SUCCESSION AND HERBIVORY:
EFFECTS OF DIFFERENTIAL FISH GRAZING ON
HAWAIIAN CORAL-REEF ALGAE[1]

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Abstract. Most general models do not include herbivory as a major agent of successional change. Potentially, herbivores can affect succession in three ways: accelerating or decelerating the rate of succession, where the sequence of dominant species is unaltered, or deflecting succession onto a new trajectory, where the species composition of dominants becomes substantially different than during ungrazed succession. We examined these alternatives for benthic algae on a coral-reef crest off Oahu, Hawaii. In this system, exposed coral-rock surfaces naturally undergo one of two major grazing regimes: (1) relatively protected inside defended territories of the damselfish *Stegastes fasciolatus* (Pomacentridae), where the benthos is dominated by filamentous algae; or (2) exposed to abundant schooling parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) outside territories, where the bottom is covered mostly by crustose algae. We compared the effects of this differential grazing on primary succession, relative to ungrazed succession, by distributing on the same date 1332 settling surfaces among three treatments: exposed inside damselfish territories, exposed just outside territories, and within fish-exclusion cages just outside territories. To balance the advantages and disadvantages of different settling surfaces, we used equal numbers of each of three kinds of 50-cm² settling plates: naturally contoured coral rock, coral rock cut into flat plates, and roughly sanded PVC plastic. To follow relative successional pathways, we sampled destructively 63 plates (21 from each grazing treatment) 17 times over 1 yr. Plates placed in the field several months before and after the main experiment suggested no seasonal differences in algal colonization. A concurrent cage-control experiment involving 144 settling plates, combined with measurements of light and water motion inside vs. outside cages, indicated that the secondary effects of cages were minor compared to the primary effect of preventing fish grazing.

In the absence of fish grazing within cages, algal succession over the year followed three stages: early dominance by simple green and brown filaments (such as *Enteromorpha rhizoidea* and *Ectocarpus indicus*), a midsuccessional stage dominated by thin and finely branched red filaments (such as *Centroceras clavulatum* and *Taenioma perpusillum*), and a late stage dominated by blades and coarsely branched thick filaments (especially *Tolypoicladia glomerulata*). Species diversity followed a unimodal pattern during ungrazed succession, declining as a few species of late-stage algae predominated.

Inside damselfish territories, succession was decelerated. The early stage was protracted and the midsuccessional stage, similar to natural assemblages inside territories, still dominated by the end of the year. Here, herbivory was of moderately destructive intensity (as measured by the density of fish bite marks that removed algal holdfasts) and fairly nonselective (as measured by comparisons of the gut contents of damselfish paired with samples of their algal mats). Algal biomass reached only about a quarter of what accumulated during ungrazed succession, but species diversity gradually increased through time. By the end of the experiment, algal species diversity was greatest inside damselfish territories compared to the other two grazing treatments.

Outside territories, where grazing was destructively intense, resulting in the removal of all erect algae, succession was strongly deflected. The early stage was quickly replaced by a low-biomass and low-diversity assemblage of crusts (such as *Hydrolithon reinboldii*) and prostrate blue-green mats (such as *Calothrix crustacea*), characteristic of natural assemblages outside territories.

Besides demonstrating the importance of herbivory during succession and providing insight on the mechanisms involved, these patterns have ramifications for explaining the maintenance of high local species diversity on coral reefs at two spatial scales. Between patches, differential grazing by territorial damselfish vs. schooling herbivores causes succession to follow different trajectories toward different algal assemblages. Within patches defined by damselfish territories, moderate grazing decelerates succession and prolongs a high-diversity midsuccessional stage. Both these patterns provide an example of predation maintaining high local diversity in tropical systems, and indicate that territorial damselfish can function as keystone species on coral reefs.

Key words: algae; coral reef; damselfish; Hawaii; herbivory; keystone species; parrotfish; predator-mediated coexistence; species diversity; succession; surgeonfish; territoriality.

INTRODUCTION

Herbivores have long been known to affect the structure of plant communities (e.g., Darwin 1859, Tansley and Adamson 1925). It follows that herbivory could be a major factor influencing succession, generally defined as a directional change in species dominance through time initiated by the opening of habitat space (Miles 1987). Following observations of the often severe impact of mammalian grazing on succession (reviews by Ellison 1960, Adams 1975, Luken 1990), early formulations of successional processes sometimes included the modifying effects of herbivores, but treated herbivores as external agents. Hypothesized effects included grazers slowing or even reversing succession (Clements 1916), "deflecting" succession from one sequence of dominants to another (Godwin 1929a), or stopping succession altogether (Tansley 1935). Field experiments subsequently showed that mammalian herbivores often tend to slow or stop succession (e.g., Hope-Simpson 1940, Watt 1981a, b, Marrs et al. 1988).

Despite these findings and the truism that consumers accompany all successions, Edwards and Gillman (1987:295) correctly concluded that "most models of succession attribute only minor importance to herbivory." Indeed, both conceptual and mathematical models often relegate herbivores to the role of external modifiers of succession in terrestrial habitats, rather than principal players driving the rate and trajectory of succession (reviews by Brown 1984, Pickett et al. 1987, Pickett and McDonnell 1989, McCook 1994). This paradox is partly explained by the fact that, besides the obvious impacts of some mammalian grazers, the roles of most herbivores during succession have been examined only recently. For example, the first experiments showing that insects can unequivocally affect the rate of early plant succession were published in the 1980s (e.g., Brown 1982, McBrien et al. 1983).

The role of herbivores in marine and freshwater successions are better documented and are often substantial (reviews for plankton: Sommer 1989, see also Sarnelle 1993, periphyton: DeNicola et al. 1990, lake macroalgae: McCormick and Stevenson 1991, stream macroalgae: Dudley and D'Antonio 1991, marine macroalgae: Sousa 1979, Lubchenco and Gaines 1981). There are probably three reasons for this difference. First, the rate of herbivory, in terms of primary production removed at a given level of productivity, is generally about three times greater in aquatic than in terrestrial systems (Cyr and Pace 1993, see Hatcher 1981 and Carpenter 1986 for data on coral-reef fishes and algae). Second, succession of freshwater and marine algae is generally more rapid than that of terrestrial plants, with shifts in dominance occurring over months rather than decades (Huntly 1991). Finally, aquatic plants and animals are often smaller and/or easier to manipulate experimentally than their terrestrial counterparts. Overall, to the extent that ecological processes are similar in

aquatic and terrestrial environments, marine and freshwater communities provide excellent model systems for understanding the roles of herbivores during succession.

In marine systems, most studies of herbivore effects on succession have been conducted in temperate rocky intertidal habitats (reviews by Sousa 1979, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Connell 1987, Farrell 1991, Sousa and Connell 1992). Interestingly, coral reefs are known to support often far more herbivores than temperate systems (reviews by Gaines and Lubchenco 1982, Horn 1989), yet there have been no detailed, long-term studies of herbivore effects on succession of reef algae. Rather, previous studies have either run for far less than a year or involved too few samples through time to resolve successional sequences of dominant species (reviews by Steneck 1988, Glynn 1990, Hay 1991, Hixon 1996). In any case, the general conclusion from previous studies has been that herbivores have profound direct and indirect effects on many components of coral-reef benthos.

