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Proceedings of the Fourth International Coral Reef Symposium, Manila, 1981, Vol. 2

FISH GRAZING AND COMMUNITY STRUCTURE OF HAWAIIAN REEF ALGAE

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ABSTRACT

On tropical reefs, intense grazing by parrotfishes and surgeonfishes is known to result in most exposed coral-rock surfaces being covered by crustose coralline algae. Substrates within damselfish territories, however, are dominated by various species of filamentous red and brown algae. While this difference is partly due to damselfish aggressively excluding other grazers from their territories, the exact effects of differential fish grazing on reef algal succession remain largely unknown. To investigate these processes experimentally, 1263 coral-rock and PVC-plastic settling plates were distributed among three field treatments: exposed inside damselfish territories, exposed outside territories, and within grazer exclusion cages. Preliminary analyses of plates sampled during the first six months of this study revealed different patterns of algal succession and species diversity. Exposed plates outside territories quickly became dominated by low-diversity prostrate green algae, which were gradually replaced by a crustose coralline assemblage. Initially, plates inside territories exhibited greater algal diversity than those within cages, though both treatments were dominated by the same filamentous species. Eventually, however, an algal assemblage of greater diversity developed on the caged plates, while communities within territories remained at an intermediate successional stage. These initial results suggest that intense fish grazing outside territories drastically alters algal succession at its earliest stages by allowing only several prostrate forms to persist, while succession within damselfish territories follows a relatively undisturbed sequence that is terminated at an intermediate stage of moderate diversity.

INTRODUCTION

The predominant role of herbivorous fishes and urchins in determining the local distribution and abundance of algae on shallow tropical reefs cannot be overemphasized (Ogden and Lobel 1978). Numerous substrate caging and grazer removal experiments have demonstrated this fact unequivocally (Stephenson and Searles 1960, Randall 1961a, Earle 1972, Ogden et al. 1973, Sammarco et al. 1974, Vine 1974, Day 1977, Wanders 1977). The principal herbivorous fishes on coral reefs are parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and territorial damselfishes (Pomacentridae) (Ogden and Lobel 1978). Intense grazing by parrotfishes and surgeonfishes 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, damselfish maintain filamentous algal mats of relatively high biomass and diversity (e.g., Brawley and Adey 1977, Lassuy 1980, Lobel 1980). At least some damselfishes can additionally both reduce the abundance of urchins (Williams 1979) and directly or indirectly inhibit coral growth (Kaufman 1977, Potts 1977, Wellington 1981) inside their territories. Thus, these fishes may be accurately labelled "keystone species" for their ability to regulate local reef community structure (Paine 1966, Williams 1980).

Beyond these general trends, the mechanisms producing these patterns and their temporal sequence remain largely unknown. We report here initial results from an ongoing controlled field experiment designed to investigate these phenomena in detail. This experiment is monitoring algal succession and associated factors inside and outside damselfish territories simultaneously on both natural and artificial substrates, and comparing these patterns with those occurring on ungrazed caged surfaces. Our discussion offers tentative speculation on two fundamental questions. First, how does differential fish grazing affect the local diversity of subtidal algae on Hawaiian reefs? Second, how does fish grazing alter algal succession in these systems?

METHODS

This section outlines our entire methodology, although our complete results will not be presented here. Our study site is located along a 600-m section

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of the subtidal windward reef crest off Coconut Island, located in Kaneohe Bay, Oahu, Hawaii. 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 and maintain algal mats. The dominant grazers here are the damselfish *Stegastes fasciolatus (=Eupomacentrus fasciolatus=Pomacentrus jenkinsi),* several surgeonfish species (especially *Acanthurus triostegus),* and juveniles of various parrotfishes (Brock et al. 1979). Urchins are rare at this site.

To minimize the bias associated with using a single artificial substrate, we followed algal succession on three types of settling plates: (1) roughly sanded grey polyvinyl chloride plastic (PVC), which had the advantages of being chemically inert and allowing virtually complete removal of attached organisms, but the disadvantage of being 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 parrotfish grazing intensity, since bite marks on this substrate were clearly visible and quantifiable. The area of each PVC and flat coral-rock settling plate was 50 cm^2. This area, as well as the sample sizes described below, were chosen from species-area and biomass-area curves obtained during a preliminary study.

