

ANTHOZOAN DOMINATED BENTHIC ENVIRONMENTS

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ABSTRACT

The coral reef ecosystem exists and persists only in virtually fully saline water of a particular temperature range, at shallow depths, where the substratum is firm. This is a consequence of the rather narrow physico-chemical tolerances of hermatypic scleractinian corals, the animals that are the main builders of reef framework. Commonly, they are also major occupiers of space in such habitats. However, in other shallow, tropical marine environments, or in the same habitats under different conditions, non-scleractinian anthozoans -- typically zoanthids and octocorals -- occupy comparable expanses of substratum. Likewise, some temperate and deep-water marine communities are dominated by anthozoans, generally actinians. Although these animals do not structure their communities physically, they are, in many respects, functionally comparable to reef-building corals. Thus, such anthozoans appear to comprise a group of ecologically equivalent (which is not to say interchangeable) benthic dominants, the distribution of which is determined mainly by physico-chemical factors, mediated and modulated -- especially on a local scale -- by biotic ones.

INTRODUCTION

Only a very small proportion of benthic environments support growth by reef-forming corals. This is because these hermatypic anthozoans do poorly at depths exceeding 50 m, on soft substrata, and in other than virtually euhaline, non-turbid, warm (typically around 20° to seldom more than 30°C) water. The vast majority of the world's benthic marine environments are therefore unsuitable for habitation by hermatypes.

Anthozoans occupy many of those environments. Among them are sea anemones that live on rocky shores of most of the world's temperate seas, pennatulaceans that can cover sandy bottoms in temperate areas, the actinian *Liponema* that dominates soft bottoms in some deep waters at high latitudes, and the azooxanthellate coral that forms banks in Norwegian fjords. At a finer level of analysis, within tropical environments broadly suitable for coral growth, zoanthids and octocorals may predominate instead. I speculate that many anthozoans of both subclasses -- not mostly clonal (asexually produced but not physically connected) or colonial (asexually produced, physically connected) species, but rarely solitary ones as well -- comprise a suite of functionally more or less equivalent species. Which ones occupy a particular environment is determined by features primarily of the physico-chemical habitat, with biotic interactions influential under some circumstances at the local scale. Empirical observations, some of which are summarized here, imply that even a slight change in the controlling factor(s) can shift the balance from one group of

anthozoans to another.

NON-REEFAL ANTHOZOAN-DOMINATED COMMUNITIES

TEMPERATE SHORES

Non-coral anthozoans predominate on many temperate shores, particularly rocky ones. The middle littoral zone in exposed areas of western North America can be carpeted with clonal beds of the sea anemone *Anthopleura elegantissima* (e.g., Ricketts et al. 1985). Its counterpart on the cold west coast of South Africa is *Bunodactis reynaudi* (see Stephenson & Stephenson 1972). In the warmer and physically more variable environment near Beaufort, North Carolina, Stephenson & Stephenson (1972) found intertidal "areas of considerable size" (page 185) occupied by *Aiptasia pallida*. Commonly such species are confined to a narrow, rather well-defined band of the littoral zone. However, on the sheltered side of Vancouver Island, the sea anemone *Metridium*, which can achieve great densities, extends a considerable distance subtidally (Stephenson & Stephenson 1972).

DEEP WATERS

Nor are temperate anthozoans confined to near-shore, shallow, or rocky habitats. Pennatulaceans occur in subtidal sand throughout the world, where they may form dense beds (Birkeland 1974). The actinian *Liponema brevicornis* was the dominant benthic species, in terms of both biomass and number, at 135 m in St. George Basin, Bering Sea, Alaska, where the bottom consists entirely of sand, mud, and silt (Dunn & Bakus 1977). Its range of occurrence is 100-1000 m, but densities at greater depths are unknown. Azooxanthellate corals can form extensive patches (Wilson 1979) and even banks (reviewed by Milliman 1974) at depths of hundreds of meters. Such records are mainly from high latitudes.