Here, we report the effects of herbivorous fishes on benthic succession on a shallow coral reef. Our previous papers on this system focused on the endpoints of succession rather than succession per se (Hixon and Brostoff 1981, 1983, 1985, Hixon and Menge 1991). Besides providing a detailed analysis of succession of reef algae, our study shows that different groups of herbivores can have very different effects on succession in the same habitat. In particular, schooling parrotfishes and surgeonfishes strongly deflect the trajectory of algal succession, whereas territorial damselfishes merely slow the successional rate. We discuss the ramifications of these processes in terms of both the mechanisms of succession and the maintenance of high species diversity on coral reefs. First, we develop the hypotheses we tested by briefly reviewing the possible effects of herbivores on succession.

Hypothesized effects of herbivory on succession

Herbivory (or any form of predation) can alter two aspects of succession: rate and trajectory. One can examine these effects either two-dimensionally, where species are typically pooled into groups by growth form and their relative abundances plotted as a function of time, or multidimensionally, which requires multivariate analyses for systems with many species. Empirically, it is important to examine both perspectives because they may produce different patterns and conclusions. Multidimensionally, succession can be viewed as a community following a path through multivariate space representing both species composition and relative abundances changing through time (Fig. 1). In the absence of herbivory, the community follows some trajectory from the disturbance that starts the successional sequence (time 0) to some arbitrary endpoint (e_1) at time t, which may or may not be a "climax"

state (Fig. 1). Besides the possibility that herbivory may have no effect on succession (Farrell 1991, Sousa and Connell 1992), there are three possible ways that herbivores can alter ungrazed succession.

Deceleration.—First, the activity of herbivores may decrease the rate of succession, such that by time t the community has changed an amount equivalent to the ungrazed system at some time less than t. In a multidimensional perspective, the community has proceeded down the same path as the ungrazed system over time t, but has not gone as far (Fig. 1). Thus, the dominant species at each successional stage do not change, just the duration of their dominance. The mechanism of deceleration is that herbivores somehow inhibit later species to the benefit of earlier species (reviews by Lubchenco and Gaines 1981, Crawley 1983, Brown 1984, Farrell 1991, Sousa and Connell 1992). In extreme cases, succession could be arrested or even reversed (Clements 1916, Tansley 1935).

Acceleration.—Alternatively, herbivory may increase the rate of succession, such that the community reaches the original arbitrary endpoint at some time less than t. Multidimensionally, the community progresses along the same successional trajectory to the same endpoint (e_1), but faster than the ungrazed system (Fig. 1). The mechanism of acceleration is opposite that of deceleration: herbivores inhibit earlier species to the benefit of later species (reviews by Sousa 1979, Lubchenco and Gaines 1981, Crawley 1983, Brown 1984, Farrell 1991, Sousa and Connell 1992).

Deflection.—Independent of the rate of succession,

PLATE 1. The territorial yelloweye damselfish, *Stegastes fasciolatus*, acts as a keystone species by prolonging a high-diversity, midsuccessional stage of benthic algae on Hawaiian coral reefs. Photo by K. E. Carpenter.

a third possibility is that herbivory causes the community to follow a different trajectory than that followed in the absence of herbivores (Godwin 1929a). In this case, early successional species are replaced by species that are either absent or rare in the ungrazed system; that is, the species composition of dominant forms changes. Thus, by time t in the multidimensional perspective, succession has led to a new endpoint (e_2 in Fig. 1) along a different pathway (sensu Glenn-Lewin and van der Maarel 1992). The mechanism of deflection is generally intense herbivory or some other disturbance that allows only resistant species to persist in the system (Godwin 1929a).

METHODS

Study system

Our study area was a 600-m section of the subtidal windward reef crest at the Coconut Island Marine Refuge, located in Kaneohe Bay, Oahu, Hawaii. This site was selected because it was not subject to fishing and other direct human perturbations. The bottom comprised a 1-m deep flat bench of dead coral rock, with occasional small patches of live coral (*Porites, Pocillopora,* and *Fungia*). Just offshore of the reef crest, the reef slope was covered by live coral (mostly *Porites compressa*) and dropped rapidly to the silty bay floor at ≈9 m depth.

The dominant grazers in this system were parrotfishes (Scaridae, *Scarus*), mostly juveniles ≈5–10 cm in total length (TL), and surgeonfishes (Acanthuridae, especially *Acanthurus* and *Zebrasoma*), mostly adults ≈15–25 cm TL. These schooling herbivores were among the most abundant fishes on this reef. At a neighboring reef, they occurred at a density of ≈0.5 fish/m², and averaged ≈25 g per fish (Brock et al. 1979). Scattered along the reef crest at our site were the permanent territories of individual yelloweye damselfish (*Stegastes fasciolatus*; Plate 1), ≈10 cm TL. At a neighboring reef, this species occurred at a density of ≈0.03 fish/
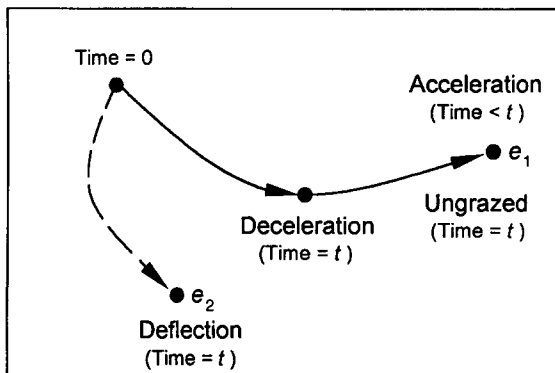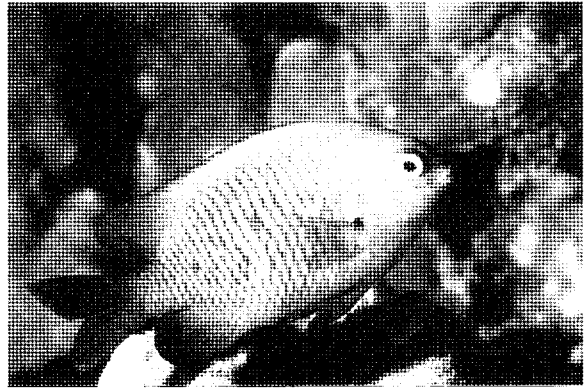

FIG. 1. Possible herbivore effects on succession in a hypothetical multivariate ordination based on species relative abundances. Each point along each curve represents a unique community in terms of species composition and/or relative abundances, such that each curve illustrates community change through time. In this particular example, ungrazed succession proceeds from left to right in multivariate space, reaching some arbitrary endpoint e_1 at time t. If herbivores cause deceleration, the community will follow the same trajectory as ungrazed succession, but not reach e_1 in the same time period. If herbivores cause acceleration, the community will reach e_1 along the same trajectory, but earlier than ungrazed succession. If herbivores cause deflection, succession will follow a different trajectory than when ungrazed, reaching a new endpoint e_2.

m^2, and averaged ≈ 40 g per fish (Brock et al. 1979). The yelloweyes defended small patches of the bottom (≈ 1 m^2) from other herbivorous fishes (Rasa 1969, Losey 1982, Hourigan 1986), thereby allowing the growth of distinct patches of filamentous algae, a pattern documented in many territorial damselfishes (e.g., Low 1971, Vine 1974, Brawley and Adey 1977, Lassuy 1980, Lobel 1980, Montgomery 1980, Mahoney 1981). Sea urchins and other large invertebrate grazers were rare at our site.

Due to territoriality by the damselfish, exposed coral-rock substrata along the reef crest were occupied by two basic kinds of benthic assemblages: (1) those outside territories, exposed to grazing by schooling parrotfishes and surgeonfishes, and dominated by low-lying crustose and prostrate algae; and (2) those inside territories, exposed to grazing by mostly the resident damselfish, and dominated by erect filamentous algae. This dichotomous pattern, first documented by Vine (1974), is common on shallow coral-reef crests (reviews by Steneck 1988, Glynn 1990, Hay 1991, Hixon 1996).