A total of 1263 settling plates were mounted horizontally and coplanarly on 18 cm × 18 cm × 10 cm concrete blocks, with four of each plate type per block. In September 1980, 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 cages were constructed of 1.3 cm × 1.3 cm galvanized wire mesh and were 60 cm × 60 cm × 30 cm in volume, so no plate was mounted closer than 15 cm from the wall of a cage. 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. These and other potential secondary effects were separated and controlled experimentally by monitoring settling plates within wall-only (no roof) and roof-only (no wall) cages.

A total of 63 settling plates (3 treatments × 3 substrates × 7 replicates) were sampled weekly for ten weeks, then monthly for six months, with a final sample at the end of one year. After being photographed, each plate was rinsed free of loose detritus and sediment (which were weighed separately), and all macroscopic animals (a consistently minor component) were removed, quantified, and identified. The relative abundance of crustose coralline algae was estimated 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. 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. (Diatoms, microscopic animals, and remaining detritus were also quantified.) This method provided an estimate of the percent relative abundance of each algal species (excluding corallines), and accounted simultaneously for both the number and size of different plants (Jones 1968b, Montgomery 1980a). These data were used to calculate standard Shannon-Weiner diversity (H') and evenness (J) indices (Poole 1974). (Because they could not be removed effectively from the plates, coralline algae were excluded from the diversity calculations.)

Comparable data for natural reef surfaces were gathered by removing nearly flat pieces of reef rock from inside and outside damselfish territories and removing all algae within 50 cm^2 quadrats. Fish gut-content samples were taken concurrently.

RESULTS

Due to textual constraints and because this project is still in progress at this writing, we present here only a portion of the data from the first six months of the study. For simplicity and brevity, these results are pooled for all three types of settling plates (except where noted), and thus are analyzed somewhat superficially. The results of the experimental cage controls, which will not be detailed here, revealed no substantial secondary effects of caging.

Comparisons of uncaged PVC plates during the first eight weeks of the succession experiment revealed that the mean number of parrotfish bite marks per plate outside damselfish territories (241) was significantly greater than that inside (15,

$P<0.001$, $n=56$ each, t-test). Thereafter, bite marks outside territories became too dense to quantify accurately. No bite marks were found on caged plates.

By the seventh week of the experiment, the total number of non-coralline algal species on all plate types became and subsequently remained relatively high within cages, slightly lower inside territories, and very low outside territories (Fig. 1A). (Total algal biomass followed a similar pattern.) While the rate of species accumulation in each treatment decreased through time, it is impossible to state presently whether or not an upper limit of species abundance had been reached after six months (Fig. 1A). Values of the Shannon-Weiner diversity index (which increases as both the number of species and the equitability of their relative abundances increase) remained relatively low outside and high inside territories (Fig. 1B). Diversity values within cages were initially lower than those inside territories, but increased erratically until they consistently exceeded those inside territories by the seventh week (Fig. 1B). By the third week of the experiment, species evenness (which increases only as the equitability of relative abundances among species increases) became consistently low outside territories and remained nearly equally high inside territories and within cages (Fig. 1C).

An examination of the simple pooled relative abundances of dominant taxa through time reveals the sources of these trends in diversity. As a result of relatively intense fish grazing, nearly all erect algal species were continuously excluded from exposed plates outside territories. Within three weeks, these plates became strongly dominated by an amorphous layer of prostrate green algae (Fig. 2A). When cultured in the laboratory, filaments of *Enteromorpha* sp. (and to a lesser extent *Cladophora* sp.) grew upward from this layer (see also Lubchenco and Cubit 1980). Gradually, the dominant coverage of prostrate greens was replaced by crustose corallines (Fig. 3). Thus, intense grazing resulted in strong dominance by a few taxa capable of surviving as relatively invulnerable prostrate forms.

