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Worldwide Distribution of the Stylasteridae (Cnidaria: Hydrozoa)*

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SUMMARY: Stylasterids show a pronounced insular distribution pattern, being found primarily off small (less than 36,000 km^2) oceanic islands, atolls, and archipelagos, and on seamounts and submarine ridges. Although lowered salinity and increased sedimentation may exclude stylasterids from the coasts of larger continental land masses, it is more likely that the availability of hard substrate and the low nutrient levels associated with steep-sided oceanic islands favor the establishment of stylasterids. Azooxanthellate Scleractinia, another calcified cnidarian taxon, have a broader distribution than stylasterids because they are assumed to be better competitors: having a greater dispersal ability, better sediment-shedding ability, and the ability of some to live on soft substrates.

Key words: Stylasteridae, insular distribution, zoogeography, azooxanthellate Scleractinia, oligotrophic waters.

INTRODUCTION

BROCH (1942) appears to have been the first to comment on the worldwide distribution of the Stylasteridae. He plotted all records of stylasterids on four world maps, coding each genus with a different symbol. Although the insular nature of the distributions is discernable from a composite of these maps, BROCH did not comment on any patterns of distribution except to note that stylasterids were absent from the northern Indian Ocean, which he attributed to a lack of collecting effort. BROCH noted that the most diverse stylasterid faunas were in Indonesia (based on HICKSON and ENGLAND, 1905) and the Aleutian Islands (based on FISHER, 1938). BROCH was in error when he stated that stylasterids were absent from Antarctica. They had been reported there by STOKES (1847) and MARENZELLER (1903). More recently, numerous Antarctic records were summarized by CAIRNS (1983). Also, all four of BROCH's maps show records of stylaterids in the Gulf of Mexico, which are not substantiated by any literature or museum records.

BOSCHMA (1953) discussed the distribution of 127 stylasterid species distinguished by him with reference to their occurrence in 24 regions in the Pacific Ocean. Like BROCH, he concluded that the most diverse faunas were in the "East Indies", off Japan, and around the Aleutian Islands. He did not discuss generalized patterns of distribution but did note the absence of stylasterids from the coasts of Korea, China, Taiwan, Indo-China, Thailand, and the Malay Peninsula, New Britain, New Ireland, the Admiralty Islands; and the Pacific coasts of Mexico, Central America, and South America.

In a revision of the western Atlantic stylasterids, CAIRNS (1986a) noted that stylasterids were never found close to continental land masses, being absent from the Gulf of Mexico and the Caribbean coasts of Central and South America, but quite common in insular environments, such as the Lesser Antilles and the Bahamas. He attributed the absence of stylasterids from off large land masses to their sensitivity to

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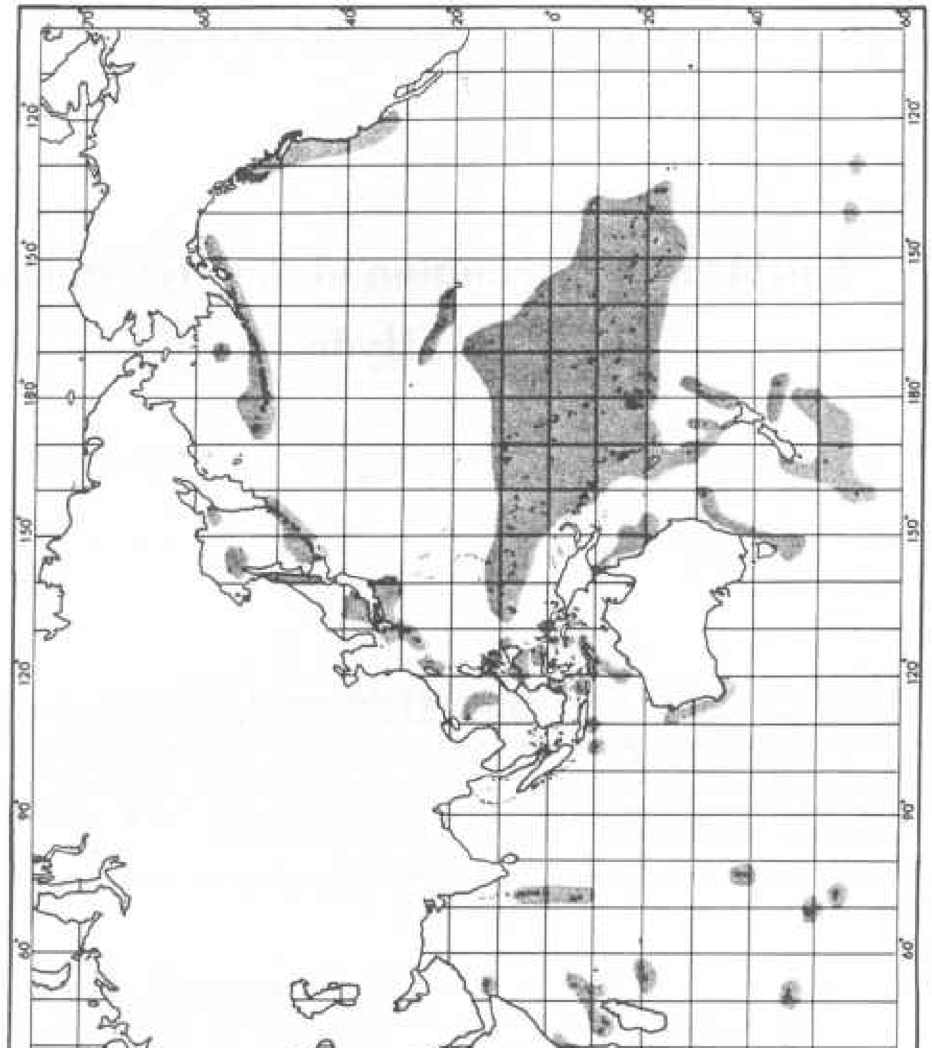

