Reports

Comparative Species Richness in Fluctuating and Constant Environments: Coral-Associated Decapod Crustaceans

Abstract. *The number of decapod species associated with the coral* Pocillopora damicornis *is compared between two regions on the Pacific coast of Panama which are of the same geologic age but differ in environmental characteristics. The relationship between number of species and coral head size does not differ between the two regions but species composition among coral heads is more variable in the fluctuating environment. Thus there are more species (55 compared to 37) associated with corals in the fluctuating environment than in the constant environment. These data impugn the concept that environmental constancy increases species richness. They support the hypothesis that species equilibrium within habitats is maintained by measurable ecological factors—in this case, the effects of a natural physical disturbance.*

The idea that species richness increases in constant, predictable environments over long periods of geologic time has become almost axiomatic in large segments of biological literature (*1*) since its independent proposal by Belt (*2*) and by Wallace (*3*) in the 19th century. However, an increasing body of data indicates that communities quickly saturate with species and remain at a relatively constant equilibrium number through long periods of time (*4*). This number is determined largely by the structural characteristics and areal extent of the habitat (*5*). The controversy may be resolved in part by examining data from habitats that are ecologically similar except for differences in environmental constancy or age. I compare here within-habitat species richness in two regions of the same geologic age but differing in environmental characteristics.

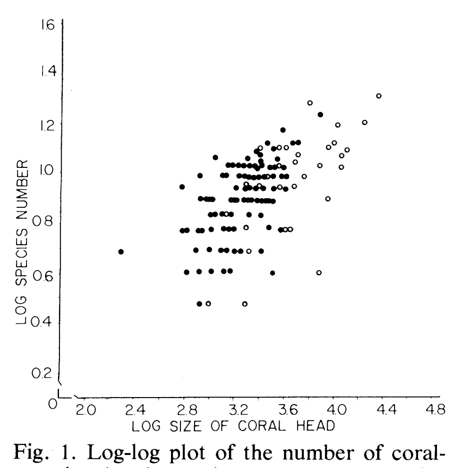

Fig. 1. Log-log plot of the number of coral-associated decapod crustacean species against the size of the coral head. Closed circles denote Uva Island and open circles the Pearl Islands. For the Pearl Islands, log y = 0.356 log x − 0.316, r = .64, P < .001, N = 35; for Uva Island, log y = 0.269 log x + 0.010, r = .48, P < .001, N = 119. There is no significant difference between the regression lines.

The branching coral *Pocillopora damicornis* (L.) and related species occur from the Indo–West Pacific to the East Pacific (*6*) under a variety of environmental conditions, which range from highly constant to highly variable in terms of measured physical and chemical characteristics on an annual time scale. Living coral heads in all these regions have an associated macrofauna that consists almost exclusively of decapod crustaceans: 96 percent of the individuals and 89 percent of the species in the Pearl Islands, Panama, and 80 percent of the individuals and 76 percent of the species at Uva Island, Panama (*7*).

The *Pocillopora*-decapod assemblage has been examined in detail in two regions (Table 1) off the Pacific coast of Panama. The *Pocillopora* communities in the Pearl Islands occur in an environment which is at present variable and has been dated by carbon-14 as 4550 ± 65 years old (*8*). Temperature, salinity, and turbidity vary greatly, temperature by as much as 12°C in 24 hours and salinity by 10 parts per thousand (ppt) during the year (*9*). The variation is seasonal, but there is a large variation from year to year, and local meteorological conditions can cause unseasonable upwelling with a concomitant drop in temperature and oxygen depletion (*10*). This community is contrasted with the *Pocillopora* community at Uva Island in the Gulf of Chiriqui. Based on growth rate data and carbon-14 dating, the reef is 2500 to 5585 years old (*8*). The present temperature variation is about 2°C and the salinity variation is about 2 ppt (*11, 12*). Thus the reefs are of the same approximate age and occur in the same biotic province (the Panamic) less than 300 km apart; yet they differ markedly in environmental characteristics.

A general description of the *Pocillopora*-decapod assemblage is given by Abele and Patton (*7*). The animals were obtained by collecting live coral heads. Individual coral heads were sealed in plastic bags and removed or were broken off into buckets and taken to the surface, where all macroorganisms (those retained by a 1-mm^2 screen, not including boring forms) were removed from the live portions of the head. The length, width, and height of the live portions of the head were measured (*13*). The dead base and occasional dead center of large heads were not measured, nor were animals collected from these portions. The sample sizes were equalized by rarefaction (*14–16*).

