species in longer cascades will likely include a higher number of indirect connections with species external to the cascade (Figure 9). For example, in a New Zealand estuary, the bivalve *Austrovenus stutchburyi* starts a five-level facilitation cascade that includes green algae, trochid snails, encrusting bryozoans and, finally, the red alga *S. atropurpurea,* which supports other inhabitants (Thomsen et al. 2016a). In this case, the persistence of *S. atropurpurea* is facultatively dependent upon all the species found at lower levels of the hierarchy and, hence, is influenced by a broad range of biotic and abiotic factors that act on any one of those levels. In fact, bivalves, snails, green algae and bryozoans are likely to respond to the alteration in pressure from different consumers, the alteration of different physical conditions or both. The number of consumers or competitors directly or indirectly interacting with species involved in the facilitation cascade, and which may modify the strength of one or more links within the cascade, is thus expected to increase with cascade length (Figure 9). This suggests that facilitation cascades are framed within local food webs and are likely to be, directly or indirectly, under the control of a broader group of species than those forming the cascade itself. The relationship between food-web complexity and stability is still highly controversial (May 1971, 1972, Mougi & Kondoh 2016), and at present, there is no empirical basis for predicting how the stability of a facilitation cascade is influenced by the complexity of the food web within which it is framed.

## Incorporation of facilitation cascades into natural resource management

Due to the role of habitat-forming species in ameliorating environmental stressors, and as hot spots of biodiversity, they are obvious targets for conservation and restoration initiatives (Crain & Bertness 2005, Byers et al. 2006, Marzinelli et al. 2014, Bayraktarov et al. 2016). With anthropogenic climate change, coastal development and food-web alterations further degrade coastal and marine ecosystems, thus facilitation cascades and the positive interactions upon which they are structured may play an increasingly important role in sustaining biodiversity (Silliman & He 2018). Facilitation cascades can enhance recovery from disturbance and thereby increase ecosystem resilience. For example, mussels increase salt-marsh cordgrass survival following drought and elevated snail-grazing stress because these bivalves enhance water storage, reduce soil salinity stress and promote the ability of cordgrass to compensate for grazing damage through their deposition of nutrients (Angelini et al. 2016).

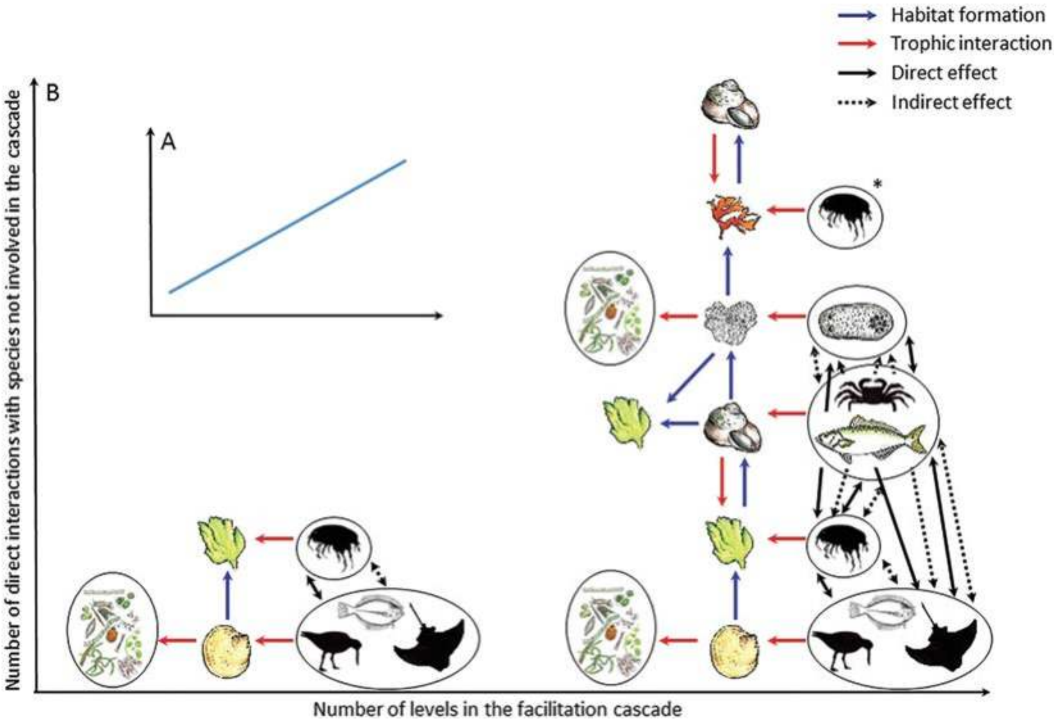

**Figure 9** (A) Predicted positive relationship between the number of levels in the facilitation cascade and the number of direct interactions with species not included in the cascade; (B) in the Avon-Heathcote Estuary, New Zealand a six-level facilitation cascade includes the cockle *Austrovenus,* the green seaweed *Ulva*, the trochid snails *Micrelenchus tenebrosus* and *Diloma subrostrata*, the nonnative encrusting bryozoan *Conopeum seurati* and the red seaweed *S. atropurpurea* (Thomsen et al. 2016a). Interactions with species that are not involved in this facilitation cascade progressively accumulate with increasing cascade length. For the sake of clarity, only positive (blue) and negative (red) direct interactions are reported among species within the cascade. In a two-level cascade, the basal habitat-former (cockle) and the secondary habitat-former (*Ulva*) are connected with two external groups of species (in circles) by trophic interactions: the cockle feed on phytoplankton and can be preyed upon by eagle rays, oystercatchers and flounders, while *Ulva* is grazed upon by amphipods. In the six-level cascade, two more groups of species are potentially accumulated, the predators of Trochids (the fish *Arripis trutta* and the crab *Cyclograpsus* spp.) and the predators of encrusting (nudibranchs). Species external to the cascade can be connected by direct (black straight line) and indirect (black dotted line) interactions (either negative or positive) and are embedded in the broader food web (not reported in the diagram). *Amphipods use both *Gigartina* and *Ulva* as a food source and, hence, interact with species at different levels of the facilitation cascade. (Drawings courtesy of E. Maggi.)

Thermal stress is an important factor limiting the distribution of marine organisms at varying scales, and facilitation cascades have the potential to extend the distribution of organisms by buffering against that stress at both the local (Angelini et al. 2016) and latitudinal scales (McAfee et al. 2016). The importance of habitat-forming organisms in buffering against thermal stress should increase with climate change as temperatures become more extreme and variable (IPCC 2015); however, the geographic distribution of those effects may not be straightforward due to the geographic idiosyncrasies of thermal regimes (Helmuth et al. 2006). These predicted changes suggest the urgency of examining facilitation cascades as a tool for mitigating the anthropogenic changes to natural systems, and of understanding the range of anthropogenic stressors beyond climate change that they may ameliorate. Similarly, shifts in food-web structure due to overharvesting of targeted species, species invasions, and changes in environmental conditions are leading to outbreaks of consumers in many systems, such as crown-of-thorn sea stars in coral reefs (Kayal et al. 2012), as well as geese (Peterson et al. 2013) and feral hogs in salt marshes (Sharp & Angelini 2016). Facilitation cascades may also play a key role in buffering against and supporting recovery after these disturbance events, although far more research is needed to untangle the mechanisms that are most important drivers of recovery.

Historically, management of marine and coastal ecosystems has focused on the protection and restoration of basal habitat-formers, using a habitat-by-habitat approach (Gillis et al. 2017). Yet, where habitat-forming species act synergistically through facilitation cascades, the full biodiversity and ecosystem service benefits of management interventions may be realized only when they protect or enhance basal, secondary and higher-order habitat-formers together (Thomsen et al. 2018). Effective management of ecosystems requires knowledge of not only the distributions of, threats to and environmental tolerances of basal habitat-formers, but also of other, dependent habitat-formers (van de Koppel et al. 2015).

## *Conservation*

In establishing and managing marine protected areas, whether the system comprehensively, adequately and representatively protects ecosystems is typically assessed based on mapping of basal habitat-formers (e.g. seagrass meadows, kelp forests, coral or shellfish reefs) and nonbiogenic habitats (e.g. rocky reefs, sandflats, or mudflats), without consideration of the distributions or dependencies of secondary habitat-formers (e.g. IUCN 1994, Agardy 1995, Great Barrier Reef Marine Park Authority 2003). This ignores the possibility that the biogenic habitat may be composed of several interacting species with important interactions of dependency among them (Thomsen et al. 2018). For example, a coral reef may have hundreds of coral, alga, and sponge species that interact and potentially facilitate one another. In ecosystems with embedded facilitation cascades (e.g. Figure 2A), secondary habitat-formers may not be uniformly distributed within basal habitat-formers. Protection of those areas with secondary habitat-formers may lead to greater biodiversity, ecosystem functioning and ecosystem service benefits than protection of those with basal habitat-formers alone (Thomsen et al. 2018). The design of marine protected areas also needs to consider the possibility of long-distance facilitation cascades, in which dependencies between habitat-formers extend beyond habitat patch boundaries (van de Koppel et al. 2015). For example, where the persistence of cockle beds is dependent on the presence of mussel beds that dissipate wave action and modify sediment properties (Donadi et al. 2013), the conservation of cockle beds requires not only protection of the cockle beds themselves, but also of the mussel beds to which they are connected. Therefore, management systems that focus on the protection of individual habitats rather than seascapes that span areas with multiple habitat-formers may be of limited conservation value (van de Koppel et al. 2015, Gillis et al. 2017).

## *Restoration*

Like conservation, restoration often focuses on the reestablishment and rehabilitation of individual habitat-formers (Hawkins et al. 2002), with little consideration of the ecological dependencies among them (Derksen-Hooijberg et al. 2018). Key processes that threaten ecological communities are often defined on the basis of the damage they cause to basal habitat-formers (Environment Australia 1999), and ecosystems are typically managed to keep disturbances below the level at which damage to basal habitat-formers occurs (e.g. Lindenmayer & Luck 2005). When restoring degraded ecosystems that comprise facilitation cascades, it may be important first to reduce environmental stressors to levels that allow the survival, growth and reproduction of both basal and secondary habitat-formers (Lewis 1982, 2005). It is plausible that in some instances, secondary habitat-formers may be more sensitive to stressors than basal habitat-formers. For example, whereas the grey mangrove

(*A. marina*), which is a basal habitat-former, is resilient to, and may even be used as a biological filter for, sewage (Chen et al. 2000), the fucalean alga (*H. banksii*, which is a secondary habitat-former that can be found entangled in the pneumatophores of the mangrove (e.g. Bishop et al. 2012), has early life history stages that are detrimentally affected by sewage (Doblin & Clayton 1995). Depending on the dispersal capabilities of basal and secondary habitat-formers and the availability of nearby sources of recruits, transplantation of one or both of these into the restoration site might also be required (Derksen-Hooijberg et al. 2018). Particularly where the secondary habitat-former is to be transplanted into the site, knowledge is needed about threshold densities, biomasses and/or trait values that must be attained by the basal habitat-former to support the secondary habitat-former. For example, *H. banksii* is only enmeshed in and retained by mangrove pneumatophores once they exceed a certain density (Bishop et al. 2013). This also implies that priority effects will be important for the establishment of facilitation cascades, and so the order and timing of restoration activities will be important.

In many cases, secondary habitat-formers may eventually recruit to the basal habitat-former following its restoration, but active restoration of secondary habitat-formers may be desired to accelerate assembly of the rest of the community. Therefore, when selecting source populations for transplants, knowledge about those phenotypes of basal habitat-formers that most effectively facilitate secondary habitat-formers and those phenotypes of secondary habitat-formers that best promote inhabitant communities will be beneficial. In some instances, methods of transplantation may also be adapted to encourage patterns and forms of growth that best support facilitation cascades. For example, just as the spacing between salt-marsh transplants may have large outcomes on transplant survival (Silliman et al. 2015), so may it also influence the enactment of facilitation cascades (Derksen-Hooijberg et al. 2018).

To maximize the probability of success, restoration projects also need to consider that dependencies among habitat-formers may occur across habitat boundaries that requires corestoration of multiple basal habitat-formers. For example, in seascapes where the persistence of seagrass is contingent on adjacent coral reefs dissipating wave energy, the restoration of seagrass will be successful only where coral reefs are either intact or functionally restored (Gillis et al. 2017).

In environments that no longer support native habitat-formers and where their restoration is not feasible, facilitation cascades that include nonnative foundation species may reinstate some of the ecosystem services once provided by native habitat-formers (Ramus et al. 2017). In such instances, actively incorporating established nonnative foundation species into management strategies may have stronger-than-expected benefits for the provisioning of coastal ecosystem services. Nevertheless, before nonnative species are actively facilitated by programs aimed at restoring ecosystem services, a thorough examination is needed (Gribben et al. 2013, Sotka & Byers 2019, Thomsen et al. 2019). Whereas the nonnative secondary habitat-former *Gracilaria* may superficially appear to enhance fish and invertebrate abundances (Byers et al. 2012, Wright et al. 2014, Ramus et al. 2017), it is unclear to what extent this represents an enhancement of production versus a redistribution of species otherwise supported by other habitats (Sotka & Byers 2019, Thomsen et al. 2019). Further, such benefits may come at the expense of unmeasured negative impacts (Gribben & Wright 2006, Gribben et al. 2009b, 2017b), such as the facilitation of toxic *Vibrio* species that cause shellfish poisoning (Gonzalez et al. 2014) or changes in denitrification (Gonzalez et al. 2013), microbial community structure and sulphur cycling (Gribben et al. 2017b, 2018) in sediment.

## *Ecological engineering*

In areas where environmental conditions are no longer suitable for basal and/or secondary habitat-formers to persist, artificial mimics of these habitat-formers may be used to reinstate some of, if not all, the functions of facilitation cascades (Thomsen et al. 2018). Whether abiotic habitat mimics will be useful surrogates for live habitat-formers is contingent on the mechanisms by which the habitat-formers support associated communities (Clark & Edwards 1999, Spieler et al. 2001; Seaman 2007). Such an approach will be most successful where the key role of the habitat-former is to provide a structural habitat, which in turn serves as a substrate for attachment, modifies resource flows (e.g. by trapping organic matter) and/or mitigates abiotic and biotic stressors (Bologna & Heck 1999, Spieler et al. 2001). Of relevance to facilitation cascades, studies comparing the communities that recruit to live habitat-formers and structural mimics (e.g. live seagrass versus artificial seagrass units) demonstrate that in many instances, the role of the habitat-formers is primarily to provide habitat structure (Cattaneo & Kalff 1979, Lee et al. 2001, Kelaher 2003).

In other cases, such as facilitation of seagrass beds and their associated communities by adjacent shellfish reefs in a long-distance cascade (van de Koppel et al. 2015), structural mimics of oyster reefs will be poor surrogates for live habitats because the mechanism by which habitat-formers are linked is a process—filtration of suspended solids from the water (Wall et al. 2008)—that depends on live habitat-formers. Whether mimics can be successfully used in place of live basal or secondary habitat-formers may also be predicted based on whether associated species are facultatively or obligately dependent on the habitat-formers. Although there are some exceptions (e.g. the epiphyte *Notheia anomala* is obligately dependent on its macroalgal host *H. banksii*; Thomsen et al. 2016b), studies utilizing artificial macrophyte mimics have shown that for many epiphytes, the biotic nature of the macrophyte involved is insignificant, with epiphytes readily growing on abiotic structures (Harlin 1973, Cattaneo & Kalff 1979). Similarly, the majority of faunal species recorded in macrophyte holdfasts are also found in surrounding habitats rather than being obligate holdfast inhabitants (Christie et al. 2003). These examples suggest that mimics are likely to be able to functionally replace components of a facilitation cascade in many ecosystems.

The concept of facilitation cascades may also be applied to the ecological engineering of artificial structures, such as seawalls, breakwaters, pontoons and pilings, to enhance their ecological value (Perkol-Finkel et al. 2012, Ng et al. 2015, Ferrario et al. 2016; for a further review of this issue, see Firth et al. 2016 and Morris et al. this issue for reviews). For example, the Elliott Bay seawall in Seattle Harbor has a textured, concrete surface aimed at promoting the growth of intertidal marine life by increasing surface area and providing crevices (Goff 2008, 2010, Haddad Drugan 2013). The design includes enlarged geometric renditions of intertidal habitat-formers of Elliott Bay, such as barnacles, mussels, anemones and rockweed, arranged vertically according to the tidal elevations at which these species would naturally be found (Haddad Drugan 2013, Figure 10). The premise of this so-called Habitat Strata concept is that these geometries will encourage the colonization and growth of secondary habitat-formers (Haddad Drugan 2013, Figure 10).

Additionally, knowledge of the mechanisms by which long-distance facilitation cascades are enacted can be applied to the design of approaches to shoreline stabilization that are a hybrid of artificial structures and living habitat-modifiers (Temmerman et al. 2013, Chee et al. 2017; also see Morris et al. this issue). For example, in environments where hydrodynamic energy is too great to allow shoreline stabilization with habitat-formers alone, artificial substrate, such as rocky rubble, is placed off shorelines to reduce wave energy to a level that allows the growth of biogenic habitat such as salt marsh (Bilkovic & Mitchell 2013) and mangrove (Hashim et al. 2010) on the landward side. The role of rocky rubble is analogous to the role of intertidal oyster reefs in promoting marsh growth by forming a barrier to wave energy in a long-distance facilitation cascade (Meyer et al. 1997).

Where habitat mimics are to be applied either in the design of coastal infrastructure or as stand-alone elements, detailed knowledge is required about how variations in the morphology of the basal and secondary habitat-formers influence the strength and enactment of facilitation cascades. For example, the structural complexity and the size (volume) of kelp holdfasts influence the diversity and abundance of associated assemblages (Norderhaug et al. 2007). As previously noted, some facilitation cascades operate only when certain threshold values of habitat-former traits are reached (Bishop et al. 2013).

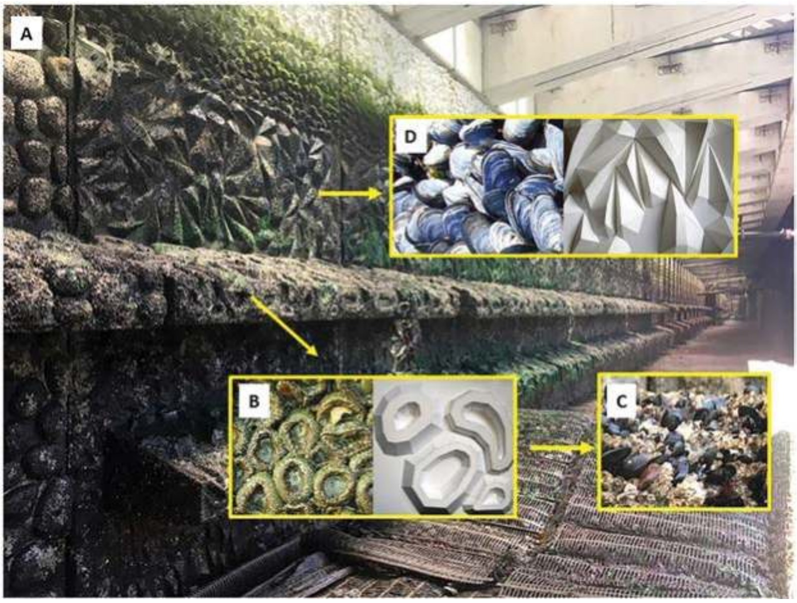

**Figure 10** The concept of a facilitation cascade may be used to ecologically engineer built infrastructure to have greater ecological value. The Elliott Bay Seawall, Seattle (A) has a textured surface that has been loosely designed to mimic the textures formed by local intertidal basal habitat-formers (B, D). These mimic basal habitat formers have, in turn, been colonized by secondary habitat-formers (C). (Photo credits (A, C) City of Seattle; (B) Haddad|Drugan.)

### *Invasive species management*

As facilitation cascades may benefit nonnative species via the same mechanisms as they benefit native species (Altieri et al. 2010, Altieri & Irving 2017), they may play a major role in the spread and proliferation of invasive species. This is particularly problematic where the nonnative species spillover from the facilitation cascade to nearby habitats. Altieri & Irving (2017) found that cobble beds adjacent to the cordgrass-mussel facilitation cascade had more than double the density of nonnative Asian shore crabs than cobble beds that were farther away. Whereas the nonnative crab was able to coexist with native crabs and prey species within the facilitation cascade due to the breadth of niche space provided (Altieri et al. 2010), outside the facilitation cascade, the nonnative species by virtue of its great abundance exerts a significant negative impact on prey species such as blue mussels (Lohrer & Whitlatch 2002). Particularly where spillover effects are apparent, effective management of nonnative species will require consideration of the role that facilitation cascades play in the proliferation of nonnatives. In such instances, whether management strategies should promote or inhibit facilitation cascades will depend on the magnitude of positive versus negative impacts, as well as the societal values placed on them.

## Key knowledge gaps

While facilitation cascades have now been documented from a large range of marine habitats, it is clear from our analysis that research has been biased towards particular habitats and types of habitat-formers. This has led to gaps in our understanding of the mechanisms by which these interactions arise and are maintained, as well as how they vary in time and space. Here, we summarize the key knowledge gaps that need to be filled to fully integrate the concept of facilitation cascades into ecological theory and management.

## *Facilitation cascades in understudied ecosystems*

From this literature review, it is evident that the study of facilitation cascades has been biased towards intertidal and shallow subtidal systems in subtropical and temperate latitudes. Thus, our knowledge of the importance of facilitation cascades to tropical, pelagic and deep-water benthic ecosystems, at very high and low latitudes, and in the Pacific and Indian Oceans is poor. Exploring facilitation cascades in these other ecosystems will allow more thorough and extensive tests of the importance of environmental stress regimes, seasonality and the size of the local species pool in shaping positive species interactions across the globe.

In addition, more information is needed on the potential role of mobile habitat-formers to start facilitation cascades. We know that drift algae can be an important secondary habitat-former in facilitation cascades once they come to settle within other habitat-formers (e.g. mangroves; Bishop et al. 2012, 2013, Hughes et al. 2014). But mobile habitat-formers have the potential to redistribute diversity through their movement within their local range (Altieri & Witman 2014), as well as transport entire communities to more distant locations (Smith 2002), and this transport process is not well understood in a cascade context.

## *Facilitation cascades initiated by nonstructural habitat-formers*

Thus far, the focus has been on facilitation cascades involving habitat-formers that physically modify habitats through their structure. Nevertheless, there are other mechanisms by which organisms may modify habitats and contribute to facilitation cascades, which need to be explored. For example, in soft sediment, bioturbating organisms, like holothurians, clams and polychaetes, can oxygenate sediment and thereby facilitate other species (Middelburg & Levin 2009), which in turn may further alter environmental conditions and promote more organisms (Biles et al. 2002, Solan et al. 2004). For example, in seagrass beds, swimming crabs excavate subtidal pools, facilitating diverse nekton assemblages that otherwise would be excluded from intertidal seagrass beds (van der Zee et al. 2016). This suggests that facilitation cascades may consist of combinations of ecosystem engineers that do and do not provide structural habitats. An additional research gap is that no studies have documented belowground facilitation cascades in sedimentary habitats, despite their likely existence. Burrowing organisms are known to enhance the aboveground structure of salt-marsh grass (Bertness 1985) and can positively influence mangrove growth and production (Smith et al. 2009). Theoretically, belowground facilitation cascades should result from the same mechanisms that drive aboveground cascades (i.e. provisioning of resources, mediation of trophic interactions and modification of abiotic conditions).

## *Understanding trait and scale-dependency across environmental gradients*

The traits, densities, patch sizes and landscape configurations of habitat-formers have important consequences for interactions between them and the associated biodiversity. Evidence indicates that both linear and nonlinear relationships can occur, including threshold effects such as the presence/absence response of oysters to pneumatophore density (Bishop et al. 2012) and mussel patch size effects of ecosystem functions in marsh (Angelini et al. 2015). To date, studies have focused on understanding how the density and traits of habitat-formers influence resource supply (e.g. physical habitat-provisioning), and more research is needed to understand the linear or nonlinear responses of environmental stressors (e.g. temperature, wave action) to the density and traits of the habitat-formers and the subsequent response of the facilitated community.

Additional research gaps that warrant attention are how biodiversity-ecosystem function relationships scale with areas in systems structured by facilitation cascades and how the body sizes and abundances of associated communities may be related to the size structure and density of the habitat formers (e.g. Angelini et al. 2015). Moreover, a deeper understanding of the importance of facilitation cascades across latitudinal gradients and whether dominant mechanisms change with latitude is required to determine whether they play important roles in controlling biodiversity and ecosystem function at large spatial scales. Addressing these knowledge gaps will deepen mechanistic understanding of when, where and at which scales facilitation cascades are most important in sustaining biodiversity and ecosystem functioning.

### *Tipping points*

Because the communities that depend on the structural habitat provided by habitat-formers may also be consumers of these (e.g. amphipods and other mesograzers on algae), there may be threshold densities at which interactions switch from positive to negative and facilitation cascades transition to trophic cascades. Understanding where these tipping points are is of high importance, given current rates of global and local change in marine ecosystems.

### *Feedbacks and cascade maintenance*

Research on facilitation cascades has largely focused on how they are established, with little attention to how they are maintained. Negative feedback may have particularly important consequences for the maintenance of facilitation cascades, as the survivorship and/or density/traits of one or both habitat-formers (e.g. Trowbridge 1993, Thomsen et al. 2013) have clear effects on each other and on the community structure. Thus, for facilitation cascades to persist, negative feedbacks should be regulated such that stability is maintained. For example, negative feedbacks may be limited by competition from other space occupiers that control the abundance of internal consumers of the habitat-formers.

Moreover, the mechanisms underpinning facilitation at higher levels of the hierarchy have received less and are often vaguely described in terms of habitat provision, without a formal assessment of whether such habitat alleviates resource limitation, provides more benign environmental conditions or reduces consumer pressure. Advancing understanding of these mechanisms, as well as their relative importance, will be key to enhancing our ability to predict variations in the strength and stability of facilitation cascades.

## Conclusion/Summary

Facilitation cascades are ubiquitous in most marine ecosystems (particularly benthic systems), in part because epibiosis is a common process (Wahl 1989). Here, we report on 100 studies (Table 1) documenting facilitation cascades, but we sense that this number greatly underestimates their relevance in structuring marine communities because they remain unexplored in some environments (e.g. deep seas) and overlooked in many others where co-occurring habitat-formers are often viewed as a single functional group rather than an assemblage of interacting species (e.g. coral reefs).

Until now, no review has integrated available studies to provide an overview of the functioning of facilitation cascades, synthesize their general importance, and identify factors that are likely to determine their importance in marine environments; our review, therefore, is both timely and overdue. For marine biologists, understanding trophic interactions (particularly trophic cascades) has been at the forefront of research agendas. Our review suggests that facilitation cascades require the same consideration if we are to fully understand the mechanisms shaping biodiversity and its important ecosystem functions across various scales and contexts.

Facilitation cascades may also provide a basis for an integrated framework inclusive of both negative (trophic) and positive (nontrophic) interactions for understanding the processes structuring ecological communities. Merging recently developed concepts in the field of facilitation cascades within food chains and trophic web theories could significantly advance our understanding of community assembly and dynamics. Such integration should allow the further development of ecological theories (inclusive of interacting positive and negative interactions) and lead to the development of more robust biodiversity conservation strategies.

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# DESIGN OPTIONS, IMPLEMENTATION ISSUES AND EVALUATING SUCCESS OF ECOLOGICALLY ENGINEERED SHORELINES

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## Abstract

Human population growth and accelerating coastal development have been the drivers for unprecedented construction of artificial structures along shorelines globally. Construction has been recently amplified by societal responses to reduce flood and erosion risks from rising sea levels and more extreme storms resulting from climate change. Such structures, leading to highly modified shorelines, deliver societal benefits, but they also create significant socioeconomic and environmental challenges. The planning, design and deployment of these coastal structures should aim to provide multiple goals through the application of ecoengineering to shoreline development. Such developments should be designed and built with the overarching objective of reducing negative impacts on nature, using hard, soft and hybrid ecological engineering approaches. The design of ecologically sensitive shorelines should be context-dependent and combine engineering, environmental and socioeconomic considerations. The costs and benefits of ecoengineered shoreline design options should be considered across all three of these disciplinary domains when setting objectives, informing plans for their subsequent maintenance and management and ultimately monitoring and evaluating their success. To date, successful ecoengineered shoreline projects have engaged with multiple stakeholders (e.g. architects, engineers, ecologists, coastal/port managers and the general public) during their conception and construction, but few have evaluated engineering, ecological and socioeconomic outcomes in a comprehensive manner. Increasing global awareness of climate change impacts (increased frequency or magnitude of extreme weather events and sea level rise), coupled with future predictions for coastal development (due to population growth leading to urban development and renewal, land reclamation and establishment of renewable energy infrastructure in the sea) will increase the demand for adaptive techniques to protect coastlines. In this review, we present an overview of current ecoengineered shoreline design options, the drivers and constraints that influence implementation and factors to consider when evaluating the success of such ecologically engineered shorelines.

## Introduction and the history of ecological engineering of shorelines

Humans have been altering coastlines for millennia (Thompson et al. 2002, Dugan et al. 2011, Ellis 2015, Loke et al. 2019), usually with little regard for the environment. Natural habitats have been replaced with artificial structures to create access, reclaim land for agriculture, industry, transport, residential use and tourism (Gittman et al. 2015, Lai et al. 2015, Chee et al. 2017) and protect growing coastal populations (Crossett et al. 2004, Nicholls et al. 2007, Firth et al. 2016b) from erosion and flooding (Burcharth et al. 2007, Kittinger & Ayers 2010, Hinkel et al. 2014). Impacts on coastal ecosystems from such developments are inevitable and range from chronic to catastrophic

(Airoldi et al. 2005a, Martin et al. 2005, Bulleri & Chapman 2010, Dethier et al. 2016, Bishop et al. 2017, Heery et al. 2017). Improving environmental conditions along artificial shorelines is critical to compensate for impacts from ocean sprawl—the proliferation of artificial structures in the marine environment (Dafforn et al. 2015a, Dyson & Yocom 2015, Firth et al. 2016b, Bishop et al. 2017, Heery et al. 2017). With climate change and sea level rise, existing shoreline protections are increasingly proving ineffective and will need substantive reassessment and reconstruction during the coming decades (Hawkins & Cashmore 1993, Nicholls & Tol 2006, Hallegatte et al. 2013, Hinkel et al. 2014, Hoggart et al. 2014, Smith et al. 2017a).

The goal of this review is to provide a framework for selecting, applying and tracking the success of ecologically engineered (hereafter 'ecoengineered') shoreline strategies (Mitsch 2012) for intertidal and shallow subtidal marine environments. The fundamental aim of ecoengineered shorelines is to build more inclusive, resilient and safe coasts for people and nature, which maximise benefits for ecosystems, society and economies (Airoldi et al. 2005a, Dafforn et al. 2015a). Because it is a relatively young discipline and innately experimental in its current form, ensuring that it is developed and applied responsibly requires that parameters and metrics for its success be clearly defined and monitored (Saleh & Weinstein 2016, Mayer-Pinto et al. 2017). In this review, we take a multidisciplinary approach in evaluating the benefits and challenges of ecoengineered shorelines and discuss metrics to evaluate success originating in the fields of coastal ecology, engineering, sociology, economics, urban planning and architecture.

Ecoengineered shorelines are in a sense the most recent stage in the development of marine infrastructure and coastal armouring, which can be traced back to before the Common Era (i.e. BC) in Egypt (Loke et al. 2019). Early ports were located in sheltered bays, river mouths and lagoons, with simple jetties and, eventually, low-crested breakwaters used in combination with natural habitats for coastal protection (Polanyi 1963, Hoyle 1989, Charlier et al. 2005). In some regions, such as China and parts of the Mediterranean, technological advances led to more extensive artificial shorelines relatively early (Franco 1996). For instance, with the discovery of pozzolanic ash hydraulic cement, the Romans started extensive underwater engineering and managed to construct solid breakwaters to protect fully exposed harbours (Jackson et al. 2017). By the Middle Ages in Europe, planting and dune belt protection were well established, as were strict environmental regulations. For instance, legal documents of 1282 and 1339 in Venice prohibited the cutting of coastal trees, picking mussels and removing sand or vegetation from beaches or dunes (Grillo 1989). In the Renaissance, Leonardo da Vinci championed the credo of 'working with Nature' ('*ne coneris contra ictum fluctus: fluctus obsequio blondiuntur*'—Nature should not be faced bluntly and challenged, but wisely circumvented) (Franco 1996). A similar idea was championed by Andries Vierlingh in his manuscript entitled *Tractaet Dyckagie*, which remains an important text regarding fundamental errors in land and water engineering management (Vierlingh et al. 1920).

The formal framing of the concept of ecoengineering is generally attributed to H. T. Odum, who proposed that ecosystems provide the biological 'design' and 'energy' required to 'engineer' socioeconomic benefits of human development (Odum 1975). He stated that 'the management of nature is ecological engineering, an endeavour with singular aspects supplementary to those of traditional engineering' (Odum 1971). Since then, the concept has gradually expanded, replacing purely 'ecological processes' with 'natural processes' to now include physical and other factors such as 'design' and 'energy' inputs (e.g. the 'sand engine/sand motor' approach for beach nourishment and flood protection that is used along the Dutch coastline; Mulder & Tonnon 2011, Stive et al. 2013, de Schipper et al. 2016). During the last 10–15 years, the practitioners involved in designing coastal defences have embraced a 'design with nature' approach, which has led to various philosophies and programmes for the delivery of ecologically minded coastal and maritime infrastructure (e.g. the programme of 'working with nature' organised by the World Association for Waterborne Transport Infrastructure (PIANC): https://www.pianc.org/working-with-nature US Army Corps of Engineers' 'engineering with nature': https://ewn.el.erdc.dren.mil/ EcoShape's 'building with nature': www.ecoshape.org).

This transition in perception and practice has been facilitated by the widening recognition of the pervasive and persistent anthropogenic changes that characterise urban areas (Bulleri & Chapman 2010, Firth et al. 2016b, Mayer-Pinto et al. 2018, Bugnot et al. 2019) and by the emergence of the 'novel ecosystem' concept, which emphasises novelty and human agency in the emergent ecological communities that are without historical precedent (Milton 2003, Hobbs et al. 2006). The novel ecosystem concept is not without controversy (e.g. Woodworth 2013, Murcia et al. 2014); however, in novel urban habitats specifically, it provides a framework for conceptualising coastal engineering projects as opportunities for the amelioration of ecosystems that are already heavily shaped by anthropogenic activity (Perkins et al. 2015, Aguirre et al. 2016). While the distinction is not always made, urban areas contain both hybrid ecosystems that may have significant novelty, as well as novel ecosystems, which, by definition, cannot return to hybrid or historical conditions (Hobbs et al. 2006). The novel ecosystem concept has arguably changed the perceived value of the urban environment, particularly in relation to its provisioning of ecosystem services to urban populations, ultimately facilitating the integration of a broader range of ecological, engineering, social and economic interests into shoreline development and management (Perring et al. 2013).

There is considerable overlap between the fields of ecoengineering and ecological restoration. Ecological restoration aims to assist the recovery of degraded ecosystems and put back their attendant services (Society for Ecological Restoration International Policy Position Statement (SER 2004). The traditional view of restoration envisaged returning an ecosystem to a predefined historical state (Hobbs & Norton 1996). Given ecosystem variability and complexity, coupled with the extent of environmental change that has occurred over recent decades, making target baselines uncertain (Palmer et al. 2016), restoring ecosystems to their former state is often impossible on human timescales (Hobbs et al. 2006). Thus, many have emphasised the importance of defining restoration to a defined target state, which is likely to be far from the original pristine condition of the ecosystem (Hawkins et al. 1999, 2002, SER 2004, Geist & Hawkins 2016, Palmer et al. 2016). Even our best efforts serve primarily to rehabilitate or repair damaged biodiversity and ecosystem processes and services, rather than comprehensively restore ecosystems (e.g. in a marine context, 'nudging nature'—Hawkins et al. 1999, 2002). Conversely *reallocation* is the process of assigning an ecosystem to a new use that may not necessarily bear an intrinsic relationship to the structure or functioning of the predisturbed ecosystem (Aronson et al. 1993). *Reconciliation* is the process of modifying and diversifying anthropogenic habitats to harbour a wide variety of native species (Rosenzweig 2003a; for further discussion, see the section entitled 'Links to theoretical and community ecology', later in this review). While some refer to restoration as the best form of ecoengineering (Bradshaw 1997), others claim that restoration encompasses ecoengineering (SER 2004). Here, we propose that ecoengineering is a broad approach that can aid restoration (Mitsch 2012), but more typically is used for rehabilitation, reallocation and/or reconciliation.

During the last decade, ecoengineered shorelines have emerged as a promising alternative to traditional coastal development (Mitsch 2012), although they are by no means a panacea for countering the negative impacts of shoreline construction, and numerous uncertainties regarding their efficacy remain (Bouma et al. 2014, Sutton-Grier et al. 2015). We emphasise that these are not a substitute for natural or even seminatural systems. Neither should such ecoengineering approaches be used to legitimise developments in sensitive habitats. In this review, our focus is on coastlines that have already become urbanised or heavily modified by land reclamation for agriculture, industry or transport infrastructure, including low-density, residential suburban sprawl. The approaches suggested here are particularly suitable when current coastal developments are being expanded or repaired. While there are examples of ecoengineered shorelines around the globe and many under development (Chapman & Underwood 2011, Firth et al. 2014, Elliott et al. 2016, Munsch et al. 2017a), a cohesive framework for developing ecoengineered shorelines and evaluating their success is presently lacking (but see relevant work by van Slobbe et al. 2013, van der Nat et al. 2016, Osorio-Cano et al. 2017, Gracia et al. 2018, Whelchel et al. 2018). This review presents the underpinning concepts, key approaches, recent developments, limitations and future trajectory of ecoengineered shoreline design. We present a framework for the development of ecoengineered shorelines by reviewing three themes: (1) core principles and approaches to ecoengineered shoreline design, (2) factors that influence implementation and (3) how to evaluate the success of ecoengineered shorelines.

## Design considerations for ecoengineered shorelines

### *Links to theoretical and community ecology*

Ecological concepts and theory provide both a vocabulary and a predictive framework to understand and manage ecosystems along the spectrum from near-pristine to highly degraded ecosystems. Thus, theory can inform policy, planning and practice. Here, we briefly introduce ecological knowledge relevant to the design of ecoengineered shorelines. We start with species-area relationships and the relationship between biodiversity and ecosystem functioning. We then discuss diversity at different scales, succession and disturbance, environmental gradients and connectivity. The aim of this section is simply to highlight some of the key theoretical underpinnings of the rapidly emerging field of designing ecologically sensitive shorelines.

#### *Species-area relationships*

Species-area relationships (SARs)—which involve one of the few widely accepted laws in ecology (Lawton 1999)—dictate that a larger area will contain a larger number of species. This pattern is observed at almost every spatial scale (Figure 1; Rosindell & Cornell 2007, O'Dwyer & Green 2010). It is manifest in highly modified shorelines, where the loss of natural habitat leads to direct loss in species (Rosenzweig 2003a). The same principle may be applied in reverse, however, to aid modifying, redesigning and diversifying anthropogenic habitats. Reconciliation ecology, which focusses on how urban and novel habitats may be used to maintain biodiversity and to provide ecosystem services, provides several examples of this (Hobbs et al. 2013, Perring et al. 2013), in both terrestrial (Rosenzweig 2003b, Kowarik 2011) and aquatic (Mitsch & Jørgensen 2004, Firth et al. 2016b) environments. While species colonisation in some of these examples occurs by accident (refer to Rosenzweig 2003b), many other examples are carefully planned and managed (see the section entitled 'Case studies and scaling up', later in this review).

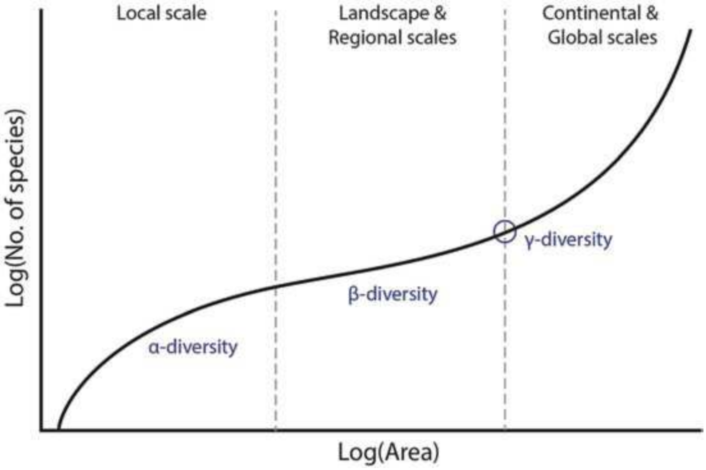

**Figure 1** Triphasic SAR. A larger area will include a larger number of species. On a local scale, alpha (α) diversity describes the number of species within a habitat, while the compositional difference in species assemblages among habitats (beta, β, diversity) is essential for achieving high gamma (γ) diversity in a region.

### *Diversity at multiple scales*

Diversity is a key theme in ecology, which underpins both the goals and assessment of many ecoengineered shoreline projects. It is frequently estimated as species richness (i.e. the total number of species present) and can be quantified at multiple spatial scales. While species richness within a habitat (alpha diversity) is useful in many instances, the compositional difference in species assemblages among habitats (beta diversity) is essential for achieving high diversity in a region (gamma diversity; Figure 1; Whittaker 1960, 1972). Specifying the scale at which ecoengineered shoreline designs aim to enhance diversity is crucial, as strategies for improving alpha and beta diversity may differ. Designs focussed on enhancing large-scale (landscape and regional scale—hundreds of metres—tens of kilometres) spatial heterogeneity and creation of various medium-scale habitat types (1–100 m) will have a positive effect on beta diversity. Those strategies focussed on increasing local-scale (<1 m) topographic and/or structural complexity (e.g. Coombes et al. 2015, Loke and Todd 2016) and ameliorating abiotic stressors (e.g. Browne & Chapman 2011, Evans et al. 2016) are more likely to have a positive effect on alpha diversity. Patches of more complex habitat, especially if they are of different types, among a background landscape of less complex habitats will also increase beta diversity (Firth et al. 2014, Evans et al. 2016).

### *Biodiversity and ecosystem functioning*

Over the last two decades, there has been a growing realisation that loss of species can compromise ecosystem functioning (e.g. biomass production, nutrient uptake; Loreau et al. 2002, Tilman et al. 2014, Oliver et al. 2015) and in turn, ecosystem services (e.g. carbon storage; Díaz et al. 2006, Cardinale et al. 2012, Isbell et al. 2014). Thus, increasing diversity would enhance the functioning of ecosystems by elevating production and nutrient cycling, as well as conveying resilience to environmental change (the insurance hypothesis; Yachi and Loreau 1999) and invasion by nonnative species (Stachowicz et al. 2002, Arenas et al. 2006, Tan et al. 2018). These processes lead to enhanced goods and services provided by biodiversity and ecosystems (i.e. provisioning, supporting, and regulating; Raffaelli et al. 2002). For both sedimentary (e.g. Solan et al. 2004) and rocky shore habitats (e.g. O'Connor & Crowe 2005, Griffin et al. 2008, 2010), experimental work has shown that species diversity and identity influence ecosystem processes such as productivity and nutrient cycling. The importance of habitat patch diversity has also been recognised for some time (e.g. Giller et al. 2004, Hawkins 2004) and more recently has been experimentally demonstrated (e.g. Griffin et al. 2009, Godbold et al. 2011, Alsterberg et al. 2017). Knowledge of the traits of species (functional diversity) can also be valuable in translating structural attributes of biodiversity into the maintenance or restoration of ecosystem processes, and hence services (Rigolet et al. 2014). Ultimately, ecoengineering aims to maximise the ecosystem services that can be delivered in seminatural and highly modified ecosystems (Dafforn et al. 2015a). Paying attention to increasing habitat patch diversity, and hence beta species diversity, is likely to pay greater dividends in terms of ecosystem functioning and provision of services.

### *Environmental gradients and connectivity*

Environmental gradients are a major influence on community composition and structure in shoreline environments (see Raffaelli & Hawkins 1996 for a review). The major gradients can be viewed as being either vertical (e.g. tidal elevation/bathymetry) or horizontal (e.g. exposure to wave action). These gradients ultimately determine what species can potentially survive in an area, with biological interactions usually proximately determining the actual assemblage in a location [e.g. experimental work by Jonsson et al. (2006) on the respective roles of wave action and grazing on breakwaters]. Disturbance regimes also vary along these gradients, but the strength and direction of these effects are frequently modified by local contingency (Underwood & Chapman 1996, Chapman et al. 2010, Bulleri et al. 2011), including small-scale topography (Johnson et al. 1998, 2003, Berntsson et al. 2000) and the vagaries of settlement by algal propagules and the larvae of invertebrates (Butman 1987, Underwood & Fairweather 1989, Fletcher & Callow 1992, Knights et al. 2012). Designs that minimise the extent to which environmental gradients are altered or intercepted are less likely to fundamentally change community structure. For example, installing hard coastal armour in an area naturally typified by coarse sand or gravel will inevitably lead to scouring of any colonising rocky shore species (Moschella et al. 2005), preventing communities from developing beyond the early successional stages.

Artificial structures often support assemblages analogous to rocky reefs jutting out from high-energy sandy beaches (Bally et al. 1984) that tend to be dominated by ephemeral early successional species. Additionally, designs perform best when they account for ecological connectivity at various scales. Changes to the movement of organisms and resources such as detritus should be avoided (Huijbers et al. 2013, Bishop et al. 2017). Arrays of structures scaling up to affect whole coastlines (e.g. Ma et al. 2014, Dong et al. 2016) can act as stepping stones for the spread of native species responding to climate change (Johannesson & Warmoes 1990, Mieszkowska et al. 2006, Keith et al. 2010, Firth et al. 2015, Huang et al. 2015, Dong et al. 2016), as well as help invasions by nonnative species (Floerl et al. 2009, Mineur et al. 2012, Airoldi et al. 2015, Bishop et al. 2017).

### *Succession and disturbance*

Novel habitats are colonised by a variety of marine organisms (Wahl 1989). When relatively constant conditions prevail, communities in novel habitats gradually shift in composition and structure through the processes of immigration and extinction (MacArthur & Wilson 1967). Connell & Slatyer (1977) proposed three models of succession: the classical model of positive facilitation of later stages by earlier colonisers, inhibition of later stages by earlier arrivals and a neutral tolerance model reflecting arrival of propagules and longevity of species. Significant disturbances, whether natural or anthropogenic, tend to push a successional sequence back to earlier stages (i.e. system retrogression; Odum 1985). Biological interactions such as grazing have been shown to break inhibition by intermediate phases such as green algae (Sousa 1979).

Classical ecological theory predicts the highest levels of diversity under moderate levels of disturbance, either in terms of intensity or frequency [the intermediate disturbance hypothesis (IDH); Connell 1978], as a low-disturbance regime leads to dominance by competitive-dominant species and strong frequent disturbances suppress most species to also result in low overall diversity (e.g. Sousa 1979). Although IDH has been challenged on both a theoretical and empirical basis (Lubchenco 1978, Fox 2013), it is well established that high levels of disturbance lead to depauperate systems comprising relatively few early successional or opportunistic taxa (Pulsford et al. 2014). As disturbances are commonplace in human-dominated environments, ecoengineering strategies that help stabilise the disturbance intensity or frequency may be beneficial (Airoldi et al. 2005b, Bulleri & Airoldi 2005, Airoldi & Bulleri 2011, Bracewell et al. 2013, Salomidi et al. 2013), increasing the likelihood that communities progress to a climax (Hawkins et al. 1983) or oscillate to and from intermediate stages.

Additionally, species or groups of species that positively influence succession can be integrated into ecoengineered shorelines through seeding (e.g. Perkol-Finkel et al. 2012, Ferrario et al. 2015, Ng et al. 2015) or targeted designs (Strain et al. 2017a). Studies on the mechanisms of succession have highlighted the importance of certain species interactions in determining the rate and direction of community development (Maggi et al. 2011). Positive interactions such as facilitation [e.g. settlement by mussels or tubicolous polychaetes enhancing the colonisation of meiofauna on hard surfaces (Dubois et al. 2002, O'Connor & Crowe 2007) or increased accumulation of leaf litter by mangrove on previously bare substrata, which aids in recruitment of juvenile nekton] may be particularly important (Bulleri et al. 2018). Organisms that serve as ecosystem engineers and foundation species also have profound impacts on the way that communities develop and, ultimately, on diversity as well (e.g. Coleman & Williams 2002, Tolley & Volety 2005, Marzinelli et al. 2014).

### *Biological invasions*

Finally, theoretical and community ecology concepts from invasion biology are also relevant for ecoengineered shoreline design, as artificial structures appear particularly prone to colonisation by nonnative species (Bulleri & Airoldi 2005, Glasby et al. 2007, Vaselli et al. 2008, Ruiz et al. 2009, Dumont et al. 2011, Dafforn et al. 2012, Mineur et al. 2012, Simkanin et al. 2012, Airoldi et al. 2015). These concepts are strongly interrelated with many of those already presented in this review, particularly diversity, connectivity, succession and disturbance. Artificial structures provide novel colonisation opportunities for nonnative species (Dafforn et al. 2012). Those located in urban areas may be subject to particularly high levels of propagule pressure ('introduction effort'), given their close proximity to known invasion hubs such as marinas and shipping facilities (Seebens et al. 2013), which is thought to strongly influence invasion risk (Lockwood et al. 2005). Urban artificial structures may also be subject to particularly high rates of disturbance (Bulleri & Airoldi 2005, Piola & Johnston 2008, Kenworthy et al. 2018) or to relatively low levels of predation by mobile consumers (Simkanin et al. 2013, Astudillo et al. 2016, 2018, Rogers et al. 2016), ultimately favouring nonnative taxa. Further, additional structural complexity, which is a key component of many ecoengineered shoreline projects (discussed further in section 'Environmentally sensitive hard defences', later in this review), can modify predator-prey interactions and potentially facilitate nonnative prey species by enhancing refugia from native predators (Barrios-O'Neill et al. 2014).

## *Fundamental design options*

The construction of artificial structures such as seawalls, groynes and breakwaters has historically been the default approach to coastal protection (Cooper et al. 2016). Artificial structures are economically and environmentally costly (Jones 1994, Airoldi et al. 2005a, Kittinger & Ayers 2010, Hinkel et al. 2014), however, contributing to the growing interest in alternatives that compensate for the negative impacts of traditional coastal infrastructure and provide multiple functions (Chapman & Underwood 2011, Francis & Lorimer 2011, Mitsch 2012, Evans et al. 2017). These alternatives can be categorised into three fundamental approaches: (1) building in design features in new or modifying existing artificial structures (termed *hard ecological engineering*; Chapman & Underwood 2011, Firth et al. 2014); (2) replacing artificial structures with sediments, vegetation and/or other habitat-forming organisms (called *soft ecological engineering*; Temmerman et al. 2013, Morris et al. 2018b) and (3) applying both soft and hard engineering approaches in combination (known as *hybrid ecological engineering*; Chapman & Underwood 2011, Bilkovic & Mitchell 2013) (Figure 2).

Many terms are used to refer to both traditionally and ecologically engineered shores. Common synonyms for artificial structures and coastal defences include coastal infrastructure, shoreline armouring, hard structures and urban structures. The term *Ecoengineered shorelines* is used to describe shorelines that have been developed or retrofitted using ecoengineering principles, via either hard, soft or hybrid approaches. Created or restored habitats are those that have undergone soft ecoengineering, and are commonly referred to as *nature-based coastal defence* (van der Nat

**Figure 2** Approaches to ecoengineered shorelines include (a) hard (tile-enhancement units installed along the seawalls at Changi, Singapore), (b) hybrid (rock fillet with saltmarsh in Chesapeake Bay, United States) and (c) soft ecological engineering (bagged oyster shell reef with saltmarsh in Chesapeake Bay).

et al. 2016, Osorio-Cano et al. 2017, Gracia et al. 2018, Sutton-Grier et al. 2018). In the United States, soft and some hybrid ecological engineering projects also fall under the commonly used term *living shorelines* (Bilkovic & Mitchell 2017).

Although the overall objective of ecoengineering is similar regardless of approach (i.e. to build shorelines for the benefit of both humans and nature; Mitsch 2012), there is a fundamental difference between hard and soft ecoengineering from a coastal defence perspective (Morris et al. 2018b). The goal of hard ecoengineering is usually to compensate for the negative impacts of artificial structures (e.g. seawall or breakwater) through enhancing biodiversity and ecological functioning while maintaining their physical integrity (e.g. Moschella et al. 2005, Burcharth et al. 2007, Chapman & Underwood 2011, Firth et al. 2014, Pioch et al. 2018). Conversely, while soft ecoengineering is usually proposed from a conservation and/or sustainability perspective (Dafforn et al. 2015a, Mayer-Pinto et al. 2017), the created or restored habitat needs to provide adequate coastal defence in addition to ecological and landscape values (e.g. biodiversity enhancement) if this technique is to replace or complement artificial structures. Although hard ecoengineering is less challenging to implement from a coastal defence perspective, there is growing evidence that created or restored habitats using soft engineering can also provide protection that is equivalent to or better than traditional engineered hard structures (Gittman et al. 2014, Smith et al. 2017a, Smith et al. 2018). As mentioned previously, soft engineering approaches and hard structures may even operate synergistically to enhance coastal protection (Smallegan et al. 2016, Vuik et al. 2016)—as successful hybrid schemes in some cases.

### *Goals and objectives*

Defining the objectives or goals is considered the most fundamental step in any restoration (e.g. Hobbs & Norton 1996, SER 2004, McDonald et al. 2016, Palmer et al. 2016) or ecoengineering project (Mayer-Pinto et al. 2017). Ecoengineered shorelines are multifunctional and are valued for their potential to accrue benefits across multiple stakeholders (Evans et al. 2017), each of whom has their own set of objectives (e.g. economic, engineering, social, ecological) that typically drive or influence the objectives of a project. Sometimes these objectives overlap—for instance, creating a wide beach could also generate space for recreation, protect inland infrastructure and form habitat for nesting shore birds (Temmerman et al. 2013). Due to the way in which projects are conceived and funded (see the section entitled ‘Implementation of ecoengineered shorelines’, later in this review), one or more of these objectives may take precedence over the others, which can lead to trade-offs. Nevertheless, multifunctionality is a key goal of ecoengineered shorelines, and thus engineering, ecological and socioeconomic outcomes should be optimised. Evaluation of the success or failure of projects needs to focus on whether these multiple objectives are achieved (see the section entitled ‘Evaluating the ecoengineered shorelines approach in practice’, later in this review).

## *Identifying the approach*

Ecoengineered shorelines range considerably in form and function and may be conceptualised along a spectrum (Moosavi 2017), from created (i.e. a habitat not historically present) or restored natural habitats at one end to ecologically engineered hard structures at the other. The most suitable approach for a site will depend on socioeconomic variables and the physical, environmental and the ecological contexts (Figure 3; Spalding et al. 2014). Shorelines should be defended only where there is something to protect (Airoldi et al. 2005a). This is usually property or infrastructure, or in some instances, ecological systems (Moody et al. 2016) or archaeological or cultural heritage (Reimann et al. 2018) threatened by inundation or erosion (Figure 3). Land reclaimed for agriculture via empoldering almost always needs some form of protection (Woltjer & Al 2007). Any form of shoreline construction or modification will pose inherent risks to marine communities and the coupled natural-human systems of which they are a part. The need for shoreline protection, therefore, must be sufficiently great to warrant assuming such risks (Airoldi et al. 2005a).

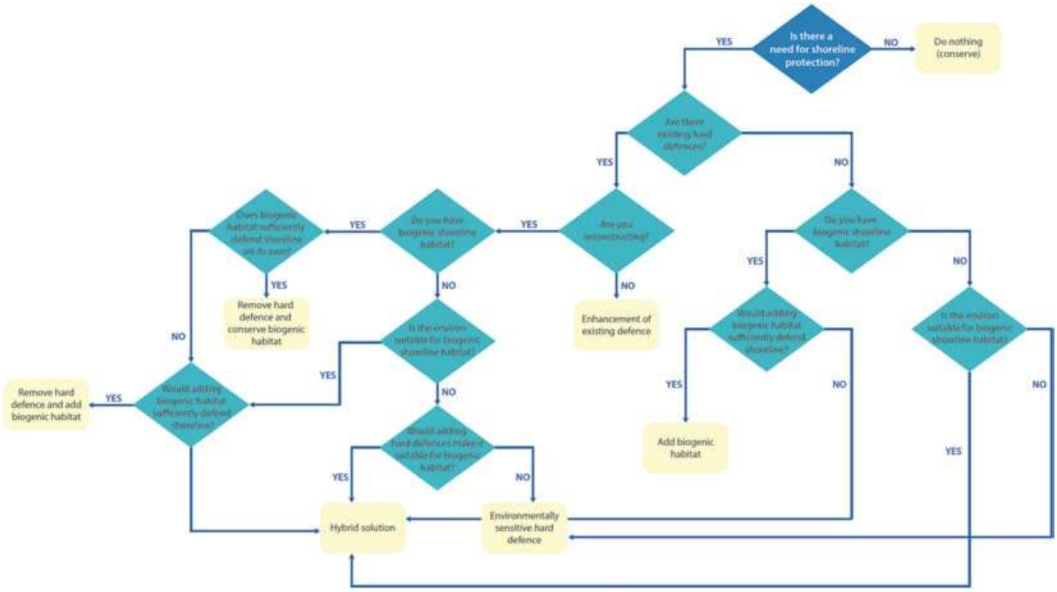

**Figure 3** A flowchart for identifying the suitable approach to ecoengineered shoreline protection. Blue diamonds indicate a decision (dark blue is the starting point), and yellow boxes indicate the ecoengineered shoreline approach to take. Biogenic habitat refers to natural or restored (i.e. soft ecoengineering) habitats. *Environmentally sensitive hard defence* refers to hard ecoengineering approaches.

In general, selecting from soft ecoengineering, a hybrid approach and environmentally sensitive hard defences requires consideration of the physical environment (particularly wave conditions; Leonardi et al. 2016) and the respective cost of each approach (Arkema et al. 2017) in the context of the main purpose of the project (e.g. creating a bathing beach or a surfing bay, as opposed to protecting an agricultural land or an ecosystem of conservation interest). At low-wave-energy sites, soft and hybrid ecoengineering approaches are often feasible (Leonardi et al. 2016, 2018, Sanford & Gao 2018). At higher-energy sites, with significant wave action from either wind or shipping, certain types of soft engineering may not persist over time or provide adequate shoreline protection (Bouma et al. 2014). Such cases necessitate hybrid approaches, or at the highest energy end of the spectrum, hard defences (Moosavi 2017).

