

## Chapter

# Skeletons of Calcareous Benthic Hydroids (Medusozoa, Hydrozoa) under Ocean Acidification

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and José Agüero*

## Abstract

The skeleton plays a vital role in the survival of aquatic invertebrates by separating and protecting them from a changing environment. In most of these organisms, calcium carbonate ( $\text{CaCO}_3$ ) is the principal constituent of the skeleton, while in others, only a part of the skeleton is calcified, or  $\text{CaCO}_3$  is integrated into an organic skeleton structure. The average pH of ocean surface waters has increased by 25% in acidity as a result of anthropogenic carbon dioxide ( $\text{CO}_2$ ) emissions, which reduces carbonate ions ( $\text{CO}_3^{2-}$ ) concentration, and saturation states ( $\Omega$ ) of biologically critical  $\text{CaCO}_3$  minerals like calcite, aragonite, and magnesian calcite (Mg-calcite), the fundamental building blocks for the skeletons of marine invertebrates. In this chapter, we discuss how ocean acidification (OA) affects particular species of benthic calcareous hydroids in order to bridge gaps and understand how these organisms can respond to a growing acidic ocean.

**Keywords:** biomineralization, Cnidaria, Hydractiniidae, Milleporidae, ocean acidification, skeleton, Stylasteridae

## 1. Introduction

Since the arrival of industrialization with the beginning of the British Industrial Revolution in 1750 to now, the accumulative concentration of carbon dioxide ( $\text{CO}_2$ ) in the atmosphere through to the year 2019 has increased to  $2340 \pm 240$  gigatonnes of  $\text{CO}_2$  ( $\text{GtCO}_2$ ), of which 25% has been sunk into the ocean [1, 2]. This human-induced sink of  $\text{CO}_2$  in the ocean produces a chemical phenomenon called ocean acidification (OA) [3]. OA decreases seawater pH, the concentration of carbonate ions ( $\text{CO}_3^{2-}$ ), and the saturation state ( $\Omega$ ) of the three primary biogenic calcium carbonate ( $\text{CaCO}_3$ ) minerals that occur in seawater and in shells and skeletons of calcifying organisms: calcite, aragonite, and magnesian calcite (Mg-calcite) [4].

Shells and skeletons of calcifying organisms play an essential role in their survival by separating and protecting them from a changing environment, as it happens with calcareous cnidarians [5, 6]. Within the phylum Cnidaria, only 17% of its extant species produce a calcareous skeleton through a process of biological transformation called biomineralization [7, 8]. The biomineralization process involves the selective extraction, transport, and uptake of biominerals from the environment

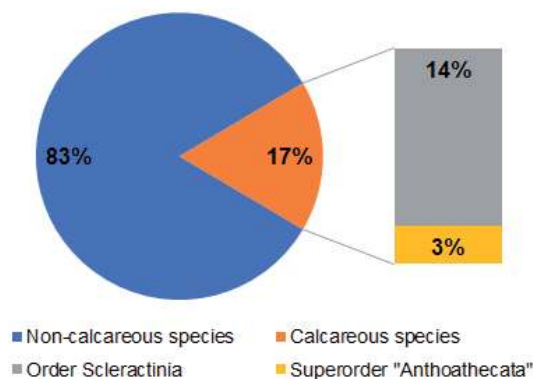
in the function of their abundance and availability for their later incorporation into functional structures under strict biological control [8].

Of the 17% of the extant cnidarians with a calcareous skeleton, 14% is represented by members of the order Scleractinia (Cnidaria, Anthozoa), while the remaining 3% is made up of species belonging to the superorder “Anthoathecata” (Cnidaria, Hydrozoa) (Figure 1) [7]. In the class Anthozoa, the biomineralization process is the best known and most widely studied, being the opposite for the class Hydrozoa [9], although they are one of the main components of zoobenthic communities, significant contributors to the building of coral reefs (Figure 2) [10–12], and also some are essential in pelagic communities due to the presence of a medusa stage [10].