The relationship between the number of species and the size of individual coral heads within each area is illustrated in Fig. 1. There is no significant difference between the slopes or intercepts of the curves for the two regions (*17*). The consistent species-area relationship argues strongly for acceptance of the hypothesis that species richness of this habitat is well predicted (and seemingly largely determined) by the areal extent and structural complexity of individual coral heads. However, the total number of

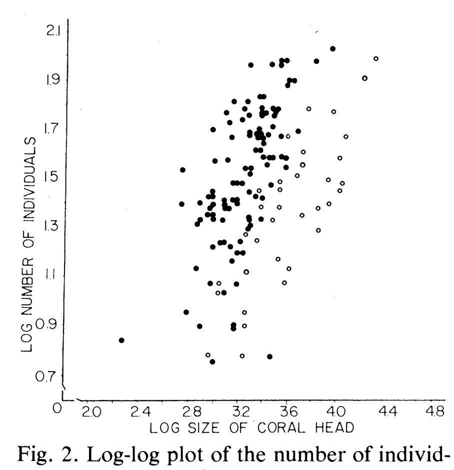

Fig. 2. Log-log plot of the number of individuals of coral-associated decapod crustacean species against the size of the coral head. Closed circles denote Uva Island and open circles the Pearl Islands. For the Pearl Islands, log y = 0.618 log x − 0.841, r = .77, P < .001, N = 35; for Uva Island, log y = 0.652 log x − 0.675, r = .58, P < .001, N = 119. There is a significant difference between the intercepts but not the slopes [see (*19*)].

Table 1. Comparative data on the *Pocillopora* coral–decapod crustacean assemblage.

Region	Age (years)	Annual sea surface temperature range (°C)	Annual sea surface salinity range (ppt)	Sample size	Species (No.)	Individuals (No.)
Pearl Islands, Panama	4500 ± 65	17–29	22–36	35	55	1107
Uva Island, Panama	2500 to 5585	28–29	31–33	35*	37 ± 2	1107*

*Randomly drawn from a sample of 119 coral heads, including 4724 individuals and 50 species.

decapod species (55) associated with *Pocillopora* in the fluctuating environment (Pearl Islands) is significantly greater ($t = 85$, $P < .001$, $N = 119$) than the number of decapod species (37) associated with *Pocillopora* in the constant environment (Uva Island). This results from a higher variance in species composition on individual coral heads in the fluctuating environment of the Pearl Islands. The decrease in species number from the Pearl Islands to Uva Island is not a random process. It results from the absence of a group of generalized species (*18*) on coral heads at Uva Island; these species occur in a wide variety of habitats, including *Pocillopora* coral. For example, the porcellanid crab, *Pisidia magdalenensis*, was the most abundant species collected on *Pocillopora* in the Pearl Islands (180 individuals). Yet not a single individual was collected among the 4724 individuals examined from 119 coral heads collected over an 8-month period at Uva Island. Other species that were relatively abundant in the Pearl Islands, such as *Heteractaea lunata* and *Lysmata californica*, were also absent from the 119 Uva samples. It is not that these species do not occur in the Gulf of Chiriqui as they occur throughout the Panamic Province; they simply occur in habitats other than pocilloporid corals.

In contrast to the situation for generalized species, the abundance of species that are either obligate commensals of *Pocillopora* or occur almost exclusively on pocilloporid corals increased at Uva. Based on a random sample of 29 coral heads from Uva taken at the same time of year as those from the Pearl Islands, *Trapezia ferruginea* increased from 91 to 147 (91 to 558 if juveniles at the coral base are considered), *Fennera chacei* from 89 to 243, and *Harpiliopsis spinigerus* from 15 to 59. This results in a change in the dominant species from Pearl to Uva: a generalist, *P. magdalenensis*, is dominant in the fluctuating environment, while a specialist, *T. ferruginea*, is dominant in the constant environment.

The population size of the coral specialists, except for *T. ferruginea*, per coral head does not change between the two regions, but each species occurs on more coral heads at Uva Island. The individual–coral head size regressions between the two areas differ significantly (*19*) in intercept but not slope (Fig. 2). This is due almost solely to an increase in abundance of juveniles and subadults of *T. ferruginea*.

I suggest that the difference in species richness between the two areas is the result of differential extinction rates generated by physical disturbance. Space is a limiting resource for many sessile marine organisms and species differ in their ability to obtain and hold space (*20*). The coral-associated decapods parallel this situation since, through their association with a sessile host, they are functionally sessile. That space is limiting is suggested by the individual-area relationship, which is consistent despite differences in species number and composition, and by the territorial activities of *Alpheus lottini* and *T. ferruginea*.