Despite growing evidence suggesting that soft and hybrid approaches are often cost effective and sufficient for protection from flooding and erosion (Spalding et al. 2014, Gittman & Scyphers 2017, Sutton-Grier et al. 2018), considerable uncertainties (both perceived and realised) remain surrounding their efficacy as coastal defences (Gedan et al. 2011, Perkins et al. 2015, Sutton-Grier et al. 2015, Arkema et al. 2017). Thus, at least some degree of hard ecoengineering is often required (Cooper et al. 2016). The value and/or importance of the property, infrastructure or ecosystem to be protected will have some bearing on the choice of approach (soft, hard or hybrid). For example, if the asset to be protected is essential to national or regional infrastructure, such as an airport, hospital or railway, there may be less willingness to accept (WTA) approaches perceived to carry greater uncertainty with respect to inundation and flood risk. Often, there is stronger support for hard engineering approaches (Gray et al. 2017) that have been more thoroughly tested over time (Sutton-Grier et al. 2015), even when they are unnecessary or less cost effective than soft or hybrid alternatives (Scyphers et al. 2014, Gittman & Scyphers 2017). In contrast, where the asset is less crucial for social and economic health or primarily of local significance, there may be a higher chance for adopting more experimental (and potentially riskier) ecoengineered shoreline approaches that provide protection under most (but not the most severe) storm events, or for which the evidence of efficacy in terms of shoreline protection is limited (but see Gittman et al. 2014, Smith et al. 2018).

Which ecoengineered shoreline approaches can and should be adopted will largely be influenced by the degree to which the environment has already been modified by anthropogenic activities (Bouma et al. 2014). In heavily modified environments, environmental degradation (e.g. by pollution and land reclamation) may result in conditions that are no longer suitable for the establishment of soft or hybrid ecoengineered shorelines (Chee et al. 2017), necessitating use of hard defences, at least in the interim, if cleanup efforts or long-term mitigation of environmental conditions are part of the development plan. The implementation of soft or hybrid approaches may also be restricted by the lack of available space, particularly in heavily urbanised settings (Saleh & Weinstein 2016). In contrast, in environments where intact and functional habitat-forming species are present, the priority should be to protect these and, where necessary, enhance their efficacy in protecting shorelines by increasing their habitat area or encouraging growth forms that are more effective in stabilising sediments, dissipating wave energy or both. Particularly at sites where the natural habitat type is sedimentary (e.g. seagrass beds, mangrove forests, saltmarshes, and dune systems), use of hard defences should be applied only where absolutely necessary, as they result in a qualitative state change from a soft- to hard-bottomed systems (Airoldi et al. 2005a).

Furthermore, the selected approach will also depend on site-specific factors such as tidal range and whether the shoreline is natural or reclaimed land. These factors will influence the space available for interventions, as well as the size and configuration required for an intervention to protect from erosion and flooding effectively (Stark et al. 2016). Importantly, as sea level rise continues to shift intertidal zones landward through coastal squeeze (e.g. Jackson & McIlvenny 2011, Torio & Chmura 2015, Luo et al. 2018), ecoengineering approaches utilising intertidal species will also need the necessary space (and capacity) for the species to retreat (Bilkovic et al. 2016). Where the tidal range is small, or the site is the result of land reclamation, there may be little intertidal area for ecoengineering approaches utilising littoral vegetation (Strain et al. 2017b), necessitating the use of subtidal species (such as shellfish, macroalgae or coral reefs) for shoreline stabilisation (Temmerman et al. 2013).

## *Environmentally sensitive hard defences*

Where hard ecoengineering approaches are deemed most appropriate, several factors typically influence the specifics of their design. The options for environmentally sensitive hard defences will depend on whether the structure is being designed de novo or whether an enhancement of an existing structure is planned.

New structures should be designed to maximise the intertidal surface area available for colonisation and to include habitat structural complexity (e.g. introducing microhabitats) that increase diversity (Loke et al. 2014, 2017) and provide refuges for target species (or their prey resources) from predators and environmental stressors (Moschella et al. 2005, Chapman & Underwood 2011, Loke et al. 2015). A greater and more heterogeneous intertidal area may be achieved by stepping structures (e.g. Barangaroo, in Sydney, Australia), sloping structures (i.e. a 45° angle as opposed to 90°), adding macroscale habitat features such as horizontal fins (e.g. Seattle seawall; for more information, see the section entitled ‘Case studies and scaling up’, later in this review) or by integrating holes of varying sizes as shelter for fish (Sella & Perkol-Finkel 2015) or invertebrates (Martins et al. 2010, Witt et al. 2012). Porous structures not only are advantageous from an engineering perspective in dampening waves (Burcharth et al. 2007), but also provide much habitat for colonisation, even if much of the additional biodiversity is hidden (Sherrard et al. 2016).

Microhabitats can be incorporated in structures by utilising heterogeneous revetment boulders rather than smooth panelled seawalls or by casting pits, grooves, water-retaining structures and other features into the concrete panel or block (Chapman & Blockley 2009, Chapman & Underwood 2011, Firth et al. 2014, 2016a, Loke et al. 2016, Strain et al. 2018b). Where possible, new structures should utilise materials that encourage the recruitment of target organisms. Recruitment will be dependent on the surface chemistry (Pomerat & Weiss 1947, Harlin & Lindbergh 1977, Anderson 1996, Neo et al. 2009) and roughness (microtopography, Köhler et al. 1999, Nandakumar et al. 2003, Coombes et al. 2015) of the structure. The colour of structures may also influence colonisation (James & Underwood 1994, Satheesh & Wesley 2010) by affecting brightness (many larvae are negatively phototactic; Bayne 1964, Raimondi & Keough 1990) and temperature (dark colours absorb while light colours reflect heat, Kordas et al. 2015, McAfee et al. 2017), although this has received little research attention. Use of local quarried rock may provide a substratum that is physically and chemically most similar to natural rocky shores (Green et al. 2012). Alternatively, the chemical composition of concrete may be altered to encourage recruitment (Sella & Perkol-Finkel 2015, McManus et al. 2018).

Options for existing structures will be more limited. They may include subtractive approaches where microhabitats and area are added by drilling holes, pits and grooves in structures (Chapman & Underwood 2011) or coring larger rock pools (Evans et al. 2016). Alternatively, additive approaches include retrofitting artificial structures with units such as complex tiles (Goff 2010, Loke & Todd 2016, Strain et al. 2017a) and water-retaining flowerpots and artificial rock pools (Chapman & Blockley 2009, Browne & Chapman 2011, Chapman & Underwood 2011, Firth et al. 2014, 2016a, Evans et al. 2016, Morris et al. 2017), which may be constructed from bioenhancing concrete materials (Sella & Perkol-Finkel 2015) or the transplantation of living, habitat-forming species (Perkol-Finkel et al. 2012, Ng et al. 2015), see review by Strain et al. (2018b).

Additionally, it may be possible to add new habitats to existing seawalls by placing boulders at the toe of each seawall (Green et al. 2012, Liversage & Chapman 2018). This also minimises scouring of the main structure by wave driven sand, gravel and cobbles (Moschella et al. 2005). Although some ecoengineered shorelines have been shown to reduce the proportion of nonnative species compared with traditional artificial structures (Sella & Perkol-Finkel 2015), an important aspect of monitoring is to ensure that the ecoengineered habitats are not favouring the establishment or spread of nonnative species (e.g. Morris et al. 2018a). Strategic choices for ecoengineered shoreline design and management surrounding invasion prevention are detailed by Dafforn (2017) and include techniques such as preseeding, managing for strong native grazer and predator populations and modifying the chemical and physical properties of ecoengineering features to facilitate the establishment of native assemblages.

The specific design of environmentally sensitive hard defences should be informed by socioeconomic and ecological goals (see the section 'Evaluating the ecoengineered shorelines approach in practice', later in this review). For example, if there is an ecological goal of biodiversity enhancement, it might be important to incorporate a diversity of microhabitats into structures, so as to maximise the number of niches (Strain et al. 2018b) and enhance beta diversity (cf. Kelly et al. 2016). In contrast, if the goal is enhancing water quality through filtration, microhabitats and chemistry that favour bivalves (or other filter feeders) should be targeted (see Strain et al. 2017a for an example of protective microhabitats that enhance bivalve survival). Morris et al. (2018c) provide a framework for deciding what interventions to apply in order to target particular functional groups of fish. Design interventions can be targeted to enhance exploited species, such as limpets in the Azores (Martins et al. 2010). Enhancing grazers will lead to less slippery and dangerous seaweeds (Jonsson et al. 2006) in areas where structures abut beaches used for recreation.

### *Soft approaches and the selection of habitat-forming species*

Soft ecologically engineered shorelines are typically founded on habitat-forming species. A variety of these species may be suitable for shoreline stabilisation, including (but not limited to) reef-forming invertebrates such as corals (Ferrario et al. 2014), oysters (Scyphers et al. 2011), mussels and worms (Moody 2012), intertidal vegetation such as mangroves and saltmarsh (Kumara et al. 2010, Gittman et al. 2014) or subtidal vegetation, such as seagrass or kelp (Dubi & Tørum 1994, Ondiviela et al. 2014). The choice of habitat-forming species for shoreline protection projects will depend on physicochemical, ecological and socioeconomic factors. First, the selected species must be able to persist, grow and reproduce under both present and projected future environmental conditions, given ongoing climate change and coastal development (Walles et al. 2016). Second, the species must be capable of forming habitat that is able to adequately protect shorelines through stabilisation of sediments or dampening of wave energy under present and projected future environmental conditions (Narayan et al. 2016, Morris et al. 2018b).

Where possible, native species should be selected over nonnative species. However, in rare instances, nonnative species may be more suitable choices due to extirpation of their native functional analogues or their greater capacity than natives to tolerate future environmental change. In the Netherlands, where native flat oysters (*Ostrea edulis*) are now functionally extinct (Beck et al. 2011) and native mussel beds (*Mytilus edulis*) have become largely overgrown by nonnative Pacific oysters, *Crassostrea gigas* (Markert et al. 2010), the nonnative oyster is being utilised as a device for shoreline stabilisation. This is because it is more suited to the present environment and is, to a large degree, functionally equivalent to the native species (da Vriend et al. 2014). Interestingly, an experimental study by Borsje et al. (2011) found that nonnative oyster beds were more effective in wave attenuation than were native mussel beds. Nonnative species, however, should not be introduced for shoreline protection purposes if they are not already naturalised in the targeted environment, or if their presence will lead to negative ecological or socioeconomic impacts that outweigh their benefits (Bunting & Coleman 2014). Ultimately, the habitat-forming species need to be self-sustaining. The probability of this may be maximised where there are nearby patches of extant natural habitat to which the population being used for ecoengineering is connected.

Socioeconomic considerations should also be taken into account when selecting species. For example, shellfish reefs may be a less desirable alternative for ecoengineering in areas subject to high human recreational activity due to risk of cuts and injury (and potential infection) from razor-sharp shells (O'Donnell 2016). Similarly, mangroves may be a socially unacceptable alternative if they facilitate the proliferation of mosquito populations, especially in areas where they are carriers of disease (Temmerman et al. 2013, Friess 2016). Conversely, certain species can be particularly desirable because they provide valued ecosystem goods or services. For instance, in areas where improvement of water quality is a key goal, living shorelines based on shellfish may not only serve to stabilise shorelines, but also improve water clarity (Allen et al. 1992, Wilkinson et al. 1996, Coen et al. 2007, Grabowski & Peterson 2007). Where the habitat-forming species provides food or raw materials, it may need to be protected from harvest so as not to compromise its role in protecting the shoreline (O'Donnell 2016). For example, the success of oyster reef restoration projects in the United States, including those for shoreline protection, is enhanced by their protection within no-take reserves (Powers et al. 2009). In Southeast Asia, firewood collection may compromise the long-term persistence of mangrove forests unless appropriate protective measures are put in place (Malik et al. 2015). Another notable socioeconomic goal can be achieved through habitat-forming species that secrete calcareous skeletons, such as oysters, corals and tube worms, through bioprotection of underlying rock or concrete, which potentially increases strength and longevity of structures (Coombes et al. 2013, 2017, Coombes, 2014).

Where habitat-forming species are being established from a baseline of zero at the shoreline site and the shoreline is already under threat from erosion or inundation, temporary protective measures may need to be in place while the habitat establishes. An example of this is the use of cultivator pots, protective matting and structures for mangrove seedlings (Krumholz & Jadot 2009, Tamin et al. 2011). These can help shield the habitat-forming species from erosion and stimulate establishment through enhanced sediment accretion, as well as protecting the shoreline from erosion until the habitat-forming species is able to attain sufficient size and/or density to fulfil the shoreline protection function. Knowledge of the configurations and morphologies of the habitat-forming species that best serve the functional role of shoreline protection will assist in determining which populations of the habitat-forming species to transplant to the site and the optimal way in which transplantation should proceed in order to achieve the desired goal. In some instances, transplantation of multiple habitat-forming species that exist in adjacent or nested configurations may best stabilise the shoreline and offer enhanced ecological cobenefits where they support unique species assemblages or promote distinct ecosystem functions (Gribben et al. this issue).

### *Hybrid approaches*

Hybrid approaches combine hard defences with natural elements, such as restoring key species or habitats by plantings and seeding. Such approaches can provide considerable benefits by helping to support broader management and conservation goals, enhancing ecosystem services and/or providing added protection beyond that of traditional hard structures (O'Donnell 2016). They enable ecological communities to be incorporated into defences at sites where they would not survive on their own or would, on their own, provide inadequate coastal protection (Sutton-Grier et al. 2015).

The configuration of natural and hard elements in a hybrid approach depends on the wave exposure of the environment, the amount of space available for transplants and the species involved. At sites where natural habitats persist and provide shoreline protection from moderate (but not large) storms, they may be fringed on their landward side by hard defences, such as seawalls or revetments, which provide the required protection from major storm events. At sites where wave action inhibits establishment of unprotected living habitat, the hard defence may be placed on the seaward side to protect the habitat from erosion. Low-crested rock sills are used to stabilise landward sediments in many instances, so that saltmarsh (Benoit et al. 2007, Bilkovic & Mitchell 2013) or mangroves (Hashim et al. 2010) can establish and grow. Hard defences and living habitat can also be interspersed. In Florida, for example, mangroves were planted in concrete cultivars that attenuate waves, accrete sediment and are designed to provide more favourable environments for survival and growth (Krumholz & Jadot 2009). This technique is also currently being implemented in Victoria, Australia (https://www.climatechange.vic.gov.au/__data/assets/pdf_file/0018/123507/Climate-Change-Innovation-Grants_funded-projects.pdf).

Generally, as wave energy increases, a greater ratio of hard defence to soft defence via a living habitat will be required. In environments with limited intertidal space, the opportunity for living habitat may be limited to small habitat pockets among hard defences (see the pocket beach example in Seattle, described in Toft et al. 2013). Nevertheless, the inclusion of these can still lead to significant biodiversity enhancement and ecosystem service provision over those provided by the hard defences alone (Spalding et al. 2013).

## Implementation of ecoengineered shorelines

The implementation of the ecoengineered shoreline approach is a complex process that is influenced by politics, public safety, community values and cost. Thus, it is not without potential risks and challenges. A major concern is dealing with communicating uncertainties and the need for adequate data (Chapman & Underwood 2011). Poor understanding of the underpinning mechanisms of common ecoengineering techniques (Gedan et al. 2011, Bouma et al. 2014) can limit the effectiveness of ecoengineered shoreline designs and lead to unanticipated changes in important ecosystem processes (Bilkovic & Mitchell 2013). There may be unintended consequences of standard ecoengineering strategies, such as enhanced structural complexity that may lead to increased accumulation of litter by shoreline structures (Aguilera et al. 2016). There is a lack of accepted and standardised criteria for evaluating their success (Perkins et al. 2015). A reputational risk is the misuse of ecoengineered shoreline concepts and terminology to justify and market expanded loss and conversion of natural habitats as ecologically desirable (Pilkey et al. 2012). However, the ecoengineered shoreline approach also has numerous potential benefits, which have already been discussed in this review, and which have been strongly emphasised in the recent research literature (Pioch et al. 2018).

The concept of working with nature has existed for centuries, but it was little less than half a century ago when the term *ecoengineering* was framed and the concept recognised (see the section entitled 'Introduction and the history of ecological engineering of shorelines', earlier in this review). Although older work on the ecology of artificial habitats exists (e.g. Plymouth and Port Erin breakwaters, United Kingdom; Southward & Orton 1954, Kain & Jones 1975) and a broader interest in the ecology (Hawkins & Cashmore 1993) and restoration of artificial marine habitats emerged in the 1980s and 1990s (e.g. Russell et al. 1983, Allen et al. 1992, 1995, Hawkins et al. 1992a,b, 1993, 1999, 2002, Allen & Hawkins 1993), research on ecoengineering of coastal structures only began to accelerate in the early 2000s (Chapman & Underwood 2011, Perkins et al. 2015, Strain et al. 2018b). In part, this increase has been prompted by growing recognition of the benefits of the ecoengineered shoreline approach (Pioch et al. 2018) the importance and relevance of which are particularly evident when considered within the context of major ecological, social and economic challenges currently faced by coastal ecosystems and human communities. It is within this context that we identify several drivers of the recent growing interest in ecoengineered shorelines, which we have broadly classified into five categories (discussed in the next sections): (1) climate change and associated sea level rise and increased flood risk; (2) coastal urbanisation, economic development and urban renewal; (3) integration in governance and policy; (4) growing public outreach and awareness and (5) advances in science and technology.

### *Climate change, the associated sea level rise and increased flood risk*

Anthropogenic climate change is placing coastal communities at risk; consequently, adaptation strategies are likely to be urgently required, especially in low-elevation coastal areas (Neumann et al. 2015, Dangendorf et al. 2017). Rising sea levels and increasingly frequent or more intense storms are leading to coastal erosion and flooding, necessitating either relocation or defence of low-lying settlements and infrastructure. By the end of this century, a rise of at least 0.25–0.55 m is projected, and about 95% of the ocean area will be affected (IPCC 2014). It is estimated that in the United States, approximately 1500 homes will be lost to coastal erosion each year for several decades, at a cost to property owners of $530 million per year (Heinz Centre 2000). These impacts of climate change are exacerbated by continued population growth in the coastal zone (Nicholls et al. 1999). Worldwide, it is predicted that by 2070, 37 million people and assets worth $13 trillion will be exposed to coastal hazards such as storms, flooding and climate variability (Nicholls & Hanson 2013). With carbon emissions still not stabilised globally, development of climate change adaptation strategies is now a priority for many jurisdictions (IPCC 2014).

Disasters such as the Indian Ocean tsunami in December 2004 and the hurricanes Katrina (2005), Sandy (2012) and Michael (2018) in the United States have drawn attention to the important role that coastal vegetation and reef-forming invertebrates play in shielding populations and property from sea level rise and storms (e.g. Danielsen et al. 2005, Gedan et al. 2011, Arkema et al. 2013). In some instances, the role that natural ecosystems play in reducing flooding is more effective than that of hard defences (Gittman et al. 2014). For example, along the east coast of the United States, damage to shorelines protected by marsh was less than along shoreline protected by bulkheads following category 1 hurricane events (Gittman et al. 2014). In several countries, including the United States, these observations, coupled with the growing need for coastal settlements and infrastructure to adapt to the threat of climate change, has led to policy that focusses attention away from hard to soft (i.e. 'living shoreline') defences as a climate change adaptational strategy (Finucane et al. 2014).

Despite the catastrophic effects that natural disasters may have on urban settlements, they can also bring about changes in public sentiment and government action. For example, Hurricane Sandy caused extensive damage to more than 650,000 homes along the east coast of the United States and claimed over 150 lives (Stewart, 2014). In response, the U.S. government provided more than $50 billion towards disaster relief and established the Hurricane Sandy Rebuilding Task Force to examine how funds might be best used to improve the resilience of communities and infrastructure to future and existing threats, including those exacerbated by climate change. The resulting Infrastructure Resilience Guidelines (Finucane et al. 2014) called for 'environmentally sustainable and innovative solutions that consider natural infrastructure options in all Federal Sandy infrastructure investments'. As a result, large numbers of living shoreline projects have now been implemented across the coastline (e.g. Tom's Cove and Assateague Beach), which are anticipated to provide not only coastal defence, but also other societal benefits.

### *Coastal urbanisation, economic development and urban renewal*

As the human population living in the coastal zone continues to increase, rapid urbanisation is transforming natural shorelines, expanding the built environment and increasing land reclamation. Developed urban shorelines are characteristically dominated by artificial structures, which have finite service life spans and need to be maintained regularly and replaced eventually (Mahmoodian et al. 2015). Urban renewal provides opportunities for converting existing coastal defences into more ecologically sustainable designs. For example, the Seattle seawall (see the section entitled 'Case studies and scaling up', later in this review) was failing and at risk of collapse should an earthquake hit, posing a public safety hazard. This, combined with the importance of the shoreline as a migratory corridor for endangered juvenile Chinook salmon, provided the opportunity to incorporate habitat improvements to the seawall reconstruction. Ecoengineered shoreline approaches will be adopted most readily where they provide clear benefits, which are in the public interest.

It is not unusual for areas of a city to be intentionally or unintentionally deindustrialised or deurbanised back to a more natural situation, and in such cases, ecoengineered shorelines can potentially play an important role. The Barangaroo Reserve in Sydney, Australia, is an example of a project driven by deindustrialisation and redevelopment. This reserve was once a concrete container terminal, but it underwent a major transformation to become a harbour foreshore park. Projects of this sort have great potential and open up huge opportunities for ecoengineered shorelines. Obsolete, locked dock basins in macrotidal estuaries in Europe have been the focus of ambitious urban renewal schemes, usually retaining the dock basins as water features or marinas and turning warehouses into housing, offices, hotels, shops, museums, art galleries and entertainment venues. One of the best studied has been the Liverpool dock system, where water quality was improved by artificial mixing and biofiltration by artificially (Russell et al. 1983) and naturally settled mussels (Allen et al. 1992, Hawkins et al. 1992a, Allen & Hawkins 1993, Wilkinson et al. 1996), leading to increases in biodiversity and healthy inner-city ecosystems of considerable conservation interest (Allen et al. 1995). The docks were much used in outreach and public engagement (Hawkins et al. 1993). Had the ecoengineered shoreline concept existed in the 1980s, considerable impetus and a body of good practice could have been deployed at the planning stage of urban renewal in Liverpool.

### *Integration into governance and policy*

Political will and shifts in governance and policy represent a strong and effective driver of ecoengineered shoreline development (Arkema et al. 2017, Sutton-Grier et al. 2018). For example, the central government of China issued a document on the use and protection of the country's coast in 2017, which specified that at least 35% of its shoreline should be maintained in a natural state by 2020 and that all proposed reclamation projects should be halted. This new national policy has sparked interest among provincial governments to invest in ecoengineered shoreline development and to convert concrete shorelines into more environmentally friendly ones by means of ecoengineering (Duan et al. 2016). At a state level, Maryland in the United States introduced the Living Shorelines Protection Act in 2008, which requires that property owners use living shorelines as the default for protection unless the owner can demonstrate the need for an artificial structure (e.g. a bulkhead) instead (Kochnower et al. 2015). Following up on European Union Directives and policy guidelines, the UK government and its devolved administrations (e.g. Wales) have given considerable emphasis on forming policy to incorporate habitat restoration and using ecoengineering in new coastal developments, including coastal defences in emerging planning guidance (see Evans et al. 2017, 2019 for detailed reviews of these efforts).

Global concerns for climate change and maintenance of biodiversity as seen in the participation of different governments in international agreements and conventions may also lead to ecoengineering options. The Paris Climate Agreement states that signatory parties 'should take action to conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases' (United Nations 2015), and the Convention on Biodiversity Conservation aims to achieve 'the conservation of biological diversity, the sustainable use of its components' (United Nations 1992). Ecoengineering is potentially one of the means that can help achieve the goals of these agreements and conventions.

### *Growing public outreach and awareness*

Public awareness of and concern about marine environmental issues are positively correlated with being well informed (Gelcich et al. 2014). Recent expanded interest in ecoengineered shorelines thus may be tied to greater education and understanding of the topic, as well as greater experience with coastal hazards that necessitate coastal defence infrastructure (Kochnower et al. 2015, Gray et al. 2017). Interviews with coastal residents in the United States suggest that awareness of and preference for ecoengineered shoreline approaches over traditional engineering are common, although so too are various misconceptions about the topic (Scyphers et al. 2014). In a recent survey of residents of four harbours in Australia and New Zealand, Kienker et al. (2018) found that level of education was positively correlated with support for marine ecoengineering. Additionally, prior knowledge about the dominant marine artificial structures in their harbour influenced how much participants in the study were willing to pay for ecoengineering (Kienker et al. 2018). A study of a variety of different stakeholders in Wales, ranging from engineers through coastal ecologists to the general public highlighted a willingness to embrace a multifunctional approach to the design of sea defences, especially if ecological objectives could also be delivered (Evans et al. 2017).

Education may result from formal programmes, such as in schools, or from community engagement in outreach activities and media articles (Figure 4). Emphasis on raising public awareness has been central to several recent ecoengineered shoreline projects. For example, the Billion Oyster Project in New York integrated curriculum development and restoration-based education programmes about the importance of oyster reefs and their ecosystem services for primary and high school students (Janis et al. 2016), which likely contributed to public awareness of the project. Local media attention has also recently increased the visibility of various ecoengineered shoreline projects, such as flowerpots on Sydney seawalls (e.g. Chapman & Blockley 2009, Browne & Chapman 2011, Morris et al. 2017).

### *Advances in science and technology*

Over the past two decades, there has been rapid growth in the understanding of how shoreline defences affect coastal ecosystems (e.g. loss of biodiversity, increase in invasive species) (Airoldi et al. 2005a, Martin et al. 2005, Bulleri & Chapman 2010), and how these negative effects may be compensated for through ecoengineered shoreline designs (Moschella et al. 2005, Perkins et al. 2015, Firth et al. 2016a, Munsch et al. 2017b, Strain et al. 2018b). It is now acknowledged that some artificial defences can cause new erosion problems or loss of public amenities (e.g. beach loss in front of seawalls; Fletcher et al. 1997). Recent research has increasingly emphasised ecoengineered shorelines as a potentially more cost-effective strategy than traditional approaches to coastal protection (Sutton-Grier et al. 2018). As studies on ecoengineered shorelines have multiplied, the accumulation of data and research findings have enabled meta-analyses pinpointing the precise ecoengineering strategies and specific circumstances under which ecoengineered shorelines are likely to be successful at meeting their stated aims (Gedan et al. 2011, Bugnot et al. 2018, Strain et al. 2018b).

**Figure 4** Various signs at ecoengineered shorelines to raise awareness and public education.

In addition, many ecoengineered shoreline strategies have themselves advanced and become more cost effective because of recent innovations in fabrication (3-dimensional printing) and materials science (e.g. ecofriendly cement mixes; Perkol-Finkel & Sella 2014). Further, advances in ecology and ecosystem science have brought insights that clarify ecological processes and the functional traits of taxa that are central to ecosystem services provided by shoreline habitats. For example, greater understanding of the role of oysters in biofiltration, habitat provisioning, sediment stabilisation and wave attenuation in New York Harbour (e.g. Coen et al. 2007, Grabowski et al. 2012) ultimately facilitates ecoengineered shoreline projects that are of ecological and social value (e.g. the Billion Oysters Project). As knowledge of coastal ecological processes and the science of ecoengineering continue to grow and support advances in technology, it is likely to drive the demand for ecoengineered shorelines.

## *Barriers to implementation*

In general, barriers may include (1) a lack of awareness by decision-makers of the available options and a failure to engage with the multiple stakeholders involved in communicating the benefits of ecoengineered shoreline approaches, (2) government policies that are insufficiently flexible to accommodate new approaches and ways of thinking and (3) an absence or paucity of science-based evidence for the success, benefits and long-term durability of innovations (see the section entitled

'Evaluating the ecoengineered shoreline approach in practice', later in this review). Additionally, there may be cultural, financial or logistic (e.g. extreme environmental degradation) barriers to adopting ecoengineered shoreline approaches. To incentivise the innovation and development of ecoengineered shoreline designs and technologies, a consistent and supportive framework is required to improve risk-to-reward ratios, particularly during the demonstration stage of technology and design development. This framework may enhance positive expectations, stimulate learning, improve the design and increase the likelihood of successful project implementation (Foxon et al. 2005).

### *Awareness and communication among key stakeholders*

For hard ecoengineered shorelines, small-scale trials have been carried out in different parts of the world over the last three decades, but medium- to large-scale implementation of ecoengineered shorelines is still in its infancy (but see the Seattle case study as one exception). For soft engineering, larger-scale implementation is more common; for instance, there has been a great effort to restore mangroves in Asia, with coastal defence as a driver in many projects (Saenger & Siddiqi 1993, Benthem et al. 1999, IFRC 2011). However, in contrast to hard ecoengineering, which has often been research driven, these larger-scale soft ecoengineering projects frequently lack scientific rigour and robust ecological-monitoring regimes (Narayan et al. 2016). Despite hot spots of research and/or implementation of ecoengineered shorelines globally, one barrier to their implementation more generally may be the wider transfer of information to relevant local, state or national governments. Even in countries that are driving ecoengineered shoreline research (like Australia, European countries, and the United States), regional (state or provincial) governments may not know about the rationale, concept and potential value of ecoengineered shoreline implementation. A better understanding of these innovations by government leaders, key stakeholders and the general public may lead to support for small-scale project trials. In turn, the success of these trials can lead to the implementation of large-scale ecoengineered shoreline projects.

Effective communication and partnerships among architects, engineers, ecologists, socioeconomic scientists and other relevant stakeholders are also important. Cross-disciplinary teams generate holistic projects through collaboration to achieve a common goal and build synergy. In particular, there is a need to build trust and better understanding among stakeholders, who often do not share the same perspective and interests (Prati et al. 2016), so as to develop ecoengineered shorelines that can fulfil both engineering requirements (i.e. shore protection and structure integrity) and ecological goals, while also providing a social benefit (Evans et al. 2017).

A better international strategy for enhancing the awareness of ecoengineered shorelines and their benefits to people and the environment is needed. The closest international tool to address this need currently is the development of an online coastal resilience mapping interface, driven by The Nature Conservancy in the United States, which has attempted to synthesise data on the coastal protection provided by intact natural habitats and to identify soft engineering projects (http://www.maps.coastalresilience.org/cities/). This tool does not include hard ecoengineered shorelines. The National Oceanic and Atmospheric Administration (NOAA) has developed a useful webpage to introduce the concept of living shorelines, with some examples (https://www.fisheries.noaa.gov/insight/living-shorelines) in the United States. In Australia, the state government of New South Wales has developed an Environmentally Friendly Seawalls guide (http://www.environment.nsw.gov.au/resources/estuaries/pubs/090328-Seawall-Guide-2012-Reprint.pdf), which summarises local projects.

Ideally, an internationally oriented ecoengineered shoreline organisation and educational website should be established, accompanied by a campaign aimed at increasing awareness at a global level. This effort could capitalise on existing networks, such as Restore America's Estuaries and the World Harbour Project, and include international organisations such as The Nature Conservancy and World Wide Fund for Nature to enhance content delivery. The strategies could include using multimedia, both conventional and Internet-based, to introduce ecoengineered shorelines and highlight illustrative projects from around the world.

### *Policies, incentives, regulations and financial instruments*

At present, specific policies that call for integrating ecological considerations into the design and construction of coastal defence and coastal development schemes through ecological engineering are generally lacking in most countries or jurisdictions. Nevertheless, ecoengineered shorelines can potentially make a significant contribution towards a wide variety of current policy objectives, such as those that support sustainable development and the maintenance of biodiversity (Naylor et al. 2012, Dafforn et al. 2015b). For example, under the United Nations Convention on the Law of the Sea (UNCLOS), states are required to protect and preserve the marine environment (Ban et al. 2014). In this context, ecoengineered shorelines could be proposed as a tool for generating more adaptive, resilient coastlines for the mutual benefit of the environment and society. Having ecoengineered shorelines on the international policy agenda may incentivise the implementation of local legislation to further support their application (e.g. the Living Shorelines Act, Maryland).

The few large-scale ecoengineered shoreline projects emerging recently (e.g. Tong King Delta and Mekong Delta, Vietnam; Grenville Bay, Grenada; Barangaroo Reserve, Carss Park and Olympic Park in Sydney; the Seattle Seawall Project, Harlem River Designing the Edge Project, Brooklyn Bridge Park, and Vancouver Conference Centre Project in the USA), if monitored efficiently for successes and failures, could provide valuable evidence to inform the adoption of ecoengineered shoreline designs, but also offer some essential information for doing a benefit-cost analysis (BCA) of any proposed ecoengineered shoreline project. Insufficient resources are usually the main barrier for any innovative development and its commercialisation (Hadjimanolis 1999). This situation is exacerbated by the lack of full accounting of the benefits associated with ecoengineered shorelines, which has rarely been performed. This is due primarily to the difficulty in assigning monetary values to the ecosystems and social services that the projects are designed to perform (see the section entitled ‘Measuring socioeconomic outcomes’, later in this review; but see Narayan et al. 2016, Reguero et al. 2018).

To date, many of the documented ecoengineered shoreline projects have been on a small scale, partly due to insufficient financial support. In most cases, local governments play a key role by providing some seed funding for conducting feasibility studies on small-scale trials of various ecoengineered shoreline designs. If a trial project proves successful, the government might proceed to conduct a large-scale implementation, depending on the policy agenda, site availability and financial resources. Unfortunately, even when money is available, in some cases the type of monitoring that is performed focusses only on proving whether a particular trial concept can or should be scaled up at a particular site (J. Miller, pers. obs.). In these cases, the opportunity to identify benefits that may apply more broadly to ecoengineered shorelines constructed in other locations is lost.

Certain countries have structured regulations that may encourage implementation of ecoengineered shoreline designs. For example, in the United States, there are regulations that demand quantitative mitigation measures for development projects, including in coastal and marine environments. These typically call for the restoration of habitat loss and/or ecosystem functions affected by the project and are often significantly higher in cases where on-site mitigation is not possible in terms of the investment expected (e.g. Ambrose 1994). Currently, mitigation measures include actual restoration work (e.g. marsh restoration, construction of artificial reefs) or purchasing mitigation credits from available mitigation banks. Ecoengineered shoreline implementation can be viewed as on-site mitigation measures, potentially offsetting some of the overall compensation and mitigation costs. This can effectively incentivise the implementation of ecoengineered shorelines; however, documentation of such cases is lacking within the United States, and currently this approach is not widely adopted in other countries.

For green buildings, there are certification and grading systems, such as those by the Leadership in Energy and Environmental Design (LEED) initiated in the United States (Humbert et al. 2006) and nowadays applied in many countries worldwide, the Building Research Establishment Environmental Assessment Method (BREEAM) in the United Kingdom (Crawley & Aho 1999) and Building

Environmental Assessment Methods (BEAM) in Hong Kong (Lee et al. 2007) in order to recognise the environmental friendliness and energy-saving efforts being adopted in the building as an incentive for the project proponent or developer to achieve the highest rating (e.g. platinum award in LEED).

Recently, the Waterfront Edge Design Guidelines (WEDG) in New York and New Jersey Harbour have been developed by the Waterfront Alliance (http://waterfrontalliance.org). The WEDG is a point-based rating system with a set of guidelines for waterfront projects in New York and New Jersey Harbour, with a view to creating resilient, ecological and accessible waterfronts (Box 1). During the evaluation process, actions taken in the planning, design, construction and even postconstruction (monitoring) process are tallied to determine how successful a project is in achieving benefits in the three core areas: resilience, ecology and access. Any project proponents can voluntarily go through the WEDG assessment to gain certification and receive advice from professional assessors to further improve the project in the plan's three aspects: shoreline protection, ecological enhancement and diverse uses of the waterfront by various stakeholders.

Thus far, the WEDG has been used to certify over a half-dozen projects spanning a range of shoreline uses, from parks to heavy industrial areas in New York City (http://wedg.waterfrontalliance.org). Recently, the WEDG has undergone a revision intended to streamline the ratings system and make it more readily applicable to shorelines outside the New York/New Jersey metropolitan

## BOX 1 THE WEDG CERTIFICATION SYSTEM FOR WATERFRONT PROJECTS ADOPTED IN NEW YORK AND NEW JERSEY

### WEDG

The WEDG employs an evidence-based approach, focussing on three key pillars of excellent waterfront design in New York and New Jersey Harbour. They include the following:

- *Resilience*: The waterfront project should reduce risks or be adaptable to the effects of sea level rise and increased coastal flooding, through setbacks, structural protection and other integrative landscaping measures.
- *Ecology*: The waterfront project should protect existing aquatic habitats and use designs, materials and shoreline configurations to improve the ecological function of the coastal zone and strive to be consistent with regional ecological goals.
- *Access*: The waterfront project should be equitable and informed by the community, enhancing public access, supporting a diversity of uses, from maritime, recreation and commerce where appropriate, thereby maximising the diversity of the harbour and waterfront.

The credit points made by the professional assessors would help guide the design process, from conceptual design through operations, and provide design performance goals for resilience, ecology and access in the following six categories:

- Category 0: Site Assessment and Planning
- Category 1: Responsible Siting and Coastal Risk Reduction
- Category 2: Community Access and Connections
- Category 3: Edge Resilience
- Category 4: Natural Resources
- Category 5: Innovation

Source: http://wedg.waterfrontalliance.org/

area. The WEDG is the first example of this kind to pave the way for developing an international certification system that will play a key role in incentivising the development of ecoengineered shorelines around the globe. Furthermore, the question is how to use the certification system to further incentivise ecoengineered shorelines. Potentially, if waterfront projects have successfully addressed the Sustainable Goals of the United Nations (https://www.un.org/sustainabledevelopment/sustainable-development-goals) and received certification by a system like the WEDG, then the project proponent could receive a tax reduction or rebate and banks could provide better loans with a lower interest rate for the project proponent. However, such arrangements are likely to depend on individual governments and banks. There is certainly a need to build more successful precedent cases to convince governments and financial institutions.

### *Engineering concerns and paucity of science-based evidence for success*

One of the biggest obstacles from an engineering standpoint is liability (Slate et al. 2007). Although regulations differ from country to country, engineers are generally responsible for ensuring public safety and can be held responsible if their projects fail. Findings of fault can result in severe economic, professional or even criminal sanctions (Baura 2006). As a result, engineers tend to be cautious and view unproven technologies/approaches with an appropriate degree of trepidation. When it comes to the design of traditional infrastructure such as buildings and bridges, engineers can rely on established codes such as the International Building Code for guidance.

For less traditional infrastructures such as coastal defence systems (i.e. seawalls, breakwaters and revetments), codes are often lacking. As a result, engineering design is often guided by a set of standard practices/approaches advocated in respected design manuals such as the *Coastal Engineering Manual* (U.S. Army Corps of Engineers 2002) and *The Rock Manual* (CIRIA et al. 2007). Absent codes, following well-vetted engineering practices provides a level of protection from professional liability should a project fail. For the engineering community to more openly embrace ecoengineered shorelines, design manuals need to be developed (Burcharth et al. 2007), or perhaps more likely, sections need to be added to existing design manuals to deal specifically with ecoengineered shoreline approaches. Such an effort needs to be led by an internationally recognised body such as the U.S. Army Corps of Engineers or Construction Industry Research and Information Association (CIRIA).

A second, related concern from an engineering standpoint is the real or perceived lack of predictability of the behaviour of certain types of ecoengineered shoreline projects with time (Bouma et al. 2014). Ecoengineered shorelines have a temporal component that is more difficult to deal with than traditional engineering materials. For example, fatigue is a well-known engineering phenomenon in which materials lose strength over time due to repetitive loading. Most traditional engineering materials have gone through enough testing that this fatigue behaviour can be predicted and planned for during design. The living element of ecoengineered shoreline projects is much less predictable (and certainly much less well studied) than the temporal behaviour of traditional materials (Bouma et al. 2014). Furthermore, some ecoengineered shoreline approaches may actually depend on the living portion of the project for properties critical to the performance of the structure. For example, if oyster growth is critical to the wave attenuation or chloride penetration prevention characteristics of a project, the threat of environmental phenomena affecting growth has a potentially devastating, cascading impact on the engineering characteristics. This can be related back to liability and the reluctance of engineers to design something whose behaviour they cannot predict. A robust evidence base on the efficacy of ecoengineered shoreline approaches was identified by some stakeholders, however, as a barrier to fuller implementation (Evans et al. 2017). Part of the problem is that the evidence is accumulating, but it is not necessarily being delivered in a readily accessible and digestible form to key practitioners, statutory bodies and legislators.

## Evaluating the ecoengineered shoreline approach in practice

Traditional artificial defence structures are constructed to protect land from erosion and flooding. Their success is typically measured from an engineering standpoint of whether protection was achieved or not. In contrast, ecoengineered shorelines are valued for their potential to provide multifunctional benefits, and thus measuring their success calls for a wider analysis. We suggest three main domains of objectives for which the success of ecoengineered shorelines may be measured:

- Ecological objectives, often stated in terms of enhancement of biodiversity or a particular species (e.g. salmon in Seattle; Munsch et al. 2017b) or the reestablishment of a habitat that provides ecosystem services such as water filtration or biodiversity provision (e.g. oyster reefs)
- Engineering objectives, which relate to the function of an engineered insertion over its projected life span
- Socioeconomic objectives, such as public acceptance, politics, recreational value, property prices and development goals (Table 1)

**Table 1** Examples of criteria for measuring the success of ecoengineered shorelines

| Category | Goals: Functions/services | Measure | Controls/reference |
|---|---|---|---|
| Ecology | Native species biodiversity | At species level: species richness, biomass, abundance, percentage of cover, percentage, community assemblage<br>At habitat level: Habitat diversity<br>At genetic level: Genetic diversity | Artificial structure<br>Natural shoreline<br>Before-after |
| | Invasive species | Number and abundance of species<br>Ratio of native to invasive species | Artificial structure<br>Natural shoreline<br>Before-after |
| | Target species | Enhancement/recovery of abundance or survival of target species | Artificial structure<br>Natural shoreline<br>Before-after |
| | Ecological functioning and processes | Integrity of biological assemblage (e.g. functional groups)<br>Biofiltration<br>Water quality<br>Primary productivity<br>Ecosystem engineers/habitat-forming species<br>Bioprotection<br>Carbon sequestration | Artificial structure<br>Natural shoreline<br>Before-after |
| | Fisheries production | Enhancement of fisheries supply<br>Usage of habitat/refuge by larvae | Artificial structure<br>Natural shoreline<br>Before-after |
| | Connectivity | Enhancement and/or reduction of connectivity | Artificial structure<br>Natural shoreline<br>Before-after |
| Engineering (risk reduction) | Energy attenuation | Wave height reduction<br>Current reduction | Natural shoreline<br>Artificial structure<br>Before-after |
| | Shoreline stabilisation | Horizontal shoreline location | Natural shoreline<br>Artificial structure<br>Before-after |

(*Continued*)

**Table 1 (Continued)** Examples of criteria for measuring the success of ecoengineered shorelines

| Category | Goals: Functions/services | Measure | Controls/reference |
|---|---|---|---|
| | Achieving adequate/desirable sedimentation dynamics | Regulating sediment accumulation | Natural shoreline<br>Artificial structure<br>Before-after |
| | Reduce flooding | Surge extent/height | Natural shoreline<br>Artificial structure<br>Before-after |
| | Structural integrity | Structural integrity<br>Durability/longevity<br>Resistance to extreme weather events | Through time<br>Natural shoreline<br>Artificial structure |
| Social | Aesthetics | Appeal to people | Before-after<br>Areas with and without interventions |
| | Tourism and recreation | Waterfront accessibility<br>People's awareness and use of the waterfront | Before-after<br>Areas with and without intervention |
| | Education | People's knowledge and awareness of coastal biodiversity and ecoengineered shorelines | Before-after<br>Areas with and without intervention |
| Governance and policy | Facilitate use of ecoengineered shorelines | Funding incentives, permits, recommendations, and regulations | Before-after |
| | Hazard mitigation | Protection of property and life | Before-after<br>Natural shoreline<br>Artificial structure |
| Economic | Shore protection insurability | Reduction of economic loss due to damage<br>Reduction of insurance premium requirement<br>Increase in property value | Before-after<br>Natural shoreline<br>Artificial structure |
| | Creation of jobs | Increase in job opportunities in landscape architecture, marine ecology, construction, tourism and fishery sectors | Before-after |
| | Business opportunity | Nurturing new businesses associated with successful waterfront | Before-after |
| | Project performance | Construction, maintenance and services provided | Artificial structure |

*Note:* The term *artificial structure* refers to a traditional engineering solution (e.g. seawalls). *Natural shoreline* refers to the intact equivalent of the created habitat (e.g. mangroves, rocky shores). A bare reference without a structure (e.g. mudflats) may also be an appropriate control for some measurements.

Metrics relating to each of these domains are essential for assessing multifunctionality and overall benefits of ecoengineered shorelines. Although a combination of these domains is becoming increasingly common in monitoring plans for ecoengineered shorelines (Yepsen et al. 2016), we show that in practice, few projects have incorporated all three (marine scientists/managers, engineers and the public; see Figure 5).

## *Measuring ecological outcomes*

Ecoengineered shorelines can be designed to meet a variety of ecological objectives, including biodiversity enhancement, invasion resistance, facilitation of specific target species, specific ecosystem

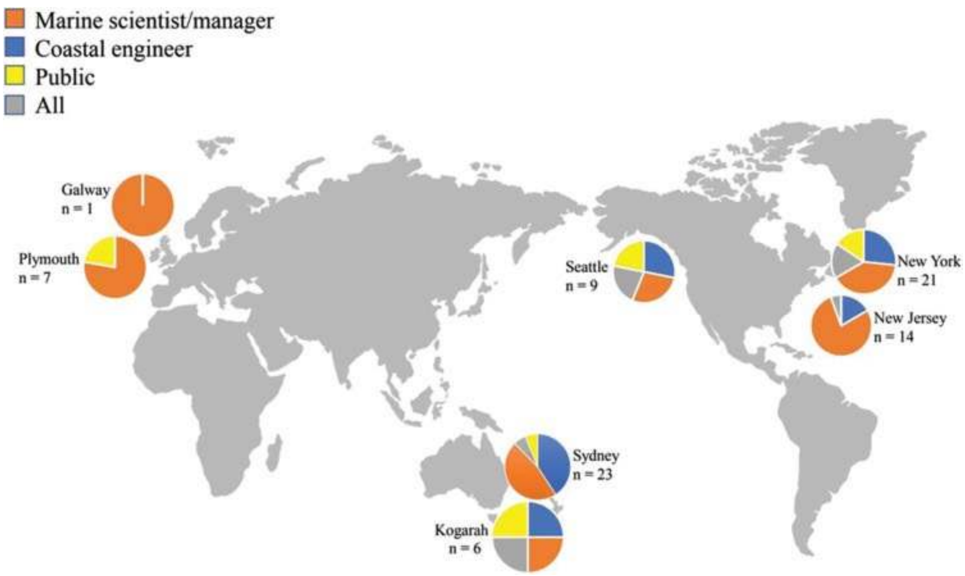

**Figure 5** The proportion of key stakeholders (marine scientists/managers, engineers, public and all three) involved in ecoengineered shoreline projects in select locations in the United States, Australia, Europe and the United Kingdom. The data were provided by researchers in these places, and the locations presented were based on where the information about stakeholder participation was available.

processes and general functioning, with the ultimate aim of provision of services (Table 1). The objectives selected depend on the type of ecoengineered shoreline project, the ecological and environmental context in which the project takes place and local societal needs and interests. Ecological objectives for hard ecoengineered shorelines tend to focus on ameliorating abiotic and/or biotic stressors that limit diversity in general, thereby enhancing focal species of conservation or commercial interest or increasing native populations or functional groups that enhance ecosystem services (Chapman & Blockley 2009, Dugan et al. 2011, Perkol-Finkel et al. 2012, Mayer-Pinto et al. 2018, Strain et al. 2018b). In contrast, where soft or hybrid ecoengineered shorelines can be constructed by establishing coastal plants, shellfish or coral reefs (Arkema et al. 2013), the main ecological focus is typically on selecting and monitoring the efficacy of specific habitat-forming organisms for coastal protection via the dampening of waves or stabilisation of sediment (Borsje et al. 2011). However, measures of ecological cobenefits, such as enhancement of biodiversity or fisheries productivity, carbon sequestration and improvement of water quality (Barbier et al. 2011, Davis et al. 2015, Sutton-Grier et al. 2015) may also be important for quantifying the success of soft and hybrid ecoengineered shorelines.

Measuring the ecological benefits of ecoengineered shorelines requires prespecifying a monitoring framework (prior to initiation) that effectively assesses changes in a specific intervention or habitat of interest (Michener 1997, Block et al. 2001). Ideally, monitoring plans compare ecoengineered shorelines with controls (i.e. unaltered artificial shorelines), as well as with ‘reference areas’ (i.e. natural habitats that the ecoengineered shorelines are seeking to mimic). In this way, planned ecoengineered shoreline interventions function as experiments (Chapman et al. 2018). Appropriate controls and reference areas depend on the type of ecoengineered shorelines being constructed. For hard ecoengineered shorelines, the relevant control is typically a new or cleared section (i.e. with any existing flora and fauna removed) of an artificial structure at the same site or at a nearby site with comparable environmental conditions, depending on the scale of the manipulation (Chapman et al. 2018), and reference sites are frequently rocky shores, the closest natural hard-substrate analogues (Chapman & Underwood 2011, Evans et al. 2016).

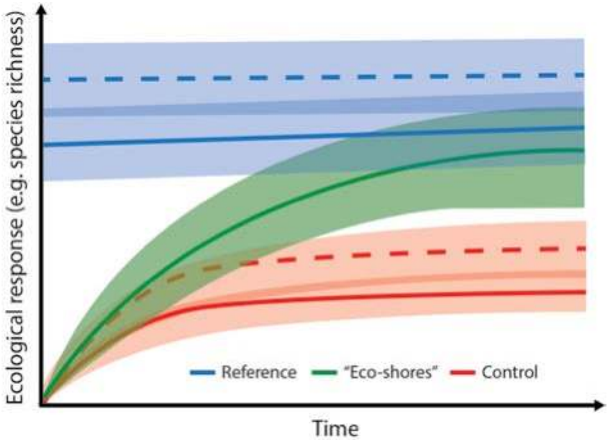

**Figure 6** A hypothetical illustration of plausible temporal changes in ecological performance of an ecoengineered shoreline and multiple control and reference sites (solid and dashed lines indicate the various sites). The shaded area around each line represents variation in a single hypothetical site or plot. It is expected that ecoengineered shorelines will enhance the targeted ecological response to be more similar to the reference habitat of interest (e.g. natural habitat), in comparison to the control (i.e. the unaltered structure), which will remain the same.

For soft-engineering interventions, controls should be established patches of the habitat type being constructed. There have also been some attempts to compare soft and hybrid interventions with 'hard' reference sites (e.g. coral reefs with breakwaters and saltmarsh with and without sills with bulkheads; Ferrario et al. 2014, Gittman et al. 2014). However, it is important to note that reference sites may have differences in physiochemical parameters, community succession and other environmental drivers, which can make comparisons between ecoengineered shorelines and reference sites difficult to interpret (Chapman et al. 2018), especially on highly modified coastlines.

Data regarding the ecological performance of reference sites can provide helpful insight into the expected natural variability in recruitment (often due to chance events in plankton) or survival of organisms (e.g. due to heat stress and predation), as well as the possible impacts from other environmental stressors over time (e.g. climate change or fishing; see Figure 6). At least two natural reference sites should be surveyed multiple times both before and after ecoengineered shoreline installation (Beyond BACI; Underwood 1991). For example, if the ecoengineered shoreline is located between two rocky shores, then both rocky shores should be used as reference sites and surveyed regularly alongside the monitoring of the ecoengineered shoreline. Equally, the effects of ecoengineered seawalls should be compared with multiple unmanipulated seawall sites (Morris et al. 2017).

Monitoring and evaluation programmes can be qualitative, semiquantitative or quantitative and may employ various sampling techniques, including visual surveys, field sensors and destructive sampling (Table 2; Burcharth et al. 2007). Generally, the time required for sampling increases as sampling methods become more quantitative. Which destructive or remote-sensing methods are appropriate will depend on the scale of assessment (e.g. whether changes in alpha, beta or gamma diversity are being evaluated) and the variables being assessed. Core variables for monitoring commonly include the number, diversity and abundance of species (Mayer-Pinto et al. 2018, Strain et al. 2018b), the growth and structure of vegetation or habitat-forming organisms and functional measurements such as filtration rates or primary production (Mayer-Pinto et al. 2018). These variables are typically compared between ecoengineered shorelines, controls and reference areas based on differences in means (Osenberg et al. 1999, Munkittrick et al. 2009, Smith et al. 2017b) and assemblage structures (Anderson 2001). Measures of effect size, such as Cohen's D or log response ratio, can also be helpful (Cohen 1988, Hedges et al. 1999, Coleman et al. 2006, Nakagawa & Cuthill Innes 2007) for quantifying the magnitude of change resulting from the intervention relative to controls and reference sites.

**Table 2** Evaluation techniques to measure the ecological and effectiveness of ecoengineered shorelines

| Technique | Method | Time scale | Effort and precision | Expectations |
|---|---|---|---|---|
| Visual | Photographs<br>Videos<br>Online outreach | Hours | Low | Initial documentation of project success or problems to address |
| Survey data | Structural amount of components (e.g. vegetation, algae, sessile invertebrates, sediments) | Year | Medium | Inform management on initial meeting of project goals |
| Statistical analysis | Evaluation based on a structured experimental design of target functions | Years | High | Validation of project goals and recommendations on further implementation |

To date, much of the experimental research on ecoengineered shorelines has been undertaken at small spatial (i.e. ranging from centimetres to metres) and temporal scales (<12 months) (Bishop et al. 2017, Chapman et al. 2018, Morris et al. 2018b, Strain et al. 2018b). Because of the effects that the shoreline form can have on ecological connectivity (Bishop et al. 2017), and with growing interest by local government agencies, nongovernmental organisations (NGOs) and developers in implementing ecoengineered shorelines at the larger scales required for coastal protection, there is a need to develop appropriate monitoring protocols for addressing ecological changes at these scales. The 12-month monitoring period undertaken by many organisations is arbitrary and probably much too short for demonstrating impacts on community structure or ecosystem functioning. Neither is there sufficient time for natural succession to take its course. For example, in an early study of colonisation of large concrete blocks placed on the outside of a Plymouth Breakwater in the United Kingdom, communities and assemblages took more than 5 years to stabilise to typical small-scale patchiness and low-amplitude fluctuations, with populations of the key grazing limpets taking considerable time (>7 years) to stabilise (Hawkins et al. 1983).

In many cases, the outcomes of ecoengineered shoreline projects at 12 months depend heavily on initial conditions (e.g. created wetland with greater cover will report success in shorter time frames than created wetlands with less cover; Mitsch & Wilson 1996). Research on wetlands suggest that 15–20 years are required to judge the success of ecoengineered shoreline projects (Mitsch & Wilson 1996). The spatial and temporal scales of ecoengineered shoreline monitoring should be linked to the generation time and geographic distribution of the communities being investigated. Developing standardised monitoring protocols and promoting their use across multiple users (e.g. the Shoreline Monitoring Toolbox in Puget Sound, Washington State; http://wsg.washington.edu/toolbox and the Hudson River in New York: Findlay et al. 2018) can help to facilitate collaborations between ecologists and the broader public (Toft et al. 2017) and may help to extend the monitoring time frames of ecoengineered shoreline projects beyond 12 months. But one size is unlikely to fit all cases, and monitoring programmes need to be tailored to the objectives of a project and its environmental and socioeconomic context.

A lack of clear project goals and appropriate monitoring and evaluation of these has hampered assessments of ecological successes and failures. For example, in an analysis of oyster reef restoration projects undertaken in the Chesapeake Bay for shoreline stabilisation or other purposes between 1990 and 2007, only 43% of projects included both the restoration and monitoring required to assess their success or failure (Kennedy et al. 2011). Similarly, of all documented marine coastal restoration projects over a 40-year period, only 61% provided information on survival of the restored organisms (Bayraktarov et al. 2016). Where monitoring has been carried out for ecological enhancements of hard defences, it has typically focussed on the success of interventions in enhancing species richness and/or the abundance of key functional groups relative to controls (see Strain et al. 2018b). Although overall species richness tends to increase with the addition of microhabitats, responses among functional groups can vary. The extent to which increased species richness is due to native versus nonnative species (Morris et al. 2018a, Strain et al. 2018b), as well as effects on ecosystem services (Mayer-Pinto et al. 2018), are rarely addressed, and yet they are important considerations for monitoring, particularly where ecoengineered shorelines are designed to meet multiple ecological objectives.

An additional limitation in measuring the success of ecoengineered shorelines in meeting ecological objectives is that unsuccessful (or only partially successful) projects are rarely documented, making it difficult to assess their frequency (see comments and an example in Firth et al. 2016a). It is likely that the incidence of failure is high, particularly for soft or hybrid ecoengineered shoreline projects in which plantings are conducted without first assessing adequate environmental suitability of the site. For example, between 1989 and 1995, only 1.52% of the 9050 ha of mangroves planted in West Bengal, India, survived (Sanyal 1998). An evaluation of the success of a the $35 million World Bank funded Central Visayas Regional Project in the Philippines indicated that only 18.4% of the 2,927,400 mangroves planted over 492 ha survived (Silliman University 1996). Plantings are especially likely to fail at sites that have not previously supported the planted species, underscoring the importance of collecting data and identifying appropriate ecological objectives prior to the implementation of ecoengineered shorelines.

### *Measuring engineering outcomes*

Ecoengineered shorelines are generally conceived to address one or more engineering objectives, which may or may not be directly related. These include shoreline stabilisation, flood mitigation, energy attenuation and sediment control. Depending on a number of factors, including the physical setting, funding source and socioeconomic considerations, one or more of these engineering objectives may take precedence and must be identified clearly so that appropriate success metrics can be defined. As with ecological objectives, the success of engineering objectives then requires the development and implementation of an appropriate framework for monitoring (Yepsen et al. 2016, Findlay et al. 2018).

Ecoengineered shorelines are generally considered successful from an engineering perspective if they achieve predetermined engineering objectives and they remain intact, such that they continue to achieve that objective over time. The former is typically referred to as the engineering *function* of the project, and the latter the engineering *form*. Engineering function and form are often (but not always) related to each other.

The specific metrics used to evaluate function depend on the engineering objectives of the project (Thayer et al. 2003). Shoreline position is an effective measure of function where shoreline stabilisation is a core engineering objective (Yepsen et al. 2016). Because shoreline position tends to be highly 3-dimensional and extremely dynamic, comparison with control sites is essential (Underwood 1994). It may be possible, however, to use an alternative, less variable measure of shoreline stabilisation, such as the marsh edge or vegetation line (Kreeger et al. 2015). Projects in which flood mitigation is an objective typically utilise flood height and/or extent as a metric for success (Yepsen et al. 2016). Although reduction in flood height compared with surrounding areas is typically easy to measure, reduction in flood extent is often more difficult and may require numerical simulations with the ecoengineered shoreline project compared to without based on past flood events (Yepsen et al. 2016). This can be particularly difficult in built environments, as even small changes in development patterns can drastically alter flood pathways and the extent of flooding.