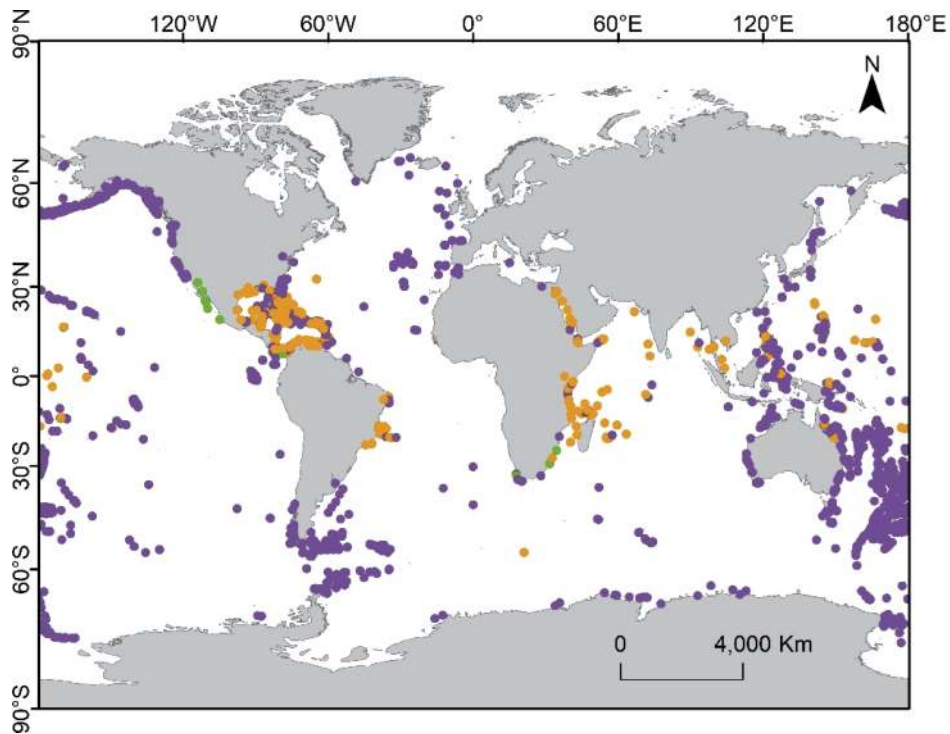
Calcareous hydroid families with a well-developed benthic polypoid stage are Milleporidae (hydrocorals, “fire corals” or millepores) with 15 species, Hydractiniidae (longhorn hydrozoans) with 4 species, and Stylasteridae (hydrocorals, lace corals, or stylasterids) with 320 species [7, 13]. These three families constitute a polyphyletic group and are commonly grouped as “calcified hydroids,” “calcareous hydrocorals,” or, simply, “hydrocorals”—terms that refer to hydroids that secrete a calcareous skeleton [14]. These calcareous structures can take the form of skeletons composed of individual spicules, spicule aggregates, or massive skeletons [15], and are responsible for providing protection and ion storage [6, 16, 17].

The calcareous skeleton of the cnidarians is always ectodermal in origin, and its mineralogy is composed exclusively of  $\text{CaCO}_3$  [18]. In the calcareous species of the class Hydrozoa, their skeletons are composed of calcite, aragonite, or both (Table 1) [9, 19–23]. Calcite and aragonite are two of the six  $\text{CaCO}_3$  polymorphs and are the most thermodynamically stable structures deposited extensively as biominerals [8]. In stylasterid species, for instance, the distribution of calcite or aragonite in their skeletons can be as follows: 100% calcite, 100% aragonite, primarily calcite with some aragonite, or primarily aragonite with some calcite [22]. When calcite and aragonite are present at the same time, the two polymorphs always occupy different anatomical sites [20]. Since the natural color of  $\text{CaCO}_3$  is white [24], the broad spectrum of colors observed in the calcareous skeletons of hydrocorals is due to the presence of carotenoproteins, symbiotic dinoflagellates of the genus *Symbiodinium*, or by the presence of microboring or euendolithic microorganisms [25–27].

Phylogenetic analysis supports the independent origins of a calcified skeleton in Hydrozoa [9, 28, 29], and the distribution of  $\text{CaCO}_3$  polymorphs in their skeletons is considered to have been produced by non-environmental causes [22]. However,



**Figure 1.** Worldwide inventory of non-calcareous and calcareous cnidarians. Own elaboration with WoRMS data [7].



**Figure 2.** Worldwide hydrocorals and longhorn hydrozoans distribution. Orange dots, Milleporidae; green dots, Hydractiniidae; purple dots, Stylasteridae. Own elaboration with OBIS data [12].

Taxa	Type of skeletogenesis	Principal mineral
Subclass Hydroidolina		
Superorder “Anthoathecata”		
Order Capitata		
Family Milleporidae	Modified spherulitic to trabecular	
<i>Millepora</i> spp.		Aragonite
Order “Filifera”		
Family Hydractiniidae	Spherulitic (with organic lamellae)	
<i>Distichozoon dens</i>		Unknown
<i>Hydrocorella africana</i>		Unknown
<i>Janaria mirabilis</i>		Unknown
<i>Schuchertinia antonii</i>		Unknown
Family Stylasteridae	Fully spherulitic or modified spherulitic to trabecular	
<i>Cheiloporidion pulvinatum</i>		Primarily aragonite with some calcite
<i>Errina</i> sp.		Primarily calcite with some aragonite
<i>Errinopsis</i> sp.		Calcite
<i>Lepidopora</i> spp.		Aragonite

**Table 1.** Types of skeletogenesis and mineral composition of skeletons in calcareous Hydrozoa [19–22].

the biomineralization process of these organisms is highly variable and strongly affected by environmental factors [30, 31] and substrate [32].