FIG. 1. — Map of all known stylasterid records.

variable hydrographic conditions near continents, such as periodically lowered salinity and turbidity (sediment load).

CAIRNS (1987a) again alluded to the insular nature of stylasterid distribution, and, in his revision of the New Zealand stylasterids (CAIRNS, 1991b), reinforced this observation by noting that most of the 59 species known from that region occurred on submarine ridges, seamounts, and small islands. Few species were found off coastal New Zealand, the exceptions being off Fiordland, the Bay of Plenty, and off North Cape. He attributed the absence of stylasterids from coastal areas to the inability of stylasterids to establish themselves in terrigenous sediment, which predominates around the broad continental margins of the North and South Islands except in the three areas in which stylasterids were found (MITCHELL *et al.*, 1989).

The objectives of this paper were to present and analyze the worldwide patterns of stylasterid distribution, to suggest explanations for this pattern, to make predictions about where stylasterids may yet be found, and to compare their distribution with that of the azooxanthellate Scleractinia.

MATERIAL AND METHODS

All published records of stylasterids, regardless of identity or depth range, were plotted on a world map (Fig. 1). BOSCHMA's (1957) comprehensive list of species and localities was a useful guide to the literature to that date, but, in general, original references were used. In addition to published records, the collections of the U. S. National Museum of Natural History provided another 150 separate data points, including the first records of stylasterids from the Hawaiian Islands exclusive of Laysan. Obviously, not all records could be plotted on one map and in some cases an envelope of occurrence is indicated. The Times Atlas of the World (1988) was used for the names and sizes of the 43 largest islands.

RESULTS

Although it might appear that stylasterids are widely and homogeneously distributed (Fig. 1), on closer examination a general pattern emerges. Stylasterids are found primarily off small "low" islands, atolls, archipelagos, seamounts, offshore reefs, and submarine ridges; they are rarely found off continental land masses or "high" continental islands. Of the 15 largest islands, those with land masses over 105,000 km^2 (e.g., approximate area of Cuba), stylasterids are either absent or extremely rare, with the notable exception of Honshu, Japan. When they do occur off these large islands, including Honshu, it is usually off a coastline with a precipitous shelf and slope. Stylasterids are also usually absent from islands having an area between 36,000 to 105,000 km^2, with the exceptions of Iceland, Mindanao, Sakhalin, Tierra del Fuego, and Kyushu. Again, most of these island exceptions have precipitous continental shelves and slopes and are on active volcanic plate boundaries. Islands smaller than 36,000 km^2 (e.g., approximate area of Taiwan), however, generally support stylasterids, with the exceptions of high islands surrounded by broad continental shelves, such as: Hainan, South China Sea and Stewart Island, New Zealand. Areas that are particularly favorable for stylasterids are: the Norfolk, Kermadec, and Macquarie Ridges, New Zealand, which together carry the highest stylasterid species diversity in the world (CAIRNS, 1991b); the New Caledonia and Loyalty Islands (H. Zibrowius, pers. comm.); the Lesser Antilles (CAIRNS, 1986a); the Aleutian Islands (FISHER, 1938); the Kurile Islands (NAUMOV, 1960); the Ryukyu Islands; the Scotia Arc (CAIRNS, 1983); the Galápagos Islands (CAIRNS, 1986b); the Azores (ZIBROWIUS and CAIRNS, 1992); the Bahamas (CAIRNS, 1986a); the Marshall Islands; the Tuamotu Islands; the Scotia Arc, Antarctic Peninsula, and most Subantarctic islands (CAIRNS, 1983); and most seamounts that rise to within 200-800 m of the surface (CAIRNS, 1982). In general, most occurrences of stylasterids are off volcanic islands and on seamounts, and thus their distribution follows plate boundaries and are associated with geological hot spots. Although stylasterids have been reported from Laysan (CAIRNS, 1978) and several unpublished records are present in the NMNH collections from other Hawaiian islands, stylasterids are surprisingly rare throughout the Hawaiian Islands.

