

Geographic Comparisons of Coral-Reef Community Processes

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ABSTRACT

Differences among geographic regions in terms of the structure and functions of coral-reef communities appear to be influenced greatly by nutrient input. Upwelling is prevalent on the western coasts of continents, major river drainage is prevalent on the eastern coasts of continents, and oceanic regions tend to be oligotrophic. Animal-plant symbionts are predominant in areas of low nutrient input where recycling of nutrients is strongly favored. At intermediate levels of nutrient input, algae respond more promptly than corals to nutrient pulses and can overgrow juvenile corals unless grazed back by herbivores. At very high levels of nutrient input, phytoplankton appear to preempt light and nutrients and raise the compensation depth of benthic algae; the phytoplankton-based foodweb replaces the benthic alga-based foodweb. Success of recruitment for species with planktotrophic larvae is occasionally facilitated by a nutrient pulse, after which increased recruitment brings about more intense competition and grazing pressure because of greater population densities.

Important factors other than nutrient input are areal extent and historical chance. The large area of the western and central Pacific makes it more modular in terms of disease and population outbreaks, and less homogeneous in species composition than is the western Atlantic. There is a decrease from west to east across the Pacific in both species numbers and non-coral habitats. An apparent lesser degree of trophic and population interconnections between coastal habitats in the Pacific may partially result from less reliable availability of non-coral habitats in Oceania. Historical chance produces particular species characteristic of one region, such as *Acanthaster planci*, *Diadema antillarum*, and *Eucidaris thouarsii*, each of which have a major role in determining community processes unique to the region. Differences in coral-reef community structure and ecological processes among geographic regions are important to take into account in the management of coral-reef resources.

INTRODUCTION

In attempting to organize a comparison among the tropical oceans, we should first examine the geographic regions within oceans. These regions (eastern continental shelf, oceanic, western continental shelf) differ in fundamental ways, and comparable regions have similarities between the Atlantic and the Pacific. A detailed presentation of the ecological differences between geographic regions of the tropical seas requires more space than the 10 pages allotted here. However, a large number of disparate local studies and observations can be conveniently summarized on a conceptual framework of nutrient availability. The hypothesis being presented is that nutrient availability affects community structure. Although this framework appears consistent with the information available at this time, it is hypothetical, based only on observation and deduction. Although all aspects need to be tested, the framework hypothesis of nutrient availability should provide a point of reference for deciding which are the important concepts to test.

We will begin with an analogy to terrestrial interregional differences. A first approximation to the general distribution of terrestrial biomes can be understood by the global atmospheric circulation of moisture. Major patterns of global circulation of atmospheric moisture are created in part by the heating of air in equatorial regions in combination with the Coriolis effect. Availability of water can strongly influence the life-forms of terrestrial communities. Deserts tend to be found at about 30°N and 30°S of the equator on the western sides of continents; temperate rainforests tend to be found about 50°N or S. As a starting point for comparisons of coral communities of different geographic divisions of the tropical oceans, we take nutrients as the analog of moisture. Major patterns in the global circulation of nutrients in tropical seas might follow a pattern brought about in part by the solar heating of the shallow waters and by the Coriolis effect. Differences among geographic regions in life-forms and trophic characteristics of the coral-reef communities might be influenced by the degree of nutrient input.

The surface waters of the tropical oceans are relatively uniformly heated throughout the year and are generally thermally stratified. Although the tropical seas cover a large area of the globe, they occupy a thin veneer over a tremendously greater volume of cold waters which lie beneath the photic zone. Nutrients are relatively dilute in the surface layers of the tropical seas, with greater concentrations found in the deeper waters beneath the photic zone in pelagic regions. A relatively high concentration of nutrients may also be bound into the biomass in shallow areas which encompass coral reef communities. This model is vulnerable to disproof in a straightforward manner if false.

The Coriolis effect might influence the distribution of nutrients on a geographic scale, bringing about major inputs of nutrients upward from below the photic zone in the eastern sides of the oceans and major inputs downward off the land masses in the western sides. The tradewinds push ocean waters away from shore and cause upwellings to be more prevalent on the western coasts of continents. Moisture-laden air from the tropical seas impinges on the eastern coasts of continents, causing rainfall, and therefore discharge from major rivers, to be more prevalent on the eastern coasts of continents. Nearly 70% of all the sediment that drains into the oceans of the world drains off the “continental” coasts of the tropical western Pacific (S.E. Asia, Indonesia, Philippines, New Guinea) and tropical western Atlantic; only 2% drains into the tropical eastern boundaries of the Pacific and Atlantic (Milliman & Meade 1983). Oligotrophic

waters are characteristic of oceanic regions far from continental shelves.