In the Pearl Islands upwelling regularly occurs from January through March, periodically lowering the temperature to 20°C, a point at which the growth rate of *P. damicornis* declines markedly or ceases, sometimes resulting in loss of soft parts from the tips of branches (*21*). Experimental data have demonstrated that *T. ferruginea* feeds on coral mucus and cannot survive on dead corals (*22*). Other coral specialists are known to feed on coral mucus (*23*) and are never found on dead corals. It is reasonable to expect some extinctions of the coral mucus–feeding specialists during this time and subsequent colonization by species such as *P. magdalenensis* and *H. lunata*. Both species are abundant on live and dead corals in the Pearl Islands but do not occur on live corals at Uva Island. In the Pearl Islands most (71 percent) of the species have similar abundances and frequencies of occurrence on coral heads (*7*). Colonization of cold-shocked corals is likely to be a largely random process, resulting in a large number of species with a low frequency of occurrence and a high variance in species composition among corals—just as observed. At Uva Island, only 300 km away, there is no upwelling and relatively little variation in physical conditions. Extinction is probably relatively rare and the dominant coral specialists increase their total population density and frequency of occurrence on coral heads.

In summary, this analysis contradicts the hypothesis that environmental constancy per se increases species richness. It also shows that there are relatively fewer specialists in the more species-rich area, in contrast to theoretical predictions (*24*). The data presented support the hypothesis that species equilibrium is maintained by measurable ecological factors.

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13. Dry weights of the coral heads were also taken for the Uva samples; dry weight and area are highly correlated ($r = .88$). There was no statistical difference between analyses in which weight and length × width × height were used as the independent variables.
14. The number of species, individuals, and coral heads sampled, including the dates, are as follows: Pearl Islands, 55, 1107, 35, June–July 1972; Uva Island, 50, 4724, 119, January, April, June, and August 1973. The regions can be compared on the basis of number of coral heads or number of individuals. Thirty-five coral heads selected at random from the Uva collections yielded 37 ± 2 species and 1175 ± 44 individuals. Using the method of K. L. Heck *et al.* [*Ecology* **56**, 1459 (1976)] 37 ± 2 species were represented in 1107 individuals randomly drawn from the Uva collections.
15. It is also important to compare the same species of coral from the same portion of the reef. The taxonomy of *P. damicornis* is unsettled and varieties have been reported by Glynn *et al.* (*12*) from both the Pearl Islands and Uva Island.

However, *P. damicornis* is the most abundant coral in both areas and attempts were made to compare only *P. damicornis*. There did not appear to be any difference in species composition among the varieties, and coral-associated decapods appear to be host specific at the generic rather than specific level. See species lists in J. S. Garth (*16*) and W. K. Patton [*Crustaceana* **10**, 271 (1966)]. Samples from the front and rear crests and front and rear flanks were compared to assess the impact of any differences in location. There was no significant difference in species composition or in the species-area relationship of deep ($N = 62$) compared to shallow ($N = 57$) portions of the reef ($t = 0.258$, $P > .5$). There were differences in density of individual species but these do not affect the present comparison.

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17. By analysis of covariance $F(1/151) < 1$ for both slopes and intercepts. By Student's t-test, $t = 1.37$, not significant for slopes; $t = 1.34$, not significant for intercepts.
18. The decapod fauna of *Pocillopora* is composed of three groups of species: (i) obligate commensals, (ii) species that most often occur on pocilloporid corals, and (iii) species that occur in a wide variety of habitats including pocilloporid corals [L. G. Abele, *Mar. Biol.*, in press; J. S. Garth (*16*)].
19. Comparison of these regressions is somewhat equivocal. A test of the slopes reveals no significant difference ($t < 1$, $P > .4$). The analysis of covariance model, assuming equal slopes, reveals a significant difference between the intercepts [Uva > Pearl, $F(1/151) = 32$, $P < .001$]. However, if the intercepts are tested using the numerical slope values derived for each region there is no significant difference between the intercepts. Visual examination of Fig. 2 supports the analysis of covariance result.
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25. I thank P. Glynn for constructive criticism and stimulating discussion and for making the coral heads from Uva Island available to me, and P. Abrams, E. Connor, W. Finney, K. Heck, E. McCoy, J. Rey, D. Simberloff, D. Strong, and K. Walters for comments. Ship time was supported by the Smithsonian Tropical Research Institute.

