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DEEP-WATER CORALS: AN OVERVIEW WITH SPECIAL REFERENCE TO DIVERSITY AND DISTRIBUTION OF DEEP-WATER SCLERACTINIAN CORALS

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ABSTRACT

The polyphyletic term *coral* is defined as those Cnidaria having continuous or discontinuous calcium carbonate or horn-like skeletal elements. So defined, the group consists of seven taxa (Scleractinia, Antipatharia, Octocorallia, Stylasteridae, and Milleporidae, two zoanthids, and three calcified hydractiniids) constituting about 5080 species, 66% of which occur in water deeper than 50 m, i.e., deep water as defined in this paper. Although the number of newly described species of deep-water scleractinian corals appears to be increasing at an exponential rate, it is suggested that this rate will plateau in the near future. The majority of azooxanthellate Scleractinia is solitary in form, firmly attached to a substrate, most abundant at 200–1000 m, and consist of caryophylliids. Literature helpful for the identification of deep-water Scleractinia is listed according to 16 geographic regions of the world. A species diversity contour map is presented for the azooxanthellate scleractinian species, showing centers of high diversity in the Philippine region, the western Atlantic Antilles, and the northwest Indian Ocean, and is remarkably similar to high diversity regions for shallow-water zooxanthellate Scleractinia. As suggested for shallow-water corals, the cause for the high diversity of deep-water scleractinian diversity is thought to be the result of the availability of large contiguous stable substrate, in the case of deep-water corals at depths of 200–1000 m (the area effect), whereas regions of low biodiversity appear to be correlated with a shallow depth of the aragonite saturation horizon.

Corals: Definition, Common Names, Species Richness, and Taxonomic Manpower

Since this symposium is focused on the taxonomy, biology, and conservation of deep-sea corals, it is appropriate at the outset to define the term *coral*. This word itself is Middle English, but derives from Old French, and in turn from Latin and Greek (see Best, 1999), and originally perhaps even from Hebrew, the word being used twice in the Old Testament. The basis for the word was probably a reference to the precious red coral of the Mediterranean, *Corallium rubrum* (Linnaeus, 1758), an octocoral with a skeleton having an attractive color and dense texture that has been used as jewelry, medicine, talisman, and currency for thousands of years, perhaps even from Paleolithic times (Hickson, 1924; Tescione, 1968). The word has even been used as a verb, meaning "to make red like coral". However, finding a consistent definition of the word coral is futile, which is not surprising since the term is not a scientific one but a layman's term that embraces a polyphyletic assemblage of several animal groups. Thus, scientific papers and books usually sidestep the issue but dictionaries and encyclopedias, which must attempt a definition, have met with limited success and lack of uniformity. The major points of inconsistency in definitions concern: (1) whether to require that corals have a continuous calcareous skeleton or one that may be disjunct (i.e., the latter qualification allowing for the inclusion of octocorals, many of which have individual microscopic calcareous sclerites but not necessarily

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a continuous calcareous axis), or (2) whether to also include cnidarians with a horn-like axis (i.e., which would allow the inclusion of the Antipatharia), and (3) whether to include non-anthozoans, such as calcified hydrozoans or even groups outside the Cnidaria. For instance, the most thorough monograph of "corals" *sensu lato* (Hickson, 1924) includes as corals not only Scleractinia, Octocorallia, calcified hydroids, and Antipatharia, but also some Bryozoa, Foraminifera, Porifera, and coralline algae. The definition proposed herein is a unique combination of elements, but attempts to include those taxa that I deduce are being currently thought of as corals.

Definition.—*Coral:* Animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous, usually microscopic, individual sclerites, or that have a black, horn-like, proteinaceous axis.

The following classification lists the seven taxa (in bold face) of corals that fit this definition, along with some of the common names that have been applied to them.

	Common names
Phylum Cnidaria (=Coelenterata)	
Class Anthozoa	
Subclass Hexacorallia (=Zoantharia)	
Order **Scleractinia** (=Madreporaria)	Hard corals, stony corals, true corals, cup corals, star corals, solitary corals, zooxanthellate corals, azooxanthellate corals.
Order **Zoanthidea** (in part)	Zoanthids, gold coral.
Order **Antipatharia**	Black corals, whip corals, wire corals, thorny corals.
Subclass **Octocorallia** (=Alcyonaria)	Soft corals, gorgonians, sea fans, sea whips, sea feathers, precious corals, pink coral, red coral, golden corals, bamboo corals, leather corals, horny corals, sea pens.
Class Hydrozoa	
Subclass Hydroidolina	
Order Anthoathecata (=Athecata)	Athecate hydroids.
Suborder Filifera	
Family **Stylasteridae**	"Hydrocorals", lace corals, stylasterids.
Family **Hydractiniidae** (in part)	Longhorn hydrozoans.
Suborder Capitata	
Family **Milleporidae**	"Hydrocorals", fire corals, millepores.

Collectively, corals that occur in deep-water have been called in the vernacular: deep-water corals, cold- or cool-water corals, ahermatypic corals, azooxanthellate corals, or just cool corals.