SHALLOW TROPICS -- REEFS AND OTHERWISE

INTER-REGIONAL VARIABILITY

At a smaller scale of analysis, within the area bounded by the set of fairly well known and narrow constraints that define suitability for reef development, anthozoan cover of hard-bottom environments varies. The best known example of geographical differences is the conventional comparison between Indo-Pacific and Caribbean reefs (Milliman 1973). Differences in structure between the two has been attributed in part to relatively recent (geologically speaking) biogeographic isolation and cooling of the Caribbean basin, resulting in differential mortality and speciation of reef organisms. A contemporary manifestation of

this history is taxonomic representation of anthozoans, with scleractinians most conspicuous and diverse in the Indo-Pacific, and alcyonarians -- especially gorgonians -- in the Caribbean (e.g., Kuhlmann 1984). (Alcyonaceans in particular may be locally important on Indo-Pacific reefs [see, e.g., Dinesen 1983] but they are relatively less conspicuous.)

INTRA-REGIONAL HETEROGENEITY

Refining the scale further, within a tropical area such as the Caribbean, or even a province such as the Great Barrier Reef or Malay Archipelago, differences in representation of various taxa of anthozoans has been repeatedly correlated with the physico-chemical environment. The coral reef ecosystem is biotically heterogeneous for a variety of reasons, among them those discussed by Grassle (1973). Thus, although called coral reefs, corals are frequently not the predominant organisms, either in terms of biomass or cover, and their distribution is not uniform. The well-known zonation of reefs is a virtually universal exemplar of this (e.g., Loya & Slobodkin 1971; Stoddart 1971; Milliman 1973; Hopley 1978).

In regions demonstrably suitable for coral growth, scleractinians seldom penetrate the intertidal zone, being physically and physiologically maladapted to that environment. On the Natal coast, where a limited number of corals do well, beds of zoanthids typically occupy the midlittoral zone (Stephenson & Stephenson 1972). Among other habitats that seem generally unsuitable for coral growth, and where alternative anthozoan groups often predominate, are those with unstable substrata and/or where disturbance is periodic. Actinians are especially common in unstable reef areas on the Caribbean coast of Panama (Sebens 1976) and zoanthids can cover large expanses on sand flats of patch reefs in Hawaii (Cooke 1979). Zoanthids dominate reef areas in Jamaica subject to periodic disturbance (Karlson 1980). Constituent species of higher taxonomic categories are not uniform in their tolerances, of course. Zonation of the three most common zoanthid species on the intertidal reef flat at Galeta, Panama, correlates with their differential sensitivity to desiccation (Sebens 1982). Vigorous wave action appears to be more inhibitory to soft than hard coral growth (Dinesen 1983, and references cited therein), explaining the complementary distributions of these groups in relatively shallow water of exposed reefs on the central Great Barrier Reef. The large sea anemones harboring clownfishes are more abundant on reefs with less-than-robust coral growth than on flourishing reefs (Mariscal 1970; Dunn 1981). Turbid shallow waters of the tropical Indo-Pacific may be dominated by clones of corallimorpharians (personal observation). Nor is complementarity with corals confined to anthozoans. For example, environments with greater than 20% living coral cover are the least favorable reef habitats for cone snails (Kohn 1983) (although diversity of the general molluscan fauna of the Chagos Archipelago exactly parallels that of corals [Sheppard 1984]).

Many of Dinesen's (1983) kite diagrams appear to show, as she asserted, a rough inverse correlation between cover of soft and hard corals on indi-

vidual reefs, but others indicate a lack of correlation or a direct one. She contested claims of earlier workers that soft corals appear more tolerant than scleractinians of adverse conditions such as turbidity. An inverse correlation, however, implies that either 1) hard and soft corals do have complementary tolerances, or 2) if competition exists between them, in certain environments one is favored and in other environments the other is. In fact, Dinesen (page 235) also found "some similarities to the cross-shelf distributions of stony corals." These apparently contradictory interpretations of the same data may both be valid, since she made comparisons across two dimensions with considerably different scales. Her claims for complementarity are for depth on single reefs; the similarity with coral distribution emerged in cross-shelf comparisons, presumably at matched depths. A similar distinction was discussed by Done (1982) in reference to hard corals.