If nutrients are generally not abundantly available in shallow tropical ocean waters and are found in far greater concentrations below the photic zone, and if nutrients have a controlling influence on community structure and function, then concentrations of nutrient input in time and space (“nutrient pulses”) could have profound effects on shallow tropical marine communities. As a general indication of the degree of influence of upwelling of nutrient-rich waters, Ryther (1969) calculated that upwelling regions are found in less than one-tenth of one percent of the world ocean surface, yet these regions supply over half the world fishery, a 500-fold inconsistency. In separately labelled sections below, I will present observations that suggest that nutrient input has a controlling effect on regional differences in trophic structure, rates of recruitment, intensity of grazing and competition, and life-history characteristics of the predominant macrofauna.

TROPHIC STRUCTURE OF COMMUNITIES ALONG A NUTRIENT-SUPPLY GRADIENT

The tropical marine region with the lowest phytoplankton production is the central oceanic Pacific (Koblentz-Mishke et al. 1970). If most of the nutrients associated with coral reefs in oligotrophic situations are temporarily bound in the biomass at any one time, and if nutrients are in short supply (neither assumption has been adequately substantiated), then organisms which recycle nutrients would be favored. Open-coast coral reefs (not enclosed harbors or lagoons) in Oceania (Micronesia, tropical Polynesia, and eastern Melanesia) are dominated by animal/plant symbionts from several phyla: hermatypic corals, alcyonaceans, tridacnid bivalves, cyanobacteria-associated sponges, *Prochloron*-associated ascidians, and others. *Prochloron*-associated ascidians “could make a major contribution to the productivity, especially in localized areas of tropical marine waters characterized by low nutrient levels and high irradiance” (Lewin et al. 1983:165). Species of *Tridacna* are favored in clear water. “*T. derasa* is restricted to oceanic environments and it is not found on fringing reefs adjacent to large land masses” (Munro & Heslinga 1983:123). Wilkinson (1986) showed that the proportion of sponges that were heterotrophic was greatest on inner shelf reefs of the Great Barrier Reef (GBR) while sponges associated with cyanobacteria became more prevalent on outer shelf reefs of the GBR.

Heterotrophic suspension-feeders that actively create water movements may be sometimes using more energy than they are acquiring when in oligotrophic waters. *Mytilus edulis* uses twice as much energy when ventilating for feeding than when not feeding (Bayne et al. 1976). G.J. Vermeij (pers. comm.) suggests that the suspension-feeding bivalves decrease in species-specific size and in numbers of species more than do animal-plant symbionts along a west-east gradient across the Pacific. He relates it to the decrease of food in the water column having a greater effect on the suspension-feeders than on the phototrophs.

In areas influenced by large land masses (the Caribbean, the continental shelf reefs of Southeast Asia, Indonesia, Philippines, and Papua New Guinea), benthic algae become dominant, presumably because of increased nutrient input by a variety of mechanisms. Nutrient input and eutrophication can stimulate the growth of benthic algae and increase rates of primary productivity (Kinsey & Domm 1974; Kinsey & Davies 1979). Human activities that

further increase nutrient input, such as land-clearing or sewage output, are associated with increases in algal biomass and sometimes decreases in coral biomass (Fishelson 1973; Banner 1974; Smith et al. 1981). Corals and other plant/animal symbionts are still prevalent, although relatively rapidly growing filamentous and fleshy algae inhibit recruitment of coral larvae by forming sediment traps among their bases (Birkeland 1977). The survival of coral recruits and thereby the abundance of corals near land masses is facilitated by the grazing of algae by herbivores (Dart 1972; Birkeland 1977; Sammarco 1980).

In regions in which even greater amounts of nutrient input occur, e.g., in regions of upwelling (Birkeland 1977), near large rivers (Collette & Rutzler 1977; Tsuchiya et al. 1986), or in lagoons of high islands (even in Oceania) subjected to heavy rainfall and terrestrial runoff, heterotrophic suspension-feeders such as boring bivalves (Highsmith 1980a), massive sponges (Wilkinson 1986), boring sponges, ascidians without symbiotic prokaryotes, and crinoids become more prevalent. With increased nutrient input, there can be more food for suspension-feeders in the form of particulate organic matter, bacteria, phytoplankton and zooplankton in the water column (Smith et al. 1981). Since most phytoplankters are single-celled plants, they have relatively large surface-to-volume ratios and can efficiently absorb nutrients. They are thereby often capable of reacting rapidly to a sudden input of nutrients. Phytoplankton blooms are often associated with input of nutrients (Salim 1960; Anderson 1964; Marsh 1977).