Once defined, it is logical to ask how many species of corals are known. Table 1 is an original compilation based on the literature (especially Cairns et al., 1999) and estimates from specialists (including F. M. Bayer, D. M. Opresko, J. van der Land, and myself) that shows that the approximate total number of corals in these seven taxa is 5080. The deep-water species (those occurring below 50 m) are estimated to account for 3336 of those species, or 65.6%, and include species from six of the seven groups, the zooxanthellate milleporids never occurring in deep water. Using a depth of 50 m to delimit deep-water corals is somewhat arbitrary, but very few zooxanthellate corals occur below this depth. As of 2005, I estimate that there are about 33 practicing taxonomists working on coral taxa: only 15 of those work on deep-water species and 10 use the molecular approach. Among those 33, eight are students, two are retired, and one is an administrator. We must therefore encourage young scientists to study the systematics of deep corals or else we will soon not be able to identify the species, much less make progress in revisionary work.

Species Richness and Characteristics of Deep-sea Scleractinian Corals

Confronted with these statistics, can we now ask if we know the true diversity (species richness) of the deep-water corals? Choosing Scleractinia as an example and to recapitulate, there are 1482 known Recent scleractinian species, 706 of which are azooxanthellate, of which 615 may be considered as deep-water Scleractinia. A graphic presentation of their rate of discovery is presented as a species accumulation curve extending from 1758 to 2004 (Fig. 1). It may appear from this graph that the rate of description is continuing at an exponential rate, with an average of 6.9 new deep-water species being described every year. However, as more fully explained by Cairns (1999a), I believe this curve is about to level off for several reasons. First, the percentage of the number of new species being encountered in large faunistic collections is steadily decreasing, and secondly, the current number of taxonomists working on deep-water Scleractinia is quite small (3.5), and elderly. Also, there are fewer large shipboard and/or submersible expeditions that collect deep-sea specimens, and collecting and research is often discouraged or impeded by regulations pertaining to international transport of specimens (e.g., CITES, alcohol limits). Although it is

Table 1. The numbers of the various types of corals, how many occur in deep water, and the number of taxonomists that study them as of mid-2005. * estimates made by Cairns, Bayer or Opresko; ** van der Land, pers. comm. (2005), based on count.

	Number of species		Practicing taxonomists			
	Number of species	Number deeper than 50 m	Total	Deep-water	Molecular approach	Comments
Scleractinia	1,482	615 (41.4%)	10	3.5	1	2 students, 1 admin.
Zoanthidea	2 (of 200)	2	2	2	1	Gerardia, 1 student
Antipatharia	*237	178 (*75%)	2	2	0	1 student
Octocorallia	**3,093	2,320 (*75%)	16	6.5	6	2 students, 2 retired
Stylasteridae	246	220 (89%)	1	1	1	1 student
Hydractiniidae	3 (of 78)	1	1	0	1	1 student; *Janaria*, *Hydrocorella*, *Polyhydra*
Milleporidae	17	0	1	0	0	
Total	5,080	3,336 (65.7%)	33	15	10	8 students, 2 retired, 1 admin.

