



Comparative depth distribution of corallimorpharians and scleractinians (Cnidaria: Anthozoa)

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ABSTRACT: We assessed whether CaCO₃ concentration of seawater may be relevant to the occurrence of members of Corallimorpharia and Scleractinia, which are very similar except for the possession by scleractinians of a calcareous skeleton. In collections of both the Challenger Deep-sea Expedition 1872–1876 and the US Antarctic (Research) Program, average depth of occurrence was significantly greater for corallimorpharians than for scleractinians. We also compared depth of occurrence relative to the position of the aragonite saturation horizon (ASH) at many localities from which specimens were collected. Nearly 25 and 50% of stations at which scleractinians were collected were below the ASH for the Antarctic and Challenger stations, respectively; 50 and 100% of the Antarctic and Challenger stations at which corallimorpharians were collected were below the ASH, respectively. Statistical analyses of these data to test whether there is a difference in the depth, relative to the ASH, at which scleractinians and corallimorpharians occur indicate a difference for the Challenger but not the Antarctic stations; more data are needed. The scleractinians that tolerate living below the ASH belong to a minority of the genera recorded in the surveys, and do not include species considered important in forming bioherms; those that occur deepest are solitary. Some deep-sea scleractinians may be unaffected by shoaling of the ASH that is predicted across all ocean basins in the near future, some may be confined to water shallower than is now the case, and others may cease producing a skeleton, becoming morphologically indistinguishable from corallimorpharians.

KEY WORDS: Corallimorpharia · Scleractinia · Corals · Sea anemones

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INTRODUCTION

Corallimorpharians (order Corallimorpharia) are anthozoans morphologically intermediate between sea anemones (order Actiniaria) and stony corals (order Scleractinia). Like a sea anemone, a corallimorpharian (Fig. 1) lacks a calcareous skeleton, but has internal morphology and nematocysts like those of a scleractinian (den Hartog 1980, Dunn 1982). Given concern that changes in seawater chemistry may affect the robustness of the skeletons of calcifying organisms or prevent formation of skeletons entirely (e.g. Orr et al. 2005, Kleypas et al. 2006, Guinotte & Fabry 2008), we sought to compare the depth distribution of deep-sea coral-

limorpharians with that of deep-sea scleractinians to infer if CaCO₃ concentration may be relevant to the occurrence of these similar animals.

Corallimorpharia has far fewer members than the 2 groups to which it is most similar (45 valid species, compared with 1632 of Scleractinia and 1069 of Actiniaria; Fautin 2008). However, like scleractinians and actinarians, corallimorpharians occur in all oceans, from polar to equatorial latitudes, and from the intertidal to at least 5 km in depth (actinarians occur in the trenches as well). Shallow temperate and deep-water corallimorpharians at all latitudes resemble scleractinian polyps (Fig. 1a), whereas most shallow tropical corallimorpharians do not, being leathery in texture with short tenta-

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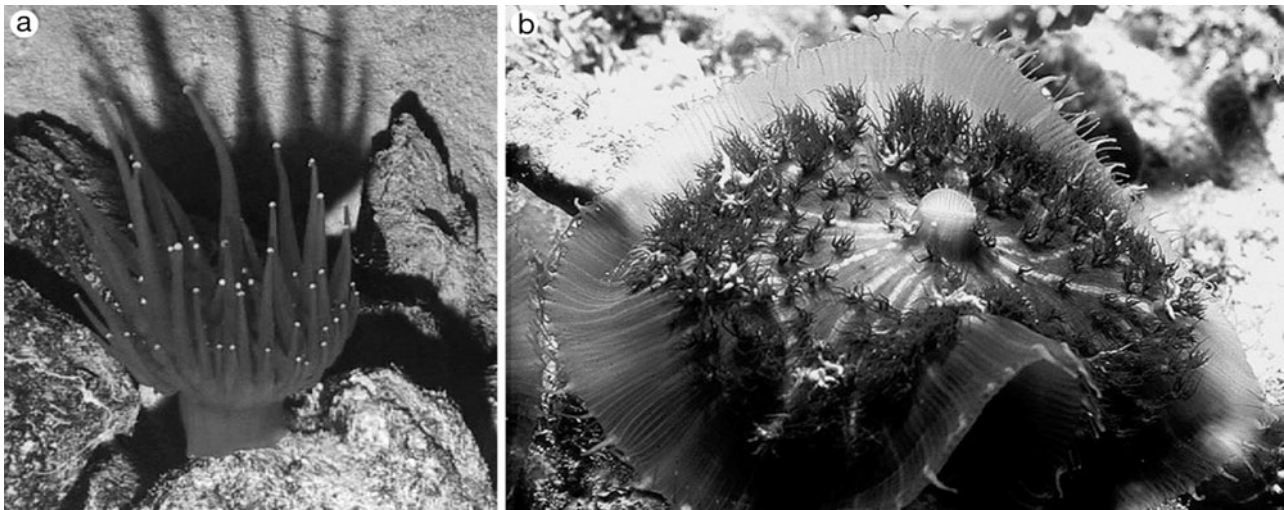


