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Two Contrasting Effects of Predation on Species Richness in Coral Reef Habitats

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Abstract

The species richness of sessile organisms on settlement panels on a coral reef was measured by the slope of a regression of $\log_e$ number of species against $\log_e$ area of sample. At a well illuminated site where panels were colonised by algae, the species richness of algae was 19% smaller on surfaces grazed by fishes than on protected surfaces. At a second site in a cave, the species richness of animals on grazed surfaces was 20% greater than on protected surfaces. These results are discussed in the light of differences between the sites. The contrasting effects of predation at the two sites are probably the result of more selective predation at the cave site than at the other site.

Introduction

One association of organisms is considered to be more diverse than another if (1) the first association contains more species than the second, i.e., if it has a greater species richness, or (2) if abundance is more evenly divided between species in the first association than the second.

Predation may increase or decrease the diversity of prey species. For example, predation increases species diversity in associations of intertidal sessile organisms (Paine, 1966, 1971, 1976), tropical forest trees (Janzen, 1970) and grassland plants (Hope-Simpson, 1940). On the other hand, Addicott (1974) concluded that predation decreased the number of species in the water-filled bracts of pitcher plants. Harper (1969), in reviewing the effects of grazing in grasslands, states that no general conclusion can be drawn as to the effects of predation on diversity.

In this study, the effects of predation on the species richness of associations of sessile organisms at two sites on the coral reef at Heron Island, Queensland, Australia, were investigated. The sites were chosen to represent two different habitats on the reef, with widely different physical conditions, and different species of predatory fish. Species richness was measured by means of an index which is described later.

Spatial heterogeneity can be important in maintaining species diversity (Menge and Sutherland, 1976). Natural surfaces on the reef almost invariably contain possible refuges such as small crevices. Flat settlement panels were, therefore, used to obtain samples of the sessile species which settle and grow at each site.

Materials and Methods

Two sites were chosen in shallow water on the reef at Heron Island, Queensland. Flat, brown "Novasteen" plastic settlement panels, measuring 220 x 240 mm and 120 x 140 mm, were suspended vertically, at least 0.3 m from the natural coral limestone, to obtain samples of the organisms which settled at each site. Site 1 was on the side of a large coral head, 6 m below the reef crest. Site 2 was in a large cave under the coral head, 1 m below Site 1. The levels of both illumination and water movement were lower at Site 2 than at Site 1.

Half of the settlement panels at each site were enclosed in cages of 20 mm mesh to exclude fish. The panels were immersed for 3 months, then collected and preserved. To reduce edge effects, areas within 10 mm of the edge of each panel were ignored when the panels were examined. In a preliminary experiment at

Site 1, where algae predominate, a number of algal species were found to be more abundant on limestone settlement surfaces than on plastic surfaces. Flat limestone settlement surfaces, made by glueing thin slices of giant clam shells to plastic panels, were therefore used at this site. At Site 2 plastic surfaces were used, as a preliminary experiment showed that there was very little difference in the abundances of species on plastic and limestone surfaces.

At Site 1, 8 sample areas of 2500 mm^2 each were examined from caged panels, and 8 from uncaged panels. At Site 2 the organisms were larger, and together, covered a smaller proportion of the settlement surfaces, so that a larger total sample area was required. I used a sample area of 5000 mm^2, and 40 samples from each of the two treatments, caged and uncaged, were examined.

I recorded the species of attached multicellular organisms larger than 0.5 mm^2 which were present in each sample. Species were given numbers when identification was not possible.

Analysis

Indices of species diversity depend on both "species richness" (the number of species in the community), and how evenly abundance is distributed among the species. Unless the entire community can be censused it is usually impossible to estimate the number of species in a community. In these cases, the two aspects of diversity cannot be estimated separately. However, if a particular relationship between the size of the sample and the number of species in the sample is assumed, then an index may be calculated from the data which describes the rate at which species are added as the sample size is increased. Such an index is called an index of species richness (Peet, 1974), although it depends both on the number of species in the community and the distribution of abundance among species. One such index was used in this paper.

For many studies of vegetation, a good empirical fit to field data is provided by the relation $S = cA^k$ (Kilburn, 1966), where S is the number of species in the sample, A is the area of the sample, and c and k are constants to be estimated from the data. c is the expected number of species in a sample of unit area, and is thus an index of "species density". k is an index of species richness in the sense discussed previously. May (1975) has derived a theoretical basis for the relation $S = cA^k$ for communities with a large number of species. The mathematical restrictions on the derivation described by May appear to be satisfied by the samples described in this paper, and I therefore assumed the relation between S and A discussed above. An alternative approach using the relation $S = a \log_e A^*$; where S is the number of species in a sample, a is an index of species richness, and A^* is the total abundance of all species together; produced very similar results. Abundances of species were measured as area of surface covered, in mm^2.

