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.

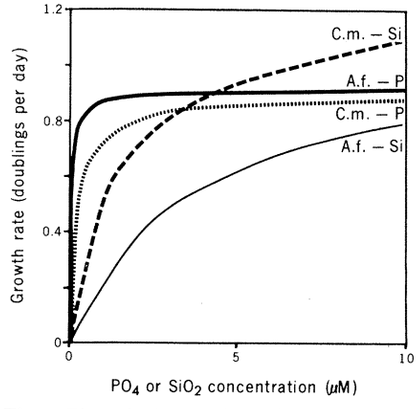

Fig. 1. The calculated Michaelis-Menten functions for *Asterionella formosa* under PO_4 limitation (thick solid line) and under SiO_2 limitation (thin solid line); the calculated functions for *Cyclotella meneghiniana* under PO_4 limitation (dotted line) and under SiO_2 limitation (dashed line). Details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

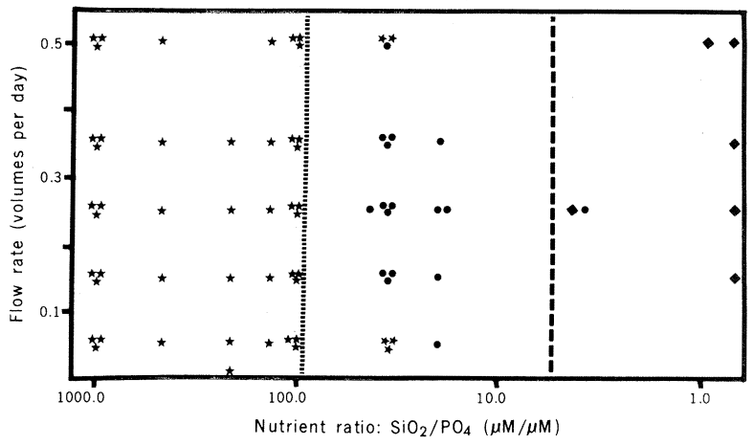

Fig. 2. Results of competition experiments at different nutrient ratios. Vertical lines at $[SiO_2]/[PO_4]$ of 97 and 5.6 are the competitive boundaries as predicted from the abilities of each species to utilize limiting phosphate and silicate. For $[SiO_2]/[PO_4] > 97$, *A. formosa* should be competitively dominant because both species are limited by phosphate. For $97 > [SiO_2]/[PO_4] > 5.6$, both species should coexist because the growth rate of each species is limited by a different resource. For $[SiO_2]/[PO_4] < 5.6$, both species are limited by SiO_2 and *C. meneghiniana* should be the competitive dominant. Symbols: stars, *A. formosa* dominant; diamonds, *C. meneghiniana* dominant; circles, stable coexistence of both species.

by two nutrients, its growth rate is determined by the concentration of that nutrient which leads to the lower growth rate (*18*). The boundary between growth rate limitation by SiO_2 or by PO_4 should occur when the concentrations of SiO_2 and PO_4 cause equal growth rates. From the Michaelis-Menten equation, growth rates are equal when

$$S_1/(S_1 + K_1) \equiv S_2/(S_2 + K_2)$$

$$S_1/S_2 = K_1/K_2$$

where S_1 and S_2 are the concentrations of nutrients 1 and 2, and K_1 and K_2 are the half-saturation constants for growth of this single species limited by nutrients 1 and 2.

From the results reported here, the boundary between PO_4 and SiO_2 limitation (*19*) for *A. formosa* should occur when $[SiO_2]/[PO_4] = 3.9/0.04 = 97$. For ratios of SiO_2 to PO_4 greater than 97, *A. formosa* should be limited by PO_4; below 97, it should be limited by SiO_2. The boundary for *C. meneghiniana* is $[SiO_2]/[PO_4] = 1.4/0.25 = 5.6$. For ratios greater than this, *C. meneghiniana* should be limited by PO_4; below this ratio, it should be limited by SiO_2. These boundaries are shown as vertical lines (Fig. 2).

This resource utilization information can be used to predict the results of nutrient-dependent competition between these two species (*20*). For $[SiO_2]/[PO_4] > 97$, both species are limited by PO_4. Under these conditions, *A. formosa*, the better competitor as predicted from PO_4 kinetics (Fig. 1), should dominate in mixed species culture. For $[SiO_2]/[PO_4] < 5.6$, both species are limited by SiO_2. In this case, *C. meneghiniana* should be the competitive dominant (Fig. 1). For nutrient ratios between 97 and 5.6, the growth rate of each species is limited by a different nutrient: *A. formosa* by SiO_2 and *C. meneghiniana* by PO_4. Under these conditions both species should coexist indefinitely in mixed species culture because an individual of one species will have a greater effect on members of its own species than on members of the other species. These are the conditions needed for coexistence as predicted by classical theory.