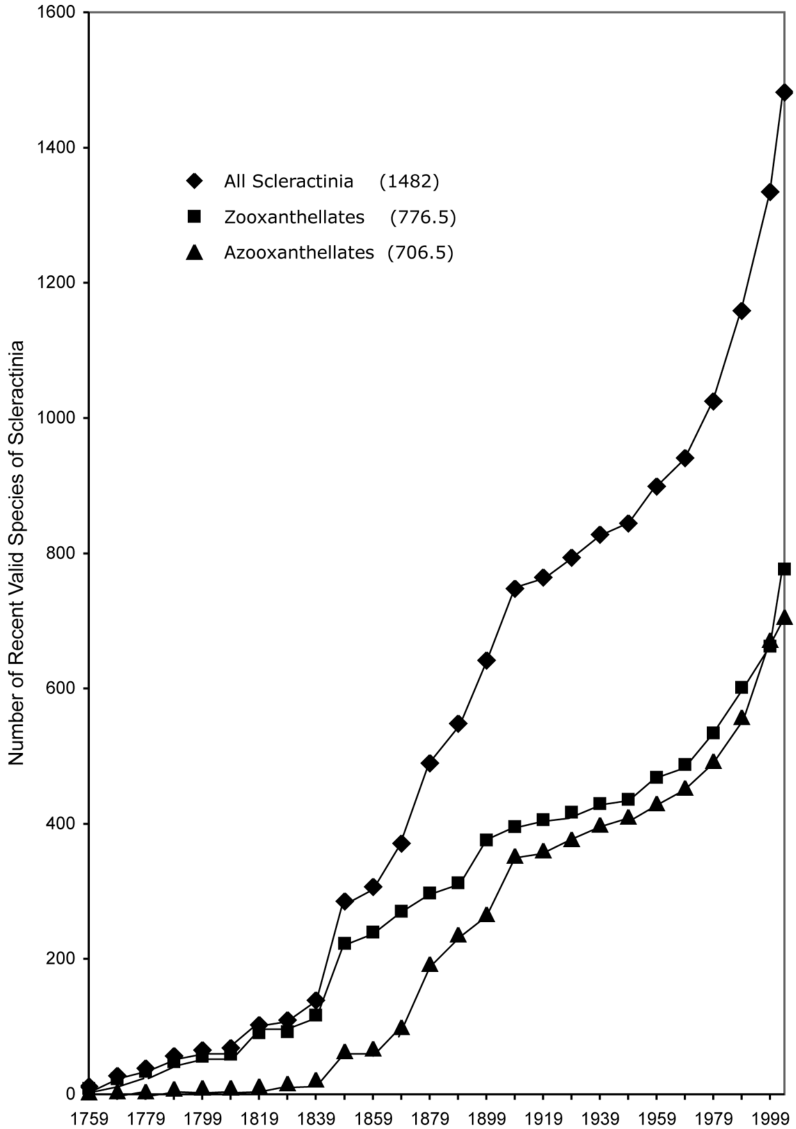

Figure 1. Cumulative number of recognized (valid) zooxanthellate, azooxanthellate, and total scleractinian species from 1759 through 2004 (modified from Cairns, 2001: fig. 1).

promising to have one student working on deep-water Scleractinia, it is also foreboding that he may not find a job in the field. Personally, after working on deep-sea scleractinian taxonomy for 30 yrs, I have switched to the study of deep-sea octocorals, which are not yet regulated by CITES.

Nonetheless, among the 706 azooxanthellate Scleractinia, certain generalizations can be made about their morphology, bathymetry, and family affiliation (update of Cairns, 2004). Most azooxanthellates (519 species, 73.5%) are solitary in habit and the remainder (187, 26.5%) are colonial. Thus, in the minority is *Lophelia pertusa* (Linnaeus, 1758), the redoubtable deep-water bank framework coral. A majority of the 706 species are firmly attached to a hard substrate: 376 species (53.3%) are attached, 265 (37.5%) are free, and 65 (9.2%) experience transverse division, resulting in an unattached corallum (an anthocyathus) from an attached base (an anthocaulus). Bathymetrically, 233 species (34.2%) occur at 0–50 m, 360 (52.9%) at 50–200 m, 431 (63.4%) at 200–1000 m, 100 (14.7%) at 1000–2000 m, and only 32 (4.7%) over 2000 m, the deepest occurring at 6328 m (Keller, 1976). The percentages add to more than 100 since many species occur in more than one depth zone, and the divisor for the total number of species was 680 (not 706), as the depth range of 26 species is unknown. Taxonomically, the largest family is the Caryophylliidae (291 species, 41.2%), followed by the Dendrophylliidae (152 species, 21.5%), Flabellidae (98 species, 13.9%), and the Turbinoliidae (56 species, 7.9%). Azooxanthellates are almost ubiquitous in the ocean, but are not known from the Bering Sea or from most of the Arctic Ocean, the most northerly record being *L. pertusa* at 71°21´N, 24°00´E in the southwestern Barents Sea off Norway (see Freiwald et al., 2004, and Fig. 2 herein).

Deep-water Scleractinia Identification Resources

Before one can apply taxonomy to solving a problem, be it zoogeographic, conservation-oriented or ecologic, one must be able to identify the species. There are literally hundreds of papers, both large and small, that describe and/or illustrate the 706 azooxanthellate species, and it is thus difficult for the beginner to know where to start. Therefore, the following papers, grouped in 16 broad geographic regions, are suggested as starting points for the identification of deep-water Scleractinia (Fig. 2). The criteria for inclusion is that the resource be useful for identification (including

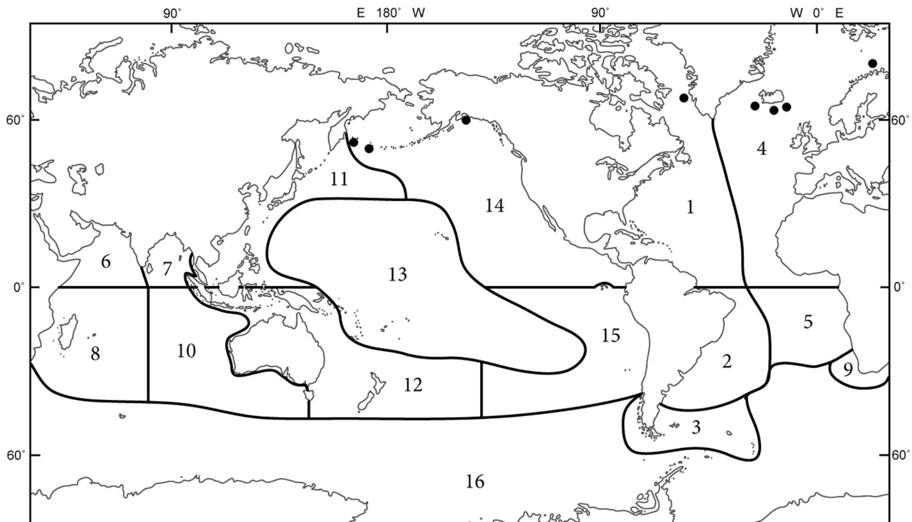

Figure 2. Sixteen geographic regions that are keyed to taxonomic literature resources in text and literature cited. Also shown are the northernmost records of scleractinian corals in the Atlantic and Pacific Oceans (circles). (1) northwestern Atlantic, (2) southwestern Atlantic, (3) southern region of South America, (4) northeastern Atlantic, (5) southeastern Atlantic, (6) northwestern Indian Ocean, (7) northeastern Indian Ocean, (8) southwestern Indian Ocean, (9) warm temperate South Africa, (10) southeastern Indian Ocean, (11) northwestern Pacific, (12) southwestern Pacific, (13) central Pacific, (14) northeastern Pacific, (15) southeastern Pacific, and (16) Antarctic and Subantarctic.

photographs, synonymies, keys, and/or taxonomic remarks) and be relatively current and available. Thus, the listed papers may not be the original faunistic account of a region, but may be the update or revision of the classical account.

