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Differential Fish Grazing and Benthic Community Structure on Hawaiian Reefs

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Introduction

Numerous field experiments have demonstrated the predominant role of herbivorous fishes in determining the local distribution and abundance of benthic algae on shallow tropical reefs (e.g., Stephenson and Searles, 1960; Randall, 1961; Earle, 1972; Vine, 1974; Day, 1977; Wanders, 1977; review by Ogden and Lobel, 1978). Intense grazing by parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) is known to result in most exposed coral-rock surfaces being covered by crustose coralline algae (e.g., Vine, 1974; Littler and Doty, 1975; Wanders, 1977; Brock, 1979). By aggressively excluding other fishes from their territories, certain herbivorous damselfishes (Pomacentridae) maintain filamentous algal mats of relatively high biomass and diversity (e.g., Brawley and Adey, 1977; Lassuy, 1980; Lobel, 1980).

The potential impact of fish grazing on benthic communities is similar to that of any other form of ecological disturbance. The "intermediate disturbance" hypothesis predicts that as the intensity or frequency of such disturbance progressively increases from zero, the species diversity of the affected community will initially increase then subsequently decrease (Connell, 1978). At low levels of disturbance, a few dominant competitors are capable of locally excluding most other species, and at high levels, many local extinctions occur. Diversity thus peaks at an intermediate disturbance level, where the coexistence of many species is maintained because their population densities are kept below levels where resources are limiting. This hypothesis has been supported by observations and experiments in several benthic marine systems subjected to physical disturbance (e.g., Connell, 1978; Sousa, 1979). To our knowledge, however, only Tansley and Adamson's (1925) study of grazing by terrestrial herbivores and Lubchenco's (1978) study of grazing by intertidal snails have experimentally demonstrated this effect occurring as a result of biological disturbance.

This paper summarizes the results of a field experiment designed to test the intermediate disturbance hypothesis for Hawaiian reef benthos subjected to differential grazing by fishes. Our prediction was that, because grazing intensity would be negligible within fish-exclusion cages, moderate inside damselfish territories, and intense outside territories, the benthic communities which developed on settling plates subjected to these three treatments would exhibit relative species diversity patterns similar to those presented in Figure 1. Our results, which will be detailed in a subsequent publication, confirmed this prediction. The data presented here are part of a broader study designed to investigate benthic succession on shallow coral reefs, the preliminary results of which have been presented elsewhere (Hixon and Brostoff, 1981).

Methods

Our study site was located along a 600-meter section of the subtidal windward reef crest off Coconut Island, located in Kaneohe Bay, Oahu, Hawaii (21°26' N Lat., 157°47' W Long.). Water depths at this site average about one meter. The substrate consists of a flat bench of dead Porites compressa coral rock, upon which damselfish establish, maintain and defend algal mats measuring less than a meter in diameter. The dominant grazers here are the damselfish Stegastes fasciolatus (= Eupomacentrus fasciolatus = Pomacentrus jenkinsi), several surgeonfish species (especially Acanthurus triostegus), and juveniles of various parrotfishes, which are the most abundant fishes on this reef (see Brock et al. 1979). Sea urchins are rare at this site.

To minimize the bias associated with using a single artificial substrate, we followed benthic succession on three types of settling plates: (1) roughly sanded grey polyvinyl chloride plastic (PVC), which had the advantages of being nearly chemically inert and allowing virtually complete removal of attached organisms, but the disadvantage of being