Fig. 1. (a) A deep-sea corallimorpharian, perhaps *Corallimorphus pilatus*, at 1798 m (photo from NOAA-HURL Archives, PI Amy Baco-Taylor). (b) A shallow tropical corallimorpharian (photo by G. Miller)

cles (Fig. 1b). Cogently, in our experience, people interested in and knowledgeable about deep-sea scleractinians may not recognize deep-sea corallimorpharians. Currently, Corallimorpharia occupies a rank identical to that of Actiniaria and Scleractinia, but during the past century it has been proposed (1) that they are really scleractinians lacking a skeleton and (2) that they belong with actiniarians (summarized by, inter alia, den Hartog 1980). Most recent molecular evidence supports Corallimorpharia as being separate from but more closely related to Scleractinia than to any other anthozoan group (Brugler & France 2007, Fukami et al. 2008, earlier data summarized by Daly & Fautin 2008). Regardless of phylogenetic details, corallimorpharians are more closely related to some corals than many of the groups referred to as 'corals' are to one another. Scleractinia and Corallimorpharia both belong to the anthozoan subclass Hexacorallia; some members of the other anthozoan subclass, Octocorallia, such as those of the family Isididae, are referred to as corals (e.g. Thresher et al. 2009).

To test whether deep-sea members of Corallimorpharia and Scleractinia differ in depth of occurrence, we compared collection records for members of the 2 taxa from comprehensive biological surveys that included data for both taxa. For 2 surveys that met our criteria, we found that, on average, corallimorpharians occur significantly deeper than scleractinians. Using data from the model of Orr et al. (2005) for carbonate saturation in seawater, we compared depth of occurrence with position of the aragonite saturation horizon (ASH) (the skeleton of a scleractinian is composed of CaCO_3 in the crystal form aragonite). The outcome of our analyses concerning whether aragonite saturation of seawater can explain the difference in depth of

occurrence of members of these taxa is ambiguous. Although some scleractinian species can tolerate living below the ASH, the ones collected deepest in both surveys were solitary. Guinotte et al. (2006) have shown that by the end of the 21st century, water at depths where 70% of deep-sea bioherm-forming scleractinians occur will be undersaturated with respect to aragonite. As a result of this shoaling of the ASH across all ocean basins in the immediate future, some scleractinians may be confined to water shallower than is now the case, and others may cease producing a skeleton. Ecosystem structure and function could be altered substantially with follow-on effects for organisms that depend on cold-water coral bioherms.

The number of records suitable for an analysis such as ours is small. The records we analyzed were from surveys not directed toward finding members of either taxon; data from surveys focused on documenting the occurrence of members of one of the taxa could be biased. We are confident that all corallimorpharians collected on the 2 surveys were included in the data we analyzed. In addition to assessing whether depth of occurrence differs between members of these 2 anthozoan groups, an aim of the present study is to stimulate, by our provisional results, the acquisition of additional data to test further the hypothesis that CaCO_3 concentration affects the occurrence of deep-sea scleractinians.

METHODS

We acquired occurrence records for scleractinians and corallimorpharians from 2 biological surveys: the Challenger Deep-sea Expedition 1872–1876 (e.g.