The northwestern Atlantic (region 1) is probably the best known region for deep-water Scleractinia, the deep and shallow-water azooxanthellates having been revised by Cairns (1979 and 2000, respectively); an illustrated key to the temperate water species is provided by Cairns (1981); and in situ color photographs of some species are given by Humann and Deloach (2002). Much less well known is the southwestern Atlantic (region 2), for which one must rely on Cairns (1979), Kitahara (2002), and a checklist of Zibrowius (1988). The cold temperate southern region of South America (region 3), west and east including the Falkland Islands, is reviewed by Cairns (1982) and Cairns et al. (2005). The northeastern Atlantic (region 4), including the Mediterranean, is also quite well known, the species being well described and illustrated by Zibrowius (1980). The work of Chevalier (1966) is also quite useful for the tropical regions of this realm. Few species have been reported from the southeastern Atlantic (region 5), the most comprehensive account being a report on 11 species collected from off Namibia, Walvis Ridge and South Africa by Zibrowius and Gili (1990).

The poorest known coral fauna is that of the northern Indian Ocean, for which no comprehensive revision exists. For the northwestern Indian Ocean (region 6: Arabian Sea, Persian Gulf, Red Sea), one must rely on early expeditionary reports, i.e., the "Investigator" (Alcock, 1898; van der Horst, 1931), the "Pola"–Red Sea (Marenzeller, 1907), and the John Murray Expedition (Gardiner and Waugh, 1938, 1939). The northeastern Indian Ocean (region 7: Bay of Bengal) is even less well known; only Duncan (1889) is available as a starting point. Cairns and Keller (1993) summarize the southwestern Indian Ocean (region 8) fauna, and Zibrowius (1974) reported 11 species from the islands of St. Paul and Amsterdam. The corals of warm temperate South Africa (region 9) are treated by Gardiner (1904), van der Horst (1927, 1938), and in a checklist by Boshoff (1981). The azooxanthellate corals of the southeastern Indian Ocean (region 10) are reviewed by Cairns (1998, western Australia) and Cairns and Parker (1992, South Australia, Victoria, Tasmania).

Within the northwestern Pacific (region 11), the tropical (Philippine) deep-water corals were partially revised by Cairns (1989) and the temperate fauna by Cairns (1994). Cairns and Zibrowius (1997) later finished the Philippine revision and added to it an account of the Indonesian corals. Ogawa et al. (2006) have also published an ongoing series of 12 revisions entitled "A revision of Japanese ahermatypic corals around the coastal region with a guide to identifications". The southwestern Pacific (region 12) fauna is also fairly well known, benefiting from revisions by Wells (1964, Queensland), Cairns and Zibrowius (1997, Indonesia), Cairns (1995, New Zealand), and Cairns (2004, New South Wales, Queensland, Northern Territories). The deep coral fauna of only part of the vast central Pacific (region 13) region is known, useful revisions or faunistic reports having been published by: Vaughan (1907, Hawaiian Islands), Wells (1954, Marshall Islands), Keller (1981, Marcus-Necker Ridge), Cairns (1984, 2006, Hawaiian Islands), and Cairns (1999b, Vanuatu and Wallis and Futuna Islands). The most recent revision of the temperate northeastern Pacific (region 14) is that of Cairns (1994), and the tropical northeastern Pacific was studied by Durham and Barnard (1952). Finally, the depauperate and poorly known tropical southeastern Pacific (region 15) has been studied by Wells (1983) and Cairns (1991), both dealing with the Galápagos fauna, and by Cairns et al. (2005), discussing the Peru–Chile fauna.

The Antarctic and Subantarctic (region 16) deep-water corals were reviewed by Cairns (1982) and the New Zealand Subantarctic islands by Cairns (1995). The classical reference to deep-water corals worldwide is the *Challenger* report by H. N. Moseley (1881).