Projects with energy attenuation as an objective typically use wave height or current velocity attenuation as a measure of success. These parameters are measured in front of (offshore) and behind (inshore) the designed wave attenuation feature and used to calculate transmission coefficients (i.e. the ratio of their measured value inshore versus offshore), which is inversely related to the dissipation of energy (e.g. Garvis 2009, Manis et al. 2015). Even though it is common for the transmission through a traditional engineering structure to increase over time as the structure breaks down, certain types of ecoengineered shorelines, such as those incorporating ecosystem engineers or biogenic taxa, are expected to become more effective over time as the biological growth helps to attenuate the incident energy (Manis et al. 2015). Projects aimed at controlling sediment deposition/erosion typically use areal extent or sediment volume to judge success. Areal extent (the net increase or decrease in land area), which is related to shoreline position, is an essential metric in projects intended to accrete or trap sediment (i.e. with features such as sills, stream barbs, and groynes). While volume change is perhaps a more complete measure of sediment control, it typically requires more effort and expense to collect and therefore it is sometimes forgone.

Metrics related to engineering form provide information about the physical integrity of specific features of ecoengineered shoreline projects. The most appropriate metrics of form depend on the type of ecoengineered shorelines being constructed. *Crest elevation* refers to the elevation of the top of an engineered or natural shoreline feature. Several of the engineering objectives defined here (e.g. wave height attenuation and flood mitigation) are strongly dependent on elevation (Armono & Hall 2003, Allen & Webb 2011, Webb & Allen 2015). Thus, stable crest elevation over time is critical to the success of an ecoengineered shoreline project. In addition to elevation, changes in slope or orientation can be indicative of potential problems. For shore-detached rock structures, changes in slope have a direct impact on the stability of the structure and its ability to dissipate waves. For shore-attached vertical structures, deflections can be indicative of problems related to scour and overtopping. For shore-attached sloping structures, changes in slope directly influence the stability of stone armouring, as well as run-up. *Scour* is a generic term referring to the erosion that occurs adjacent to a hard feature. Scour occurs naturally in front of cliff faces and around rocks, but it also can be caused by built features such as bulkheads and seawalls. It can occur in front of (toe scour), adjacent to (flanking or end effects) or behind (leeside scour) structures.

Another important component of engineering monitoring is inspection of structural performance in terms of integrity of materials or construction units (Burcharth et al. 2006). Structural integrity can be broadly used to describe the physical integrity of an ecoengineered shoreline project, considering the wide range of types of structure this includes. Despite being designed in a manner that facilitates ecological enhancement, often the main objective of an ecoengineered shoreline project is to provide a structural solution. When considering a composite structure, such as a riprap or revetment, structural integrity can be evaluated according to the displacement of individual units from the structure (Burcharth et al. 2006). For solid structures such as a seawall, structural integrity can be about the physical degradation of the overall structure and the constituent components. A *component* is defined as an individual structural member, and the collection of such members such as piles, pile caps, decks and fittings makes up the structure. When dealing with soft and hybrid solutions, such as marshes or marsh sills, some of these components are living, including marsh plantings and items derived from natural materials such as coir logs. In addition to assessing the overall condition of the structure, each individual component should be rated (NYCEDC 2016). Monitoring techniques include visual site inspections (described in further detail later in this review), taking core samples of concrete/rock armour and more standard concrete testing such as chloride or water penetration and compressive strength (Sagoe-Crentsil et al. 2001). In certain cases, more sophisticated measures can be made using probes for corrosion progress and density (Castaneda et al. 2017).

The techniques used to evaluate the metrics discussed here vary depending on the project type, the monitoring budget and the technical abilities of the monitor. Some of the more common tools and techniques are described here; however, the list is far from exhaustive (Yepsen et al. 2016). The simplest approach for measuring distances, areas and volumes is to establish a localised survey grid and to measure distances and elevations with respect to known, fixed points. Although more expensive and requiring more expertise, utilising a survey-grade global positioning system (GPS) can improve both the accuracy (on the order of centimetres, both horizontally and vertically) and the efficiency of data collection compared with simpler approaches. Light detection and ranging (LiDAR), a remote-sensing method, can increase the accuracy and efficiency of surveys even further, but this technology is often out of reach for most ecoengineered shoreline projects due to the expense and expertise required. An emerging approach, which offers many of the advantages of LiDAR at a fraction of the cost, is the utilisation of recreational grade drones and 'structure from motion' techniques. Structure from motion utilises photogrammetric techniques to piece together 3-dimensional information from a series of 2-dimensional photographs (Turner et al. 2016). Some techniques are capable of providing information about slope/inclination, and simple inclinometers can be used to complement low-cost/low-tech techniques.

Simple water-level/wave staffs can be used to estimate water levels and wave heights (Lapann-Johannessen et al. 2015). More advanced techniques include low- and high-frequency pressure gauges, ultrasonic wave/water level gauges and electronic wave/water-level staffs (high frequency is required for wave measurements in shallow water). Current attenuation is probably the most difficult parameter to measure, due to the expense and difficulty involved in obtaining current measurements. On large-scale schemes, satellite imaging can also be used for monitoring the structural integrity of the project (Yepsen et al. 2016).

Ecoengineered shorelines are often designed for a life span of 25, 50 or even 100 years, and thus they require longer periods for success evaluation. Nonetheless, short-term monitoring (1–2 years postdeployment) of key structural performance criteria (such as cracking or corrosion) can provide more immediate measures of success (Thayer et al. 2003). Levels I, II and III describe standard levels of structural inspection and are based on the American Society of Civil Engineers (ASCE) *Waterfront Facilities Inspection and Assessment Manual* (Waterfront Facility Inspection Committee 2015). Level I examination is a visual inspection that does not require any structural components to be cleaned, and so it can be completed most rapidly. Level II examination is focussed on identifying damaged or deteriorated areas that may be hidden by marine organisms or surface materials. Level III examination is more involved and often entails the use of both nondestructive testing (NDT) techniques and partially destructive techniques. This can include extracting material samples (cores) of the concrete or wooden structure for off-site testing or *in situ* surface hardness testing (NYCEDC 2016). For example, the structural performance of bioenhanced concrete pile encasements constructed in Brooklyn Bridge Park to restore the load-bearing capacity of the pier piles, while generating valuable habitat for marine flora and fauna, was monitored 1 and 2 years postdeployment through Level II inspections (Perkol-Finkel & Sella 2015). These findings, as well as the results of the ecological monitoring for the project, were submitted to the New York State Department of Environmental Conservation to validate the structural and ecological performance of the structure. This was required for acceptance of the bioenhanced structure to provide mitigation credits towards the overall project.

As the field of ecoengineering is relatively new and project budgets are often limited after construction, longer-term monitoring data (>5 years postdeployment) are rare. Nonetheless, as risk reduction and engineering performance are key components of many ecoengineered shoreline projects, it is important to conduct such tests and revisit installations several years after deployment. A recent example is the biological and structural monitoring of a bioenhanced breakwater section in Haifa Port, Israel, where Sella and Perkol-Finkel (unpubl. data) revisited the installation 6 years postdeployment. Biological monitoring included on-site visual and photographic surveys, as well as structural monitoring via a combination of visual inspection and core samples for structural integrity of the bioenhanced concrete.

Long-term monitoring plans should also aim to identify and quantify changes in the structural performance due to the increased presence of marine life. As these natural systems develop and their presence increases over time, they will affect the structure's performance and interact with the surrounding environment. For example, marine growth could increase the crest height of a breakwater and further dissipate local wave energy, or alternatively marine growth on a pile encasement could alter flow patterns and change drag forces around the structure (Yacouby-Al et al. 2014).

### *Measuring socioeconomic outcomes*

Few ecoengineered shoreline projects have achieved socioeconomic success, despite the capacity of healthy coastal habitats to provide a plethora of ecosystem services that are valuable to humans (Barbier et al. 2011). For instance, the complex habitat structure provided by vegetated coastal habitats or biogenic reefs creates a nursery habitat for commercially important invertebrate and fish species (Beck et al. 2001, Heck Jr et al. 2003). Shellfish reefs filter nutrients and metals from the water, which can increase water quality (Gifford et al. 2004, 2005, Kellogg et al. 2013, Smyth et al. 2013, Onorevole et al. 2018); similarly, seaweeds can sequester nutrients and heavy metals, as well as carbon (Chung et al. 2011, Henriques et al. 2015, Yang et al. 2015, Krause-Jensen & Duarte 2016). Further, the basis of soft ecoengineering or living shorelines comes from the observation that natural, intact habitats can protect against erosion and flooding (Shepard et al. 2011, Arkema et al. 2013, Temmerman et al. 2013).

There is growing evidence of the efficacy of ecoengineered shorelines in providing and enhancing many of the ecosystem services associated with natural ecosystems (Gittman et al. 2014, 2016, Davis et al. 2015, Onorevole et al. 2018). Nevertheless, their value in providing these services will depend on the identity of the habitat types included in ecoengineered shoreline designs, their density and configuration and the characteristics of the environment in which they are placed (Piehler & Smyth 2011, Smyth et al. 2015). For example, Smyth et al. (2015) found that the relationship between oyster density and denitrification was weakly positive at ambient nitrogen concentrations, but at elevated nitrogen concentrations, it was nonlinear, increasing from low to medium oyster densities but declining at high densities. Overall, it is expected that the ecosystem services provided by an ecoengineered shoreline will increase over time as the habitat becomes established and grows. Even well-established ecoengineered shorelines are unlikely to attain the same level of ecosystem functioning as natural, intact habitats. This is due to trade-offs between engineering, ecological and socioeconomic objectives that result in a design that is suboptimal for ecosystem service provision. Simultaneous monitoring of ecological, engineering and socioeconomic objectives is needed to investigate trade-offs, but it is seldom done.

While there have been attempts to value economically the ecosystem services provided by estuarine and coastal systems (e.g. Costanza et al. 1997, 2014, Barbier et al. 2011), attempts to value the services provided by ecoengineered shorelines holistically have been lacking (Beck et al. 2018, Reguero et al. 2018). Economic valuation involves assigning quantitative values to the goods and services provided by various habitats and is a useful way to compare benefit-cost ratios of management scenarios (Spurgeon 1999). For ecoengineered shorelines, an ultimate economic goal may be that its benefit-cost ratio exceeds that of alternative artificial structures. However, economic valuation can be challenging for ecosystem services because not all of them have a market value. Goods and services with a market value can be evaluated based on revenue increases—for instance, when ecoengineered shorelines increase the production of commercially important seafood species (e.g. Martins et al. 2010), marine-derived pharmaceuticals and raw products, such as firewood. Where there are no markets for services, indirect pricing methods can be used to establish the (revealed) willingness to pay (WTP) or willingness to accept (WTA) compensation for the availability or lack of these services (de Groot et al. 2002).

A variety of indirect methods may be applied to the valuation of ecoengineered shorelines. First, the economic value of shoreline protection may be determined using avoided damages or replacement costs (de Groot et al. 2002, Rao et al. 2015), such as the avoided damage to coastal properties after a storm in areas with an ecoengineered shoreline protecting the coast. This evaluation could be in comparison to a nearby, unprotected shoreline or, alternatively, a nearby artificial structure with a similar exposure (Gittman et al. 2014). The latter contrast enables an analysis of how maintenance and replacement costs following a storm compare between ecoengineered shorelines and artificial structures.

Second, the hedonic pricing model, which works on the premise that the price of a marketed good (e.g. houses) is related to structural, neighbourhood and environmental characteristics, may be applied to ecoengineered shorelines (Landry & Hindsley 2006). Coastal property protected with ecoengineered shorelines may differ in value compared to property with no coastal protection or property protected with hard structures (Landry & Hindsley 2006). House prices are directly related to beach width (Pompe & Rinehart 1994) and other environmental attributes, such as the open/green space provided by wetlands, which can positively influence prices in urban areas (Mahan et al. 2000) and negatively influence them in rural areas (Bin & Polasky 2005). Additionally, house prices are influenced by perceived risk to flooding and erosion (Jin et al. 2015).

A third method for quantifying the value of ecoengineered shorelines is the willingness of a representative sample of individuals to pay for services they provide (de Groot et al. 2002). This can be evaluated in terms of the time and cost that recreational users spend travelling to a site to take advantage of its amenities (Spurgeon 1999). As with the other indirect methods, WTP can be compared between ecoengineered shorelines, shorelines with traditional structures and shorelines without structures. Ideally, WTP may also be compared for a given site before and after ecoengineered shoreline construction.

In addition to such economic valuations, ecoengineered shorelines may be valued in terms of their social benefits and ability to effect policy change. Throughout history, cultures, knowledge systems, religions, heritage values and social interactions have been influenced by the nature of ecosystems (Hassan et al. 2005). Moreover, humans have always shaped the environment to enhance the availability of such services. Ecoengineered shorelines may enable the public to reclaim the water's edge, bringing people back to urban waterfronts (Sairinen & Kumpulainen 2006) for leisure activities and experiences. They can improve shoreline aesthetics, promote public visitation, increase cultural output (Hortig et al. 2001, Reise 2003, Claesson 2011) and be valuable for scientific investigation and environmental education (Krauss et al. 2008, Mitsch et al. 2008). Social impacts can be assessed using a variety of methods, ranging from simple counts of visitation numbers and frequencies and research and education programmes, through to more complex assessments of changing perceptions (Maas & Liket 2011). Questionnaires and participatory mapping of such elements as use values (Brown & Hausner 2017, Strain et al. 2019) are common tools for assessing use and perceptions. Increasingly, technologies such as immersive landscape theatres and virtual reality are also being used to investigate perceptions of aesthetic change (Wang et al. 2013, Miller et al. 2016) and may be suitable for before-and-after assessments.

Policy impacts of ecoengineered shoreline projects take a number of forms (Keck & Sikkink 1998), which makes their measurement challenging. New, highly visible and successful ecoengineered shorelines can provide the first step in influencing policy where ecoengineered shorelines are not currently part of the political agenda. In drawing attention to the utility of ecoengineered shoreline approaches, such projects may persuade governmental or other influential stakeholders to endorse international declarations or conventions, securing procedural change at the domestic and international levels and changes in policy (e.g. changes in legislation or budget allocations). This route could start with the avocation of national or international guidelines for best practices in the construction of shoreline protection schemes.

Procedural changes may include the development of permitting processes or funding schemes that enable the use of and incentivise investment in ecoengineered shorelines for coastal defence. This has the potential to lead to policy changes to support ecoengineered shoreline investments as part of the increased investment in coastal infrastructure. These political effects need to lead to on-the-ground changes in key stakeholders, such as private landholders that are implementing coastal protection works or developers that can declare ecoengineered shorelines as part of the tender (Keck & Sikkink 1998). In the United States, there has been some progress towards investing in living shoreline approaches through policy drivers securing procedural (e.g. green bonds and infrastructure banks used to fund nature-based coastal defence in Massachusetts) and legislative changes (e.g. the Living Shoreline Act in Maryland; Sutton-Grier et al. 2018). There are guides to monitoring and evaluating policy influence (e.g. Reisman et al. 2007, Jones 2011). The method starts with the development of a theory of change (Reisman et al. 2007) that describes a set of activities (e.g. ecoengineered shoreline pilot project), outputs (e.g. design guidelines for ecoengineered shorelines), outcomes (e.g. change to ecological or social system as a result of activity), impacts (i.e. the overall contribution of the outcomes to the goal) and goals (i.e. overall project objective). The outcomes are the target for measuring success, which may be through the impact of research, media uptake, or stakeholder surveys (see Jones 2011).

## *Adaptive management in response to monitoring outcomes*

Assessment of the efficacy of ecoengineered shorelines in meeting objectives, using monitoring and evaluation programmes, is essential to the success of present and future projects. Due to the relative immaturity of the discipline, there is a paucity of data demonstrating how project design and environmental and socioeconomic context influence project success. Such data are critical to informing the design of future ecoengineered shorelines and fine-tuning existing projects to increase their efficacy. Ecoengineering of community structure and ecosystem functioning along urban shorelines is complicated by uncertainties over costs and potential benefits and long-term sustainability (Temmerman et al. 2013), making it difficult for governments to legislate for ecoengineered shorelines. Uncertainty increases over time (Bouma et al. 2014), as natural variability, management objectives and economic constraints can all influence the success of ecoengineering.

Adaptive management is a structured decision-making strategy to govern social-ecological systems that embraces their complexity and uncertainty, providing opportunities for learning and adapting to change (Folke et al. 2005). It rests on the recognition that urban landscapes and seascapes need to be understood and managed as complex, adaptive social-ecological systems and points to the importance of actively managing resilience, here defined as the capacity to persist with functional integrity under changing social and environmental conditions. The feedback between learning and decision-making is a defining feature of adaptive management, with learning contributing to management by helping to inform decision-making and management contributing to learning through interventions that are useful for investigating resource processes and impacts (Williams 2011). Fundamental steps in the process include the articulation of clear objectives (ecological, engineering and socioeconomic), identification of management alternatives, predictions of management consequences, recognition of key uncertainties and quantitative assessment of outcomes.

Interest in and application of adaptive management have grown steadily over the last few decades (Chaffin et al. 2014), and this tool has been recommended as particularly useful in urban ecosystem restoration (Hychka & Druschke 2017) and ecoengineering (Mayer-Pinto et al. 2017). Indeed, the urban setting offers unique opportunities to address environmental issues, while at the same time delivering wide-reaching benefits to the multiple stakeholders and users of marine urban waterfronts. There is also an urgent imperative to create urban infrastructure and environments that are more resilient to climate-related risks. Even though examples of real-scale implementations are limited, scientific knowledge and technologies are being developed to provide adaptive solutions for ecoengineering. Examples include ecosurfaces that can be ecologically retrofitted with further enhancement if monitoring data suggest that the original objectives are not being met (Morris et al. 2018c), optimising the timing and frequency of maintenance interventions to infrastructure by incorporating knowledge of the life histories of species (Airoldi & Bulleri 2011), limiting the social barriers to ecoengineering via better understanding of the social perceptions and expectations through social surveys and interviews (Kienker et al. 2018) and/or providing quantitative data on the cost-effectiveness of various management options (Reguero et al. 2018).

## Case studies and scaling up

As is the case for any significant coastal or urban development, scaling up ecoengineered shorelines at any site should make economic sense—so long as *all* costs and benefits are factored into that calculation, including valuing environmental and societal benefits and the costs of traditional development. As with valuation of environmental assets generally, this is still a new field, and the ecoengineered shoreline concept includes a diversity of approaches and technologies. Thus, it is difficult to make any global statements about the cost-benefit ratio for living shorelines across all possible sites and approaches. However, it is instructive to examine projects where the balance between ecology, engineering and socioeconomic factors has played out with varying degrees of success. Three case studies (in Seattle, the East and Gulf coasts of the United States, and Sydney) are described next, and they represent hard, soft and hybrid designs, respectively. Their implementation and evaluation are also outlined. They cover a range of project types, physical settings, engineering objectives and habitats. Although all the projects are multiobjective in nature, the drivers of each project and the metrics used to evaluate them differ.

### *Case Study 1: Hard ecoengineering: Seattle, Washington*

After a large earthquake in 2001, the Elliott Bay Seawall in Seattle, built between 1916 and 1934, was failing and at risk of collapse in the event of another moderate-sized to large earthquake, posing a public safety hazard. Because of the scale of the city's infrastructure, replacement of the wall had an intense, hard engineering focus. However, the need to replace the failing wall with a structure designed to modern earthquake standards also provided the opportunity to ecologically enhance the heavily modified foreshore areas (Cordell et al. 2017). The adjacent estuarine waters are an important migratory corridor for juvenile Chinook salmon (*Oncorhynchus tshawytscha*), which is listed as threatened under the U.S. Endangered Species Act, and the new structure was designed to provide ecological complexity and a well-lit environment conducive to migration, foraging and refuge for salmon and other species, thus incorporating ecological components into traditional poured concrete walls (Munsch et al. 2017a).

Key to the success of this project was social buy-in, as habitat improvement for juvenile salmonids has great cultural, recreational and economic importance in the region. The Seattle waterfront is also a vibrant hub of the city, including many business, tourism, recreation, transportation, shipping and port activities. This social aspect is considerable, especially given the public funding involved on the project and the sense of place that a broad array of user groups depend upon for a connection to the water.

The design and implementation of the Seattle seawall habitat enhancements developed during a decade of studying habitat enhancements for juvenile salmon in Elliott Bay. Information gathered from testing seawall design options with experimental panels that had enhanced texture and slope and overhead light penetrating surfaces (LPSs) allowed for proof of concept at the metre scale that was incorporated into the final seawall design at the kilometre scale (Cordell et al. 2017, Figure 7). Additional components incorporated into the final seawall design came from the success of a project at the nearby Olympic Sculpture Park, which at the 100-m scale created an intertidal bench and a pocket beach (Toft et al. 2013). Data gathered from these smaller-scale projects allowed for scaling-up of ecoengineered shoreline implementation (see the section entitled 'Process of scaling-up successful projects', later in this review, for more discussion).

The final design for Seattle's seawall included: (1) placement of intertidal benches (stone-filled marine mattresses) and creation of an artificial beach, designed to mimic a shallow-water, low-gradient habitat; (2) incorporation of crevices and ledges into the seawall face, with the goal of increasing complexity and enhancing production of invertebrates and algae and (3) addition of LPSs (glass blocks) in the cantilevered sidewalk above the seawall, intended to provide a light corridor to

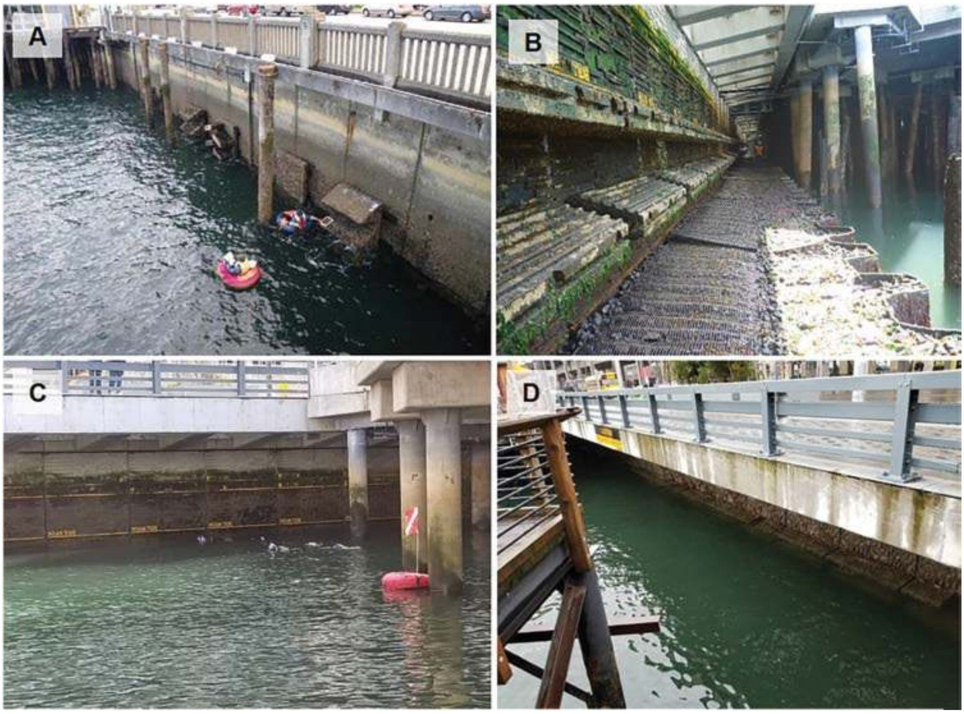

**Figure 7** (A) Monitoring algae and invertebrates on experimental habitat test panels on the Seattle seawall before reconstruction; (B) habitat enhancements incorporated into the new seawall, including projections and texturing on the wall and marine mattress benches; (C) snorkelling to survey fish at a mean tide when the bench is inundated; (D) view from an adjacent pier showing a cantilevered sidewalk with light penetrating surfaces consisting of glass blocks.

enhance juvenile salmon outmigration and feeding and to potentially improve productivity under piers (Figure 7).

There is an associated time scale with such a large, hard ecoengineering scheme, highlighting that implementation of ecoengineering projects is not just a matter of spatial scale. Experimental seawall panels were deployed in 2008 and monitored for 4 years, experimental LPSs were deployed in 2013 and monitored for 1 year, the Olympic Sculpture Park was created in 2007 and monitored both before and after enhancement from 2005 to 2011 and the first phase of the Seattle seawall rebuild was completed in 2017, with the second phase yet to be initiated. The experimental stages were needed to ensure the ecoengineered habitats met ecological (i.e. enhanced salmon habitat), engineering (i.e. no compromise to structural stability of seawall) and socioeconomic (i.e. community acceptance) outcomes.

### *Case Study 2: Soft ecoengineering: living shorelines on the East and Gulf coasts*

The ‘living shorelines’ approach emerged in the 1970s through many examples of bank erosion control and shoreline stabilisation using saltmarsh plantings in Chesapeake Bay (Garbisch & Garbisch 1994). This technique is regarded as successful at providing shoreline protection that is adaptive to sea level rise, in addition to cobenefits such as habitat and food resources for fish and other wildlife or improved water quality (Craft et al. 1999). However, it was recognised that the creation or restoration of saltmarsh alone only provided sufficient coastal protection in low-energy environments. This resulted in the development of the 'hybrid living shoreline' approach, which incorporated varying degrees of hard structure to reduce energy and allow living shorelines to be applied in a wider range of environmental conditions (Garbisch & Garbisch 1994; Figure 8).

Key to the living shorelines technique is that construction must conserve, create or restore natural shoreline functions, in addition to providing coastal defence. In order to retain ecological functioning, strong emphasis is placed on maintaining the connection between terrestrial and marine systems (Bilkovic et al. 2017), a link that is severed by traditional artificial defences, such as bulkheads. In Chesapeake Bay, rock sills are widely used in combination with saltmarsh plantings for additional coastal protection (Figure 8). However, although such a design is regarded as successful for coastal defence, the addition of these hard structures in a soft-bottomed environment results in ecological trade-offs through enhancing filter feeders that colonise the sill at the expense of deposit-feeding infauna, with potential consequences for nutrient cycling (Bilkovic & Mitchell 2013).

There is increasing interest in using oyster-reef living shorelines for coastal protection. In response to the loss of native oyster populations (*Crassostrea virginica*; Beck et al. 2011), restoration techniques, originally applied for fishery enhancement and increasing oyster populations, have been adopted with the primary objective of other services, such as coastal defence and enhancement of water quality. Oysters need a hard substratum for settlement, which led to a diversity of oyster-reef structures being developed. These include loose shell, bagged shell and oyster mats and a number of precast concrete or steel structures (e.g. Oyster Castles®, Ready Reef™, Reefball™, ReefBLK℠, ShoreJAX™, Oysterbreak™ and Wave Attenuating Units®) (Hernandez et al. 2018). Unfortunately there is a lack of scientific or engineering data to support the use of one approach over another. This

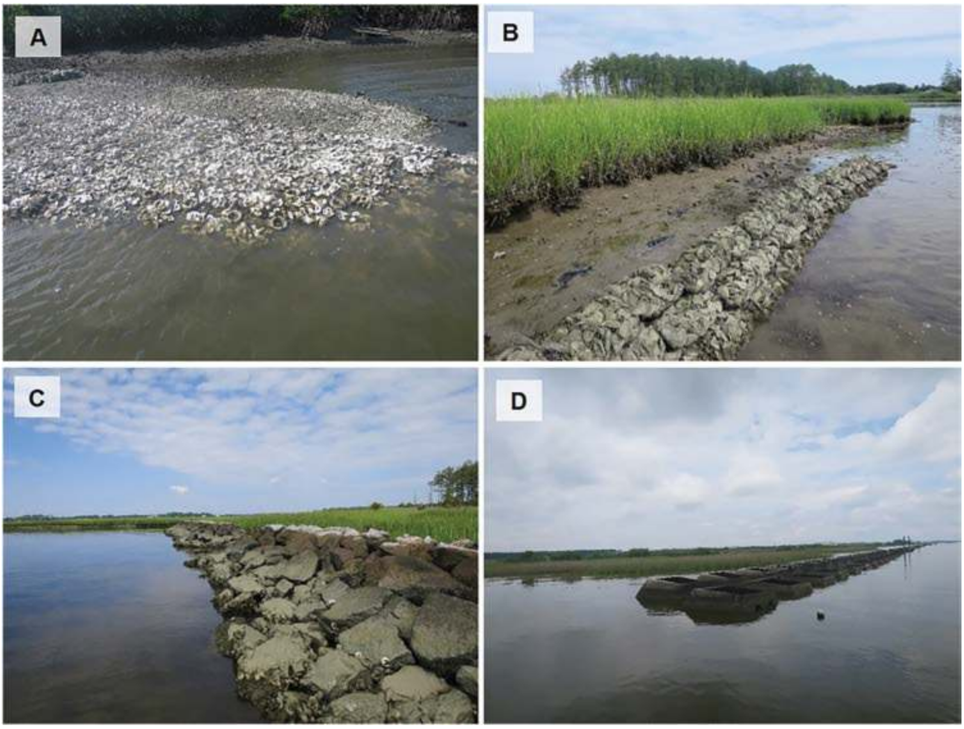

**Figure 8** Examples of living shorelines projects along the East and Gulf coasts, United States. (A) Restored oyster reefs using oyster mats; (B) bagged shell oyster reef living shorelines with saltmarsh; (C) rock sill with saltmarsh and (D) wave-attenuating units with saltmarsh.

has prevented the development of universal design guidelines appropriate for living shorelines, which has limited their wider application (Narayan et al. 2016, Morris et al. 2018b). Recent studies have tried to gauge public perceptions of living shorelines to help inform management of coastal hazards (Gray et al. 2017). Future research to optimise living shoreline design for coastal protection using the minimum amount of hard material or optimising the placement of hard material for species colonisation (e.g. oysters) will further enhance their ability to provide multiple functions and services.

### *Case Study 3: Hybrid ecoengineering: Sydney*

The emphasis of many foreshore projects is to construct efficiently engineered armouring structures that protect infrastructure, but these frequently have negative impacts on the intertidal environment (Bulleri & Chapman 2010, Ma et al. 2014, Firth et al. 2016b). Projects within the Georges River estuary, including Carss Bush Park Seawall in New South Wales, Australia, have examined foreshore infrastructure design from both scientific and engineering approaches, to not only develop an ecologically responsive foreshore design, but also ensure the successful construction and long-term structural integrity of projects (Figure 9).

The Carss Bush Park project aimed to design and construct infrastructure that allows natural coastal processes, such as tidal ingress, to influence the foreshore. Numerous habitat structures were introduced into what was a highly degraded environment. These included rock pools at varying intertidal levels, longer foreshore slopes and crevices, mudflats for mangrove and benthic organisms, a 'naturalised' creek line and endangered saltmarsh benches (Heath 2017, Strain et al. 2018a). The objective of creating such a diverse intertidal zone is to connect the foreshore with previously

**Figure 9** Carss Bush Park Foreshore before construction (A and C) and after construction, including saltmarsh (B) and intertidal habitats (D).

developed ecoengineering projects and natural foreshore areas in order to expand the connectivity of estuarine/marine ecosystems within the Georges River (Strain et al. 2018a).

The design and construction of this project have led to improvements in the natural fish and seaweed biodiversity in the artificial rock pools (Heath and Moody 2013, Bugnot et al. 2018, Strain et al. 2018b), while also increasing the social values of the Georges River foreshore (Heath, pers. obs.). Combined with other successful ecoengineering projects along the Georges River, a cumulative improvement in habitat availability has been achieved. The project also incorporates adaptability to future climate change, ensuring its aesthetics and ecological benefits are not affected by sea level rise.

The project design reflected its heavy recreational use and the highly urbanised nature of the location by encouraging the reconnection of the community to the foreshore and Kogarah Bay. This was critical to ensuring the local community's support (Heath, pers. obs.). Landscaping was important in making the ecoengineered shorelines scheme aesthetically pleasing to a broad sector of the community and to promote usability.

The designs also provided environmental benefits, not only with the introduction of intertidal habitats, but with the utilisation of existing seawall sections to create large saltmarsh benches (Heath 2017, Strain et al. 2018a). The use of sections of existing infrastructure in stage 1 reduced the volume of material leaving the site, while also creating the tidal barrier necessary for the saltmarsh to thrive. Critical to the design was ensuring that the saltmarsh was sporadically inundated with saline water during king (spring)–tide events but not affected by all tidal events. By keeping sections of the existing seawall in place, it was not necessary to build new structures or reclaim land from Kogarah Bay as alternative designs required.

While restoration of the Georges River intertidal foreshore to natural conditions is not achievable due to its highly urbanised state (Alyazichi et al. 2015), the foreshore ecoengineering projects outlined previously show how ecological enhancement along a highly urbanised shoreline can be achieved. These ecoengineering projects protect public land from flooding and erosion, improve native biodiversity (Heath & Moody 2013, Bugnot et al. 2018, Strain et al. 2018b) and habitat connectivity (Strain et al. 2018a), with the potential to restore other ecosystem services (e.g. nutrient cycling and carbon sequestration), while developing relationships with the community through educational and recreational engagement (Heath 2017).

## *Process of scaling up successful projects*

To date, most hard and soft ecoengineered shorelines have focussed on rehabilitating or adding a single type of habitat at the site scale (Scyphers et al. 2011, Davis et al. 2015, Strain et al. 2018b). Enhancements to seawalls are typically at the scale of metres or less (Strain et al. 2018b), while living shorelines are typically constructed at scales of less than a hectare (e.g. Scyphers et al. 2011, Davis et al. 2015). In contrast, the scale at which marine ecosystems are degraded by shoreline development is typically in the order of 10–1 million ha (Edwards & Gomez 2007). To benefit large-scale processes and a broad range of species (Bishop et al. 2017), the scale and complexity of ecoengineered shorelines, as for restoration projects more generally, need to be much larger than is commonly considered today (Naveh 1994, Hobbs & Norton 1996, Soulé & Terborgh 1999).

The scaling-up of ecoengineered shorelines may, conceivably, be achieved in several ways. First, beneficial approaches piloted at small scales may simply be applied to larger areas and more sites. For example, the 1.2-km Elliott Bay seawall (in Seattle; see the section entitled 'Case studies and scaling up', earlier in this review) includes textured and sloped surfaces that were initially experimented on at the metre scale (Cordell et al. 2017). Similarly, the approximately 1-km-long New York Living breakwaters project, due to be built following the 'Rebuild by Design' competition (http://www.rebuildbydesign.org/our-work/all-proposals/winning-projects/ny-living-breakwaters), incorporates features such as bioenhanced concrete blocks and tide-pool armouring units that have previously been deployed at demonstration scales (Perkol-Finkel & Sella 2015, Sella & Perkol-Finkel 2015).

It should be noted, however, that because many ecological processes are highly scale dependent (Turner 1989, Wiens 1989, Levin 1992), failure of a particular approach to enhance a desired function at a small scale does not necessarily preclude its efficacy at a larger scale. Hence, interventions need to be designed with the scale of the targeted ecological processes in mind.

There are several reasons why ecoengineered shorelines of larger areas may be expected to yield greater ecological benefits than their smaller counterparts. Ecological theory suggests that the number of species supported by an ecosystem increases with habitat area (see the section entitled 'Links to theoretical and community ecology', earlier in this review; Arrhenius 1921, Gleason 1922). Projects of larger scale are also more likely to incorporate the heterogeneity required to facilitate ecological processes critical to ecosystem function (MacArthur & Wilson 1967, Rosenzweig 1995, Tews et al. 2004). Small areas of habitat are generally considered to be more susceptible to disturbances, as the probability that an entire habitat patch is affected decreases with increasing size (MacArthur & Wilson 1967, Meurant 2012).

Additionally, related to living shoreline projects, wave attenuation increases with distance inside habitat patches, although the magnitude of such protection is the greatest in the first few metres, with the benefits of additional width much diminished (Peterson et al. 2004, Bradley & Houser 2009, Manca et al. 2012). To date, these predictions remain largely untested and the question of how benefits of ecoengineering scale with extent remains a key unknown. Some functions may be expected to scale linearly with areal extent; for example, water filtering capacity may increase linearly with the density or biomass of filter-feeders supported by the ecoengineered shoreline. In contrast, biodiversity, and the ecosystem functions that depend on it, may display a nonlinear pattern of increase to a maximum value, beyond which further increases in area have no effect (Yachi & Loreau 1999, Thébault & Loreau 2006). Monitoring common sets of variables across projects of smaller and larger area would enable future meta-analyses that address relationships between ecoengineered shoreline extent and community structure and function. Furthermore, studies that monitor the benefits of ecoengineered shorelines also require the costs (e.g. facilitation of nonnative species) to determine the optimal area of interventions. Modelling studies that include data on the dispersal capabilities of target and nontarget pest species might assist in identifying the locations at which ecoengineering initiatives may be applied to the greatest benefit (Bishop et al. 2017).

Second, scaling-up may involve increasing the complexity of projects to include multiple habitats. Ecoengineered shoreline projects that include multiple components will increase not only alpha-, but also beta-diversity, and hence ecosystem function (see the section entitled 'Links to theoretical and community ecology', earlier in this review). Many marine species require multiple habitat types in which to complete their life history (Thorpe 1988, Krumme 2009, Sheaves 2009). Hence, building ecoengineered shorelines of a single habitat type may fail to provide the resources needed for species across their life history (Bishop et al. 2017, Morris et al. 2018c). However, whether the inclusion of multiple habitats in ecoengineered shorelines is desirable or not will depend on the identity (i.e. native versus nonnative) and function of the species they support, goals of the intervention (e.g. bolstering the population of a species that depends on multiple habitat types increasing ecosystem function in a severely degraded urban environment, restoring natural habitat configurations) and, potentially, also whether the ecoengineered shoreline is present in an area that historically supported multiple or a single habitat type.

Both the Seattle waterfront (see the section entitled 'Case studies and scaling up') and the New York Living Breakwaters projects exemplify how multiple habitat types may be included in hard-engineering projects. The breakwaters include 'Reef Streets', which add habitat for marine life, as well as intertidal crests, which further increase the complexity and diversity of available habitats. Bioenhancing concrete units are embedded into the breakwaters' fabric, providing targeted enhancement measures. These include multifunction armour units and tide-pools, which by their surface complexity and macro design increase the available surface area to be utilised as habitat and enhance the ecosystem services provided by structure (http://www.rebuildbydesign.org/our-work/all-proposals/winning-projects/ny-living-breakwaters). The GreenShores project in Pensacola, Florida, which created more than 12 ha of oyster reefs, saltmarsh and seagrass habitat along 3.2 km of urban waterfront, is an example of a living shorelines project targeting multiple habitat types (DEP 2012). The sizes of, distances between and identity of habitat patches should be informed by knowledge of the seascape ecology of target species and communities. In addition to the ecological benefits of large-scale projects, there may be significant socioeconomic benefits. As the scale of ecoengineered shoreline projects increases and they are progressively more grounded in science, an economy of scale is expected to emerge. At present, however, the evidence for economies of scale in restoration projects is weak due to their almost universally small scale (Bayraktarov et al. 2016). In some instances, there may even be an inverse economy of scale caused by large-scale projects proceeding without adequate systems knowledge (Turner & Boyer 1997). Additionally, large-scale projects may generate more media and public interest, which may in turn lead to greater opportunities for cofunding and investment.

Several core elements typify projects that have successfully scaled up. These include vision, prior knowledge, technological capacity, financial viability and social licence (Menz et al. 2013). Manning et al. (2006) identify the preemptive constraint of vision as a major impediment to scaling up restoration more generally and suggest stretch goals and backcasting as two potential approaches to overcome this. *Stretch goals* are ambitious, long-term goals that can be used to inspire creativity and innovation (Manning et al. 2006). *Backcasting* involves visualising a desired end point and then retrospectively developing a pathway to that point (Manning et al. 2006). Prior knowledge and technological capacity are commonly built through small-scale pilot studies. For example, the Seattle Waterfront project (see the section entitled 'Case studies and scaling up', earlier in this review), which, among other goals, sought to provide a suitable habitat for juvenile salmon foraging and migration, was designed following years of studying the mechanisms by which urban structures affect juvenile salmon (e.g. Munsch et al. 2014, 2015, 2017a). It built on small-scale demonstration projects, experimenting on the efficacy of proposed interventions at mitigating these impacts (Goff 2010, Toft et al. 2013).

The division of large-scale projects into multiple stages can also assist in ensuring their success. Lessons from earlier stages can be used to inform later stages using an adaptive management approach (see the section entitled 'Adaptive management in response to monitoring outcomes', earlier in this review). Such an approach was used in the Pensacola Green Shores project (DEP 2012).

Worthwhile questions include: What happens if there is failure at the experimental stage? Does it feed back in a different way in the process of scaling-up? Arguably, success and failure are opposite ends of the spectrum of learning that an experiment can provide (Firth et al. 2016a), and both can be used to inform implementation at a larger scale. Instrumental to this line of thought is representing failure in a way that acknowledges the causal mechanisms and generates reasons with an eye to future applications. Social licence is built through engaging stakeholders in all steps of the project, from the planning to the implementation and ongoing monitoring and evaluation phases.

The availability of funding can be a major impediment to large-scale restoration projects (Manning et al. 2006). As previously noted, most research on the ecoengineered shoreline approach has occurred in developed countries (in particular Australia, European countries and the United States). Nevertheless, investment in restoration projects in developing countries can achieve up to 30 times more unit area of habitat than developed countries on a dollar-for-dollar basis, or up to 200 times more unit area when accounting for the local value of the U.S. dollar in developing nations (Bayraktarov et al. 2016). Data on the success of ecoengineered shorelines are urgently needed from developing countries to inform the development of large-scale ecoengineering in these areas.

## Concluding comments

In summary, while the protection of all-natural ecosystems remains the ideal conservation strategy, the presence of urban and novel artificial habitats should not be ignored. Given their ubiquity in many countries and increasing prevalence in general, there is a real imperative to compensate for the negative impacts that seawalls and other artificial coastal defences have on shorelines. Examples of ecological engineering efforts around the world have shown that this is possible, but in general, few projects have taken an interdisciplinary approach to setting goals, monitoring and evaluation. This means that there is a paucity of information on the multifunctionality of various ecoengineered shoreline approaches, inhibiting the development of benefits-cost analyses and/or guidelines that could be adopted at national or international scales.

Most of the projects to date have been done on a small scale and in isolation. The adoption of more standardised monitoring techniques that included ecological, engineering and socioeconomic evaluation would enable a more holistic approach to the evaluation and wider implementation of the ecoengineered shoreline approach globally. Proven techniques are urgently needed so that governments, policymakers and international organisations seeking sustainable development goals related to coastlines and oceans have the capacity to develop guidelines, policies and regulations that promote ecoengineered shoreline strategies, where all-natural solutions are not feasible. Greater investment in design, experimentation and development of ecoengineered shorelines could have multiple benefits in improving habitat, biodiversity, water quality and reductions in seaborne waste, resulting in improved access to and appreciation of waterfronts. Doing so would move current options beyond a prime focus on structures with industrial or defensive functions and to a holistic approach with environmental goals with multiple applications at a range of scales.

More examples of successful ecoengineered shorelines are required to demonstrate their potential to provide coastal protection, enhance biodiversity and ecosystem services and increase people's enjoyment. In order to change the way that future coastal defences look and function, ecoengineered shoreline designs generated through interdisciplinary collaborations (e.g. between architects, engineers, ecologists, social scientists and coastal managers) need to be encouraged. Nonetheless, it is important to note that, as in most large-scale engineered intervention, the success of a project at one locality (e.g. Seattle Seawall Project) does not necessarily mean that the same approach will be successful in others (i.e. one size is unlikely to fit all), due to differences in government policies, ecological goals, site-specific environmental conditions, financial support and other socioeconomic factors. As the success of projects from engineering, ecological and socioeconomic standpoints is demonstrated by a sound evidence base, stakeholders will become more invested in ecoengineered shoreline development, initiating the support of government and the development of relevant policy.

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# CONSEQUENCES OF ANTHROPOGENIC CHANGES IN THE SENSORY LANDSCAPE OF MARINE ANIMALS

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## Abstract

Human activities are altering a wide range of key marine cues at local and global scales, and it is important to know how animals may respond. Species survival and performance depend on the ability of individuals to successfully extract and interpret information from their environment about preferred abiotic conditions and the presence of prey, predators, competitors, mates and suitable habitats. Such information is made available via a wide range of abiotic and biotic cues that can be detected by organisms through various sensory modalities. Global anthropogenic changes, however, are rapidly altering the sensory landscape ('cuescape') and behaviour of animals by modifying the production, transmission and interpretation of critical natural cues, as well as introducing novel anthropogenic cues. To date, most studies have focussed on how animals respond to such changes rather than investigating how the cues themselves are changing. Because the responses that individuals show ultimately depend on factors affecting both the generation and reception of cues, better integration is needed to understand how these factors ultimately affect individual performance. This review provides a holistic assessment of how multiple cues (e.g. sounds, visual cues, chemicals, salinity, temperature and electromagnetism) are being altered at different spatial and temporal scales in marine habitats. Natural cuescapes are being modified by humans and novel anthropogenic cues are being introduced into the ocean, both of which can directly and indirectly alter the diversity and strength of natural cues. Examples are provided of how species might respond to such changes, focussing on what coping and adaptation mechanisms are available for species to persist in a future ocean. While 'sensory generalist' species may prevail in marine environments with diminishing or masked natural cues, some 'sensory specialists' might sustain themselves via sensory compensation, behavioural plasticity or avoidance of detrimental cues in the short term, or via genetic adaptation in the longer term. Due to the rapid loss of natural cuescapes, alternative research agendas are needed to monitor and measure multicue changes throughout the oceans. Together with mechanistic and field studies of animal responses, such research can inform management by identifying the species most at risk and the areas that may be suitable for cuescape preservation.

## Introduction

The marine environment produces a complex mixture of thousands of chemical, auditory, visual and other physicochemical cues, and marine organisms have adapted to isolate and distinguish relevant information against a noisy background of multiple cues (Kingsford et al. 2002). These cues are critical for vital processes, such as finding food and habitats, pelagic orientation of larvae, avoiding predators and locating mates (Myrberg & Fuiman 2002, Hay 2009, Pohnert et al. 2007). Behaviours ranging from microscale habitat selection to navigation across ocean basins rely on individuals receiving and correctly interpreting relevant environmental cues. However, anthropogenic activities are having an increasing impact on the production, transmission and composition of natural environmental cues at all spatial scales. When this interference with natural cues affects critical processes, such as mating, competition, foraging and predator avoidance, there are consequences for individual performance, and ultimately population viability (Schmidt et al. 2010, Wong & Candolin 2015). To date, most research effort related to cue alteration in the sea has focussed on how animals might respond (e.g. Tuomainen & Candolin 2011, Radford et al. 2014, Clements & Hunt 2015, Nagelkerken & Munday 2016, Cattano et al. 2018, Goldenberg et al. 2018, Kelley et al. 2018), rather than how the multitude of cues themselves are changing. In particular, the impacts of artificial auditory cues (e.g. due to increased shipping, noise from marine construction and sonar and seismic surveys) on animal behaviour has received considerable attention (Slabbekoorn et al. 2010, Francis & Barber 2013, Swaddle et al. 2015, Shannon et al. 2016), with much emphasis on altered communication in cetaceans (Au et al. 2000). Increases of artificial chemical pollutants in the marine environment (Bernhardt et al. 2017) and their impacts on animal behaviour and populations have also been widely investigated (Zala & Penn 2004, Lurling & Scheffer 2007). However, the modification of natural cues by humans is much more ubiquitous and pervasive than artificial sounds and chemical pollution. Besides the introduction of many artificial cues into the marine environment, humans are also directly and indirectly altering the diversity and strength of natural cues. In fact, there are very few natural cues that are not being modified by humans in some way.

With the rapid global changes that are occurring in marine environments (e.g. warming, ocean acidification or marine pollution) there is the need for a more complete and integrated understanding of how humans are altering multiple, interacting environmental cues that influence the performance and persistence of marine species. This can improve our understanding of how populations, communities and ecosystems are being affected by human impacts at local and global scales, and also provide potential opportunities for mitigation of human activities to help preserve natural cuescapes. Ecosystems as we know them today will probably no longer smell, look, feel or sound the same to animals in the near future, but we still have a limited understanding of how humans are modifying natural cuescapes. Perhaps most important, we need to establish if marine species have sufficient phenotypic plasticity or genetic adaptive potential to adjust to rapidly changing cuescapes.

This review identifies the major changing environmental cues in the sea and focuses on how abiotic and biotic cues are modified via (1) alterations to naturally produced cues (acoustic, visual, thermal, chemical and salinity cues); (2) the introduction of novel anthropogenic cues (acoustic, light, and electromagnetic) that can mask or alter natural cues and (3) altered transmission of environmental cues due to direct or indirect human disturbances (e.g. climate change, ocean acidification, eutrophication, or habitat degradation). Physical cues (sound, light, temperature, and electromagnetism) are considered first, followed by chemical cues and salinity. The effects of chemical pollutants have been reviewed elsewhere (e.g. Zala & Penn 2004, Lurling & Scheffer 2007) and are not dealt with here. After characterising changing environmental cues, the various ways in which animals may cope with or adapt to altered cues are assessed, and the necessary research to better understand the consequences of altered sensory cues for marine animal populations and communities is identified. Finally, we evaluate the implications of changing cuescapes for conservation management. Overall, this review provides a novel overview and synthesis of the wholesale changes that are occurring to biologically relevant cues in the marine environment, as well as the prospects for adaptation by species and mitigation by humans.

## Physics of cues and sensory modalities

Each sensory modality of marine animals is influenced by a unique set of physical and chemical characteristics of the environment, the fundamentals of which are broadly understood for the marine environment (Apel 1987). At a basic level, a sensory modality involves the transmission of a signal from a source to a receiver—the sensory organs of an organism. For modalities operating over a distance (e.g. hearing and vision) signal strength typically decreases with distance between the source and receiver, though sometimes in a nonuniform and nonlinear fashion. Anthropogenic factors can influence the magnitude, type and patterns of cue sources, as well as the transmission efficiency, thereby influencing detection range (Table 1). For contact sensory modalities (e.g. temperature and salinity), the organism senses the surrounding seawater environmental conditions and (for motile organisms) their spatial gradients. A range of excellent books have been published that provide extensive detailed information on sensing in aquatic animals, such as Atema (1988), Lenz et al. (1997), Collin & Marshall (2003), von der Emde et al. (2004) and Brown et al. (2007). Only a very brief overview of the basic physics of common environmental cues is given here, and attention is drawn to some of the sensory modalities used by marine animals to intercept these cues.

### *Sound*

Sound generated by vibrations at a source is transmitted through seawater at a speed of about 1500 m/s as pressure waves with alternating zones of compression and rarefaction. Relevant frequencies range from very low (as low as a few hertz) to high frequencies (greater than 25 kHz). Propagation losses occur simply due to spreading of sound waves away from the source, as well as frequency-dependent attenuation processes, such as absorption by seawater and the seabed, and scattering by suspended particles, organisms, the sea surface and seabed. High-frequencies are attenuated rapidly and propagate only a relatively short distance (kilometres), while long-distance propagation (>1000 km) is possible for low frequencies (Apel 1987, Wilcock et al. 2014). Acoustic energy loss at low frequencies is pH dependent because of chemical relaxation of dissolved ions (borate-boric acid and magnesium carbonate). Addition of atmospheric $CO_2$ to seawater, and the resulting increase in hydrogen ion concentration and reduction in pH, lead to reduced sound attenuation (Brewer et al. 1995). Sound waves undergo refraction, or wave bending, due to vertical and horizontal variations in sound speed that depend on temperature, salinity and pressure. Long-distance propagation involves sound ray paths with multiple reflections from the sea-surface or ray trapping in the deep sound channel (Apel 1987).

Sound reception is found in most marine taxa and occurs via diverse organs, including ears with an outer tympanum in mammals, an inner ear with otoliths in fishes (connected to the swim bladder in some species), a variety of cutaneous receptors and statoliths in invertebrates, lateral line systems with neuromasts in fishes and other means of sensing and focussing vibrations, including the jaw in dolphins and other odontocetes (Au & Hastings 2008, Mooney et al. 2012, Ladich & Schulz-Mirbach 2016). A comprehensive overview of hearing capabilities and underlying mechanisms in fishes can be found in Webb et al. (2008).

### *Light*

Natural light (photons) in the sea comes ultimately either from sunlight (including moonlight) or from *in situ* fluorescence, bioluminescence, or Raman scattering. Photons are both absorbed and reflected by organisms and the seabed, resulting in visual cues. Seawater is relatively transparent in visible bands of the electromagnetic spectrum (400–760 nm). Transmission is modulated by attenuation processes (absorption and scattering) that are strongly wavelength dependent; more rapid attenuation occurs for ultraviolet wavelengths and longer visible wavelengths (yellow, orange and red) relative to shortwave visible bands (violet, blue and green), leading to a shift in light spectra

**Table 1** Overview of how different cues are altered in their production, transmission and reception due to local and global stressors, with some examples of their effects on ecological processes.

| Cue type | Local/global change stressor | Type of change | Cue |  |  | Ecological processes affected (examples) | Key references |
|---|---|---|---|---|---|---|---|
|  |  |  | Production | Transmission | Reception |  |  |
| Sound | Noise pollution | Physical | ✓ |  | ✓ | Foraging, predator avoidance, settlement, metabolism, metamorphosis, migration, survival, communication, mating | Popper & Hastings (2009), Slabbekoorn et al. (2010), Fewtrell & McCauley (2012), Shannon et al. (2016) |
|  | Habitat degradation | Biological | ✓ |  | ✓ | Settlement, metamorphosis | Rossi et al. (2017), Gordon et al. (2018) |
|  | Overfishing | Biological | ✓ |  |  | Settlement | Coquereau et al. (2017), Bertucci et al. (2016) |
|  | Ocean acidification | Biological | ✓ |  | ✓ | Settlement | Rossi et al. (2016a,b) |
|  | Ocean acidification | Chemical |  | ✓ |  | Settlement, migration, communication | Ilyina et al. (2010) |
|  | Weather changes | Physical | ✓ |  |  | Migration | Knutson et al. (2010) |
|  | Ocean warming | Physical |  | ✓ |  | Settlement | Wilcock et al. (2014) |
| Visual | Light pollution | Physical | ✓ |  |  | Foraging, migration, spawning, settlement, survival | Aubrecht et al. (2008), Davies et al. (2014) |
|  | Eutrophication | Physical |  | ✓ |  | Foraging, predator avoidance, mating | Jarvenpaa & Lindstrom (2004), Wong et al. (2007) |
|  | Sedimentation | Physical |  | ✓ |  | Foraging, predator avoidance, mating, settlement, colour vision | Leahy et al. (2011), O'Connor et al. (2016) |
|  | Weather changes | Physical | ✓ | ✓ |  | Foraging, growth, survival, predator avoidance | Suursaar et al. (2012), Filippino et al. (2017) |
|  | Habitat degradation | Biological | ✓ | ✓ | ✓ | Foraging, predator avoidance, settlement, competition, timing of plankton blooms | Obryk et al. (2016), Boström-Einarsson et al. (2018) |
|  | Ocean warming | Biological | ✓ | ✓ |  | Settlement, stress levels, foraging | McCormick et al. (2010), Norin et al. (2018) |
|  | Ocean acidification | Chemical |  |  | ✓ | Predator avoidance | Chung et al. (2014) |

*(Continued)*

**Table 1 (Continued)** Overview of how different cues are altered in their production, transmission and reception due to local and global stressors, with some examples of their effects on ecological processes

| | | | Cue | | | | |
|---|---|---|---|---|---|---|---|
| Cue type | Local/global change stressor | Type of change | Production | Transmission | Reception | Ecological processes affected (examples) | Key references |
| Temperature | Ocean warming | Physical | ✓ | | ✓ | Activity rhythms, migration, smolting, reproduction, sound production | Visser & Both (2005), Pankhurst & Munday (2011) |
| | Ocean acidification | Chemical | | | ✓ | Settlement | Pistevos et al. (2017b) |
| | Heat pollution | Physical | ✓ | | | Migration, activity rhythms | David et al. (2007) |
| Electromagnetic | Ocean infrastructure | Physical | ✓ | | | Migration, reproduction, survival, growth | Öhman et al. (2007), Gill et al. (2012) |
| Chemical | Eutrophication | Chemical/ biological | ✓ | ✓ | | Mating | Mesquita et al. (2003), Fisher et al. (2006) |
| | Ocean acidification | Chemical/ biological | ✓ | ✓ | ✓ | Predator avoidance, movement, mating, foraging, reproduction, settlement, homing | Chivers et al. (2014a), Roggatz et al. (2016)<br>Williams et al. (2019) |
| | UV light | Physical | | ✓ | | Predator avoidance | Chivers et al. (2014b) |
| | Habitat degradation | Biological | ✓ | ✓ | ✓ | Predator avoidance, settlement, homing | McCormick & Lönnstedt (2016), McCormick et al. (2017) |
| | Sedimentation | Physical | | ✓ | | Conspecific recognition | Lecchini et al. (2017) |
| | Acid rain | Chemical | | ✓ | ✓ | Predator avoidance | Brown et al. (2002), Hardege et al. (2011) |
| | Plastic pollution | Chemical | ✓ | | | Foraging, survival, growth | Savoca et al. (2016), Mattsson et al. (2017) |
| | Ocean warming | Chemical | ✓ | ✓ | ✓ | Mating | Lienart et al. (2016) |
| Salinity | River regulation | Chemical | ✓ | ✓ | | Settlement | Vorosmarty & Sahagian (2000), Meynecke et al. (2006) |
| | Ocean acidification | Chemical | | | ✓ | Settlement | Pistevos et al. (2017b) |
| | Ocean warming | Physical | ✓ | | | Plankton blooms, settlement, activity rhythms | Reebs (2002), Payne et al. (2013) |

and monochromatic light with increasing depth (Mobley 1994). Irradiance declines approximately exponentially with depth, with visible light levels dropping to about 1% of surface values by 10 m (red) to 100 m (blue). In productive environments, biological materials (e.g. chlorophyll, chromophoric dissolved organic carbon, and detrital particles) contribute substantially to additional light attenuation (absorption and scattering); suspended sediments (turbidity) can also sharply reduce water clarity in coastal zones and bottom layers. Sufficient light exists in the mesopelagic zone (about 100–1000 m) for vision. Underwater visibility depends on target size, contrast and transparency, as well as light attenuation, with typical sighting depths of metres to many tens of metres depending on conditions (Johnsen 2014).