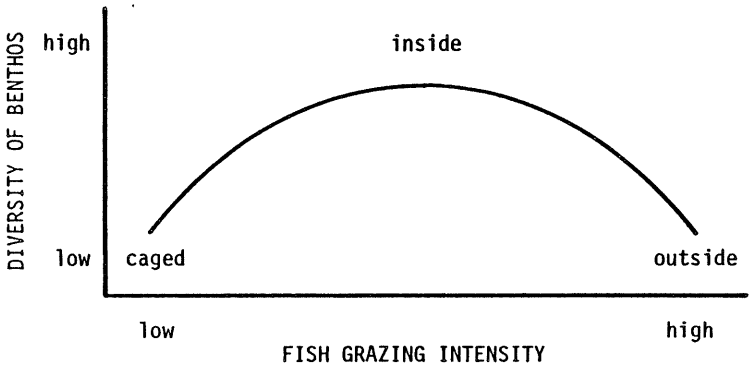

Figure 1. Predictions of the intermediate disturbance hypothesis for the maintenance of local benthic diversity as a function of three levels of fish grazing intensity: within fish-exclusion cages, inside damselfish territories, and outside territories. See text.

an unnatural substrate; (2) flatly cut Porites coral rock, which had the advantages of being the natural substrate and allowing removal of nearly all attached organisms, but the disadvantage of being unnaturally flat; and (3) naturally contoured Porites coral rock, which had the advantage of being the natural substrate in both composition and relief, but the disadvantage of irregular contours precluding exact area measurements. The PVC plates additionally provided a measure of relative fish grazing intensity, since individual bite marks, although present on all three substrates, were clearly visible and countable on this substrate alone. The area of each PVC and flat coral-rock settling plate was 50 cm^2. This area, and the sample sizes described below, were chosen from species-area and biomass-area curves obtained during a preliminary study.

A total of 1344 settling plates were mounted horizontally and coplanarly on 112 concrete blocks, each measuring 18 cm x 18 cm x 10 cm and supporting four of each plate type. In September 1980, 96 of these blocks were distributed simultaneously and evenly among three field treatments: inside territories (exposed nearly exclusively to damselfish grazing); outside territories (exposed mostly to parrotfish and surgeonfish grazing); and within cages (protected from fish grazing). Blocks were arranged in sets of three, such that a given territory contained one exposed block, with one exposed and one caged block located several meters outside the territory at approximately the same depth and degree of wave exposure. (The presence of a block within a territory did not appear to disturb the resident damselfish, but a cage caused obvious disturbance. Hence, all cages were necessarily placed outside territories.)

The cages were constructed of 1.3 cm x 1.3 cm galvanized wire mesh and were 60 cm x 60 cm x 30 cm in volume, so no plate was mounted closer than 15 cm from the wall of a cage. Exterior cage surfaces were prevented from fouling by the intense grazing activity of fishes, while interior surfaces were periodically cleaned by divers. (The effects of the cages on water motion and light penetration were measured with dissolving plaster-of-Paris "clod-cards" [Doty, 1971] and comparative photometer readings, respectively. A cage-control experiment, involving 16 settling-plate blocks and including wall-only [no roof] and roof-only [no wall] cages, tested these and other potential secondary effects. These data will be reported in detail elsewhere.)

During the succession experiment, 63 settling plates (3 treatments x 3 substrates x 7 replicates) were sampled without replacement each week for ten weeks, then each month for six months, with a final sample (reported here) at the end of one year. Thus, a total of 1071 settling plates were sampled during the one-year duration of the experiment (September 1980 to September 1981).

After being photographed, each plate was rinsed free of loose detritus and sediment (which were analyzed separately), and all macroscopic animals were removed, counted, and identified. The relative abundance of crustose coralline algae was estimated visually as percent cover. The remaining algae were then scraped from the plate, wet weighed, examined microscopically, dry weighed, and ash weighed. The naturally contoured coral-rock plates were examined microscopically only, since accurate area measurements were impossible.