Azooxanthellate Scleractinian Species Diversity Contour Lines ("Isopanspecific" Lines)

The species diversity map (Fig. 3) is based on reliable lists of species from 95 regions, which in turn are based on hundreds of sources and is meant to represent only a first approximation of the true diversity of deep-water azooxanthellate corals in the world. The contour lines were drawn by hand, not computer algorithm. Nonetheless, certain trends can be seen. There are three regions of high biodiversity, the most diverse being the region bordered to the north by the Philippines and to the southeast by New Caledonia, including New Guinea and the northeastern coast of Australia. Species diversities of 120–157 occur in this region. A second, and much smaller, biodiversity center with up to 81 species occurs in the Caribbean, and includes the region from Cuba through the Lesser Antilles. A third region, equal to the Caribbean in richness, is the northwestern Indian Ocean (79 species). Two smaller, isolated regions of high diversity are the southwestern Indian Ocean (51 species) and off Brazil (46 species). The diversity centers and attenuation of contour lines are remarkably similar to those demonstrated for shallow-water coral genera (Wells, 1954; Stehli and Wells, 1971; Rosen, 1971, 1981; Veron, 1985, 1995), even though these two kinds of corals occur in very different environments, and species, not genera, are the subject of the azooxanthellate contours. Both mappings also include the same three major regions of high diversity, all of which are located on the western margins of ocean basins with depauperate faunas in the eastern margins. The azooxanthellate mapping differs, of course, in having attenuated contour lines that extend into the temperate and even polar regions, a much more significant presence in the eastern Atlantic, and fewer species in the tropical Pacific islands, but a consistent if small presence off temperate and Subantarctic islands. The contour lines support the generalized conclusions of previous analyses of deep-water coral species distribution (Rosen, 1981; Keller, 1998). Rosen's (1981) analysis concerned only the North Atlantic, in which he found the highest numbers of species in temperate latitudes, whereas Keller's (1998) analysis was worldwide and concluded that the greatest number of deep-water species occurred in the northern hemisphere tropics on the western sides of oceans.

Many explanations have been proposed to explain the regional high diversity of zooxanthellate Scleractinia, one of the most common being the effect of temperature (Wells, 1954; Stehli and Wells, 1971; Rosen, 1971, 1981): warmer water (25–28 °C) favors speciation, cooler water inhibits the ability for reproduction. Others (Stehli and Wells, 1971; Rosen, 1971, 1981) emphasize the "area effect", i.e., the tendency for more species to occur in large, spatially heterogeneous regions that are relatively stable over time (the stability-time hypothesis of Sanders, 1968). Salinity, both higher and lower than oceanic, has also been suggested to be a factor (Rosen, 1971), as well as the effect of surface oceanic currents on dispersal of larvae (Rosen, 1971; Veron, 1985, 1995). Most of these hypotheses are thoroughly discussed by Rosen (1981,