Light receptors in marine animals vary from photosensitive dermal spots in some invertebrates to well-developed photoreceptors and complex eyes in crustaceans, cephalopods and vertebrates (Nicol 1960). Many invertebrates have photoreceptors in the integument that respond to variation in illumination but cannot resolve form. Crustaceans have compound eyes comprising many subunits, each acting as a directional photoreceptor. By contrast, cephalopods and vertebrates have eyes with a lens capable of focussing an image on the retina. The information about the light environment that can be gathered by eyes includes intensity, temporal change, spatial distribution, spectral distribution and polarization pattern (Cronin 1988). Mantis shrimps (Stomatopoda) have one of the most complex (compound) eyes, with up to 12 different photoreceptors and a capacity to see ultraviolet, visible and polarized light (Thoen et al. 2014). Lythgoe (1980) provides more details on vision in fishes.

### *Temperature*

Seawater temperatures change relatively slowly in response to external heating and cooling because of the large heat capacity of seawater, requiring about 4000 J to raise the temperature of 1 kg of seawater by 1 °C. Variations in surface water temperature occur from net air–sea heat exchange associated with solar heating and longwave, sensible and latent cooling. Large seasonal temperature ranges of >10 °C occur in surface waters in temperate regions, with smaller ranges in equatorial and polar environments. Similar to salinity, subsurface temperature generally changes more slowly with time, except near oscillating fronts, and is controlled by ocean circulation and turbulent mixing.

Relatively little is known about the mechanisms of thermosensing in marine organisms. Various marine animals can respond to very small changes (as low as 0.03 °C) in temperature (Murray 1971). Thermosensing can be accomplished using the ampullae of Lorenzini in rays and sharks (Akoev 1990) and via cutaneous nerves in bony fishes (Murray 1971). For some fish species, it has been postulated that photoreceptors can also act as thermoreceptors (Nisembaum et al. 2015).

### *Electromagnetism*

Electrical currents from electrons moving in submarine cables (e.g. electricity or telecommunication) generate low-frequency electromagnetic fields that can penetrate the surrounding water column over relatively short distances of $10^0$–$10^2$ m (Öhman et al. 2007, Boehlert & Gill 2010). Alternating current (AC) creates both electrical and magnetic fields, while direct current (DC) creates only magnetic fields. Induced magnetic field anomalies overlie the local geomagnetic field (Kavet et al. 2016), and additional electrical field effects can arise from ocean currents and organisms moving through AC-cable generated magnetic fields.

The detection of weak electric fields in marine animals can occur through the induction of electrical signals in specialized receptor cells (Collins 2010). Electroreceptors in the epithelium of some fishes can provide information about the intensity, spatial configuration and the source direction of weak electric fields (Collins 2010). Elasmobranchs have specialized organs with jelly-filled ampullary electroreceptors that are particularly sensitive to the detection of weak electromagnetic fields and use them for orientation and prey detection (Kalmijn 1982, Josberger et al. 2016).

### *Chemicals*

Chemical cues are transmitted by the physical transport of specific molecules from a source to a sense organ. Many organisms can smell a wide range of organic and inorganic compounds, typically of relatively small molecular size, and cues may consist of a few distinct compounds, a family of related compounds or a broad chemical mix. The physical transport of chemical signals in the sea is scale dependent and is modulated by advective flow, turbulence and molecular diffusion at very small scales—the Batchelor microscale of tens to hundreds of microns (Mann & Lazier 2006, Glover et al. 2011). Chemical signal strength decreases away from a source because of turbulent physical dispersion and possibly chemical degradation or alteration of cue molecules. Spectra of marine chemical concentrations (and also salinity and temperature) tend to be red-shifted, with the largest variations at long wavelengths (and time scales), affecting the time/space scales over which organisms can detect changes in the environment. Time scales for turbulent horizontal diffusion increase with distance, varying from seconds to minutes at organism scales to hours to days (for distances <1 km) to days to weeks (ocean submesoscale about 1–10 km) (Okubo 1971), and turbulent stirring can result in highly patchy and rapidly changing tracer patterns on submesoscale and smaller scales.

Chemoreceptors may be located anywhere on the bodies of marine animals. Moreover, they may be distributed widely over the body, or localized in certain tissues or organs (e.g. rhinophores, osphradium, and antennae), including the nose, which can range from an open pit to a complex, enclosed structure with nares to focus water flow over a dense field of olfactory receptors (Laverack 1988). Olfactory organs typically work either in pulsed sniffs and flicks, or continuously in laminar flow (Atema 1988). Taste receptors form an additional component of the chemoreceptory apparatus of many marine species (Caprio 1988).

### *Salinity*

Salinity, a measure of the amount of dissolved salts in seawater, primarily reflects the concentrations of conservative, inorganic ions (e.g. $Na^+$, $Mg^{2+}$, $Cl^-$), and absolute salinity is reported in grams per kilogram. The proportion of the major ions is effectively constant in almost all ocean environments, and modern techniques quantify salinity from seawater conductivity, the ability of seawater to conduct an electrical current that scales with the amount of charged ions. Ocean salinity typically ranges from 34 to 37 on the conductivity-based Practical Salinity Scale, with substantially lower values in polar regions and coastal areas near river mouths. Surface salinity varies in response to net precipitation minus evaporation, while subsurface values reflect advection and both vertical and horizontal turbulent mixing.

Changes in salinity are detected by marine organisms through a variety of molecular and ionic osmoreceptors (Ortiz 2001, Fiol & Kültz 2007). Internally, changes in the extracellular osmolarity are detected by osmoreceptors and baroreceptors in the brain, vasculature, renal system and other tissues (Seale et al. 2012).

## Alterations to cuescapes

### *Global change and ocean soundscapes*

Oceans and coastal seas are filled with natural abiotic sounds created by various physical phenomena (e.g. waves, rain, wind, and storms) and earthquakes (geophony), as well as natural biotic sounds created by soniferous animals (biophony). Biological sounds are particularly diverse and complex and emitted across a wide range of frequencies (15 Hz–200 kHz; Hildebrand 2009, Wilcock et al. 2014). Many marine organisms, ranging in size from small shrimp to large whales, actively make sounds to help find mates, fend off predators, catch prey or defend their territory (Swaddle et al. 2015), or passively create sounds as a result of their biological activities (Radford et al. 2008, Lillis et al. 2014). Because sound travels five times faster and over much greater distances in water

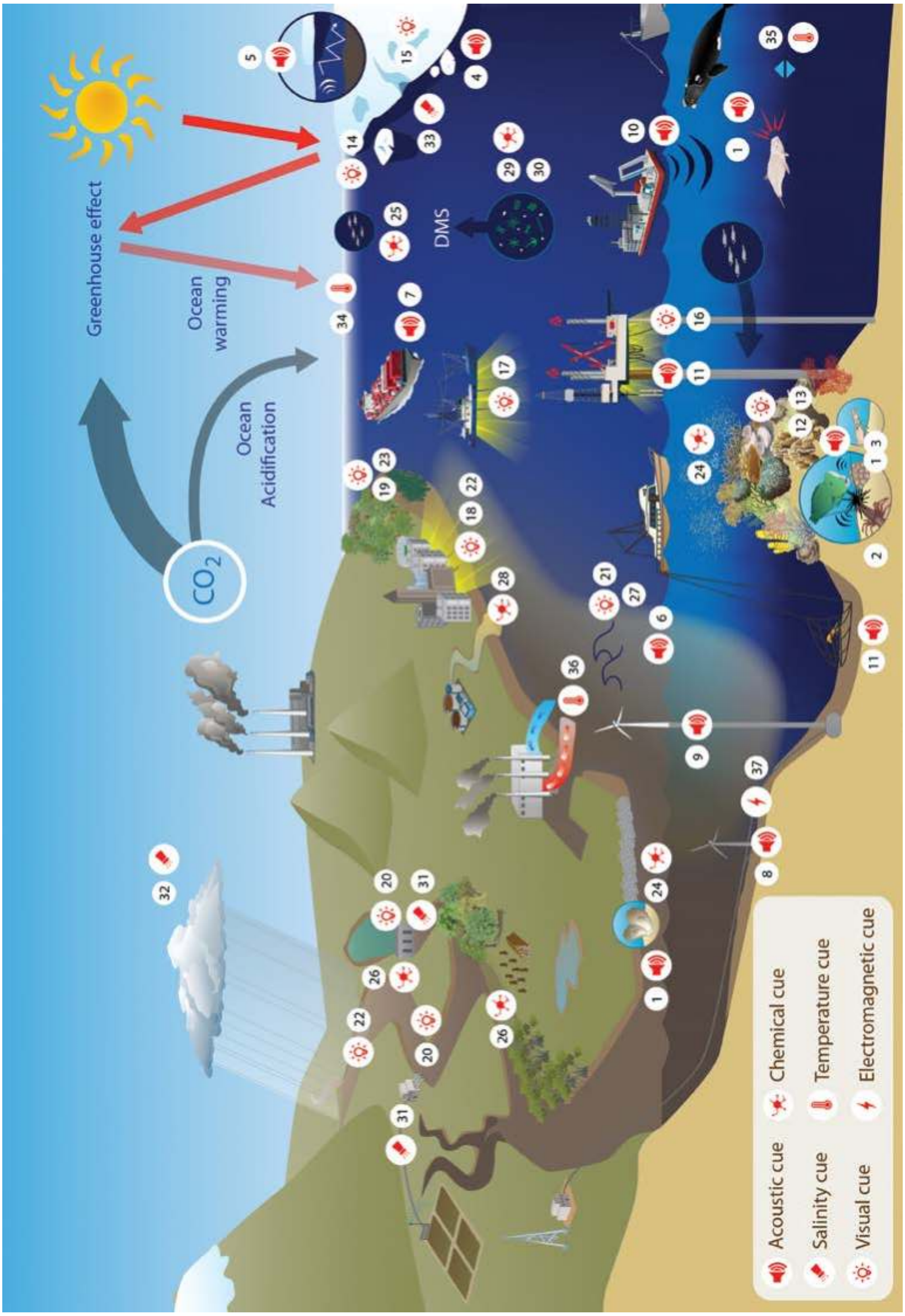
Greenhouse effect
Ocean warming
Ocean Acidification
$CO_2$
DMS
Acoustic cue
Salinity cue
Visual cue
Chemical cue
Temperature cue
Electromagnetic cue

Figure 1

**Figure 1 (Continued)** Overview of major natural and anthropogenic cues that are being altered by local, regional, and global anthropogenic stressors. *Sound cues*: 1. diversity of soniferous species, 2. predators controlling the abundance of soniferous species, 3. behaviour of soniferous species, 4. sound of melting sea-ice/icebergs, 5. sound transmission under sea-ice, 6. intensity of wave sounds, 7. vessel engines, 8. underwater turbines, 9. offshore windfarms, 10. sonar and seismic surveys, 11. anthropogenic vibrations. *Visual cues*: 12. background coloration and patterning of habitats, 13. habitat structural complexity, 14. thickness of sea-ice, 15. degree of snow cover on sea-ice, 16. gas flaring and illumination by offshore (oil) platforms, 17. commercial nocturnal (squid) fishing, 18. lighting of coastline urban developments, 19. coastline vegetation that filters terrestrial sediment and nutrient runoff, 20. artificial regulation of river and sediment flows, 21. coastal wave action and turbidity, 22. terrestrial run off from altered rainfall, 23. wave energy reduction by offshore habitats. *Chemical cues*: 24. chemical cues from habitats and species, 25. chemical cues from introduced and range-extending species, 26. land-based chemical cues delivered by river flow and terrestrial run off, 27. sedimentation effects on chemical cue sensing, 28. eutrophication effects on chemical cues, 29. dimethylsulfide (DMS) production by phytoplankton, 30. microplastics mimicking DMS cues. *Salinity cues*: 31. river regulation change, 32. changing rainfall patterns, 33. ice melt. *Temperature cues*: 34. (seasonal) temperature cues, 35. depth of thermoclines, 36. cooling water from plants. *Electromagnetic cues*: 37. submarine electricity/ telecommunication cables. Illustration by Animate Your Science (www.animate-science.com). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

than in air, it acts as a reliable orientation cue and enables long-distance communication. The importance of biotic sounds has been best studied in relation to communication and echolocation in cetaceans (Au et al. 2000, Miller et al. 2004, Janik et al. 2006), as well as being an orientation cue for the pelagic larvae of many reef-associated animals such as fishes, corals, crustaceans and molluscs (Simpson et al. 2005, Montgomery et al. 2006, Vermeij et al. 2010, Huijbers et al. 2012, Lillis et al. 2014).

### *Modification of natural soundscapes*

Humans are altering many aspects of natural abiotic and biotic marine soundscapes, through both direct and indirect perturbation (see Figure 1 and Table 1). Abiotic sound cues are being altered through climate change and ocean acidification. Changing weather patterns will lead to altered storm dynamics and to changes in wave, ocean current and precipitation patterns (Knutson et al. 2010), altering the geophony of the oceans. In polar regions, climate change is altering sea-ice habitat, with a reduction of total iceberg and floating sea-ice volumes and enhanced rates of summer sea-ice melting (Post et al. 2013). Because ice melting creates loud sounds that are emitted over thousands of kilometres, smaller volumes of ice that melt at faster rates potentially lead to shorter but stronger seasonal sound peaks (Matsumoto et al. 2014).

Biotic sound cues are being altered through direct impacts, such as overfishing of sound-producing species, which is increasingly leading to a silencing of the ocean (comparable to a 'silent spring' due to loss of bird life from potential overuse of pesticides; Carson 1962). Soniferous animals such as whales have been harvested, in some cases to near-extinction (Roman & Palumbi 2003, Lotze et al. 2006). Likewise, many sound-producing coastal species such as sea urchins and fishes (e.g. grunters, croakers, foraging parrotfishes) are heavily targeted by commercial and subsistence fisheries in some locations (Hughes 1994, Andrew et al. 2002) or have suffered from massive die-offs (e.g. *Diadema antillarum* urchins; Lessios et al. 1984). Natural oyster reefs have been severely degraded globally by overexploitation (Kirby 2004); yet, when intact, these systems create important soundscapes that facilitate settlement by oyster larvae and other animals (Lillis et al. 2014). Overexploitation of species can also cause increases in biological sounds, such as in cases where urchin predators (e.g. rock lobsters or monacanthids) are overfished, leading to urchin population explosions (e.g. *Centrostephanus rodgersii*, Ling et al. 2009). Feeding urchins create a clearly distinguishable and loud chorus at night when they scrape algae off hard substratum (Rossi et al. 2016b), and these sounds are amplified through their egg-shaped skeletons (Radford et al. 2008).

Biotic cues are also being altered through the degradation and modification of living marine habitats. Mass coral bleaching due to warming ocean temperatures, for example, can instigate phase shifts from coral-dominated to macro-algal dominated habitats, resulting in losses of reef-building organisms (Anthony et al. 2011, Nagelkerken & Connell 2015). This diminishes habitat quality and availability for soniferous animals (e.g. snapping shrimp) and consequently production of biological sounds (Rossi et al. 2017, Gordon et al. 2018). Other major causes of habitat degradation result from destructive fishing practices, coastal pollution, eutrophication and sedimentation (Lotze et al. 2006). For example, habitat loss in kelp forests and seagrass beds due to nutrient pollution and ocean acidification decreases the overall biological sound levels of these habitats, largely attributable to lower sound production by snapping shrimp (Alpheidae; Rossi et al. 2017). Consequently, larval fish are no longer attracted to the sounds of these habitats (Rossi et al. 2016a). Likewise, fished and degraded reefs have quieter and more depauperate soundscapes (Piercy et al. 2014, Coquereau et al. 2017), resulting in decreased settlement of larval fishes (Gordon et al. 2018).

Biotic cues are further being altered through behavioural changes in soniferous animals. Increased temperature can alter sound production and reception in fishes (Ladich 2018). Elevated $CO_2$ interferes with brain neurotransmitter function in various fishes and invertebrates, leading to a range of altered or reversed behavioural responses (Heuer & Grosell 2014, Watson et al. 2014). This includes altered and reduced sound production by noisy snapping shrimp (Rossi et al. 2016b), which are amongst the most common sound producers in coastal areas worldwide. Nevertheless, we currently know almost nothing about how ocean acidification alters sounds production by marine animals (Nagelkerken & Munday 2016).

### *Sound pollution*

Aside from altering natural soundscapes, humans are also introducing novel anthropogenic sounds to the sea (anthrophony). With the rapidly increasing industrialization of the oceans, biological sounds are being masked by unnatural abiotic sounds from ocean vessels, in-water turbines for renewable energy, offshore wind farms, sonars for military applications, ocean exploration, commercial fishing, pile driving near harbours and coastal developments and seismic surveys for oil and gas exploration (Hildebrand 2009, Wilcock et al. 2014). While most of these sounds are produced around urbanized coastal areas, ships with increasingly powerful engines are creating sound pollution globally (Malakoff 2010). Ship noise can travel over tens of kilometres and can reduce the range of sound detection of whale calls by other whales from about 1000 km to just 10 km (Slabbekoorn et al. 2010). Anthropogenic sounds can mask biological sounds used for animal communication and navigation (Slabbekoorn et al. 2010), alter a wide range of behaviours (Table 1), increase mortality rates (McCauley et al. 2017) and may even cause physical damage to sensory systems and other body parts (McCauley et al. 2003, Shannon et al. 2016).

In addition to the introduction of anthropogenic noise, human activities increase vibrations within the seabed as a result of bottom trawling (Berghahn et al. 1995), dredging (Robinson et al. 2011), pile-driving (Tsouvalas & Metrikine 2014), oil and gas drilling (Greene 1987) and transport of oil in submarine pipelines (Olunloyo et al. 2007). Some benthic fishes and a range of benthic invertebrates that are associated with soft substrata, such as molluscs and lobsters (Roberts et al. 2015, Miller et al. 2016), show altered behaviour or increased trauma or mortality in response to anthropogenic vibrations transmitted through the substratum (Roberts & Elliott 2017), but the longer-term effects on individuals and populations are still unknown. In scallops (Bivalvia, Pectinidae), for example, behavioural alterations include a reduction in normal behaviours (e.g. valve closure response and speed of recessing into the sediment) and an increase in nonclassical behaviours (e.g. a flinch response to air gun noise) (Day et al. 2017).

### *Alterations to sound transmission*

Besides changes to sound production, human perturbations alter underwater sound transmission (Table 1). Reduced ocean pH and increased seawater temperature both reduce noise absorption, leading to better and longer-distance noise transmission (Ilyina et al. 2010, Wilcock et al. 2014). However, the increased physical transmission of sounds due to higher temperature and lower pH (Udovydchenkov et al. 2010, Reeder & Chiu 2010) has a relatively small effect compared to anthropogenic noise sources and cannot sufficiently buffer the loss of natural sound production due to human and climate change effects on marine habitats and species. Furthermore, sound transmission is altered in the presence of sea-ice cover (Alexander et al. 2013), and hence increased presence or absence of ice cover due to climate change can alter polar underwater soundscapes.

## *Global change and visual seascapes*

Light and water clarity play a key role in the ecology of most shallow-water marine animals. In clear-water habitats, animals depend heavily on vision to perceive their environment. The ability to see and not be seen affects important processes, such as predator avoidance, foraging, competition and sheltering (Utne-Palm 2002). However, human perturbations are altering the production, reception and transmission of important visual cues (see Figure 1 and Table 1).

### *Modification of natural visual seascapes*

Abiotic visual cues are being altered in some locations, with changes to the light environment experienced by marine species. For example, the polar light environment is changing markedly due to the reduced extent and thickness of sea ice, less snow cover on sea ice and earlier sea-ice melt in summer (Clark et al. 2013). Light acts as an important seasonal cue, affecting such activities as the timing of plankton blooms and vertical migration by zooplankton (Berge et al. 2009). Earlier light availability and altered vertical mixing regimes during spring potentially lead to mismatches between phytoplankton and zooplankton blooms (Montes-Hugo et al. 2009, Obryk et al. 2016), can alter polar food webs and vertical carbon fluxes and can modify entire biological communities via light competition (Post et al. 2013, Clark et al. 2013). Receding sea ice can also enhance vision-based foraging in fish due to increased light availability (Langbehn & Varpe 2017). Furthermore, altered ultraviolet B exposure due to atmospheric changes related to climate change can increase predator inspection behaviour by fish (e.g. three-spined sticklebacks, *Gasterosteus aculeatus*; Vitt et al. 2017).

Biotic visual cues are being altered due to habitat loss, as well as indirect climate change effects. These perturbations can alter the visual patterning and cues of seascapes, with consequences for its inhabitants. For example, coral bleaching has been intensifying (Donner et al. 2005, Hughes et al. 2017), with coral reefs experiencing a reduction in their architectural complexity worldwide (Alvarez-Filip et al. 2009). Such changes to habitat coloration, structural complexity and surface area modify the visual perception of animals, including the visibility of prey to their predators and vice versa. This can result, for example, in higher stress levels in fish associated with bleached host anemones (e.g. anemone fish, *Amphiprion chrysopterus*; Norin et al. 2018), and riskier behaviour and higher mortality of fish on bleached or dead corals (e.g. damselfish, Pomacentridae, McCormick et al. 2010, Lönnstedt et al. 2014, Boström-Einarsson et al. 2018). Furthermore, dead or bleached corals provide less effective visual and spectral cues for settling fish and coral larvae than live corals (Feary et al. 2007, Foster & Gilmour 2016), while reduced coloration of degraded reefs diminishes the effectiveness of camouflage of prey species against complex backgrounds (Marshall et al. 2003). Moreover, visual habitat selection by juvenile fish can depend on the presence and size of other individuals and whether they belong to the same or other species (e.g. snappers, *Lutjanus fulviflamma*; Igulu et al. 2011); hence, modification of species community structure due to fishing might affect settlement patterns and habitat preferences of early-stage marine species.

### *Artificial light pollution*

Comparable to anthropogenic sounds, humans are also polluting the oceans with abiotic visual cues such as artificial light, which can mask or alter the natural underwater light environment.

Offshore fishing vessels (particularly squid fisheries, which use strong lights as attractants), oil platforms (which use artificial lighting, as well as gas flares) and coastal development (particularly along beaches, coastal suburbs and harbours) emit large amounts of artificial light, which is even visible from space at night (Aubrecht et al. 2008). This can alter the communication, reproduction, recruitment, migration and foraging actions of some marine animals in the immediate vicinity and enhance mortality rates by increased visibility to nocturnal predators (Davies et al. 2014). Artificial light can also mask natural light cues, such as moonlight, potentially disrupting animal migrations. The best-studied case of the latter is the attraction to artificial beach light by hatching sea turtles that normally orient towards moonlight reflected from the sea surface (Tuxbury & Salmon 2005).

### Alterations to light transmission

Humans are affecting the transmission and spectral composition of natural visual cues by altering habitats that maintain high water clarity and by exacerbating the influx of terrestrial materials that reduce water clarity. Riparian vegetation and coastal vegetation such as mangroves, saltmarshes and seagrasses stabilize terrigenous sediments and take up allochthonous nutrients (Gillis et al. 2014), but these habitats have suffered substantial losses in cover globally (Lotze et al. 2006). Owing to changes in land use (i.e. urbanization, forestry, agriculture, river regulation, deforestation, and mining) and weather patterns, increasing loads of sediment, nutrients and particulate organic matter are being released into coastal areas via rivers, artificial channels, stormwater runoff, groundwater discharge and coastal erosion (Howarth et al. 2000, McCulloch et al. 2003). Increased concentrations of particulate and dissolved matter also alter the light environment by reducing visibility and increasing the scattering of natural light, whereas eutrophication leads to plankton blooms that significantly decrease water clarity. Such changes minimize the transmission of relevant visual cues and can affect a range of behaviours such as foraging (e.g. tropical damselfish; Johansen & Jones 2013), activity levels (damselfish; Leahy et al. 2011), habitat choice (damselfish; O'Connor et al. 2016), breeding coloration (three-spined sticklebacks; Wong et al. 2007) and mate selection (Seehausen et al. 1997; e.g. gobies, *Pomatoschistus minutus*; Jarvenpaa & Lindstrom 2004).

Climate change alters weather patterns, leading to increased storm frequency, storm severity and precipitation in some regions, including elevated frequency of extreme events (Knutson et al. 2010, Donat et al. 2016). Resulting changes in water motion increase sediment resuspension, while increased rain in urbanized coastal areas and greater areas of impervious surfaces (e.g. streets, car parks and other paved areas) can increase direct runoff rates and river sediment loads into the sea. Likewise, sea level rise and loss of shallow reefs due to climate change lead to reduced coastal protection by reefs and increased coastal erosion and sediment resuspension (Gillis et al. 2014, Saunders et al. 2014). On the other hand, some human activities reduce sediment fluxes to the coast via reduced river flow to estuaries (e.g. due to dams, river water extraction for irrigation; Syvitski et al. 2005), while the same is likely to happen at locations that are forecast to receive less precipitation due to climate change. The effects of these changes in turbidity on animal behaviour are almost completely unknown and undocumented.

## Global change and temperature cues

### Alterations in phenology

Seasonal changes in water temperature act as a strong natural abiotic cue for many biological processes (see Figure 1 and Table 1), including timing and magnitude of spawning (Pankhurst & Munday 2011; e.g. salmon in freshwater; Otero et al. 2014), smolting (salmon in freshwater; Björnsson et al. 2011) and activity rhythm (fishes in general; Reebs 2002). With the oceans warming due to climate change (Roemmich et al. 2012), threshold temperature cues will occur earlier during the spring season (as well as later during autumn), changing the onset and duration of migration and spawning (Philippart et al. 2003). Changes to the seasonal timing of temperature thresholds may also cause a mismatch with other coupled cues, such as light. For example, an altered photoperiod–temperature coupling can affect the timing and rate of reproduction in polychaete worms (Lawrence & Soame 2009). Additionally, climate change can cause predator-prey mismatches in cases where predators and prey respond to different environmental cues (Edwards & Richardson 2004, Visser & Both 2005). For example, spawning of mollusc larvae may occur earlier in the season due to climate change, but phytoplankton blooms are limited by spring light intensity, and hence a mismatch occurs between spawning of larvae and their food availability (Philippart et al. 2003). Temperature can also act as a cue for timing of feeding, with higher temperatures causing a switch from daytime to nighttime feeding in fish (e.g. salmon parr, *Salmo salar*; Fraser et al. 1993). Changes to other physical characteristics of seawater can further alter behavioural interactions of animals towards temperature change. For example, ocean acidification can alter the response towards temperature cues in larval fish (e.g. marine barramundi; Pistevos et al. 2017b).

### *Alterations in ocean stratification*

Ocean surface warming and polar freshening will tend to increase vertical stratification and reduce surface mixed-layer depths in most locations over seasonal time scales (Bopp et al. 2013) and thus modify the location, timing and water depth of thermoclines (Boyd et al. 2008), affecting feeding behaviour. For example, the presence and location of a thermocline can act as a foraging cue for marine birds, as it is indicative of enhanced feeding opportunities (Pelletier et al. 2012).

### *Point-source warming of water bodies*

Humans are also directly elevating water temperatures at very local scales via the release of heated water used for cooling purposes in (nuclear) power plants and desalination plants (Raptis et al. 2016, Ma et al. 2017). Due to the large amounts of cooling water needed, these plants are often located near rivers, estuaries or coastal seas. Continuous outputs of hot water can mask the local seasonal water temperature fluctuations (Miri & Chouikhi 2005) that act as natural phenological cues for species in these particular locations (e.g. copepods; David et al. 2007).

## *Humans and electromagnetic cues*

Electromagnetic fields can act as abiotic navigational cues for marine animals. Several marine taxa, such as some bony fishes (e.g. salmon and eels; Putman et al. 2013, Cresci et al. 2017), elasmobranch fishes (Kalmijn 1982), invertebrates (e.g. lobsters; Lohmann 1985), reptiles (e.g. turtles; Lohmann & Lohmann 1996) and mammals (e.g. whales; Walker et al. 1992) can sense the Earth's geomagnetic field. It has been demonstrated that at least some of them can use this information for long-distance navigation in the ocean (Wiltschko & Wiltschko 2005, Bottesch et al. 2016). With the growing pressure to replace fossil fuels with renewable sources of energy, the development of large offshore wind farms or tidal turbines is rapidly increasing (Figure 1). The electricity they generate is transported to shore via long submarine cables that create localized artificial electromagnetic fields—a phenomenon that is also observed with long-distance submarine telecommunication cables (Öhman et al. 2007). Artificial electromagnetic fields can affect animal behaviour and physiology within the vicinity of these structures (Öhman et al. 2007, Gill et al. 2012). Electrosensitive species can either be attracted or repelled by such fields, depending on their strength (Gill 2005). For example, swimming speed was reduced during the long-distance migration of European eels (*Anguilla anguilla*) as they passed over a high-voltage submarine cable (Westerberg & Lagenfelt 2008).

## *Global change and chemical cuescapes*

Chemical cues are ubiquitous in the marine environment, and most aquatic species rely on these info-chemicals to inform themselves of their surroundings. These cues can indicate the presence and quality of food, predators, hosts, competitors, conspecifics and habitat (Hay 2009). They are also crucial to major life history events in many marine species, such as adult migrations to spawning sites (Scholz et al. 1976) and larval navigation and orientation to juvenile habitats (Leis et al. 2011, Igulu et al. 2013). Alterations to chemical cues, therefore, can have serious consequences for a range of key ecological processes, such as recruitment, survival, reproduction and predation (Lurling & Scheffer 2007). Humans are modifying the production of natural chemical cues, as well as altering their persistence, composition and transmission and also introducing novel chemical cues into the ocean (see Figure 1 and Table 1).

### *Modification of natural chemical cuescapes*

Biotic chemical cues are naturally produced by many habitats and their associated biological communities, but humans are altering marine habitats directly via habitat destruction and indirectly via climate change (Sunday et al. 2017). These stressors alter species compositions and drive regime shifts that create environments that smell different than undisturbed habitats. For example, ocean warming and acidification reduce the abundance and alter the biochemistry of calcareous crustose algae (Nagelkerken & Connell 2015, Webster et al. 2011, 2013), which deliver the principal chemical cues for settlement of coral larvae that sustain new coral-reef growth. Anthropogenically degraded reefs smell different than healthy reefs, and their chemical cues are dispersed over shorter distances (Lecchini et al. 2014), resulting in lower attractiveness to fish and coral larvae, potentially reducing species population replenishment via reduced settlement (Dixson et al. 2014). However, the effects may be species specific. For example, O'Leary et al. (2017) found no difference in settlement by temperate abalone larvae (*Haliotis rufescens*) on crustose algae (*Peyssonnelia* spp.) that had been exposed to reduced pH for several months. Furthermore, the larvae of some reef species use chemical cues of coastal plants to locate settlement sites on reefs (e.g. jellyfish, *Cassiopea xamachana*; Fleck & Fitt 1999; anemone fish, *Amphiprion percula*; Dixson et al. 2008; grunts, *Haemulon flavolineatum*; Huijbers et al. 2008), and coastal deforestation will diminish the strength of such cues. Besides directly modifying the abundance and community structure of benthic ecosystems, climate change can indirectly alter benthic vegetation—and hence the chemical cues they emit—either by changing the metabolites they produce or changing the behaviour of herbivorous animals. For example, elevated $CO_2$ affects the weeding behaviour by herbivorous damselfish, *Parma alboscapularis* (which act as ecosystem engineers), leading to changes in benthic algal communities (Ferreira et al. 2018).

Further, humans are extracting large numbers of fishery species from the oceans, leading to alterations in their abundance, and therefore also the aroma of natural seawater. For example, oyster reefs provide indirect chemical habitat cues that attract predators to reef-associated prey (e.g. clam prey and crab predators; Wilson & Weissburg 2013), but oyster reefs are degraded and overfished across most of their biogeographic distribution (Kirby 2004). Climate change is prompting species range shifts, resulting in the occurrence of new species from lower latitudes in subtropical, temperate and polar regions (Poloczanska et al. 2013). For example, temperature-driven range extensions of coral reef herbivores lead to the overgrazing of macroalgae in some temperate systems, causing altered community structures of benthic vegetation (Verges et al. 2014). Alien species are increasing due to introductions (Hooper et al. 2005), with further spread facilitated by climate change (Walther et al. 2009, Raitsos et al. 2010). Such large alterations to species' community structures by the introduction of new species are likely to lead to novel or altered chemical cuescapes.

### *Introduction of allochthonous chemical cues*

Regulation of river flows, altered land use and changing weather patterns are causing increasing volumes of abiotic and biotic chemicals of terrestrial origin to be released into coastal seas (Howarth et al. 2000, McCulloch et al. 2003, Davis et al. 2015). Introduction of foreign biotic cues via coastal eutrophication is a major global contributor in urbanized areas. For example, sewage effluents and agricultural runoff can disrupt chemical communication between males and females and affect fish mating (Fisher et al. 2006).

Similarly, increased sedimentation can lead to a loss of attraction to conspecific chemical cues (e.g. in shrimp, *Stenopus hispidus*, and damselfish, *Chromis viridis*; Lecchini et al. 2017). Many diadromous species use or imprint on chemical cues from estuaries to locate suitable recruitment of spawning areas, with salmon as a classic example (Scholz et al. 1976). Salmon (*Oncorhynchus* spp.) seem to use magnetism to navigate in the open ocean (Putman et al. 2013), but once in the vicinity of coastlines, they switch to olfactory cues to locate their natal streams. Alterations of riparian habitats and flow regimes are very likely to alter the olfactory cues from these rivers that guide individuals upstream (Leonard et al. 2012). Juvenile salmon can also suffer from olfactory impairment due to small changes in pH of freshwater from acid rainfall (Leduc et al. 2009), while ocean acidification can reduce the sensitivity of salmon to chemical cues that are used for avoiding predators and homing to natal streams (Ou et al. 2015, Williams et al. 2019). Clearly, any disruption to the long-distance navigational and migration abilities of salmon and other diadromous species will have consequences for their population viability.

### *Alterations to chemical cue transmission*

Anthropogenic changes to the marine environment not only alter the production, but also the transmission, composition and persistence of biotic signalling cues in the ocean (Table 1). Conspecific alarm cues, for example, are key info-chemicals that allow species to learn how to distinguish predators from nonpredators and therefore are directly linked to individual survival and species population dynamics (Ferrari et al. 2010). Elevated seawater temperature (Lienart et al. 2016), ocean acidification (Chivers et al. 2014a), acid rain (Brown et al. 2002), increased ultraviolet radiation (Chivers et al. 2014b) and habitat degradation (McCormick & Lönnstedt 2016) can all affect the integrity, persistence and efficacy of these alarm cues. For example, fishes on dead corals (e.g. damselfish, McCormick et al. 2017) suffer greater mortality than on live corals because the efficacy of alarm cues is reduced in degraded habitats. Pheromones are the key info-chemicals that are used for mating but are altered by low pH (Hardege et al. 2011) and by humic acids that are commonly found in eutrophic waters (Mesquita et al. 2003). Peptides are one of the most important classes of signalling molecules, used for a range of activities like foraging, reproduction, settlement and homing, but they have impaired functionality at low pH due to changes in their overall charge and structure (Roggatz et al. 2016). Finally, dimethyl sulphide (DMS) is a common and key info-chemical used by seabirds (Nevitt & Haberman 2003), penguins (Wright et al. 2011) and whale sharks (Dove 2015) to locate areas with high food abundance in the open ocean at spatial scales of metres to thousands of kilometres (Hay 2009). Ocean acidification reduces the production of this important chemical cue (Nagelkerken & Connell 2015), although eutrophication can offset this reduction in coastal waters (Gypens & Borges 2014). Microplastic concentrations are rapidly increasing in the ocean (Wright et al. 2013, Law & Thompson 2014), and they emit DMS-like cues that lead to enhanced plastic ingestion by seabirds (Savoca et al. 2016); this can cause behavioural disorders in fish (Mattsson et al. 2017) and invertebrates (Seuront 2018).

## *Global change and salinity cues*

Salinity gradients can act as important abiotic cues for marine larvae to locate coasts, estuaries and rivers, especially for diadromous species (Kingsford et al. 2002, Goldstein & Butler 2009, Serrano et al. 2010). Climate change is forecast to result in more variable precipitation patterns, as well as overall increases or decreases (depending on location and season) in total annual precipitation (Zhang et al. 2007), with direct consequences for estuarine and near-shore seawater salinity (Durack et al. 2012) through altered runoff, flooding and river flow regimes (Figure 1). Such changes in freshwater loads, fluxes and salinity levels can change fish diel activity patterns (e.g. yellow-fin bream, *Acanthopagrus australis*; Payne et al. 2013), modify fish shoaling behaviour (e.g. Pacific blue-eye, *Pseudomugil signifer*; Herbert-Read et al. 2010) and alter the dependability of salinity cues for homing or migrating animals, which has consequences for fisheries production (e.g. barramundi, *Lates calcarifer*; Meynecke et al. 2006). Climate change is further reducing the overall extent of, but increasing the melting rates of, marine-terminal glaciers, coastal sea ice and snow (Jacobs et al. 2002), altering freshwater inputs and salinity patterns in polar coastal waters. Humans are also indirectly altering the responses of animals towards salinity cues because warming and ocean acidification can interfere with the use of these cues by migrating organisms (Edeline et al. 2006, Pistevos et al. 2017b). For example, Pistevos et al. (2017b) showed that ocean acidification can reverse the aversion to estuarine waters by marine larval barramundi of specific life stages. Similarly, attraction of migrating glass eels (*Anguilla anguilla*) to freshwater and allochthonous cues is altered by ocean acidification conditions (Borges et al. 2019).

Transmission of salinity cues to coastal seas is being altered by human land-based activities. For example, dam construction, river regulation, deforestation and freshwater extraction for irrigation have all led to severely reduced and less variable discharges of freshwater into estuaries and coastal seas worldwide (Vorosmarty & Sahagian 2000) (see Figure 1 and Table 1).

## Adaptive responses to altered cuescapes, including future research needs

The foregoing review reveals the ubiquitous human alteration of natural abiotic and biotic cuescapes in the sea (i.e. the spatially heterogeneous amalgamation of environmental cues) across a wide range of spatial scales, as well as how this might affect individual performance and population success. The ramifications of our analysis are that human perturbations of natural cuescapes will have substantial effects on the future resilience of populations of marine animals, and hence the functioning of marine ecosystems. Not only are humans altering natural cuescapes by direct point-source perturbations, they are also altering the Earth's global environment indirectly via long-term alterations to weather patterns, sea-surface temperature, pH, currents and other hydrographic features (Figure 1). The fact that cue alterations operate across different spatial and temporal scales (Figure 2) and the effects vary depending on the cue considered, type of cue alteration, species-specific threshold levels, geographic locality and habitat type has made progress in this field relatively slow and challenging. Moreover, interactive effects of stressors and cue changes may alter species responses in ways that cannot be predicted based on research focussing on single cues or stressors (Przeslawski et al. 2015, Pistevos et al. 2017a).

Advancing our understanding of how alterations to marine cuescapes affect species and ecosystems is complicated by the fact that local and global stressors alter the production, composition, persistence and transmission of sound, visual, chemical, salinity, temperature, electromagnetic and other cues, as well as the ability of marine animals to intercept, evaluate and respond appropriately to relevant cues (Table 1). Nevertheless, while many species may be detrimentally affected, others will be less so if they can avoid, acclimatize (e.g. sensory compensation, behavioural plasticity) or genetically adapt to these environmental changes (Figure 3; Kelley et al. 2018). There is an urgent need to advance research on these topics, as these adaptive responses may significantly alter species sensitivities in nature, as opposed to predictions based on short-term experiments from laboratory environments (Munday et al. 2013, Goldenberg et al. 2018).

### *Avoidance*

Avoidance may be the first response by animals to an altered environment. For example, large visual predatory fishes actively avoid turbid areas, as it interferes with their foraging and causes physiological stress (Utne-Palm 2002). Whales have been shown to avoid areas with artificial air-gun sounds (Dunlop et al. 2017). Species can also avoid negative cue changes through temporal avoidance. For example, yellow-fin bream (*Acanthopagrus australis*) can shift their feeding activity from day to night in response to increased rainfall in estuaries due to changes in hydrological variables and altered predation risk/foraging efficiency trade-offs (Payne et al. 2013).

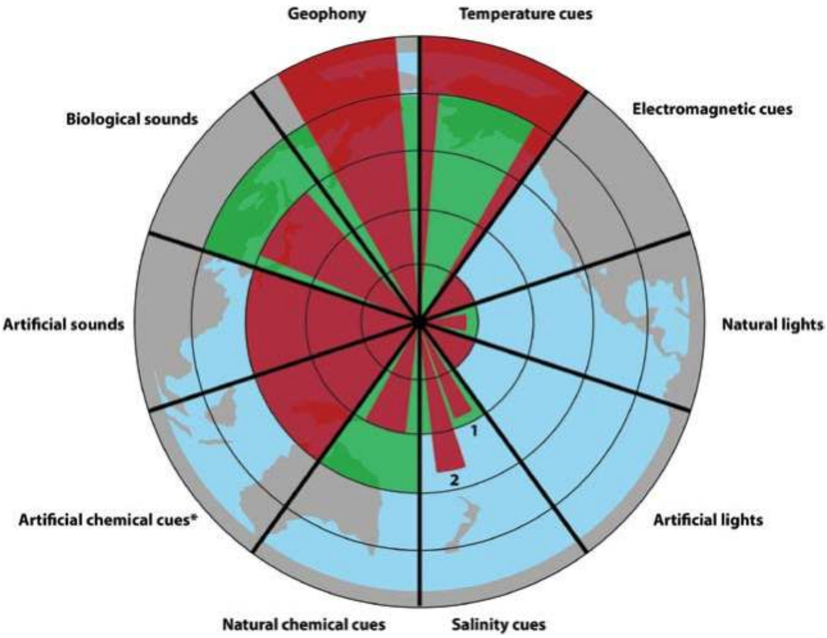

**Figure 2** Potential alteration in spatio-temporal occurrence of major natural and anthropogenic ocean cues due to local and global anthropogenic stressors as discussed in the text. Width (persistence in time) and length (propagation in space) of the sectors indicate the relative scales at which the various cues (labels outside the large circle) predominate under natural conditions (green) and how they might increase or decrease in the future (red). The direction and magnitude of change can differ among locations and systems, but here the expected predominant changes are shown. Sizes of sectors are not to scale. 1: example of salinity cue change under reduced precipitation; 2. example of salinity cue change under increased precipitation.* The map is centred on the Pacific Ocean to emphasize the vast volume of ocean habitat (relative to land) that is susceptible to anthropogenic cue changes. Illustration by Animate Your Science (www.animate-science.com).

Ontogeny also plays a role, with younger stages occupying different habitats (with different cue dependencies and alterations) and having different cue preferences and mobility than older life stages (Lecchini et al. 2007, Leis 2007, Huijbers et al. 2012). Moreover, avoidance in one life stage may have consequences for subsequent ones. For example, a modified response by pelagic larvae to orientation cues may alter their dispersal and hence change gene flow and metapopulation structuring (Swaddle et al. 2015). *

The effectiveness of avoidance will depend on the spatial scale and predictability at which cues are altered and the spatial scale at which species can respond to the cue alteration. For example, coastal species are more affected by changes to cues of terrestrial origin than oceanic species, while sessile animals are more limited at avoiding negative cues than mobile species. Animals will also be better at avoiding predictable (regular or gradual) cue changes, as opposed to the sudden onset of adverse cues (e.g. air guns). A consequence of avoidance could be a contraction in species range and reduction in abundance because there is less suitable environment available to occupy (Dixson et al. 2014, Gordon et al. 2018). However, detailed insights into threshold levels at which different species avoid or can cope with altered cues, and how this will affect species survival and distribution in nature are still lacking.

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[*] Artificial chemical cues are not discussed in this review, but have been included here for completeness.

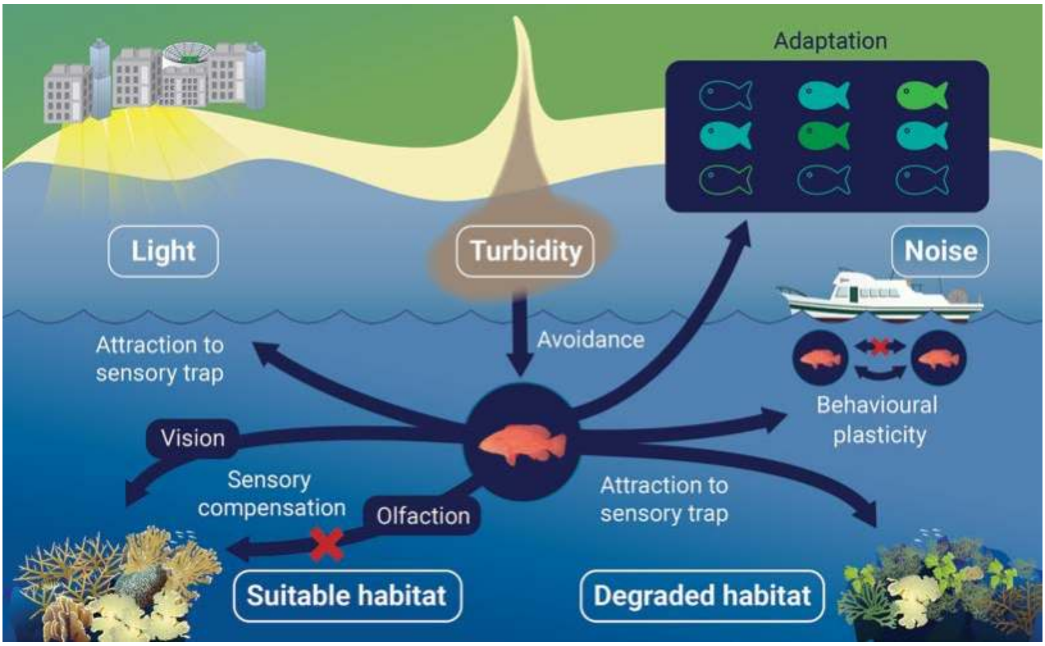

**Figure 3** Potential organismal strategies and responses to changing cuescapes that form a critical part of future research agendas. Examples of cue changes are provided within boxes, while species responses are shown as stand-alone text. 'Vision' and 'Olfaction' refer to examples of sensory modalities used by organisms to sense environmental cues. Behavioural plasticity: crossed-out double-arrowed straight line represents masking/disturbance of, e.g. communication between organisms, by anthropogenic cues; double-arrowed curved line represents adjustments in communication mode (indicative of plasticity). Adaptation: differently coloured fish represent offspring with different phenotypes/genotypes that will undergo natural selection under an altered environment. Illustration by Animate Your Science (www.animate-science.com). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

### *Sensory compensation*

Animals have some capacity to cope with sensory dysfunction or loss of cue functionality through redundancy of sensory modalities. When one sensory modality becomes less sensitive or dysfunctional, or when a particular environmental cue becomes weaker, altered, or lost, individuals may still extract relevant information about their environment from the remaining functional senses and cues (Goldenberg et al. 2018). For example, although ocean acidification disrupts the ability of larval fish to distinguish among chemical habitat cues, appropriate habitat choice occurs when visual habitat cues are present at the same time (e.g. damselfish; Devine et al. 2012). Likewise, under conditions of increased turbidity, damselfish rely more heavily on chemical than visual cues to detect potential predators (Leahy et al. 2011), and they can rely on senses other than vision to recognize potential predators through social learning (Manassa et al. 2013).

On the other hand, changes to one cue can affect the functioning of other sensory channels, such as anthropogenic noise affecting visual signalling in cuttlefish (*Sepia officinalis*; Kunc et al. 2014). Because the use of multiple cues or sensory modalities often improves the accuracy of the information about the environment, partial loss of sensory or cue functionality could still have some negative effects on individual performance. It remains difficult to predict, however, the extent to which partial loss of sensory function ultimately affects individual fitness. However, ecological complexity can buffer the negative impacts of global change stressors (Goldenberg et al. 2018), and studies in natural laboratories subject to elevated $CO_2$ have shown that some species can prevail even if they suffer from a dysfunction of some senses (Nagelkerken et al. 2016, 2017). There is an urgent need for research on this topic, as sensory compensation may form an important buffering mechanism against climate stressors for individuals in nature.

### *Sensory and behavioural plasticity*

The impacts of cue alterations often increase when cue changes have low predictability, sudden onset, high degree of overlap with natural cues (in case of anthropogenic cues), or overlap with the thresholds within which sensory modalities operate (Francis & Barber 2013). Weaker cues or reduced sensing capacity may have little biological effect if the necessary thresholds are still attained (e.g. when cues are overrepresented). Animals may also be able to use cues of reduced strength by making temporal adjustments. This could involve extending the time frame in which sensory information is gathered to allow for better detection, or waiting until favourable conditions return in case of episodic cue alterations (e.g. windows in which anthropogenic noise or light emission is minimized; Radford et al. 2014). For example, sea bass (*Dicentrarchus labrax*) exposed to ocean acidification (about 1000 µatm $pCO_2$) must be up to 42% closer to a cue source in order to detect it (Porteus et al. 2018), but some species might adjust to this situation by increasing cue search times.

Individuals may be able to acclimatize to altered cuescapes over time. For example, fishes initially exhibit negative behavioural responses to sounds from vessels, pile-driving and seismic surveys, but these effects are absent after several weeks of exposure to the same noise (e.g. damselfish and sea bass; Nedelec et al. 2016, Radford et al. 2016). Likewise, cat sharks (*Scyliorhinus canicula*) can show rapid, albeit short-term habituation to artificial electric fields (Kimber et al. 2014). Alternatively, animals could adjust their sensory signalling and cue reception, such as through a change in the duration, frequency or amplitude of sound communication in response to noise pollution (Rosenthal & Stuart-Fox 2012). Moreover, some species of cetaceans and seals are capable of enhancing cue detectability using binaural effects (comparison of sounds received at both ears) when the relevant cue and masking cue originate from different directions (Erbe et al. 2016). The capacity for fine-tuning sensory systems to respond to reduced cue strength or increased interference is largely unknown for most marine species and most cues, but it could be an important mechanism by which animals adjust to changes in the cuescapes available to them.

Finally, animals may offset loss in cue strength by adjusting their behaviour. For example, in risky environments with presence of predators, damselfish reduce their activity and foraging levels with increasing turbidity due to sedimentation (Leahy et al. 2011). Another mechanism to cope with environmental change is associative learning (Chivers et al. 2014a). Animals can exhibit behavioural plasticity by learning how to respond to environmental changes by observing the associated responses of other more experienced or resilient individuals from the same or other species (McCormick & Lönnstedt 2016). The degree to which species can rely on phenotypic plasticity to respond to altered cuescapes needs further study, as it is a strong determinant of species ability to cope with environmental change (Munday et al. 2013, Crozier & Hutchings 2014).

### *Adaptation*

Cuescape changes can act as strong agents of selection across physiological or behavioural phenotypes (Swaddle et al. 2015). For example, due to their competitive strength, larger sand goby males (*Pomatoschistus minutus*) can attract several females, while some smaller males may not be able to mate at all; but turbid conditions interfere with the sexual selection process, and mating success becomes more evenly distributed among different-sized males (Jarvenpaa & Lindstrom 2004). Likewise, environmental stressors may favour individuals with greater boldness. Such traits are often heritable, and therefore cue alteration can select for certain behavioural phenotypes (Sih et al. 2004). Similarly, selection could favour genotypes with the greatest sensory sensitivity to detect cues of reduced strength or altered composition. Clearly, populations with a substantial genetic variation in the response to environmental cues have greater scope for adapting to changing cuescapes (Munday et al. 2013). Some species may already exhibit polymorphisms that are preadapted to different cuescapes, which would likely enhance adaptive potential through differential selection on favoured genotypes (Delhey & Peters 2017).

Plasticity and adaptation can also interact in unexpected ways that could influence adaptive capacity. For example, Welch & Munday (2017) demonstrated that individual variations in behavioural response to alarm cues exhibited by damselfish at elevated $CO_2$ are heritable, and therefore the fish should adapt, but this adaptive potential is obscured by nonadaptive plasticity when fish are permanently exposed to elevated $CO_2$ for many weeks. Furthermore, genetic correlations between traits associated with different sensory systems could constrain the rate of adaptation or lead to reduced performance in competing sensory modalities (Munday et al. 2013, Laubenstein et al. 2019). Understanding the relationship between plasticity and adaptive potential will be critical to predicting the ability of species to adjust to future changes in cuescapes.

### *Sensory traps*

Changing cuescapes can facilitate maladaptive responses by attracting animals to habitats and environments that do not enhance fitness or population viability (Schlaepfer et al. 2002). For example, many aquatic animals are positive phototactic, and artificial lighting during nighttime can alter natural behaviour, leading to increased mortality from visual predators or suboptimal visual habitat selection (Davies et al. 2014). Likewise, ocean acidification can interfere with neurological functioning in fishes and invertebrates and enhance maladaptive choices, such as attraction of tropical barramundi larvae to temperate reef sounds or artificial sounds (Rossi et al. 2018), and of larval clownfish (*Amphiprion percula*) to chemical cues of irrelevant coastal habitats (Munday et al. 2009). Some species will benefit, however, from the effects of sensory traps on other species, such as increased foraging opportunities in artificially lit areas that aggregate prey, in degraded habitats with reduced hiding opportunities for prey and in areas with higher turbidity (for nonvisual predators). The emergence of sensory traps due to anthropogenic impacts and the specific mix of species that are most sensitive to the presence of such traps will affect future species' community structures, but it is still an understudied field. Understanding behavioural responses to altered cues is a complex task. For example, individual animals are more likely to respond to novel cues if they are more similar to cues to which the species has responded in the recent evolutionary past, while some cues elicit behavioural responses only when more than one relevant cue is present (Sih et al. 2011).

## Technological advances to study cuescape changes

The inherent interdisciplinary nature of the challenge of changing cuescapes calls for different and novel research approaches. Much of our present knowledge about the possible effects of changing marine cuescapes comes from manipulative experiments that identify and quantify potential organism responses to alterations in the environment. Carefully designed laboratory experiments can provide information on the sensitivity (or, conversely, the resilience) of organism physiology and behaviour to changing cues, but they cannot give insight into responses at higher levels of biological organization (Goldenberg et al. 2018). Larger-scale and more complex mesocosm studies of predator-prey, competition and other community responses are emerging (e.g. Alsterberg et al. 2013, Goldenberg et al. 2017, Sswat et al. 2018, Ullah et al. 2018), and field manipulation experiments in natural laboratories are providing insight into species responses in a more natural context (e.g. Fabricius et al. 2014, Nagelkerken et al. 2016, 2017, 2018). Changing local regulations and enforcement of controls on sources of marine pollution could also provide opportunities to mimic manipulation studies, and studies across geographic ranges and natural gradients could be used to assess whether there are variations in organism sensitivity to changing cues within different subpopulations or whether community composition varies concomitantly (e.g. Goniea et al. 2006, Kroeker et al. 2016, Vargas et al. 2017). Multistressor approaches are critical because of the possibility of nonlinear synergistic or antagonistic interactions among changing cuescape stressors (e.g. Breitburg et al. 2015), which could alter the capacity to adjust through plasticity or genetic adaptation (Gaitán-Espitia et al. 2017).

There is also an urgent need to obtain more detailed information across space and time about how marine cuescapes are changing. Global- and regional-scale ocean observational networks are in place for some physical environmental cues (e.g. temperature and salinity), and other networks are in progress about other elements, such as pH (e.g. Global Ocean Acidification Observation Network, www.goa-on.org). By comparison, while there is growing interest in monitoring environmental sound and anthropogenic noise pollution, sound monitoring is not always well integrated with other ocean environmental observations. Observational networks typically are built to address specific scientific questions or applications, such as ocean heat uptake, long-range weather forecasting and monitoring commercial fish stocks. For cuescape research, the challenge will be to develop networks with co-located measurements of key environmental cues, targeting regions of high susceptibility. Such networks also should benefit from the growing capabilities of autonomous sensor data on moorings and mobile platforms (e.g. gliders, profiling floats, autonomous subsurface and surface vehicles), satellite and airborne remote sensing, as well as data management systems that can deliver comprehensive data sets to users in nearly real time.

Modelling frameworks are needed to integrate across physical (e.g. cuescape changes) and biological (e.g. behavioural responses) research elements and support resource management and conservation efforts. In principle, models provide a dynamic tool for extrapolating conditions in undersampled seas, assessing cascading effects across food webs and forecasting an uncertain future, with the possibility of novel environmental conditions and biological communities (e.g. McNamara et al. 2011). However, model performance and confidence are restricted by both limited observations and conceptual understanding. Regional ocean models and Earth system models already incorporate many of the required cuescape elements, such as seawater temperature, salinity and pH (Bopp et al. 2013), but considerably more work is required to add other environmental cues and the accompanying biological responses. Further, improved techniques are needed for local and regional downscaling for many applications.

## Management implications

Human alterations to natural cues are likely to simplify natural cuescapes (Figure 2), which can be detrimental for biological diversity, as it reduces the diversity of fundamental cue niches. Moreover, many cues are being altered concurrently and at unprecedented rates, and stressor effects can be exacerbated by other detrimental processes, such as species overexploitation and habitat destruction. Changing cuescapes will favour individuals and species that have greater natural tolerance to changes in environmental cues, with consequences for community structures. Novel communities with altered species composition are the most likely longer-term outcomes of altered cuescapes. Species with broad environmental tolerances, plasticity, or polymorphism are the likely winners in the face of global cue changes. Overall, sensory generalists are likely to increase in abundance to the detriment of sensory specialists (Killen et al. 2013). This may not only affect species diversity and abundances at local scales, but ultimately can also affect humans when it concerns species of significant ecological or fisheries importance.

Coastal areas will experience the most dramatic changes in multiple cues at the same time, as this is the environment where most human perturbations occur and where cue changes from land-based activities are superimposed onto changes in marine cues. Furthermore, habitats that are naturally rich in the production of natural cues (e.g. coral reefs), or those that experience the most extensive human cue alterations (e.g. coastline developments), will form hot spots of cuescape changes. Transmission of cues varies depending on the type of cue considered, and changes to cuescapes can occur across very great distances (e.g. sounds) or be more localized (e.g. artificial lights; Figure 2). Mapping of such hot spots and overlaying of multiple cuescape changes can identify the areas at greatest risk and inform policy and management.

Management efforts need to focus on mitigating negative effects on natural cues and reducing the frequency, duration and intensity of novel (anthropogenically induced) cues. However, the capacity to manage and mitigate cue alteration will vary among cues. While stressors such as light and sound pollution can be managed at a local scale to reduce impacts, global stressors such as rising temperature and declining pH cannot be significantly altered in the short term. While technological advances have increased the presence of anthropogenic cues in the ocean, they also provide opportunities to reduce them. For example, technology exists to make ship engines quieter, while anthropogenic lights along coastlines and beaches could be adjusted in their direction, intensity and wavelengths to reduce impacts on animals. Likewise, sound and light pollution by vessels and infrastructure could be confined in space through regulations that limit pollution to specific shipping lanes, fishing zones or development areas. Preservation of coastal vegetation and minimising artificial river regulation could reduce the influx of considerable quantities of terrestrial cues into coastal areas, while protection of large biogenic habitats (e.g. seagrass beds, coral reefs, oyster reefs, or kelp forests) can maintain the production of natural cues. Overall, diverse options are available to regulate coastal construction and pollution by concentrating the impacts in space and time, avoiding such impacts during important animal migrations or at critical foraging or spawning sites, and the use of more advanced techniques that create fewer and less detrimental artificial cues.