To estimate the number of species in samples of different sizes I used the following procedure. The samples from each site and treatment combination were arranged in three random orderings. Each ordering was considered in turn. The number of species in the first sample was counted, and the second sample was then combined with the first to form a larger sample. After the number of species in the combined sample had been counted, the next sample was added. This process was repeated until all the samples had been combined. Thus, a random ordering of a set of samples yielded estimates of the number of species in samples of increasing size. As I used three orderings, I obtained three estimates for each size of sample. I calculated the mean of $\log_e (S)$, where S is the number of species in the sample, for each sample size, and used a regression of $\log_e (S)$ on $\log_e (A)$, where A is the area of the sample, to estimate the constants c and k in the assumed relation $S = cA^k$ discussed above.

Results

Regressions on $\log_e (S)$ against $\log_e (A)$ for all site and treatment combinations were significant ($P = 0.01$, Table 1). The constants c and k estimated by these regressions were compared by means of a multiple-regression technique using dummy variables (Draper and Smith, 1966). The index of species density (c) was significantly higher for caged than for uncaged surfaces ($P = 0.01$), but did not differ significantly between sites (Table 2). Therefore, at both sites predation reduced the number of species living together on small areas.

For caged surfaces there was little difference in the value of the index of species richness (k) between sites (Table 1), but at Site 1, k was significantly smaller ($P = 0.01$) on uncaged than caged surfaces and at Site 2 k was significantly greater ($P = 0.01$) on uncaged than on caged surfaces (Table 2). Therefore, predation by fish reduced

Table 1. Results of regressions of $\log_e$ (number of species) against $\log_e$ (area of sample)

Site and treatment	Regression constants[a]		R^{2b}	No. of samples	F value and significance[c]
	C	k			
Site 1					
Caged surfaces	11.508	0.343	0.9922	8	760.0 S
Uncaged surfaces	5.641	0.278	0.9857	8	410.0 S
Site 2					
Caged surfaces	10.979	0.343	0.9881	40	3162.6 S
Uncaged surfaces	6.013	0.410	0.9671	40	1116.1 S

[a] Regression equation has form $\log_e (S) = \log_e (C) + k \log_e (A)$.
[b] R^2 = Proportion of total sum of squares attributable to the regression.
[c] S = Significant value of F at P = 0.01.

Table 2. F values and associated degrees of freedom from an analysis of differences in regression constants between sites and caging treatments

Effect tested by the regression analysis	F value	Associated degrees of freedom	Significance[a]
Effect on constant C of:			
Caging treatment	64.184	1,88	S
Sites	0.012	1,88	ns
Interaction	0.320	1,88	ns
Effect on constant k of:			
Caging at Site 1	70.814	1,12	S
Caging at Site 2	23.818	1,76	S

[a] S = Significant value of F at P = 0.01; ns = not significant at P = 0.01.

species richness at Site 1 whereas it increased species richness at Site 2.

These results are based on settlement panels which were immersed for 3 months. Other evidence (Day, unpublished data) suggests that similar results would be obtained from panels immersed for a longer period. Caged panels immersed for 6 months in caves on the reef at Heron Island were often covered completely by 3 or 4 species of ascidians, whereas uncaged panels immersed for 6 months in caves supported a large number of species. On the other hand, caged panels suspended at well-lit places similar to Site 1 for 6 months were covered by a wide variety of algal species. My observations indicate that the results are applicable to natural surfaces provided that small refuges from predation, such as crevices, are not considered.

Discussion and Conclusions

Characteristics of both prey and predators may be important in determining the effect of predators on the diversity of prey (Addicott, 1974). The prey species at the 2 sites I investigated were similar in many respects. At both sites the prey were sessile, and predators created patches of free space by removing prey organisms. Furthermore, at both sites competitive interactions between prey species appeared to be important. At Site 1 some species of algae were abundant only on grazed surfaces, which suggests they might have been suppressed on protected surfaces where a number of other species were abundant. At Site 2 some species of encrusting organisms grew over and smothered other species.

As described in "Results", a few species of ascidians eventually monopolized protected settlement panels in caves, whereas interactions between algal species on protected panels did not lead to the monopolization of these panels by a few species, at least within 6 months. However, the settlement panels considered here were immersed for 3 months only, and the caged panels from Site 2 were not dominated by a few species of ascidians.