Rehbock 1992, Langmuir 2004, Perry & Fautin 2004) and the US Antarctic Research Program (USARP; now termed the US Antarctic Program) as assembled in the online resource 'Hexacorallians of the World' (Fautin 2008). To obtain the data used, on the opening page of 'Hexacorallians of the World' (<http://hercules.kgs.ku.edu/Hexacoral/Anemone2>) select 'Distributional Data,' then successively select from the list of menus 'Expedition' and 'Name.' When an expedition name is selected from the pick list or typed into the search box, a map of the stations for that expedition appears, and a list of specimens from that expedition can be selected to display. Records can be downloaded in XML.

In our analyses, we used the names published in the data sources except for the few cases in which the same specimen was referred to a different genus in a subsequent publication; in these we referred the species to the genus in which it was most recently placed. Although all published records we used are vouchered by museum specimens, we did not examine the specimens themselves.

The 50 volumes that constitute the results of the Challenger Expedition include 2 chapters on scleractinians, one by Moseley (1881) on deep-sea corals and one by Quelch (1886) on shallow-water, reef-building corals. Although most specimens dealt with in the chapter by Quelch (1886) seem to have been collected by shore parties, members of 5 species were collected at one numbered sampling station 8 fathoms deep. Because those specimens occurred in such shallow water and were recorded nowhere else in the Challenger Expedition reports, we did not include any data from Quelch (1886) in our analysis. The data in a preliminary report by Moseley (1876) are included in the later report (Moseley 1881), but since publication of the formal results, additional specimens collected on the Challenger Expedition have been identified. Our analyses include those in publications by Cairns & Zibrowius (1997) and Cairns et al. (2005); we do not include those by Brook (1892) because they concern shallow-water species and lack station numbers, from which we infer that they were taken in shore collections.

Our analyses include all published records of corallimorpharians from the Challenger Expedition. Hertwig (1882a,b,c, 1885, 1888) inventoried the Challenger sea anemones *sensu lato* (members of orders Actiniaria and Corallimorpharia), but in a short paper, Moseley (1877) described the 2 species of corallimorpharians included by Hertwig (1882a,b). Hertwig (1888) described a third species of corallimorpharian from the Challenger Expedition.

Most of the occurrences in the Antarctic and sub-Antarctic we analyzed were for specimens collected under the auspices of the USARP in the 1960s and 1970s using the ships 'Eltanin', 'Hero', and 'Islas

Orcadas'. The publication documenting scleractinians was written by Cairns (1982) and that on corallimorpharians was written by Fautin (1984).

We compared depth of occurrence for scleractinians versus corallimorpharians collected on the Challenger Expedition and under the auspices of the USARP. Our analysis was based solely on presence at a station; we did not consider the number of individuals sampled. The significance of the differences we found was assessed with the Mann-Whitney *U*-test, a non-parametric statistic equivalent to the parametric *t*-test. For all statistical tests, we accepted as significant *p*-values less than 5%.

We compared the depth of each station at which at least one specimen was collected to the ASH at that location for the subset of stations for which ASH data were available. Values for ASH depth are based on the model outputs described by Orr et al. (2005); modeled ASH data are lacking for some enclosed regions, including the Weddell and Ross Seas. Modeled data are available for the years 1765 and 1994; for the stations where data for both years are available, our results were identical, but we used the 1994 data because only they are available for some stations. To determine if the proportion of stations below the ASH at which corallimorpharians were collected differed from the proportion at which scleractinians were collected, we used Fisher's exact test (a statistic that is more accurate than the chi-squared test when expected values are small).

RESULTS

Fig. 2 plots the Challenger stations from which corallimorpharians and scleractinians were collected, and Fig. 3 plots the Antarctic and sub-Antarctic localities. Table 1 presents comparative data for the animals collected by the Challenger, and Table 2 for those collected in Antarctic and sub-Antarctic waters. The value for the Mann-Whitney *U*-test assessing the null hypothesis that scleractinians and corallimorpharians for the 2 data sets combined occur at equal depth was $p = 0.00003$ for 1-tailed and 0.00006 for 2-tailed.