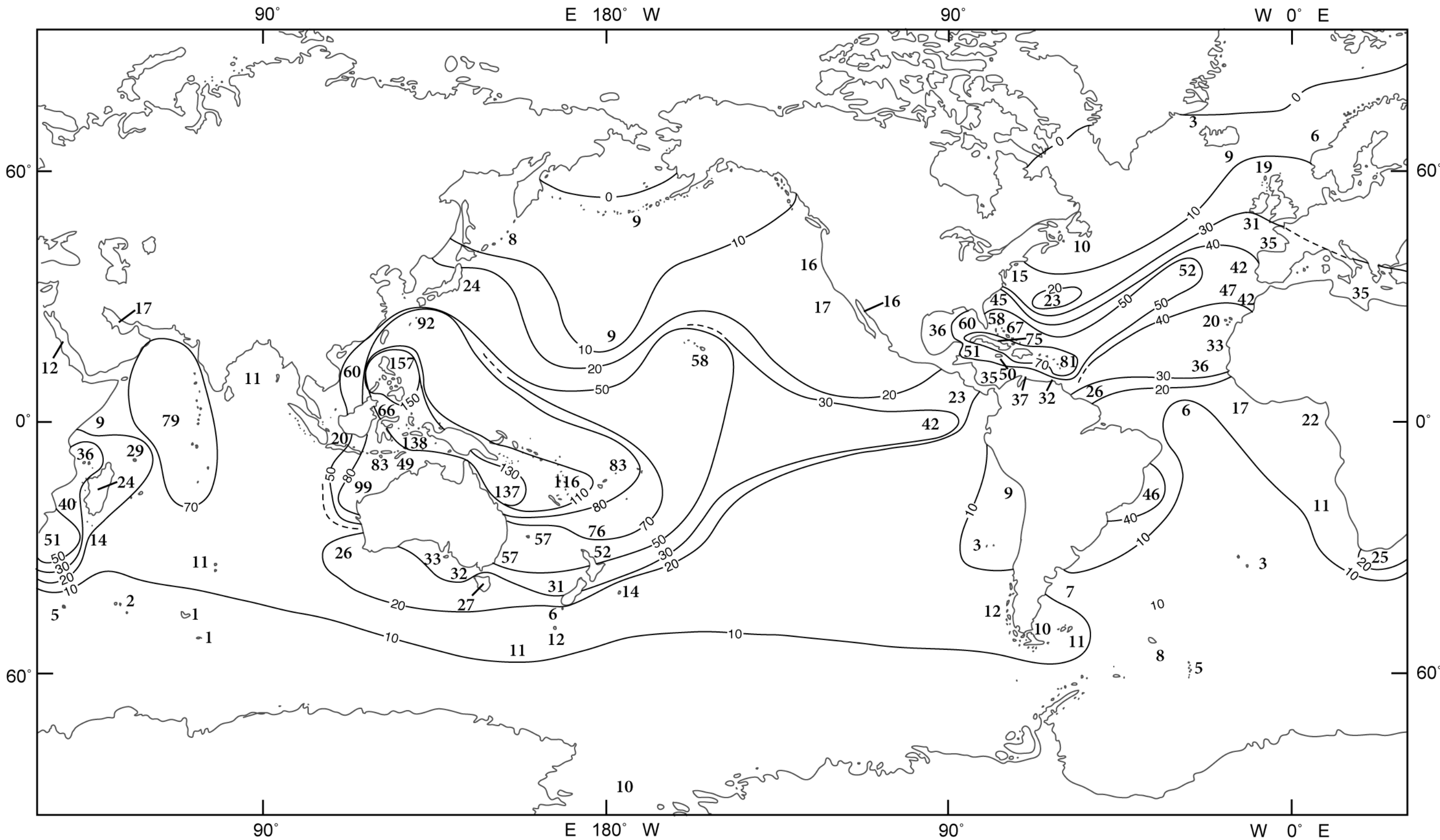

Figure 3. Species diversity contours of the 706 species of azooxanthellate Scleractinia. Three high diversity regions (northern hemisphere) and two secondary high diversity regions (southern hemisphere) are indicated. See text for discussion.

1984), Fraser and Currie (1996), and Veron (1995: 51), the latter concluding that the biogeographic patterns of zooxanthellate and azooxanthellate should have little in common. It is not the point of this section to explain why zooxanthellate species occur where they do, but simply to point out the similar distribution patterns of the two ecological groups.

Although each azooxanthellate species probably has an optimal temperature range for reproduction, it is unlikely that temperature is the only factor controlling distribution and is probably much less important than it is for shallow water corals. For instance, the average temperature and depth ranges of a typical western Atlantic azooxanthellate (derived from Cairns, 1979: table 1) is 6–15 °C and 250–1225 m, respectively. If these species were strictly tied to a temperature range, one might expect to find them in shallower water in higher latitude (tropical submergence), but this is not the case for most species. Nor do Antarctic species occur in particularly shallow water. Nonetheless, the low numbers of species in the polar regions are undoubtedly influenced by the cold temperature found there. Salinity may have a regional effect, large rivers such as the Amazon producing a fresh water barrier to azooxanthellate distributions even at great depth, but overall this appears to be a minor influence. The effect of currents on dispersal is certainly pronounced in shallow water corals but the currents and their effects are poorly known in deep water. The area effect thus seems to be the most logical explanation for the high diversity of deep-water corals on the western margins of oceans. The Philippine to New Caledonian shelf and slope region is the most extensive contiguous area of substrate at 200–1000 m depth (the prime depth for azooxanthellate corals) in the world, providing geographically complex (hard, muddy, and sandy) substrates that are available for colonization. Smaller, but equal in geographic complexity and availability for colonization, is the Caribbean Antillean arc. The area effect created by a large archipelago of islands and seamounts might also explain the relatively high diversity around the Hawaiian Islands and Galápagos. But then why are there so few species in the topographically inviting region of the upper boreal North Pacific, including the Aleutian and Kurile Islands, which is idyllic for deep-water stylasterids and octocorals but contains only 12 species of Scleractinia? Recent evidence (Guinotte et al., 2006) indicates that the depth of the aragonite saturation horizon (ASH) may be a limiting factor in deep-water coral occurrence, with few or no scleractinian corals occurring in water below this level because of the difficulty of extracting calcium carbonate to form skeletons. Indeed, this horizon is quite shallow in the Aleutian region of the North Pacific (about 100 m) and perhaps not coincidentally eight of the 12 species known from this region occur in shallow water above the ASH, the other four being very deep-living micrabaciids, which are noted for their unique adaptations to living in a low calcium carbonate environment by decreasing their skeletal weight (Squires, 1967; Owens, 1984). None of the 12 are habitat-forming species. As noted above, stylasterids are common in this same region, and although most stylasterids have aragonitic coralla, a small percentage of species have calcitic coralla (Cairns and MacIntyre, 1992). Most of the Aleutian species having calcitic coralla, which therefore may allow these species to have a greater bathymetric range as calcite has a deeper saturation horizon. Furthermore, the sclerites of octocorals are calcitic. Other regions having a low ASH (such as the eastern Pacific, Bay of Bengal, and off southwestern Africa) are also regions of low scleractinian diversity. Thus, although the area effect may be an important cause of regional high diversity of deep-water corals, other factors such as the calcium carbonate saturation depth may limit diversity in other regions; temperature, salinity, and currents may also play subsidiary roles.

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Literature Cited

Alcock, A. 1898. An account of the deep-sea Madreporaria collected by the Royal Indian Marine survey ship Investigator. Indian Museum, Calcutta. 1–29.

Best, M. B. 1999. Corals as speaking stones. Geol. Mijnbouw 78: 141–145.

Boshoff, P. H. 1981. An annotated checklist of southern African Scleractinia. S. Afr. Ass. Mar. Biol. Res., Oceanogr. Res. Inst., Durban, Invest. Rep. 49: 1–45.

Cairns, S. D. 1979. The deep-water Scleractinia of the Caribbean and adjacent waters. Stud. Fauna Curaçao Other Carib. Isl. 57: 1–341.