Experimental design

Following protocols reviewed by Foster and Sousa (1985) and Vadas (1985), our basic experimental design was to compare primary succession on settling surfaces placed under three different grazing regimes: ungrazed, exposed inside damselfish territories, and exposed outside territories. Because microhabitats for coral-reef algae can vary abruptly at small spatial scales (Carpenter 1990), it was important to control for microhabitat differences per se independent of the grazing treatments. As detailed in this section, we accomplished this design by destructively sampling groups of identical settling plates that were the same age, at the same orientation and depth, and as physically close as possible, while still ensuring different grazing regimes and statistical independence. For each experiment, all plates were placed in situ on the same date, then samples of plates were removed and analyzed periodically over the course of a year to document succession.

Settling plates.—To minimize any bias associated with using a single kind of settling plate, we followed succession on three types of surfaces, which had complementary advantages and disadvantages: (1) naturally contoured pieces of sun-dried *Porites* coral rock, which had the advantage of being the natural substratum in both composition and relief, but the two disadvantages of irregular contours precluding exact area measurements and introducing variance due to intrinsic between-plate differences; (2) *Porites* coral rock cut into flat square plates, which had the advantages of being the natural substratum, providing standardized replicates, and allowing accurate area measurements, but the disadvantage of being unnaturally flat; and (3) flat and roughly sanded polyvinyl chloride plastic

(PVC), which had the advantage of fish bite marks being most readily countable on these surfaces (see *Laboratory analyses* below), but the disadvantage of being an unnatural substratum (albeit virtually chemically inert).

Elsewhere, we compared the relative effects of these different settling surfaces on the benthic assemblages that developed within each grazing treatment (Hixon and Brostoff 1985). Essentially, these substrata supported very similar assemblages within each treatment, with two exceptions occurring only in the relatively high grazing intensity treatment outside damselfish territories: (1) PVC plates were overgrown more rapidly by crustose algae than were coral plates, due to parrotfishes being able to scrape and clear the surface of coral plates; and (2) naturally contoured coral plates supported more species than flat plates, due to the crevices providing refuges from predation (Hixon and Menge 1991). Therefore, for the present analysis, we paired identical plate types among grazing treatments (see *Data analyses* below).

The area of each flat settling plate was 50 cm^2, and that of each irregular coral plate was approximately the same. This area was chosen from the asymptote of species-area curves obtained from larger plates (up to 225 cm^2) during a preliminary study several months before the main experiment. (Note that early succession during the preliminary study was the same as that during the main experiment.)

We mounted 1332 plates (444 of each substratum type) horizontally on 111 concrete blocks using a nontoxic cement ("Liquid Nails"). This arrangement allowed groups of four natural coral plates, four flat coral plates, and four flat plastic plates lying on the same plane to be exposed as a single module to virtually identical conditions in situ (Fig. 2A, see also Fig. 1 of Hixon and Brostoff 1985, and Fig. 13–2 of Foster and Sousa 1985).

Grazing treatments.—On 19 September 1980, all 111 settling-plate modules were distributed in the field evenly among three grazing treatments: (1) exposed outside damselfish territories to grazing by parrotfishes and surgeonfishes; (2) exposed inside territories, defended by and grazed mostly by the resident damselfish; and (3) within grazer-exclusion cages (see *Cages and controls* below). Modules were arranged in situ in sets of three, such that a given damselfish territory (37 in all) contained one exposed module, with one exposed and one caged module located about a metre outside the territory at approximately the same depth, orientation, and degree of wave exposure (Fig. 2B). (The presence of a module within a territory did not appear to disturb the resident damselfish, but a cage did. Thus, all cages were necessarily placed outside territories.)

Sampling design.—Sets of settling plates were removed from the field for analysis 17 times during the year-long experiment: 10 weekly samples, followed by 6 monthly samples, followed by a final sample at day
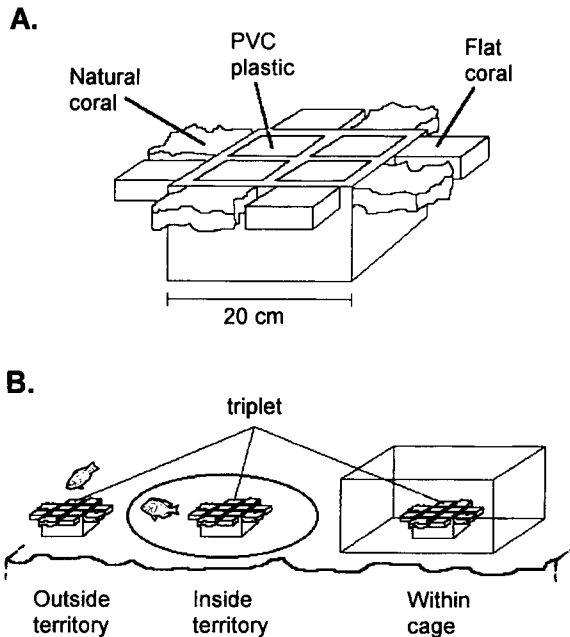
A.

B.

FIG. 2. (A) Concrete-block module supporting four settling plates of each of three substratum types. (B) Spatial arrangement of settling-plate modules in and near each damselfish territory, showing how three plates of identical substratum type and orientation comprised one "triplet" for comparing the three grazing treatments. Perspective is looking onshore at the edge of the reef crest.

365. Each sample comprised 63 plates, representing 3 grazing treatments × 21 replicate plates (7 of each substratum type), for a total of 1071 plates analyzed.

Samples were selected randomly in a way that controlled for microhabitat differences between plates independent of grazing treatment, thereby ensuring that the only major differences among compared plates were their grazing regimes. First, to control for any larger scale environmental differences along the 600 m length of reef crest comprising our study site (none were apparent), the site was arbitrarily divided into seven sections of roughly equal length (each containing 5–6 damselfish territories). From each section on each sampling date, we removed one randomly selected set of nine settling plates (three of each substratum type from each grazing treatment). Second, to control for any smaller scale environmental differences due to the orientation of plates on modules, plates of the same type removed from each grazing treatment were from identical positions on their respective modules. This sampling design provided a "triplet" of plates of identical age, substratum type, depth, and orientation, differing as much as possible only in grazing regime (Fig. 2B). Such triplets provided the basis for statistical comparisons between grazing treatments (see *Data analyses* below).

Cages and controls

Grazer-exclusion cages were constructed of 1.3 × 1.3 cm galvanized wire mesh and were 60 × 60 × 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, whereas interior surfaces were periodically cleaned by divers.

Besides excluding grazers, cages cast shadows, alter water motion, and protect benthic invertebrates from predation. Any of these secondary effects could produce artifactual differences between treatments independent of grazing intensity (review by Dayton and Oliver 1980). Therefore, we not only measured these effects, but also ran a separate cage-control experiment. We measured total light intensity inside and outside cages in situ on calm, cloud-free days at 0900 ($n = 10$ paired measurements), 1200 ($n = 5$), and 1500 ($n = 10$) using a LI-COR LI-185 quantum meter (see Foster et al. 1985, Ramus 1985). We measured relative water motion inside and outside cages as the 48-h mass loss of 58 pairs of dissolving "clod-cards" (Doty 1971, see also Denny 1985, Foster et al. 1985), which are simply nodules of plaster of Paris molded in standard ice trays. Preweighed clod-cards were mounted horizontally on the same kind of concrete blocks used to mount the settling plates. We placed these blocks inside and outside cages in situ immediately adjacent to experimental cages on eight dates distributed over the course of the succession experiment. After removal from the field, each clod-card was dried at 60°C for at least 72 h, until constant mass was attained. The relative mass loss of the dissolving clod-cards inside vs. outside cages provided a crude measure of relative water motion.