Table 3 presents occurrence data for scleractinians and corallimorpharians from those Challenger and Antarctic and sub-Antarctic stations for which modeled ASH data exist. For Scleractinia, the number of genera to which those species belong is also shown as a proportion of the total number of genera in the data set (all corallimorpharians belong to *Corallimorphus*). ASH data were available for 159 localities for scleractinians (40 Challenger stations, 119 Antarctic and sub-Antarctic stations) and 15 for corallimorpharians (5 Challenger stations, 10 Antarctic and sub-Antarctic

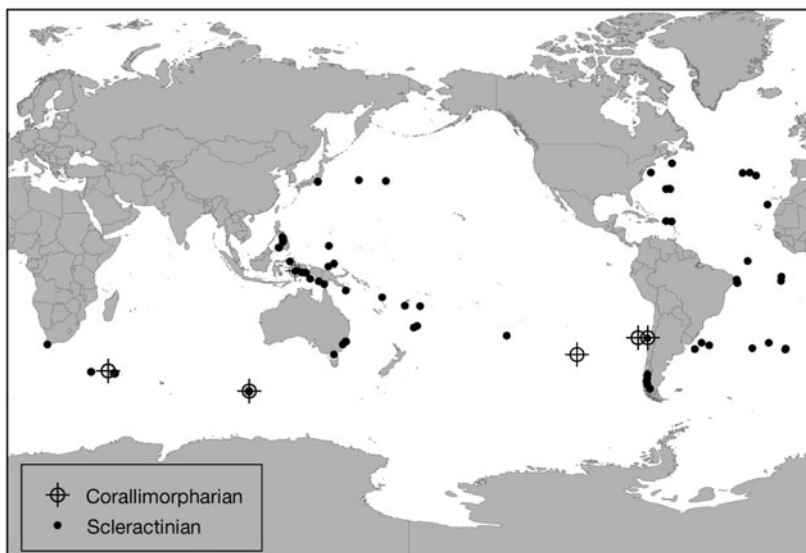


Fig. 2. Challenger Expedition stations from which corallimorpharians and scleractinians were collected

stations). For the Challenger Expedition, ASH data were available for 5 of the 6 stations at which corallimorpharians were collected and 40 of the 71 stations at which scleractinians were collected. For the Antarctic, ASH data were available for 10 of the 12 stations at which corallimorpharians were collected and for 119 of the 187 stations at which scleractinians were collected.

Average depth of occurrence was calculated for the 20 Antarctic species for which we had 3 or more

records (69 for *Flabellum impensum*). The values were rather continuous from 62 m (5 records for *Sphenotrochus gardineri*, range 9 to 116 m) to 757 m (3 records for *Enallopsammia rostrata*, range 333 to 1028 m). The 4 species with the deepest average depths of occurrence were *Flabellum apertum* (7 records, mean 971 m, range 587 to 1647 m), *Flabellum truncum* (4 records, mean 1333 m, range 587 to 1896 m), *Fungiacyathus marenzelleri* (10 records, mean 2056 m, range 300 to 4840 m), and *Leptopenus antarcticus* (5 records, mean 2182 m, range 2005 to 2384 m); the 4 deepest records were of *Fungiacyathus marenzelleri* (mean 3598 m, range 2836 to 4840 m). For the Challenger data, only 3 species were recorded at 3 or more stations: *Desmophyllum ingens* (3 records, mean 341 m, range 256 to 448 m), *Solenosmilia variabilis* (3 records, mean 654 m, range 256 to 768 m), *Bathyactis symmetrica* (14 records, mean 3196 m, range 1829 to 5304 m). According to Cairns (1982), some, but not all, of the Challenger records under the name *Bathyactis symmetrica* refer to *Fungiacyathus marenzelleri*; the name *B. symmetrica* has been applied to 5 species, all members of the genus *Fungiacyathus* (Fautin 2008).