For microscopic examination, the algae from a single plate were spread uniformly within a glass petri dish and scanned to determine the total number of species present. A total of 100 randomly selected points within the dish were then examined under 100-power magnification, and the alga occupying the central point of each ocular field was recorded. The total number of species per plate observed by this method was almost invariably identical to that determined by complete scanning, indicating that we had adequately sampled the local species "universe" (see Peet, 1974). This method thus provided an estimate of the proportional relative abundance of each algal species (excluding corallines), and accounted simultaneously for both the number and size of different plants (see Jones, 1968; Montgomery, 1980). Coralline algae could not be removed effectively from the plates; however, no more than two coralline species occurred throughout our study site (see also Littler and Doty, 1975).

The measurement of species diversity has always been a controversial topic because each proposed index contains inherent bias (Hurlbert, 1971; Peet, 1974). To minimize this problem, we analyzed our relative abundance data using seven different diversity measures: (1) the total number of species found on all plates within one treatment and (2) the mean number of species per plate within one treatment, both of which are the only truly objective measures of diversity (Poole, 1974); (3) the Shannon-Wiener index (H'), a traditionally popular measure for which statistical analyses have been derived (Pielou, 1966; Hutcheson, 1970); (4) the exponentiated Shannon-Wiener index and (5) the reciprocal of the Simpson index, which are most sensitive to changes in the proportions of rare and common species, respectively, and which are related by Hill's (1973) unifying notation; (6) Pielou's (1966) evenness index (J), which measures the equitability of relative abundances among species; and finally (7) dominance, which is simply the proportional abundance of the most common species, an inverse measure of evenness advocated by May (1975).

Results

Table 1 summarizes the results of the final sample of 63 settling plates after a one-year exposure to the three field treatments, along with previous data on relative grazing intensities. For simplicity and brevity, these results are pooled for all three types of settling plates (except where noted below). The "approximate t-test" of Sokal and Rohlf (1969), which assumes and compensates for unequal variances, was used for comparisons of mean parameter values between treatments. Diversity (H') comparisons were calculated according to Poole (1974). The results of the cage-control experiment, which will not be detailed here, revealed no substantial secondary effects of caging.

Comparisons of uncaged PVC plates during the first ten weeks of the succession experiment revealed that the mean number of fish bite marks per plate outside damselfish territories was significantly greater than that inside. Thereafter, bite marks on plates outside territories became too dense to count accurately. No bite marks were found on caged plates. Thus, fish grazing was most intense outside territories, intermediate inside territories, and nonexistent within cages.

Inversely correlated with this pattern of grazing intensity, the mean ash-free dry-weight biomass of noncoralline algae on the PVC and flat coral-rock plates after one year was significantly greatest within cages,

Table 1. Summary data on the benthic communities that developed on settling plates after a one-year exposure to the three field treatments (n = 21 each, except for invertebrates per plate and ash-free dry-weight biomass, for which n = 14 each). The data on fish bites per plate were gathered during the first 10 weeks of the succession experiment (n = 63 each). Significance levels are given for comparisons of adjacent means (approximate t-tests). Species diversity (H') comparisons were calculated according to Poole (1974). See text.

	Outside Territories		Inside Territories		Within Cages
Primary Grazer:	Parrotfishes		Damselfish		None
Bites / Plate:	269.6	***	14.9	***	0.0
Inverts / Plate:	1.7	*	34.3	ns	48.8
Algae--					
Biomass (g/m^2):	6.2	***	28.6	***	10.3
Species Total:	13		20		17
Species / Plate:	3.8	***	7.9	**	5.3
Diversity (H'):	1.16	***	2.19	***	1.85
Evenness (J):	0.45		0.73		0.65

***: P<0.001, **: P<0.01, *: P<0.05, ns: not significant (P>0.05).

moderate inside territories, and low outside territories. Correspondingly, the mean number of invertebrates per plate after one year was greatest within cages and inside territories, and negligible outside territories. By rank abundance, these invertebrates included mostly holothuroidean and stomatopod postlarvae, as well as small polychaete worms, harpacticoid copepods, and several rarer taxa.