The cage-control experiment started in February 1981, and thus overlapped both spatially and temporally with the main succession experiment. The experimental design was identical to the main experiment, except that it involved 144 settling plates distributed among 12 modules and included four treatments: (1) exposed in the open vs. (2) exposed under a roof-only (no-wall) cage, comparisons that tested for shading effects at high grazing intensity; and (3) enclosed within a wall-only (no-roof) cage, with the walls extending upward a metre to the sea surface, vs. (4) enclosed within a complete cage, comparisons that tested for shading effects at low grazing intensity. The wall-only cages were exposed to direct sunlight for just under half the day. (We were unable to test water-motion effects independent of grazing intensity because even low walls tended to exclude fishes.)

Three times during the cage-control experiment (91, 147, and 231 d since beginning) a sample of 48 plates (4 cage treatments × 12 replicate plates comprising four of each substratum type) was removed from the field without replacement to compare the attached epibenthic assemblages (see *Sampling design* above). Note that, within each grazing treatment, succession during the cage-control experiment was the same as that during the main experiment, which had started 5 mo earlier (M. A. Hixon and W. N. Brostoff, *unpublished data*).

Laboratory analyses of settling plates

Plates from the main succession experiment and the cage-control experiment were analyzed identically. When removed from the field, each place was immediately sealed in a separate plastic bag in situ to minimize the loss of any resident organisms. All plates were analyzed the same day they were collected. After being photographed, each plate was rinsed free of loose detritus and sediment (which were analyzed separately), and all macroscopic animals were removed and counted.

We measured the relative intensity of destructive (i.e., holdfast-removing) grazing among treatments as the "standing crop" of visible fish bite marks on plates. These were bites that had scraped the substratum and so had removed algal holdfasts and potentially influenced species relative abundances. Such bite marks were mostly made by parrotfish, but also included those by surgeonfish and damselfish. Although bite marks were evident in the same relative patterns among the three plate types, they were most readily countable on the PVC plates, which we used for our counts. Bite marks on plates exposed outside damselfish territories became too dense to quantify accurately above a density of ≈ 400 bites/50 cm², so we conservatively used this value for plates with too many bite marks to count.

The relative abundance of algal crusts and prostrate mats on each settling plate was estimated visually as percent cover using a gridded overlay (see Dethier et al. 1993). Because the remaining algae were morphologically similar (mostly filamentous) and grew in mixed-species stands, their relative abundances could not be estimated macroscopically. This situation required destructive sampling, which Schoener and Greene (1981) have shown to provide the same results as nondestructive methods. The algae were scraped from the plate and spread evenly within a glass petri dish. The dish was first scanned microscopically to determine the total number of species present. To estimate the relative abundance of each species, 100 random points within the dish were then examined under $100\times$ magnification, and the alga occupying the central point of each ocular field was recorded (Jones 1968). 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" (Peet 1974).

Following microscopic examination, each petri dish was wet weighed, dry weighed, and finally ash weighed to determine ash-free dry mass (AFDM) algal biomass. (The naturally contoured coral plates were examined microscopically only, since accurate area measurements were impossible.) Drying was at 60°C for at least 72 h, until constant mass was attained, and ashing was at 500°C for 16 h (Brinkhuis 1985, DeWreede 1985).

Natural algal assemblages

Three times during the year-long succession experiment (October 1980, June and September 1981), we removed eight pairs of pieces of natural substrata from inside and outside damselfish territories. Each sampled substratum was located ≈ 1 m from its pair mate, at the same depth and exposure, and no territory was sampled more than once. Approximately 50 cm² flat and horizontal sections of these samples of coral rock were subjected to the same laboratory analyses as the settling plates to provide a comparison of natural assemblages inside and outside territories. Because differences between sampling dates were negligible, data were pooled for comparison with settling-plate data ($n = 24$ pairs).

Data analyses

Our experimental design exposed replicate settling plates to different grazing regimes, but otherwise identical as possible microenvironments. This design allowed analysis by various approaches; repeated-measures analyses were not essential because each plate was examined only once (Winer 1971). We chose paired-comparison analyses because this approach emphasizes the matching of similar replicates (Sokal and Rohlf 1981), which was facilitated by the "triplet" design of our samples (see *Sampling design* above). Our sample sizes were sufficiently high that the results of parametric and nonparametric univariate tests converged, so we report the more conservative nonparametric tests (Z statistic of Wilcoxon signed-ranks tests for paired comparisons). All tests were run on the SYSTAT microcomputer package (Wilkinson 1990).

For multivariate analysis, we present the ordination procedure of detrended correspondence analysis (DCA, Hill and Gauch 1980), using the DECORANA microcomputer routine (Hill 1979). Despite some controversy on the absolute patterns produced by this method (Wartenberg et al. 1987, Peet et al. 1988, Jackson and Somers 1991), DCA has proven to be a useful way to visualize relative successional trajectories (e.g., Archer et al. 1988, Halpern 1988, DeNicola et al. 1990, Gibson and Brown 1992, see also James and McCulloch 1990). In particular, DCA illustrates successional trajectories as an ordination of sequential samples in "species space" (cf. Fig. 1), and provides a reciprocal ordination of species in "sample space," thereby showing where along the trajectory each species was most common.

To minimize the bias associated with any one species diversity index (reviews by Peet 1974, Magurran 1988), we compared diversity between treatments using four different measures: richness (S), which is simply the number of species, the Shannon-Wiener Index (H'), the exponentiated H', and the reciprocal of the Simpson Index. The latter two measures are most sensitive to changes in the proportions of rare and common species, respectively, and are related by Hill's (1973) unifying notation. To examine evenness, we used both Pielou's (1966) J and "dominance," which is simply the proportional relative abundance of the most common species, an inverse measure of evenness advocated by May (1975). Because all measures provided the same rela-

tive patterns of diversity and evenness, we report here only S, H', and J.

Feeding selectivity of fishes

As will be clear from our results, the schooling parrotfishes and surgeonfishes in our study, considered as a group, consumed any erect algae presented to them. Indeed, in our system, erect algae naturally occurred only within damselfish territories or within crevices. Algal species that were strongly chemically protected appeared to be absent in our system (reviews by Hay and Fenical 1988, Hay 1991). M. E. Hay (*personal communication*) suggested that intense grazing in our system may have prevented erect algae from reaching a size where chemical deterrence was effective. Moreover, algae that are allegedly well-defended chemically can nonetheless be highly susceptible to fish grazing (Lewis 1985).

To determine the feeding selectivity of damselfish grazing on mature algal mats inside their territories, we removed 30 actively feeding fish from an adjacent reef, along with the portion of each individual's algal mat where it was feeding at the time of capture. Samples were taken early during daily feeding to insure that the foregut contents were from the portion of the territory we sampled. Both the fresh foregut contents and the algal-mat samples were subjected to the same microscopic examinations used to determine the relative abundances of algae on the settling plates (see *Laboratory analyses of settling plates* above).