Relative abundance patterns inside territories and within cages were much more similar to each other than to those outside territories. As comparative indicators of grazing intensity, prostrate green and coralline algae were relatively minor components of both treatments, but were consistently more abundant within territories (Fig. 2B and C, Fig. 3). Both treatments were dominated sequentially by the green filamentous *Enteromorpha lingulata* J. Agardh, during the first several weeks of the experiments, followed by the brown filamentous *Ectocarpus indicus* Sonder for about the next ten weeks (Fig. 2B and C). Thereafter, substrates inside damselfish territories remained dominated by *Ectocarpus,* while those within cages became dominated by two similar red algae, *Centroceras clavulatum* (C. Agardh) Montagne and *Ceramium fimbriatum* Setch and Gard. (Fig. 2B and C). Subsequent samples unreported here have verified this incipient trend. Note that the relative abundance of *Ectocarpus* (and *Enteromorpha)* within cages exhibited a definite gradual decline through time (Fig. 2C), while that within territories remained relatively stable (Fig. 2B).

Preliminary analyses of quadrat samples from natural reef surfaces suggested that fully mature algal communities had not yet developed on the settling plates after six months. Uncaged plates outside damselfish territories had attained an average of 20% cover of coralline species (Fig. 3B), while natural reef surfaces exhibited well over 50% cover. Consequently, non-coralline species diversity on the plates ($H'=1.23$, Fig. 1B) was significantly greater than that on natural reef surfaces ($H'=0.97, P<0.01$, $df=52$, t-test). Uncaged plates inside territories were dominated by *Ectocarpus* (43% relative abundance) after six months (Fig. 2B), while natural reef surfaces were dominated by *Gelidium* sp. (35%) and *Polysiphonia rhizoidea* Meñez (28%). However, overall species diversity on the plates ($H'=1.89$, Fig. 1B) was virtually identical to that on natural surfaces ($H'=1.87$).

Comparisons between the samples from natural reef surfaces revealed that both species diversity ($H'=1.87$ vs. 0.97) and dry weight biomass (206 vs. 80 g/m^2) were significantly greater inside damselfish territories than outside ($P<0.001$. $n=8$ each, Mann-Whitney U-test), with species evenness ($J=0.68$ vs. 0.70) being nearly identical. Therefore, although algal succession on the settling plates was apparently incomplete after six months, the existing communities exhibited the same relative patterns in diversity as those on natural reef surfaces.

DISCUSSION

How does differential fish grazing affect the local diversity of subtidal algae on Hawaiian reefs? These initial results indicate that the answer to this question may depend upon the successional stage considered. During the first six weeks of our experiment, damselfish territories (intermediate grazing intensity) exhibited greater algal diversity than either caged substrates (no grazing) or exposed uncaged substrates (high grazing intensity), suggesting an "intermediate disturbance" effect (sensu Connell 1978). After six weeks, however, caged substrates consistently exhibited the greatest diversity, suggesting an inverse relationship between grazing intensity and algal diversity. Lassuy (1980) observed this latter pattern in another damselfish system at Guam.

Previous experimental studies of marine herbivore systems have suggested that each of these two patterns occurs as a function of the relationship between grazer food preferences and algal competitive abilities (e.g., Day 1977, Lubchenco 1978). Where herbivores selectively graze competitively in-