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Ecological Competition Between Algae: Experimental Confirmation of Resource-Based Competition Theory

Abstract. *All possible outcomes of ecological competition, including stable coexistence, were observed in laboratory studies of two species of freshwater diatoms potentially limited by phosphate and silicate. The relative abundance of these nutrients determined the outcome of competition. The observed conditions of coexistence and competitive displacement agree with those predicted solely from the abilities of each species to acquire and utilize limiting nutrients. Coexistence occurred only when the growth rate of each species was limited by a different resource. These results may help explain the regional coexistence in nature of an otherwise paradoxically high number of algal species.*

All planktonic algae require essentially the same nutrients, which they obtain from a commonly held resource pool. Classical ecological competition theory predicts that, under idealized conditions (*1*), the one species best able to acquire and use the limiting resource should displace all other competing species. If this prediction is correct, lakes and oceans should contain few species of algae. Marine and fresh waters usually contain more than 30 species of phytoplankton in apparent competitive coexistence within any small parcel of water (*2, 3*). Hutchinson termed this discrepancy between nature and theoretical prediction the "paradox of the plankton" (*2*). Many theories have been proposed to explain this. One class of explanations emphasizes that the spatial complexity and temporal variability of nature are a violation of the idealized conditions assumed in classical theory (*2–4*). A second stresses the possibility that differing mortality rates, from differential grazing and settling, may minimize interspecific competition (*5*). Another hypothesizes that, even under idealized conditions, coexistence should be possible if species differ in their ability to acquire and utilize resources (*6, 7*). Although such differences have been demonstrated (*8*), experimental confirmation of a resource-based theory of competition has been lacking. The results reported here show that the steady-state outcome of nutrient competition between two species can be predicted solely from the ability of each species to obtain and use nutrients for growth.

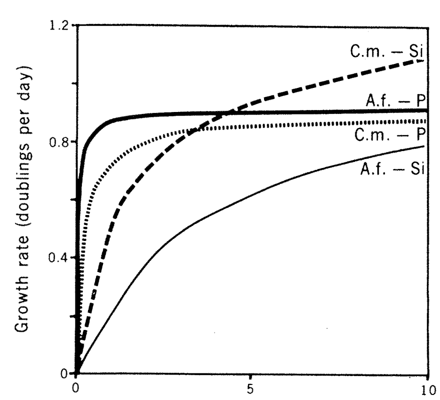

Fig. 1. The calculated Michaelis-Menten functions for *Asterionella formosa* under PO_4 limitation (thick solid line) and under SiO_2 limitation (thin solid line); the calculated functions for *Cyclotella meneghiniana* under PO_4 limitation (dotted line) and under SiO_2 limitation (dashed line). Details are given in the text and (*14*).

The freshwater diatoms studied, *Asterionella formosa* and *Cyclotella meneghiniana*, occur together in mid-latitude lakes. Both species were bacteria-free clonal isolates (*9*). All experiments were performed in controlled-culture laboratory conditions (*10*). The two potentially limiting nutrients for the competition experiments, phosphate (PO_4) and silicate (SiO_2), often limit growth rate in lakes (*11, 12*). The first experiments determined the abilities of each species to use limiting concentrations of PO_4 or SiO_2. Competition experiments between both species, grown together in flow-through (semicontinuous) culture, were then performed.

If the growth rate of a species is limited by a nutrient, its growth rate will depend on the amount of that nutrient available. At low concentrations of the nutrient, growth rate is almost directly proportional to concentration. As concentration increases, a maximal rate of growth is approached. The Michaelis-Menten equation is commonly used to describe the relationship between growth rate and concentration (*8, 13*):

$$\mu = \mu_{max}[S/(S + K)]$$

where μ is the growth rate, μ_{max} is the maximal growth rate, S is the concentration of the limiting nutrient, and K the concentration which leads to half-maximal growth rate, called the half-saturation constant.

The growth response of each species, cultured singly, to limiting concentrations of PO_4 and SiO_2 was determined experimentally (*14*). The results were fit to the Michaelis-Menten equation (Fig. 1). The maximal growth rates of the two species do not differ significantly ($P > .95$) (*15*). *Asterionella formosa* has a K for phosphate-limited growth of 0.04 μM PO_4, significantly lower ($P > .95$) than the K of 0.25 μM PO_4 for PO_4 limited growth of *C. meneghiniana*. If both species were grown together under PO_4 limitation, *A. formosa* should be the competitive dominant (*16*). Under SiO_2-limited growth conditions (Fig. 1), $K = 1.4$ μM SiO_2 for *C. meneghiniana* and $K = 3.9$ μM SiO_2 for *A. formosa*. The half-saturation constants are significantly different ($P > .95$). If both species were limited by SiO_2, *C. meneghiniana* should be the superior competitor (*17*).

If a single species is potentially limited