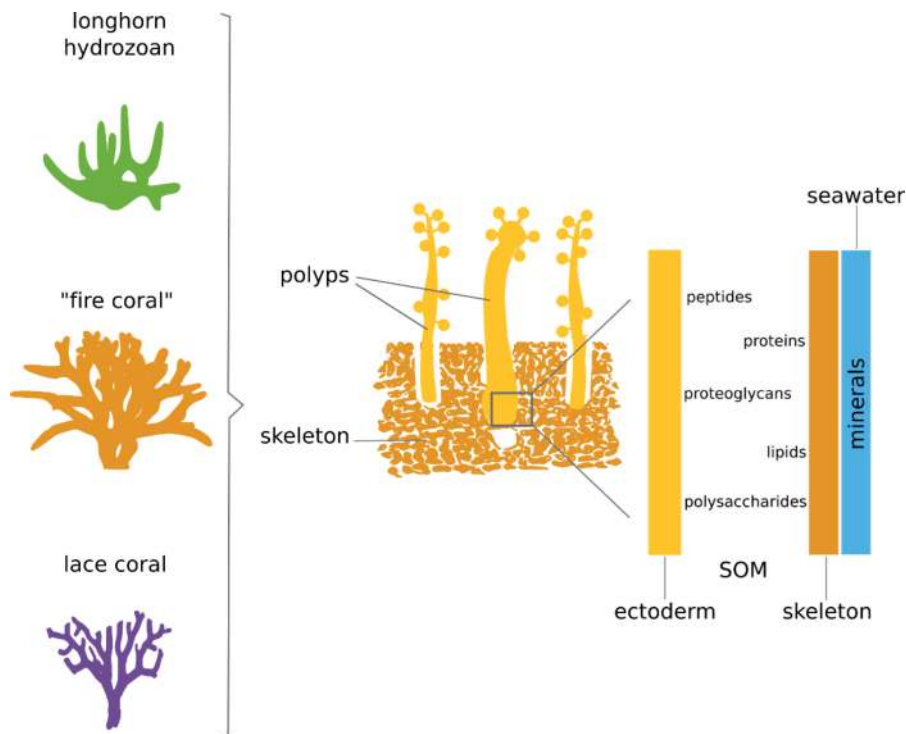
## 2. Skeletogenesis and OA

The biomineralization process is practically unknown to calcareous hydroids. Sorauf [21] summarizes some hypotheses about the biomineralization process of some Hydrozoa, and there has been no review about it to date. The basic structure is of the spherulitic growth of a principal mineral controlled by organic substrates to form pillars in which the spherulites are in part compartmentalized by a skeletal organic matrix (SOM), which forms an irregular matrix with compartments but does not form sheaths for individual crystal growth. In the class Hydrozoa exist three types of skeletogenesis, and the principal minerals involved are the  $\text{CaCO}_3$  polymorphs aragonite or calcite (**Table 1**) [19–22].

In addition to biomineralization,  $\text{CaCO}_3$  plays a significant role as second messenger to control exocytosis, cortical reactions in eggs, and muscle contraction [33]. In some hydractinids,  $\text{CaCO}_3$  is required for larval motility [34], induction of metamorphosis [35], and secretion of adhesive material during the latter [34].

The biocrystallization, such as sclerotization, is derived from the ectoderm, which produces a SOM that controls the spacing of nucleation sites and limits the size or shape of spherulites [21, 36]. The organic secretions may be composed of peptides, proteins, proteoglycans, lipids, and polysaccharides, which, as a whole, are known as the template for mineralization [21, 37]. It is known that this template is involved in most, if not all, stages of biomineral formation, from transport, through nucleation and growth, to structure stabilization (**Figure 3**) [37].

According to an analysis of SOM homologs in cnidarians, including Hydrozoa, several proteins related to biomineralization were identified [38]. Extracellular



**Figure 3.** Schematic representation of the hypothetical skeletogenesis process on calcareous hydroids.

adhesion proteins and carbonic anhydrases homologs were the most common proteins found (e.g., in *Millepora alcicornis*, *Millepora complanata*, and *Millepora squarrosa*). Homolog proteins include enzymes such as peptidase-1 and peptidase-2 as well as acidic proteins like SAARP-1, SAARP-2, acidic SOMP, CARP4, CARP5, Integrin-like and two SAARP-like proteins; those proteins are involved in calcite formation [39]. Two galaxin ortholog proteins (Galaxin and Galaxin-2) [38] have been fully characterized by the calcifying matrix of scleractinian corals [40]. More interestingly, carbonic anhydrases, which are known to precipitate  $\text{CaCO}_3$  in different calcareous organisms [41], have been identified in Hydrozoa species, CruCA-4, and Putative CA [38]. Finally, in contrast to scleractinian corals, Hydrozoa species did not show small cysteine-rich proteins (SCRiPs) [38], whose function in corals is still unclear.

In some calcareous hydroids, a progressive capability to produce a similar SOM to that of scleractinian corals has been observed, with individual control of crystal growth [21]. Also, the calcification process of stylasterid and millepore species has been compared with that of scleractinian corals [42]. This calcification process includes uptake and transport of materials, production of organic secretion, the formation of tissue cavities where calcification may take place, and the deposition of  $\text{CaCO}_3$ ; these processes may be influenced differently by environmental conditions, and be affected by OA [43, 44].

