Community Structure of Coral Reefs on Opposite Sides of the Isthmus of Panama

Abstract. *Competition for space among reef corals includes interspecific destruction by extracoelenteric digestion, rapid growth, and overtopping. No Caribbean species excels in all strategies, and on western Caribbean coral reefs there is a positive correlation between coral abundance and diversity. On eastern Pacific coral reefs, however,* Pocillopora damicornis *excludes other corals, and on these reefs there is an inverse relation between coral abundance and diversity, except in areas where disturbances, such as* Acanthaster *predation, offset space monopolization.*

The eastern tropical Pacific and the western Caribbean have been separated for only 3 million to 5 million years (*1*), yet they are strikingly different in the taxonomic composition and arrangement of their faunas. In this report the community structure and composition of coral reefs on opposite sides of the Isthmus of Panama are compared. The effects of physical and biological processes, especially predation and competition, on the production and maintenance of these communities' structures are assessed.

On reefs where crowding occurs, corals are space-limited. As in other benthic environments (*2*), it can be expected that the resolution of this competition will be a major determinant of the community's structure. Due to their dependence on zooplankton for food (*3*) and on light for their symbiotic algae (*4*), the corals' growth form as well as growth rate is important in space competition. Some corals have overtopping morphologies, as found in plant species for growing over and shading out neighboring individuals (*5*). Another mode of competition is to eat neighboring corals. Lang (*6*) has shown that certain species, when they come into physical contact with other species, can extrude their mesenterial filaments, digest away the living tissue of the neighboring coral, and then overgrow the exposed skeleton. In the Caribbean (*6*) and the eastern Pacific (*7*), corals are arranged in a hierarchy such that species higher up the scale are capable of digesting all those beneath them (position on this scale is referred to here as digestive dominance). This is complicated only by occasional equalities where no digestive interaction is observed between the touching species. Normally the hierarchy is inflexible and does not depend on the physiological state or age of the interacting corals (*6*).

Despite conspicuous examples of biological interactions that occur on reefs, many of the fundamental controls over the location and intensity of reef development are purely physical. Factors such as temperature and salinity fluctuations, heavy sedimentation, low light penetration (*8*), and storm or wave damage (*9*) are important. In their extremes, these stresses can exclude certain species or prevent the accumulation of coral biomass in an area. Only in areas of moderated physical regimes where coral growth is favored do the complex biological controls influence the division of biomass among coral species.

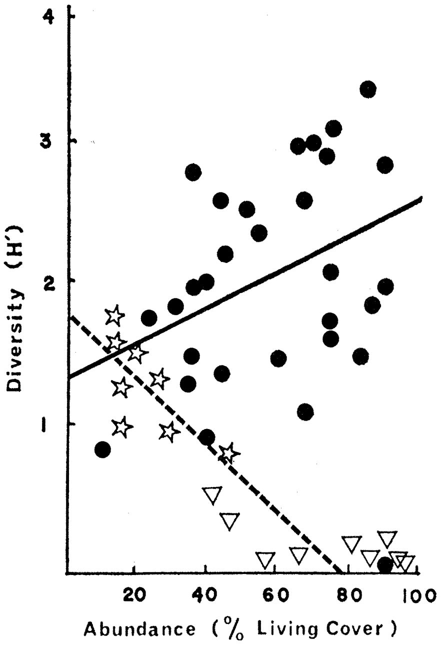

Fig. 1. For transects along Caribbean and eastern Pacific coral reefs, species diversity, *H'*, is plotted against coral abundance (percentage of transect line covering living coral) (*12*). A positive correlation is found for Caribbean transects (closed circles); correlation coefficient $r = +.41$, significant at $P < .025$. The number of species under the transect also correlates positively with the abundance of coral under the transect; $r = +.56$ and $P < .01$. For eastern Pacific transects with (open stars) and without (open triangles) *Acanthaster* predation, $r = -.91$, significant at $P < .001$. The number of species under the transect also correlates negatively with abundance; $r = -.76$, with $P < .001$.