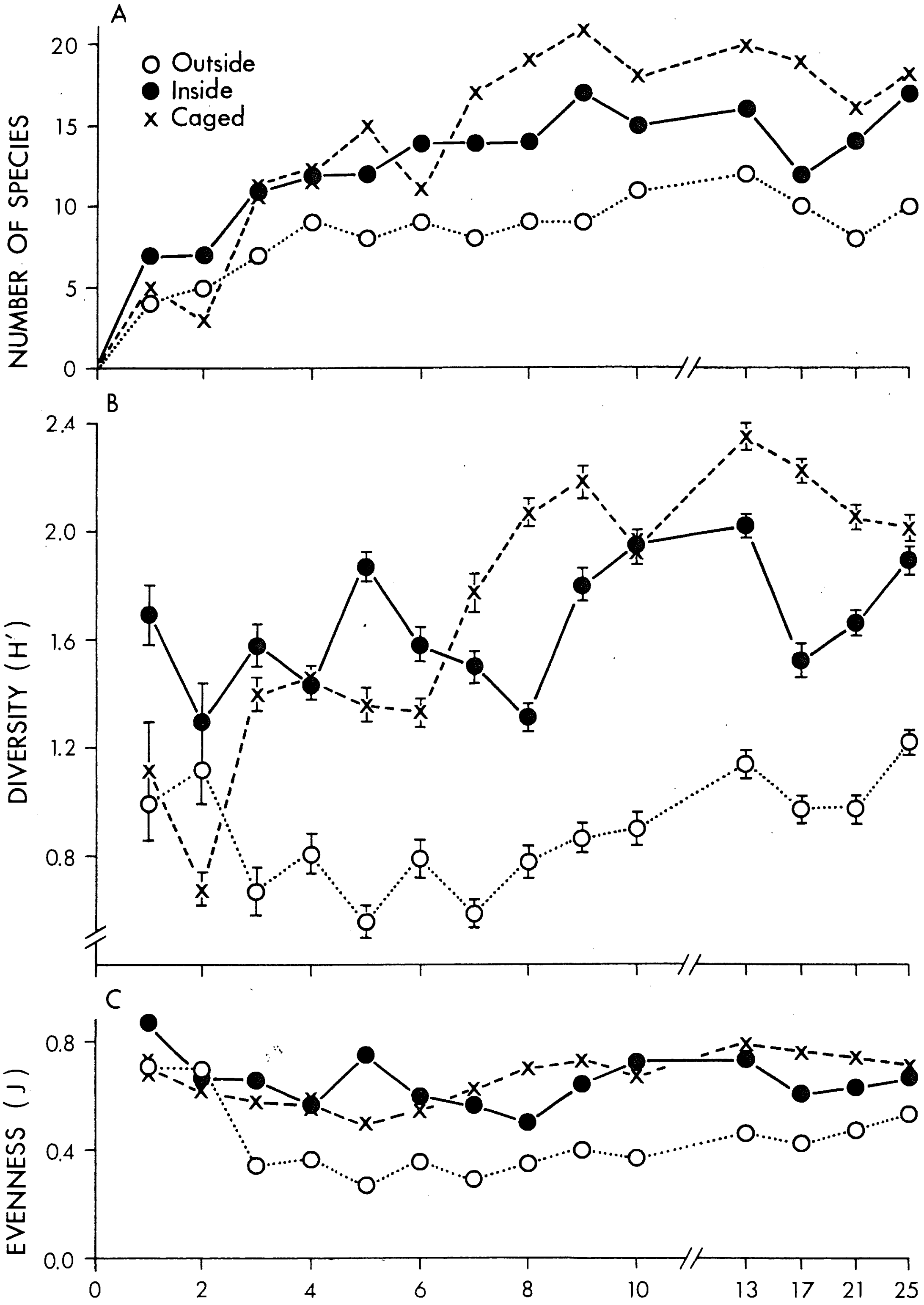

Figure 1. Temporal patterns in (**A**) the total number of species, (**B**) diversity, and (**C**) evenness of non-coralline algae in settling plates exposed outside and inside damselfish territories and within grazer exclusion cages. Each point represents data from 21 plates. Diversity value intervals are ± standard errors calculated according to Poole (1974).