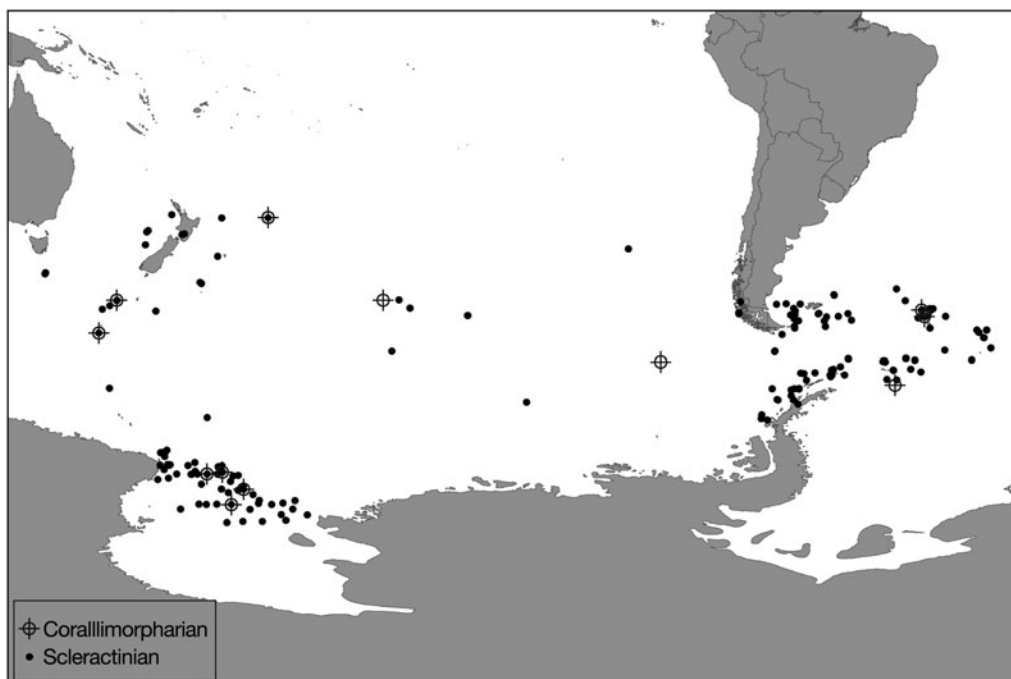


Fig. 3. Antarctic and sub-Antarctic stations from which corallimorpharians and scleractinians were collected

Table 1. Comparison of scleractinians and corallimorpharians collected by the Challenger Expedition. The values for the Mann-Whitney *U*-test assessing the null hypothesis that Challenger scleractinians and corallimorpharians occur at equal depth are $p = 0.003883$ for 2 tails and $p = 0.001942$ for 1 tail

	Species	Stations (Both occurred at 3 stations)	Records	Depth range (m)	Average depth (m)
Scleractinia	81 (76 ^a) (in 33 genera)	71	174	18–5304	1404
Corallimorpharia	3 (all <i>Corallimorphus</i>)	6	7	2515–3950	3142

^aNumber identified to species; 5 were identified only as sp.

Table 2. Comparison of scleractinians and corallimorpharians collected in the Antarctic and sub-Antarctic mainly under the auspices of the US Antarctic Research Program. The values for the Mann-Whitney *U*-test assessing the null hypothesis that Antarctic and sub-Antarctic scleractinians and corallimorpharians occur at equal depth are $p = 0.00584$ for 2 tails and $p = 0.00292$ for 1 tail

	Species	Stations (Both occurred at 8 stations)	Records	Depth range (m)	Average depth (m)
Scleractinia	37 (36 ^a) (in 19 genera)	187	286	9–4840	634
Corallimorpharia	2 (Both <i>Corallimorphus</i>)	12	12	132–4410	1600

^aNumber identified to species; 1 was identified only as sp.

Table 3. Proportion of stations for which there are data on the aragonite saturation horizon (ASH; as of 1994) where scleractinians and corallimorpharians were collected deeper than the ASH. 'Stations' refers to the proportion of stations at which members of each taxon were collected that were deeper than the ASH (regardless of the number of species reported at that station). 'Species' refers to the portion of species reported from at least 1 station deeper than the ASH (regardless of whether other specimens of the species were reported from depths shallower than the ASH). The denominator is the total number of species in the data set (as shown in Tables 1 & 2). The null hypothesis for Fisher's exact test was that there is no difference in the proportion of stations below the ASH from which scleractinians and corallimorpharians were collected

Surveys	Scleractinia	Corallimorpharia	Fisher's exact test (p)
Challenger			
Stations	18/40 (45%)	5/5 (100%)	0.028
Species	42/81 (52%)	3/3 (100%)	
	in 9/33 (27%) genera		
Antarctic and sub-Antarctic			
Stations	27/119 (23%)	5/10 (50%)	0.119
Species	15/37 (41%)	2/2 (100%)	
	in 9/19 (47%) genera		
Combined surveys			
Stations	45/159 (28%)	10/15 (67%)	0.0063