Coral reefs of the eastern Pacific are composed predominantly of monospecific stands of *Pocillopora damicornis* Linn. (= *P. lacera* Verrill?) (*10–12*). In areas where coral coverage is high, the space is monopolized by this species; in areas with less coverage, space is progressively less monopolized; thus, the inverse relation between species diversity and the abundance of living coral is produced (Fig. 1). Several factors contribute to the high proportion of *Pocillopora*. In localities most favorable to reef development, *Pocillopora* has a maximum growth rate [up to 6 cm per branch per year (*13*)] an order of magnitude greater than that of any other eastern Pacific coral. This rapid growth rate is coupled with an overtopping morphology and high digestive dominance. Field studies (*7, 14*) place *Pocillopora* near the top of the digestive dominance hierarchy, followed by species in the genus *Pavona*, and finally species of *Porites*. Such a dominance interaction can be observed in nature (Fig. 2). Finally, *Pocillopora* is able to inhabit water depths near the low tide mark, even being awash at lowest spring tides. It is for these reasons that this coral occupies a high proportion of the substrate suitable for coral growth in the eastern Pacific.

Reversal of space monopolization is possible through a variety of disturbances (*2, 15*). Most interesting is predation by *Acanthaster planci*, the crown of thorns starfish (*14*). All of the transects with the highest diversity (starred points in Fig. 1) come from reefs with a high frequency of coral predation by *Acanthaster*; the transects with lower diversity come from reefs where *Acanthaster* is rare (Islas Secas) or absent (Islas Perlas). The same number of species is found on both kinds of reef; the increase in the number of species observed under the transect for the preyed-on reefs (Fig. 2) is due to an increase in abundance in these species, making them common enough to be counted by the transect method employed (*12*). Although the relative abundances of the coral species change markedly, for the most part, the order of abundance does not. On all reefs *Pocillopora* is most abundant, followed by *Pavona*, with very little coverage contributed by the rest of the fauna. Totaling the amount of coral coverage on the two kinds of reef (Fig. 2) shows that the reefs with a high frequency of *Acanthaster* have almost one-third less coral biomass than those lacking the starfish. By cropping down the coral, the starfish leaves space where other species, in addition to *Pocillopora*, can (and do) colonize in areas once exclusively occupied by *P. damicornis*. Differential recolonization rates as well as differential predation can cause the observed shift in relative abundances. The Indo-Pacific character of the fauna indicates that eastern Pacific coral larvae are capable of colonizing reefs from long distances.

In addition to localized *Acanthaster*, there are a number of cosmopolitan corallivores capable of producing bare spaces for coral settlement. The feeding rates of a guild of corallivorous fishes, a gastropod, and two paguridean decapods are described by Glynn *et al.* (*7*); these corallivores consume approximately one-third of the new growth of *Pocillopora* communities each year. Such predation is significant, especially when compounded by *Acanthaster* predation (*16*). Thus, there is a considerable biological component in the production and maintenance of eastern Pacific coral community structure. Because of the broad taxonomic base of this control, it can be said to be interphyletic in origin.

On the Caribbean side of Panama, areas most favorable to reef growth have coral densities comparable to those observed on the eastern Pacific reefs, but the areas of maximum coverage, instead of being monopolized by one species, have the greatest number of species and the highest species diversity (Fig. 1). Goreau and Goreau (*17*) noted that except for several acroporids, which calcify relatively rapidly, no consistent relation exists between a coral's calcification rate and its prevalence on a Jamaican reef. This is similar to the situation on the Atlantic side of Panama, but opposite to that on the Pacific side. A partial explanation for these interoceanic differences is suggested by a comparison of the growth rates of Caribbean coral species with their dominance ranks. In the eastern Pacific, rapid growth and high digestive dominance are present in the same species. In the Caribbean, the opposite is true: The species that calcify and grow most rapidly (those in *Acropora, Porites*, and *Agaricia*) are the least capable of eating other species, while the species that grow most slowly (those in *Scolymia, Mussa, Isophyllia, Mycetophyllia, Isophyllastrea*, and *Meandrina)* are highest on the digestive dominance scale. Furthermore, none of the strong aggressors employs an overtopping morphology, as is found in the weak genera *Acropora* and *Agaricia*. As a speculation, high digestive dominance and rapid growth rate may represent physiological alternatives which, to date, have not evolved together in one Caribbean species. There appears to be a balance of abilities divided among the Caribbean corals such that no one species is competitively superior in acquiring and holding space. The effect of this balance of competitive abilities is to retard, even in high-density situations, the rapid competitive exclusion that takes place on undisturbed eastern Pacific reefs. In areas where physical factors allow for the accumulation of coral biomass, a large number of species coexist. Hence, for the Atlantic side of Panama there is a positive relation between diversity and abundance.