About the biochemical process underlying the response of hydrocoral *M. alcicornis* in acidified waters, it has been found that the calcification process in the hydrocoral was not affected by a wide range of seawater pH (8.1–7.5) under experimental conditions [30]. Besides, it is mentioned that the Ca-ATPase plays an essential role in the biomineralization as maintenance a steady-state net calcification rate in the hydrocoral, especially under scenarios of moderate (pH 7.8) and intermediate (pH 7.5) acidification of seawater, but under a scenario of severe acidification (pH 7.2) of seawater, the hydrocoral is not able to maintain a steady-state net calcification rate [30]. On the other hand, physiologically, the exposure to seawater acidification induces oxidative stress with consequent oxidative damage to lipids and proteins, which could compromise hydrocoral health [45]. However, a reduction in the calcification process was not observed in *Millepora platyphylla* despite having been exposed to OA conditions [46].

Some effects in other calcareous organisms, for instance, anthozoans, sea urchins, and mollusks by OA are: slowdown of their calcification rates; changes in gene expression consistent with metabolic suppression; increased oxidative stress; potential effect on symbiotic zooxanthellae; decrease in matrix proteins; reduction of carbonic anhydrase protein; increased calcite growth; structural disorientation of calcite crystals; fragile skeletons that reduce protection from predators and changing environments, affect the expression of the gene encoding Ca-ATPase enzymes and the enzymatic activity itself [30, 44, 47–49].

OA not only affects the skeleton of the calcareous hydroids, but it can also affect the other phases of its life cycle, for instance, the medusa stage of millepores, since it has been recently recorded that cubomedusae suffer from higher mortality when subjected to OA conditions (pH 7.5) [50].

### 3. Implications, threats, and consequences of OA

The response of hydrocorals to the changes they face in their environment remains unknown, especially how they are affected by anthropogenic activities such as the increase in the concentration of  $\text{CO}_2$  in the atmosphere, causing an increase in sea surface temperature (SST) and a decrease in seawater pH. The chemistry of

OA is better understood from their implications for calcifying marine fauna and their hosts or associations. Skeletons of hydrocorals and longhorn hydrozoans are known to host abundant and diverse symbiotic organisms, for instance, with photosynthetic dinoflagellates (generally referred to as zooxanthellae), and maintain associations with micro and macroboring organisms, and grazers. The macroboring organisms (MIO) include cyanobacteria, green and red algae, fungi, and lichens [51]. The macroboring organisms (MAO) comprise ascidians and sponges [42], while in the grazers encompass echinoderms, mollusks, polychaeta, crustaceans, and fish [42, 52].

Of the three families of extant calcareous hydroids, only “fire corals” have a symbiotic relationship with zooxanthellae [42]. The zooxanthellae are essential for the “fire corals” to achieve their calcification process, keep their rate of calcification constant, as well as speed up a calcareous deposition in the function of the environmental conditions [43]. Loss of this association from hydrocoral tissue is responsible for the white color observed, aptly named bleaching [53]. When “fire corals” experiment stress occurs bleaching, or the paling zooxanthellate decline and the concentration of pigments within the zooxanthellae fall, where each zooxanthella may lose 50–80% of its photosynthetic pigments [54]. The stress can be induced by a plethora of factors, singly or in combination, and among them we have: anomalously low and high temperature, solar radiation, subaerial exposure, sedimentation, freshwater dilution, inorganic nutrients, high concentrations of xenobiotics, presence of pathogens such as protozoan and bacterium, OA, among others [54, 55]. Recently, it has been observed that hydrocorals can select their symbionts zooxanthellae, depending on environmental conditions, which can confer an advantage on how to face ongoing human-driven climate change [56].

The mechanism underlying the observed bleaching response was not explicitly investigated, some hypotheses are that changes in seawater chemistry influence bleaching thresholds by altering the functioning of the carbon-concentrating mechanism (CCM), photoprotective mechanisms (such as photorespiration for instance), or direct impacts of acidosis; therefore, the acidification effects on coral bleaching are uncertain and review of other aspects, for instance, levels of the other abiotic factors such as light and nutrients, photoacclimation and photoprotection responses, molecular genetics, as well as studies that imply the understanding of integral processes about host-algae are recommended to understand the role that zooxanthellae may play in the ability of corals to cope with these anthropogenic changes in the ocean [53, 57, 58].

The MIO distribution within the skeletons occurs through contact with the substrate of settlement as MIO already colonizes it, and their colonization occurs early in the development of the corals and expands at slower rates than the hydrocoral growth [27]. Since stylasterid corals do not host zooxanthellae, such an arrangement may be beneficial throughout the life of the coral, despite some losses to its skeleton density due to dissolution by MIO; moreover, the boring microflora within corals have a mutualistic relationship, helping corals survive better during bleaching events, because these MIO may satisfy the nitrogen quantities required by live hydrocorals for their balanced growth, also considering that MIO are the major primary producers and agents of microbioerosion dissolving large quantities of  $\text{CaCO}_3$  with a potential in buffering seawater [59].