Clearly, anthozoans do not occupy the entire benthic environment in these habitats. Indeed, if they did, complementary distributions would be a tautology, since one group would necessarily diminish as another thrived. Cover of soft corals off Laing Island, Papua New Guinea, was claimed by Tursch & Tursch (1982) to be inversely proportional to hard coral cover. This is not true relative to the entire area (their figure 3). It is if only area covered by living organisms is considered (their figure 5), but in this case is tautologous, since members of the third category -- "others" -- are virtually absent in water shallower than 4 m. Reichelt et al. (1986) did line-transect surveys of the benthos on two of the reefs Dinesen (1983) studied. For each of the six environments on each reef, I compared the percentage cover of hard corals (their first eight categories) and soft ones (categories SC and GO). A slightly negative but insignificant rank correlation was obtained with both Kendall's and Spearman's non-parametric statistics. The negative correlations were considerably stronger, although still insignificant, based on percentage of live cover.

ECOLOGICAL EQUIVALENCE

EQUIVALENT ANTHOZOANS

The anthozoan species that are the subject of this paper play a similar role in their communities. Like all cnidarians, they are carnivorous, actively capturing prey through use of nematocysts. (Many harbor zooxanthellae, from which they obtain fixed carbon, but that is not an essential point of similarity; cf. also Coates & Jackson 1987). Central to the ecological equivalence of these animals is their ability to dominate significant amounts of benthic space through long periods (at least years). Nematocysts enable anthozoans of some species to defend space from both conspecifics and heterospecifics (e.g., Francis 1973, Hartog 1977, Chornesky 1983), but they are not essential to the similarity, either. Spatial dominance is related to sessility. Most of these equivalent animals are immovably fixed, although some actinians and alcyonaceans can creep, sea pens may drift (Birkeland 1974), and *Liponema* is able to roll (Dunn & Bakus 1977).

Space dominance is strongly tied to contiguosity of the modules (the polyps). This is typically achieved by means of asexual reproduction, resulting in clones or colonies, which also carries a genetic implication -- that large expanses may be covered by one or a few genotypes persisting far longer than the lifespan of a single module (Hughes & Jackson 1980). Thus, most solitary actinians (among them the majority studied by Sebens 1976) and ahermatypes are excluded from this category. Liponema is apparently exceptional in this regard -- disjunct individuals are densely distributed over considerable extents of bottom. It is remotely possible that they can reproduce through regeneration of tentacles, which are deciduous (Dunn & Bakus 1977). Moreover, some of the clownfish anemones are so large that an individual can occupy an area equal to that covered by many hundred scleractinian or zoanthid polyps (Dunn 1981). One species -- Heteractis magnifica -- is solitary in part of its range, and clonal elsewhere; in either form it can dominate significant areas of the benthos (Allen 1972; Dunn 1981).

The majority of solitary anthozoans, which includes cerianthids and most actinians, and colonial species that are never benthic dominants, are excluded from this assemblage. Sebens (1976, page 67) included actinians and corallimorpharians on shallow Panamanian reefs in "a guild of sessile carnivores." In fact, all cnidarians are carnivores, and nearly all polyps (the only body form of anthozoans) are sessile. Yet, I believe that even those living sympatrically do not, ipso facto, belong to a single guild, a term as coined by Root (1967, page 335) to mean "a group of species that exploit the same class of environmental resources in a similar way," including "all sympatric species involved in a competitive interaction, regardless of their taxonomic relationship." While, strictly speaking, it is true that all anthozoans have a common way of making a living -- a legacy of their common ancestry -- they are not all ecologically equivalent in many respects. Moreover, competition has been documented in few of the cases I have cited of species in sympatry, and the significance of these patterns extends to allopatric species.