DISCUSSION

The average depth at which corallimorpharians occurred was significantly greater than that for scleractinians ($p < 0.01$) in data from both the Challenger Expedition and the USARP, and for the 2 data sets

combined, although the depth range of scleractinians exceeded that of corallimorpharians in both surveys (Tables 1 & 2). This may be a demonstration of the pattern of habitat partitioning in anthozoans identified by Fautin (1989). The Antarctic and sub-Antarctic are lower in diversity of both scleractinians and corallimorpharians, despite samples having been taken at more than twice as many Antarctic and sub-Antarctic stations as Challenger stations (Tables 1 & 2). This is not surprising given that the Challenger sampled over 100° of latitude, from 43.07°N (Stn 48, northwest Atlantic) to 64.3°S (Stn 153, southern Indian Ocean). Average depth of collection for both scleractinians and corallimorpharians is about half that in the Antarctic and sub-Antarctic as for the Challenger, supporting the idea of latitudinal submergence/emergence (e.g. Ekman 1953, Franz et al. 1981).

Because these animals are so similar except for the scleractinian aragonitic skeleton, we reasoned that saturation of seawater with respect to aragonite might be responsible for the difference in their depth of occurrence; CaCO_3 in the seawater is presumably physiologically relevant for scleractinians but not for coral-

limorpharians. Consistent with that hypothesis, the proportion of stations below the ASH at which corallimorpharians occurred was twice that for scleractinians. The differences in this proportion were significant for the Challenger data and all the data combined, but not for the Antarctic and sub-Antarctic data. Our findings are suggestive but not conclusive; further testing of the hypothesis that seawater chemistry is responsible for the clear difference in depth of occurrence of members of these 2 taxa requires additional data. More occurrence data for deep-sea corallimorpharians and scleractinians from unbiased sources, which are difficult to obtain, may help clarify the importance of seawater chemistry to the lives of animals of these taxa, and as models for carbonate saturation in seawater are refined and extended to places not now covered, the data we used can be reassessed.

Although it is widely held that scleractinians evolved from an anemone-like animal that developed a skeleton (e.g. Scrutton 1999), based on morphology, Hand (1966) suggested that sea anemones descended from scleractinians in a process that included loss of the skeleton. Likewise, a phylogeny using radioimmunoassay (Fautin & Lowenstein 1994) found Scleractinia ancestral to both Corallimorpharia and Actiniaria. Veron (1995) proposed that the scleractinian skeleton has evolved and been lost repeatedly. In the detailed scleractinian phylogeny of Romano & Cairns (2000), the calcareous skeleton was inferred to have evolved independently as many as 4 times. Medina et al. (2006) found corallimorpharians to be nested among scleractinians, which they interpreted as supporting the idea of lability of the skeleton. By contrast, Daly et al. (2003), Brugler & France (2007), and Fukami et al. (2008) found Corallimorpharia to be the sister taxon to Scleractinia rather than being nested within Scleractinia. Contrary to the assertion by Fukami et al. (2008), the topology of Corallimorpharia as the sister taxon to Scleractinia rather than being nested within Scleractinia does not, in itself, logically refute the 'naked coral hypothesis' (e.g. Fautin & Lowenstein 1994, Stanley & Fautin 2001), which holds that the skeleton exists under conditions of favorable seawater chemistry and disappears when conditions become unfavorable. Although the most parsimonious explanation may appear to be that the skeleton arose in the common ancestor of Scleractinia after the branch point with Corallimorpharia, if time is taken into consideration, as it was by Fautin & Lowenstein (1994) and Medina et al. (2006), that branch arose at a time when scleractinians existed, as attested to by fossils. None of these phylogenetic analyses included deep-sea corallimorpharians.

Evidence is growing that some scleractinians can survive without their skeletons. Goreau & Goreau (1959, p. 247–248) reported that 'polyps of starving

corals [taxon not specified] are able to detach themselves completely from the corallum. In this phase they can stay alive for some weeks without showing any evidence of renewed skeletogenesis although they are able to ingest food normally.' Sammarco (1982, p. 57) coined the term 'polyp bail-out' for the abandonment of their skeleton by polyps of the scleractinian *Seriato-pora hystrix* under stress, which he described as both an 'escape response' and a 'mode of asexual reproduction.' Sammarco (1982, p. 57), who observed this in the field and the laboratory, found that some polyps can secrete a new skeleton. Home aquarists have observed fleshy scleractinians crawl out of their skeletons (P. Alderslade pers. comm.); one can speculate that stress may cause such behavior. Although the skeleton presumably protects corals, skeletonless anthozoan polyps can survive in nature: witness the existence of corallimorpharians and sea anemones.