It is also instructive to note where stylasterids are not found. In addition to their absence from large islands, they are also absent or extremely rare from the coasts of North, Central, and South America; Africa; the northern Indian Ocean and the Asian coast to the Sea of Japan; Australia; and off New Zealand. None have been found in the Canadian, Alaskan, or Soviet Arctic, regardless of island size. Northernmost records of stylasterids in the North Pacific are 58° 17′ N in the Gulf of Alaska (FISHER, 1938), 58° 02.3′ N in the Okhotsh Sea (NAUMOV, 1960), and about 57° N off Pribilof Island in the Bering Sea (CAIRNS, 1991a). The northernmost record in the North Atlantic is 68° 30′ N off Norway (ZIBROWIUS and CAIRNS, 1992). Stylasterids are conspicuously absent from the Gulf of Mexico, with one exception off Veracruz (HORTA-PUGA and CARRICART-GANIVET, 1990), and in the Mediterranean, with the exception of the Straits of Messina (ZIBROWIUS and CAIRNS, 1992). Records that appear to be off continents in Figure 1 are invariably well off the continental coast, either at the continental slope (e.g., Blake Plateau and off Brazil); on fringing or barrier reefs (e.g., Great Barrier Reef, Belize barrier reef); off small, steep-sides islands near a continent (e.g., Zanzibar, Pemba, Socotra); or adjacent to precipitous continental slopes (e.g., off northwestern Cuba and the fiords of Iceland, Chile, Norway, Fiordland of New Zealand).

DISCUSSION

CAIRNS (1986a, 1991b) suggested three reasons why the distribution of stylasterids is primarily insular in nature, one of which was their possible sensitivity to fluctuating salinity associated with river discharge from large islands and continental land masses. Although this may be a factor, it requires testing, especially in order to separate the effects of lowered salinity from possible effects of high sediment and nutrient levels in river discharges. Stylasterids are generally absent from areas of high suspended sediment discharge, such as off the Amazon Delta, the Gulf of Mexico, the Gulf of Guinea, the Mediterranean, the Bay of Bengal, the Persian Gulf, off southeast Asia, and the Bering Sea (MILLIMAN and MEADE, 1983). In one of the few studies on the natural history of stylasterids, OSTARELLO (1973) noted that settling of particulate matter was extremely harmful to young colonies, those planulae that settled on vertical surfaces tending to fare much better. Whereas siltation and suspended particulate matter may help to explain why stylasterids are absent from certain regions, it does not necessarily explain their presence in others. Azooxanthellate Scleractinia, the other major group of calcified Cnidaria, are often common in regions of sedimentation. One factor that may explain this difference in distribution is that the polyps and tentacles of azooxanthellate Scleractinia are, in general, larger than those of stylasterids (polyp diameter: 1.5-65.0 mm vs 0.7-3.0 mm, respectively), and thus the larger-tentacled Scleractinia may be more efficient at sediment shedding than the stylasterids.

A third hypothesis, related to sediment loading, pertains to the stylasterids' requirement of a hard substrate on which to settle and grow. OSTARELLO (1973) noted a preference for settlement on vertical surfaces and CAIRNS (1991b) suggested that stylasterids were rare off the coasts of New Zealand possibly because the two large islands were surrounded by relatively broad continental shelves covered with terrigenous sediment. The only areas around New Zealand having a nonterrigeonous (biogenic calcareous gravel or volcanic) cover are off Fiordland South Island, the tip of North Cape, and several areas in the Bay of Plenty (MITCHELL *et al.*, 1989) and these are the only areas of coastal New Zealand that support stylasterids. This seems to be a general correlation worldwide: stylasterids are common off small, low islands and seamounts with narrow shelves and precipitous slopes that have little terrigenous sediment cover and present the opportunity for attachment and support of colonies. In contrast, they are absent or quite rare from continents and continetal islands having broad shelves and relatively thick terrigenous sediment cover. Another reason why azooxanthellate Scleractinia occur off continental land masses and stylasterids do not may be that, whereas both taxa require a hard substrate on which to settle, approximately one-third of the azooxanthellate scleractinian genera subsequently (post-settlement) live free on the substrate, which is often soft. All but *Conopora adeta* (see CAIRNS, 1987b) of the 243 known Recent stylasterid species are firmly attached to hard substrates that are large enough to support them without shifting.