All seven indices indicated that the diversity of noncoralline algae was significantly greatest inside damselfish territories compared to that either within cages or outside territories. Because of this, only the values of four representative measures are presented in Table 1. Thus, the treatment subjected to intermediate grazing intensity exhibited the greatest diversity of algae.

By rank mean proportional abundance, the dominant erect algae on settling plates located inside territories included the filamentous species Centroceras clavulatum (C. Agardh) Montagne, Ectocarpus indicus Sonder in Zollinger, and Polysiphonia rhizoidea Meñez, which together accounted for only 29.9% of the algae present. On the other hand, plates within cages were stongly dominated by Tolypiocladia glomerulata (C. Agardh) Schmitz, which alone accounted for 47.5% of the algae present. Plates outside territories were covered mostly by crustose coralline algae.

Discussion

The results of this experiment suggest that fish grazing does indeed control the local distribution and abundance of benthos on flat coral-rock surfaces of at least one shallow Hawaiian reef. Grazing intensity increases progressively from surfaces within fish-exclusion cages to those inside damselfish territories (subjected to grazing mainly by a single damselfish) to those outside territories (subjected to intense grazing by numerous parrotfishes and surgeonfishes). With increased grazing, the biomass of erect algae and the abundance of associated small invertebrates expectedly decreases, while the coverage of crustose coralline and prostrate algae increases.

These results also support our prediction that differential fish grazing has intermediate disturbance effects on algal species diversity in this system (see Figure 1). The diversity of algae by seven different measures was significantly greatest at intermediate grazing intensity within damselfish territories.

What are the mechanisms that produced this pattern? Outside territories, intense nonselective grazing by parrotfishes and surgeonfishes simply eliminates most erect algae and associated fauna, leaving only a low-diversity assemblage of grazer-resistant prostrate and crustose forms (see also Brock, 1979; Lobel, 1980). Within cages, where fish grazing is effectively prevented, algal succession proceeds without interruption as prostrate and crustose forms are overgrown. This results in an initial relatively rapid increase in both diversity and biomass, such that after six months algal diversity is actually greater within cages than inside territories (Hixon and Brostoff, 1981). However, following this intermediate stage, diversity characteristically decreases as several late-successional species become dominant (review by Connell, 1978). The ultimate result is that, within one year, the diversity of algae within cages falls below that inside damselfish territories.

Inside territories, grazing by a single resident damselfish apparently maintains the relatively high algal diversity characteristic of intermediate successional stages (see Connell, 1978). Lubchenco (1978) provides data suggesting a possible mechanism by which damselfish might accomplish this effect. Her series of experiments on intertidal snails and algae suggest that intermediate disturbance effects on algal diversity occur where herbivores selectively consume or otherwise remove competitively dominant species. Previous studies suggest that territorial damselfishes are often selective grazers (Lassuy, 1980; Lobel, 1980; Montgomery, 1980), and may additionally "weed-out" undesirable species from their algal mats (Foster, 1972; Lassuy, 1980; Irvine, this volume). Ongoing paired comparisons of the gut contents of our local damselfish relative to the species composition of their algal mats will determine whether or not similar mechanisms occur in our system, although many hours of field observation have revealed no evidence of weeding behavior (Hixon, unpublished).

In any event, it is apparent that territorial damselfishes are capable of enhancing and maintaining the local diversity of reef algae through intermediate disturbance effects. Other studies have also determined that these fishes are able to control the local abundance of living coral (Kaufman, 1977; Potts, 1977; Wellington, 1981) and sea urchins (Williams, 1979, 1980, 1981). Thus, territorial damselfishes may be considered true "keystone species" (sensu Paine, 1969) for their ability to regulate benthic community structure on tropical reefs.

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Literature Cited

Brawley, S. H., and W. H. Adey. 1977. Territorial behavior of three-spot damselfish (Eupomacentrus planifrons) increases reef algal biomass and productivity. Env. Biol. Fish. 2:45-51.

Brock, R. E. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol. 51:381-388.