In conditions of very high nutrient input and low rates of flushing, the phytoplankton-based food-web appears to replace the benthic alga-based food-web. It has been calculated that if phytoplankton reaches a density of 2 g m^{-3} , a compensation depth originally at 100 m depth would be moved to 3.5 m depth (Ryther 1963). In effect, the benthic algal community and the food-web it supports would be eliminated below 3.5 m. (Phytoplankton could also reduce the amount of nutrients in the water column available to the benthic algae.) In coral communities in the northern Gulf of Thailand, with large amounts of river drainage and terrestrial runoff, fleshy and filamentous benthic algae were very sparse below 4 m depth (Kamura & Choonhabandit 1986; Tsuchiya et al. 1986). Schooling herbivorous fishes (scarids, acanthurids, siganids, kyphosids) were completely absent despite the adequacy of the habitat for other fishes, as evidenced by the presence of at least 31 other families of coral reef fishes amounting to 832 kg ha^{-1} (Menasveta et al. 1986). Herbivorous damselfishes were present, but they maintained their territories at shallow depths of 3-4 m. Although the scleractinian community consisted of 85 hermatypic species (21 of which were acroporids), heterotrophic suspension-feeders (bivalves, barnacles, massive sponges) were also predominant (Tsuchiya & Lirdwitayapaisit 1986; Tsuchiya et al. 1986). Planktivorous fishes were prevalent in the reef-fish community.

This geographic pattern in trophic structure of coral communities along a gradient of nutrient input is found on a smaller scale within regions influenced by nutrient input and residence time of water. The Gulf of Chiriqui, unlike the adjacent Gulf of Panama, does not have upwelling, and corals are predominant (Glynn et al. 1972). Heterotrophic sponges, bivalves, and ascidians are predominant even in Oceania in situations in which an enclosed lagoon or harbor is next to a high island (e.g., the lagoons of Pohnpei and Truk in the Carolines, Apra Harbor at Guam). This nutrient input/trophic structure gradient is found at other ecological scales of reference. C.R. Wilkinson & A.C. Cheshire will discuss cross-shelf gradients in this symposium.

A change in rate of nutrient input over time can also bring about a change in trophic structure of a benthic community at one location. A population of heterotrophic sponges increased 5-fold in biomass when a sewage outfall commenced operation off Grand Cayman Island in the Caribbean (Rose & Risk 1985). When the sewage outfall was diverted from Kaneohe Bay, Oahu, Hawaii, the amount of particulate carbon in the water column, and the density of phytoplankton, zooplankton, and heterotrophic suspension-feeders all decreased (Smith et al. 1981). Before the sewage diversion, over half of the total benthic biomass of the bay was in the southeastern quarter of the bay near the sewage outfall. This rich benthos was composed predominantly of heterotrophic suspension-feeders: conspicuous sponges, tunicates, polychaetes, barnacles and molluscs (Smith et al. 1981). Upon diversion of sewage, the mainly heterotrophic total biomass in the southeastern sector decreased from 505 to 145 metric tons and the benthic community began to revert to a more typical phototrophic coral-reef community (Smith et al. 1981).

Productivity can be high and sustain large amounts of biomass in coral reefs in oligotrophic regions because A) the primary producers are fixed relative to the advection of nutrients in the waters over them and because B) the nutrients taken up from the water are recycled at several levels. Scales at which recycling takes place include: 1) microbiological, 2) physiological (between animal and plant tissues of symbionts), 3) between trophic levels (e.g., the demersal plankton is largely supported by the detrital food-web, coral mucus is consumed by animals at several levels in the food-web, fish-feces can be recycled in the diets of fishes up to five times before coming to rest), 4) hydrodynamic (by eddies, gyres, increased residence time of water in lagoons and other enclosed coastal features), and 5) through retention of organic detritus and plankton by current-producing suspension-feeders such as sponges and by motile demersal plankton, planktivorous fishes and invertebrates.

The proportion of organic material that is exported from coral reefs in oligotrophic regions is less than the proportion of production exported from “mesotrophic” seagrass beds (Wiebe 1987) or from “planktotrophic” communities in regions of upwelling (Ryther 1969). Geographic variation in the relative proportions of benthic algal production that go directly to the herbivore and detrital food-webs may also result from geographic differences among coral reef communities in the relative influence of herbivorous fishes and echinoids (cf. section on Faunal Differences).