A fourth possible explanation for the observed distribution of stylasterids is suggested here. It has been noted (e.g., EMLEN, 1977) that a nutrient pulse will favor r-selected species, to the partial exclusion of K-selected species over the short term. BIRKELAND (1987, 1989) and VERMEIJ (1990) noted that marine areas having low nutrient levels (oligotrophic regions) support K-strategists that recycle nutrients (e.g., zooxanthellate corals), whereas higher nutrient levels favored r-strategists, such as benthic algae, heterotrophic suspension feeders, and finally phytoplankton blooms, in that order. One of the marine regions with the lowest nutrient level is the central oceanic Pacific (KOBLENTZ-MISHKE *et al.*, 1970; BERGER, 1989), e.g., off small, low islands; in deep water; and on continental slopes far from the coast. Although stylasterids are all azooxanthellate and thus do not tightly recycle nutrients, they do, in general, fit the description of a K-strategist (Pianka, 1970; Sanders, 1979), having: slow growth, slow response to environmental change, a long life, iteroparous reproduction, and brooded planulae. Therefore, they may be outcompeted by more aggressive species in high nutrient waters, finding refuge in low nutrient level and/or less competitive environments, such as cryptic habitats (caves) and in deep water (Sanders, 1979; Thayer, 1989). A specific example is the observed distribution of marine invertebrates in the southern fiords of New Zealand. The upper 4 m of fiord water is characterized as low salinity and light absorbing (due to inclusion of detritus and tannins) and thus not conducive to algal growth (Grange, *et al.*, 1981). The same authors concluded that interspecific competition is thereby reduced, allowing the settlement of sessile epifauna (e.g., Brachiopoda, Antipatharia) at lesser depths than ordinarily. To rephrase their interpretation, I would suggest that the dark, freshwater lens reduces the number of aggressive opportunistic species typically found at shallow depth, allowing the typically deeper-water, less competitive species (e.g., stylasterids) to colonize unusually shallow water. For example, *Stylaster eguchii*, which has a depth range of 15-1483 m, occurs in shallow water only in the New Zealand fiords (Cairns, 1991b).

The broader distribution of azooxanthellate Scleractinia in higher nutrient waters may imply that they are better competitors, which may be explained, in part, by the ability of some azooxanthellate species (Fadlallah, 1983; Harrison, 1985) to broadcast their gametes, whereas all stylasterids brood their planula to an advanced stage, which often settle very close to the parent colony.

CONCLUSIONS

Although a lowered salinity or increase in sedimentation may help to explain the absence of stylasterids from continental land masses, it is more likely that a combination of availability of hard substrate (providing attachment and subsequent support) and low nutrient levels produces the insular distribution illustrated in Figure 1. Marine environments that usually have both hard substrates and low nutrient levels are small (low), steep-sided, volcanic islands, atolls, and seamounts. Based on these factors, I would predict stylasterids to eventually be found off the following islands and seamounts: Atlantic — Bermuda, St. Helena, Challenger and Argus Banks, Cayman Islands, and Trindade; eastern Pacific — Juan Fernández Islands, St. Felix Island, Clipperton, Revilgegado Islands, and Easter Islands; Pacific — New Britain, New Ireland, Admiralty Islands, Nauru, Aotea Seamount, and Bonin Islands; Indian Ocean — Andaman and Luccadive Islands, Mentawaian Archipelago west of Sumatra, and Cocos-Keeling Island; Subantarctic — South Sandwich Islands and Bouvet.

The correlation of the presence of stylasterids to oceanic hard substrates and low nutrient levels is not absolute. For instance, the common shallow-water *Distichopora violacea* is found off Laing Island, northern New Guinea, in hypertrophic, sediment-laden waters (Boero, pers. comm.). In this case, I would suggest an ecological study of this species, such as the kind done by Ostarello (1973), which might explain why *D. violacea* is successful in that environment and how it differs ecologically or morphologically from other stylasterids.

Azooxanthellate Scleractinia, the other major calcified cnidarian taxon, has a much broader distribution than stylasterids, often occurring off continental land masses. Factors contributing to its broader distribution are hypothesized to be: a greater ability to shed sediment, the ability of some species to live on soft bottoms, and its greater dispersal ability, altogether making it a better competitor in those environments.

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