Feeding selectivity of damselfish was calculated by comparing the algae in each fish's foregut to the algae available in its algal mat using the method of Johnson (1980). The preference index produced by this method $(-\bar{t})$ is a symmetrical open-ended measure, with values near zero indicating consumption of prey in the same proportions that they occur in the habitat. Johnson's method has several desirable features, including that it (1) is insensitive to the inclusion or exclusion of rare or doubtful species; (2) employs ranks of selection and availability and thus is relatively insensitive to inaccurate or biased measurements; and (3) provides significance tests, including Snedecor's F for testing overall selectivity ($F [I - 1, J - I + 1]$ where $I = 22$ algal species and $J = 30$ damselfish guts), and the Waller–Duncan procedure for multiple comparisons of food items (Waller and Duncan 1969). The Waller–Duncan procedure is desirable because it minimizes the chances of both Type I and Type II error (Johnson 1980).

RESULTS

Cage controls

Water motion.—Comparisons of clod-card mass loss estimated that the cages reduced water motion by an average (± 1 SD) of only $4.3 \pm 5.5\%$ ($n = 58$ pairs). This outcome was not surprising given that the study site was in a bay protected by a barrier reef, and rarely subject to high water motion.

Light intensity.—Quantum-meter readings showed that the cages decreased total light intensity an average (± 1 SE) of $24.4 \pm 3.4\%$ at 0900 ($n = 10$ pairs), $18.6 \pm 3.8\%$ at 1200 ($n = 5$), and $20.8 \pm 2.4\%$ at 1500 ($n = 10$). Total light intensity at noon averaged 1016 ± 51 μmol photons$\cdot$m$^{-2}\cdot$s^{-1} inside cages and 1248 ± 7 μmol photons$\cdot$m$^{-2}\cdot$s^{-1} outside cages. Note that both these light levels are 10 times greater than those known to saturate the photosynthetic rate of a broad variety of algae (Luning 1981, Littler and Littler 1992), indicating that shading was not an important artifact negatively affecting photosynthesis. Conversely, because photosynthesis by some shallow-reef algae can be photoinhibited at midday (Hanelt 1992), it is also possible that shading by cages may have actually provided a benefit to the enclosed algae.

Cage-control experiment.—Two direct tests of the possible effects of shading were provided by the cage-control experiment. First, comparisons of results from complete cages vs. roofless cages (which still excluded fishes but received more direct sunlight) tested for shading effects in the absence of fish grazing. Six of 30 paired comparisons between these treatments were significant (Table 1). Despite no differences in algal species richness, evenness (*J*) and consequently composite diversity (*H'*) were greater in the wall-only treatment on day 91 of the experiment (Table 2), but not subsequently (Table 1). Algal biomass was also greater in the wall-only treatment for most of the experiment (147 and 231 d since the start of the experiment), suggesting possible negative effects of complete cages independent of shading, but also indicating that any positive effect of reduced photoinhibition was not substantial (Table 2). Despite these differences, there were few ramifications in terms of other parameters, especially in the long run. In particular, only the density of herbivorous invertebrates and the relative abundance of one algal growth form (complex red filaments, see *Patterns of algal succession* below) were greater in the wall-only treatment, and only on day 147 (Table 2), with no differences by the end of the experiment (Table 1).

Second, comparisons of results from open plots vs. roofs with no walls tested for shading effects in the presence of grazing fishes. In this case, only 2 of 30 paired comparisons between the treatments were significant, slightly more than would be expected by chance alone (Table 1). Despite no difference in algal species richness, evenness and consequently composite diversity were slightly greater in the roof-only treatment at the end of the experiment (Table 2).

In summary, the cage-control data indicated that the secondary effects of the fish-exclusion cages were negligible, compared to the primary effect of preventing fish grazing, for several reasons. First, water motion was not substantially altered by the cages because the study was conducted in a low-flow area. Second, light levels appeared to be photosynthetically saturating both

TABLE 1. Summary of results of cage-control experiment. Table entries show statistical significance of differences due to shading. Comparisons of complete cages and roofless cages with walls extending to the surface (wall only) tested for shading effects in the absence of grazing fishes. Comparisons of open plots and roofs with no walls (roof only) tested for shading effects in the presence of grazing fishes. Each comparison of each parameter involved 12 pairs of settling plates sampled on each date (91, 147, and 231 d since the start of the experiment), except for grazing intensity (four pairs of plates) and algal biomass (eight pairs of plates). Paired comparisons were by Wilcoxon signed-ranks tests (see Table 2 for details of significant comparisons).

	Complete cage vs. wall only (grazing fish absent)			Open plot vs. roof only (grazing fish present)		
	Elapsed time			Elapsed time		
Parameter	91	147	231	91	147	231
Grazing intensity (bite marks/50 cm²)	NS	NS	NS	NS	NS	NS
Algal biomass (g AFDM/50 cm²)	NS	*	**	NS	NS	NS
Herbivorous invertebrates (no./50 cm²)	NS	**	NS	NS	NS	NS
Relative abundance by growth form						
Simple green/brown filaments	NS	NS	NS	NS	NS	NS
Complex red filaments	NS	*	NS	NS	NS	NS
Thick filaments and blades	NS	NS	NS	NS	NS	NS
Crusts and blue-green mats	NS	NS	NS	NS	NS	NS
Algal species diversity						
Richness (no. species/50 cm²)	NS	NS	NS	NS	NS	NS
Evenness (J)	*	NS	NS	NS	NS	*
Composite diversity (H')	*	NS	NS	NS	NS	*

* $P \leq 0.05$, ** $P \leq 0.01$, NS not significant ($P > 0.05$).

inside and outside cages, and the cages did not substantially affect any potential midday photoinhibition. Third, the number and magnitude of differences between treatments during the cage-control experiment were relatively small compared to those during the main succession experiment (see *Patterns of algal succession* below).

General effects of differential fish grazing

Grazing intensity.—Throughout the succession experiment, the intensity of destructive (i.e., holdfast-removing) grazing, as measured by the density of fish bite marks, differed greatly among treatments ($P \ll 0.001$ for all paired comparisons). Grazing intensity was greatest outside damselfish territories (averaging 326 bites/50 cm²), moderate inside territories (averaging 31 bites/50 cm²), and undetectable within grazer-exclusion cages (Fig. 3A).

Algal biomass.—For the 1st mo of the experiment (plate samples 1–4, days 7–28), there was negligible biomass (ash-free dry mass, AFDM) on all plates (Fig. 3B). For the next 2 mo (samples 5–11, days 35–91), there was no difference between the plates within cages and those inside territories (both averaging 0.14 g AFDM/50 cm², $P > 0.05$), these standing crops being 10 times greater than that outside territories (averaging 0.01 g AFDM/50 cm², $P \ll 0.001$). After 3 mo (samples 12–17, days 119–365), algal biomass was significantly greatest within cages (averaging 0.40 g AFDM/50 cm²), intermediate inside damselfish territories (0.13 g AFDM/50 cm²), and lowest outside territories (0.04 g AFDM/50 cm², $P \ll 0.001$ for all paired comparisons).

Thus, algal standing crop ultimately varied inversely with grazing intensity (Fig. 3A, B).

Invertebrates.—Several lines of evidence demonstrated that differences between treatments were due to differential grazing by fishes rather than by invertebrates. Large mobile invertebrates were rare in this system and were never seen on or near the settling plates, including at night. Of particular interest, however, were potentially herbivorous small invertebrates (including gastropod molluscs, polychaete worms, and amphipods and other small crustaceans). If sufficiently abundant, these mesoherbivores could potentially affect algal relative abundances independently of fish grazing, as Brawley and Adey (1981) documented in a large aquarium (see also Brawley 1992). However, such effects did not occur on the reef flat adjacent to our reef-crest system (Brostoff 1988*a*), where the density of mesoherbivores reached 55 animals per 50-cm² plate (SD = 30, n = 304; Brostoff 1988*b*). Carpenter (1986) also detected no substantial effects of mesograzers in the Virgin Islands (see also Hay et al. 1987).