DENSITIES OF RECRUITMENT

Disparate observations of differences in densities of recruitment of animals with planktotrophic larvae between years of large and small amounts of river discharge or rainfall, and between areas with or without upwelling, suggest that survival of planktotrophic larvae may be related to nutrient input. Space on the upper surfaces of fouling panels was occupied by macroorganisms 3 to 6 times faster in an area of upwelling on the Pacific coast of Panama than on the Caribbean coast of Panama (Meyer & Birkeland 1974). Major population increases of certain species with planktotrophic larvae have been significantly associated with river discharge (Aleem 1972; Sutcliffe 1972,1973) or rainfall (Chidambaram & Menon 1945; Ben-Tuvia 1960; Birkeland 1982), suggesting an input of nutrients from terrestrial runoff may have been influential. The density of barnacle settlement on the coast of England has been observed

to increase with phytoplankton density (Barnes 1956) and the density of barnacle larvae in Kaneohe Bay decreased greatly when sewage input (presumably with nutrient input) was diverted (Smith et al. 1981).

If larval survival and recruitment were more successful in nutrient-rich water columns, then one would expect to find large numbers of individuals towards the younger end of the age distributions to be characteristics of nutrient-rich areas. Thresher (1987) observed that the ratio of juvenile to adult resident damselfishes was greatest in the nutrient-rich waters of the eastern Pacific, intermediate in the Caribbean, and least of all in the Indo-West Pacific. This decreasing gradient of recruitment to adult standing stock corresponds to a decreasing gradient of productivity in the water column (Koblentz-Mishke et al. 1970). This is consistent with the hypothesis that productivity in the water column favors larval survival, but of course there are numerous possible alternative explanations. Nevertheless, Thresher's observations could have important implications and they should be followed with further field studies.

INFLUENCE OF RECRUITMENT ON GRAZING PRESSURE

Increased rates of successful recruitment could contribute to greater standing stocks of reef fishes. Population densities of fishes which graze benthic organisms appear to be 5 to 20 times greater on the Pacific coast of Panama than densities of fishes of the same or comparable genera on the Caribbean coast of Panama (Glynn et al. 1978; Birkeland 1987). Grazing pressure on the benthos by fishes has been observed to be greater on the Pacific coast of Panama than in the Caribbean (Birkeland 1971, 1977, 1987; Glynn 1972; Earle 1972; Vermeij 1978; Hay & Gaines 1984).

The grazing pressures on sponges by fishes appear to differ between the Pacific and Caribbean coasts of Panama to a greater extent than can be explained by the differences in the abundances of grazing fishes alone (Birkeland 1987). Behavioral changes in foraging with increased population density may compound the grazing pressure. *Holocanthus passer* on the Pacific coast usually forages in large schools while *Holocanthus app.* in the Caribbean are usually found alone or in pairs. Schooling behavior should increase foraging efficiency (Pitcher & Magurran 1983). Field experiments have shown that the scarcity of large sponges in eastern Pacific coral communities is undoubtedly because of grazing and not because of the physical environment or availability of reproductive propagules (Birkeland 1987). Sponges and other suspension-feeders actually appear to grow faster in the eastern Pacific, but they rarely reach a large size in locations exposed to grazing by fishes. As prey become scarce beyond a lower threshold, the predator will have to generalize its diet (Ivlev 1961; Werner & Hall 1974). If a number of the more abundant species become generalized in diet, the schools of abundant generalist grazers would be more likely to indiscriminantly graze small organisms before the prey reached a size at which their defensive mechanisms become effective.

INFLUENCE OF RECRUITMENT ON INTENSITY OF COMPETITION

Despite the greater grazing pressure on the Pacific coast of Panama than on the Caribbean coast, the accumulation of biomass was also greater (Birkeland 1977). The greater rate of occupation of space on the fouling panels on the Pacific coast was partially a result of greater

rates of recruitment (Meyer & Birkeland 1974). The greater rates of biomass accumulation by the fouling communities was probably also a result of greater rates of recruitment combined with greater rates of growth. The biomass accumulated over 77 days by the heterotrophic fouling communities in a region of upwelling on the Pacific coast of Panama was 6 times the biomass of phototrophic communities on the Caribbean coast and 12 times the biomass of phototrophic communities at small islands 6 to 14 km off the Caribbean coast (Birkeland 1977). The fouling panels were on the exposed coasts of both the eastern Pacific and the Caribbean, not in protected backwater lagoons or harbors.

The competition for space on initially bare substrata is apparently more intense in areas of high rates of nutrient input. In the oceanic western Pacific, recruitment of corals to bare substrata appears to be limited at least partially by the availability of planulae in the water column (Birkeland et al. 1982; Wallace 1985). In the Caribbean, algae quickly dominate bare substrata and coral recruitment is facilitated by the grazing of algae by herbivores (Birkeland 1977; Sammarco 1982). In regions influenced by upwelling, heterotrophic suspension-feeders dominate the substrata below about 5 or 8 m depth and there is very little coral recruitment by larvae (Birkeland 1977; Richmond 1985, 1987).