Existing marine reserves could aid in the preservation of healthy cuescapes by limiting anthropogenic cues within their boundaries. As such, differences in natural cuescapes inside and outside marine protected areas (MPAs) might provide a tool to study the effect of modified cuescapes on ecological communities and animal behaviours. Healthy cuescapes inside reserves could help support natural processes that underpin species population replenishment, maintenance and diversity. Such reserves might not maintain the full range of natural cuescapes all at once, but they still could provide healthier cuescapes than degraded areas. Also of interest is the designation of remote areas with relatively unaffected cuescapes (e.g. Pacific islands) as reserves to preserve and study relatively pristine cuescapes.

## Conclusions

Six main conclusions can be drawn from this review:

- Marine cuescapes are being rapidly altered by local, regional and global stressors. This includes changes to the production of natural cues themselves (sound, chemical, visual, temperature, salinity or electromagnetic); the introduction of multiple anthropogenic cues (sound, light and chemical) that mask natural cues, create more noisy backgrounds, or act as ecological traps through maladaptive responses by organisms; and changes to the transmission of cues (e.g. due to changes in water properties such as pH, temperature, turbidity and the presence and thickness of sea ice).
- Marine cuescapes are being altered at different spatiotemporal scales. Coastal urbanized areas are likely to become hot spots of changes to multiple cues, most of which will occur over relatively short distances. Increasing anthropogenic cues in open oceans, on the other

hand, are typically present for extended time periods (for artificial light) or travel over long distances (for artificial sounds).

- Marine cuescape changes can alter behavioural and physiological responses by marine animals. These responses depend on the species, life stage, functioning and sensitivity of sensory modalities, and sensory pathways considered. Responses to altered cues might change over time due to habituation or sensory compensation. Because many behaviours that are important for individual fitness can be affected, cuescape changes can have cascading effects on population replenishment and community structure.
- Numerous species are expected to be negatively affected to some extent by degrading cuescapes, but ‘sensory generalists’ are less likely to be affected or might even prevail over ‘sensory specialists’.
- Some species might adopt various behavioural strategies that help them cope with and persist in a changing environment in a future ocean. Such strategies include avoidance of local detrimental cues, compensation by other sensory modalities, behavioural plasticity and genetic adaptation. Understanding such coping mechanisms is an urgent research priority because, despite their prevalence in nature (and therefore their potential importance), these mechanisms have been little studied.
- Species survival and reproduction rely to a large degree on individuals extracting relevant information from their surrounding environment. The habitats of most species are highly complex due to species interactions and environmental control over species behaviour and performance. Moreover, species may adjust to changes to single environmental cues, but they have less plasticity to cope with multiple cue changes. There is a need for research agendas that lead to improved understanding of changes to cuescapes across different spatiotemporal scales, and that include mechanistic and *in situ* studies to establish the range of species’ responses to such changes, as well as improved modelling approaches that can generate predictions about the communitywide effects of changed cuescapes—both now and in the future.

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# BIOLOGY AND ECOLOGY OF THE GLOBALLY SIGNIFICANT KELP *ECKLONIA RADIATA*

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## Abstract

*Ecklonia radiata* is one of the most widespread kelps globally, dominating temperate reefs throughout much of Australasia and southeastern Africa. Throughout much of its range, it is the only laminarian kelp and hence plays a key role in facilitating biodiversity and driving food webs, and it underpins immense ecological and socioeconomic values. This review synthesises the growing literature on *E. radiata* from its phylogeny and distribution through to its biology, ecology and recent changes.

It provides an assessment of the state of knowledge and identifies gaps in our understanding of this important species. Despite being tolerant of a wide range of abiotic conditions, recent environmental change has caused direct and indirect loss of *E. radiata* forests, with extensive areas transitioning to turf and urchin barrens. Ongoing climate change may require application of multifaceted and novel strategies to increase its resistance and resilience to future conditions. By integrating variation across space, time and environmental change, this review provides a description of the current status and possible future trajectories of *E. radiata* forests.

## *E. radiata:* A globally significant species

One of the most widely distributed kelps globally is *Ecklonia radiata* (C. Agardh) J. Agardh (Figure 1). In contrast to many other kelp forest ecosystems, where multiple laminarian species coexist (Steneck & Johnson 2013, Wernberg et al. 2019), *E. radiata* often forms monospecific forests as it is the only laminarian kelp throughout much of its range (Figure 1). The ecological and socioeconomic importance of *E. radiata* has long been recognised (e.g. Bolton & Anderson 1994, Steinberg & Kendrick 1999). However, in contrast to other widespread and dominant kelp taxa such as *Macrocystis* (Graham et al. 2007) and *Laminaria* (Bartsch et al. 2008), there have not been any recent systematic assessments of our knowledge of the species. The only review of the species was 25 years ago by Bolton & Anderson (1994) as part of their review of the genus *Ecklonia*. Since then, significant work has been done on many aspects of the species. Indeed, a search for '*Ecklonia radiata*' in the core collection of the Web of Science (22 April 2018) revealed that 88% of 427 records have been published since 1994.

This review synthesises the literature on the phylogeography (see the section entitled 'Phylogeny and distribution'), ecophysiology (see the section entitled 'Ecophysiology and environmental drivers') and population biology (see the section entitled 'Life history, dispersal and recruitment') of *E. radiata*, as well as the community ecology (see the section entitled 'Community ecology of *Ecklonia* forests') and recent changes in and future threats to *E. radiata* forests (see the section entitled 'Recent changes and future threats'). The synthesis concludes that although our current scientific understanding of the biology and ecology of *E. radiata* spans broad scales of space, time

**Figure 1** *Ecklonia radiata* forests support diverse ecological communities, economic values and cultural significance. It is the only laminarian kelp throughout much of its distribution, where it often forms dense monospecific forests. (All photos by the authors and Andrew Green.)

and scientific disciplines, common trajectories of ecological change warrant continued inquiry and integrated management interventions to ensure the long-term integrity and persistence of *E. radiata* kelp forests (see the section entitled 'Conclusion').

## Background

### *Kelp forests: The foundation of temperate reef ecosystems*

Ecologically dominant species play a critical role in creating and maintaining many ecosystems. Through their influence on the local abiotic environment and biotic interactions, organisms such as trees, marsh grasses, mangroves, corals and seaweeds drive the structure and function of associated communities. In addition to providing biogenic habitats and food, they support a range of other ecosystem services, such as influencing landscape-scale energy flows, biogeochemical cycles (including carbon and nitrogen) protection against severe weather (storms, floods, waves etc.) and provision of harvestable resources. Consequently, there is a keen interest in understanding the past, present and future trajectories of these important species.

Seaweeds (macroalgae) are dominant habitat-forming species across at least ~25% of the world's coasts, particularly at temperate and polar latitudes (Schiel & Foster 2006, Bolton 2010, Steneck & Johnson 2013, Filbee-Dexter et al. 2019). Seaweeds are among the fastest-growing plants on Earth, and they contribute substantially to the structure and energy that support the incredible biodiversity and production for which many marine ecosystems are renowned. Seaweed species within the order Laminariales (Ochrophyta; brown algae) are often referred to as *kelp,* although the term is sometimes used more broadly (Bolton 2010, Fraser 2012, Steneck & Johnson 2013, Bolton 2016, Wernberg et al. 2019). Kelps provide many of the same ecological functions underwater as trees on land, and like terrestrial forests, which are typically defined simply by the presence of trees, kelp ecosystems are best described as *kelp forests* (Wernberg & Filbee-Dexter 2019).

### *Kelp forests and humans*

Temperate rocky coasts where kelp forests dominate play an important role for humans in both extant and historical contexts. There is a long history of use of kelp by indigenous people around the world, both as food and as tools (Kuhnlein & Turner 1991, Lightfoot & Parrish 2009, Clarke 2011). For example, along the rocky coasts of southern Africa, early humans relied on mussels, limpets and other marine organisms associated with kelp forests, providing necessary omega-3 fatty acids and trace elements required for brain function and development (Compton 2011). A tight relationship between humans and kelp ecosystems is also the basis of the *kelp highway theory,* which proposes that the colonisation of maritime peoples from Asia to the Americas during the end of the Pleistocene was strongly facilitated by making extensive use of the resource-rich kelp forests found around the Pacific Rim (Erlandson et al. 2007, 2015). Despite being comprised of different kelp taxa, these ecosystems shared the key property of supporting a wealth of coastal resources including seaweeds, shellfish, fish, marine mammals and seabirds, which required minimal adaptive adjustments for migrating coastal peoples. In Australia, aboriginal people used kelp as food and to make water-carrying vessels and footwear (Akerman 2005, Clarke 2011) and as part of cultural and ceremonial activities (Thurstan et al. 2018). The stipe and fronds of *E. radiata* were roasted and eaten as food, and selected parts were also made into utensils (Wesson 2009).

Kelp forests contribute substantial ecosystem services to human populations representing large economic values (Smale et al. 2013, Vásquez et al. 2014, Bennett et al. 2016, Blamey & Bolton 2017). In contrast to other marine ecosystems such as coral reefs, however, there are surprisingly few studies quantifying these values (Bennett et al. 2016). Nevertheless, it has been estimated that *E. radiata* forests contribute more than $10 billion per year ($1400/ha/yr) to the gross domestic product (GDP) in Australia alone through direct values from activities such as recreational and commercial fishing and tourism (Bennett et al. 2016). The total value of kelp forests, however, far exceeds this if also considering indirect and less tangible values such as biodiversity, coastal protection, nutrient cycling, fisheries enhancement and carbon storage. Moreover, the bequest value of kelp forests to coastal communities (i.e. the value they have to people simply knowing that they are there for future generations) is immense but immeasurable (DPI 2014). Considering these indirect values, seaweed habitats are the third-most-valuable ecosystem globally (Costanza et al. 2014).

## Phylogeny and distribution

### *Phylogeny and global distribution*

Laminarian kelps (Order: Laminariales) are thought to have emerged in the Northern Hemisphere about 80 million years ago. In contrast, dominant groups, including *Ecklonia*, were derived more recently (ca. 25 Ma; Silberfeld et al. 2010). Colonisation of the Southern Hemisphere by kelp species, however, may be more recent (Silberfeld et al. 2010, Rothman et al. 2017). On the east coast of Australia, phylogeographic histories of species, including *E. radiata,* are shallow, suggestive of origins <3 Ma (Durrant et al. 2015). The genus *Ecklonia* has previously been placed in different families, including Laminariaceae, Alariaceae and Lessoniaceae. Although these families are still recognised, gene transcriptomics now place *Ecklonia* in a new family, Arthrothamnaceae (Jackson et al. 2016).

The relationships of species within the genus *Ecklonia* have only recently become clear with comprehensive molecular studies (Figure 2). A phylogenetic study concluded that Northern Hemisphere and Southern Hemisphere *Ecklonia* species form separate clades (Rothman et al. 2015). Moreover, all the Southern Hemisphere samples studied (including *Ecklonia brevipes* from Australia), with the exception of South African *E. maxima*, formed a single species: *E. radiata* (Rothman et al. 2015). In addition, the species of *Eisenia* and *Eckloniopsis* fell within the *Ecklonia* clade, and thus *Eisenia bicyclis* and *Eckloniopsis radicosa* were resurrected and the new combination *Ecklonia arborea* proposed (formerly *Eisenia arborea*).

These findings radically change the accepted global distribution of the genus *Ecklonia*. *Ecklonia sensu lato* is thus the most globally widespread kelp genus and grows in all oceans. It is also the most warm-tolerant genus of the Laminariales (tom Dieck 1993, Terada et al. 2016, as *E. radicosa*). The origins of the genus, however, are still not clear. Although the genus *Ecklonia* appears to be more speciose in the northwest Pacific suggestive of Northern Hemisphere origins, the species identities in this region have not been clearly defined using molecular methods.

*Ecklonia radiata* displays a great deal of morphological variation throughout its range, even on small spatial scales (e.g. Womersley 1987, Stegenga et al. 1997, Wernberg et al. 2003a), confusing species identity. A number of morphological variants have been subsumed into *E. radiata*, including *E. biruncinata, E. exasperata* and *E. richardiana*. There have been historical records of *E. radiata* (or species currently considered synonymous with *E. radiata*) in a number of world regions. The type of *E. biruncinata* Bory was a specimen collected by D'Urville in Concepcion, Chile. This appears to be an error, as there is no other evidence that *E. radiata* (as *E. biruncinata*) is present in South America. Collections have been made of populations of *Ecklonia* in Northwest Africa (Mauritania, Senegal) and neighbouring islands (Canary Islands, Cape Verde Islands), particularly in upwelling and deeper sites. Some of these specimens were given the name *E. exasperata* (e.g. Kützing specimens in Leiden from Canaries and Cape Verde, Willem Prudhomme van Reine, pers. comm.). The *E. exasperata* type is from Tasmania, and this species is considered synonymous with *E. radiata*. The material from Mauritania was described as *E. muratii* by Feldmann (1937), and this name has been used more widely for the northeast Atlantic *Ecklonia* (Guiry & Guiry 2018). These putative *E. radiata* populations have not yet been sequenced, and their species identity and phylogenetic relationships remain unclear. Similarly, *Ecklonia* occurs in an upwelling zone on the northern Indian Ocean coast of Oman. These populations have always been described as *E. radiata*,

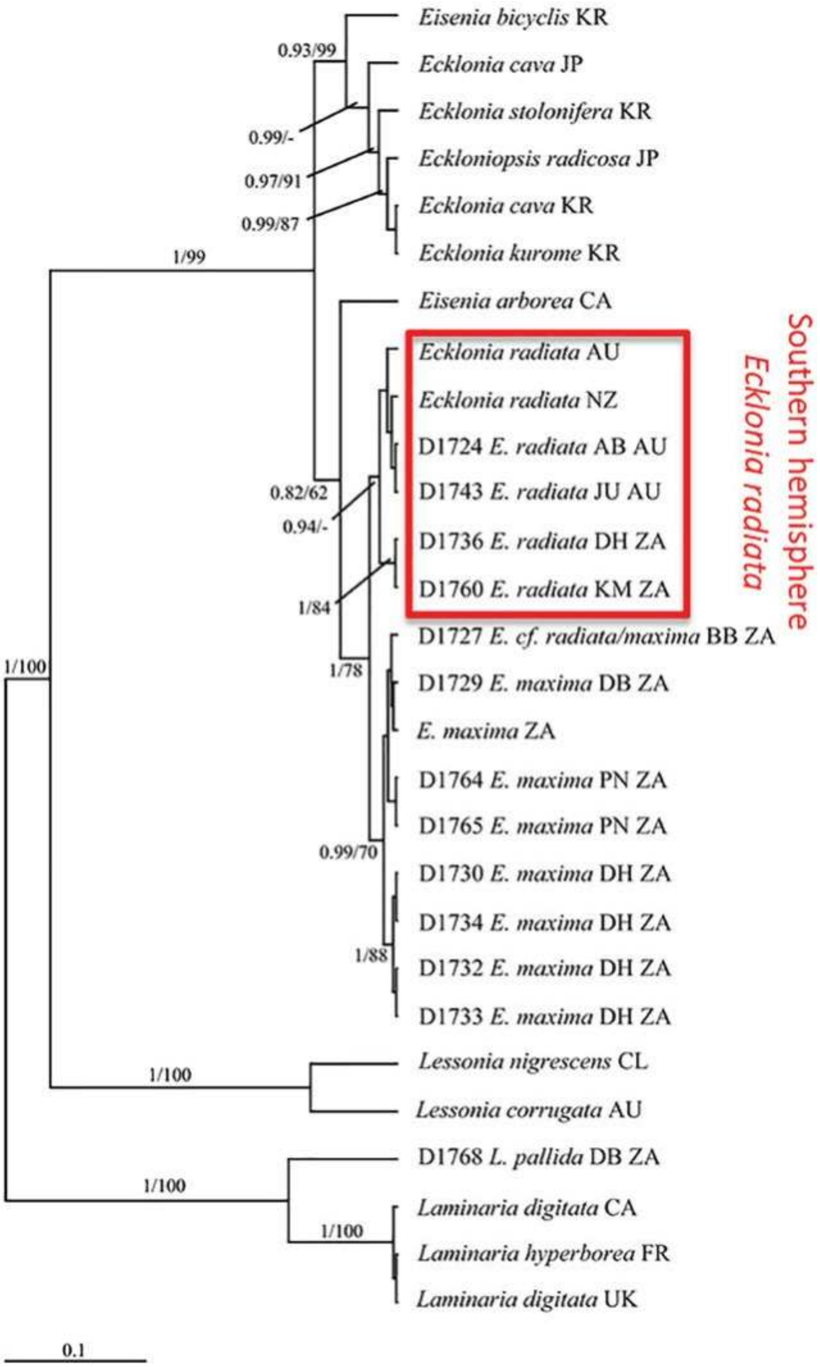

**Figure 2** Phylogeny of *Ecklonia* and closely related species, showing all Southern Hemisphere *E. radiata* (Australia, New Zealand and South Africa) forming a distinct clade. Putative *E. radiata* specimens have been collected from Oman, Mauritania, Senegal and the Canary and Cape Verde Islands. However, molecular investigation is required to unequivocally confirm species identities. (Bayesian phylogeny based on concatenated rbcL/ITS alignment, from Rothman, M.D. et al.: A molecular investigation of the genus *Ecklonia* (Phaeophyceae, Laminariales) with special focus on the southern hemisphere. *Journal of Phycology*. 2015. **51**, 236–246. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission.)

also without molecular evidence on taxonomic relationships. It is clear that specimens of *E. radiata* collected outside the Southern Hemisphere require molecular investigation to confirm the species identity and ascertain the true distribution of this widespread kelp.

## *Continental distribution of E. radiata*

As marine organisms, kelps are restricted upwards in the intertidal zone as they become increasingly limited by desiccation and other factors. In contrast to some other laminarian kelps, which can form extensive forests in the lower intertidal zone (e.g. species of *Undaria*, *Postelsia*, *Laminaria*), *Ecklonia radiata* is only occasionally found in the intertidal zone, suggesting that it is a true subtidal species with very low tolerances to desiccation (Larkum & Wood 1993). The exception is in South Africa, where *E. radiata* mostly inhabits the low intertidal/shallow subtidal (John Bolton, pers. obs.). However, the ecological performance of *E. radiata* has not been examined in a desiccation framework, implying that the mechanisms underpinning its absence from the intertidal zone remain speculative. Alternative, but less likely, models that need to be tested experimentally include competitive exclusion, grazer damage, light inhibition or ultraviolet (UV) damage.

Throughout its distribution in the Southern Hemisphere, *E. radiata* can be found on most subtidal rocky substrata from ~27°S to 48°S, except in South Africa where it is largely confined to the southeast coast, although deeper populations have recently been confirmed in Mozambique at 24°S (Figure 3). In Australia, *E. radiata* is found on temperate and subtropical rocky reefs along the entire continent and adjacent islands poleward of ~27°S (e.g. Houtman Abrolhos, Western Australia; Tasmania; Moreton Island, Queensland) (Womersley 1987, Connell & Irving 2008, Wernberg et al. 2011c, Marzinelli et al. 2015b). This includes reefs on the open coast, as well as within estuaries such as Sydney Harbour (Coleman 2013, Johnston et al. 2015), where it is also found growing on artificial structures such as jetties (Marzinelli 2012). *E. radiata* occurs subtidally from the low tide mark to approximately 40-m depth, although large forests have been found at 60 m or more at the northern limit of its distribution on the Australian east coast (Marzinelli et al. 2015b), and to 80 m at its northern limit in New Zealand (about 30°S, Nelson et al. 2018). The vertical distribution and abundance of *E. radiata* varies with latitude and is related to physical factors such as light

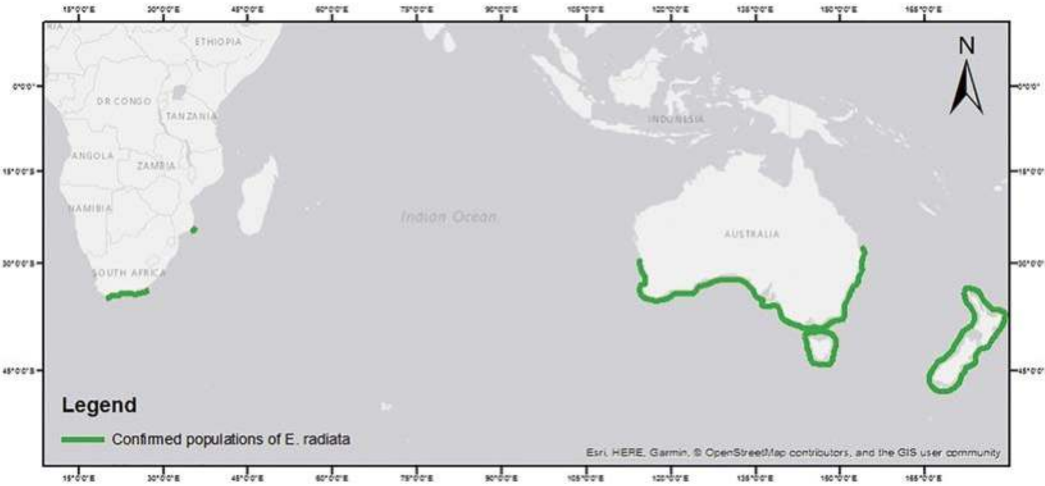

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**Figure 3** Distribution of *Ecklonia radiata* in the Southern Hemisphere. Putative *E. radiata* populations are also found in the Northern Hemisphere (Oman, Mauritania, Senegal and the Canary and Cape Verde Islands), although they remain to be confirmed using molecular methods and are not shown here.

availability and water temperature, as well as biological processes such as grazing, resulting in marked biogeographical variation (Connell & Irving 2008, Marzinelli et al. 2015b).

On the east coast of Australia, *E. radiata* typically forms monospecific stands that are patchy (Underwood et al. 1991a, Connell & Irving 2008). In shallow waters (<~20 m), these patches can be driven by winter storm disturbances on small scales (Kennelly 1987a) and on larger scales, patches decrease in size and frequency south from around 32°S, representing a negative relationship to sizes and frequencies of sea urchin barrens formed by *Centrostephanus rodgersii* (Connell & Irving 2008). The range expansion of *C. rodgersii* to the northeast coast of Tasmania since about the 1950s has led to substantial changes from reefs dominated by dense forests of *E. radiata* and other seaweeds to sea urchin barrens (Johnson et al. 2005a, Johnson et al. 2011). In deeper waters (>about 30 m), the occurrence and abundance of kelp generally increase with latitude, despite some small-scale variability (Marzinelli et al. 2015b). Sea urchin barrens generally do not occur at these depths (but see Perkins et al. 2015); instead, reefs without kelp are dominated by sponges, solitary ascidians, byozoans and other encrusting invertebrates (Ferrari et al. 2018). At lower latitudes, the combination of high light availability and a significant decrease in water temperature at depths >30–40 m (<20°C in early summer) appears to maintain kelp forests at 30–60 m or more, with abundances that match dense forests at the highest latitudes (Marzinelli et al. 2015b). However, in shallower water at similar low latitudes, *E. radiata* stands become increasingly disjunct and rare (Vergés et al. 2016), presumably due to higher summer sea temperatures and greater herbivory, but also due to patchiness in availability of rocky reef habitat.

On the south and west coasts of Australia, *E. radiata* forests are much less patchy and typically occur in mosaics of mixed species with large canopy-forming fucoids (e.g. *Cystophora* spp., *Scytothalia dorycarpa*), covering most of the rocky reefs (Connell & Irving 2008, Wernberg & Connell 2008, Wernberg et al. 2011c, Coleman & Wernberg 2017). The distribution of *C. rodgersii* is limited to the east coast, and the absence of this herbivore from the continental south and west coasts may explain the marked differences in small-scale distribution patterns and patchiness of *E. radiata* compared with the east coast (Connell & Irving 2008). In shallow waters, the total extent of reef coverage by *E. radiata* and other fucoids does not change with latitude; however, the structure of the habitat does, with more monospecific stands of *E. radiata* at lower latitudes, presumably as cool-adapted fucoids disappear (Wernberg et al. 2003b, Wernberg et al. 2011c). Recent anomalies in water temperature during a strong marine heatwave caused significant reductions in the cover of fucoids at lower latitudes (Smale & Wernberg 2013), strengthening the latitudinal differences in heterogeneity, although these anomalies also led to strong declines of *E. radiata*, causing shifts from canopy-dominated to turf-dominated reefs at low latitudes (Wernberg et al. 2013a, Wernberg et al. 2016a). This pattern has also been observed along the east coast (Vergés et al. 2016; also see the section entitled 'Recent changes and future threats', later in this review).

*Ecklonia radiata* is the dominant laminarian kelp on rocky reefs throughout mainland New Zealand (Shears & Babcock 2007) but presumably due to the higher latitudes of the New Zealand coasts, strong biogeographical patterns are not as evident as in Australia. On the northeast coast of the North Island, *E. radiata* forms extensive monospecific stands at depths >8 m (Schiel & Choat 1980, Schiel 1990, Shears & Babcock 2007) and can extend beyond 30 m in clear water (Grace 1983). It is found at lower densities at shallower depths, where it occurs in mixed stands with fucoids. *E. radiata* often has a bimodal distribution with depth in northern New Zealand due to the presence of sea urchin (*Evechinus chloroticus*) barrens, which can dominate between 3–17 m depths (Choat 1982, Shears & Babcock 2007). In southern New Zealand, *E. radiata* does not form extensive forests and is mostly restricted to shallower depths (<15 m) and usually occurs in mixed stands with several other species of seaweeds (Choat & Schiel 1982, Schiel 1990, Shears & Babcock 2007). *E. radiata* is notably rare in some regions, such as the west and southeastern coasts of the South Island (Shears & Babcock 2007). *E. radiata* has not been recorded in the Chatham Islands or in the sub-Antarctic Auckland Islands (Schiel 1990), except in the Snares Islands (Bolton & Anderson 1994). It occurs as far north as the Kermadec Islands (~29°S; Nelson et al. 2018).

In South Africa, *E. radiata* is mostly confined to the south and east coasts (Figure 3), where it forms a distinct subtidal fringe in sheltered habitats. It does not dominate the shallow subtidal, as it does in much of its Australasian distribution. The westernmost populations are around 60 km east of the southernmost point of Africa, the major biogeographical break of Cape Agulhas, and there is a single population further west at Bordjiesrif, on the Cape Peninsula (Rothman et al. 2015). There are also little-known subtidal populations on the Agulhas and Alphard Banks and at 25–30 m on Middle Bank (Tommy Bornmann, pers. comm.). At the eastern end of the distribution, *E. radiata* grows in the subtidal fringe only as far as the boundary between the Eastern Cape and KwaZulu-Natal provinces (Port Edward, De Clerck et al. 2005). The species occurs, however, in deeper subtidal populations, to at least 50 m and to the extreme northeast of South Africa (Sodwana), and specimens were recently collected from the subtidal in Mozambique (Kerry Sink, pers. comm.). The west coast kelp forests of the southwest coast of South Africa are dominated by the much larger *E. maxima*, which, until recently, was geographically separated from *E. radiata*. Around 2006, *E. maxima* extended its distribution approximately 70 km eastward, where the two species now grow on the same shores at De Hoop (Bolton et al. 2012) and may hybridise (Bolton & Anderson 1987, Rothman et al. 2015).

## Ecophysiology and environmental drivers

*Ecklonia radiata* grows and reproduces across about 20° of latitude, from the shallow subtidal to a depth greater than 40 m (even as deep as 70–80 m in some places; Richmond & Stevens 2014, Nelson et al. 2018), and on reefs exposed to a wide range of hydrodynamic forces (Phillips et al. 1997, Goldberg & Kendrick 2004, Thomsen et al. 2004, Wernberg & Thomsen 2005, Wing et al. 2007, Connell et al. 2008a, Smale et al. 2011, de Bettignies et al. 2012). This wide distribution suggests that *E. radiata* has broad tolerance to many environmental conditions. A range of abiotic conditions, including both physical state factors (temperature, water motion, sediments, chemistry (salinity, pH and oxygen levels)) and resources (light, space/substratum and nutrients) may limit the performance and distribution of *E. radiata*. While individual conditions and resource levels have direct effects, they never affect *E. radiata* in isolation but rather interact in synergistic or antagonistic ways. This is particularly true for temperature, which affects all biological processes from subcellular enzyme kinetics to biogeographic distributions (Kordas et al. 2011). It is also important to note that performance responses may be different for gametophyte and sporophyte stages, as well as among different stages of sporophyte growth (juveniles versus adults) (Wood 1987, Thomsen et al. 2004, Franco et al. 2017), and knowledge about all life stages is required to fully understand what drives and limits population distribution (Russell et al. 2012).

### *Growth and primary production*

The primary meristem of *E. radiata* is located just above the junction between the stipe and the primary blade. Consequently, growth and primary production can be quantified by punching a hole at the base of the central lamina above the meristem and measuring linear extension and biomass accumulation (BA) over time (Figure 4A, Mann & Kirkman 1981). These measurements have been done from the subtropical waters of the Houtman Abrolhos Islands (28°S) to the cooler waters of Doubtful Sound in New Zealand (45°S). Despite widely different environmental conditions, almost everywhere, individual kelps grow fastest in the austral spring (September–November) and slowest in late summer and autumn (February–April) (Table 1). These patterns tend to coincide with the periods when water temperatures are coolest and warmest, respectively, although the temperature maxima and minima differ. For example, the summer temperatures at the Houtman Abrolhos often exceed 24°C, while in Doubtful Sound, summer temperatures rarely exceed 20°C. For *E. radiata*, similar rates of primary blade growth have been recorded in New South Wales, South Australia and southern New Zealand ranging from 0.06 to 0.42 cm/day, and these are within the range recorded for other members of the order Laminariales (see Table 1 and Miller et al. 2011). Within this broad

**Table 1** Growth rates (linear blade extension using hole punch method) and production in *E. radiata* over a range of studies, depths and locations

| Location | Extension (cm/ind/d) | Production (g/ind/d) | Depth (m) | Study |
|---|---|---|---|---|
| Western Australia: Abrolhos, 28° | 0.03–0.2 | | 2 | Hatcher et al. (1987) |
| Western Australia: Jurien, 30° | | 0.7–6.3$^{w}$ | 9–12 | Bennett et al. (2015a) |
| Western Australia: Marmion, 32° | 0.07–0.22 | 0.55–3.63$^{w}$ | 2.5–17.3 | Bearham et al. (2013) |
| Western Australia: Marmion, 32° | 0.08–0.3 | | 5–10 | Hatcher et al. (1987) |
| Western Australia: Marmion, 32° | | 0.9–3.8$^{w}$ | 8–11 | de Bettignies et al. (2013b) |
| Western Australia: Marmion, 32° | | 0.4–4.6$^{w}$ | 9–12 | Bennett et al. (2015a) |
| New South Wales: Port Jackson, 33.8° | 0.08–0.20 | 0.23–0.59$^{d}$ | 1.5 | Larkum (1986) |
| Western Australia: Hamelin 34° | | 1.1–5.6$^{w}$ | 9–12 | Bennett et al. (2015a) |
| South Australia: West Island, 35° | 0.08–0.22 | 0.16–0.79$^{d}$ | 3–12 | Fairhead & Cheshire (2004a) |
| New Zealand: Doubtful Sound, 45° | 0.06–0.45 | 0.14–1.38$^{d}$ | 15 | Miller et al. (2011) |

*Note:* w = wet weight and d = dry weight.

trend, growth is also positively correlated with the amount of light available (Fairhead & Cheshire 2004a, Bearham et al. 2013).

In a comprehensive study of *E. radiata* growth in southwestern New Zealand, growth rates were measured bimonthly for 15 months at two wave-exposed outer coast sites and one wave-sheltered fjord site (Miller et al. 2011), the seasonal patterns of growth were similar across all sites, with higher rates (0.4 cm/day) during spring (September–October) compared 0.1 cm/day in winter. However, growth rates were not correlated to a particular environmental parameter (light, inorganic nitrogen supply and water motion). However, while spring growth rates were higher than those of other seasons, those in spring 1999 (0.2 cm/day) were half those of spring 1998, illustrating variations that may be driven by differences in the environment between years.

Growth rate can also be expressed as biomass accumulation (BA, g dw/alga/day) if the dry mass is measured (Fairhead & Cheshire 2004a). BA of individuals for sites in Australia and New Zealand range from 0.12 to 0.98 g dw/alga/day (see Table 4 in Fairhead & Cheshire 2004a, Miller et al. 2011). In southern New Zealand, BA was similar for the wave-exposed and sheltered sites and (similar to linear growth) was maximal in spring. At West Island, South Australia, BA followed a similar seasonal pattern to that observed in New Zealand, with spring and summer rates being about 4 times greater than those in winter. Also, BA was lower at 3 m compared to 5, 10 and 12 m: this was because the tissue at 3 m was less dense; that is, it had less mass per unit area and was not related to linear growth rate, which was greater at 3 m compared to the other sites. In contrast, in northern New Zealand (Novaczek 1984a) and Perth, Australia (Kirkman 1989), BA was similar for samples taken at different depths. Light and temperature can have positive effects on BA, but the strength of these relationships vary with season, being stronger in spring and summer (Bearham et al. 2013).

Adding knowledge of population density (individuals per square meter) provides an estimate of primary production (g dw/m/day). BA primary production rates range from 0.43 to 12.1 g dw/ind/day (Miller et al. 2011) and again, are in the range of other Laminariales. In a New Zealand fjord, kelp density at outer-coast wave-exposed sites was much greater than that of the inner wave-sheltered site, resulting in a wave-exposed BA production rate that was five times greater than that of the wave-sheltered site, despite there being no difference in growth rates (Miller et al. 2011). Similarly, BA production rate was greater in deep (~15 m) compared to shallow water, while growth rates were comparable (Novaczek 1984a, Kirkman 1989).

Measurements of net primary production (g C/m$^2$/day) for *E. radiata* are rare because carbon loss must be taken into account. Carbon loss due to tissue erosion can be measured using the hole-punch method (Mann & Kirkman 1981, de Bettignies et al. 2013b), and knowledge of tissue carbon content.

**Figure 4** Measurements of *Ecklonia radiata* growth and productivity can be taken using methods including (A) tagging plants and 'hole-punching' to measure growth of the primary blade, which can be converted to biomass accumulation, (B) Pulse amplitude modulated (PAM) chlorophyll fluorescence to measure the rate of transport of electrons through photosystem II, which is increasingly used as a proxy for gross photosynthesis and (C) photorespirometry chambers to measure oxygen metabolism. (All photographs by the authors.)

However, the release of dissolved organic carbon (DOC) has not been measured for *E. radiata* or most other kelps, even though this can be a major carbon loss. For example, 14% of *Macrocystis pyrifera* (Reed et al. 2015) and 26% of *Laminaria hyperborea* (Abdullah & Fredriksen 2004) production is released as DOC. To circumvent the limitations of *in situ* measurements, particularly relating to DOC, Rodgers & Shears (2016) used a physiological model to estimate primary production in relation to depth and season. The model showed that net primary production (NPP) was greater in shallow (6 m) compared to deep (14 m) water and was higher in summer (2.7–4.5 g C/m$^2$/day) compared to other seasons, with winter NPP close to zero at both depths. Of the few studies that have quantified erosion for *E. radiata* (Novaczek 1984a, Miller et al. 2011, de Bettignies et al. 2013b), results are difficult to compare because the methods used differ. However, one consistent finding is that erosion comprised a substantial proportion of the total biomass produced, a pattern consistent with kelps elsewhere (Krumhansl & Scheibling 2012). de Bettignies et al. (2013b) found that rates of erosion were highest during the austral autumn (when kelps grew slowly), and that this led to negative net production during this period. In contrast, in spring, kelps grew quickly and erosion was low, resulting in high net production. These patterns explained long-observed intra-annual trends in kelp biomass (e.g. Kirkman 1984, Wernberg & Vanderklift 2010). Whether via erosion or dislodgement, a high proportion of kelp production is exported beyond the kelp forest (see the section 'Community ecology of *Ecklonia* forests', later in this review, and Figure 8).

### *Photosynthesis and respiration*

Photosynthesis and respiration have mainly been measured in the laboratory on small pieces of blade tissue (e.g. Stæhr & Wernberg 2009), and only rarely on whole individuals in the field (but see Fairhead & Cheshire 2004a, Rodgers et al. 2015, Figure 4C). Primary productivity of *Ecklonia radiata* is within the range of other Laminariales (Fairhead & Cheshire 2004a,b). At West Island, South Australia, primary productivity was five times greater, at 3 m (maximum about 2400 μmol $O_2$/m$^2$/day) than at 10 m (500 μmol $O_2$/m$^2$/day) throughout the year. Although there were some differences in rates of productivity in different months, there was no clear seasonal pattern at either depth (Fairhead & Cheshire 2004a).

Photosynthetic parameters, derived from photosynthesis (*P*) versus irradiance (*E*) curves, are a simple tool that has been used in conjunction with pigment content to examine how *E. radiata* acclimates (photoacclimation) to various irradiances. $P_{max}$ is the maximum photosynthetic rate when light availability does not limit photosynthesis and the initial slope of the *P* versus *E* curve (α) is a measure of the light-harvesting ability at subsaturating irradiances. The compensation irradiance (*Ec*) is the irradiance at which net photosynthesis balances respiration, and $E_k$ is the light saturation point. A strong gradient of light is found along Doubtful Sound, a fjord in southwestern New Zealand and provides a natural laboratory for studying mechanisms of photoacclimation in *E. radiata*, which grows at sites with maximum irradiances ranging from 650 to 1250 μmols photons/m$^2$/s$^2$ (measured at a 1-m depth in November 2000, Miller et al. 2006). $P_{max}$ was similar at the five sites studied because the content of both chlorophyll *a* and accessory pigments was greater at low light compared to higher-light sites, which resulted in a greater ability to harvest light at low irradiances (i.e. increased α, Miller et al. 2006). Additionally, for the low-light sites, $E_k$ was lower than at the high-light sites, as was $E_c$ because of lower respiration rates. There was also a morphological acclimation, with blades being larger and thinner (i.e. greater surface area to volume ratio) at the low-light compared to high-light site, thought to reduce self-shading within the thallus.

Fairhead & Cheshire (2004b) studied photoacclimation of *E. radiata* in West Island, South Australia, at four depths during seven months of the annual cycle. The $P_{max}$ tended to be greater in winter (May and June) compared to other times of year, for the four depths (3, 5, 10 and 12 m) studied. Alpha (α) was steeper and $E_k$ lower in winter than summer, which is similar to the New Zealand fjord study (Miller et al. 2006). However, at West Island, the differences observed in $P_{max}$, α and $E_k$ were not explained by chlorophyll and accessory pigment content; although these parameters did vary with month, there were no clear patterns with season or depth.

Temperature affects all cellular processes, and therefore varying temperatures can influence photosynthetic and respiration rates. Respiration by *E. radiata* increases with increasing temperature, and adjustments of both $E_c$ and $E_k$ help maintain a positive carbon balance with increasing temperature (Stæhr & Wernberg 2009). The optimal temperature for net photosynthesis of *E. radiata* in Western Australia is 24°C, and rates decline at higher and lower temperatures, whereas respiration rates increase with increasing temperature between 0 and 30°C. The result is a thermal performance breadth ranging from 21.2°C to 26.5°C, and with relatively little variation across locations with different temperature regimes (Wernberg et al. 2016b). These tests, however, covered only a relatively narrow range of temperatures. In contrast to optimum temperatures, the temperature responsiveness differs between respiration and photosynthesis (Stæhr & Wernberg 2009, Wernberg et al. 2016b). Respiration rises faster than photosynthesis and peaks later, leading to a mismatch and inability to maintain positive carbon balance at higher temperatures. These differences likely have consequences for the capacity of these populations to respond to disturbances (Wernberg et al. 2010) and could be underpinned by genetic differences (Wernberg et al. 2018).

## *Carbon acquisition and pH*

Based on widespread patterns in carbon-stable isotopes (i.e. typical ranges are between −24 and −14: Fenton & Ritz 1989, Vanderklift & Bearham 2014), *Ecklonia radiata* is a bicarbonate using seaweed that employs a carbon-concentrating mechanism or mechanisms (CCMs) to increase the supply of $CO_2$ to the enzyme Rubisco, which in turn fixes $CO_2$ into organic material (Beer et al. 2014). In an experiment in which the supply of $CO_2$ was increased, simulating the supply predicted for 2100 (i.e. ocean acidification), the $\delta^{13}C$ of *E. radiata* became less negative (i.e. it increased), indicating greater uptake of $CO_2$ in the future (Britton et al. 2016). It has been hypothesised that greater $CO_2$ use in a future high-$CO_2$ ocean will enhance seaweed growth (Hepburn et al. 2011), but this may not be the case for *E. radiata,* as rates of photosynthesis and growth were unaffected by $CO_2$ supply in the laboratory (Britton et al. 2016) and in the field (Connell et al. 2018). This finding for *E. radiata* is similar to that of another Laminariales, *Macrocystis pyrifera*, which has at least two mechanisms for bicarbonate acquisition—an AE transporter plus external carbonic anhydrase (Fernández et al. 2014). However, for most seaweeds, including *E. radiata*, the types of CCM are unknown, but elucidating these mechanisms will be key to understanding responses to ongoing ocean acidification (Cornwall et al. 2017).

Numerous manipulative experiments that seek to examine the influence of pH on *E. radiata* have shown limited direct effects (Connell & Russell 2010, Connell et al. 2013, Provost et al. 2017, Connell et al. 2018). However, it may not be so much mean changes in pH that influence kelp, but rather normal diel fluctuations in pH that occur in supposedly healthy kelp forests (as a direct result of photosynthesis and respiration by the resident seaweeds), which benefit growth of juvenile sporophytes (Britton et al. 2016). In contrast, there is great potential for an increase in indirect effects of pH on *E. radiata* through competitive displacement (Connell et al. 2018), a result that appears commonly across widely different parts of the globe using contrasting methods (Connell et al. 2013). Carbon enrichment increases the growth of ephemeral algal species (turfs) which do not have CCMs but do have minor direct effects on *E. radiata* (Falkenberg et al. 2013a). This leads to a switch in competitive advantage, whereby turfs replace *E. radiata* (Connell et al. 2008b, Gorman et al. 2009). *E. radiata* forest collapse is worsened when the increased production of turfs is exacerbated by reduction in its consumption by herbivores (Connell & Ghedini 2015). What this means is that small cumulative increases in carbon enrichment drives a much greater consequence than would be predicted from linear effects measured between competitors (e.g. *E. radiata* versus turfs) because these interactions are embedded within a broader network of change that propagates collapse.

## *Nitrogen uptake, C:N ratios and enrichment*

Nitrogen is the nutrient that most commonly limits seaweed primary production. It is available in two dissolved inorganic forms, nitrate $\left(NO_3^-\right)$ and ammonium $\left(NH_4^+\right)$, the supply of which varies with season. Nitrate is available at higher concentrations in winter compared to summer, whereas ammonium is available at low concentrations year round (Hurd et al. 2014). *Ecklonia radiata* from Doubtful Sound, New Zealand, has nitrate uptake rates (at 10 μM) ranging from 0.13–1.6 μmol/gdw/s, compared to a slightly greater range for ammonium uptake of 0.07–3.0 μmol/gdw/s (Miller et al. 2006). In this system, nitrate and ammonium are available at similar concentrations (2–4 μM) for most of the year, and so make a similar contribution to primary production. However, this likely depends on the relative availability: *Ecklonia maxima* in South Africa takes up nitrate and ammonium simultaneously and at similar rates, but because the supply of nitrate in this upwelling system is much greater than that of ammonium, ammonium accounts for only 4% of total N acquired (Probyn 1985).

The ratio of tissue carbon to nitrogen (C:N) is a useful indicator of whether or not nitrogen is limiting primary production. Values of ~15–20 indicate nitrogen sufficiency for kelps, whereas those >20 indicate nitrogen limited growth. In southern New Zealand, C:N ratios of *E. radiata* range from 18 to 52 and are between 18 and 30 for most months, except between February and May when they can be >30 and >50 at wave-exposed and -sheltered sites, respectively (Miller 2004). In summer (i.e., December) in Western Australia, C:N ratios ranged from 25 to 44 and were positively correlated with temperature across a latitudinal gradient (Stæhr & Wernberg 2009). These results indicate that nitrogen may be limiting primary production throughout much of the year, with greater limitation during summer, at wave-sheltered and warm sites. Enrichment of nitrogen in South Australia caused the spring increase in biomass of *E. radiata* to triple (August–October), with a concomitant increase in $\delta^{13}C$ of tissue and decrease in the C:N ratio (Falkenberg et al. 2013b). These results are consistent with observations of the oligotrophic nature of the south coast (Connell 2007a), with high C:N ratios of kelp under ambient conditions indicating N-limitation, while the lower ratio under enrichment indicating lower N-limitation. Variation in such limitations among taxa have implications for the competitive balance of major ecosystem components under conditions of increased resource availability (Connell 2007b).

The transfer of nitrogen across ecosystem boundaries is considered one of the more important forms of natural resource subsidy, owing to its strong influence on both biological and abiotic characteristics of recipient systems (Polis et al. 1997). The degree to which nitrogen subsidies mediate kelp loss is contingent on both ambient and historical concentrations (Gorman et al. 2009) and the capacity of the system to assimilate additional nutrients (Marczak et al. 2007). Indeed, losses of *E. radiata* forests are greater where the difference in nitrogen availability between land and sea is larger (Gorman et al. 2009). The loss of *E. radiata* forests from nitrogen overloading represents the cumulative effect of failure of kelp to recover from pulse events (e.g. storms) that remove individuals or patches of individuals (Connell et al. 2008b). Eutrophication increases the accumulation of turfs and sediments following localised disturbances, preventing the recruitment of kelp (Gorman & Connell 2009). These localised impacts may be unconnected in time and space, but over many years, they coalesce and become substantial across broader areas (Connell et al. 2008a). Consumption by herbivores may buffer the expansion of turfs during nutrient enrichment (McAllister & Bornman 1972, Sarnelle 1992, Russell & Connell 2005) and other resource perturbations (Ghedini et al. 2015, McSkimming et al. 2015). By keeping turf abundance in check and maintaining turf-free space, herbivores facilitate *E. radiata* recruitment and persistence (Gorman & Connell 2009).

### *Temperature*

Laminarian kelps are generally considered cool-water organisms (see the section entitled ‘Phylogeny and distribution’, earlier in this review), but *Ecklonia* is the most temperature-tolerant genus in the order and many species are found in warm-temperate and subtropical waters. Biogeographically, *E. radiata* is found between about 8°C and 25°C (Bolton & Anderson 1994), and temperature is a significant determinant of the regional distribution of *E. radiata* (Wernberg et al. 2011a,b, Martinez et al. 2018) although physiological (adaptation) and biological (competition, herbivory) mechanisms can offset simple relationships between ocean temperature and local abundances (Connell & Irving 2008, Wernberg et al. 2010).

Metabolic processes such as photosynthesis and respiration show strong temperature dependency. In Western Australia, photosynthesis increases until about 24°C, after which it declines rapidly (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b). Respiration, on the other hand, increases beyond about 24°C, driving a mismatch at high temperatures that implies that the seaweeds cannot maintain a positive carbon balance at high temperature (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b). Physiological studies of sporophytes in Western Australia found only minor variation in optimum temperature across populations 6° latitude/4°C apart (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b), suggesting little local adaptation in adult sporophytes. Nevertheless, the temperature dependency of both photosynthesis and respiration varied considerably depending on the local environment with lower Q10 values under warmer conditions (photosynthesis Q10: 3.35–1.45 and respiration Q10: 3.82–1.65), presumably an adaptation to keep metabolic rates under control in warm environments (Wernberg et al. 2010). Temperature can also act antagonistically with other stressors such as ultraviolet radiation B (UVB). For example, Xiao et al. (2015) demonstrated that negative effects of higher UVB on photosynthesis and growth were alleviated at warmer temperatures, possibly due to induction of photo-repair. At higher temperatures and UVB, *E. radiata* also decreased accessory pigments in the thallus (Xiao et al. 2015).

In Australia, *E. radiata* sporophytes are generally larger, have more reproductive tissue, grow faster and have lower mortality in cooler than in warmer waters (Hatcher et al. 1987, Mabin et al. 2013). Reduced growth and productivity have also been associated with seasonally warm water (Fairhead & Cheshire 2004a,b, Bearham et al. 2013). Temperature also affects reproduction and gametophyte development (Novaczek 1984a,b,c, Mohring et al. 2014). The optimum temperature for gametophyte development is broad, but shows regional differences consistent with thermal adaptation (12°C–20°C, New Zealand, Novaczek 1984a,b,c, 18°C–22°C, South Africa, Bolton & Anderson 1987, 18°C–23°C, Australia, Mohring et al. 2014). Still, lethal temperatures for gametophytes appear to be well above maximum temperatures experienced in the field (Novaczek 1984a,b,c, Mohring et al. 2014) suggesting that this life stage is not limited by high temperatures. It is, however, possible that minimum temperatures for gametophyte growth and reproduction set the cool limit for the species (Novaczek 1984a,b,c).

Temperature can alter interactions among *E. radiata* and its competitors, grazers and associated predators. Intraspecific competition is weaker where water temperatures are warmer, and canopy cover facilitates rather than competes with recruits (Wernberg et al. 2010, Bennett et al. 2015b). Warming waters can also drive mismatches between consumption and predation, whereby urchin grazing on *E. radiata* increases but consumption pressure on urchins (by lobsters) decreases at higher temperatures, driving accelerated kelp loss (Provost et al. 2017). The interactive effects of temperature and $CO^2$ can indirectly affect *E. radiata* via positive effects on kelp competitors. For example, warmer temperatures increased the proliferation of turf competitors, particularly under elevated $CO^2$, which may inhibit kelp recruitment and recovery in future oceans (see the section entitled 'Recent changes and future threats', later in this review; also see Connell & Russell 2010). In conclusion, temperature affects all aspects of the biology of *E. radiata* from evolutionary scales and patterns of distribution through to contemporary impacts on physiology and biology. It interacts with other environmental and biological drivers through direct and indirect mechanisms to modify extant patterns and response to change.

## *Water motion: Waves*

Water motion is a fundamental environmental state condition that affects all marine organisms. In marine systems, waters are never stagnant, and like other seaweeds (Hurd 2000), hydrodynamic forces affect the performance of *Ecklonia radiata*. Tidal currents play a relatively minor role in most places where *E. radiata* is found, and wave exposure is by far the dominant hydrodynamic force affecting the species. *E. radiata* is found across a wide range of wave exposures (Phillips et al. 1997, Turner & Cheshire 2003, Goldberg & Kendrick 2004, Thomsen et al. 2004, Fowler-Walker et al. 2005, Fowler-Walker et al. 2006, Wernberg & Thomsen 2005, Wing et al. 2007, Smale et al. 2011, de Bettignies et al. 2012), but typically it becomes increasingly replaced by other canopy-forming seaweeds (*Cystophora* spp., *Sargassum* spp.) and turf-forming species at low wave exposures and by other canopy-forming seaweeds (e.g. *Scytothalia* and *Phyllospora*) or sessile invertebrates at very high wave exposures (Turner & Cheshire 2003, Coleman et al. 2008, Wernberg & Connell 2008).

Wave forces are essential to break down boundary layers around the thallus, remove waste products and increase nutrient uptake rates (Hurd 2000). However, during storms, wave forces can result in pruning (removal of part of the frond) or dislodgment (removal of the entire kelp) from the substratum. Fully grown *E. radiata* can withstand water velocities of 2–5 m/s (Thomsen et al. 2004, de Bettignies et al. 2013b). *In situ* biomechanical pull-tests show that *E. radiata* often break above the meristem (pruning) at a force of 150–250 N, suggesting that recovery could be possible. This occurred more frequently on hard (igneous rock) compared to soft (sedimentary rock) substrata (Thomsen et al. 2004). On soft substrata, such as limestone rock, adult kelps typically break at the reef, often removing part of the rock and thereby resetting succession (Thomsen et al. 2004). Biomechanical measurements and calculations also suggest that *E. radiata* recruits are a lot less limited by wave forces than adults, as drag increases disproportionally with frond size compared to the attachment strength (Thomsen et al. 2004). Consequently, break velocities for adult *E. radiata* (2–5 m/s) are much lower than that for recruits (10–25 m/s). Moreover, *E. radiata* holdfasts are often found in fused aggregates, which appear to decrease dislodgment frequency through morphological changes and thallus compaction during the drag phase of the wave cycle (Wernberg 2005).

It is commonly observed that kelps have substantial morphological changes to reduce drag and increase attachment strength in response to wave exposure. Several studies suggest that *E. radiata* respond to wave forces by being smaller, having narrow laterals and blades, fewer spines, larger holdfasts and thicker blades and laminae (Fowler-Walker et al. 2005, Wing et al. 2007, Miller et al.

2011). Still, not all studies have reported consistent effects of wave exposure on specific morphological traits (Wernberg & Thomsen 2005). One reason could be that at peak flow velocities, *E. radiata* compacts (Wernberg 2005) such that only size (surface area), not morphological traits, influences dislodgement and thereby survival (de Bettignies et al. 2013a). A tagging study of thousands of *E. radiata* from Western Australia found relatively low and constant dislodgement rates across seasons and wave exposures (de Bettignies et al. 2015), despite stronger wave action in winter and on exposed reefs. It was suggested that winter reduction in biomass through frond erosion, reduces kelp size (and hence drag) and thereby decouples the expected relationship between dislodgment, season and wave exposure (de Bettignies et al. 2013b, de Bettignies et al. 2015), as has also been indicated for other laminarian species (Johnson & Mann 1986).

While most biomechanical studies of *E. radiata* have focussed on 'healthy' kelps, small perforations are common in kelp thalli (cf. Figure 9). Tissue break-force tests show that holes and tears to the *E. radiata* thallus reduces the strength, extensibility, toughness and stiffness of the tissue by up to 82% and can dramatically increase susceptibility to breakage during storms (de Bettignies et al. 2012). These wounds can be found at all wave exposures, but they are most prevalent in early winter, suggesting that wounds accumulate over summer when waves are generally small (Lemm et al. 1999) and that wounded parts of the thallus break off as storms pick up in autumn and winter (de Bettignies et al. 2012). The ecological implication is that this pruning reduces kelp size and hydrodynamic drag and ultimately lowers the risk of fatal dislodgment during severe winter storms. Hence, where storms drive loss, they tend to sever individuals from above the holdfast rather than detaching the holdfast from rock (Goodsell & Connell 2005a).

### *Sediments and sedimentation*

Sedimentation and turbidity are among a broad spectrum of land- and ocean-based activities, coupled with continued growth of the human population (Ruffin 1998, Airoldi 2003) and migration to coastal areas, that are driving unprecedented and complex changes in water chemistry (Boesch et al. 2001) and ecology of kelp forests (Connell 2007b, Filbee-Dexter & Wernberg 2018). *Ecklonia radiata* forests generally prevent the accumulation of sediment and turfs under their canopy (Melville & Connell 2001, Connell 2003a, Wernberg et al. 2005) and adult plants can survive and grow under a range of sediment loads. However, there appears to be a bottleneck at attachment and burial of microscopic stages (cf. the section entitled 'Ecophysiology and environmental drivers', earlier in this review) by sediment (Connell 2007b). Hence, *E. radiata* is rare or sparsely distributed in areas with extensive sedimentation, but variations in sedimentation with light and abrasion provide a strong set of physical conditions (Irving & Connell 2002, Connell 2005) that drive heterogeneity among various canopy types (Turner & Cheshire 2003, Connell 2007a).

### *Substratum and space*

Hard substratum is of fundamental importance to kelp, providing space for settlement and growth of the holdfast structure. *Ecklonia radiata* can create extensive monospecific forests on a variety of rock types, including sandstone, limestone, granite and basalt (Underwood et al. 1991b, Wernberg et al. 2003b, Thomsen et al. 2004, Tuya et al. 2008, Tuya et al. 2009), with one study suggesting that densities are higher on limestone than granite reefs (Harman et al. 2003). *E. radiata* can be found on pebbles, boulders and large extensive reefs, where the minimal size of inhabitable rock can be predicted from the thallus size (which scale with attachment strength), its drag and wave exposure (the imposed force) (Thomsen et al. 2004, Thomsen & Wernberg 2005). *E. radiata* can also be dominant (with densities of >25 kelp/m$^2$) regardless of topographic complexity, ranging from simple to very complex reef topographies (Toohey 2007), although with higher density on low- compared to high-relief reefs (Harman et al. 2003). *E. radiata* readily settle on artificial substrates (e.g. Smale et al. 2011) and can often be found on the vertical surfaces of coastal infrastructure, such as pier-pilings and seawalls (Marzinelli 2012, Marzinelli et al. 2018). No studies have looked at the importance of microtopography, such as cracks and crevices, although such features likely increase the settlement and attachment strength of gametophytes and provide a refuge from predators (Franco et al. 2015, Bolton et al. 2018).

## Life history, dispersal and recruitment

### *Life cycle, reproduction and phenology*

*Ecklonia radiata* has a typical laminarian life cycle, with alternations between a microscopic haploid gametophyte stage and macroscopic diploid sporophyte stage (Figure 5). *E. radiata* does not produce sporophylls. Instead, zoospores develop within the tissue of the main lamina and basal part of the laterals. When reproductively mature, sporogenic tissue becomes visible as slightly discoloured raised patches (Figure 5A). Zoospore production in *E. radiata* can be as high as ~1000–2000/mm$^2$ of lamina (Mohring et al. 2014) and seasonal timing of zoospore production appear to vary geographically. In Western Australia, peaks in both the presence of sori (Figure 5A) and zoospore (Figure 5B) release occur from mid-summer (January) to the end of autumn (May) and are positively correlated with seawater temperature and occur synchronously across the coast (Mohring et al. 2013a,b). It has been suggested that the timing of maximum zoospore production and release occurs when conditions are optimal for gametophyte germination, growth and subsequent sporophyte development, and this may be a strategy to increase success against competing algae (Mohring et al. 2013b). In contrast, in Tasmania, *E. radiata* has sori and produces zoospores throughout the year, but often with peaks in autumn and winter when seawater is coldest (Sanderson 1990, M. Tatsumi, unpbl. data). However, even though zoospores are produced throughout the year in Tasmania, they are not always viable—particularly during the summer (M. Tatsumi, unpbl. data). As well as external environmental factors, the amount of zoospores released per plant will reflect lamina morphology/size, with lamina length being a strong predictor of the amount of reproductive tissue (Mabin et al. 2013). The onset of sorus production appears to depend on thallus size and season, not age (Novaczek 1984a). In New Zealand, frond surface area needed to be at least 300 cm$^2$ and stipe diameter around 14 mm (Novaczek 1984a) for thalli to become reproductive. The fact that size (lamina length) is a strong predictor of the amount of reproductive tissue indicates that morphological changes in response to human impacts (e.g. warming) are likely influence the overall reproductive capacity in *E. radiata* (Mabin et al. 2013).