__________. 1981. Marine flora and fauna of the northeastern United States. Scleractinia. NOAA Tech. Rep. NMFS Circ. 438: 1–14.

__________. 1982. Antarctic and Subantarctic Scleractinia. Ant. Res. Ser. 34: 1–74.

__________. 1984. New records of ahermatypic corals (Scleractinia) from the Hawaiian and Line Islands. Occas. Pap. Bishop Mus. 25(10): 1–30.

__________. 1989. A revision of the ahermatypic Scleractinia of the Philippine Islands and adjacent waters, Part 1: Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae. Smithson. Contrib. Zool. 486: 1–136.

__________. 1991. A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands. Smithson. Contrib. Zool. 504: 1–32.

__________. 1994. Scleractinia of the temperate North Pacific. Smithson. Contrib. Zool. 557: 1–150.

__________. 1995. The marine fauna of New Zealand: Scleractinia (Cnidaria: Anthozoa). N. Z. Oceanogr. Inst. Mem. 103: 1–210.

__________. 1998. Azooxanthellate Scleractinia (Cnidaria: Anthozoa) of Western Australia. Rec. Western Aust. Mus. 18: 361–417.

_________. 1999a. Species richness of Recent Scleractinia. Atoll Res. Bull. 459: 1–12.

_________. 1999b. Cnidaria Anthozoa: deep-water azooxanthellate Scleractinia from Vanuatu, and Wallis and Futuna Islands. Mem. Mus. Natl. Hist. Nat. 180: 31–167.

_________. 2000. A revision of the shallow-water azooxanthellate Scleractinia of the Western Atlantic. Stud. Nat. Hist. Carib. Reg. 75: 1–231.

_________. 2001. A brief history of taxonomic research on azooxanthellate Scleractinia (Cnidaria: Anthozoa). Bull. Biol. Soc. Wash. 10: 191–203.

_________. 2004. The azooxanthellate Scleractinia (Coelenterata: Anthozoa) of Australia. Rec. Aust. Mus. 56: 259–329.

_________. 2006. New records of azooxanthellate Scleractinia from the Hawaiian Islands. Occas. Pap. Bishop Mus. 87: 45–53.

_________ and N. B. Keller. 1993. New taxa and distributional records of azooxanthellate Scleractinia (Cnidaria, Anthozoa) from the tropical south-west Indian Ocean, with comments on their zoogeography and ecology. Ann. S. Afr. Mus. 103: 213–292.

_________ and I. G. MacIntyre. 1992. Phylogenetic implications of calcium carbonate mineralogy in the Stylasteridae (Cnidaria: Hydrozoa). Palaios 7: 96–107.

_________ and S. A. Parker. 1992. Review of the Recent Scleractinia (Stony Corals) of South Australia, Victoria and Tasmania. Rec. S. Aust. Mus., Mono. Ser. 3: 1–82.

_________ and H. Zibrowius. 1997. Cnidaria Anthozoa: Azooxanthellate Scleractinia from the Philippine and Indonesian regions. Mem. Mus. Natl. Hist. Nat. 172: 27–243.

_________, V. Häussermann, and G. Försterra. 2005. A review of the Scleractinia (Cnidaria: Anthozoa) of Chile, with the description of two new species. Zootaxa 1018: 15–46.

_________, B. W. Hoeksema, and J. van der Land. 1999. Appendix: list of extant stony corals. Atoll Res. Bull. 459: 13–46.

Chevalier, J.-P. 1966. Contribution à l'étude des Madréporaires des côtes occidentales de l'Afrique tropicale, parts 1 and 2. Bull. l'Inst. Fond. d'Afr. Noire (I.F.A.N.) 28: 912–975, 1356–1405.

Duncan, P. M. 1889. On the Madreporaria of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by John Anderson, F. R. S., Superintendent of the Museum. J. Linnean Soc. 21: 1–25.

Durham, J. W. and J. L. Barnard. 1952. Stony corals of the eastern Pacific collected by the Velero III and Velero IV. Allan Hancock Pac. Exped. 16: 1–110.

Fraser, R. H. and D. J. Currie. 1996. The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. Am. Nat. 148: 138–159.

Freiwald, A., J. H. Fosså, A. Grehan, T. Koslow, and J. M. Roberts. 2004. Cold-water coral reefs. UNEP-WCMC, Cambridge, U.K., 1–84.

Gardiner, J. S. 1904. The turbinolid corals of South Africa, with notes on their anatomy and variation. Mar. Invest. S. Afr. 3: 97–129.

___________ and P. Waugh. 1938. The flabellid and turbinolid corals. John Murray Exped. 1933–34 Sci. Rep. 5: 167–202.

___________ and _______. 1939. Madreporaria excluding the Flabellidae and Turbinolidae. John Murray Exped. 1933–34 Sci. Rep. 6: 225–242.

Guinotte, J. M., J. Orr, S. D. Cairns, A. Freiwald, L. Morgan, and R. George. 2006. Climate change and deep-sea corals: will chemical and physical changes in the world's oceans alter the distribution of deep-sea bioherm-forming scleractinians? Front. Ecol. Environ. 3: 141–146.