Micro and macrobioerosion under undisturbed natural conditions are essential mechanisms in  $\text{CaCO}_3$  recycling; however, these bioerosion processes can proceed faster if OA weakens the substrate, also facilitating in this way the bioerosion by grazers [60]. Furthermore, OA does not affect the siliceous sponges as directly as other marine taxa, which are heavily dependent on  $\text{CaCO}_3$  at various life history stages like cnidarians, mollusks, and many crustaceans species with tiny pelagic

larval forms [61]. These siliceous sponges represent a threat when settling on calcareous substrates by the process of weakening the skeleton by their bioeroder action; nevertheless, thermal stress appears to weaken calcifiers more strongly than bioeroding sponges [62].

Other impacts include shifts in competitive interactions with non-reef builders such as macroalgae, sponges, soft corals, ascidians, and corallimorpharians; the competition impacts the recruitment, growth, and mortality of coral organisms [63].

## 4. Conclusion

This review of current literature concerning the effects of OA on hydrocorals and longhorn hydrozoans and their proposed mechanisms shows that targets are numerous, and therefore it is difficult today to give a conclusion. Besides, several of the findings correspond to anthozoans and specific areas or under laboratory or modeling conditions. On the other hand, it has been shown that each species has a different response, some are more sensitive than others, and some show strategies to survive under conditions of anthropogenic climate change. As proposed by Luz [45], further studies that use metabolomics and proteomics techniques are necessary to help identify different response pathways in hydrocorals exposed to acidic conditions.

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## Conflict of interest

The authors declare no conflict of interest.

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## References

- [1] O'Brien PK. Deconstructing the British industrial revolution as a conjuncture and paradigm for global economic history. In: Horn J, Rosenband LN, Smith MR, editors. *Reconceptualizing the Industrial Revolution*. United States of America: MIT Press; 2010. pp. 21-46. Available from: <http://www.jstor.org/stable/j.ctt5hhgdm.6>
- [2] Friedlingstein P, Jones MW, O'Sullivan M, Andrew RM, Hauck J, Peters GP, et al. Global carbon budget 2019. *Earth System Science Data*. 2019;**11**(4):1783-1838. Available from: <https://www.earth-syst-sci-data.net/11/1783/2019/>
- [3] Caldeira K, Wickett ME. Anthropogenic carbon and ocean pH. *Nature*. 2003;**425**(6956):365. DOI: 10.1038/425365a
- [4] Gattuso J-P, Hansson L. Ocean acidification: Background and history. In: Gattuso J-P, Hansson L, editors. *Ocean Acidification*. Pondicherry: Oxford University Press; 2011. pp. 1-20
- [5] Watabe N. Shell. In: Bereiter-Hahn J, Matoltsy AG, Richards KS, editors. *Biology of the Integument 1: Invertebrates*. 1st ed. Berlin, Heidelberg: Springer-Verlag Berlin, Heidelberg; 1984. pp. 448-485. DOI: 10.1007/978-3-642-51593-4\_25
- [6] Tidball JG. Cnidaria: Secreted surface. In: Bereiter-Hahn J, Matoltsy AG, Richards KS, editors. *Biology of the Integument: Invertebrates*. Berlin, Heidelberg: Springer Berlin Heidelberg; 1984. pp. 69-78. DOI: 10.1007/978-3-642-51593-4\_7
- [7] WoRMS. Cnidaria; 2019 [cited 01 December 2019]. Available from: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1267>
- [8] Mann S. In: Mann S, editor. *Biomineralization: Principles and Concepts in Bioinorganic Materials Chemistry*. 1st ed. New York, United States: Oxford University Press; 2001. 198 p. (Oxford Chemistry Masters)
- [9] Miglietta MP, McNally L, Cunningham CW. Evolution of calcium-carbonate skeletons in the Hydractiniidae. *Integrative and Comparative Biology*. 2010;**50**(3):428-435. DOI: 10.1093/icb/icq102
- [10] Di Camillo CG, Bavestrello G, Cerrano C, Gravili C, Piraino S, Puce S, et al. Hydroids (Cnidaria, Hydrozoa): A neglected component of animal forests. In: Rossi S, Bramanti L, Gori A, Covadonga O, editors. *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. 1st ed. Cham, Switzerland: Springer International Publishing; 2017. pp. 397-427. DOI: 10.1007/978-3-319-21012-4\_11
- [11] Weber JN, Woodhead PMJ. Stable isotope ratio variations in non-scleractinian coelenterate carbonates as a function of temperature. *Marine Biology*. 1972;**15**(4):293-297. DOI: 10.1007/BF00401388
- [12] OBIS. Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO; 2019 [cited 02 November 2019]. Available from: <http://www.iobis.org>
- [13] Cairns SD. Deep-water corals: An overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science*. 2007;**81**(3):311-322. Available from: <https://www.ingentaconnect.com/search/article?option1=tka&value1=deep.water+s+corals.+An+overview+with+special&pageSize=10&index=1>
- [14] Amaral FMD, Steiner AQ, Broadhurst MK, Cairns SD. An overview