Once *E. radiata* zoospores are released, they have the ability to swim for at least 24 h (although they often do so for only 1–2 h), until they settle onto the substratum and germinate into male or female gametophytes (Figure 5C). Given the size of both zoospores (~5 μm) and gametophytes (~100–400 μm; Mabin et al. 2013, Mohring et al. 2014), the settlement of *E. radiata* is usually difficult to measure directly, and little is known about the processes that influence these very early life history stages in the field. The understanding of gametophytes is largely limited to laboratory studies. Gametophyte recruitment (i.e. densities) can be quantified in the laboratory at various times post-settlement up until the fertilisation of oogonia (Mabin et al. 2013, Mohring et al. 2013b, Mohring et al. 2014, Tatsumi & Wright 2016). After 12–15 days (by which time gametogenesis has typically occurred), successful recruitment of gametophytes (i.e. as a percentage of zoospores released) ranges between 0% and 50% (Mohring et al. 2013b). Gametophyte recruitment peaks between 16°C and 20°C and generally declines with increasing temperature (Mohring et al. 2013a, Mohring et al. 2014), increasing light (above 40–60 μmol photon/m$^2$/s) and decreasing zoospore density (Tatsumi & Wright 2016). Nonetheless, *E. radiata* gametophytes appear to be among the most temperature tolerant in the Laminariales, with an upper temperature tolerance of 26°C (New Zealand, Novaczek 1984a; and South Africa, Bolton & Anderson 1987) to 28°C (Australia, tom Dieck 1993). The size of gametophytes varies between regions and is generally greatest at temperatures between 13°C and 15°C (New Zealand, Novaczek 1984a), 20°C–22°C (South Africa, Bolton & Anderson 1987;

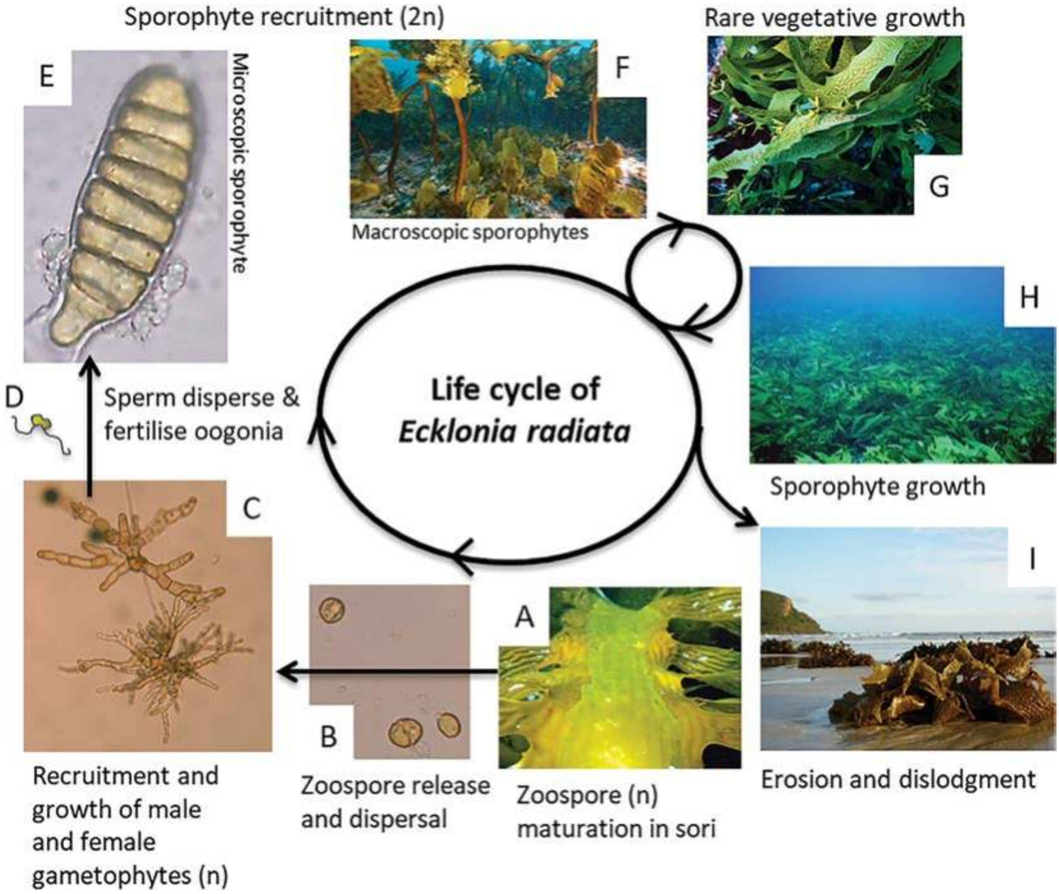

**Figure 5** Life cycle of *Ecklonia radiata* from sorus tissue to kelp forest and detritus. (A) Macroscopic sporophytes become reproductive bearing sori (seen as slightly raised tissue) that release motile zoospores (B). Zoospores settle and grow into separate male and female gametophytes (C). (D) Sperm disperse and oogonia on female gametophytes are fertilised and juvenile (E) microscopic and (F) macroscopic sporophytes (in the understorey) develop. Sporophytes recruit and grow through stages 1, 2 and 3 (Kirkman 1981), often forming (H) dense, monospecific forests. (G) In some populations, known only in the Capes region in Western Australia, sporophytes can reproduce vegetatively. (I) Sporophytes are often dislodged or eroded during storms and detritus transported into other habitats where they provide important spatial subsidies (see the section entitled 'Community ecology of *Ecklonia* forests'). (All photos by the authors and Nahlah Abdullah Alsuwaiyan.)

and Western Australia, Mohring et al. 2013b, 2014), 16.5°C–22°C (Tasmania, Mabin et al. 2013) and at higher light levels (Novaczek 1984b, Tatsumi & Wright 2016). Thus, it appears overall that gametophyte recruitment is susceptible to increasing temperatures and light, but those conditions result in better growth. In the field, low-light conditions that are best for gametophyte recruitment are found beneath the *E. radiata* canopy; light beneath the canopy varies as a function of season, time of day and canopy cover, but it is typically <100 μmol photon/m$^2$/s and can be reduced by as much as 95% (<10 μmol photon/m$^2$/s) compared to above the canopy (Wernberg et al. 2005, Tatsumi & Wright 2016). Temperature and light also influence egg production, with with most rapid egg production for South African *E. radiata* (as *E. biruncinata*) in the range of about 15°C–19°C, but eventual maximum egg production per female at about 22°C (Bolton & Anderson 1987), a similar pattern is also seen for *E. radiata* in New Zealand (Novaczek 1984c). In addition, other factors including sedimentation, scour, grazing and pollutants are likely to affect these small gametophytes, but studies are scant.

Sporophytes are visible after 30–35 days (laboratory-grown microscopic sporophytes are clearly visible at this time, about 500 µm; Figure 5E). Recruitment appears to be negatively affected by high temperature (no sporophyte development at temperatures >22°C; Mabin et al. 2013) and low light (no sporophyte development <10 µmol photons/m$^2$/s; Tatsumi & Wright 2016). Bolton & Anderson (1987) measured growth of 5 week-old sporophytes (c.1 mm in length) in South African *E. radiata* (as *E. biruncinata*) and found that they survived and grew over 2 weeks from 4°C to 26°C, with a broad optimal range for growth from 15°C to 22°C. Again, knowledge of processes affecting young sporophytes are biased towards laboratory studies due to the difficulties in finding and measuring microscopic states in the field. Although very small sporophytes have been measured in the field using an underwater microscope (Kennelly & Underwood 1984), recruitment in the field is usually measured when sporophytes are visible to the naked eye (i.e. stage 1 sporophytes, Kirkman 1981, Figure 5F) and have already undergone early post-recruitment mortality. Nevetheless, survivorship during the transition from microscopic to macroscopic recruitment in *E. radiata* has been estimated as ~0.6% (Tatsumi & Wright 2016), which is similar to other kelps for which this transition has been measured in the field (Schiel & Foster 2006).

Surviving *E. radiata* sporophytes are predominately perennial. The exception is at the Houtman Abrolhos Islands, off Western Australia, where plants could be annual (Hatcher et al. 1987). Stipe growth ring analyses suggests that individuals can be up to 10 years old in some places (Novaczek 1981), although in many other places, individuals are considerably younger, with maximum ages of 2–4 years (Larkum 1986, Andrew 1993, Wernberg 2005). Demographic modelling of tagged kelp populations from the same site studied by Novaczek indicate that while average age of mature plants in undisturbed deep water stands may reach 7 years (Haggitt 1999), disturbances such as dieback (Cole & Babcock 1996) shorten longevity to around 3 years and even as short as 1 year in shallow water stands (Haggitt 1999).

Although *E. radiata* generally exhibits a typical alternation of generations (haplodiplontic) life history strategy, vegetative reproduction from the thallus Has been described in one population from Western Australia (Coleman & Wernberg 2018). Vegetatively reproducing sporophytes of *E. radiata* (Figure 5G) were formerly identified as a separate species, *E. brevipes*, first described from New Zealand (Huisman 2000), but recent genetic studies have revealed that Australian *E. radiata* and Australian *E. brevipes* are genetically similar and likely a single species (Rothman et al. 2015). Taxonomic relationships of the Western Australian '*brevipes*' variant to the type locality of *E. brevipes* from New Zealand remains unknown. Despite strong morphological differences, *E. radiata* and *E. brevipes* are only weakly genetically differentiated where they co-occur in Western Australia, likely because *E. brevipes* can still undergo a haplodiplontic life cycle and interbreed with *E. radiata* (Coleman & Wernberg 2018). Hence, it is likely that *E. brevipes* is a vegetatively reproducing morph of *E. radiata* and it is treated as such here. The propensity for vegetative propagation of this morph is huge, with up to 20 small, clublike haptera (rudimentary holdfasts) produced on the margins of secondary laminae of each adult sporophyte (Coleman & Wernberg 2018). Although a similar form of vegetative reproduction has been described from drift *E. radiata* from New Zealand (Lindauer 1945), what is unique about Australian *E. radiata* is that vegetatively produced haptera eventually make contact with the substratum, attach to rocks by lodging in cracks and crevices and are subsequently torn off the parent plant, creating a new clonal individual (Lindauer 1945, Lindauer et al. 1961) and becoming a functional part of the local kelp forest community. This mode of vegetative reproduction is unique among seaweeds and higher plants because it involves the reversal in polarity of growth and meristematic tissue, with the apex of the thallus becoming the holdfasts of new individuals (Lindauer 1945).

## *Dispersal and population connectivity*

Dispersal and gene flow are critical ecological processes that connect populations and facilitate population recovery and persistence. Gene flow within and among populations ensures adequate genetic diversity to allow populations to respond to changing environmental conditions and stressors. *Ecklonia radiata* can disperse via three modes; zoospores, sperm and detached fertile drift material. There are few field studies on *E. radiata*. Studies on spore and sperm dispersal in other Laminariales suggest that sperm only disperse the small distances (centimetres) over which pheromones from the female gametophyte are effective (Reed 1990, Maier et al. 2001), and this is perhaps why self-fertilisation is common (Raimondi et al. 2004). Dispersal of zoospores (Reed et al. 1988) and detached fertile drift material (Hernández-Carmona et al. 2006) are the likely modes of longer distance dispersal. Zoospores may disperse widely within local populations (kilometres; Gaylord et al. 2002, Reed et al. 2004, Gaylord et al. 2006) but rapidly decline thereafter (among reefs). Similarly, fertile drift material of *E. radiata* is negatively buoyant and may disperse over long distances only via rafting with co-occurring buoyant species (e.g. *Sargassum* spp.).

Given the microscopic size of propagules, directly measuring dispersal is difficult. Dispersal measurements rely on direct observations of recruitment or indirect genetic methods. These latter techniques estimate gene flow and dispersal in sporophytes (microscopic gametophytes have never been observed in the field), so the relative contribution of dispersal modes is unknown, and each may play a key role in the population genetics of *E. radiata*. Population genetic studies on *E. radiata* using neutral microsatellite markers (Dolman & Coleman 2009) have identified that genetic structure around the Australian continent is weak, suggesting widespread gene flow that is mediated by the strength and direction of prevailing ocean boundary currents (Coleman et al. 2009, Coleman et al. 2011b, Figure 6) acting on shallow phylogeographic histories (Durrant et al. 2015). Strong relationships exist between the relative strength of each of Australia's boundary currents and overall genetic structure ($F_{ST}$) of *E. radiata* populations within those currents (Coleman et al. 2011b (Figure 6), Wernberg et al. 2018). Moreover, continental scale estimates of pairwise population genetic structure ($F_{ST}$) are positively correlated with oceanographic dispersal time (Coleman et al. 2013a, Figure 6).

On regional scales, dispersal and gene flow of *E. radiata* populations are also positively correlated with oceanographic dispersal time and the strength of prevailing currents, but the

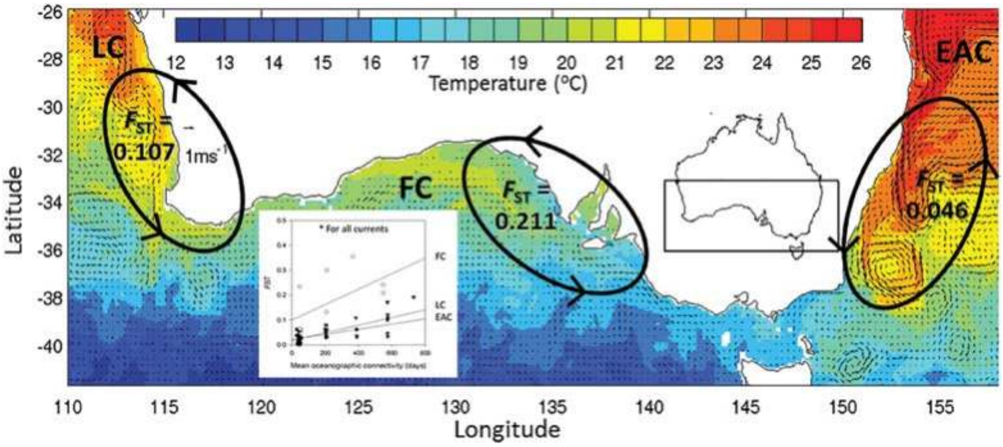

**Figure 6** Genetic estimates of population connectivity ($F_{ST}$) of *E. radiata* within each of Australia's boundary currents: The East Australian Current (EAC), the Flinders Current (FC) and the Leeuwin Current (LC). Overlaid on an example of current strength, direction and temperature over a 6-day period in the austral autumn (Adapted from Coleman, M.A. et al. 2011b. *Journal of Ecology* **99**, 1026–1032). The inset graph shows positive correlations between mean oceanographic connectivity time and genetic structure ($F_{ST}$) within each boundary current. (Adapted from Coleman, M.A. et al. 2013a. Temperate shelf water dispersal by Australian boundary currents: implications for population connectivity. *Limnology and Oceanography: Fluids and Environments*, 2013. **3**, 295–309. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission.)

complexities of latitude and effective population size are apparent (Coleman et al. 2009). For example, populations of *E. radiata* at the low-latitude margins on both the east and west coasts of Australia have lower genetic diversity (expected heterozygosity and number of alleles), suggesting lower effective population size and limited dispersal (Coleman et al. 2011b, Wernberg et al. 2018). This is likely a result of limited connectivity from higher latitudes due the predominately poleward flow of boundary currents, as well as fragmentation of populations because rocky reef habitat is limited (New South Wales, Coleman et al. 2011a) or populations have undergone declines (Western Australia; Smale & Wernberg 2013, Wernberg et al. 2013a, 2016a, Provost et al. 2017, Vergés et al. 2016). Regardless, the erosion of genetic diversity within these populations combined with limited and declining connectivity (Coleman et al. 2017) confer on low-latitude *E. radiata* populations a limited ability to respond to climatic change and disturbance (Wernberg et al. 2010, Wernberg et al. 2018).

Dispersal and gene flow in seaweeds are often determined by local factors, including coastal topography such as bays, beaches and river mouths (e.g. Faugeron et al. 2001, Billot et al. 2003, Coleman & Brawley 2005b, Coleman et al. 2011a, Muhlin et al. 2011, Coleman et al. 2019), position on the shore (Engel et al. 2003) and other barriers to dispersal (Coleman & Brawley 2005a, Durrant et al. 2015, Durrant et al. 2018). However, the role of these small-scale processes in influencing dispersal and connectivity in *E. radiata* are less well understood. Coastal topography (the presence of bays and estuaries) does not appear to limit dispersal in open coastal populations of *E. radiata* (Coleman 2013). However, prevailing patterns of water movement within estuaries (waves versus tides) may influence scales of dispersal (Coleman 2013, Coleman et al. 2019). A focus on small-scale studies and more powerful genetic markers (e.g. single-nucleotide polymorphisms) may be required to properly discern spatial patterns of genetic structure in *E. radiata*. Given its key role as a foundation species throughout its range, this information will be important to consider in marine protected area (MPA) planning (Coleman et al. 2011a, Durrant et al. 2014) and other conservation initiatives, such as rehabilitation (Campbell et al. 2014a, Wood et al. 2019).

Understanding patterns of dispersal and gene flow in *E. radiata* are in their infancy, and we know little from its range outside of Australia. Further, power to detect subtle genetic structure can now be greatly enhanced with advances in technology such as next-generation sequencing, which allows large sections of the genome to be interrogated via methods such as genotyping by sequencing (GBS; e.g. Elshire et al. 2011). These modern genetic techniques, which also examine functional areas of the genome potentially under selection, will pave the way for a more holistic understanding of *E. radiata* ecology and response to environmental change.

## *Settlement and recruitment*

Settlement in benthic marine species is usually recognised as the termination of the pelagic phase (dispersal, as discussed previously) and the beginning of the benthic phase, while recruitment involves the survival of settled individuals to a defined point in time, often when they can be seen in a population (Keough & Downes 1982, Rodriguez et al. 1993). Thus, for *Ecklonia radiata,* settlement can be defined as the attachment of planktonic zoospores to the benthos and their initial morphogenetic changes into male and female gametophytes, while recruitment includes the subsequent growth and survival of gametophytes and the development of the sporophyte (the latter grows from the oogonia on the female gametophyte after fertilisation of the oogonia by antherozoids). Given that little is known about the settlement of gametophytes, other than from laboratory studies (cf. the section entitled ‘Ecophysiology and environmental drivers’, earlier in this review), here, we focus on the recruitment of sporophytes into macroscopic *E. radiata* populations and the factors that influence them.

The ontogenetic development of the macroscopic sporophytes can be classed into three life stages based on thallus complexity and gross morphology; stage 1 (main thallus up to 15 cm), stage 2 (15–70 cm) and stage 3 (20–90 cm) (Kirkman 1981). Densities of macroscopic *E. radiata* recruits in the field vary markedly in space and time, with substantial small-scale spatial variation in recruit densities on scales of metres and kilometres (Wernberg 2009), indicating that a range of processes acting on those scales are likely to influence recruitment patterns. These processes include canopy loss (from storms) and increased light, temperature, scour, sedimentation, competition with understory algae and grazing. Recruitment in *E. radiata* has been described as seasonal, with high recruitment into clearings when gaps in the canopy form in winter (Kennelly 1987b) or spring (Schiel 1988), but slow recruitment when clearings are opened up at other times of the year. In some cases, if canopy removal occurs when spore production is low (e.g. late spring) and remaining sporophytes are sparse, then development of turf algae can minimise or prevent subsequent recruitment of *E. radiata* (Kriegisch et al. 2016). In Australia and New Zealand, stage 1 recruits appear in greatest abundance in October–November (early spring) and grow through stage 2 to stage 3 adults in 3–6 months depending on light levels (Kirkman 1981, Novaczek 1984a, Schiel 1988). The size and morphology of stage 3 kelps varies greatly from place to place (Wernberg et al. 2003a) but also exhibits seasonal variations as a consequence of growth in spring and summer and erosion in autumn and winter (Kirkman 1981, Kennelly 1987b, Wernberg & Vanderklift 2010, de Bettignies et al. 2015).

As in the laboratory for microscopic sporophytes, high light has positive effects on macroscopic sporophytes in the field. A number of studies have shown increased recruitment of *E. radiata* under increased light following the creation of experimental gaps in the canopy (Kirkman 1981, Kennelly 1987b, Goodsell & Connell 2002, Carnell & Keough 2014, Flukes et al. 2014). However, the scale of sporophyte removal is another important consideration because if the canopy becomes too sparse, light too high or both, then lack of spores and development of turf algae (in response to elevated light and absence of sporophyte blades sweeping the substratum) can lead to collapse of kelp recruitment (Kriegisch et al. 2016). Where the opening of gaps in the canopy results in elevated recruitment, it is not known whether these patterns are the result of zoospore settlement and subsequent sporophyte recruitment after gap creation or the postrecruitment growth of existing dormant microscopic gametophytes and sporophytes (Carney & Edwards 2006) that respond rapidly to the increased light. However, the effects of increased light appear to interact with temperature: On large scales in southwestern Australia, increased recruitment and post-recruitment growth occurred in zero canopy (high-light) environments at cooler sites, but the opposite result occurred at sites that were 2°C–4°C warmer (Wernberg et al. 2010). The changes to the subcanopy light environment can also have indirect negative effects on *E. radiata* recruits as higher light also increases the abundance of understory algae (Toohey et al. 2004, Flukes et al. 2014) which can inhibit *E. radiata* recruitment (Kennelly 1987a, Tatsumi & Wright 2016). This inhibition can occur via competition for light, or when turf algae enhances sedimentation, which may further inhibit sporophyte recruitment (Kennelly 1987b, Connell 2003b, Connell 2005, Valentine & Johnson 2005a,b, Gorman & Connell 2009).

Determining post-recruitment mortality (stage 1, Kirkman 1981) requires tagging recruits in the field and following them through time. This has only been done a handful of times for *E. radiata*. Wood (1987) followed tagged recruits for 7 months in three experimental treatments and found that post-recruitment mortality ranged from 86% in an unmanipulated (full-canopy) treatment, 58% in a canopy-removal treatment to 24% in a canopy-removal treatment with shading. The post-recruitment mortality of tagged macroscopic recruits can be quite low. For example, survivorship of recruits to 30 days after canopy clearing was typically 70%–90%, being higher on topographically simple compared to complex reefs (Toohey & Kendrick 2007). After canopy removal, post-recruitment mortality does not appear to be due to physical removal of thalli from storms, but it has been attributed to photo-inhibition on exposure to high light (Wood 1987, Toohey & Kendrick 2007). In natural stands of *E. radiata* in northeastern New Zealand, the annual probability of survival for recruits was 17% based on 526 tagged recruits monitored quarterly (Haggitt 1999).

## Community ecology of *Ecklonia* forests

*Ecklonia radiata* has a wide range of direct and indirect effects on other species by providing an arena where they can find resources and allies and avoid stress and enemies (Figure 7). Underpinning these ecological services are various forms of mutualism, habitat provision and modification and interaction chains such as trophic cascades, competition cascades and facilitation cascades (Thomsen et al. 2010).

### *Non-trophic ecological processes*

Non-trophic direct and indirect facilitation processes associated with *Ecklonia radiata* have been documented from biogeographical and landscape scales (Fowler-Walker & Connell 2002, Anderson & Millar 2004, Irving et al. 2004b, Tuya et al. 2009, Vanderklift et al. 2009) to individuals and small patches (Taylor & Cole 1994, Taylor 1998) to smaller sub-individual scales such as holdfasts (Smith et al. 1996, Goodsell & Connell 2002, Anderson et al. 2005a, Anderson et al. 2005b, Coleman et al. 2007, Goodsell & Connell 2008, Smith et al. 2014).

*Ecklonia radiata* provides fundamental habitat space for many sessile and mobile species. For example, diverse microscopic bacterial films, protists and algae coat the thallus surface (Mazure & Field 1980, Russell et al. 2005, Marzinelli et al. 2015a) and macroscopic epiphytes and sessile animals are abundant especially on older parts of the thallus and the holdfast (Fletcher & Day 1983, Jennings & Steinberg 1997, Russell et al. 2005, Marzinelli et al. 2009). These communities of sessile epibionts are generally more abundant on *E. radiata* from areas of relatively low water motion or light levels, on artificial structures like pilings (Marzinelli et al. 2009, Marzinelli et al. 2011) and in areas with high nutrient levels (Russell et al. 2005). For example, epiphytes are typically less common under high-wave action, as fronds are abraded and cleaned by whiplash (Fletcher & Day 1983). Mobile epibionts on *E. radiata* are relatively sparse compared to canopy-forming fucoid seaweeds with finer branching structure

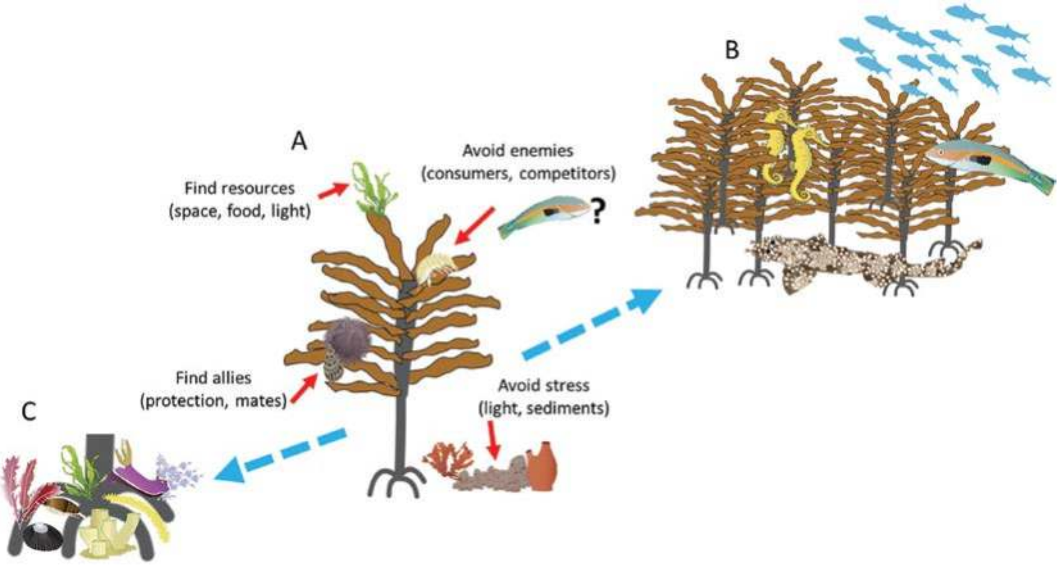

**Figure 7** Mechanisms of non-trophic facilitation. (A) *Ecklonia radiata* provides ecological services to other species including stress and enemy avoidance and resource and ally provisioning. These services scale from (A) individuals up to (B) patch and landscape scales and (C) down to sub-individual structures of *E. radiata*. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/.)

(Taylor & Cole 1994, Taylor 1998, Tuya et al. 2008, Marzinelli et al. 2016), and epibiont diversity lower (Marzinelli et al. 2016, Coleman & Wernberg 2017). Nevertheless, the highly variable morphology of *E. radiata* (Wernberg et al. 2003a, Fowler-Walker et al. 2006, Wernberg & Vanderklift 2010) may increase the number of microhabitats and thereby allow for co-existence of more diverse communities of sessile and mobile species, as shown for crinkled *E. radiata* fronds that were inhabited by more epibiota compared to smooth fronds (Fletcher & Day 1983, Jennings & Steinberg 1997, Fowler-Walker et al. 2005).

Epibiota on *E. radiata* also varies across space and time (Taylor 1998) with higher animal densities recorded at intermediate depths (6 m, with mean densities up to 200 animals per 100 g WW alga) (Table 2), perhaps because of variation in water motion and sedimentation with depth (Taylor & Cole 1994). Herbivorous gastropods can be highly abundant in *E. radiata* forests in northern New Zealand (Freeman & Creese 2011), but they tend to be rare at offshore islands (Choat & Schiel 1982, Shears & Babcock 2004). Similarly, gastropod assemblages are more abundant and species-rich in *E. radiata* forests on inshore than offshore reefs in Western Australia and vary across latitudes (Tuya et al. 2008, Wernberg et al. 2008).

Positive effects on epiphytes can lead to facilitation cascades becasue high *E. radiata* epiphyte loads can increase the abundance of mesofauna (Jennings & Steinberg 1997). However, once a sessile species has colonised *E. radiata*, increased competition may also occur, such as when epiphytic bryozoa outcompete epiphytic hydroids (Fletcher & Day 1983). Mobile species inhabiting *E. radiata* fronds are typically dominated by crustaceans, gastropods and polychaetes but most of them are generalists and can also be found in other habitats (Fletcher & Day 1983, Taylor & Cole 1994, Jennings & Steinberg 1997, Taylor 1998).

Kelp forests provide an arena to find intraspecific or interspecific allies, such as through facilitation cascades (Thomsen et al. 2010, Bell et al. 2014, Figure 7). In these cascades, *E. radiata* is the primary foundation species, facilitating intermediate species, through chemical (Steinberg 1984, 1985) or physical (Amsler et al. 1999) mechanisms, and thereby increasing the performance and survival of focal species (associational defences). For example, Bell et al. (2014) documented an intricate facilitation cascade whereby the sea urchin *Holopneustes purpurascens*, with its tube feet, rearranged the architecture of *E. radiata*'s fronds to create so-called ‘safe houses’ for the snail *Phasianotrochus eximius*, which thereby experienced less predation and dislodgement from waves. In addition, *E. radiata* can provide physical habitat where organisms find mating partners, such as weedy seadragons, *Phyllopteryx taeniolatus*, inhabiting *E. radiata* forests in New South Wales, Australia (Sanchez-Camara & Booth 2004).

Like other habitat-forming species, *E. radiata* can provide a space to avoid enemies (competitors and predators). Most enemy-avoidance mechanisms are direct, as small mobile animals can simply escape predation by hiding between blades and holdfasts (Smith et al. 1996, Goodsell & Connell 2002, Anderson et al. 2005b, Coleman et al. 2007). Because many of these small, mobile species are also herbivores, it can be difficult to separate whether the main facilitation mechanisms (in addition to direct feeding on *E. radiata*) are feeding on biofilms and epiphytes attached to *E. radiata*, or whether they are engaging in predator avoidance. Thus, similar to finding allies, proposed mechanisms for avoiding enemies have received little experimental research scrutiny. Further, some studies show that predation risk for some species is greater inside structurally complex *E. radiata* habitats than in nearby unvegetated habitats (Farina et al. 2014), suggesting that *E. radiata*'s role in mediating predator avoidance is highly species-specific.

Canopy-forming seaweeds, like *E. radiata*, may facilitate other species by reducing abiotic stress, in particular through frond abrasion and scouring, sedimentation, UV light and natural light—and possibly water motion and temperature as well (e.g. Bennett & Wernberg 2014, Bennett et al. 2015b). Light absorption by *E. radiata* results in a darker sub-canopy environment with less UV stress to provide a more benign habitat for light sensitive understory species (Kennelly 1989, Connell 2003a, Irving et al. 2004a, Wernberg et al. 2005, Marzinelli et al. 2011, Coleman & Kenelley 2019). For example, removal of *E. radiata* canopies results in rapid bleaching, reduced

**Table 2** Number of supported species/taxa associated with various structural components of *Ecklonia radiata*

| Region | Location | Number of supported species/presence | | | | | | | | | Study |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Understory/ canopy | Holdfast | Epibiota | Microbial | Macroinverts | Sponges | Fish | Bryzoans | Annelids | |
| Australia | Continental | X | | | X | | | | | | Connell & Irving (2008), Irving et al. (2004b), Marzinelli et al. (2015a) |
| Australia | WA | 82 | 160 | | | X | | X | | | Coleman et al. (2007), Crawley & Hyndes (2007), Harman et al. (2003), Toohey (2007), Toohey et al. (2004), Toohey & Kendrick (2008), Tuya et al. (2008, 2009), Wernberg et al. (2003a,b, 2005), Kendrick et al. (1999) |
| Australia | SA | 16 | | | | X | | X | | | Baker & Edyvane (2003), Connell (2003b), Daume et al. (1999), Fowler-Walker & Connell (2002, 2007), Goodsell & Connell (2005b), Goodsell et al. (2004), Irving & Connell (2006), Jenkins & Wheatley (1998), Melville & Connell (2001) |
| Australia | TAS | 51 | | | | X | 1 | X | 1 | | Edgar & Barrett (1999), Flukes et al. (2014) |
| Australia | VIC | 9 | | 37 | | 5 | | X | 1 | 1 | Fletcher & Day (1983), Jones (1992), O'Hara (2001) |
| Australia | NSW | X | 385 | 8–11 | X | X | X | 35 | | | Andrew, N. L. (1993), Bell et al. (2014), Curley et al. (2002), Ettinger-Epstein & Kingsford (2008), Fulton et al. (2016), Marzinelli et al. (2009, 2011, 2012, 2014, 2016, 2018), Marzinelli (2012), Roberts & Scanes (1999), Smith (2000), Smith & Simpson (1992), Smith et al. (1996), Smith & Simpson (1993), Steinberg (1995a), Wright et al. (1997), Zagal et al. (2013) |
| New Zealand | North East | | 351 | | | | | 42 | | | Anderson et al. (2005a,b), Anderson and Millar (2004) |

photosynthesis of both encrusting coralline algae (Irving et al. 2004a) and foliose red algae (Toohey et al. 2004, Wernberg et al. 2005) or both. Wave forces result in kelp blade whiplash and abrasion of the bottom, and thereby inhibit sediment accumulation (Kennelly 1989, Connell 2003a, Toohey et al. 2004, Wernberg et al. 2005, Irving & Connell 2006). There have been some discrepancies, however, in relation to whether understory species are predominantly facilitated by kelp through abiotic light and sediment reduction, or if abrasion has a more indirect effect because it can reduce recruitment and growth of fast-growing turfs, articulate calcifying algae or fucoids (Kennelly 1989, Melville & Connell 2001, Irving et al. 2004a, Toohey et al. 2004, Wernberg et al. 2005). Indeed, the latter example represents a novel competition cascade (Levine 1999, Thomsen et al. 2010), where *E. radiata*, through abrasion and light reduction, outcompetes strong competitors for light and space (e.g. fucoids) and thereby allows coexistence of weak (e.g. encrusting algae) competitors with various resource requirements.

Similar facilitation mechanisms scale up to larger *E. radiata* stands and down to specific structural components of an individual thallus (Figure 7). Upscaling of *E. radiata* individuals to stands of various landscape configurations, densities, and with mosaics of stands with interspersed gaps allows large species to find food and allies and avoid enemies (Andrew & Jones 1990, Jones 1992, Harman et al. 2003, Tuya et al. 2009, Vanderklift et al. 2009, Newcombe & Taylor 2010, Smith et al. 2014). Moreover, there is an emerging understanding of *E. radiata* forest soundscapes that carry decision-making information needed for some species to locate resources and evaluate their quantity and quality. The presence of *E. radiata* forests produces distinct soundscapes, and loss of these forests causes a reduction in biological sound (Rossi et al. 2017).

Facilitation of communities associated with *E. radiata* holdfasts has been a frequent focus of study. Compared to *E. radiata* fronds, holdfasts provide a more stable habitat for attachment of sessile taxa such as barnacles, tube-forming polychaetes, hydroids, bryozoan, tunicates and sponges (Smith et al. 1996, Anderson et al. 2005b, Goodsell & Connell 2005b, Coleman et al. 2007). In addition, the interstitial spaces among the holdfast's haptera provide a unique 3-dimensional environment for mobile species, dominated by crustaceans and polychaetes (Smith & Simpson 1992, Smith et al. 1996, Anderson et al. 2005b, Goodsell & Connell 2005b, Coleman et al. 2007). These holdfast assemblages are highly diverse and contain many rare taxa (Goodsell & Connell 2005b, Coleman et al. 2007). For example, Smith et al. (1996) quantified 125,605 individuals representing 386 species (152 families and 10 phyla) from 258 holdfasts collected from northern New South Wales. Similar collections from northeastern New Zealand showed similarly high diversity, with 351 taxa (213 families and 15 phyla) associated with 80 holdfasts (Anderson et al. 2005a,b). Faunal communities associated with holdfasts differ with holdfast size and age (Anderson et al. 2005a) and depth (Goodsell & Connell 2002, Coleman et al. 2007).

Because of the insular structure and high biodiversity, holdfast communities have been used as a model system of island biogeography and landscape ecology to test hypotheses related to habitat size (Smith et al. 1996, Anderson et al. 2005b), isolation and edge effects (Goodsell & Connell 2002). Holdfast assemblages have also been used as a tool to detect impacts from anthropogenic stressors like sewerage discharge (Smith & Simpson 1992, Smith & Simpson 1993, Smith et al. 1996, Smith 2000). Artificial holdfasts can also be used as natural mimics (supporting up to 30 families; Magierowski 2006) and test hypotheses about community assembly and post-recruitment interactions (Magierowski & Johnson 2006).

## *Direct trophic interactions and food webs*

Only a small number of invertebrate and fish species feed directly on adult *Ecklonia radiata*. The main consumers of kelp are sea urchins: in New Zealand, *E. chloroticus* (Choat & Schiel 1982), and in southeastern Australia, *C. rodgersii* (Andrew 1993, Andrew & Byrne 2001, Connell & Irving 2008). Also in southeastern Australia, in Port Phillip Bay (Kriegisch et al. 2016) and in Tasmania (Sanderson et al. 1996, Johnson et al. 2004, Pederson & Johnson 2007), *E. radiata* forests are subject to destructive grazing by the red sea urchin *Heliocidaris erythrogramma*. *H. erythrygramma* is also the main kelp-eating urchin throughout southern and western Australia, although the species here is mostly drift feeding (Vanderklift & Wernberg 2010). At high densities, these species are capable of removing entire kelp forests, grazing not only the blades and meristem, but also the base of stipes, a behaviour that results in accelerated canopy loss (Andrew & Jones 1990). If high densities of urchins are sustained, canopy loss can result in a shift towards urchin barrens, a system with no macroscopic foliose algae that is instead dominated by turf algae or crustose coralline algae (Choat & Schiel 1982, Fletcher 1987, Andrew & Underwood 1989, Underwood et al. 1991b, Andrew 1993, Andrew & O'Neill 2000, Johnson et al. 2004, Johnson et al. 2005a, Johnson et al. 2005b, Ling 2008, Johnson et al. 2011, Coleman & Kennelly 2019). Sea urchin overgrazing fundamentally transforms the ecosystem structure and dynamics of temperate reefs (Lawrence 1975, Filbee-Dexter & Scheibling 2014, Ling et al. 2015), leading to a loss of biodiversity and biomass in former *E. radiata* forests (Ayling 1981, Babcock et al. 1999, Ling 2008, Salomon et al. 2008) and declines of important commercial species (Johnson et al. 2005b, Johnson et al. 2011).

In contrast to sea urchins, gastropod grazing on *E. radiata* is relatively minor in terms of biomass consumed (Fletcher 1987). Small gastropods living on *E. radiata* seem mainly to graze either epiphytes or the old eroding end of the primary blade rather than live *E. radiata* tissue, though some (e.g. *Phasianotrochus eximius*) do directly consume *E. radiata*. Large turbinid gastropods readily consume *E. radiata* recruits in the laboratory (Wernberg et al. 2008, Miranda et al. 2019), and gastropod grazing may play an important role in supressing the recruitment of *E. radiata* and other algae in habitats where mature sporophytes have been removed (Ayling 1981, Choat & Andrew 1986, Fletcher 1987, Falkenberg et al. 2014, Ghedini et al. 2015, McSkimming et al. 2015). Smaller epifauna, such as amphipods and isopods, also graze on *E. radiata* (Taylor & Steinberg 2005). The lysianassid amphipod *Orchomenella aahu* has been associated with localised mass mortality of *E. radiata* in northeastern New Zealand (Haggitt & Babcock 2003), and Newcombe & Taylor (2010) found that amphipods not only grazed epiphytes on *E. radiata*, with some species grazing directly on its fronds.

*Ecklonia radiata* dominates the diet of only a handful of temperate fishes: *Olisthops cyanomelas* in eastern Australia (Jones 1992), several species of *Kyphosus* in Western Australia (Vanderklift et al. 2009, Bennett et al. 2015c) and *Odax pullus* and *Kyphosus sydneyanus* in New Zealand (Clements & Choat 1993, Moran & Clements 2002). At lower-latitude reefs, *E. radiata* is now also targeted by tropical and subtropical fishes, such as *Siganus fuscescens* and *Kyphosus* spp. (Bennett et al. 2015a,b, Vergés et al. 2016, Zarco-Perello et al. 2017), as these have moved poleward with ocean warming. Seasonal aggregations of *O. cyanomelas* can clear patches within *E. radiata* forests, but with little impact as they grow back annually (Andrew & Jones 1990). However, as is the case with grazing gastropods, the main ecological role of fish grazing may be in suppressing kelp recruitment, particularly following disturbance (Bennett et al. 2015c). Grazing by the temperate damselfish *Parma mccullochi* is hypothesised to maintain habitat heterogeneity on reefs in Western Australia by reducing or preventing the recruitment of large brown algae, including *E. radiata* within habitat patches (Saunders et al. 2015) or in larger spatial contexts following large-scale mortality of *E. radiata* (Bennett et al. 2015a,b).

*Ecklonia radiata* can be a high-preference food target, relative to other large, fleshy macrophytes, for important echinoid herbivores and some large gastropods in Australia and New Zealand (Schiel 1982, Andrew 1986, Steinberg & van Altena 1992, Cole 2001, Taylor & Steinberg 2005, Vanderklift & Wernberg 2008). It often supports high growth and reproduction for these herbivores (Andrew 1986, Steinberg & van Altena 1992). However, like many large, fleshy brown algae, it is often less frequently consumed than many other smaller, more delicate species, particularly by smaller gastropods or crustaceans (Taylor & Steinberg 2005, Wernberg & Goldberg 2008). There are exceptions to this trend (Williamson et al. 2004, Taylor & Steinberg 2005), including the arboreal sea urchin *Holopneustes purprascens* (Steinberg 1995a) and the amphipod *Allorchestes compressa*, which consumes detrital or detached *E. radiata* at higher rates than other less fleshy algae (Robertson & Lucas 1983).

*Heliocidaris erythrygramma* has also been observed to preferentially retain and consume detached *E. radiata* (Vanderklift & Wernberg 2008). In perhaps the most comprehensive analysis of consumption of temperate Australasian macroalgae including *E. radiata* by diverse herbivores, Taylor & Steinberg (2005) found that the feeding preferences of small mesograzers differed from that of larger grazers such as urchins. Much of the research on trying to understand the reasons for selectivity in feeding by herbivores for *E. radiata* in Australia and New Zealand, relative to other (brown) algae, has focussed on the effects on herbivores of the brown algal secondary metabolites known as *phlorotannins*. Phlorotannins are a mixture of complex polyphenols that are ubiquitous in brown seaweeds and have a role in both herbivore deterrence and cell wall formation (Schoenwaelder 2002).

Although levels of phlorotannins in temperate Australasian brown, including *E. radiata*, algae are typically very high (Steinberg 1989, van Hees et al. 2017), variation in levels among these different species do not affect herbivore selectivity for these seaweeds (Steinberg & van Altena 1992, Steinberg 1995a). Extracted, purified phlorotannin mixtures also do not generally deter feeding by Australasian herbivores, including dominant echinoid herbivores such as *E. chloroticus* or *C. rodgersii*, even at high levels, in contrast to their effects on North American (Steinberg & van Altena 1992, Steinberg 1995a) and European (Pavia et al. 1997) herbivores. Estes & Steinberg (1989) and Steinberg (1995b) proposed that these broad-scale biogeographic differences in algal chemical defences and herbivore response were a consequence of a trophic cascade in evolutionary time, driven by the absence of a key predator—sea otters—in Australasia. There is also no evidence for induction of higher levels of phlorotannins in *E. radiata* following simulated herbivory (Steinberg 1994), though induction of phlorotannins is known for other species of *Ecklonia* (Molis et al. 2006). Interestingly, some herbivorous fish such as *K. sydneyanus or O. pullus,* which consume *E. radiata* in Australia and New Zealand, have complex gut morphologies or high gut pH, which likely serve to deactivate phlorotannins.

Other factors affecting selectivity by herbivores for *E. radiata* are less well explored but may include thallus toughness and nutritional content (McShane et al. 1994) or possibly the production of other secondary metabolites (e.g. terpenoid, Hay & Fenical 1988) and secondary pigments (e.g. fucoxanthins). Finally, it should be emphasised that consumption and feeding selectivity are not the only factors that affect the impact of herbivores on *E. radiata* forests, with foraging behaviour (Andrew 1988), the physical environment (Shears et al. 2008), ecological context, particularly predators (Babcock et al. 1999, Shears & Babcock 2002, Spyksma et al. 2017a) and other aspects of the life history or habits of the herbivores (Steinberg 1995a) also playing key roles.

## *Indirect interactions and trophic cascades*

Some of the first descriptions of subtidal coastal habitats in Australia and New Zealand were characterised by the juxtaposition of *Ecklonia radiata* forests and barrens habitat dominated by crustose coralline algae (Choat & Schiel 1982, Grace 1983, Underwood et al. 1991b). This configuration of habitats was generally considered to be the characteristic state of subtidal reefs, However, questions soon arose about whether this was in fact the case, or whether the barrens were created and maintained because of unnaturally high densities of sea urchins that resulted from other factors—principally reduced numbers of predators that allowed urchin populations to flourish. Such interactions, where impacts at higher trophic levels result in indirect effects at lower trophic levels, are known as *trophic cascades*. The existence of trophic cascades is difficult to demonstrate because experiments at realistically large spatial scales are problematic. However, a combination of factors has shown that trophic cascades do take place in *E. radiata* forests and suggest that extensive *E. radiata* canopies, rather than urchin barrens, are the more natural state of these subtidal reefs.

In New Zealand the creation of marine reserves allowed predator populations (mainly the lobster *Jasus edwardsii* and snapper *Pagrus auratus*) to recover to a point where they reduced the abundance of urchins (*E. chloroticus*) sufficiently to allow kelp forests to return to from formerly barrens habitat, while barrens outside the reserves persisted (Babcock et al. 1999, Shears & Babcock 2003, Spyksma et al. 2017b). On the coast of eastern Australia, especially south of Sydney, barrens maintained by *C. rodgersii* also exist over extensive areas (Andrew & O'Neill 2000, Connell & Irving 2008), but there is no evidence from relatively young reserves in this area, that predator populations have recovered enough to reverse the trophic cascade (Coleman et al. 2013b, Coleman et al. 2015). These heavily populated coastlines have historically been subject to intense fishing pressure, so barrens are likely maintained through a combination of this harvesting legacy and ongoing climatic change that facilitates urchin transport (Coleman et al. 2017), recruitment and survival (Ling et al. 2009). Change in the ocean climate in southeast Australia as a result of increased eddy propagation of the East Australian Current (EAC; Ridgway 2007) has led to transport and establishment of *C. rodgersii* into Tasmania, precipitating large-scale transformation of kelp forests to barrens (see the section entitled 'Recent changes and future threats', later in this review).

In New Zealand, the transition from urchin barrens back to *E. radiata* forest has largely been attributed to the direct consumption of sea urchins by predators that result in an overall decline in sea urchin density (Babcock et al. 1999). However, sea urchins inside marine reserves exhibit a cryptic behaviour, occupying cracks and crevices (Shears & Babcock 2003, Spyksma et al. 2017b). This cryptic behaviour has been directly linked to increased predation risk (Spyksma et al. 2017b), suggesting that both density and behaviourally mediated interactions are important in the predator–sea urchin–kelp trophic cascade.

Indirect effects also structure maintenance of kelp-turf regime shifts, particularly in the context of resource enrichment. Consumption by herbivores may buffer the expansion of turfs during nutrient enrichment (McAllister & Bornman 1972, Sarnelle 1992, Russell & Connell 2005) and other resource perturbations (Ghedini et al. 2015, McSkimming et al. 2015). By keeping turf abundance in check and maintaining turf-free space, herbivores facilitate *E. radiata* recruitment and persistence (Gorman & Connell 2009). Increases in nutrient and sediment loads, which tend to go together, are likely to have detrimental effects on kelp forests, particularly in those regions where populations of herbivores are naturally ineffective, sparse or subject to decline (Ghedini et al. 2015). The aggregate of such changes in consumption can generate a mechanism of trophic compensation that stabilises community productivity in varying environments (Connell & Ghedini 2015). The reality is that alteration of both producers (e.g. nutrient-driven change) and consumers (e.g. extraction of consumers) require attention to the synergies they may create. In Port Phillip Bay, Australia, negative top-down effects of sea urchin grazers overwhelm positive bottom-up effects of enhanced nutrient loading on *E. radiata*, and local elevation of nutrients does not change the urchin density at which overgrazing or kelp recovery from overgrazing occurs (Kriegisch et al. 2016). Similarly, in South Australia, herbivory increases with nutrient enrichment so that the boosted effects of nutrients on turfs are negated (Falkenberg et al. 2014). By better recognising the environmental conditions which maintain or disrupt the balance between the processes of production and consumption (Ghedini & Connell 2016), it may be possible to improve forecasts regarding the probability of habitat stasis or shifts.

### *Context dependency and variation in the occurrence of trophic cascades*

While regime shifts and trophic cascades provide graphic demonstrations of the importance of *Ecklonia radiata* within its ecosystem, it is important to note that throughout a lot of its range in New Zealand and Australia *E. radiata* is not subjected to high levels of grazing by fish or sea urchins and sea urchin barrens do not exist. Most commonly, *E. radiata* forests occur as near monospecific canopies or as mixed *E. radiata*/fucoid canopy (Schiel 1990, Fowler-Walker & Connell 2002, Shears & Babcock 2007, Connell & Irving 2008, Wernberg et al. 2011c). Urchin barrens are more prevalent in northern than in southern New Zealand (Shears & Babcock 2007, Schiel 2013), and in southern compared to northern New South Wales in eastern Australia (Glasby et al. 2017). Furthermore, within regions such as northern New Zealand, the extent of urchin barrens varies with depth and wave exposure. Consequently the effects of trophic cascades involving the indirect effects of predators on kelp forests is considered highly context dependent (Shears et al. 2008). To date, the cascading effects of fishing on kelp forests have been demonstrated only from northern New Zealand and Tasmanian reefs.

The reasons for the weak interaction between grazing echinoids and large brown algae across much of the range of *E. radiata* is not completely clear, but due to the widespread effects of fishing on top predators, such as lobster, it is unlikely that top-down impacts are limiting urchin populations across most of Australasia. Various lines of evidence suggest that lack of grazing pressure stems from bottom-up processes that control urchin recruitment. A case in point is the extension of the East Australia Current, which has resulted in not only the direct transport of *C. rodgersii's* larvae to Tasmania (Johnson et al. 2005a), but also the creation of oceanographic conditions suitable for *C. rodgersii* development at higher latitudes than previously (Ling et al. 2009). Across many parts of the New Zealand coastline, high levels of sedimentation inhibit the settlement and survival of *E. chloroticus* (Andrew & Choat 1985, Walker 2007), decreasing recruitment levels and resulting in low urchin population densities (Shears et al. 2008). The arid coastlines of southern and southwestern Australia are characterised by clear waters and are relatively free of fine sediment, but they also lack urchin barrens habitat. *Centrostephanus tenuispinus* is morphologically similar to *C. rodgersii* and is present on these coasts, but never highly abundant, possibly because of the relatively oligotrophic conditions that reduce the likelihood of dense recruitment. *C. rodgersii* larvae have been shown to have an extended larval phase of 3–5 months (Huggett et al. 2005), making them highly dependent on a consistent planktonic food supply. Understanding the drivers of variation in kelp forest structure and ecological processes at this scale remains a significant knowledge gap.

### *Ecosystem processes and trophic cascades*

Ecosystem models focussed on reefs at Gisborne on the central eastern coast of New Zealand show that production by the seaweed canopy (mostly *Ecklonia radiata*) comprised almost an order of magnitude greater biomass than any other primary producer and contributed almost half of the total detrital budget to the system (Pinkerton et al. 2008). Seaweed (canopy) also make up a significant proportion of the diets of lobster, herbivorous invertebrates, phytal/infaunal invertebrates and herbivorous fish (16%, 30%, 39% and 23%, respectively (Pinkerton et al. 2008). *E. radiata* is estimated to be similarly important to food webs on the west coast of Australia, although there a higher proportion of primary production is consumed directly, and less than 25% goes through detrital food web pathways (Lozano-Montes et al. 2011). This model has been used to simulate and predict the ecosystem effects of recent loss in *E. radiata* canopy as a result of the 2011 heatwave (Wernberg et al. 2016a) on the central coast of Western Australia. A simulated persistent loss of 50% of the *E. radiata* canopy was projected forward for 33 years and showed declines in biomass at all levels of the food web, including key groups such as invertebrates (–38%), target fishes (–24%); rock lobster (–21%); herbivorous fish (–9%) (Hector Lozano-Montes, unpublished data). Also, the total biomass of the system declined (~10%), and an important loss in diversity (about 11%) measured by the Shannon Diversity Index was predicted by the model at the end of 2050. In addition, models have been used to identify thresholds and recommend management targets to avoid regime shifts from *E. radiata* forests to urchin barrens (Marzloff et al. 2016a).

### *Fate of production and trophic subsidies*

Like most other kelps globally (Krumhansl & Scheibling 2012), *Ecklonia radiata* is not extensively consumed directly across much of its range. Instead, most biomass is lost through exudation of nutrients and polysaccharides, erosion of small fragments and dislodgment of entire individuals (Jennings &

Steinberg 1994, Hyndes et al. 2012, de Bettignies et al. 2013b). Dislodged *E. radiata* material is often exported beyond the reef on which the kelp grows, providing spatial subsidies (*sensu* Polis et al. 1997) to organisms that live in distant habitats. Large fragments of *E. radiata* accumulate on beaches (Figure 8), in seagrass meadows and on reefs, where they are eaten by numerous species of herbivores ranging from amphipods, sea urchins and fish to weevils (Wernberg et al. 2006, Vanderklift & Wernberg 2008, Crawley et al. 2009, Vanderklift & Wernberg 2010, Mellbrand et al. 2011). *E. radiata* is not the only macrophyte in such accumulations of wrack, but it tends to decompose faster (Gladstone-Gallagher et al. 2016) and be consumed at greater rates than most other macrophytes (Crawley & Hyndes 2007). The combination of the amount of material available and the relatively high rates of consumption means that *E. radiata* wrack is likely to be disproportionately more important than other species (Robertson & Lucas 1983, Vanderklift & Kendrick 2005). Experimental additions of kelp to beach sediments have sometimes (but not always) confirmed that such subsidies increase the abundance and richness of fauna (but see Bishop et al. 2010, Mellbrand et al. 2011, Bishop & Kelaher 2013). This in turn propagates to higher trophic levels, with evidence that detached macrophytes contribute to the nutrition of organisms from fish to spiders (Crawley et al. 2009), although no studies have unambiguously quantified the contribution of kelp alone.

Smaller particles of kelp suspended in the water are also likely to be an important food source for a diverse array of organisms, especially as they can travel orders of magnitude farther than large kelp detritus particles (Wernberg & Filbee-Dexter 2018). Experimental studies on the northeast coast of New Zealand have shown that organic carbon fixed by *E. radiata* is an important food source fuelling nearshore food webs, comprising 57% of the diet for mussels and 34% for oysters (Salomon et al. 2008). Plants may also benefit from kelp-derived resource subsidies as shown in Western Australia, where seagrasses and seagrass epiphytes take up nitrogen leaching from dislodged kelp exported to the seagrass meadows (Hyndes et al. 2012).

In addition to being a trophic subsidy to other ecosystems, *E. radiata* detritus can end up in habitats with capacity to sequester carbon, such as seagrass meadows, saltmarshes, mangroves or the continental shelf (Wernberg et al. 2006, Hill et al. 2015). Indeed, allochthonous carbon can contribute as much as 50% of the total organic carbon sequestered in seagrass meadows (Kennedy et al. 2010). Kelp also contain refractory compounds that are not fully broken down (Trevathan-Tackett et al. 2015), and the presence of seaweed derived carbon in deep sea sediments suggests that this could potentially be an important source of the carbon sequestered (Krause-Jensen & Duarte

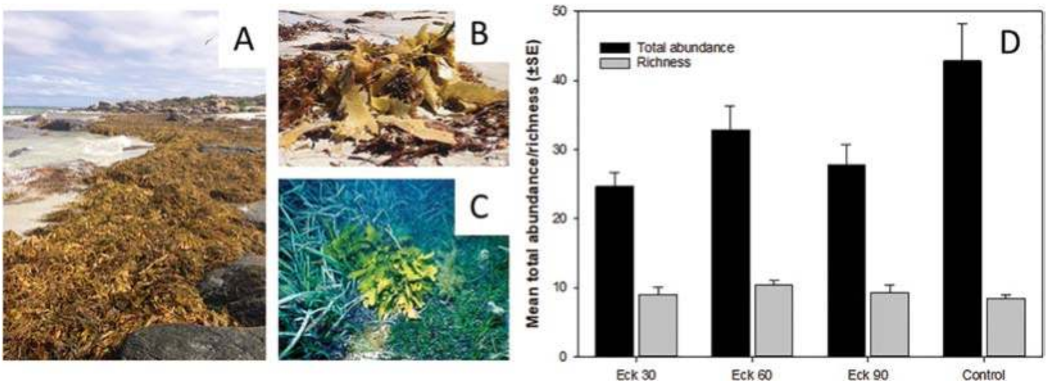

**Figure 8** Detritus in the form of fragments and whole plants of *Ecklonia radiata* are transported into other habitats, including sandy beaches (A, B) and seagrass beds (C), where they break down and fuel marine food webs. (D) Relative to unenriched procedural controls, the total abundance was lower but richness greater of fauna in sediments enriched with 30, 60 or 90 grams of *E. radiata* detritus. (Data from Bishop et al. 2010. Photographs by the authors.)

2016). The large quantities of carbon stored in living kelp biomass have the potential to contribute significantly towards blue carbon sequestration. For *E. radiata*, however, future research is needed to quantify the ultimate fate of detached kelp wrack.

## *Microbial communities*

Extensive microbial diversity is found within the microbiomes associated with marine organisms (Thompson et al. 2017), and these may be critical for the normal development and functioning of eukaryotic hosts (Egan et al. 2013, McFall-Ngai et al. 2013, Bourne et al. 2016). Kelps, and seaweeds more generally, are covered in microorganisms, and the importance of surface-associated microbes on the functioning of seaweeds is increasingly recognised (Egan et al. 2013). Changes in surface-associated microbial communities can have significant effects on host seaweeds, ranging from development and recruitment (Marshall et al. 2006, Morris et al. 2016), photosynthetic capacity (Marzinelli et al. 2015a), fecundity (Weinberger et al. 2007, Campbell et al. 2011) and survival (Egan et al. 2013, Peters 2015). Recently, there has been an increasing focus on understanding the interactions between microbiomes and large habitat-forming kelps because of their ecological importance (e.g. Bengtsson et al. 2010, Clasen & Shurin 2015, Marzinelli et al. 2015a, McKeown et al. 2017). Of these, *Ecklonia radiata* is probably the most studied kelp species (Thompson et al. 2017).