Hickson, S. J. 1924. An introduction to the study of recent corals. Manchester at the University Press, London. 257 p.

Horst, C. J. van der. 1927. Eupsammid corals from South Africa. Union of S. Afr. Fish. Mar. Biol. Surv. Rep. No. 5. for the year 1925. Spec. Rep. No. 1.2: 1–7.

_______________. 1931. Some solitary corals from the Indian Ocean. Rec. Indian Mus. 33: 3–12.

_______________. 1938. *Balanophyllias* from the Cape of Good Hope. Ann. Mag. Nat. Hist. 2: 139–145.

Humann, P. and N. Deloach. 2002. Reef coral identification: Florida Caribbean Bahamas, including marine plants, second edition. New World Publications, Inc., Jacksonville. 278 p.

Keller, N. B. 1976. The deep-sea madreporarian corals of the genus *Fungiacyathus* from the Kurile-Kamchatka, Aleutian Trenches and other regions of the world oceans. Trudy Instit. Okean. 99: 31–44 [in Russian, English translation deposited at Smithsonian].

__________. 1981. The solitary madreporarian corals. Pages 28–39 *in* A. P. Kuznetsov and A. N. Mironov, eds. Benthos of the submarine mountains Marcus-Necker and adjacent Pacific regions. P. P. Shirshov Institute of Oceanology, Moscow.

__________. 1998. Spatial distribution of the azooxanthellate Scleractinia (Cnidaria, Anthozoa). Okeanologiya 38: 227–232.

Kitahara, M. V. 2002. Sistemática dos corais de profundidade do sul do Brasil, Thesis, Universidade do Vale do Itajaí, Itajaí. 134 p.

Marenzeller, E. von 1907. Expedition S. M. Schiff "Pola" in das Rote Meer. Zoologische Ergebnisse 24. Über den Septennachwuchs der Eupsamminen E. H. Denkschr. Kais. Akad. Wissensch., Math.-naturwissen. Classe 80: 1–12.

Ogawa, K. 2006. A revision of Japanese ahermatypic corals around the coastal region with guide to identification. Part 12. *Truncatoflabellum, Placotrochus* and *Placotrochides.* Nankiseibutu (Nanki Biol. Soc.) 48(1) 13–20.

Owens, J. M. 1984. Microstructural changes in the Micrabaciidae and their ecological and taxonomic implications. Paleont. Amer. 54: 519–522.

Rosen, B. R. 1971. The distribution of reef coral genera in the Indian Ocean. Pages 263–299 *in* D. R. Stoddart and C. M. Yonge, eds. Regional variation in Indian Ocean coral reefs. Symp. Zoological Society of London, 28, The Zoological Society of London, London.

____________. 1981. The tropical high diversity enigma - the corals'-eye view. Pages 103–129 *in* P. H. Greenwood, ed. The evolving biosphere. Cambridge University Press, Cambridge.

____________. 1984. Reef coral biogeography and climate through the Late Cainozoic: just islands in the sun or a critical pattern of islands? Pages 201–262 *in* P. J. Benchley, ed. Fossils and climate. John Wiley and Sons, Chichester.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243–282.

Squires, D. F. 1967. The evolution of the deep-sea coral family Micrabaciidae. Stud. Trop. Oceanogr. 5: 502–510.

Stehli, F. G. and J. W. Wells. 1971. Diversity and age patterns in hermatypic corals. Syst. Zool. 20: 115–126.

Tescione, G. 1968. The Italians and their coral fishing. Fausto Fiorentino, Napoli. 490 p.

Vaughan, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. Bull. U. S. Nat. Mus. 59: ix + 427 p.

Veron, J. E. N. 1985. Aspects of the biogeography of hermatypic corals. Proc. Fifth Int. Coral Reef Cong., Tahiti 4: 83–88.

___________. 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. USNW Press, Sydney. xiii + 321 p.

Wells, J. W. 1954. Recent corals of the Marshall Islands: Bikini and nearby atolls, Part 2, Oceanography (Biologic). Geol. Surv. Prof. Pap. 260-I: 382–486.

_________. 1964. Ahermatypic corals from Queensland. Univ. Queensland Pap., Dept. Zool. 2: 107–121.

_________. 1983. Annotated list of the scleractinian corals of the Galápagos. Pages 212–291 *in* P. W. Glynn and G. M. Wellington, eds. Corals and coral reefs of the Galápagos Islands, University of California Press, Berkeley.

Zibrowius, H. 1974. Scléractiniaires des Iles Saint Paul et Amsterdam (sud de l'Océan Indien). Tethys 5: 747–778.

___________. 1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique Nord-Oriental. Mem. Inst. Oceanogr. Monaco 11: 1–284.

___________. 1988. Les coraux Stylasteridae et Scleractinia. Les rapports des campagnes à la mer MD 55/Brésil à bord du "Marion Dufresne" 6 May–2 June 1987 87-03: 132–136.

___________ and J.-M. Gili. 1990. Deep-water Scleractinia (Cnidaria: Anthozoa) from Namibia, South Africa, and Walvis Ridge, southeastern Atlantic. Sci. Mar. 54: 19–46.

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