- of the shallow-water calcified hydroids from Brazil (Hydrozoa: Cnidaria), including the description of a new species. *Zootaxa*. 2008;**1930**(1):56-68. DOI: 10.11646/zootaxa.1930.1.4
- [15] Lowenstam HA, Weiner S. In: Lowenstam HA, Weiner S, editors. *On Biomineralization*. 1st ed. USA: Oxford University Press; 1989. 324 p
- [16] Chapman DM, Histology C. In: Muscatine L, Lenhoff H, editors. *Coelenterate Biology Review and New Perspectives*. 1st ed. UK: Academic Press; 1974. pp. 1-92. Available from: <http://www.sciencedirect.com/science/article/pii/B9780125121507500062>
- [17] Harrison FW, Ruppert EE. In: Harrison FW, Ruppert EE, editors. *Microscopic Anatomy of Invertebrates, Volume 2, Placozoa, Porifera, Cnidaria, and Ctenophora*. 1st ed. United States of America: Wiley; 1991. 456 p. (Microscopic Anatomy of Invertebrates)
- [18] Cuif J-P. Calcification in the Cnidaria through time: An overview of their skeletal patterns from individual to evolutionary viewpoints. In: Goffredo S, Dubinsky Z, editors. *The Cnidaria, Past, Present and Future: The World of Medusa and her Sisters*. Cham: Springer International Publishing; 2016. pp. 163-179. DOI: 10.1007/978-3-319-31305-4\_11
- [19] Moore RC, Wells JW, Harrington HJ, Hill D, Boschma H, Hyman LH, et al. *Coelenterata*. In: Moore RC, editor. *Treatise on Invertebrate Paleontology*. USA: Geological Society of America, Incorporated; 1956. pp. 1-106
- [20] Lowenstam HA. Coexisting calcites and aragonites from skeletal carbonates of marine organisms and their strontium and magnesium contents. In: Miyake Y, Koyama T, editors. *Recent Researches in the Fields of Hydrosphere, Atmosphere and Nuclear Geochemistry*. 1st ed. Tokyo, Japan: Editorial Committee for Sugawara Volume; 1964. pp. 373-404
- [21] Sorauf JE. Biomineralization, structure and diagenesis of the coelenterate skeleton. *Acta Palaeontologica Polonica*. 1980;**25**(3-4):327-343
- [22] Cairns SD, Macintyre IG. Phylogenetic implications of calcium carbonate mineralogy in the Stylasteridae (Cnidaria: Hydrozoa). *PALAIOS*. 1992;**7**(1):96-107. Available from: <http://www.jstor.org/stable/3514799>
- [23] Cairns SD. In: Cairns SD, editor. *Stylasteridae (Cnidaria: Hydrozoa: Anthoathecata) of the New Caledonian Region*. Paris: Muséum national d'Histoire naturelle; 2015. 362 p. (Mémoires du Muséum national d'histoire naturelle)
- [24] Al Omari MMH, Rashid IS, Qinna NA, Jaber AM, Badwan AA. Calcium carbonate. In: Brittain HG, editor. *Profiles of Drug Substances, Excipients and Related Methodology*. 1st ed. USA: Academic Press; 2016. pp. 31-132. Available from: <http://www.sciencedirect.com/science/article/pii/S1871512515000229>
- [25] Rønneberg H, Fox DL, Liaaen-Jensen S. Animal carotenoids—Carotenoproteins from hydrocorals. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*. 1979;**64**(4):407-408. Available from: <http://www.sciencedirect.com/science/article/pii/030504917990292X>
- [26] LaJeunesse T. Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology*. 2002;**141**(2):387-400. DOI: 10.1007/s00227-002-0829-2
- [27] Pica D, Tribollet A, Golubic S, Bo M, Di CCG, Bavestrello G, et al. Microboring organisms in living stylasterid corals (Cnidaria, Hydrozoa). *Marine Biology Research*.

2016;12(6):573-582. DOI:  
10.1080/17451000.2016.1169298

[28] Lindner A, Cairns SD, Cunningham CW. From offshore to onshore: Multiple origins of shallow-water corals from Deep-Sea ancestors. *PLoS One*. 2008;3(6):e2429. DOI: 10.1371/journal.pone.0002429

[29] Mendoza-Becerril MA, Jaimes-Becerra AJ, Collins AG, Marques AC. Phylogeny and morphological evolution of the so-called bougainvilliids (Hydrozoa, Hydroidolina). *Zoologica Scripta*. 2018;47(5):608-622. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1111/zsc.12291>

[30] Marangoni de BLF, Calderon EN, Marques JA, Duarte GAS, Pereira CM, e Castro CB, et al. Effects of CO<sub>2</sub>-driven acidification of seawater on the calcification process in the calcareous hydrozoan *Millepora alcicornis* (Linnaeus, 1758). *Coral Reefs*. 2017;36(4):1133-1141. DOI: 10.1007/s00338-017-1605-6