Corroborating previous work, potentially herbivorous invertebrates were generally rare on our settling plates (Fig. 3C), and in fact, their per plate abundance was positively correlated with algal biomass (r = 0.28, n = 546, $P \ll 0.001$). Potential mesograzers averaged only 0.15 animals per 50-cm² plate outside damselfish territories, 0.66 animals/50 cm² inside territories, and 2.42 animals/50 cm² within grazer-exclusion cages ($P \ll 0.001$ for all paired comparisons). Other small invertebrates, including harpacticoid copepods, oysters, and recently settled larvae of sea cucumbers and mantid shrimps, showed the same pattern (M. A. Hixon and

TABLE 2. Significant comparisons from cage-control experiment (see Table 1). Each comparison gives means ($\pm$ 1 SE) for 12 pairs of settling plates sampled on a given date (except for algal biomass, where eight pairs of plates were sampled). Paired comparisons were by Wilcoxon signed-ranks tests (Z statistic).

Parameter	Elapsed time (d)	Treatment comparison		Z	P
		Complete cage vs. wall only			
Algal species diversity					
Evenness (J)	91	0.08 $\pm$ 0.02	0.16 $\pm$ 0.03	2.14	0.03*
Composite diversity (H')	91	0.07 $\pm$ 0.02	0.16 $\pm$ 0.03	2.30	0.02*
Herbivorous invertebrates (no./50 cm^2)	147	0.67 $\pm$ 0.23	2.83 $\pm$ 0.87	2.55	0.01**
Relative abundance by growth form					
Complex red filaments	147	26.08 $\pm$ 7.82	43.92 $\pm$ 10.76	1.99	0.05*
Algal biomass (g AFDM/50 cm^2)	147	0.17 $\pm$ 0.02	0.23 $\pm$ 0.04	2.10	0.04*
	231	0.22 $\pm$ 0.03	0.64 $\pm$ 0.08	2.52	0.01**
		Open plot vs. roof only			
Algal species diversity					
Evenness (J)	231	0.56 $\pm$ 0.05	0.70 $\pm$ 0.05	1.96	0.05*
Composite diversity (H')	231	0.78 $\pm$ 0.08	1.02 $\pm$ 0.08	2.20	0.03*

* $P \leq 0.05$, ** $P \leq 0.01$.

W. N. Brostoff, *unpublished data*). Lobel (1980), Klumpp et al. (1988), and Zeller (1988) also found more small invertebrates inside damselfish territories than outside.

Only one species of coral, *Pocillopora damicornis*, recruited to the settling plates. Only 28 juvenile colonies, each occupying <0.5 cm^2, were sampled at various times throughout the experiment (never more than four on one sampling date). Most of these coral spat occurred on PVC plates within grazer-exclusion cages.

Patterns of algal succession

A total of 40 algal species were sampled during the succession experiment, including 5 blue-greens (Cyanophyta), 9 greens (Chlorophyta), 5 browns (Phaeophyta), and 21 reds (Rhodophyta). Several species were identifiable only to genus because they were small or immature, not found as larger individuals elsewhere, and could not be isolated and cultured successfully. As detailed in the Appendix, the 40 species were classified before analysis into four growth forms, analogous to Littler and Littler's (1980) "functional forms" and Steneck and Dethier's (1994) "functional groups": (1) simple green and brown filaments of relatively thin and unbranched structure (7 species); (2) red filaments of thin but finely branching structure (12 species); (3) thick, coarsely branching filaments and blades of relatively robust structure (13 species); and (4) crusts and prostrate blue-green mats (8 species). Note that, to some extent, these growth forms can intergrade in that some of these species can assume more than one form (see Lubchenco and Cubit 1980, Dethier 1981, Lewis et al. 1987, Hanisak et al. 1988). However, with one exception, each species occurred as a single growth form during our study. The exception was a felt-like green crust, which, based on microscopic examination of laboratory cultures, appeared to be anastomosing basal holdfasts of *Enteromorpha* and *Cladophora* (see Moss and Marsland 1976). Because this crust was ex-

tremely different from the upright forms of these species, we classified it separately.

Because species within each growth-form group were morphologically similar and occurred in mixed-species stands, they appeared to be ecological equivalents (see Littler and Littler 1980, Steneck 1988, Steneck and Dethier 1994). Moreover, it was virtually impossible to distinguish individual species within such mixed-species stands macroscopically, suggesting that fish may have similarly discriminated among the algae as several growth forms as opposed to tens of species. Therefore, to examine both levels of perception, we focused our univariate analyses on the four algal growth forms and our multivariate analyses on all 40 species.

By growth form.—For clarity and to facilitate different kinds of comparisons, changes in the relative abundances of the algal growth forms among grazing treatments are illustrated both by treatment (Fig. 4) and by form (Fig. 5). The ungrazed successional sequence within cages followed three distinct stages: an early stage (less than $\approx$100 d into the experiment) dominated by green and brown filaments, a midsuccessional stage (100–300 d) dominated by red filaments, and a late stage (greater than $\approx$300 d) dominated by thick filaments and blades (Fig. 4A). Green and brown filaments were significantly more abundant than the other forms for the first 10 samples 7–70 d into the experiment ($P \ll 0.001$, $n = 210$ pairs, $Z = 11.1$–12.1), and red filaments dominated the five samples between days 120 and 230 ($P \ll 0.001$, $n = 105$ pairs, $Z = 3.7$–5.5). At the last sample on day 365, thick filaments and blades were significantly more abundant than all other forms ($P \ll 0.001$, $n = 21$ pairs, $Z = 3.6$–3.7), except red filaments ($P = 0.41$, $n = 21$ pairs, $Z = 0.8$). The dominant four species in the final assemblages within fish-exclusion cages were *Tolypiocladia glomerulata* (47.5% overall relative abundance), *Antithamnion* sp.
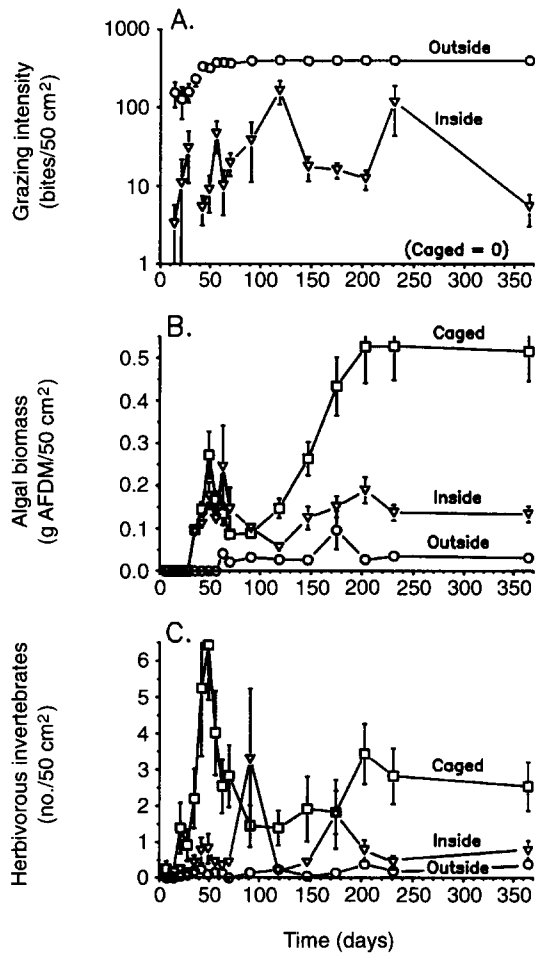
FIG. 3. Patterns of (A) destructive (i.e., holdfast-removing) grazing intensity, measured as the density of fish bite marks, (B) algal biomass, and (C) the density of small herbivorous invertebrates during succession. Each point gives the mean (±1 SE) of (A) 7, (B) 14, and (C) 21 settling plates, respectively. Grazing treatments are: caged = within fish-exclusion cage; inside = exposed inside damselfish territory; outside = exposed outside territory. On this and subsequent similar figures, sample intervals are weekly for 10 wk, then monthly for 6 mo, followed by the final sample at the end of 1 yr.
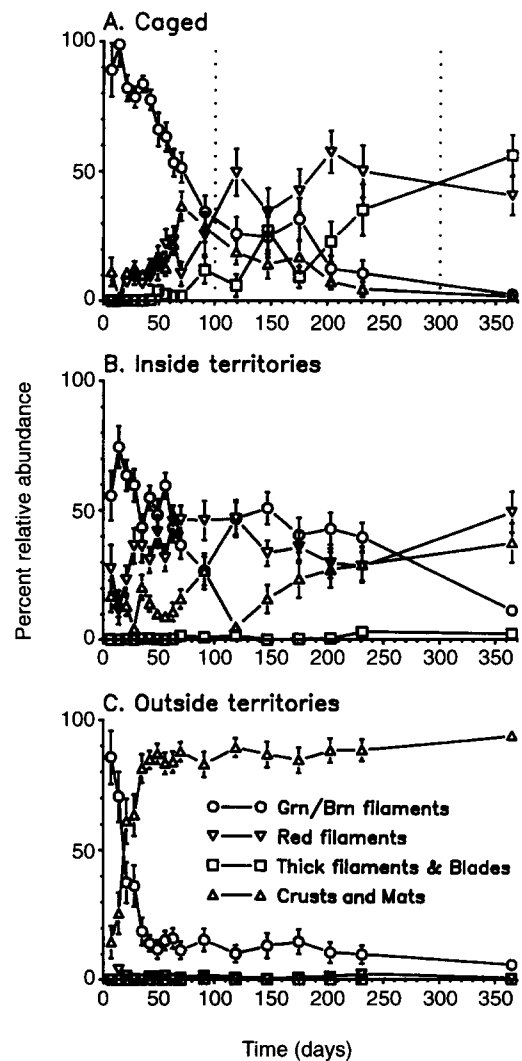