The microbiome of *E. radiata* is very diverse, and a large component of it is unique (Marzinelli et al. 2015a, Roth-Schulze et al. 2016, Beattie et al. 2018). A characterisation of microbial community structure from surfaces of *E. radiata* at multiple spatial scales spanning the entire latitudinal distribution along the east and west coasts of Australia and encompassing three biogeographic provinces (Waters et al. 2010) showed high bacterial and archaeal taxonomic diversity. Over 80% of the >8000 operational taxonomic units (OTUs, roughly equivalent to *species* for eukaryote ecologists) identified in this study had never previously been found elsewhere (Marzinelli et al. 2015a). The relatively small number of OTUs that could be classified taxonomically belonged to ~230 families and 50 phyla (Marzinelli et al. 2015a).

Surface-associated viruses are another component of *E. radiata*'s microbiome that also appear to be extremely diverse. A recent study characterising the virome on the surfaces of *E. radiata* revealed a similar pattern to that observed for bacteria and archaea, with ~80,000 virus-like reads identified from metagenome sequencing, of which over 80% did not match any previously described viral sequences (Beattie et al. 2018). Preliminary analyses of fungal diversity on *E. radiata* targeting internal transcribed spacer (ITS) deoxyribonucleic acid (DNA) sequences are also showing striking patterns of diversity, with many of the ITS sequences previously unknown (Ezequiel Marzinelli & Peter Steinberg, unpublished data).

The structure (relative abundance of taxa) of *E. radiata*'s diverse microbial communities also differ significantly from those associated with other co-occurring seaweed species, seagrasses and inert surfaces (rocks) and are largely distinct from those in the water column (Roth-Schulze et al. 2016). Characteristics of the host, such as physio-chemical properties, rather than host phylogeny, appear to influence the type of taxa colonising the surfaces, leading to strong host specificity (Marzinelli et al. 2015a, Roth-Schulze et al. 2016).

There are strong spatial and temporal variation in *E. radiata*'s bacterial, archaeal (Marzinelli et al. 2015a) and fungal (Ezequiel Marzinelli & Peter Steinberg, unpublished data) surface-associated communities. This variation is related to temperature and light availability, and to a lesser extent to wave exposure (Marzinelli et al. 2015a). Interestingly, however, these patterns break down for microbiomes associated with stressed hosts. A putative disease of *E. radiata* characterised by tissue bleaching was consistently found in the large-scale continental surveys of Marzinelli et al. (2015b), with >50% of the individuals sampled in each population showing signs of bleaching at the end of summer, when the water is warmer (Marzinelli et al. 2015a). Bleaching affected kelp individuals by reducing their photosynthetic capacity (Marzinelli et al. 2015a). Host condition (healthy versus

**Figure 9** Progression of tissue bleaching and degradation (Left to right) associated with temperature-mediated change in the microbiome of *Ecklonia radiata*. (From Qiu, Z. et al. *Proceedings of the Royal Society B-Biological Sciences* 2019. Photographs by the authors.)

bleached) overrode effects of geographic location or environmental variables on the structure of the kelp-associated microbiome (Marzinelli et al. 2015a).

These results suggest that environmental change may indirectly affect *E. radiata* via changes in the associated microbiome that can lead to disease. Indeed, a large-scale die-back of *E. radiata* in New Zealand was associated with high abundances of virus-like particles on the kelp blades, which showed signs of tissue decolouration, bleaching and degradation (Cole & Babcock 1996, Easton et al. 1997). Experiments provide further support for this idea, as warming and acidification mesocosm conditions mimicking future ocean conditions have been shown to cause changes in *E. radiata*'s microbial community structure, followed by tissue bleaching and subsequent degradation (see Figure 9; Qiu et al. 2019). Some of the bacteria that become abundant under such conditions are also abundant on bleached kelp in the field (Marzinelli et al. 2015a, Qiu et al. 2019) and on kelp growing on artificial structures such as pier-pilings (Marzinelli et al. 2018), which are typically in poor condition relative to kelp on adjacent natural rocky reefs (Marzinelli 2012, Marzinelli et al. 2012). Such changes in the microbiome can potentially mediate ecological interactions such as grazing and fouling (Marzinelli et al. 2011, Campbell et al. 2014b, Marzinelli et al. 2018), which can lead to strong detrimental effects on kelp populations and major declines.

Two significant challenges for the study of the kelp holobiont are to understand functional interrelationships and to determine cause-and-effect relationships between hosts, microbiomes and environmental change. Analyses of functional genes via metagenomic sequencing on *E. radiata* and co-occurring macrophytes have found that abundances of genes related to enzymes involved in the breakdown of iduronate—a component of mucopolysaccharides, characteristic of brown seaweeds—were much higher on *E. radiata* than on other macrophytes or inert surfaces (Roth-Schulze et al. 2016). Thus, while *E. radiata*'s microbiome shares functional properties with microbes from other surface-associated habitats, it also hosts microbes that mediate host specificity (Roth-Schulze et al. 2016). Determining causation involves manipulating the microbiome, either via the addition or removal of specific taxa, or through changes in abundances of targeted taxa. Some of these approaches involve culturing and isolating the microorganisms associated with kelp, which can also allow identifying taxa that can potentially enhance host resilience to environmental stressors, providing new tools for management of these ecosystems (see the section entitled 'Recent changes and future threats', next).

## Recent changes and future threats

*Ecklonia radiata* forests are dynamic ecosystems, responding to natural and human-driven changes in the environment. Across Australia, climate-induced changes to ocean boundary currents have underpinned recent marine heatwaves (e.g. Wernberg et al. 2013a, Oliver et al. 2017) and gradual warming (Johnson et al. 2011, Vergés et al. 2016), which have driven dramatic changes

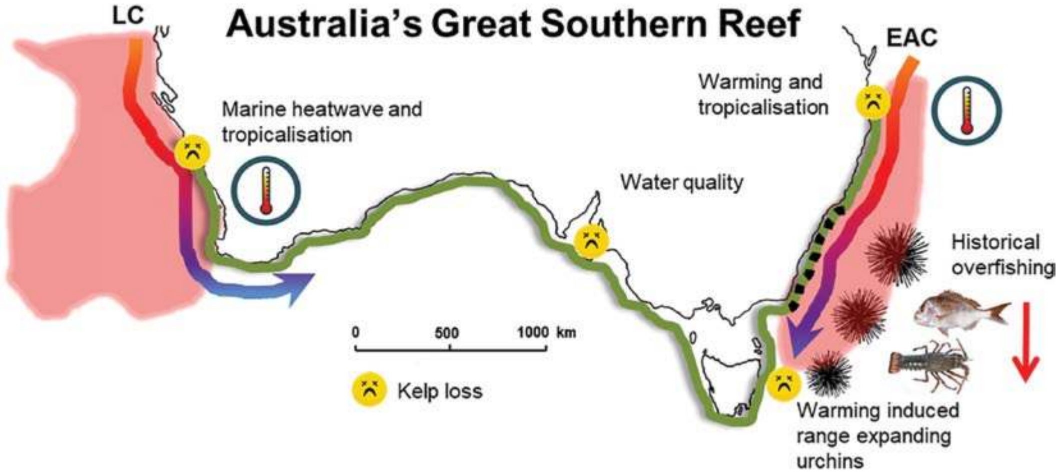

**Figure 10** Overview of *Ecklonia radiata* loss across Australia, showing the various regional drivers. Both the East Australia Current (EAC) and Leeuwin Current (LC) transport warm water poleward (Wernberg et al. 2013b) with warming (east) and heatwaves (west) precipitating *E. radiata* loss at low latitudes. The red areas indicate warming hot spots, where the rate of warming is in the top 10% globally. *E. radiata* loss at higher latitudes on Australia's southeast coast (Tasmania) is an indirect result of the warming and strengthening flow of the EAC, facilitating the recent transport and survival of urchin larvae leading to transitions to barrens habitat. Barrens represent about 50% of the reef from about 33° latitude on the east coast. Historical overfishing of urchin predators along the east coast likely impedes *E. radiata* recovery. On the south coast, loss of *E. radiata* forests have been associated with declining water quality and the expansion of turfs.

to *Ecklonia radiata* forests over contemporary time scales (Figure 10). At the same time, human-driven changes in resource (eutrophication, Connell 2007b) and consumer (fishing, Ling et al. 2009) levels have reinforced these changes (Wernberg et al. 2011a). A common result of these changes is the transition from complex kelp-dominated states towards more simplified turf and barrens states, a global phenomenon (Filbee-Dexter & Scheibling 2014, Filbee-Dexter & Wernberg 2018). Similar persistent losses of *E. radiata* forests have not been observed in New Zealand, likely due to the complexities of changing boundary currents and higher latitudes (Shears & Bowen 2017), or South Africa, where intensification of upwelling has caused localised cooling and expansion of some marginal kelp forests (Bolton et al. 2012).

### *Warming and marine heatwaves*

*Ecklonia radiata* forests in eastern and western Australia and southeastern Africa are located in global warming hot spots, regions where the rate of warming over the past 50 years is in the top 10% globally (Hobday & Pecl 2014). This accelerated warming is driven by a strengthening of poleward flowing boundary currents (Wu et al. 2012), carrying warm, nutrient-poor water from low to high latitudes. Background warming has caused range shifts in seaweeds, invertebrates and fish inhabiting temperate reefs and *E. radiata* forests (Last et al. 2011, Wernberg et al. 2011b, Poloczanska et al. 2013, Bennett et al. 2015c), leading to substantial changes in performance, composition and interactions within kelp forest communities (Vergés et al. 2014). To date, similar changes in species distributions or ecosystem states have not been observed in New Zealand kelp forests, where there has been minimal long-term warming (Shears & Bowen 2017).

There is a general consensus that ocean temperatures surrounding most *E. radiata* kelp forests will continue to increase (but see Bolton et al. 2012), although the pattern and magnitude of warming will depend on the trajectory of global $CO_2$ emissions. Warming could, at least initially, lead to localised expansion of *E. radiata* where more temperature-sensitive canopy-forming fucoids disappear (Wernberg et al. 2011c, Bennett et al. 2015a, Coleman & Wernberg 2017, Martinez et al. 2018). Nevertheless, species distribution models for Australia based on the RCP 2.6 (conservative) and RCP 6.0 (intermediate) $CO_2$ emission scenarios predict that a major poleward range contraction of *E. radiata* is likely within the coming 85 years (Martinez et al. 2018). Although *E. radiata* is currently found across the entire south coast and to about 27°S on the east and west coasts, it could become highly restricted to southeastern Australia and Tasmania (Figure 11), losing as much as 49% and 71% of its current distribution under the RCP 2.6 and RCP 6.0 $CO_2$ emission scenarios, respectively (Martinez et al. 2018). These projections do not consider additional effects of increasing frequency of marine heatwaves and tropical herbivores (as discussed next), synergies with other increasing human stressors such as eutrophication (Russell et al. 2009) or continued expansion of urchins into southern reefs (Coleman et al. 2017) that are predicted to be the only suitable habitat for *E. radiata* under future scenarios (Martinez et al. 2018).

As a consequence of the human-induced increase in mean ocean temperature, there has also been an increase in discrete extreme temperature events known as *marine heatwaves* (Hobday et al. 2016) an upwards trend that will likely continue (Oliver et al. 2017, Oliver et al. 2018). In 2011, Western Australia experienced the worst marine heatwave in recorded history, with *E. radiata* forests experiencing temperature anomalies exceeding 4°C–5°C for several weeks. Over a few weeks, kelp forests collapsed entirely or were severely decimated across several hundred kilometres of coastline (Wernberg et al. 2016a), presumably as their lethal temperature threshold was exceeded (Smale & Wernberg 2013, Wernberg et al. 2016b, Figure 12). The magnitude of heatwave impact was negatively correlated with genetic diversity within *E. radiata* populations (low diversity populations were completely extirpated), suggesting that genetic diversity and population connectivity may underpin adaptive responses and resilience in these kelp forests (Wernberg et al. 2018). At their low-latitude distribution, kelp forests failed to recover due to increased fish grazing (Bennett et al. 2015a,b) and expansion of turf competitors (Wernberg et al. 2016a); 8 years later, these reefs remain dominated by turf (Figure 12; Thomas Wernberg, pers. obs.). Interestingly, a subsequent unprecedented marine heatwave in Tasmania

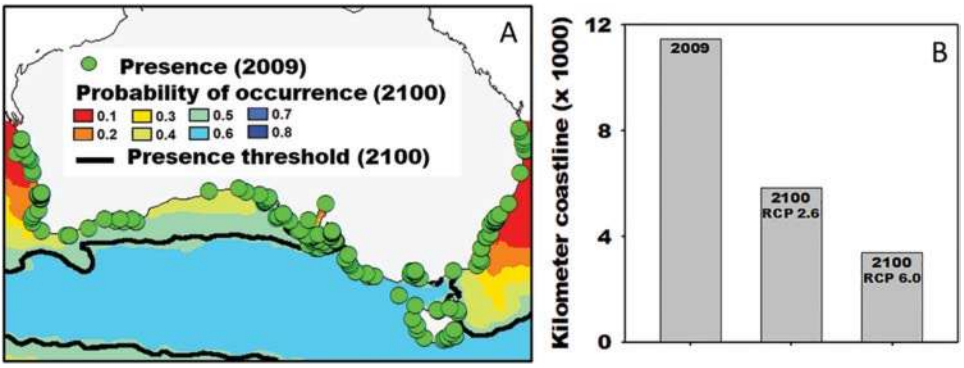

**Figure 11** Distribution of *Ecklonia radiata* in Australia, now and projected into the future. Herbarium specimens lodged in the major Australian herbaria until 2009 (green dots) show *E. radiata* distributed all along the south coast and far up the east and west coasts of the continent (A). Species distribution models projecting the extent of suitable habitat (blue area between the black presence thresholds) for *E. radiata* in 2100 under the RCP 2.6 (conservative) (map not shown) and RCP 6.0 (intermediate) (B) scenarios of greenhouse gas emissions suggest there will be a major range contraction, isolating *E. radiata* to the southeastern corner of the continent and Tasmania, over the coming 85 years, even under optimistic emission projections. These estimates do not consider the additional impacts of increasingly severe marine heatwaves, range-shifting tropical herbivores or increased competition from turfs. (After Martinez, B. et al. 2018. *Diversity and Distributions* **24**, 1350–1366.)

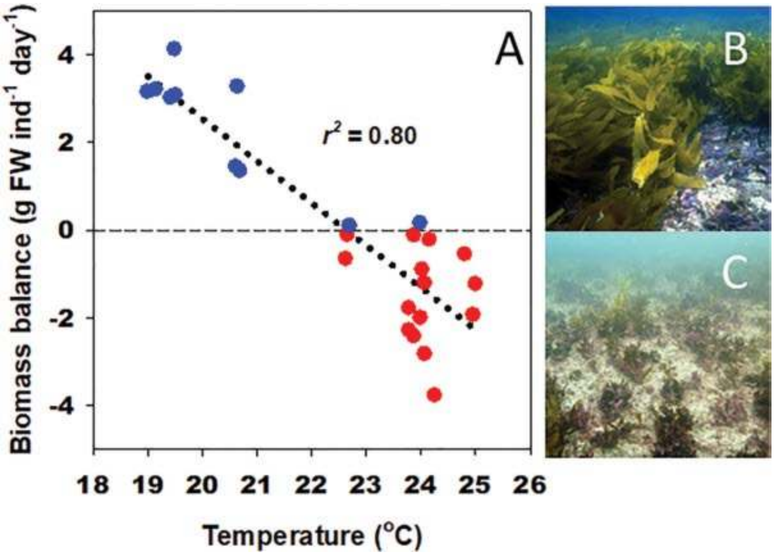

**Figure 12** Along the west coast of Australia, the balance between *Ecklonia radiata* production and erosion becomes negative (i.e. the kelps shrink, red dots) when temperatures exceed about 23°C (each point represents the average of measurements on 15 kelp at a point in space and time, Wernberg unpublished data) (A). During the 2011 marine heatwave, temperatures exceeded this threshold across vast swathes of coastline for several weeks. Dense and healthy *E. radiata* kelp forests in Kalbarri (Western Australia) in 2005 prior to the heatwave subsequently collapsed (B), and the reef was colonised by sediment-laden algal turf (C). (Photographs by the authors).

did not cause a similarly catastrophic response in *E. radiata*, although several kelp associated taxa were negatively affected (Oliver et al. 2017). Differences in thermal tolerances as a consequence of relative position with the distributional range are the most likely explanation for the difference in impacts between Western Australia (warm range margin) and Tasmania (cool range centre) (Wernberg et al. 2013a, Bennett et al. 2015a).

## *Overgrazing: Tropicalisation and urchin incursion*

One of the main impacts of climate change at the warm range edges of *E. radiata* forests is due to new species interactions emerging as a result of tropicalisation; that is, an increase in the proportion of tropical and warm-water species where temperate species previously dominated (Vergés et al. 2014). In particular, increases in the abundance of tropical and warm-temperate herbivores have been linked to declines of *E. radiata* in both eastern (Vergés et al. 2016) and western Australia (Wernberg et al. 2016a, Zarco-Perello et al. 2017). Novel kelp-herbivore interactions are leading to the decline of *E. radiata* and the maintenance of alternative turf-dominated reefs via both direct consumption of macroscopic sporophytes and enhanced grazing on algal turfs, which prevents kelp re-establishment and provides high resilience to these novel ecosystems (Bennett et al. 2015c, Vergés et al. 2016). Although more than 90 herbivorous fish species have expanded their distribution into temperate reefs worldwide (Vergés et al. 2014), only a small number of species appear to be able to consume adult *E. radiata*. In particular, the rabbitfish *Siganus fuscescens* and sea chubs *Kyphosus* spp. have been implicated in the loss of *E. radiata* in both eastern and western Australia (Vergés et al. 2016, Zarco-Perello et al. 2017) and also in Japan for *Ecklonia cava* (Yamaguchi 2010, Yamaguchi et al. 2010). In contrast, a much larger number of species appear to be implicated in enhanced turf grazing in tropicalised reefs, including multiple species of parrotfish (*Scarus* spp.) and surgeonfish *Acanthurus* spp. (Bennett et al. 2015c, Basford et al. 2016, Vergés et al. 2016).

Although low-latitude *E. radiata* populations are mostly being replaced by turf communities in Australia (Bennett et al. 2015c, Vergés et al. 2016), there is also evidence of some coral species expanding their distribution in eastern Australia (Baird et al. 2012) and other species expanding in cover in Western Australia (Tuckett et al. 2017). In southeastern Japan and southern Korea, some sites that used to be dominated by *E. cava* and other canopy formers have undergone a profound regime shift and are now dominated by fast-growing *Acropor*a and other corals (Tribble & Randall 1986, Denis et al. 2013, Vieira et al. 2016).

In Tasmania, strengthening of the East Australia Current and incursion of warmer water into Tasmania have resulted in greater transport, survival and development of sea urchin (*C. rodgersii*) larvae and increased urchin reproduction (Ling et al. 2008), precipitating the formation of barrens and widespread loss of *E. radiata* and *M. pyrifera* kelp forests (Johnson et al. 2005b, Ling 2008, Johnson et al. 2011) and associated biodiversity (Ling 2008). Although barrens are now widespread in northeastern Tasmania, they remain incipient farther south, where urchins coexist with high-canopy cover of seaweeds (Johnson et al. 2011). The prevalence of urchin barrens is facilitated by a lack of predation pressure on *C. rodgersii* by large lobsters, which have been historically overfished (Ling et al. 2009). This may be further exacerbated in warmer oceans because of decreased predation pressure of lobsters on urchins and increased grazing of urchins on kelp, resulting in accelerated loss of *E. radiata* forests (Provost et al. 2017). It has been shown through large-scale experiments (Johnson et al. 2013) and modelling (Johnson et al. 2013, Marzloff et al. 2013, Marzloff et al. 2016b) that while large lobsters in largely intact *Ecklonia* forests are capable of preventing the ongoing spread of these barrens, rehabilitation of extensive urchin barrens by building lobster biomass is highly unlikely even if lobster fishing is ceased over many decades. This is because of the magnitude of the hysteresis in the lobster–urchin–kelp dynamic (Babcock et al. 2010, Johnson et al. 2013). Indeed, in New Zealand, such regime shifts took decades within MPAs once predators were protected (Shears & Babcock 2003, Marzloff et al. 2016b). In Tasmania, lobsters are also the principal predator of the urchin *H. erythrogramma* (Pederson & Johnson 2007), which also overgrazes *Ecklonia* to form urchin barrens, but only in relatively sheltered bays and at smaller scales. Densities of *H. erythrogramma* often appear to be only just sufficient to maintain barrens (Johnson et al. 2004), and anecdotal evidence suggests that persistence of *H. erythrogramma* barrens is typically more ephemeral than extensive *C. rodgersii* barrens, which appear to persist indefinitely.

### *Predicted changes to dispersal and connectivity*

Given that gene flow in *Ecklonia radiata* (and their competitors/herbivores) is largely dependent on passive dispersal (e.g. by currents, waves, tides), future changes to these vectors of dispersal will have important implications for population genetic parameters (Coleman et al. 2017), population demography and ability of *E. radiata* to respond to and recover from disturbances (Wernberg et al. 2018). Boundary currents globally are predicted to change under future scenarios of ocean change, with changes not only to temperature, but also hydrodynamics. In particular, in addition to warming, the strength of Australia's boundary currents are predicted to change in contrasting ways. The Leeuwin Current, in Western Australia, is predicted to weaken (Sun et al. 2012) and the East Australia Current is predicted to strengthen, separate at and penetrate into higher latitudes (Sun et al. 2012, Cetina-Heredia et al. 2014), with dispersal in eddies also predicted to increase (Matear et al. 2013, Cetina-Heredia et al. 2014, Oliver et al. 2015). Dispersal of *E. radiata* among populations may thus change in divergent ways, with a decrease on the west coast and an increase on the east coast.

Simulations of change in oceanographic connectivity along the east coast of Australia demonstrate that dispersal of organisms (including *E. radiata*) will be impacted, and this effect may be mediated by pelagic larval/propagule duration (Cetina-Heredia et al. 2015, Coleman et al. 2017). Specifically, under a future climatic scenario (A1B), dispersal in *E. radiata* shows a general trend of enhancement in a poleward direction and weakening in an equatorward direction (Coleman et al.

2017). This implies that already declining, low-latitude *E. radiata* forests will receive less gene flow and limited chance for genetic rescue under future scenarios of change. The intricacies of dispersal among populations along the coast are complex, however, and temporal variation within climatic scenarios is great (Coleman et al. 2017). To date, these projected changes to dispersal largely do not take into account the effects of temperature-mediated survival and performance of propagules (but see Cetina-Heredia et al. 2015) or adults (Figure 11, Martinez et al. 2018), which must be integrated to more accurately predict how dispersal and connectivity of *E. radiata* might change in the future.

### *Carbon and nitrogen emissions*

Carbon and nitrogen are two of the most limiting resources on land and in the sea, and their increasing liberation through human activities within both realms is unprecedented (Vitousek 1994). Both affect water quality, and public concern over coastal water quality is renowned. Resource enrichment (e.g. nitrogen from terrestrial runoff or carbon from fossil fuel combustion) represents a persistent enigma for those who manage biogenic habitats, as enrichment often acts as a direct positive effect (i.e. resource, Connell & Russell 2010; also see the section entitled 'Life history, dispersal and recruitment', earlier in this review), but also as an indirect negative effect (i.e. stressor; Burkholder et al. 2007), where it favours faster-growing and opportunistic competitors such as turf-forming algae (Connell et al. 2013). Modern societies 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). Kelp loss due to nutrient overenrichment is driven by the stimulation of seaweed turfs that typically trap sediment to form a semiconsolidated matrix that inhibits recruitment of *Ecklonia radiata* (Gorman & Connell 2009). This reversal of competitive dominance, whereby normally ephemeral turfs persist year round to displace kelps, is also enhanced by $CO_2$ enrichment (Connell et al. 2018). In locations where kelps have been lost to the indirect effects of nutrient pollution (e.g. Adelaide, South Australia), the public have valued the improvement of water quality to be worth 100 s of millions of dollars that they would be prepared to pay (MacDonald et al. 2015). Nevertheless, researching the best ways to mitigate resource liberation is challenging, because of the complexity of understanding a complex system of buffering interactions (Goldenberg et al. 2018) that is prone to tipping points (non-linear cause effects; Connell et al. 2017b), that are lagged and not immediate (Connell et al. 2008a) and indirect rather than direct (Connell et al. 2013). What we do know is that co-limitations between nitrogen and carbon work in tandem to drive kelp loss in a high-$CO_2$ world (Falkenberg et al. 2013b). Whether together or separately, they provide the resources under which turfs expand and inhibit recruitment of *E. radiata* (Connell & Russell 2010).

Resource enrichment of algae can propagate into enhanced reproduction of herbivores that increase grazing intensity (Heldt et al. 2016, Connell et al. 2017a), but also create a mismatch between herbivore production and food demands of carnivores (Nagelkerken & Connell 2015). The effects of resource enhancement on kelp forests, therefore, are mediated by this shifting balance between the propagation of resource enrichment and its consumption across trophic levels. Top-down responses by herbivores and their predators can accelerate or reverse kelp loss (Goldenberg et al. 2018). When considered in conjunction with concomitant warming, herbivory has been observed to decline during warming events, which provides kelp-competitors (e.g. turfs) a refuge from herbivory (Mertens et al. 2015).

A key challenge for science and management of resource liberation is its duality; it can act as both a direct positive effect (i.e. resource, Connell & Russell 2010) and as an indirect negative effect (i.e. stressor; Connell et al. 2018). To date, research tended to focus on direct effects, reflecting the idea that the strongest drivers in ecosystems are direct. Yet, we increasingly recognise that indirect effects that affect production and consumption of habitats are often some of the strongest (Harley et al. 2017), and because they are often surprising (Hughes et al. 2013), they are underestimated in terms of their ubiquity and strength.

## *Mitigation and mechanisms that buffer change*

Whilst the collapse of kelp systems highlights their susceptibility to local and global change (e.g. Wernberg et al. 2011a), it also emphasises a need to explore mechanisms that can buffer, reduce or reverse the extent of change (Connell & Ghedini 2015). Hence, understanding the range of mechanisms that can enhance community persistence in the face of rapid environmental change is a central theme of current ecological research. These could include active mitigation through intervention, genetic/genomic manipulation or increasing resilience through protected areas or better understanding of ecological interactions and compensatory dynamics.

Restorative actions can enable recovery to the defined historical habitats in some degraded systems. Others are resilient to restoration efforts as they have either undergone a shift to an alternative persistent state with a strong basin of attraction or the dynamic equilibrium between alternative states has shifted (Suding et al. 2004, Johnson et al. 2011, Lotze et al. 2011). It is the existence of these alternative stable states and their resilience to restorative actions (i.e. the magnitude of hysteresis) that underlie many of the difficulties in anticipating the potential for re-establishment of historical habitats (Beisner et al. 2003). Restorative actions in which loss of *Ecklonia radiata* forests has been a direct result of climatic changes (particularly at low-latitude margins) are unlikely to be successful, given that predicted ongoing and increasing change are exceeding the thresholds of *E. radiata* to survive (Wernberg et al. 2013a). Restoration of trophic structures via the designation of MPAs (Babcock et al. 2010) and/or urchin culling (Andrew & Underwood 1993) may be successful, particularly when done together. Urchin culling alone, however, is not a long-term solution to *E. radiata* loss. Not only is it extremely resource and cost intensive (Sanderson et al. 2016), but culling by divers cannot tackle the scale of barrens and the depths to which they occur (Johnson et al. 2011). Moreover, slow incursion of adult urchins and continued recruitment of larvae back into newly established forests prevent long-term success without ongoing intervention (Tracey et al. 2015) such as to rebuild populations of urchin predators (Marzloff et al. 2013, Marzloff et al. 2016b).

In the case of urchin barrens formation, in which both the magnitude of hysteresis and the spatial extent of the problem is large, it has been suggested that the best use of limited resources is to attempt to prevent further barrens formation but not to attempt restoration of extensive barrens back to kelp forest (Johnson et al. 2017). In Tasmania, it is clear that rebuilding populations of large, predation-capable lobsters can be effective in arresting ongoing barrens formation in kelp forests and incipient barrens, but it is unlikely to have any effect in restoring kelp forests on extensive urchin barrens (Johnson et al. 2013, Marzloff et al. 2013, Marzloff et al. 2016b). The extensive urchin barrens in Tasmania are likely to be an enduring feature of the coastline unless innovative approaches currently under trial (e.g. development of smart automated robotics to locate and remove urchins) meet with success. Manipulative experiments have shown that restorative actions to reverse shifts from algal turfs back to barrens require transplantation of adult kelps to reinstate environmental conditions (high scour and low light) that inhibit turf growth and sediment accumulation, as well as provide a source of spore supply. However, all forms of intervention and restorative actions that seek to reverse regime shifts are unlikely to be successful in the long term unless conditions that precipitated shifts (e.g. poor water quality) are also improved.

MPAs may play a role in increasing resilience of *E. radiata* forests to climate stress or providing sources for reseeding or recolonisation in landscapes of increasing degradation. Many MPAs globally limit not only extractive activities, but also are protected by legislation that limits other activities that may affect marine biota. As such, MPAs may indirectly increase resilience of *E. radiata* to climate change by reducing interacting stressors such as coastal development and pollution. In addition, if MPAs can protect existing *E. radiata* forests in general landscapes of degradation, then these areas will be important sources of dispersal for recovery of denuded areas or donor populations for restoration efforts (Coleman et al. 2011a, 2017). However, to date, there is no empirical evidence that MPAs have played either of these roles for *E. radiata*. Certainly, MPAs have played a significant indirect role in recovery of *E. radiata* forests in New Zealand following historical fishing (Babcock et al. 2010). However, where urchin barrens are pervasive and widespread and climate-mediated dispersal of urchin larvae continues, such trophic cascades are unlikely to be realised even with significant restoration of predator populations (see above).

An emerging and topical component of future conservation and management of marine habitats, including *E. radiata* forests, centres on the concepts of enhancing resilience through genetic or genomic manipulation (Coleman & Goold 2019). Termed *assisted adaptation* or *assisted gene flow*, the general concept is that by introducing better-adapted (to a particular stressor of interest) genotypes into populations, it may be possible to boost the resilience of those populations to future stress (Aitken & Whitlock 2013). A similar concept is *genetic rescue,* whereby the fitness of small or genetically depauperate populations is enhanced through assisted immigration (Whiteley et al. 2015). Although such ideas have been employed in terrestrial systems and aquaculture for centuries (such as selective breeding), the advent of sequencing technologies and the ability to identify loci (and genotypes) that are selected for under certain environmental conditions now makes this a reality for natural marine systems. Indeed, such technology opens the possibility to design bespoke assisted adaptation strategies to boost resilience against a variety of stressors, if loci under selection can be linked to certain stressors of interest (e.g. temperature, pollution, nutrient input, grazing tolerance).

Despite its promise, caution must be taken to avoid outbreeding depression or disrupting adaptation to additional (non-target) stressors (Aitken & Whitlock 2013). In addition, unintended ecological surprises may arise when a change in one species resilience results in alteration to interactions among species (e.g. competition). Gene-editing technologies are an additional emerging area that could transform the resilience of organisms to stress some day (Coleman and Goold 2019). This could be coupled with manipulations of the associated microbiome to enhance resilience (see the section entitled ‘Community ecology of *Ecklonia* forests’, earlier in this review). Despite the fact that both these concepts present ethical challenges and debate, they should remain within discussions about conservation tools for the future (Filbee-Dexter & Smajdor 2019).

Future generations may also place greater value on research that seeks to understand the circumstances in which environmental change is resisted. Critically, knowledge of stabilising processes may be useful to managers in circumstances where kelp loss is undesirable and preventable. The erosion of stabilising processes releases the culminated potential of change (Ghedini et al. 2015), such that stability was, actually, long undermined before collapse. Such lagged responses have been considered as ‘living dangerously on borrowed time during slow, unrecognised regime shifts’ (Hughes et al. 2013). Whilst system collapse and its drivers are, in fact, readily observable, stability and its drivers remain among the least-studied processes in ecology (Connell & Ghedini 2015).

By bolstering the processes that compensate for change and thereby stabilise kelp forests, we may enable them to resist future shocks. A key symptom of systems undergoing negative change is loss of biodiversity, the very factor that appears to buffer the direct, negative effects of human activities (Hautier et al. 2015). Where communities are more complex, they tend to be more stable because of the inherent capacity for compensatory dynamics among the web of species interactions (Goldenberg et al. 2018). Hence, the relatively simple rule of thumb of conserving diversity may actually be one of the more tractable levers of management. In this regard, given the diversity of fucoids and range of environments they occupy, they may replace *E. radiata* as habitat-forming kelps for habitat and energy provision.

The cover of fucoids on many shallow reefs across southern Australia exceeds that of *E. radiata* (Cresswell et al. 2017). *E. radiata* and fucoids, however, support different communities and abundance of economically important species (e.g. Marzinelli et al. 2014) and are not entirely functionally equivalent (see review by Coleman & Wernberg 2017). Moreover, with the possible exception of some species of tropical *Sargassum*, the potential for fucoids to replace *E. radiata* as the dominant habitat formers on temperate reefs is less likely at lower latitudes on Australia’s east coast, where fucoids are generally lacking and *E. radiata* forms monospecific forests.

## Conclusion

Over evolutionary and contemporary scales, *Ecklonia radiata* has adapted to a wide range of environmental conditions; from about 27°S to 48°S throughout Australasia and southeastern Africa, it occurs on hard substrates from the shallow subtidal down to mesophotic reefs at about an 80-m depth. Such extreme variations in environmental conditions appears to drive great morphological plasticity, which has confused the species' identity. As such, identifying the true distribution of *E. radiata* requires molecular confirmation, particularly of putative Northern Hemisphere populations. There has been an enormous growth in our understanding of *E. radiata* and the ecosystems that it supports over the past 25 years, especially in Australasia, while gaps exist for other parts of its range. Wherever *E. radiata* occurs, however, it plays a major role in determining patterns of subtidal biodiversity and ecosystem structure. From individual holdfasts to entire forests, *E. radiata* supports thousands of species, underpins food webs and represents immense scientific, economic and social values.

Of concern is that climate change, especially warming and other anthropogenic stressors are driving the loss of *E. radiata* forests, and while there are regional differences in the drivers of this loss, there is ubiquity in patterns of change. Regime shifts to undesirable states (algal turfs or urchin barrens) are a common consequence of *E. radiata* loss and are accompanied by strong hysteresis making restoration difficult. Restorative activities will need to move beyond simply abating stressors and incorporate multifaceted intervention strategies that could include combinations of removing competitors and grazers, restoring the trophic structure of *E. radiata* forests and emerging interventions such as genetic rescue, assisted gene flow and adaptation (Coleman & Goold 2019). Despite a general landscape of contemporary loss, the evolutionary history of *E. radiata* has shaped a temperature-tolerant, plastic and widely distributed species that may be among the best-placed kelps to adapt or tolerate future oceans. Simultaneously, science must continue to generate understanding and discover novel solutions to ensure that these underwater forests survive and flourish in a future of increasing change.

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# A REVIEW OF BIOPHYSICAL MODELS OF MARINE LARVAL DISPERSAL

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## Abstract

Larval dispersal is arguably the most important but least understood demographic process in the sea. The likelihood of a larva dispersing from its birthplace to successfully recruit in another location is the culmination of many intrinsic and extrinsic factors that operate in early life. Empirically estimating the resulting population connectivity has been immensely difficult because of the challenges of studying and quantifying dispersal in the sea. Consequently, most estimates are based on predictions from biophysical models. Although there is a long history of dispersal modelling, there has been no comprehensive review of this literature. We conducted a systematic quantitative review to address the following questions: (1) Is there any bias in the distribution of research effort based on geographical or taxonomic coverage? (2) Are hydrodynamic models resolving ocean circulation at spatial scales (resolution and extent) relevant to the dispersal process under study? (3) Where, when and how many particles are being tracked, and is this effort sufficient to capture the spatiotemporal variability in dispersal? (4) How is biological and/or behavioural complexity incorporated into Lagrangian particle tracking models. (i.e. are key attributes of the dispersal process well captured.)? Our review confirms strong taxonomic and geographic biases in published work to date. We found that computational 'effort' (i.e. model resolution and particle number) has not kept pace with dramatic increases in computer processor speed. We also identified a number of shortcomings in the incorporation of biology, and behaviour specifically into models. Collectively, these findings highlight some important gaps and key areas for improvement of biophysical models that aspire to inform larval dispersal processes. In particular, we suggest the need for greater emphasis on validation of model assumptions, as well as testing of dispersal predictions with empirically derived data.

## Introduction

Marine ecosystems cover nearly 75% of the Earth's surface and harbour over 25% of global biodiversity (Scheffers et al. 2012), with recent estimates suggesting a total number of marine species in the range of 700,000 to 1 million (Appletans et al. 2012). At present, there are nearly 200,000 accepted species of marine animals (>80% of currently described marine biodiversity; WoRMS Editorial Board 2017). Developing a broad understanding and appreciation for this diversity is daunting, particularly as research effort in biological disciplines is terrestrially focussed (Lawler et al. 2006, Caliman et al. 2010, Trimble & van Aarde 2012) and the limited transfer of scientific knowledge across the land-sea interface has hampered the growth of marine biology and ecology as disciplines, despite calls for greater collaboration and integration (e.g. Menge et al. 2009). As Steele

(1991) so clearly articulated over a quarter century ago, the physical characteristics of marine and terrestrial environments operate over different spatiotemporal scales, with important consequences for how organisms interact with each other and the environment. The question of whether these environmental differences result in contrasting biological or ecological outcomes across systems requires explicit recognition and testing (Webb 2012).

## *The ubiquity of complex life cycles in the sea*

One example of how environmental differences lead to dissimilar ecological outcomes is in the nature of complex life cycles. Although many terrestrial animals exhibit complex life cycles in which different developmental stages occupy different niches and/or habitats (Wilbur 1980), this life-history pattern is more common and striking in the ocean, particularly in the context of benthic marine animals where relatively sedentary adult stages give rise to pelagic larvae. For these animals, transitions between life stages coincide with transitions not just among benthic habitat patches (e.g. coral and rocky reefs) but also with the overlying pelagic environment. The terrestrial analogy is those species that spend time in air, yet this habitat transition is usually temporary, as air provides almost none of the resources needed for survival. In contrast, benthic marine species that produce planktotrophic (feeding) larvae can spend weeks to months feeding and developing while in the pelagic environment (Keough & Swearer 2007).

Pelagic larval development is the dominant developmental mode among benthic marine species (Young 1990). Out of the thirty phyla of marine animals, there are only four phyla with benthic lifestyles (Gastrotricha, Gnathostomulida, Nematoda and Tardigrada) that lack species with pelagic larvae (Pechenik 1999). While there has been some debate over the ultimate drivers for the evolution of pelagic larval stages (e.g. Pechenik 1999, Burgess et al. 2016), the prevalence of this development mode combined with the dynamic nature of ocean currents means dispersal, the movement of individuals away from their birth location, over ecologically relevant scales is likely to be characteristic of the great majority of benthic marine animals most of the time.

## *The importance of dispersal and population connectivity*

Despite its fundamental importance to understanding the ecology and evolution of benthic marine organisms, dispersal is arguably the least-understood demographic process in the sea. Because most marine species spawn large numbers of tiny pelagic offspring that suffer extreme mortality while being dispersed by ocean currents (Thorson 1950, Cowen & Sponaugle 2009, Metaxas & Saunders 2009, White et al. 2014, Johnson et al. 2015), small changes in survival and ocean circulation can have profound consequences to the dynamics of marine populations. Successful dispersal, the movement of individuals from their birth to their recruit location, can lead to large recruitment pulses (e.g. Hjort 1914) that are capable of sustaining populations of long-lived species for decades (i.e. the storage effect, *sensu* Warner & Chesson 1985). Successful dispersal can also connect groups of local populations (population connectivity—the dispersal of individuals among populations) into a metapopulation (i.e. a population of populations, *sensu* Levins 1969), with the dynamic nature of marine environments causing widely varying demographic rates within and among subpopulations (Bertness et al. 1991, Phillips 2005). How such demographic heterogeneity influences marine metapopulations depends on knowledge of the spatiotemporal scales over which populations are connected via larval dispersal (e.g. Hjort 1914, Gaines and Bertness 1992, Kinlan et al. 2005, Noonburg et al. 2015, Shima et al. 2015). Identifying these scales has important management implications, as it sets the spatial scales for assessing, among other things, environmental impacts and recovery from disturbances (Reed et al. 2000), the spatial structure of exploited fisheries (Botsford et al. 2009), broad-scale conservation planning (Trakhtenbrot et al. 2005, Treml & Halpin 2015) and the design of marine reserve networks (Roberts 1997, Shanks et al. 2003, Gaines et al. 2010).

### *The components of successful dispersal*

Whether an individual larva is ultimately successful in dispersing from its birthplace to its recruit location depends on the culmination of a suite of intrinsic and extrinsic processes operating in early life (Pineda et al. 2009). In a previous study, Treml et al. (2015a) presented a framework for describing the four stages of population connectivity—the three stages of dispersal (Clobert et al. 2009) and the final stage of recruitment (post-settlement survival to reproduction), which determines reproductive population connectivity, dispersal of individuals that survive to reproduction (Pineda et al. 2007, Shima & Swearer 2010), and is important in evolutionary models of dispersal (Travis et al. 2012). This framework outlines the key drivers acting upon each stage of connectivity, capturing the biophysical complexity of this process for benthic marine species with biphasic life cycles (Figure 1). Stage 1 is the initiation of emigration in which some number of propagules (gametes, larvae or spores) are spawned. The parameters important in this stage are related to reproductive output (i.e. adult abundance, fecundity, egg quality and fertilisation success). Stage 2 is transport and movement,

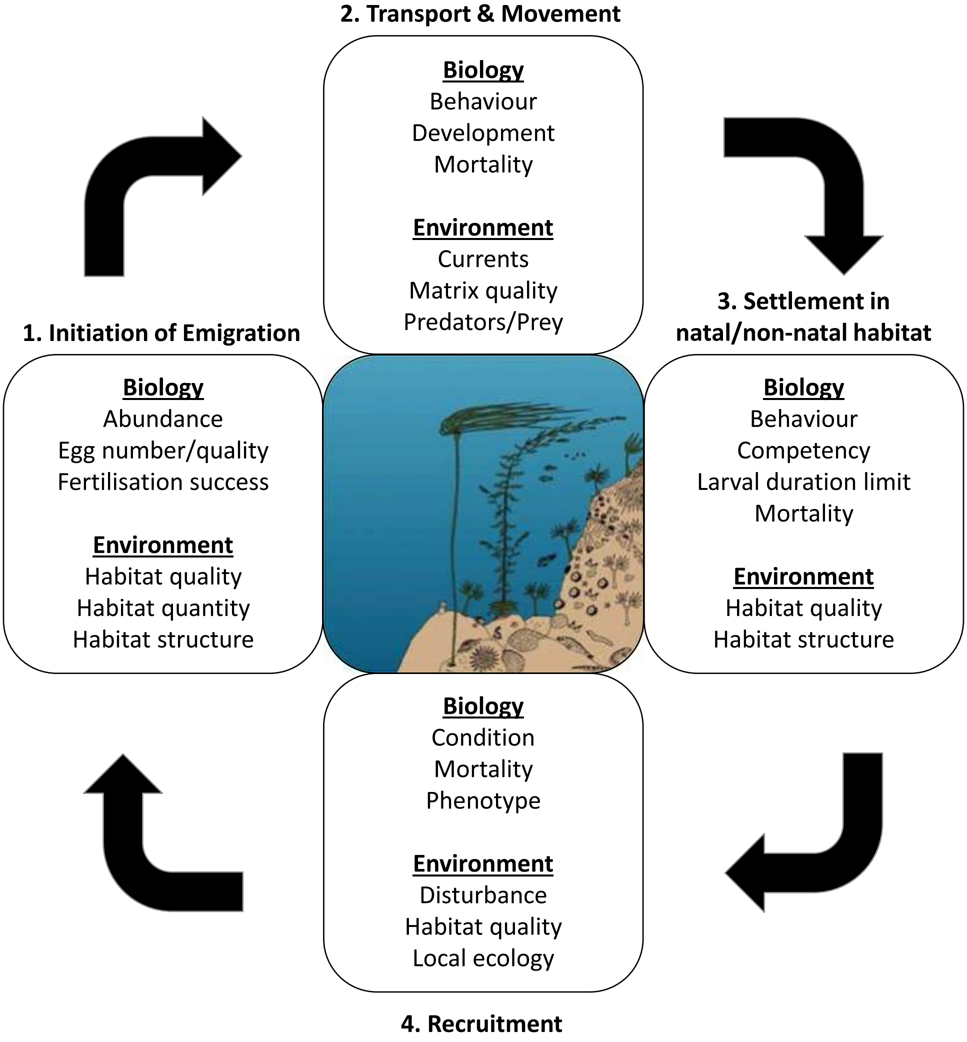

**Figure 1** The four stages of successful larval dispersal, resulting in population connectivity in benthic marine organisms. (Modified from Treml, E.A. et al. 2015a.)

where the disperser's trajectory is determined both by the potential advection and turbulence of currents and the motility and behaviour of individuals. Transition through this stage depends on larval survival and development rates, particularly sensory and motility capabilities that determine behaviour, and the extrinsic roles of currents and the spatial structure of the pelagic environment (i.e. the quality of the ocean matrix and the abundance of predators and prey). Stage 3 is settlement, which marks the end of the dispersal period and occurs when dispersers actively settle into some suitable habitat patch, either within the natal source site or in a non-natal location. This stage can also be biophysically complex and governed by intrinsic (settlement competency window—from competency to duration limit of the larval period, behaviour, motility and sensing) and extrinsic (habitat quality and structure) factors, which all influence the likelihood of survival during this habitat transition. Stage 4 is recruitment, which occurs when some settlers survive and mature to reproduce, thereby contributing to subpopulation demographics and gene flow. Recruitment into the adult stage is determined by individual growth and survival to maturation, which are influenced by habitat quality (including nursery grounds), disturbance, local ecology (competition and predation) and individual condition and phenotype. Together, these four stages capture the full biophysical complexity of the processes determining population connectivity.

## *Methods for estimating dispersal: The rise of the machines*

Empirically generating this level of insight into the connectivity process, even for a handful of species, has been immensely difficult because of the challenges of studying and quantifying dispersal in the sea. Not only do most marine animals produce large numbers of minuscule larvae that suffer high mortality and that can be difficult to identity to the level of species, but they typically spend days to months developing in the water column, where they are subject to transport by ocean currents, potentially over large distances away from their natal population (Swearer et al. 2002, Cowen & Sponaugle 2009). These spatiotemporal scales make the tracking of larvae virtually impossible, except in the rare cases where it is possible to follow larvae *in situ* (e.g. the short-lived and large larvae of ascidians; Olson 1985). As such, most estimates of dispersal are based either on indirect empirical methods (e.g. parentage analysis, genetic assignment tests, fluorescent staining, enriched stable isotope labelling, and assignment tests using environmental markers) that rely on the collection of successful dispersers to determine where they came from [and usually not how they got there, but see Shima & Swearer (2009, 2016) for applications of fish otolith elemental time series to reconstruct dispersal histories] or on theoretical estimates of potential dispersal trajectories based on biophysical models (for reviews of these methods, see Levin 2006, Cowen & Sponaugle 2009, Jones et al. 2009, Leis et al. 2011).

Although these approaches have different strengths and weaknesses depending on the spatial and temporal scales of interest, empirical approaches for quantifying demographic connectivity are often logistically and financially costly and provide only snapshot estimates of dispersal, usually for a few sample sites and over limited geographical scales. Consequently, biophysical models have long been the dominant approach for estimating potential dispersal patterns and resulting connectivity outcomes in marine systems, even with the development of new methods and technologies fueling the rapid rise in empirical marine larval dispersal research over the past fifteen years (Figure 2; see also Jones 2015). Since 1980, 77% of marine larval dispersal research per year has been modelling studies (mean [95% confidence interval (CI)] annual proportion of studies: 0.766 [0.791–0.812]), and this pattern has remained constant over time (linear regression of proportion of modelling studies against publication year: slope parameter estimate (95% CI) = −0.0007 (−0.0051–0.0036), $n = 38$, $p = 0.724$).

## *Horizon scan—How well are we doing?*

Given the long history of coupling Eulerian ocean circulation models with Lagrangian particle tracking models to predict patterns of larval dispersal, it seems to be an appropriate time to assess

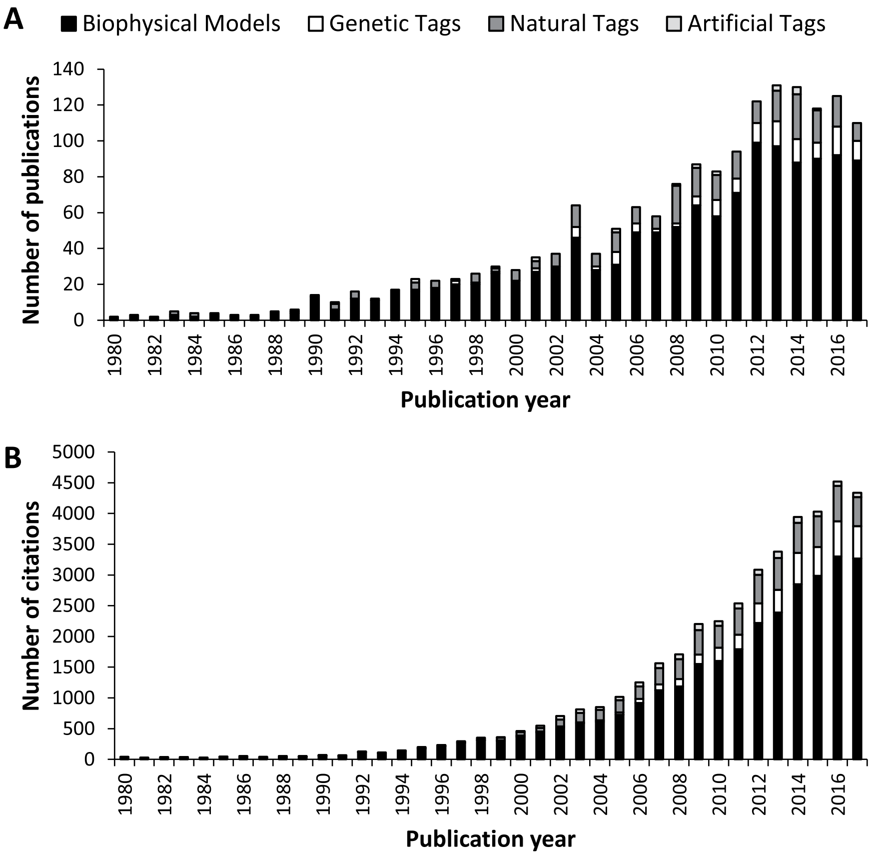

**Figure 2** Temporal trends in (A) publication and (B) citation rates for the principal theoretical (biophysical models) and empirical (genetic, natural and artificial tags) methods for estimating contemporary marine larval dispersal. Data are based on an ISI WoS publication search and citation report (performed on 1 May 2018) using the following Boolean search terms, with additional refining based on article titles and abstracts: *Biophysical Models*—(larv* OR propagul* OR egg*) AND (transport* OR retention OR dispers* OR connectivity OR 'residence time*') AND (hydrodynamic* OR numerical OR biophysical OR lagrangian) AND (model* OR simulation*); *Genetic Tags*—(larv* OR propagul* OR egg*) AND (transport* OR retention OR dispers* OR connectivity OR 'residence time*') AND (parentage OR 'genetic assignment'); *Natural Tags*—(larv* OR propagul* OR egg*) AND (transport* OR retention OR dispers* OR connectivity OR 'residence time*') AND (microchemistry OR 'natural tag*' OR 'natural mark*' OR 'natural signature*' OR 'natural composition*' OR 'chemical tag*' OR 'chemical mark*' OR 'chemical signature*' OR 'chemical composition*' 'elemental tag*' OR 'elemental mark*' OR 'elemental signature*' OR 'elemental composition*' OR 'environmental tag*' OR 'environmental mark*' OR 'environmental signature*' OR 'environmental composition' OR 'geochemical tag*' OR 'geochemical mark*' OR 'geochemical composition*' OR 'geochemical signature*' OR 'multielemental mark*' OR multielemental signature*' OR multielemental tag*' OR 'multielemental composition'); *Artificial Tags*—(larv* OR propagul* OR egg*) AND (transport* OR retention OR dispers* OR connectivity OR 'residence time*') AND (artificial OR fluorescent OR calcein OR *tetracycline OR alizarin OR 'enriched stable isotop*' OR 'isotop* ratio') AND (mark* OR signature OR tag). Given the differences in publication history among methods and incomplete reporting for 2018 at the time of analysis, trends were trimmed to cover the 37-year period from 1980 to 2017.

our efforts at incorporating biological complexity into such modelling efforts and what consequences this might have for our understanding of actual dispersal and population connectivity. Although several studies have assessed sensitivities of modelled dispersal patterns to both particle-tracking (e.g. Simons et al. 2013) and biological-input parameters (e.g. Paris et al. 2007, Peck & Hufnagl 2012, Robins et al. 2013, Treml et al. 2015a), there has been no specific review of this extensive body of research (however, see Bryan-Brown et al. 2017 for a broad review of marine population connectivity studies across empirical approaches).

To address this knowledge gap, we conducted a systematic quantitative review of studies that used hydrodynamic models and Lagrangian particle tracking with at least some level of biological relevance to investigate larval dispersal in marine environments. The resulting database was then used to answer the following questions:

- Is there any bias in the distribution of research effort based on geographical or taxonomic coverage?
- Are hydrodynamic models resolving ocean circulation at spatial scales (resolution and extent) relevant to the dispersal process under study?
- Where, when and how many particles are being tracked, and is this effort sufficient to capture the spatiotemporal variability in dispersal?

## A systematic quantitative review of marine larval dispersal studies using Lagrangian biophysical models

### *Development of the database*

We performed a literature search on 31 October 2017 using the ISI Web of Science and the following Boolean search term: (larv* OR propagul* OR egg*) AND (transport* OR retention OR dispers* OR connectivity OR 'residence time*') AND (hydrodynamic* OR numerical OR biophysical OR Lagrangian) AND (model* OR simulation*). This resulted in an initial list of 1089 references. No additional references were identified through other sources. The titles and abstracts of all references were screened to eliminate irrelevant studies ($n = 594$). As the purpose of the review was to evaluate biophysical models of larval dispersal, we excluded references that only modelled ocean circulation, with no particle tracking ($n = 25$) and references that were not conducted on animals with pelagic larval development ($n = 8$). Overall, this resulted in a final data set of 524 records (from 462 references—see Appendix).*

### *Criteria used to evaluate studies*

A range of information was extracted from each study that can be broadly grouped into seven categories: geographical context, study animal, hydrodynamic model, particle-tracking model and the three stages of dispersal (initiation of emigration, transport and movement and settlement in natal/non-natal habitat) (Table 1). These criteria were chosen in order to answer the questions posed in our review.

## The distribution of research effort

Geographical and taxonomic bias in research efforts can limit inference and obscure a general understanding of larval dispersal.

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* Access to this database is available to potential collaborators—contact the lead author for more information.

**Table 1** Criteria used to characterise biophysical modelling studies of marine larval dispersal

| Category | Data | Description |
|---|---|---|
| Geographical context | Year of publication | |
| | Country of author | Country of lead author at time of publication |
| | Country of study | Left blank if the study was across multiple countries |
| | Ocean/major sea of study | Arctic Ocean, Atlantic Ocean (Baltic Sea, Mediterranean Sea, North Atlantic, South Atlantic), Indian Ocean, Pacific Ocean (North Pacific, South Pacific), South China Sea, Southern Ocean |
| | Type of dispersal environment | Continental shelf, deep sea, embayment, open coastline |
| Study animal | Taxonomic details | Class, phylum, genus, species; generic categories include generic benthic animal, coral, fish, particle, reef animal, reef fish |
| | Habitat type of adult life stage | Animal (parasitic), benthic (demersal), pelagic; left blank if study was on a 'generic' species |
| | Habitat type for benthic species | Coral reef, estuary, rocky reef, reef/soft sediment, soft sediment; left blank if study was on a 'generic' species |
| | Commercial relevance | Fished, not fished, unknown |
| Hydrodynamic model | Software used | Name of programme, proprietary, unstated |
| | Dimensionality | 2-dimensional, 3-dimensional |
| | Area of model domain (km$^2$) | Calculated by drawing polygons in Google Earth and calculating the area of the polygon using http://www.earthpoint.us/Shapes.aspx. Three methods were used to determine the polygons: (1) If boundary coordinates were available, points were plotted as place-marks, and a polygon drawn using the place-marks and the coastlines as boundaries. (2) If only maps were available, boundaries were extrapolated from latitude and longitude coordinates. (3) In cases where maps were provided but with no grid references, then boundaries were inferred from the coastline shapes and any textual references provided. This was done separately for small and large domains in studies that used nested models. |
| | Horizontal cell type | Fixed, variable, unstated |
| | Horizontal cell resolution (m) | Maximum (finest) and minimum (coarsest) |
| | Maximum depth of model domain (m) | Calculated as follows: (1) the maximum modelled depth, or (2) if whole water column was modelled, the maximum depth of the modelled domain, with values taken from http://webapp.navionics.com/ |
| | Vertical cell type | Fixed, variable, unstated |
| | Vertical cell number (if fixed) | N/A |
| | Vertical cell thickness | Fixed, variable, unstated |
| | Vertical cell resolution (m) | Maximum (finest) and minimum (coarsest) |
| Particle-tracking model | Software used | Name of programme, proprietary, unstated |
| | An IBM? | Yes, no |
| | Model run duration (days) | N/A |
| | Total number of larvae released | N/A |
| Initiation of emigration | Release location | Constant spacing, even spread over a specified area, habitat as proxy for populations, known populations, unstated |
| | Release amount/location | Constant, scaled to habitat area, scaled to observed number of dispersers, scaled to population size, unstated |

(*Continued*)

**Table 1 (Continued)** Criteria used to characterise biophysical modelling studies of marine larval dispersal

| Category | Data | Description |
|---|---|---|
| | Release times | Single, multiple at constant rate over arbitrary window, multiple with known times |
| | Released during known spawning season? | Yes, no |
| | If single release, number/ location | N/A |
| | If single release, duration of release (min) | N/A |
| | If multiple releases, release frequency (h) | N/A |
| | If multiple releases, total release duration (days) | N/A |
| Transport and movement | Larval mortality? | Yes, no, unstated |
| | Larval mortality type | Fixed-generic, fixed-species specific, variable-environmentally dependent, variable- state dependent |
| | Behaviour mode | Active, passive only for an initial period, passive throughout development, unstated |
| | Vertical movement? | Yes, no, unstated |
| | Vertical movement type | Constant, constant buoyancy, variable with age/size |
| | Vertical swimming speed used (cm/s) | Minimum and maximum |
| | Horizontal swimming? | Yes, no, unstated |
| | Horizontal swimming type | Constant, variable with age/size |
| | Horizontal swimming speed used (cm/s) | Minimum and maximum |
| | PLD | Fixed, fixed competency window, set by duration of model run (unlimited), unstated, variable- modelled, variable- from collected settlers |
| Settlement in natal/ non-natal habitat | Time to competency (min PLD) (days) | N/A |
| | Maximum PLD (days) | N/A |
| | Settlement type | If within habitat zone/detection distance before end of model run, if within habitat zone/detection distance at end of PLD, if within habitat zone/detection distance before end of PLD, if within habitat zone/detection distance and competent to settle, location at end of PLD, location at end of run, no settlement, other, unstated |
| | Habitat detection present? | No, yes—fixed, yes—variable |
| | Habitat detection distance (km) | Minimum and maximum |

## *Geographical coverage*

We used sea-surface area (of oceans or other predefined regions) to generate an expected distribution of research effort (i.e. the predicted distribution of published studies in the absence of any bias) and found a clear and striking pattern of over-representation of published studies from European/North American waters (i.e. the North Atlantic Ocean and Mediterranean and Baltic seas) and an under-representation of studies in the Southern Hemisphere (South Pacific and Southern oceans) and the Indian Ocean [$n = 521$ (three global scale studies were removed), $df = 9$, $X^2 = 1749.466$, $p < 0.0001$;

Figure 3A]. This pattern is qualitatively similar to that observed by Bryan-Brown et al. (2017). Given the global distribution of leading research universities ( www.timeshighereducation.com), this pattern is unsurprising, and others have observed similar geographical distributions of ecological research (Lawler et al. 2006, Trimble & van Aarde 2012, Hale & Swearer 2016). Research efforts are concentrated closer to shore (76% of studies), with 12% of them from coastal embayments and 64% from open coastlines. A total of 18% of studies are from the continental shelf, and 6% are from the deep sea. Although we are unable to evaluate these against an expected distribution, it seems clear that more studies are needed for more offshore and/or deepwater taxa.