The success of larval recruitment of scleractinians is inversely related to rate of nutrient input and inversely related to the success of planktotrophic larvae. Both planktotrophic larvae and benthic suspension-feeders are possibly positively influenced by food supply in the water column. Planula larvae contain large amounts of lipids, and even zooxanthellae (Richmond 1987), and so are probably less dependent upon food-supply in the water column, and after settlement will actually do better in low nutrient environments because of less competition for space. The predominance of animal/plant symbionts (mainly corals), benthic algae, or heterotrophic suspension-feeders in the early stages of occupation of bare substrata is presumably a major factor in the determination of the characteristics of the surrounding community.

LIFE-HISTORY CHARACTERISTICS OF PREDOMINANT SPECIES

Observations of fouling communities suggest that filamentous algae, fleshy algae, and many small suspension-feeding animals, such as barnacles and bivalves, are able to respond relatively directly (with accelerated growth) to increased inputs of nutrients, suspended organic matter, or plankton. Competition for space and grazing pressure both increase under conditions of high nutrient input (Birkeland 1977, 1987). Observations also suggest that, for unknown reasons, animal/plant symbionts apparently do not accelerate growth as rapidly or to the degree that small upright algae and heterotrophic suspension-feeders are able. Animal/plant symbionts are typically adapted to low nutrient conditions (Muscatine & Porter 1977). Once a coral colony reaches adequate size, its position is relatively secure. However, when a strong pulse of nutrients occurs, a recently settled coral has little chance of surviving the rapid takeover of space by heterotrophic suspension-feeders and algae (Birkeland 1977).

Reaching a refuge in a size, that is, a large enough size for defensive mechanisms to become effective, becomes less probable as nutrient input increases. As grazing intensity increases, algae with chemical or structural defenses against herbivory are incidentally grazed before they reach a recognizable threshold in size. This may apply to corals as well (Sammarco 1980,

1985). Intense grazing by generalists (characteristic of areas of high nutrient input) sets back succession, while grazing by specialists facilitates succession (Birkeland et al. 1985).

The hypothesis presented here is that the average time available to reach a refuge in size from competition or from grazing decreases along a gradient of increasing nutrient supply. A problem with testing this in the field is that there are many uncontrolled variables involved when comparing different species in different areas. The necessary program for testing the hypothesis may involve observing the outcome of raising a selected set of corals, algae, bivalves, sponges and grazing fishes under controlled nutrient-supply treatments in large aquaria.

RESPONSES TO SEA-LEVEL CHANGES

It has been predicted that there will be a rise in sea level over the next century. A number of factors are potentially involved in determining the responses of coral reefs to the increasing rate of sea level rise. Two of the possible geographic differences in responses are influenced by relative rates of nutrient input.

Hallock & Schlager (1986) found evidence in the geological record that "drowned reefs" and carbonate platforms do not keep up with rises in sea level during periods of excess nutrient input. They proposed that increased nutrient input stimulates phytoplankton growth and thereby reduces water transparency, and increases competition for space and bioerosion by heterotrophs. This is consistent with the geographic variation in trophic structure of coral reefs (Birkeland 1987) and with the sequence of events in Kaneohe Bay (Smith et al. 1981). This suggests that reefs in Oceania should be expected to respond more favorably to a rise in sea level than reefs on continental coasts, other factors held constant. The geographic patterns of abundances of echinoids and of *Acanthaster planci* also suggest that reefs in Oceania may be expected to respond more favorably to a rising sea level, perhaps indirectly as a result of low levels of recruitment of echinoderm larvae being associated with low levels of nutrients. Grazing by echinoids is one of the factors determining whether a reef is accreting or eroding. This factor varies geographically and with time. Grazing by *Eucidaris thouarsii* was sufficient to limit reef growth in the Galapagos prior to the El Niño of 1982-1983 (Glynn & Wellington 1983), after which there has been a net bioerosion of the Galapagos reefs (P.W. Glynn pers. comm.). When abundant, diadematids are considered inimical to coral recruitment (Sammarco 1980), while schooling herbivorous fishes, which are predominant in the oceanic Pacific, are often beneficial (Birkeland 1977). Diadematids are more prevalent in the western Atlantic and continental-shelf Pacific than in Oceania. Likewise, outbreaks of *Acanthaster planci* and *Echinometra mathaei* occur on continental margins or on high islands. Because of these possible effects of terrestrial runoff on increased productivity in the water column and on outbreaks of echinoderms, the ability of a coral-reef system to respond to a rise in sea level by increased rate of accretion will probably vary geographically, with oceanic atolls having the lower rate of bioerosion and predation on corals.