FIG. 4. Patterns of relative abundance of four algal growth forms (see Appendix) during succession: (A) within fish-exclusion cages (note shifts in dominance at approximately day 100 and day 300, indicated by vertical dotted lines), (B) inside damselfish territories, and (C) outside territories. Each point gives the mean (±1 SE) of 21 settling plates.

(10.2%), *Acanthophora spicifera* (8.1%), and *Ceramium fimbriatum* (7.2%).

Succession inside damselfish territories was decelerated relative to inside fish-exclusion cages. Early dominance by green and brown filaments persisted over 230 d into the experiment, and red filaments (rather than thick filaments and blades) still dominated at the end of the year (Fig. 4B). Green and brown filaments were significantly more abundant than the other forms for the first 16 samples, up to day 230 ($P \leqslant 0.001$, $n = 336$ pairs, $Z = 4.5$–15.3). At the end of the experiment, red filaments were significantly more abundant than all other forms ($P < 0.001$, $n = 21$ pairs, $Z = 3.2$–3.6), except crusts and blue-green mats ($P = 0.37$, $n = 21$ pairs, $Z = 0.9$). The dominant four species in

the final assemblages inside damselfish territories were *Centroceras clavulatum* (29.1% overall relative abundance), *Calothrix crustacea* (21.1%), *Taenioma perpusillum* (9.5%), and *Oscillatoria lutea* (7.4%). The blue-green *Calothrix* and *Oscillatoria* were largely epiphytic on the red filaments (see also Lobel 1980).

The differences between ungrazed succession within cages and moderately grazed succession inside damselfish territories were due to, first, reciprocal variation in the abundances of green/brown filaments (Fig. 5A) and red filaments (Fig. 5B), and second, the near absence of thick filaments and blades inside territories (Fig. 5C). On the one hand, green and brown filaments were significantly more abundant within cages for the first 11 samples from day 7 to 91 ($P \leqslant 0.001$, $n = 231$
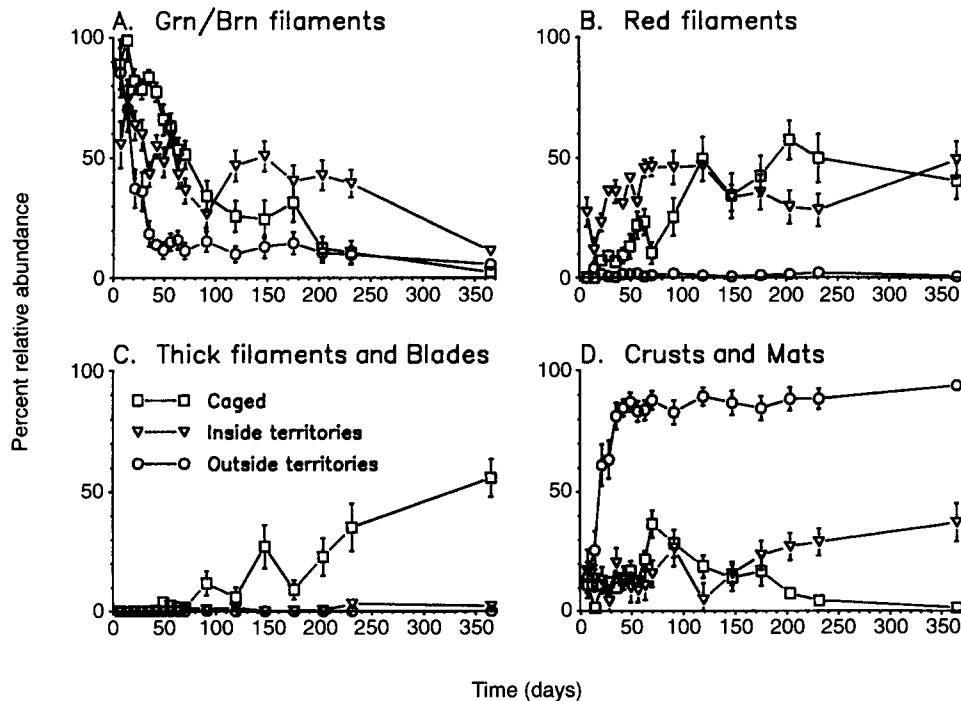
FIG. 5. Patterns of relative abundance of four algal growth forms during succession: (A) simple green and brown filaments, (B) thin and finely branched red filaments, (C) thick and coarsely branched filaments and blades, and (D) crusts and prostrate blue-green mats. Each point gives the mean (± 1 SE) of 21 settling plates. Grazing treatments are: caged = within fish-exclusion cage; inside = exposed inside damselfish territory; outside = exposed outside territory.

pairs, $Z = 6.7$), and more abundant inside territories thereafter ($P \ll 0.001$, $n = 126$ pairs, $Z = 5.4$). On the other hand, red filaments were more abundant inside territories for the first 11 samples ($P \ll 0.001$, $n = 231$ pairs, $Z = 8.6$), and more abundant within cages for half of the subsequent 6 samples ($P = 0.005$, $n = 63$ pairs, $Z = 2.8$). Crusts and mats were of low abundance in both treatments, although they were significantly more abundant inside territories for the last three samples (Fig. 5D, $P \ll 0.001$, $n = 63$ pairs, $Z = 5.0$).