[31] Olgúin-López N, Hernández-Elizárraga VH, Hernández-Matehuala R, Cruz-Hernández A, Guevara-González R, Caballero-Pérez J, et al. Impact of El Niño-southern oscillation 2015-2016 on the soluble proteomic profile and cytolytic activity of *Millepora alcicornis* ("fire coral") from the Mexican Caribbean. *PeerJ*. 2019;7:e6593. DOI: 10.7717/peerj.6593

[32] Vago R, Pasternak G, Itzhak D. Aluminum metallic substrate induce colossal biomineralization of the calcareous hydrocoral *Millepora dichotoma*. *Journal of Materials Science Letters*. 2001;20(11):1049-1050. DOI: 10.1023/A:1010972727293

[33] Alberts B, Johnson A, Lewis J, Morgan D, Raff M, Roberts K, et al. Myosin and actin. In: Alberts B, Johnson A, Lewis J, Morgan D, Raff M, Roberts K, et al., editors. *Molecular*

*Biology of the Cell*. 6th ed. United States of America: Garland Science; 2014. pp. 915-925

[34] Dandar-Roh AM, Rogers-Lowery CL, Zellmann E, Thomas MB. Ultrastructure of the calcium-sequestering gastrodermal cell in the hydroid *Hydractinia symbiolongicarpus* (Cnidaria, Hydrozoa). *Journal of Morphology*. 2004;260(2):255-270. DOI: 10.1002/jmor.10220

[35] Thomas MB, Edwards NC, Ball BE, McCauley DW. Comparison of metamorphic induction in hydroids. *Invertebrate Biology*. 1997;116(4):277-285. Available from: [www.jstor.org/stable/3226859](http://www.jstor.org/stable/3226859)

[36] Knight DP. Sclerotization of the perisarc of the calyptoblastic hydroid, *Laomedea flexuosa*: 1. The identification and localization of dopamine in the hydroid. *Tissue & Cell*. 1970;2(3):467-477. Available from: <http://www.sciencedirect.com/science/article/pii/S0040816670800453>

[37] Ehrlich H. Chitin and collagen as universal and alternative templates in biomineralization. *International Geology Review*. 2010;52(7-8):661-699. DOI: 10.1080/00206811003679521

[38] Conci N, Gert W, Sergio V. New non-Bilaterian transcriptomes provide novel insights into the evolution of Coral Skeletomes. *Genome Biology and Evolution*. 2019;11(11):3068-3081. DOI: 10.1093/gbe/evz199

[39] Rahman MA, Tamotsu O. Aspartic acid-rich proteins in insoluble organic matrix play a key role in the growth of calcitic sclerites in alcyonarian coral. *Chinese Journal of Biotechnology*. 2008;24(12):2127-2128. DOI: 10.1016/S1872-2075(09)60003-0

[40] Fukuda I, Ooki S, Fujita T, Murayama E, Nagasawa H, Isa Y, et al. Molecular cloning of a cDNA encoding a

- soluble protein in the coral exoskeleton. Biochemical and Biophysical Research Communications. 2003;**304**(1):11-17. Available from: <http://www.sciencedirect.com/science/article/pii/S0006291X03005278>
- [41] Zoccola D, Innocenti A, Bertucci A, Tambutté E, Supuran CT, Tambutté S. Coral carbonic anhydrases: Regulation by ocean acidification. Marine Drugs. 2016;**14**(109):1-11. DOI: 10.3390/md14060109
- [42] Lewis JBBT. Biology and ecology of the hydrocoral *Millepora* on Coral reefs. In: Southward AJ, Young CM, Fuiman LA, editors. Advances in Marine Biology. UK: Elsevier; 2006. pp. 1-55. Available from: <http://www.sciencedirect.com/science/article/pii/S0065288105500014>
- [43] Strömngren T. Skeleton growth of the hydrocoral *Millepora complanata* Lamarck in relation to light. Limnology and Oceanography. 1976;**21**(1):156-160. DOI: 10.4319/lo.1976.21.1.0156
- [44] Erez J, Reynaud S, Silverman J, Schneider K, Allemand D. Coral calcification under ocean acidification and global change. In: Dubinsky Z, Stambler N, editors. Coral Reefs: An Ecosystem in Transition. Dordrecht: Springer Netherlands; 2011. pp. 151-176. DOI: 10.1007/978-94-007-0114-4\_10
- [45] Luz DC, Zebraal YD, Klein RD, Marques JA, Marangoni LF de B, Pereira CM, et al. Oxidative stress in the hydrocoral *Millepora alcicornis* exposed to CO<sub>2</sub>-driven seawater acidification. Coral Reefs. 2018;**37**(2):571-579. DOI: 10.1007/s00338-018-1681-2
- [46] Brown D, Edmunds PJ. Differences in the responses of three scleractinians and the hydrocoral *Millepora platyphylla* to ocean acidification. Marine Biology. 2016;**163**(3):62. DOI: 10.1007/s00227-016-2837-7
- [47] Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, et al. Anthropogenic Ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature. 2005;**437**(7059):681-686. DOI: 10.1038/nature04095
- [48] Doney SC, Fabry VJ, Feely RA, Kleypas JA. Ocean acidification: The other CO<sub>2</sub> problem. Annual Review of Marine Science. 2009;**1**(1):169-192. DOI: 10.1146/annurev.marine.010908.163834
- [49] Fitzner SC, Phoenix VR, Cusack M, Kamenos NA. Ocean acidification impacts mussel control on biomineralisation. Scientific Reports. 2014;**4**(1):6218. DOI: 10.1038/srep06218
- [50] Chuard PJC, Johnson MD, Guichard F. Ocean acidification causes mortality in the medusa stage of the cubozoan *Carybdea xaymacana*. Scientific Reports. 2019;**9**(1):5622. DOI: 10.1038/s41598-019-42121-0
- [51] Tribollet A, Pica D, Puce S, Radtke G, Campbell SE, Golubic S. Euendolithic Conchocelis stage (Bangiales, Rhodophyta) in the skeletons of live stylasterid reef corals. Marine Biodiversity. 2018;**48**(4):1855-1862. DOI: 10.1007/s12526-017-0684-5
- [52] Carpenter RC. Invertebrate predators and grazers. In: Birkeland C, editor. Life and Death of Coral Reefs. 1st ed. New York: Springer US; 1997. pp. 198-229
- [53] Kirk Nathan L, Weis VM. Animal-symbiodinium symbioses: Foundations of coral reef ecosystems. In: Hurst CJ, editor. The Mechanistic Benefits of Microbial Symbionts. 1st ed. Cham, Switzerland: Springer International Publishing; 2016. pp. 269-294. DOI: 10.1007/978-3-319-28068-4\_10
- [54] Glynn PW. Coral reef bleaching: Facts, hypotheses and implications. Global Change Biology. 1996;**2**(6):495-509. DOI: 10.1111/j.1365-2486.1996.tb00063.x