FAUNAL DIFFERENCES

Diadematid echinoid populations may be an order of magnitude more dense in the Caribbean

and in continental shelf regions of the western Pacific than in Oceania (Sammarco 1985; Birkeland 1985, 1988). In view of the fact that diadematids have planktotrophic larvae, one might hypothesize that the geographic pattern may result in part from relative rates of nutrient input and associated success of larval recruitment (Birkeland 1988). Within the Caribbean, *Diadema antillarum* populations are an additional order of magnitude more dense on coral reefs which have been heavily fished (Hay 1984). This may result from reduced predation pressure from balistid fishes and reduced competition from herbivorous fishes which have been removed by overfishing (Hay 1984). In contrast to the Caribbean, diadematids are not considered to have a major influence at One Tree Island on the Great Barrier Reef. Echinoids are generally disregarded, presumably because of their scarcity, while herbivorous fishes and some invertebrates are considered influential (Hatcher 1982).

The foraging styles of particular species may have profound effects on differences in the trophic patterns of coral-reef communities. Although it is dangerous to generalize from only two studies, works by Carpenter and Hatcher may be providing important clues for patterns that warrant further research. An annual average of 97% of the shallow water benthic algal production entered the animal community by herbivory in the Caribbean (Carpenter 1986), while an annual average of 20 to 70% of the algal production entered the animal community by herbivory in 7 habitats across a reef on the Great Barrier Reef (Hatcher 1982). This may be because *Diadema antillarum* is the herbivore with the major impact in the areas studied by Carpenter, and herbivorous fishes had the greatest influence in Hatcher's study. *D. antillarum* has a relatively limited foraging range (Carpenter 1984) as compared to herbivorous fishes, and when populations are dense, *D. antillarum* graze the substratum in a relatively generalized manner, removing much of the algal biomass. Schooling herbivorous fishes are relatively motile, can forage over larger ranges than can echinoids on a daily basis, and so they can feed more selectively (Carpenter 1984). Selective feeding by herbivorous fishes, even though intense, facilitates succession (Birkeland et al. 1985). This produces a standing stock of morphologically tough or chemically defended algae that is not directly consumed by herbivores.

Although we may have the goal of establishing a deterministic theory of community structure, interoceanic comparisons show us that individual species, whose presence may be a result of historical chance in evolution, can have a profound effect on community structure. Outbreaks of corallivorous gastropods (*Drupella* spp.) occur in the western Pacific, but major outbreaks on such an influential scale of counterparts are unknown for the Atlantic. The thin and ephemeral sponge (*Terpios* sp.), containing blue-green algae in its tissues, can overgrow and kill large areas of corals in the western Pacific (Bryan 1973). Sponges overgrow corals in the Atlantic, but Atlantic species of sponges are relatively sedentary.

Major interoceanic differences in community structure and function can be attributed to the presence of particular species. Often species in one ocean have no counterpart in the other. For example, Vermeij (1987) listed a variety of taxa that contained species of corallivores in the Pacific, but did not have corallivores in the Atlantic. *Acanthaster planci* is one of 9 or 10 species of Pacific asteroids that include coral tissue or coral mucus in their diets (Birkeland 1988). No Atlantic asteroids feed on reef-building corals to any influential degree. The impact of predation by *A. planci* on coral-reef communities during high levels of population density can have a substantial effect on the coral reef community through several trophic levels and across hectares of area. It can alter the size distributions and relative abundances of coral

species, facilitate the increase in abundances of algae, alcyonaceans, and sponges, decrease the abundances of corallivorous fishes, and increase the abundances of herbivorous fishes. All these things happen more drastically in the Indo-Pacific than in the Caribbean because *A. plani* is in the species pool.

INTERCONNECTIONS BETWEEN COASTAL HABITATS

Coral-reef communities appear to have more trophic interactions and population interconnections with seagrass and mangrove habitats in the Caribbean than in the Pacific (Ogden & Gladfelter 1983; Birkeland 1985). Although fishes in the Pacific do move between habitats to feed, there appears to be less influence of neighboring habitats on fish community structure in the Pacific (Birkeland and Amesbury 1988) than in the Caribbean (Ogden and Zieman 1977). This is consistent with the conclusions of Sale (1980) who found between-habitat diversity to be considerably higher in the Central Pacific, while within-habitat diversity did not differ as much. A higher between-habitat diversity with a uniform within-habitat diversity indicates a lower portion of the species being found together in the same habitat.