Brock, R. E., C. Lewis, and R. C. Wass. 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. Mar. Biol. 54: 281-292.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Day, R. W. 1977. Two contrasting effects of predation on species richness in coral reef habitats. Mar. Biol. 44:1-5.

Doty, M. S. 1971. Measurement of water movement in reference to benthic algal growth. Bot. Mar. 14:32-35.

Earle, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshure Bay, with an annotated list of plants. Sci. Bull. Los Angeles Natur. Hist. Mus. 14:17-44.

Foster, M. S. 1972. The algal turf community in the nest of the ocean goldfish, Hypsypops rubicunda. Proc. 7th Int. Seaweed Symp. 1:55-60.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432.

Hixon, M. A., and W. N. Brostoff. 1981. Fish grazing and community structure of Hawaiian reef algae. Proc. 4th Int. Coral Reef Symp. 1: in press.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon Formula. J. Theor. Biol. 29:151-154.

Jones, R. S. 1968. A suggested method for quantifying gut contents in herbivorous fishes. Micronesica 4:369-371.

Kaufman, L. 1977. The threespot damselfish: effects on benthic biota of Caribbean coral reefs. Proc. 3rd Int. Coral Reef Symp. 2:559-564.

Lassuy, D. R. 1980. Effects of "farming" behavior by Eupomacentrus lividus and Hemiglyphidodon plagiometopon on algal community structure. Bull. Mar. Sci. 30:304-312.

Littler, M. M., and M. S. Doty. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of Porolithon. J. Ecol. 63:117-129.

Lobel, P. S. 1980. Herbivory by damselfishes and their role in coral reef community ecology. Bull. Mar. Sci. 30:273-289.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.

May, R. M. 1975. Patterns of species abundance and diversity, p. 81-120. In: M. L. Cody and J. M. Diamond (eds.) Ecology and evolution of communities. Belknap-Harvard; Cambridge, Mass.

Montgomery, W. L. 1980. The impact of non-selective grazing by the giant blue damselfish, Microspathodon dorsalis, on algal communities in the Gulf of California, Mexico. Bull. Mar. Sci. 30:290-303.

-----. 1980. Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. J. Exp. Mar. Biol. Ecol. 47:9-24.

Ogden, J. C., and P. S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Env. Biol. Fish. 3:49-63.

Paine, R. T. 1969. A note on trophic complexity and community stability. Am. Nat. 103:91-93.

Peet, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5:285-307.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 10:131-144.

Poole, R. W. 1974. Introduction to quantitative ecology. McGraw-Hill; New York, N.Y.

Potts, D. C. 1977. Suppression of coral populations by filamentous algae within damselfish territories. J. Exp. Mar. Biol. Ecol. 28: 207-216.

Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42:812.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. Freeman; San Francisco, Ca.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60: 1225-1239.

Stephenson, W., and R. B. Searles. 1960. Experimental studies on the ecology of intertidal environments at Heron Island. I. Exclusion of reef fish from beach rock. Aust. J. Mar. Freshwater Res. 2:241-267.

Vine, P. J. 1974. Effects of algal grazing and aggressive behaviour of the fishes Pomacentrus lividus and Acanthurus sohal on coral-reef ecology. Mar. Biol. 24:131-136.

Wanders, J. B. W. 1977. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: the significance of grazing. Aquatic Botany 3:357-390.

Wellington, G. M. 1981. The role of competition, niche diversification, and predation on the structure and organization of a fringing coral reef in the Gulf of Panama. Ph.D. diss., University of California at Santa Barbara.

Williams, A. H. 1979. Interference behavior and ecology of threespot damselfish (Eupomacentrus planifrons). Oecologia 38:223-230.

-----. 1980. The threespot damselfish: a noncarnivorous keystone species. Am. Nat. 116:138-142.

-----. 1981. An analysis of competitive interactions in a patchy back-reef environment. Ecology 62:1107-1120.