There is also experimental evidence that production of a coral's skeleton can be sensitive to CaCO_3 saturation state. Fine & Tchernov (2007) demonstrated that under conditions of low pH, the skeleton of 2 species of scleractinians dissolved, and the animals, although ceasing to deposit a skeleton, persisted. Moreover, the polyps separated physically, as Sammarco (1982) also found. Such 'naked' polyps are indistinguishable from corallimorpharians, which do not form colonies, although those of many or all species can propagate asexually and those of some species tend to live in clonal aggregations. When pH was increased, the animals resumed calcifying (Fine & Tchernov 2007). Thus, the abandonment of its skeleton by fleshy corals in home aquaria might be stimulated by the low saturation state of CaCO_3 that is typical of such aquaria. It is perhaps significant that the water in which Sammarco (1982) kept his corals, at the Australian Institute of Marine Science, came from offshore and was circulated in a flow-through system (P. W. Sammarco pers. comm.). Such seawater would be expected to be more saturated in CaCO_3 than water used by home aquarists.

The similarity between some deep-sea corals and corallimorpharians has long been noted. In his remarks in the Challenger proceedings that accompanied the description of the new genus and species *Corallimorphus profundus*, Moseley (1877, p. 301) stated, 'Similar or kindred forms were often dredged in deep water by the 'Challenger.' They seem closely allied to the simple disk-shaped corals, such as *Stephanophyllia*, in which the tentacles are also knobbed and disposed at the margin, and on the surface of the disk, in a closely similar manner. They have further similar thread-cells [nematocysts] to these solitary corals, and, indeed, appear to differ from them only in having no calcareous corallum developed. Indeed, in one species of

Stephanophyllia, obtained in deep water, the calcareous skeleton was in a most rudimentary condition, being a mere delicate network of calcareous trabeculae. So like in appearance were these forms of Actininae to the living corals, that it was only by feeling them as they were found in the dredge that I became convinced that they had no calcareous skeleton, and I macerated several in caustic potash in the hopes of finding traces of a corallum present in them. They seem to approach these disk-like corals very closely, and possibly to represent forms from which the corals were developed.'

Implicit in most discussions of the lability of the scleractinian skeleton is the idea that scleractinian taxa differ in sensitivity to CaCO₃ concentration in seawater—so some may be unable to survive without a skeleton. Our data show that some scleractinians are capable of living well below the ASH, and some appear to occur mainly or exclusively in relatively deep water (e.g. *Fungiacyathus marenzelleri*, *Lep-topenus antarcticus*, and many species of *Flabellum*). However, most of the species included in our analyses do not form bioherms, and the species that occur the deepest—like those referred to by Moseley (1877) above—are solitary. Indeed, in our data, none of the 6 species considered by Guinotte et al. (2006) to be 'deep-sea bioherm-forming corals' occurred deeper than the ASH. Thus, we infer that colonial species will be especially affected by decreased CaCO₃ saturation, either by being unable to persist in the altered waters or, as in the colonial species studied by Fine & Tchernov (2007), ceasing to form a skeleton and losing tissue connection between polyps. The potential loss not only of skeletons but of coloniality with diminishing CaCO₃ saturation has implications for ecosystems in which coral colonies provide structure, attachment surfaces, and refuges for hundreds of species.

Scleractinians that live in the deep sea may be physiologically adapted to harvest scarce ions effectively and/or their skeletons may be protected from the corrosive water by being covered by thick or unbroken tissue. Thus, although reduction of CaCO₃ saturation in the near future will likely affect many scleractinians, it is unlikely to affect members of all taxa equally or in the same ways. Some may simply be unable to survive in water of diminished CaCO₃ saturation, and so will be found shallower and shallower as time goes on; some may be able to persist as they are, and some may remain where they are but cease making a skeleton, and so be grossly indistinguishable from corallimorpharians.

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