The smaller areal extent and interconnection by water currents of the Caribbean (Wust 1964) lead to a more homogeneous distribution of marine species and coastal habitats than in the Pacific. Fish communities may overlap less in the central Pacific because the frequency and reliability of encountering mangroves and seagrasses become less from west to east across the Pacific. Coral-reef fishes in the central Pacific may be less well adapted to movements between habitats as they pass through their life-history stages because other habitats are available less consistently than they are in the Caribbean.

REPRODUCTION

Thresher (1982, 1987) documented differences in the reproductive biology (egg size, early life history, reproductive morphology and physiology, social behavior) of confamilial fishes from different geographic regions. Some western Pacific demersal-spawning fishes produce eggs with an average volume of up to nearly an order of magnitude larger than their western Atlantic confamilials (Thresher 1982). Thresher (1987) observed that the geographical variation in egg size of confamilial demersal-spawning reef fishes appeared to vary inversely with primary productivity in the water column. Small egg volume correlates with 1) small size of larvae at hatching, 2) a narrower range of prey sizes that can be taken at first feeding, 3) a shorter time to irreversible starvation if acceptable food is not found, and 4) an increased duration of larval period (Thresher 1987). Thus, Thresher (1987) suggested that selection for more numerous smaller eggs occurred in regions where the microzooplanktonic prey were either more abundant or more predictable in occurrence. In this regard, Thresher's (1982) data on egg sizes generally fit the pattern of primary productivity (Koblentz-Mishke et al. 1970).

The reproductive biology of scleractinians also varies geographically, whether considered in terms of the coral community or individual species (Richmond 1987). Scleractinians experience mass spawnings on the Great Barrier Reef, but tend to spawn at different times in the Red Sea (Harrison et al. 1984; Shlesinger & Loya 1985; Willis et al. 1985). Richmond (1985, 1987)

documented that *Pocillopora damicornis* reproduces asexually by fragmentation or by “polyp bail-out” in the eastern Pacific and mainly by sexual reproduction in Oceania. Likewise, Sammarco (1987) noted that *Acropora* spp. in the Caribbean reproduce mainly by fragmentation and on the Great Barrier Reef mainly by planulation. Highsmith (1980a, 1980b, 1982) reported that even colonies of massive species are replicated by fragmentation, especially in areas of high productivity where bioerosion and predation are more intense.

Wallace (1985) found that acroporid coral recruits grow much more slowly than was previously reported in the literature. The first two or three years after settlement are especially hazardous for corals in regions of high nutrient input, but less so in oligotrophic regions where larval abundance, rather than competition for space, may be relatively important in determining the abundance of recently settled corals (Birkeland 1977; Birkeland et al. 1982; Wallace 1985). Reattachment of broken branches is a possible mechanism for proliferation with an immediate refuge in size, and fragmentation appears more prevalent in nutrient-rich environments. Richmond (pers. comm.) is finding that some of the geographic differences in the reproductive biology of *Pocillopora damicornis* has a genetic basis. However, since bioerosion and predation increase with nutrient input, some of these geographic differences in prevalence of asexual reproduction, especially for massive species, may result directly from environmental interactions.

INTEROCEANIC COMPARISONS OF THE EVOLUTIONARY PROCESSES

Two concepts of geographic differences in intensities of evolutionary processes have been presented, one by G.J. Vermeij and another by D.C. Potts. Vermeij (1978) compiled evidence that indicated an escalation of adaptive traits between predators and prey and between competitors. The escalation was greatest in the Indo-West-Pacific, intermediate in the eastern Pacific, and least in the tropical Atlantic. Vermeij (1987) further documented that escalation is stimulated by high rates of productivity of the community. His studies indicate that geographic differences in rates of nutrient input can lead to geographic differences in intensity of evolutionary processes.

Potts (1983, 1984) noted that the scleractinian fauna of the Indo-Pacific is largely homogeneous, with relatively few endemic species, and with the component species having a high level of intraspecific variability. He deduced that frequent changes in sea level during Pliocene-Quaternary glaciations maximized intraspecific variation, but disrupted the evolutionary processes from approaching completion (speciation or extinction) for scleractinians. He also suggested that although speciation was inhibited in scleractinians because of the frequency of sea-level changes in relation to generation times of corals, these same environmental fluctuations might have accelerated speciation in organisms with much shorter generation times.