- [55] Eakin CM, Lough JM, Heron SF. Climate variability and change: Monitoring data and evidence for increased coral bleaching stress. In: van Oppen MJH, Lough JM, editors. Coral Bleaching: Patterns, Processes, Causes and Consequences. 1st ed. Berlin, Heidelberg: Springer Berlin Heidelberg; 2009. pp. 41-67. DOI: 10.1007/978-3-540-69775-6\_4
- [56] Rodríguez L, López C, Casado-Amezua P, Ruiz-Ramos DV, Martínez B, Banaszak A, et al. Genetic relationships of the hydrocoral *Millepora alcicornis* and its symbionts within and between locations across the Atlantic. Coral Reefs. 2019;38(2):255-268. DOI: 10.1007/s00338-019-01772-1
- [57] Lesser MP. Coral bleaching: Causes and mechanisms. In: Dubinsky Z, Stambler N, editors. Coral Reefs: An Ecosystem in Transition. 1st ed. Dordrecht: Springer Netherlands; 2011. pp. 405-419. DOI: 10.1007/978-94-007-0114-4\_23
- [58] Albright R. Ocean acidification and coral bleaching. In: van Oppen MJH, and Lough JM, editors. Coral Bleaching: Patterns, Processes, Causes and Consequences. Cham, Switzerland: Springer International Publishing; 2018. pp. 295-323. DOI: 10.1007/978-3-319-75393-5\_12
- [59] Tribollet A. The boring microflora in modern coral reef ecosystems: A review of its roles. In: Wisshak M, Tapanila L, editors. Current Developments in Bioerosion. 1st ed. Berlin, Heidelberg: Springer Berlin Heidelberg; 2008. pp. 67-94. DOI: 10.1007/978-3-540-77598-0\_4
- [60] Schönberg CHL, Fang JKH, Carreiro-Silva M, Tribollet A, Wisshak M. Bioerosion: The other ocean acidification problem. ICES Journal of Marine Science. 2017;74(4):895-925. DOI: 10.1093/icesjms/fsw254
- [61] Conway KW, Whitney F, Leys SP, Barrie JV, Krautter M. Sponge reefs of the British Columbia, Canada Coast: Impacts of climate change and ocean acidification. In: Carballo JL, Bell JJ, editors. Climate Change, Ocean Acidification and Sponges: Impacts Across Multiple Levels of Organization. 1st ed. Cham, Switzerland: Springer International Publishing; 2017. pp. 429-445. DOI: 10.1007/978-3-319-59008-0\_10
- [62] Schönberg CHL, Fang JK-H, Carballo JL. Bioeroding sponges and the future of coral reefs. In: Carballo JL, Bell JJ, editors. Climate Change, Ocean Acidification and Sponges: Impacts Across Multiple Levels of Organization. 1st ed. Cham, Switzerland: Springer International Publishing; 2017. pp. 179-372. DOI: 10.1007/978-3-319-59008-0\_7
- [63] Chadwick Nanette E, Morrow KM. Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N, editors. Coral Reefs: An Ecosystem in Transition. 1st ed. Dordrecht: Springer Netherlands; 2011. pp. 347-371. DOI: 10.1007/978-94-007-0114-4\_20