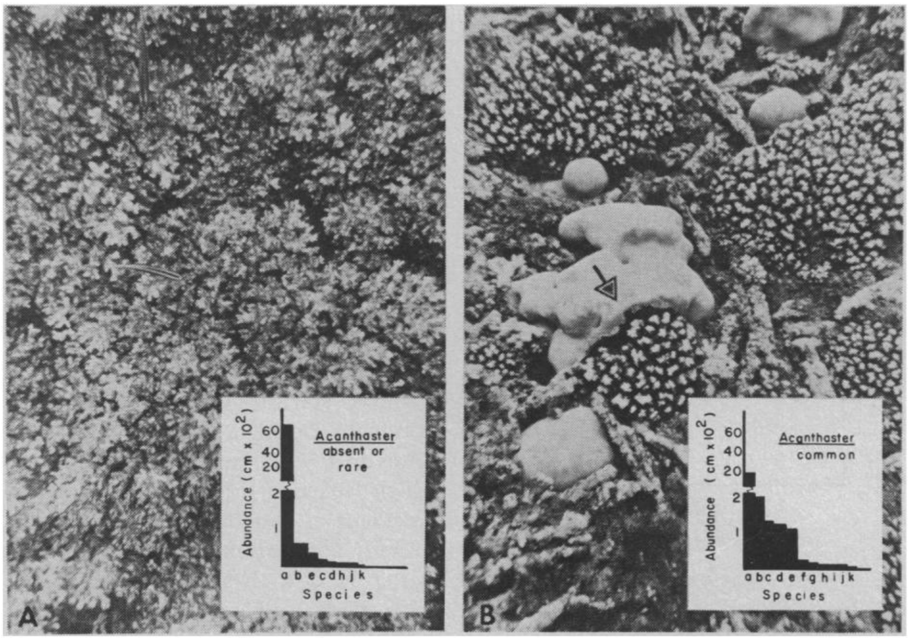

Fig. 2. Eastern Pacific *Pocillopora* reef crests. (A) Monospecific stand of *P. damicornis* where *Acanthaster* is absent (Islas Perlas); (B) crest where *Acanthaster* is common (Isla Uva). Note the black, killed area (arrow) on the margin of the white *Pavona clivosa* colony in the center of (B). This dead area is an outline of the neighboring branched *Pocillopora* colony whose mesenterial digestive filaments were seen extruded onto this *Pavona* colony at the region of contact. Note the lower coral cover but higher number of species on this reef section. The white tips of the *Pocillopora* colonies in (A) and (B) are due to predation by various corallivorous fish; each area is roughly 0.75 m^2. The number of centimeters of transect covering each species of coral on eastern Pacific reefs is shown in the bar graphs for reefs where *Acanthaster* is absent or rare [none to one individual per 50,000 m^2 in (A)] and where it is common [one or more individuals per 100 m^2 in (B)]. (a) *Pocillopora damicornis, Pocillopora elegans*, (c) *Pavona varians*, (d) *Millepora* sp., (e) *Porites californica*, (f) *Porites panamensis*, (g) *Pavona clivosa*, (h) *Psammocora brighami*, (i) *Pavona ponderosa*, (j) *Pavona gigantea*, and (k) *Tubastrea aurea*.

One exception occurs (bottom Caribbean point in Fig. 1) in extensive shallow-water reef flats composed almost exclusively of *Porites furcata*. In San Blas, off the Atlantic coast of Panama, this species was observed to survive a 1-hour exposure to air at midday without apparent morphological damage, as well as a continuous 3-hour flow of silt-laden river water with a salinity of 19 parts per thousand, which followed the first torrential rain of the 1972 wet season. *Porites furcata* is at the bottom of the digestive dominance hierarchy (*6*), but its physiological tolerance to desiccation and surface salinity fluctuations allows it to escape in shallow water the competitive interactions which, under normal circumstances, would prevent its monopolization of space on the reef.

The destruction by predation of at least one-third of new coral growth per year observed in the eastern Pacific appears to be absent from the Caribbean.