Although they share some fundamental attributes, ecologically equivalent species differ among themselves in important ways. It is those dissimilarities -- mainly in terms of physiological tolerances -- that account for contrasts in distribution. This is most easily appreciated where the differences are greatest, as between conspicuously different environments on the global scale, e.g., shallow tropical seas and the cold-temperate littoral. But I believe it can be validly extended to the local level where they may minimize or preclude competition. Hermatypic corals have such narrow physiological tolerances, that even a slight alteration of physico-chemical parameters (such as bottom type or water clarity) will serve to favor anthozoans of another group over them, or vice versa. At a finer level of analysis, the distributions of corals are clearly correlated with what is known of the animals' physiological tolerances and of magnitude/variation in relevant physico-chemical factors (e.g., Pichon 1972; Loya 1976; Dittley 1978; Claereboudt & Bouillon 1987; Tomasotik & Sander 1987). I conclude that only at the finest level, where species with basically

similar physiologies coexist, does the opportunity for competition arise.

The major difference between corals and other anthozoans, of course, is the extent to which the former structure their environment. Even in this respect there is a spectrum, from framework-building scleractinians (as well as the hydrocoral Millepora and alcyonarians Tubipora and Helopora), through entirely soft-bodied forms. The skeletogenic alcyonarians that make important contributions to reef carbonate sediments but, with rare exceptions (e.g., Konishi 1981), not to the framework occupy an intermediate point. Thus, although the effect on the environment of their having lived differs among the groups, in life anthozoans are fundamentally ecological equivalents of one another in many important respects.

NON-EQUIVALENT ANTHOZOANS AND OTHERS

Comparisons can be made across taxa and time, as well as through space. Some shallow temperate and tropical environments, such as piers and pilings, support heavy growth of hydroids -- also sessile carnivores. These cnidarians impart a certain physical structure to their environments, providing habitats for many smaller organisms, especially crustaceans (e.g., Ricketts et al. 1985). They are not comparable to the anthozoan communities, however, in their ephemeral (commonly seasonal) nature. Their structural contribution of chitinous exoskeletons is also transient. Likewise bryozoans, some of which can be similar to dominant anthozoans in being able to monopolize space through over-growth and other competitive mechanisms, but which are mostly relatively delicate and often seasonal (Ryland 1979). They, like sponges, rarely dominate a zone or ecosystem. Barnacles and mussels predominate in certain zones of many temperate shores (Stephenson & Stephenson 1972). All of these filter-feeders provide some structure to their environments, but function very differently from the actively carnivorous anthozoans in their communities.

Contemporary bioherms other than those formed by cnidarians are of minor significance and generally short-lived (Heckel 1974). This has been true throughout the Cenozoic, as well as much of the Mesozoic (rudistids were important in the Cretaceous). Although some Paleozoic bioherms were dominated (at different times and in different places) by stromatoporoids, sponges, echinoderms, bryozoans, and molluscs, those formed by cnidarians (rugose and tabulate corals) were also significant (Heckel 1974). It appears likely, given the similarity of ecological roles among the contemporary anthozoans discussed here, that early in their history, some cnidarians -- reef corals and soft-bodied, space-dominating, reefal and non-reefal anthozoans -- assumed a role not unlike that of modern reef corals.

PATTERNS AND PROCESSES

There are three possible patterns in relative abundance of any two organisms. Their abundance may vary together, which implies that they have similar ecological requirements, so that conditions under which one thrives favor the other as

well. There may be no systematic correlation between the two when they are seemingly responding independently to different aspects of the environment. Finally, an inverse relationship may exist between them. I have cited above quantitative studies that provide examples of anthozoans illustrating each.