The constrasting effects of predation on species richness at Sites 1 and 2 may be explained by differences in the foraging behaviour of predators.

The most important predators at Site 1 were herbivorous scarid and acanthurid fishes. The scarids scrape surfaces covered with algae, leaving broad toothmarks. Observations of the pattern of fish scrapes on panels exposed to fish for short periods at Site 1 indicate that the fish aim for small areas of dense algal growth, irrespective of

which species are present in those areas. As a result of this foraging behavior, each part of a surface would eventually be scraped. Choat and Robertson (1975) recorded about 300 scrapes m^{-2} h^{-1} on nearby coral heads covered by algae.

Pomacanthid and balistid fishes were important predators of sessile organisms at Site 2 and in other caves on Heron Island reef. These fish search for and remove colonies of ascidians and arborescent ectoprocts. I have observed that they attack the organisms on cave walls far less frequently than the scarid fishes feed.

The difference in the intensity of predation at the two sites may partly explain the contrasting effects of predation on species richness at each site. Emlen (1973) and Addicott (1974) have argued that intense grazing will result in a reduction of the diversity of prey organisms, whereas mild predation may lead to an increase in prey diversity. Paine and Vadas (1969) found that after sea-urchins were removed from rocks and pools a large number of new algal species colonised these areas, but that after periods of 2 or 3 years one or two species predominated where the urchins had been removed. They suggested that algal diversity would be increased by intermittent grazing by urchins, whereas severe grazing led to low algal diversity.

The effect of predation on prey diversity may depend on whether the predators select particular species of prey, and which species they select. Paine (1966) proposed that prey diversity is determined by the extent to which predators prevent the monopolisation of resources by one species. This implies that a predator which selects competitively dominant species of prey in preference to other species will be most effective in increasing prey diversity. The sea stars studied by Paine (1966, 1971, 1974) select dominant species. Similarly, host-specific seed-eating insects prevent species of tropical forest trees from becoming abundant, so that space is made available for a large number of tree species (Janzen, 1970, 1973).

At my Site 1, the herbivorous fish apparently do not select particular species. In the face of this non-selective grazing, only those species of algae which colonise new surfaces rapidly may become abundant on grazed surfaces. Some species of filamentous algae, for example *Ectocarpus* spp. and *Lophosiphonia* sp. were much more abundant on the uncaged panels than on the caged panels. Most species of algae however, were severely reduced in abundance on the uncaged compared with the caged surfaces.

In caves such as that at Site 2, the more selective fish predators effectively prevent the eventual monopolization of space for settlement and growth by species of ascidians. They also remove species of arborescent ectoprocts. As the species which covered the largest areas on the caged panels at Site 2 were arborescent ectoprocts and compound ascidians, the effect of predation on the settlement panels was to reduce the numbers of the most abundant species. Predation led to a more even distribution of abundance between species on the grazed panels.

The predatory fish at Site 2 reduced the number of species on small areas of surface, but as many of the species attacked occurred occasionally on uncaged samples, species were added more rapidly as the sample size was increased. The increased species richness on the panels subject to predation at Site 2 was therefore the result of a change in the distribution of abundance between species, rather than a change in the number of species which could occur on the grazed surfaces. This illustrates that indices of species richness such as the one used here are sensitive to the relative abundances of species as well as the number of species, and also that it may be misleading to use the number of species in a sample of fixed size to compare communities, as is done by some authors.

Why did not the predatory fish at Site 2 completely eliminate the species they selected from the unprotected panels? Because the fish in caves feed on some of the sessile species and not on others, the cave walls, or settlement panels, covered with sessile organisms must appear to be spatially heterogeneous to the fish. As a result, the fish would have to search far longer for some prey items than others (Smith, 1972). If a man were searching for coloured stones lying on a mosaic he would have to search much longer for some stones than others. Therefore, a few of the selected prey items would survive for long periods on unprotected surfaces, and the species subject to predation would never be entirely eliminated.

At Site 1, the herbivorous fish attacked all the organisms on the panels. The fish treated the surfaces of the panels as homogenous areas.

In many respects both the communities investigated here are similar to the communities investigated by Paine (1966, 1971). The prey are sessile, and appear to compete for space. Paine found that predation by sea stars increased species diversity. The sea stars, like the fish at Site 2 in the present study, selected

some species of potential prey and not others. The contrasting effects of predation on species richness at the two sites investigated here are best explained by the fact that whereas the fish at Site 2 were selective predators, the fish at Site 1 were not selective predators.

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