The results of 73 competition studies conducted at various ratios of SiO_2 to PO_4 and at various flow (dilution) rates (*21*) are in general agreement with these predictions (Fig. 2). Two single-species control cultures tested at each nutrient ratio and flow rate showed that each species was able to exist by itself under all conditions tested. Any competitive displacement observed in mixed species cultures must be the result of interactions between the two species. The competitive displacement of *C. meneghiniana* by *A. formosa* when both species are limited by PO_4 (ratio greater than 97) agrees with the predicted results. The displacement of *A. formosa* by *C. meneghiniana* under SiO_2 limitation is also as predicted. Competitive displacement often required 10 to 25 days even under conditions of rapid turnover (*22*). Stable coexistence was observed in the predicted range of nutrient ratios (*23*). The actual boundary between dominance by *A. formosa* and stable coexistence of both species has an apparent curvature toward lower ratios at both high and low flow rates (Fig. 2). There are not sufficient data near the other boundary to determine if it is also curved.

Long-term coexistence of competing species was observed only when the growth rate of each species was limited by a different nutrient. This supports the ecological concept that as many competing species can coexist as there are limiting resources (*6, 7, 24*). This experimentally demonstrates the plausibility of one hypothesis (*7*) used to explain the paradox. It has not been demonstrated that there are enough limiting resources for this mechanism to explain the coexistence of so many species in nature (*25*).

An alternative theory which helps explain the paradox states that many patches of water that differ in the species they favor exist contemporaneously. Coexistence is thought to be due to the continual development of patches that "decay" before competitive displacement can fully occur (*3*). If these patches have a lifetime less than the 10 to 25 days required for competitive displacement in vitro, numerous species may be able to exist together in a nonequilibrium state. The results reported indicate that each patch might tend not toward dominance by a single species but toward a multispecies assemblage. The species composition of an assemblage would be determined by which nutrients were potentially limiting in each patch. Perhaps Hutchinson was correct in suggesting that there is insufficient time for competitive exclusion to occur during the summer in temperate lakes because of the slowness of competitive exclusion and the nonequilibrium conditions in lakes.

The results reported confirm the ability of resource utilization information to predict the steady-state outcome of competition. If similar cases can be found, it would indicate that theories of competition based on the abilities of species to utilize resources could be a powerful tool in understanding the structure and dynamics of natural communities (*12, 13, 26*).

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References and Notes

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10. Light-dark cycle of 12 : 12, light from fluorescent bulbs at about 100 μein m^{-2} sec^{-1}; 20° ± 0.5°C; algal medium WC, described by R. R. L. Guillard and C. J. Lorenzen [*J. Phycol.* **8**, 10 (1972)].
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14. Unpublished results obtained with S. S. Kilham. Culture flasks of WC medium (*10*) were inoculated with nutrient-starved cells at a density of about 500 cells per milliliter, and allowed to grow for 4 days, with cell counts made daily. Initial nutrient concentrations did not decrease more than 25 percent by day 4 because of the low cell density at the start of the experiments. Growth rate at each initial concentration was estimated by a least-squares linear regression of logarithm to base 2 of cell counts versus day. These data were fitted to the Michaelis-Menten equation by a nonlinear regression [by the method of C. I. Bliss and A. T. James, *Biometrics* **22**, 573 (1966)] which provides confidence limits about the mean.
15. A *t*-statistic was used to test significant differences of all means with significance stated.
16. Both PO_4 uptake and PO_4-limited growth rates at various concentrations of PO_4 are needed to make this conclusion. Short-term (batch) PO_4 uptake experiments with both species, cultured singly, revealed no significant differences ($P > .95$) in K or in the maximal rate of PO_4 uptake between the two species. Because uptake abilities are not significantly different, the species best able to convert low PO_4 levels into growth should be the superior competitor.
17. The SiO_2 uptake experiments revealed no significant differences in K or in the maximal rate of SiO_2 uptake between the two species. Thus, *C. meneghiniana* should be the competitive dominant when both species are limited by SiO_2.
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19. Nutrient ratios are employed here for ease of presentation of experimental results. Under controlled culture conditions in which only specific nutrients may be limiting growth rate, use of ratios should be valid. For natural situations, absolute concentrations and supply (turnover) rates of all relevant nutrients should be used.
20. I present this simple model of steady-state competition to illustrate the potential power of resource utilization theory. Numerous other interpretations, based on more physiologically realistic models, are possible and are in preparation. This model illustrates what may be an essential aspect of any resource-based model: stable, steady-state coexistence occurs only when the growth rate of each species is limited by a different resource.
21. The ratio of SiO_2 to PO_4 in the influent medium was adjusted as shown (Fig. 2). This approximates steady-state concentration ratios for which the simple mathematical analysis presented is valid. In all cases, the absolute concentrations of PO_4 and SiO_2 were low enough that only SiO_2 or PO_4 should be limiting growth rate. Cultures were diluted manually daily by removing a portion and replacing it with medium. Flow rates are expressed as the ratio of the volume removed per day to the total culture volume.
22. A species was considered competitively displaced when it comprised less than 5 percent (by number of cells) in a mixed species culture. Mixed cultures were started with each species in equal abundance.
23. These cultures showed no shift in the proportions of each species between about day 20 and day 42, when experiments were generally terminated.
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27. Supported by a University of Michigan Rackham predoctoral fellowship to D.T. and by NSF grant GB-41315 to P. Kilham. I thank P. Kilham, S. S. Kilham, J. Adams, J. Porter, D. Wethey, B. Hazlett, J. Vandermeer, and a reviewer for comments and C. Kott for assistance with experiments. This work is part of a dissertation submitted in partial fulfillment of the Ph.D. degree at the University of Michigan.