Although these observations are preliminary, the direct intraphyletic interaction of coral versus coral in the Caribbean seems less modified by predation pressure than on some eastern Pacific coral reefs (*18*). Space is produced in the Caribbean by slower means, such as the slump or collapse of larger coral heads due to intense boring by sponges and bivalves (*19*). This might be analogous to the creation of space in highly dense rain forests by tree fall (*20*) and seems sufficient to offset the slow competitive exclusion which would occur if the system were left totally undisturbed. Elsewhere in the Caribbean, weather disturbances such as hurricanes are probably of major importance to shallow-water coral community organization as well, but Panama does not have such severe disturbances.

In looking at species succession, Pielou (*21*) found that species diversity increased over time for some small plots of young temperate forest trees. She concluded that natural thinning by interspecific competition caused the decrease in segregation and dominance by single species, the result being an increase in the local diversity. While few data exist for reef succession, most phases of Caribbean coral succession may prove to be similar to this pattern, whereas, without large-scale physical or biological disruptions, eastern Pacific coral succession may prove to be the opposite. In support of this, Grigg and Maragos (*22*) have shown that, all else being equal, coral communities on the oldest lava flows in Hawaii have the lowest diversities and that the same negative relation between diversity and abundance exists in Hawaii as on the eastern Pacific reefs. They suggest that interspecific competition of the kind outlined above might be the cause for this decrease in diversity over time. Additional support for this hypothesis comes from their observation that in areas exposed to heavy swell and periodic storm damage, abundance remains low and diversity high, regardless of the age of the colonized surface. In Hawaii, where coral fauna and reefs are similar to those of the eastern Pacific, storm and swell damage may act as a diversifying force in the same way as *Acanthaster* predation does in the eastern Pacific.

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18. The outcome of connecting these two oceans with a sea-level canal is problematic, but what little predictive evidence exists is ominous: eastern Pacific *Acanthaster* are capable of eating all of the Caribbean coral species so far fed to them (*11*). Why should Caribbean species have any resistance to predators with which they have never come in contact? Further, while dominance experiments between eastern Pacific and Caribbean corals have not been tried, analogy with Indo-Pacific and Caribbean species—the Indo-Pacific species killed even the most aggressive Caribbean corals [J. C. Lang, thesis, Yale University (1970)]—is disturbing, considering the close systematic relationship between the eastern Pacific and the Indo-Pacific corals (*10, 11*).
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23. I thank W. D. Hartman, G. E. Hutchinson, R. K. Trench, D. C. Rhoads, and P. W. Glynn for advice and criticism throughout this research. K. G. Porter, D. H. Janzen, S. T. Hubbell, L. Johnson, J. C. Lang, D. S. Wethey, and S. Ohlhorst have provided helpful comments. Supported by a Smithsonian predoctoral fellowship, NSF grant GA-30970, and a grant-in-aid of research from the Society of Sigma Xi.

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Studies of Squeezing: Handedness, Responding Hand, Response Force, and Asymmetry of Readiness Potential

Abstract. *Eleven subjects squeezed an electronic dynamometer, at each of three force levels, with both their right and left hands. In right-handed subjects the premovement "readiness" potentials were larger over the hemisphere contralateral to the responding hand. Left-handed subjects show contralateral dominance when responding with the right hand but not when responding with the left hand. The data suggest that in the potentials studied there is a component associated with the preparation to perform a specific movement, rather than with generalized preparatory processes.*

Slow cortical potentials that precede self-paced voluntary movement (*1–4*) have excited much interest. Although they may provide a useful tool for the study of the physiological mechanisms underlying voluntary movement, considerable controversy still remains. Especially prominent have been suggestions that these potentials represent either diffuse arousal mechanisms or, alternately, postresponse proprioceptive activity (*3, 4*). We present evidence that these potentials are associated with the execution of specific movements, rather than with diffuse, arousing, preparatory processes. This we infer from the fact that the amplitude, and scalp distribution, of these potentials is strongly determined by parameters of the subject's movement. We also show that the degree of hemispheric asymmetry of these potentials is different in right- and left-handed subjects.

Of the four components of movement-related electrocortical potentials which have been described (*1*), we are concerned here with a ramp-shaped negative potential that begins to develop 800 to 1000 msec prior to the movement (N1). Vaughan and his co-workers (*1, 4*) have referred to the entire complex of potentials as the "motor"