These clear geographic biases in research efforts may skew our perceptions of the relevant scales and processes that shape dispersal. For example, islands that are more than 5 km apart (effectively, habitat patchiness for many benthic and demersal marine species) are two to three times more abundant in the tropics than in temperate latitudes (Leis et al. 2013). Because scales of habitat patchiness

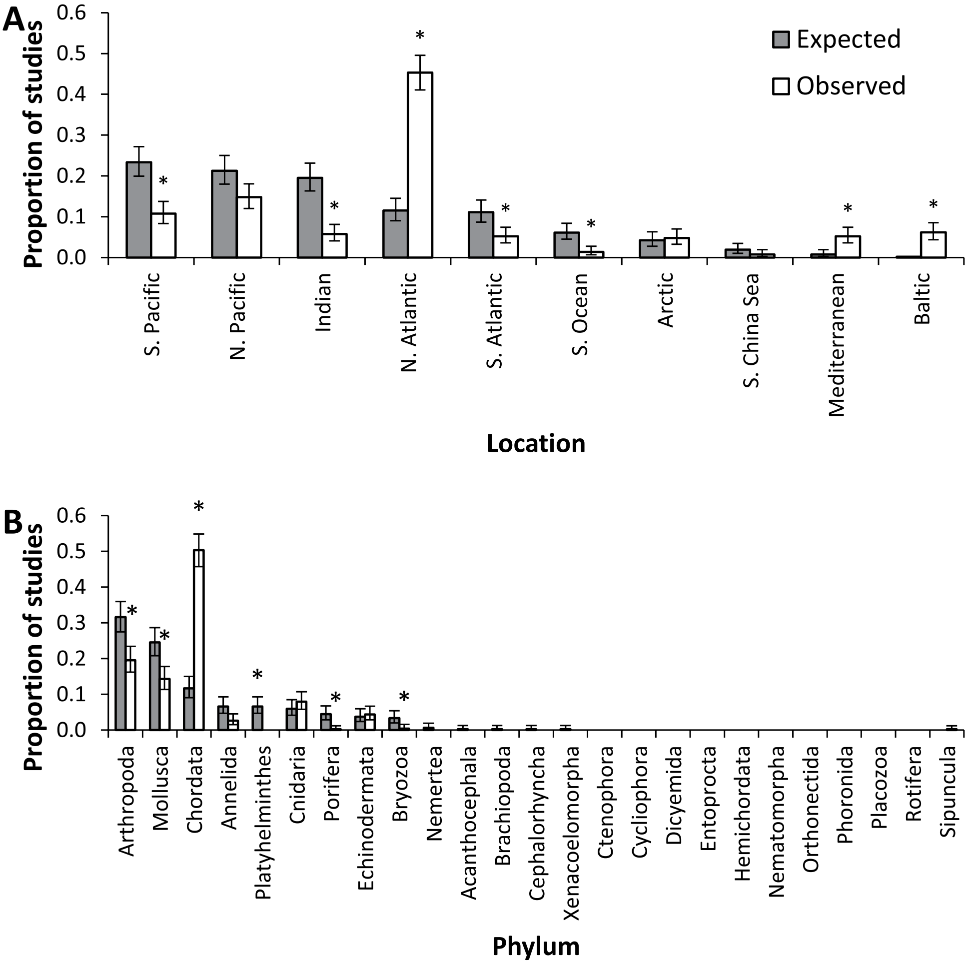

**Figure 3** Distribution of research effort based on study (A) location and (B) phylum. The expected numbers of studies by location were based on a frequency distribution of surface ocean area (in km$^2$) among the 10 major oceans and seas. (Data from Eakins & Sharman 2010.) The expected numbers of studies by phylum were based on a frequency distribution of accepted species among the 25 marine animal phyla with pelagic larvae. (Data from the World Register of Marine Species; accessed 1 December, 2017).) Error bars are 95% CI based on the Wilson score interval method for sample proportions. (*indicates significant deviation from expected.)

relative to dispersal potential have important ecological consequences (e.g. Pinsky et al. 2012), an over-representation of studies from certain latitudes could lead to perceptions about dispersal and connectivity that do not necessarily hold for other areas. Also, regional variations in ocean circulation can lead to different predictions of dispersal trajectories and distances. For example, differences in amplitude, rotational speed and direction of eddies in the Northern and Southern hemispheres (Chelton et al. 2011), as well as regional differences in geostrophic velocities among major ocean basins (Gray & Riser 2014), are likely to result in variable dispersal outcomes. Dispersal outcomes will also be a function of larval life histories, which vary considerably among biogeographic regions (e.g. Marshall et al. 2012). In short, dispersal and patterns of population connectivity are likely to be context-dependent, and if the goal is to achieve a more general understanding, then this requires a widening of the geographical coverage in dispersal modelling studies.

### *Taxonomic coverage*

Most studies (78%) have been conducted on species with benthic adult life stages; 20% focus on species with pelagic adults, and 2% target species with parasitic adult life stages (51 out of the 524 studies modelled generic particles/taxa). Of the 369 studies conducted on a benthic species, most (43%) focussed on reef-associated species (coral reefs: 24%; rocky reefs: 19%), with a further 28% looking at sediment-associated species, 12% at estuarine species (split evenly between rock- and sediment-associated species) and 17% at generalist (reef and sediment) species. This distribution of research effort reflects a bias towards reef-associated species, given that the majority of benthic habitat is sedimentary. Based on the frequency distribution of currently accepted marine species among animal phyla with larval development, there is also a taxonomic bias in research effort, with considerable overrepresentation of chordate (i.e. fish) studies and under-representation of studies on arthropods, molluscs, flatworms, sponges and bryozoans [$n = 455$ (sixty-nine studies of generic taxa were excluded), $df = 24$, $X^2 = 803.618$, $p < 0.0001$; Figure 3B]. In part, this bias is driven by a strong focus on commercially important species (79.8% fished versus 20.2% not fished; $df = 1$, $X^2 = 126.247$, $p < 0.0001$), with 93% of chordate studies on fished species. Again, as with other reviews of ecological research, taxonomic biases are not uncommon (e.g. Caliman et al. 2010, Bryan-Brown et al. 2017). Nonetheless, these biases almost certainly mean that the great diversity of larval developmental modes, morphologies, behaviours and life histories (e.g. Young et al. 2002) is unevenly represented. For example, this has resulted in spurious differences in estimates of marine larval dispersal based on different methods (e.g. Kinlan & Gaines 2003). If the goal is a more holistic understanding of dispersal across the full spectrum of marine biodiversity, then broader taxonomic coverage is clearly needed.

## Matching the physics to the biology

Although there exists a long and rich history of observations and, more recently, modelling of open ocean circulation (see Semtner 1986 and Talley et al. 2011 for historical perspectives), most of the research efforts on dispersal and connectivity appear to be driven by the interests of benthic ecologists (this is an inference based upon the over-representation of studies on benthic species and nearshore habitats). We contend that many of these research efforts use models that may be better suited to offshore regions (which has remained a strong focus of oceanographers), and in at least some instances, the models may fail to capture important features of the nearshore coastal zone where larvae of many benthic marine species are born, settle, and may even complete their entire development (e.g. Morgan et al. 2018a). Modelling the nearshore environment is notoriously difficult, as hydrographic features of the coastal zone (e.g. breaking waves, tides, runoff, and upwelling) result in ocean circulation dynamics that operate at finer temporal and spatial scales than are typically observed or modelled (Largier 2003, Nickols et al. 2012, Morgan et al. 2018b, Shanks and Morgan 2018). In situations where dispersal outcomes are largely driven by physical transport, this spatiotemporal mismatch means that the underlying modelled ocean circulation patterns (which advect Lagrangian particles) may often fail to capture dispersal at the relevant scales for many marine species (Largier 2003, Nickols et al. 2012).

### *Dimension and resolution of the model domain*

Overall, most (84%) of the 524 studies used 3-dimensional hydrodynamic models. Model domain extent varied enormously, ranging from $4 \times 10^{-6}$ to $3.5 \times 10^{8}$ km$^2$ in area and going to maximum depths of 2.7–10,000 m. Across studies with reported information, model resolution varied by eight orders of magnitude in the horizontal dimension (median cell size: 3.5 km; range: 13 cm to 110 km; $n = 498$ studies) and was strongly correlated with model domain size (Figure 4A). Most models used fixed regular grids (67%), with a moderate number of studies using curvilinear or variable mesh

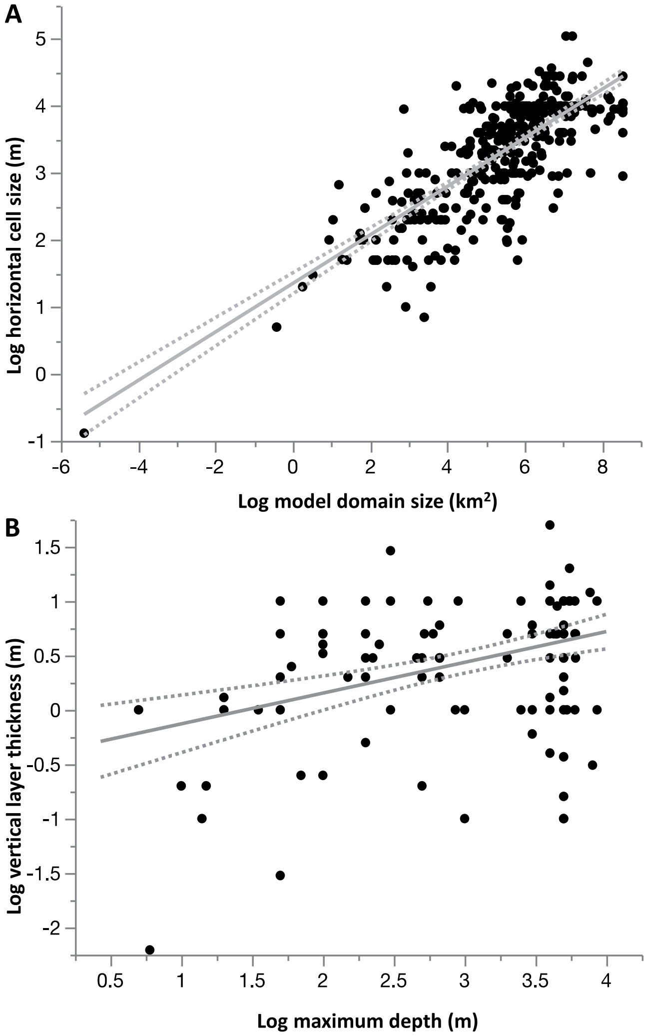

**Figure 4** Relationships between (A) horizontal model cell size and model domain size ($R^2_{\text{adj}} = 0.564$, $F_{1,494} = 640.397$, $p < 0.0001$), and (B) minimum vertical layer thickness (i.e. discretisation) and maximum depth ($R^2_{\text{adj}} = 0.133$, $F_{1,128} = 20.707$, $p < 0.0001$). When nested and/or terrain-following models were used, we used the highest (finest) resolution reported. Model fits are linear regressions (with 95% CI).

sizes (20%) or nested models (9%), with the remaining 4% unstated. For studies using 3-dimensional models, 77% used a fixed number of vertical layers; a further 6% used variable (dynamic) layers and 17% were unstated. For studies using a fixed number of layers, they ranged from 2 to 128 layers (median: 30). Most studies used variable layer thicknesses (e.g. 59% were terrain following); a further 12% used fixed thicknesses, and the remainder (29%) did not provide this information. Vertical resolution varied by three orders of magnitude (median layer thickness: 5 m; range: 1 cm to 50 m) and was only weakly related to the model's maximum depth (Figure 4B). What these results clearly show is a lack of consistency in how well resolved oceanographic models are, even when accounting for differences in domain size (residual unexplained variance: 43% horizontally, 90% vertically).

### *Are we keeping pace with computational advancements?*

Although downscaling models will likely improve the representation of velocity flow fields, particularly along topographically complex coastlines, substantial computational costs are incurred. Computational costs scale in proportion to the number of cells and the number of time steps in the model (Kim et al. 2014); for example, increasing a 3-dimensional model resolution by a factor of two (i.e. twice the number of meridonal cells, zonal cells and depth cells and twice the number of time steps) would increase the computational requirements by approximately sixteen times (or even more, depending on maximum velocities and model stability). Over the past 35 years of larval dispersal modelling, advancements in computer technology [e.g. processor power, cache, random access memory (RAM), graphics processing units (GPUs)] mean that these computational costs, in terms of time and money have decreased and are continuing to decrease. This begs the question of whether hydrodynamic model resolution has increased over time, and if so, whether the rate of increase is proportional to increases in computational speed (after accounting for the scaling of computational costs).

After adjusting for the effect of model domain size on horizontal resolution (see Figure 5), model resolution has been getting finer (on average) with time (Figure 5A), a decrease in cell size of 49% over the 35 years of published studies. Over a comparable time period (26 years), computational speed (based on a single-thread performance of CPUs) has increased by over 800% (Figure 5B). If downscaling is beneficial because it usually leads to better representation of fine-scale current velocities acting on larvae (particularly nearshore), then the rate at which this has occurred over the past three decades has not been limited by computing power. This, of course, does not account for the fact that downscaled models may necessarily include more equations, more parameters, and therefore more memory requirements, which may contribute to this slower-than-expected increase in resolution.

### *Is the tail still wagging the dog?*

Although more coarsely resolved velocity fields have been shown to realistically capture long-distance dispersal pathways, particularly among offshore islands where oceanic conditions can lead to greater spatial coherence in velocity fields (e.g. Davies et al., 2015; Treml et al. 2015b; Liggins et al. 2016), there is the possibility that they can lead to biases in characterising the spread of particles from release locations in more coastally dominated environments and for more local-scale questions. Several recent simulation studies have shown that both estimates of transport distances and direction, as well as the relative dispersion of particles, are very sensitive to model resolution, over both short (50–800 m, 1–12 h; Lynge et al. 2010) and long (0.8°–0.56°, 1–30 days; Putman & He 2013) length and time scales, respectively. In the case described in Putman & He (2013), finer-resolved models more closely matched *in situ*, near-surface drifter trajectories. Small-scale flow conditions, such as those found in coastal boundary layers, can lead to greater particle retention times and a reduction in the mean but an increase in the variance of dispersal distances (e.g. Nickols et al. 2012). These findings are intriguing and suggest that future efforts at downscaling models in coastal ecosystems may lead to more evidence for greater local retention times for some particles, as well as greater maximum dispersal distances.

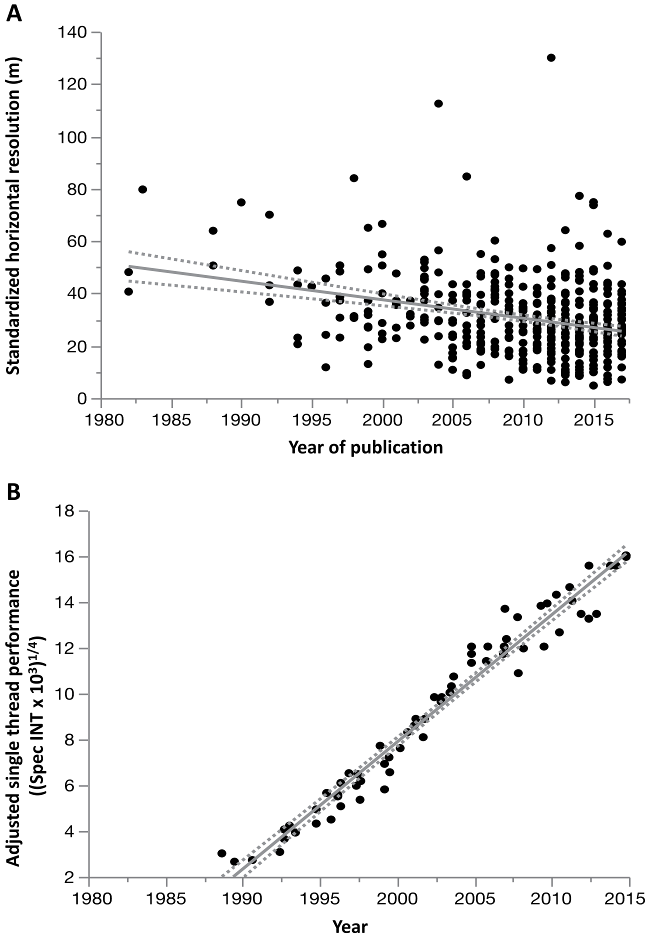

**Figure 5** (A) Relationship between standardised horizontal model resolution (cell size) and year of publication ($R^2_{\text{adj}} = 0.090$, $F_{1,494} = 49.948$, $p < 0.0001$), and (B) trends in computer processing efficiency (as measured by single-thread performance (SpecINT × $10^3$) of CPUs) over time ($R^2_{\text{adj}} = 0.964$, $F_{1,64} = 1740.411$, $p < 0.0001$). Horizontal model resolution was standardised to account for the effect of domain size. This was done by saving the residuals of the linear regression in Figure 4A, adding those residuals to the mean log horizontal resolution and back-transforming to the original units. The single-thread performance data were downloaded from https://www.karlrupp.net/2015/06/40-years-of-microprocessor-trend-data/. These computer processing efficiencies were adjusted by a 1/4-power weighting, as computational costs for a 3-dimensional hydrodynamic model generally increase with model resolution in proportion to cell size$^{-4}$ (e.g. Kim et al. 2014). Model fits are linear regressions (with 95% CI).

### *Characterising the dispersal process*

Because of the computation costs associated with estimating velocity fields, Lagrangian particle-tracking models run most efficiently when they are run offline or independent to the ocean model (e.g. Jones et al. 2016). Determining how many particles to release and from how many locations represent trade-offs between computational time and precision. Releasing too few particles, from too few locations within a source area/patch or all at once can result in poor characterisation of the underlying variability in potential dispersal trajectories from that source (Brickman & Smith 2002). Although the optimal number of particles to release will depend (at least in part) on what question is being asked, the findings of Jones et al. (2016) suggest that releasing <1000 particles per location is likely to result in considerable error in estimates of dispersal and population connectivity. In contrast, Simons et al. (2013) found the minimum number of particles per location in their model domain ranged from 2800 to 5900 for tracking times of 15 and 30 days, respectively.

Relevant studies in our database ($n = 299$ with reported data) released between 72 and $4.9 \times 10^{17}$ particles (median: 464,495 particles) in total, with particles being released over a period of 0.15 to 2,523,744 days (median: 365 days). 38% of studies released particles in a single event/location (Figure 6A). The remainder implemented multiple releases, either within a fixed window (43%), a predicted spawning window (2%), or a known spawning window (11%); 6% of studies provided no information on timing of particle release. For the studies that used a single release ($n = 110$), the number released ranged from 1 to $1 \times 10^7$ particles (median = 1000), with 90% of studies releasing simultaneously. For studies with multiple releases ($n = 168$ out of 327, with reported details), the number of particles released from each location ranged from 1 to $4.2 \times 10^7$, with a median of 178. Release intervals ($n = 252$) ranged from 1 second to 1 year (median: 72 h). Surprisingly, the number of particles released has not increased over time, suggesting that computational power is an unlikely limiting factor [linear regression of the log number of particles released per location against publication year: slope parameter estimate (95% CI) = 0.013 (−0.026–0.051), $n = 167$, $p = 0.514$].

Taken together, these findings raise the possibility that in some instances, the shape of the potential or realised dispersal kernel is not effectively being described: more than one-third of studies released only at a single time and about 50% of studies released fewer than 1000 particles per location. Avoidance of error due to undersampling will require careful consideration of sample size, release locations and times, duration of tracking, biophysical complexities in relation to the questions of interest and the precision required to answer them. These model parameter values will be system specific and should be informed by a sensitivity analysis (as has been suggested by others, including North et al. 2009 and Simons et al. 2013).

## Initiation of emigration

Benthic marine invertebrates and fishes are some of the most fecund animals on Earth. Given the stochastic nature of larval transport in coastal oceans (e.g. Siegel et al. 2008), the precise locations and timings of spawning can profoundly affect dispersal outcomes (e.g. Treml et al. 2012, Robins et al. 2013, Treml et al. 2015a).

### *Location, location, location*

Although the majority (44%) of studies released particles from known spawning/population locations (Figure 6B), the remainder either used habitat as a proxy (25%) or distributed releases evenly (19%) or with constant spacing (11%) within a target area (with a further 1% unstated). Spawning locations can strongly affect dispersal distributions due to differences in local oceanographic conditions, particularly along topographically complex coastlines. For example, it is well known that many marine species migrate to spawn in areas that are more favourable for larval retention (the member-vagrant hypothesis, Sinclair 1988). We recently showed that estimates of a range of dispersal and metapopulation metrics were strongly influenced by the location of larval release (Treml et al. 2015a), even when known release locations were only tens of kilometers apart. For species that are common and strongly associated with a particular habitat type (e.g. reef-associated), the habitat is likely to be a suitable proxy for spawning location. For species that are more mobile, however, knowing where spawning occurs will be important.

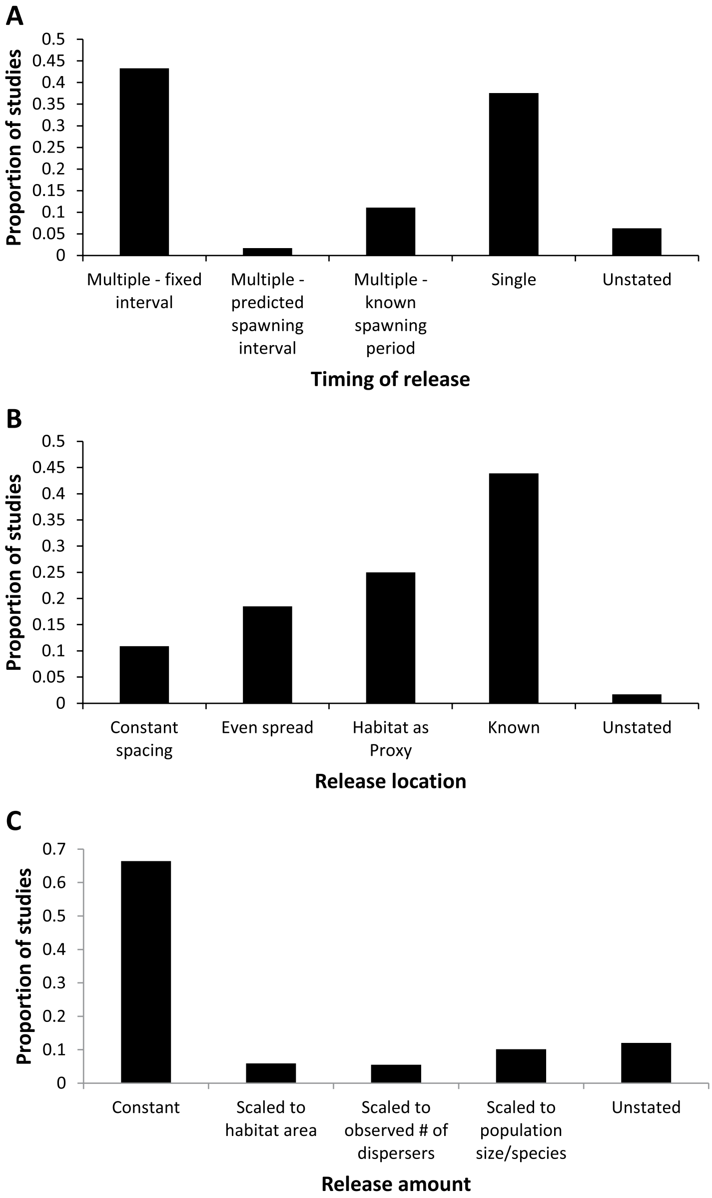

**Figure 6** The distribution of modelling studies based on (A) how and when particles were released, (B) where particles were released and (C) the number of particles released from each location and event (for studies with multiple releases), as described in Table 1.

### *Timing is everything*

Only 13% of studies released particles during a known (11%) or predicted (2%) spawning period (Figure 6A). Reproductive timing in marine invertebrates and fishes exhibits tremendous diversity over diel, lunar, seasonal and annual time scales, with many of the adaptive explanations for particular spawning times related to offspring transport/dispersal (e.g. Robertson 1991, Morgan & Christy 1995). Using an environmental marker approach, Carson et al. (2010) detected consistent seasonal differences in directionality of alongshore transport of larvae of two mussel species in southern California due to seasonal changes in the dominant current direction. As each species spawns primarily in different seasons, this led to differences in the predominant dispersal direction and resulting connectivity patterns, highlighting the importance of knowing the phenology of a species. Several recent modelling studies corroborate this conclusion by illustrating that both the timing (Romero-Torres et al. 2017) and frequency (Kough & Paris 2015) of spawning can have profound impacts on dispersal and population connectivity predictions. Given these findings, there is a clear need for models to incorporate more realistic spawning patterns.

### *Accounting for spatial variability in production*

Successful dispersal between populations is not simply dependent upon a non-zero probability of larval transport from spawning to settlement locations (potential connectivity— the probability of dispersing between populations); it also requires that a sufficient number of larvae are spawned to result in at least some settlement (realised connectivity— the product of larval production and potential connectivity or the number of individuals that disperse between populations) (Watson et al. 2010). To date, most (66%) modelling studies released the same number of particles per location to estimate a probability of potential connectivity, with only 16% rescaling this relative probability to a realistic dispersal rate using population size (10%) or habitat area (6%) as an estimate of reproductive output (Figure 6C). This is likely because most studies are focussed on estimating the potential for dispersal/connectivity. These potential connectivity predictions, however, may not represent realistic dispersal rates and connectivity strengths because they do not account for the effects of larval production. Thus, they cannot be directly compared to empirical estimates (which, are by definition, measures of realised connectivity). Accounting for spatiotemporal variability in propagule production rates can result in fundamentally different predictions about dispersal and connectivity (e.g. Hameed et al. 2016, Castorani et al. 2017). Modelling efforts that can incorporate such information will be more ecologically relevant and should be a priority for future work.

## Transport and movement

### *Larval mortality*

Estimates of realised connectivity require consideration of both the numbers of propagules released and their chances of survival. Surprisingly, 70% of models did not consider mortality. Of those that did, only 29% (8.7% overall) used a species-specific mortality rate (Figure 7). Furthermore, the

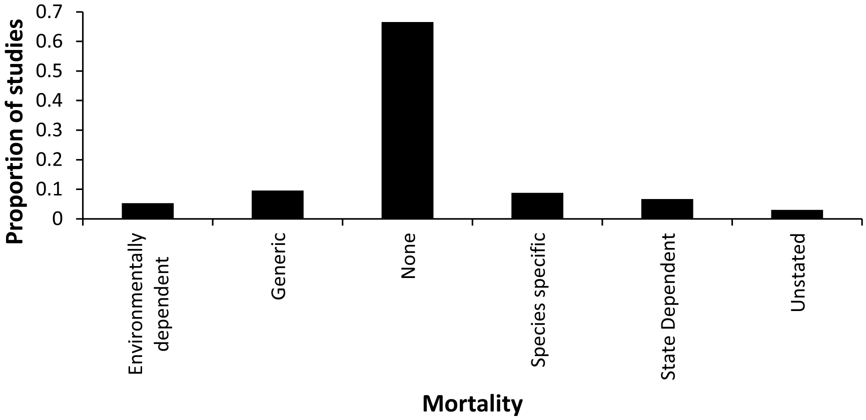

**Figure 7** The distribution of modelling studies based on the parameterisation of mortality, as described in Table 1.

likelihood of models including a mortality rate has actually marginally decreased over time (logistic regression: $R^2 = 0.03$; likelihood-ratio $X^2 = 18.499$, $df = 1$, $p < 0.0001$). This limitation is, in part, a consequence of the fact that empirical estimates of mortality in the wild are rare, and those that are available are highly variable and uncertain even within taxa, ranging by more than two orders of magnitude (White et al. 2014). Most estimates suggest a mortality rate of approximately 20% per day, but several recent studies suggest this may be an overestimate (e.g. White et al. 2014, Johnson et al. 2015). Coincidentally, the 30% of models that incorporated mortality used a median rate of 18% per day (range: 0.1%–95%).

There is also ample empirical evidence that mortality rates are not constant during larval development (e.g. Cushing 1975, Leggett and DeBlois 1994, Houde 1997). However, only 7% of models allowed mortality to vary as a function of age, size or stage (e.g. stage duration hypothesis, Cushing 1975; bigger-is-better hypothesis, Bailey & Houde 1989). Regardless of the shape of the function, mortality is one of the biggest biological drivers of variation in modelled dispersal patterns and connectivity outcomes (e.g. Cowen et al. 2000, Paris et al. 2007, Treml et al. 2015a). Over the past two decades, there has been considerable development in coupling individual based models (IBMs) to hydrodynamic and particle-tracking models to investigate the drivers of variation in larval mortality (see Peck & Hufnagl 2012 for a recent review). Such approaches seem to be a fruitful avenue for improving mortality functions, including time- and space-varying components, in future dispersal modelling research.

### *Duration of the settlement window*

In most marine species, settlement can occur only once a larva becomes developmentally competent. Competency can arise from very early to quite late in the larval dispersal phase, and it continues up to the point when a larva dies or loses its capacity to settle (Anderson 1988, Leggett and DeBlois 1994). The maximum length of the pelagic larval phase [pelagic larval duration (PLD)], or the limit of competency, is arguably the most well studied biological trait that influences the dispersal potential of marine animals. Despite considerable evidence that many species exhibit high variability in age at settlement (e.g. Victor 1986), 50% of studies used a fixed larval duration (i.e. 'the music stops' — individual either settles or dies when PLD reached), 26% used a fixed competency window (i.e. a range over which an individual could settle), and 16% used a variable PLD (i.e. individuals took varying times to reach the PLD), with the remainder either unlimited (4%) (i.e. until the end of the model run) or unstated (1%) (Figure 8A). For studies that modelled a particular species (as opposed to a generic disperser), modelled PLDs were on average 30 days (170%) longer than observed durations for a given phyla (range: 7 days shorter to 69 days longer; 70% less to 642% more). These differences, however, were not statistically significant, given the high among-species variation within taxa (Figure 8B). This suggests that modelled dispersal distances could be overestimates for most marine species. This possibility is supported by empirically derived relationships between PLD and dispersal distance (e.g. Shanks 2009; but see D'Aloia et al. 2015) and genetic metrics (e.g. Selkoe & Toonen 2011), and because modelled predictions of dispersal and population connectivity are sensitive to variation in larval duration (e.g. Treml et al. 2015a, Defne et al. 2016).

### *Behaviour*

The past three decades of efforts to model marine larval dispersal have coincided with an increasing appreciation for the important role that behaviour can play in larval transport (Kingsford et al. 2002, Queiroga & Blanton 2005, Levin 2006). Particles have evolved from being entirely passive, to vertically migrating, and more recently, to active swimming, with the capacity for independent movement and decision-making (see Leis 2006 for a comprehensive review of the role of behaviour in the biology of larval fish).

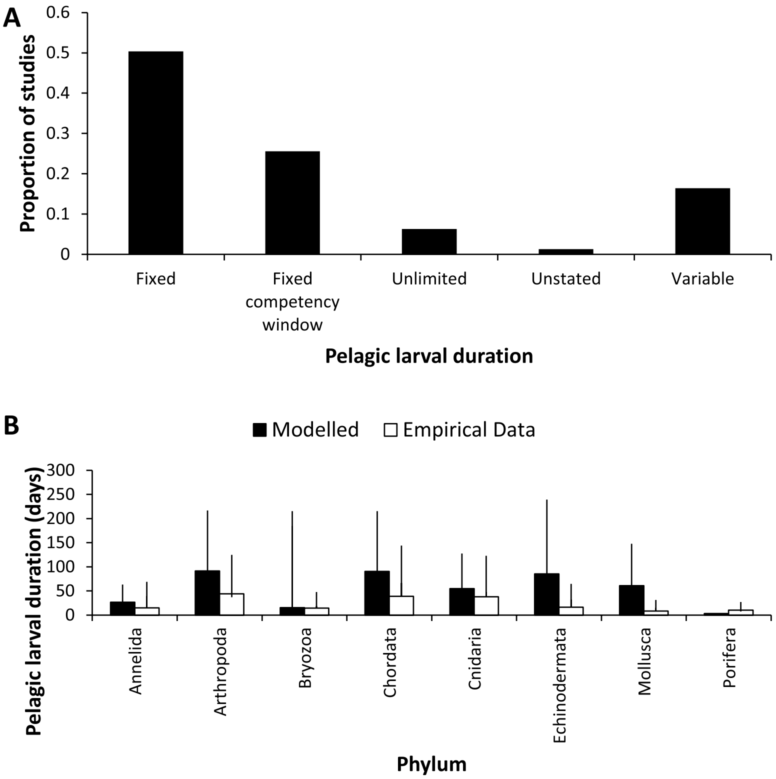

**Figure 8** The (A) distribution of modelling studies based on the parameterisation of pelagic larval duration (PLD), as described in Table 1; and (B) mean (95% CI) PLD from modelling ($n = 454$) and empirical ($n = 383$) studies across eight phyla. (Data from empirical studies were redrawn from Figure 1 in Bradbury et al. 2008.)

### *Dispersal as a passive or active process*

The pervasive viewpoint for many years was that larvae were planktonic, subject to the vagaries of ocean currents, with active movements operating at much smaller scales and in relation to foraging and predator avoidance (e.g. Blaxter 1969). This perspective also dominates biophysical modelling, surprisingly not changing over time, as the likelihood of models assuming passive larvae has actually marginally increased based on the year of publication (Logistic regression: $R^2 = 0.006$, Likelihood-ratio $X^2 = 4.116$, $df = 1$, $p = 0.0425$). Overall, 56% of studies assumed that larvae were passive throughout development, 41% of studies modelled active behaviour throughout the larval period (36%) or after an initial passive period (3%), with a further 3% not reporting this detail (Figure 9A). Like larval mortality, larval behaviour is notoriously difficult to observe and measure, particularly in the field, and is currently an active area of research.

### *Vertical movement*

It is well recognised that small changes in vertical position of larvae can have a large influence on horizontal transport (e.g. Fortier & Leggett 1983, Queiroga & Blanton 2005, Huebert et al. 2011), and that some animals actively modify their vertical position to avoid predators, find food and take advantage of directional changes in currents (e.g. selective tidal-stream transport; Forward and Tankersley 2001, Kunze et al. 2013). Despite this fact, more than half of models (53%) only had passive dispersal (i.e. no behavioural control over the vertical position in the water column), with the remainder of the models incorporating fixed (18%: 15% swimming and 3% buoyancy) or variable

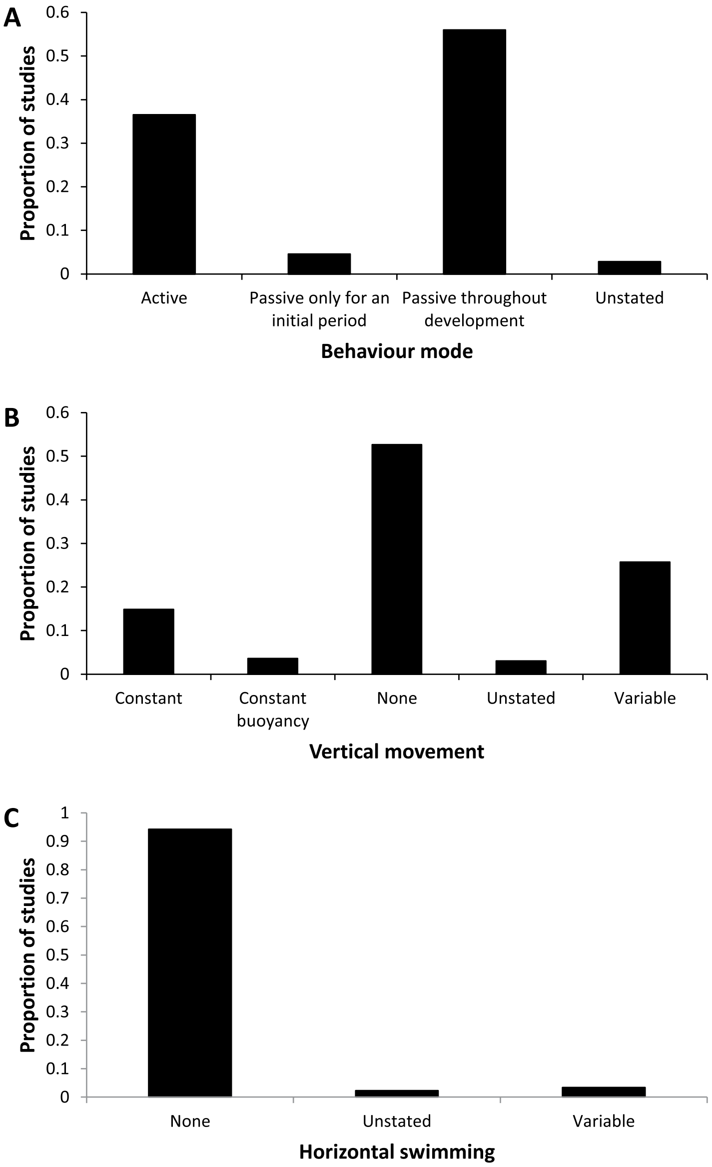

**Figure 9** The distribution of modelling studies based on the parameterisation of (A) behaviour mode, (B) vertical movement and (C) horizontal swimming, as described in Table 1.

(26%; i.e. changing with stage, age, size or environment) speeds of active dispersal (3% of studies were unstated) (Figure 9B). Given the sensitivity of modelled predictions to even small changes in vertical positioning (e.g. Fiksen et al. 2007, Robins et al. 2013), this indicates a clear need for species-specific knowledge of the biophysical processes that influence the depth distributions of larvae during development.

### *Horizontal swimming*

There is considerable evidence, particularly for coral reef fishes, that at least late-stage larvae are capable of swimming *in situ* at speeds that exceed mean currents (e.g. Leis et al. 2009) and thus have the capacity to behaviourally modify their transport, both in terms of advection and diffusion. Nevertheless, 95% of studies (Figure 9C) did not incorporate horizontal swimming (93.5% when only considering studies on fishes), and of the 18 known studies that did, over 70% were published in the past five years. The challenge now is gaining a better understanding of why larvae actively move (see Allen et al. 2018 for a recent review of movement ecology of marine animals with complex life cycles) so that appropriate, rule-based behavioural algorithms can be incorporated into biophysical dispersal models (see Willis 2011, Staaterman & Paris 2014 for reviews and discussion of modelling approaches).

## Settlement in natal/non-natal habitat

Settlement, the transition from pelagic to benthic environments and subsequent metamorphosis into the benthic juvenile stage, is a critical period in the life of marine animals with complex life cycles. Choosing a suitable settlement location has important consequences for future growth, survival and reproduction.

### *Competency*

The transition between pelagic and benthic habitats can occur only if larvae are developmentally competent to settle. Species can vary considerably in how long they can remain competent (e.g. Scheltema 1971, Hadfield & Strathmann 1994), with evidence that in some species, individual larvae can delay settlement to exploit more favourable settlement times (e.g. Forward et al. 2001, Robertson et al. 1999, Shima et al. 2018) or until encountering more favourable settlement habitat (e.g. Pechenik 1990, Raimondi & Keough 1990). However, only 40% of published studies modelled some form of a competency window (e.g. using an age range or variable cutoff, Figure 10A). For the remaining studies, settlement was either simply defined by the end of the PLD (28%) or model run (8%), not modelled explicitly (22%), or imposed using a different and/or unspecified criterion (2%). We recommend greater consideration of parameters related to competency periods, as these can affect the likelihood of both local retention and long-distance dispersal (e.g. Kinlan and Gaines 2003, Connolly & Baird 2010, Treml et al. 2015a).

### *Habitat detection and settlement*

The settlement stages of benthic marine invertebrates and fishes use a variety of sensory cues (e.g. auditory, olfactory, mechanical and visual) to detect and orientate towards settlement habitat (Crisp and Ryland 1960, Rodriguez et al. 1993, Thompson et al. 1998, Montgomery et al. 2001, Kingsford et al. 2002, Fuchs et al. 2018). This ability, combined with vertical and horizontal swimming capacity, means that behaviourally mediated habitat detection, selection and settlement is probably characteristic of most marine species, particularly fishes, and at distances that can influence dispersal patterns (e.g. Montgomery et al. 2006, Gerlach et al. 2007). However, this trait has not been incorporated into biophysical dispersal models; only 5% of published studies included either a fixed (4%) or varying (1%) ability to detect settlement habitat from some distance away (Figure 10B). Algorithms that probabilistically implement active settlement behaviours (e.g. integrating realistic horizontal and vertical swimming and habitat detection distances; Staaterman & Paris 2014, Treml et al. 2015a) may be a useful way forward.

## Recruitment

Realised dispersal and population connectivity depend on whether dispersers survive to exert some demographic influence on local populations.

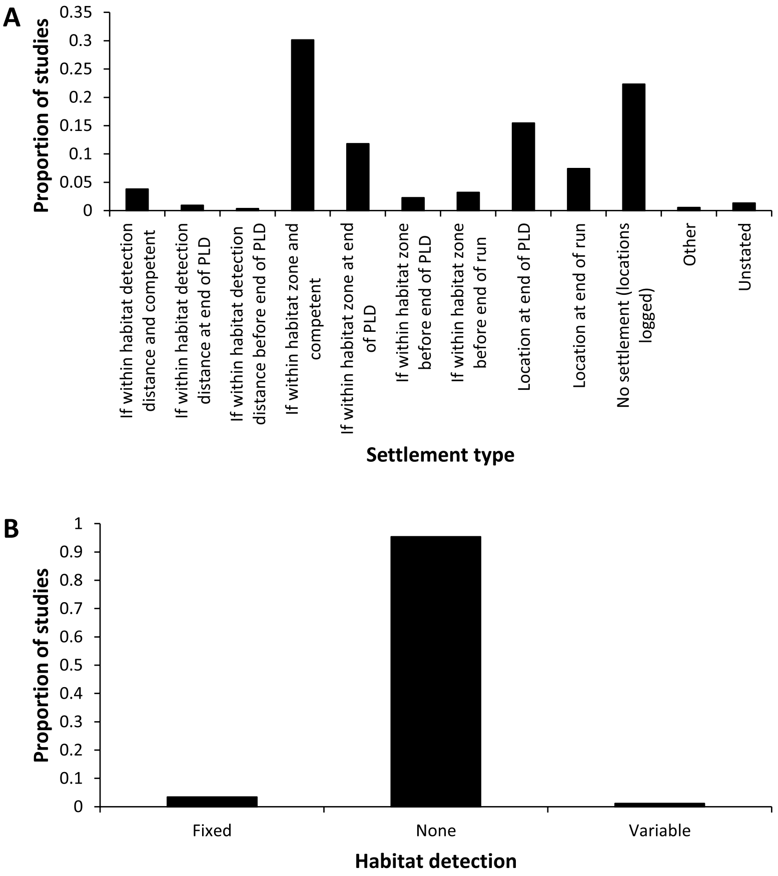

**Figure 10** The distribution of modelling studies based on the parameterisation of (A) settlement type and (B) habitat detection capability, as described in Table 1.

### *You have to survive to be counted*

Post-settlement mortality of benthic marine animals is variable, and rates may exceed 30% (Gosselin & Qian 1997) or even be up to 95% (Doherty et al. 2004) within the first 24 h. Mortality rates may be even higher when dispersers settle into poor-quality habitats (e.g. Burgess et al. 2012), or when they are phenotypically mismatched to settlement habitat (i.e. when an individual that is specialised to one environment settles to an alternative environment where it incurs a reduction in fitness; Marshall et al. 2010). Additional studies—particularly ones that evaluate the spatiotemporal variation of habitats and phenotype-environmental interactions, as well as for species that also transition between juvenile nursery and adult breeding habitats—would be valuable.

### *Dispersal history and condition matter*

Metamorphosis is not a new beginning (Pechenik 2006), and dispersal history and the resulting impacts on larval quality can carry over into the juvenile stage (Phillips 2004) and cause differential effects (Fischer and Phillips 2014), such as selective mortality (Shima & Swearer 2010), with important consequences for population stability (Noonburg et al. 2015) and metapopulation persistence (Shima et al. 2015). As far as we are aware, these effects have not yet been incorporated into biophysical models of dispersal and population connectivity.

## Conclusions and future directions

Over 75% of all marine larval dispersal studies have been based on biophysical models, and this trend is likely to continue for the foreseeable future. Our synthesis of this body of literature indicates that while models are improving in their biological realism, incorporating the bio-complexity of the four stages of successful dispersal, as outlined in Figure 1, has only been realised in 2 out of the 524 studies reviewed (Treml et al. 2015a,b). Fewer than 50% of studies considered any single key biological parameter other than larval behaviour (61%, Figure 11). In part, this is due both to the limitations of the model platforms used and a lack of empirical data for model parameterisation.

### *Reporting standards*

A major challenge in compiling the data for this review was the lack of a standard way of reporting, particularly in relation to hydrodynamic model details and particle release statistics (Figure 12). While only 6% of studies failed to provide details for any individual parameter, on average, 38% of studies were missing details for at least one. One of the primary bottlenecks in the utilisation of ecological models, in general, is the lack of proper documentation (e.g. Hoch et al. 1998). We suggest

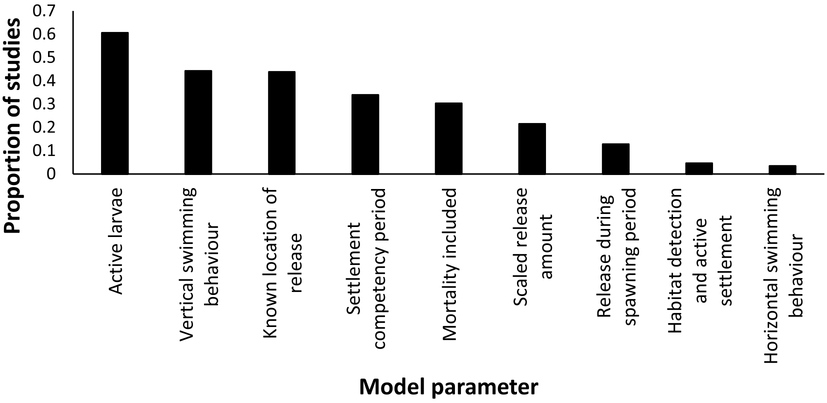

**Figure 11** The proportion of studies that included each of the key biological traits related to realised dispersal as outlined in stages 1–3 of Figure 1. Traits are arranged in decreasing proportion of studies. Proportions were calculated separately for each trait.

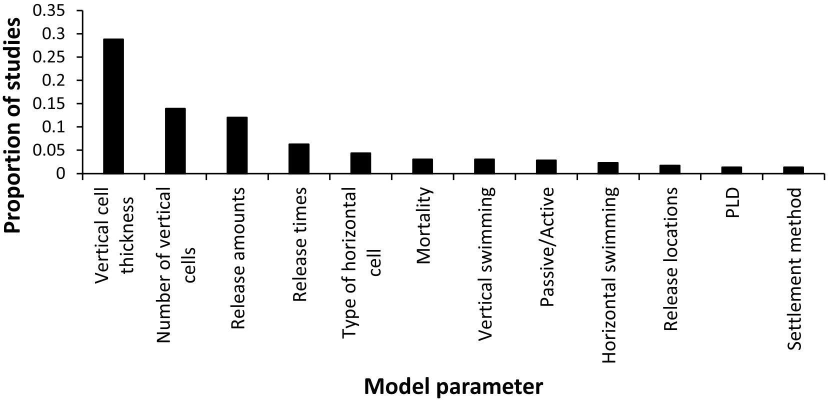

**Figure 12** The proportion of studies that did not report details or settings of key model parameters.

that the exemplary manual of recommended practices for biophysical modelling by North et al. (2009) could serve as a template for developing such standards for documentation.

## *One model to rule them all*

A striking outcome of this review was documenting just how many hydrodynamic and particle-tracking models have been used in studies of marine larval dispersal (Figure 13). Some of this diversity reflects the evolution of available modelling platforms, but many are proprietary or commercial in nature, limiting their accessibility to and uptake by a broader research community.

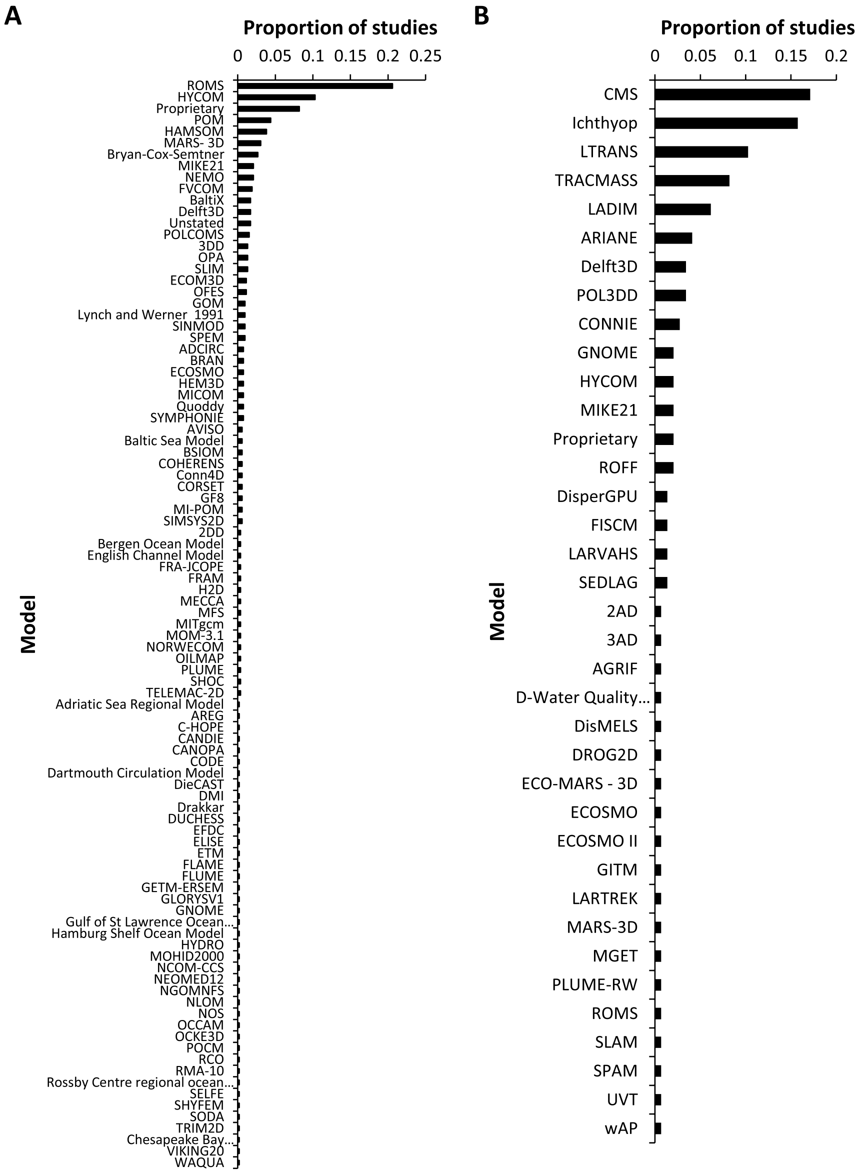

**Figure 13** The distribution of studies based on the (A) hydrodynamic and (B) particle-tracking model used.

Increasingly, researchers are using open-source hydrodynamic models (e.g. regional ocean modelling system [ROMS], hybrid coordinate ocean model [HYCOM]) and making offline Lagrangian particle tracking models with increasing levels of biological complexity (e.g. connectivity modelling system [CMS], Ichthyop, lagrangian transport model [LTRANS], Tracmass, marine geospatial ecology tool [MGET]) available to other users. However, most of the innovation remains siloed to particular models or research groups instead of a collective effort being invested into one or a few platforms. We suggest that the value of biophysical models in studies of marine larval dispersal and its broader implications will be enhanced through more coordinated and collaborative efforts among researchers.

## *Data limitations*

Despite previous requests (e.g. Metaxas & Saunders 2009), we continue to need more empirical research to make models of marine larval dispersal better. In relation to some complexities (e.g. mortality), there simply are not enough field-based estimates. This is problematic when interactions between life-history traits, such as the timing and duration of propagule release, the numbers of larvae spawned, the onset and duration of settlement competency and the magnitude and variability in mortality, can lead to wildly varying dispersal outcomes. For other traits, we have gained considerable insights, such as larval locomotory and sensory capabilities (reviewed in Chia et al. 1984, Montgomery et al. 2001, Queiroga & Blanton 2005, Leis 2006). In this context, the issue is not so much a lack of empirical data, but in how such behavioural knowledge can and should be incorporated into models of dispersal. Yes, larvae can swim and detect benthic habitat from afar, but the question of whether these capabilities influence dispersal and settlement patterns directly or indirectly, such as in response to ocean physics, particularly in the coastal zone (Pineda & Reyns 2018) or as a by-product of responses to predators and prey (Woodson & McManus 2007), remains a major challenge. It also raises an important caveat about how models can be improved to more realistically capture the dispersal process in light of data limitations. As Sir Robert May (2014) sagely said in his concluding remarks on the uses and abuses of mathematical models:

> Perhaps the most common among abuses, and not always easy to recognize, are situations where mathematical models are constructed with an excruciating abundance of detail in some aspects, whilst other important facets of the problem are misty or a vital parameter is uncertain to within, at best, an order of magnitude. It makes no sense to convey a beguiling sense of ‘reality’ with irrelevant detail, when other equally important factors can only be guessed at. Above all, remember Einstein’s dictum: ‘models should be as simple as possible, but not more so’.

## *Model validation*

Models generate predictions about larval dispersal and population connectivity, which should be tested and validated against empirical observations. To date, only 33 studies have generated estimates of dispersal from biophysical models that have been combined (in all cases) with genetic data. In none of these studies were genetic estimates used (or intended) to validate model predictions. Instead, biophysical models were largely used to generate estimates of oceanographic distance to feed into models of gene flow (see the Supplementary Information 1 in Nolasco et al. 2018).

To our knowledge, Nolasco et al. (2018) is the only study to explicitly compare modelled versus observed dispersal estimates for the purpose of model testing and evaluation. They show that connectivity matrices generated from the chemistry of larval mussel shells and a biophysical model became more concordant when uncertainties in larval origins were accounted for appropriately. What is clearly needed are more empirical observations of dispersal and population connectivity that can be used to compare against simulations from biophysical dispersal models with varying levels of biological complexity and parameter settings (Pineda et al. 2007).

### *Downscaling the physics and upscaling the behaviour*

Many hydrodynamic models do not capture a variety of the coastal oceanographic features (e.g. coastally trapped waves and boundary flows, frontal convergences and divergences, internal waves, etc.) that larval biologists have long known to exert important influences on larval transport. This is because many models do not extend into the nearshore, but also because resolving the structure of advective currents depends on the physics of the model, which is limited by the grid resolution of the model. As models move into the nearshore environment, downscaling will be important in order to capture smaller-scale physical processes, but these models will also need extensive field observations for model testing and validation (e.g. Taebi et al. 2012). Small-scale, subgrid processes are usually approximated using stochastic models for diffusion, which often assume a constant rate to approximate the random (and passive) spread of larvae. This is problematic as many of these processes result in spatial heterogeneity; for example, areas of convergence (fronts, thin layers) will reduce rates of diffusion.

Although most research has focussed on how larval behaviour affects advection, there is growing awareness of its relevance to diffusion as well. Several recent studies suggest that at least larval fishes can have shared dispersal histories, suggesting that they travel in cohesive groups (e.g. Ben-Tzvi et al. 2012, Shima & Swearer 2016). Given this can happen from a very early age, it suggests a significant level of behavioural control on the rate of diffusion. Larvae travelling in groups has important implications for dispersal. There is compelling theoretical and empirical evidence that animals travelling in groups are better able to navigate than individuals (Berdahl et al. 2018), and this has been recently shown for larval fishes (Irisson et al. 2015). This finding suggests that behavioural interactions among larvae can scale up to influence dispersal, but this sort of dynamic has yet to be incorporated into particle-tracking algorithms.

### *The ghost in the machine?*

*The Concept of Mind* (Ryle 2000), originally published in 1949, is a critique of René Descartes, who believed in dualism, the idea that the human mind is not physical—that it exists independent of the human brain. Its author, Gilbert Ryle, referred to this idea as the “ghost in the machine.” We suggest that this idiom is a useful metaphor for the dualism in our modelling of dispersal—that behaviour exists independently of the physical state of a larva (i.e. its body). Much of the early modelling assumed that larvae were passive; only the physical state was relevant to dispersal outcomes. In recent decades, models have begun to incorporate behavioural algorithms in recognition of the fact that larvae are active participants in their dispersal. However, much of this effort has occurred independent of the physical state of the larva. There is, however, growing evidence that the movement decisions made by individual animals are informed by their local environment (context dependence) and internal state, such as its growth, age or condition (phenotype dependence; Clobert et al. 2009). Biophysical dispersal models that break through this dualism will be an important innovation moving forward.

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[*] Access to this database is available to potential collaborators—contact the lead author for more information.

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