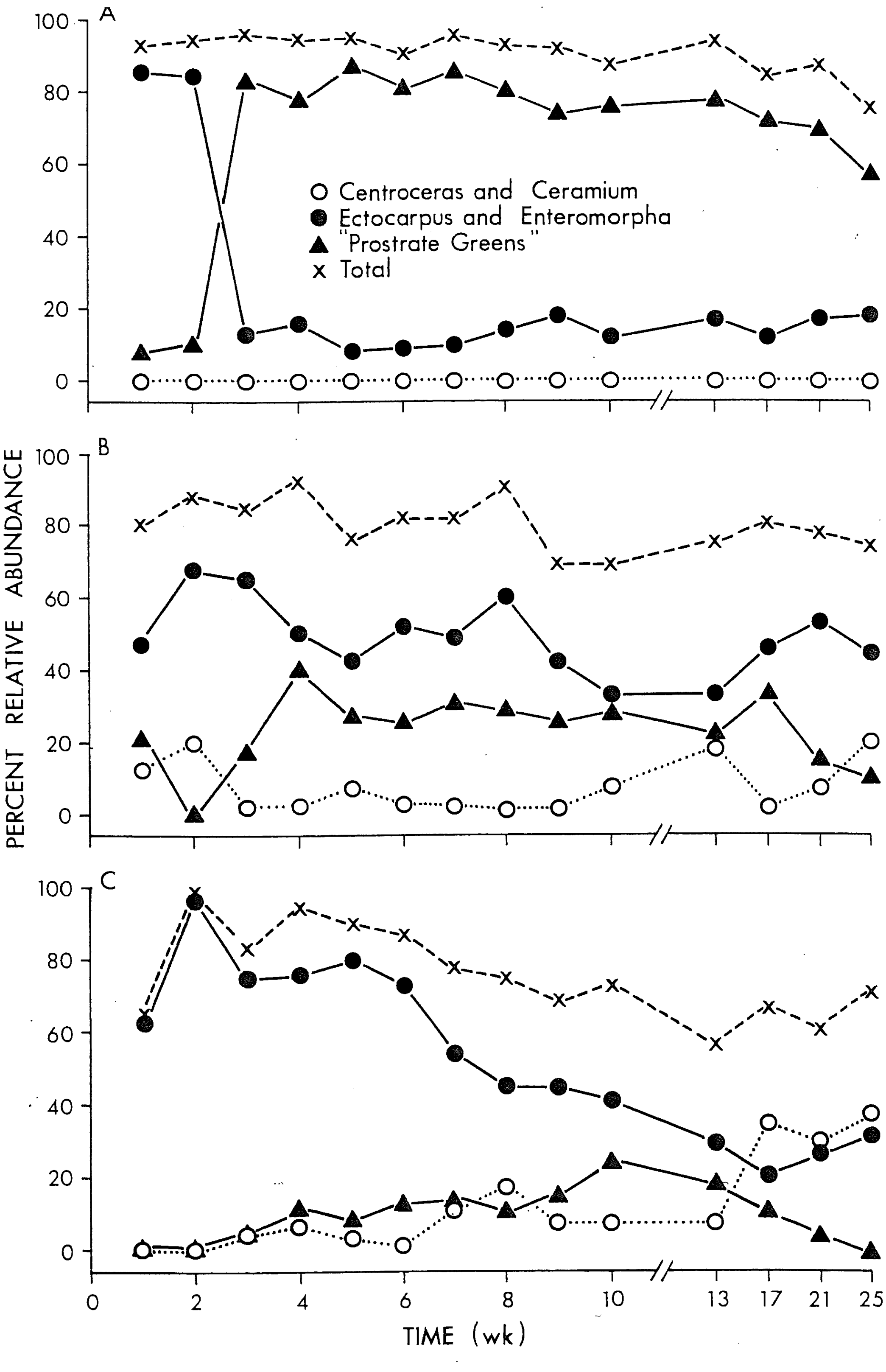

Figure 2. Temporal patterns in the percent relative abundance of the dominant algae on settling plates located (**A**) outside damselfish territories (**B**) inside territories, and (**C**) within cages. Each point represents a pooled sample of 63 plates. *Centroceras* and *Ceramium* are plotted together because they consistently co-occurred at similar abundance. *Ectocarpus* and *Enteromorpha* are plotted together because the former nearly completely replaced the latter after several weeks.

ferior algae (Lubchenco 1978) or are entirely nonselective (Day 1977), increased grazing intensity results in decreased algal diversity as rare species are progressively eliminated. Available field evidence suggests that Hawaiian parrotfishes and surgeonfishes are nonselective grazers of the dominant algae present on our settling plates (Randall 1961b, Jones 1968a, Hobson 1974, Brock 1979), although *Acanthurus triostegus* will exhibit preferences under controlled laboratory conditions (Randall 1961b). Territorial damselfishes, on the other hand, have been found to be either nonselective (Montgomery 1980 a, b) or selective grazers (Lassuy 1980, Lobel 1980, Montgomery 1980b). Preliminary analyses of *Stegastes fasciolatus* diets in relation to available algae tentatively suggest that our local damselfish is a relatively selective grazer. However, we are presently unable to conclude that this species prefers competitively inferior algae. If this preference is verified by ongoing analyses, then the inverse relationship between grazing intensity and algal diversity that occurred during the latter part of our experiment will be adequately explained.