A major contrast between the Caribbean and the Indo-West Pacific systems was proposed to be in their resilience. Potts (1986) described the Indo-West Pacific as a “globally robust and resilient mosaic of regional and local, oceanic and shelf, systems, linked by long-distance dispersal, but buffered by substantial spatial barriers” and the Caribbean as a system that “behaves locally, regionally and globally as a single system with few barriers to dispersal and little buffering from biological or physical disturbance”. In support of this generalization, it

might be noted that the diadematid disease of 1981 in the Pacific was apparently contained within the Hawaiian Islands (Birkeland 1988), while the diadematid disease of 1983 spread throughout the western Atlantic from Panama to Bermuda in about one year (Lessios et al. 1984). Incidents of coral bleaching or diseases of sponges have occurred over large areas of the Caribbean. Outbreaks of *Acanthaster planci* are generally restricted to individual provinces within the Indo-Pacific (e.g., the Great Barrier Reef, the Ryukyus, Samoa, Hawaii).

Whereas the size of the Pacific Basin may have provided some buffer to the temperature changes from Pleistocene glaciations, this very size may be a factor in allowing a build-up of a larger pressure differential along the equator, leading to an El Nino Southern Oscillation with greater disruptive influences than anything comparable in the Caribbean.

WHY EXAMINE GEOGRAPHIC DIFFERENCES?

Some feel that it is not useful to examine patterns over a geographic scale because the processes involved occur on a local scale. Upwellings and rivers occur in each geographic region, they are merely more predominant in some. Furthermore, it is difficult to make valid comparative studies between geographic regions because habitats may not be strictly comparable. Most importantly, it is argued that we must develop our understanding of the factors that control variance at the within-reef level before can properly examine variance at the geographic level. The within-reef factors are complex enough that we may never reach the stage at which it will be valid to examine reefs from a larger perspective. The effects of local factors are more spectacular because they are often visible first-hand. Geographic patterns might not be so obvious. In our beginning analogy, the tendency for deserts to be on the west sides of continents around 30° latitude is not so visible as the rainshadows in the lee of some high islands. Likewise, the differences between coral-reef communities in the lagoon and on the seaward slope of an oceanic high island may be more obvious than the differences between the coral-reef communities on the seaward slopes of reefs on continental margins and on oceanic islands.

So why be interested in geographic patterns?

First, there are some important phenomena, such as the El Nino Southern Oscillation, that we cannot understand on a small scale. Second, “processes important for understanding coastal fisheries dynamics may be driven by events a whole ocean away. Parochialism is a dangerous attitude of mind for fisheries oceanographers at any latitude” (Longhurst and Pauly 1987:44). Documentation supporting this statement is provided in the book on the ecology of tropical oceans by Longhurst and Pauly (1987). Third, similar ecological patterns may involve different causal factors when they occur at different scales. Geographic comparisons across the tropical Pacific and Atlantic have upwelling to the east and terrestrial runoff to the west, a pattern in common with cross-shelf surveys across the Great Barrier Reef. Nevertheless, the causal processes for upwelling, the role of current patterns and the Coriolis effect differ profoundly at these two scales of study. Fourth, generalizations for coral-reef communities derived from research done in separate tropical seas have produced different conclusions and these have resulted in misdirected controversies. The controversies were sometimes misdirected in that the differences had resulted from true ecological differences among the geographic regions rather than from matters of interpretation. For example, the differences between the

Caribbean and the eastern Pacific in grazing intensity by fishes corroborate both sides of a previous debate between Bakus (1964) and Randall & Hartman (1968). The differences in points of view between scientists working on reef-fish communities in the Caribbean and in the western Pacific may result from geographic differences in the relative importance of resource limitation (competition) and recruitment limitation (Thresher 1987).

But the most urgent reason for attempting to understand geographic differences in ecological processes is that human populations, technology, and commercial fisheries are developing rapidly along tropical coastlines. Recognition of basic differences in coral-reef systems under different situations should prompt us to keep these differences in mind when formulating resource management plans. An economy based on the export of biomass might be feasible in a region subjected to strong nutrient input such as upwelling. A service-based economy, exporting items other than biomass (e.g., culturing pearls at atolls such as Takapoto in the Tuamotus) or dealing in tourism, might be more sustainable over the long term in an oligotrophic region. If we shelve consideration of regional differences until we thoroughly understand within-reef processes, we might be too late to foresee problems arising from applying uniform resource management policies to a variety of conditions.

ACKNOWLEDGMENTS

I thank Marlin J. Atkinson, Bruce and Annamarie Hatcher, Robert E. Johannes, Egbert G. Leigh, Ernest A. Matson, Stephen G. Nelson, Robert T. Paine and Geerat J. Vermeij for their time in reading an earlier draft and patiently giving helpful suggestions. The flaws and obvious weaknesses that remain are my fault. I am grateful to Bert Leigh for his persistently prodding me to put these ideas on paper.

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