The pattern exhibited by two ecologically equivalent groups can differ with scale. On a global scale, hard and soft corals show similar patterns -- both have relatively few, mostly ecologically insignificant species in temperate areas, whereas many species of both taxa occupy large areas in the shallow tropics. Clearly these groups have broadly similar needs and physiological tolerances, doing well in the tropics, poorly outside. Differences, however, are evident on a finer scale. Considering only the tropics, soft corals are relatively more conspicuous and diverse in the Caribbean than in the Indo-Pacific (e.g., Kuhlmann 1984). Complementarity is in even greater evidence at a local scale, especially with depth (e.g., Fishelson 1970; Dinesen 1983).

Complementarity is the pattern most frequently documented in the literature, often as evidence of competitive exclusion. Alternatively, the cause may be purely physico-chemical, with different taxa having diametrically opposite requirements, or, at least, one being tolerant to conditions in which the other does poorly or cannot survive. The physiological tolerances of *Anthopleura elegantissima* and *Acropora palmata* are so different that it is highly unlikely that the former could survive in the shallow Caribbean, and it is certain that the latter could not live in the rocky intertidal of the northeast Pacific. Clearly, the physiological tolerances of these ecologically equivalent animals determine their ranges, an extreme example of mutually exclusive distributions that have nothing to do with competition. A real-life example of this is the common explanation for different dominant anthozoans on Indo-Pacific and Caribbean coral reefs -- an historical one (Glynn 1973; Milliman 1973).

Impressionistic and even quantitative correlational data do not reveal causes. Assessing the relative importance of factors governing distribution and abundance blur most when considering species of similar tolerances, which, even when sympatric, may have disparate sensitivities to facets of their environment. Competition can exist between hard and soft corals (e.g., Sammarco et al. 1983). The lack of correlation I found between those two groups in published studies by Dinesen (1983) and Reichelt et al. (1986) suggest that animals of the two groups are responding to different factors in the environment, or to the same factor(s) in different ways. I conclude that competition is important only at the ultra-local scale (Buddemeier & Hopley this symposium) -- the level of the individual colony -- and has minimal influence on the larger scale patterns with which this paper is concerned. Although *Zoanthus* is competitively inferior to corals, it is the most abundant benthic organism on the east back reef of Discovery Bay, Jamaica, because of its ability to survive periodic disturbance and/or recolonize surfaces thereby exposed (Karlson 1980). In this case, too, the issue of competition seems of more theoretical than practical significance, and

physical forces dominate. It is possible that pre-emptive competition, which differs from interference competition (e.g., Underwood & Denley 1984), may be important in some instances. For example, Fishelson (1970) speculated that actinians carpeting large expanses of shallow substratum in the Red Sea prevent coral settlement.

The patterns that are the subject of this paper are generally too large in scale to be amenable to experimental manipulation. However, there are an increasing number of reports on degradation in coral reefs, due to human or other activity, that constitute inadvertent experiments. Least useful in addressing the issue of critical environmental factors are those that document only hard coral disappearance, omitting mention of what, if anything, replaces it (e.g., Dustan & Halas 1987, concerning Key Largo, Florida). Reef corals in Kaneohe Bay, Hawaii, deteriorated as a result of environmental stress in the form of sewage and terrigenous run-off, and were replaced by zoanthids (Cooke 1976; Smith et al. 1982). This rare small-scale experiment provides evidence of what is obvious on the global scale -- that physico-chemical factors are very important in governing which species of anthozoans dominate, or even survive. That predictability of coral reef communities increases with spatial scale (Green et al. 1987) is a reflection of distribution of this group of equivalent anthozoans being controlled by physico-chemical rather than biotic factors. The lack of predictability at the smallest scale, I conclude, is because 1) that is the level at which biotic interactions can have an effect, and 2) small perturbations in the physico-chemical environment that shift the balance subtly, favoring one taxon over another, are the least quantifiable and even identifiable.

ACKNOWLEDGMENTS

I thank C. Birkeland, R.W. Buddemeier, R.J. Cuffey, S.V. Smith, and an anonymous reviewer for their critical reading and suggestions that improved this paper.

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