As for the initial pattern we observed, Lubchenco (1978) provides data suggesting that where herbivores are selective for competitively superior algae, a unimodal relationship exists between grazing intensity and algal diversity. Low grazing

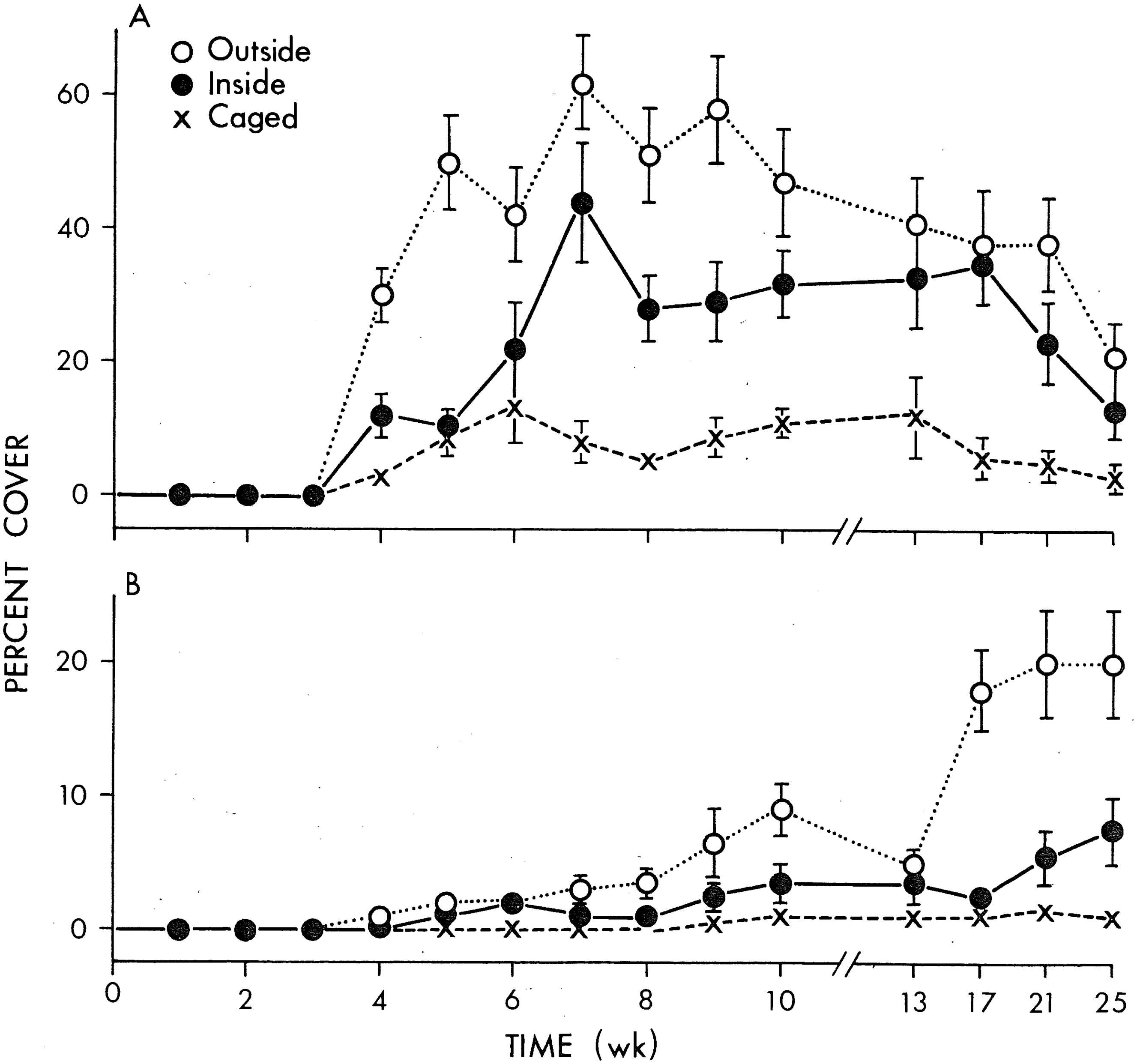

Figure 3. Temporal patterns in the percent of (**A**) prostrate green algae and (**B**) crustose coralline algae on settling plates. The symbols are identical to those in Fig. 1. Each point represents the mean of 14 plates (excluding naturally contoured coral-rock plates) with 95% confidence intervals.