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Potassium-Argon Ages from the Galápagos Islands

Abstract. *Potassium-argon ages of eight volcanic rocks from some of the geologically oldest flows exposed in the Galápagos Archipelago indicate that the Galápagos Islands have a probable maximum age of 3 million years. Rocks from six islands were dated; the oldest are from Española (3.2 ± 0.2), Sante Fe (2.7 ± 0.1), and Plazas (4.2 ± 1.8 million years). The new data suggest that the Galápagos Islands are younger than previously supposed on the basis of marine magnetic anomaly dating, but they are older than most previously dated rocks from the Galápagos.*

The Galápagos Islands have been of interest to biologists since 1835, when Darwin (*1*) noted their relative isolation from any major land mass, their geologic youthfulness, and the differentiation of species on and within the island archipelago. The age of the islands is important to any biological, evolutionary, geo-

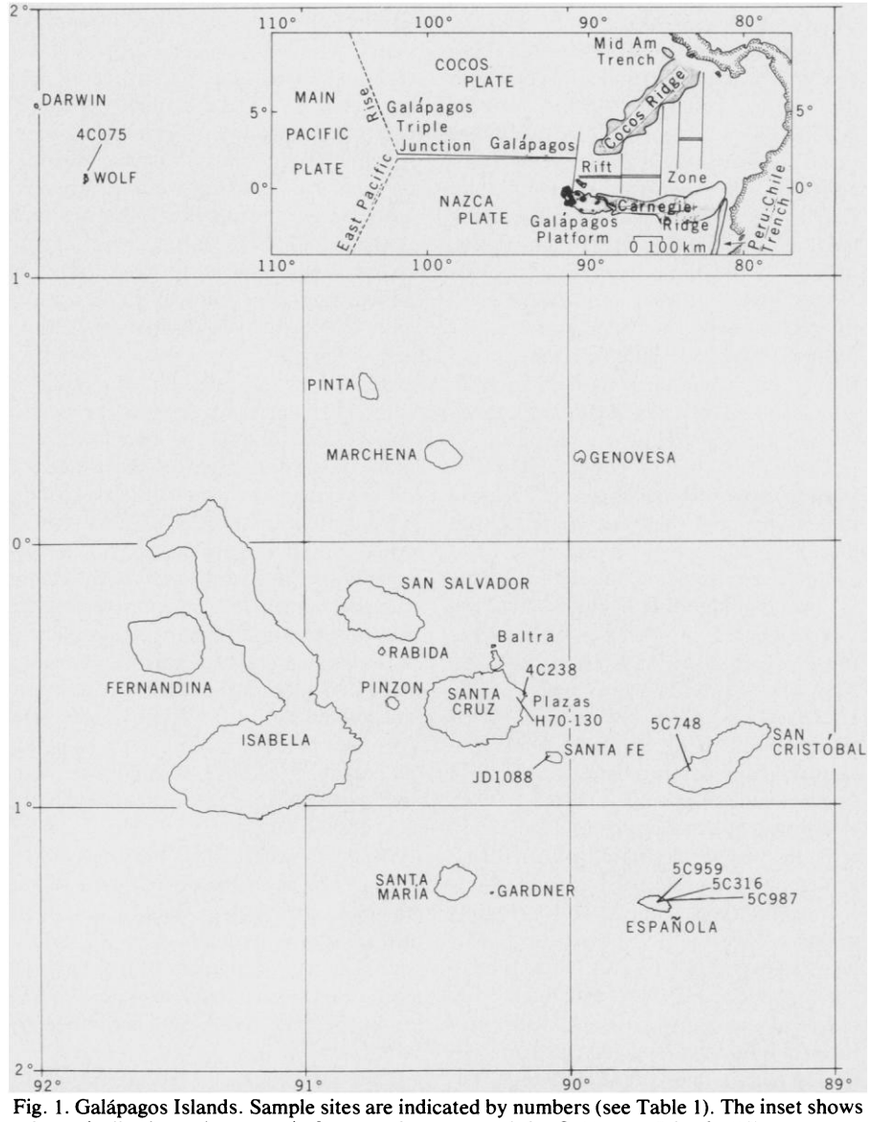

Fig. 1. Galápagos Islands. Sample sites are indicated by numbers (see Table 1). The inset shows schematically the major tectonic features that surround the Galápagos Islands (*15*).