allows competitively dominant species to eliminate inferior forms (low diversity); moderate grazing disproportionately reduces dominant species thus allowing inferior forms to persist (high diversity); and high grazing intensity eliminates most species (low diversity)(see also Connell 1978). However, it is doubtful that this model adequately explains the results during the first several weeks of our experiment for two reasons. First, space *per se* was surely not limiting on the plates during this period, thus precluding extensive competitive exclusion among the algae. Second, it seems unlikely that damselfish could forage selectively among the relatively small algal thalli that occurred during this period. We suggest instead that the initially high algal diversity on plates placed inside damselfish territories was simply a function of the close proximity of these substrates to an abundant source of colonizing spores provided by the surrounding dense algal mat (see also Hruby and Norton 1979). Thus, in spite of an initial relatively rapid accumulation of species within territories, damselfish grazing eventually reduced algal diversity relative to that on ungrazed caged surfaces.

How does fish grazing alter algal succession on Hawaiian reefs? It is apparent that the intense feeding activity of parrotfishes and surgeonfishes outside damselfish territories drastically alters succession at its earliest stages. Within three weeks, typical early successional species, such as *Enteromorpha*, are reduced to prostrate forms that are subsequently slowly replaced by crustose corallines (see also Doty 1967). This apparently typical pattern has been observed during similar field experiments on Caribbean reefs (Wanders 1977), as well as during microcosm experiments in Hawaii (Brock 1979). Intense fish grazing in these systems simply excludes erect foliose algae from flat surfaces, allowing only grazer-resistant prostrate and crustose forms to persist.

Inside territories, on the other hand, the relatively moderate and selective feeding activity of damselfish may maintain an intermediate stage of algal succession, rather than drastically altering its initial course. During the first three months of our experiment, the rank abundances of algal taxa were nearly identical inside territories and within cages, with *Ectocarpus* dominating. However, the last three monthly samples revealed that the ungrazed caged communities had proceeded to a stage dominated by *Centroceras* and *Ceramium*, while territory communities remained dominated by *Ectocarpus*. Although natural territory surfaces are dominated by other species, suggesting that succession will continue on the plates still in the field, these results indicate that succession is at least inhibited if not controlled by damselfish grazing (see also Montgomery 1980a). It has been suggested for other damselfish systems that this pattern is maintained by selective grazing (e.g., Montgomery 1980b) and/or removal of certain algal species by "weeding" (e.g., Lassuy 1980). While *Stegastes fasciolatus* appears to be a selective grazer, many hours of field observation have revealed no evidence of weeding behavior (Hixon, unpublished).

Regardless of the intrinsic mechanisms of succession involved (Connell and Slatyer 1977), these preliminary data indicate that differential fish grazing does indeed regulate the community structure of Hawaiian reef algae. By the conclusion of our experiment, many more details of this phenomenon will be revealed. Such information may ultimately make it possible to control the structure of benthic reef communities by manipulating the abundance of territorial damselfish relative to other grazing fishes. In any event, it is obvious that the effective management of coral reef systems must recognize the important role of herbivorous fishes.

ACKNOWLEDGEMENTS

We wish to thank R. Day, M. Doty, M. Foster, P. Jokiel, P. Lobel, J. Lubchenco, S. Smith, and W. Sousa for useful discussions on experimental design and methods. R. Brock, M. Doty, P. Jokiel, R. Kinzie, G. Losey, A. Perry. J. Stimson and W. Walsh kindly reviewed the manuscript and made many helpful suggestions. This project would not have been possible without the generous field assistance of the "Macho-ettes": C. Agegian, L. Bell and A. Perry. The senior author's participation in this symposium was made possible by a University of Hawaii Faculty Travel Grant. This research was primarily funded in sequence by a National Science Foundation National Needs Postdoctoral Fellowship and a University of Hawaii Biomedical Research Support Grant, both awarded to the senior author. We also thank M. Doty and B. Cooil of the U.H. Department of Botany (S. Siegel, Chairman) for generously providing laboratory space and equipment, and the U.H. Department of Zoology (S. Townsley, Chairman) and Hawaii Institute of Marine Biology (P. Helfrich, Director) for additional logistic support.

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