Succession outside territories followed a much dif-

TABLE 3. Characteristics of nine settling plates (out of 1035 supporting detectable algae) excluded from detrended correspondence analysis of algal succession. Grazing treatments are exposed outside damselfish territories, exposed inside territories, and within fish-exclusion cages. Plate types are naturally contoured coral rock and PVC plastic. The dominant algal species and its percent relative abundance are listed for each plate.

Age (d)	Treatment	Type	Dominant (%)
7	outside	natural	*Nostoc spumigena* (100)
7	inside	natural	*Nostoc spumigena* (100)
7	inside	natural	*Nostoc spumigena* (88)
7	caged	natural	*Nostoc spumigena* (100)
14	inside	natural	*Nostoc spumigena* (100)
63	caged	PVC	*Spyridia filamentosa* (97)
147	caged	PVC	*Spyridia filamentosa* (100)
147	caged	natural	*Padina* sp. (100)
365	caged	natural	*Spyridia filamentosa* (84)

ferent trajectory than in the other grazing treatments. Early successional green and brown filaments dominated for only the first 2 wk, and were rapidly replaced by crusts and prostrate mats, which strongly dominated for the remainder of the experiment (Figs. 4C and 5D). Within the crusts and mats (and unlike the other growth forms), there was a nested succession of the green crust gradually decreasing in cover as that of the crustose coralline *Hydrolithon reinboldii* increased (Hixon and Brostoff 1981). The dominant four species in the final assemblages outside damselfish territories were the green crust (42.6% overall relative abundance), *Calothrix crustacea* (23.4%), *Hydrolithon reinboldii* (19.9%), and *Oscillatoria lutea* (7.7%).

By species.—Successional patterns examined at the level of algal species by detrended correspondence analysis (DCA) reflected and corroborated those observed at the level of growth forms. Because 36 settling plates from the first 3 wk of the experiment supported no detectable algae, they were excluded from analysis. The first run identified nine additional plates supporting "outlier" algal assemblages, which caused the scores of the remaining plates to "collapse" along the first axis. All the outliers were plates that had become strongly dominated by a single species, especially the blue-green *Nostoc spumigena* on five plates during the first 2 wk and the red filament *Spyridia filamentosa* on three other plates later during the experiment (Table 3). Removing these outliers for the second DCA run

resulted in relatively high eigenvector values for the first and second axes (0.78 and 0.55, respectively), indicating high correlation between the sample and species configurations (Hill and Gauch 1980). By far, most variation was detected along the first axis.

The second DCA of 1026 settling plates sampled over 17 dates during the year (Fig. 6A) showed that, on average, succession inside damselfish territories followed the same trajectory as within fish-exclusion cages (running from left to right on the ordination, originating from an axis 1 score of ≈100). However, succession proceeded at a much slower rate inside territories and covered only about half the ordinated distance as within cages. Succession outside territories followed a completely different trajectory (starting at the same origin, but running from right to left on the ordination).

The accompanying ordination of the 40 algal species illustrates how each species corresponded with the 17 samples of settling plates; each species is located in a position that "reciprocally averages" its distribution among samples (Fig. 6B). To facilitate interpretation of Fig. 6B, the center of gravity of groups of species by growth form are plotted in Fig. 6C, after eliminating one rare outlier species from each group. Comparing Fig. 6C with Fig. 6A corroborates the pattern that ungrazed succession within cages proceeded in three stages: early domination by green and brown filaments to midsuccessional dominance by red filaments to late domination by thick filaments and blades (cf. Fig. 4A). Succession inside damselfish territories followed the same trajectory, but did not reach the final stage (cf. Fig. 4B), and succession outside territories progressed directly from early green and brown filaments to persistent crusts and prostrate mats (cf. Fig. 4C).

Patterns of species diversity

We examined changes in algal diversity during succession from two perspectives, "global" (among-plates) and "local" (within-plate), within each grazing treatment. At the global level, pooling all plates on each of the 17 sampling dates, composite diversity (H') initially increased on ungrazed caged plates, peaked ≈3 mo into the experiment, and subsequently declined and appeared to stabilize sometime after day 200 (Fig. 7A). This pattern was paralleled by and was due mostly to changes in species richness (Fig. 7B) rather than evenness (J), which was relatively constant (Fig. 7C). Maximum global richness within cages peaked at 21 species ≈2 mo into the experiment.

In contrast, composite diversity inside damselfish territories gradually increased until it exceeded values within cages sometime after day 200 (Fig. 7A). This pattern was also due largely to changes in species richness, which reached a maximum of 20 species at the end of the experiment (Fig. 7B). Species evenness was comparable between these two treatments throughout the experiment (Fig. 7C). Plates outside territories ex-

hibited the lowest global richness, evenness, and composite diversity of all treatments throughout the year.

At the local level of individual plates, comparisons among grazing treatments followed two stages. For the first 11 samples (day 7 to day 91), patterns within fish-exclusion cages and inside damselfish territories were nearly identical, and all three measures of diversity were always lowest outside territories (Fig. 8). On only three dates during this period were there significant differences between caged plates and those inside territories (H' in territories was greater than that in cages at days 14, 35, and 42; $P = 0.006–0.04$, $n = 21$ pairs each, $Z = 2.0–2.8$). Outside territories, diversity values were usually significantly lower than those either within cages or inside territories (46 of 66 paired Z tests).

From about day 90 onward, there was a pronounced decline in all three measures of local diversity within cages, which tended to level-off after day 150 (Fig. 8). For the last five samples (days 147–365), average composite diversity was greatest inside damselfish territories, intermediate outside territories, and lowest within cages (Fig. 8A). However, by the end of the experiment, the difference between caged plates and plates outside territories was not significant (caged vs. outside: $P = 0.54$, $Z = 0.6$; caged vs. inside: $P = 0.002$, $Z = 3.1$; outside vs. inside: $P = 0.01$, $Z = 2.5$; $n = 21$ pairs each). These differences were due mostly to the richness component of diversity (Fig. 8B), since average evenness was comparable inside and outside territories in the last five samples (Fig. 8C).

In summary, during the year-long succession experiment, global algal species diversity among all plates pooled followed a unimodal pattern within fish-exclusion cages, gradually increased inside damselfish territories, and was always lowest outside territories (Fig. 7). Local or within-plate species diversity was comparable within cages and inside territories and lowest outside territories for the first 3 mo of the experiment. Thereafter, diversity declined within cages such that diversity was greatest inside territories by the end of the experiment (Fig. 8). Additionally, across all samples inside territories and within cages, there was a weak but highly significant negative relationship between all three measures of algal diversity and algal biomass (H': $r^2 = 0.11$; S: $r^2 = 0.11$; J: $r^2 = 0.06$; $P \ll 0.001$ and $n = 364$ plates each, excluding biomass values of zero during the 1st mo of the experiment).

Comparisons of settling plates with natural substrata

The samples of natural coral rock removed from inside and outside damselfish territories supported algal assemblages of unknown ages and histories. Consequently, comparing these samples with the settling plates provided only an approximate estimate of how closely succession on the plates had converged toward nearby reef assemblages by the end of the experiment. To provide as realistic a contrast as possible, we com-
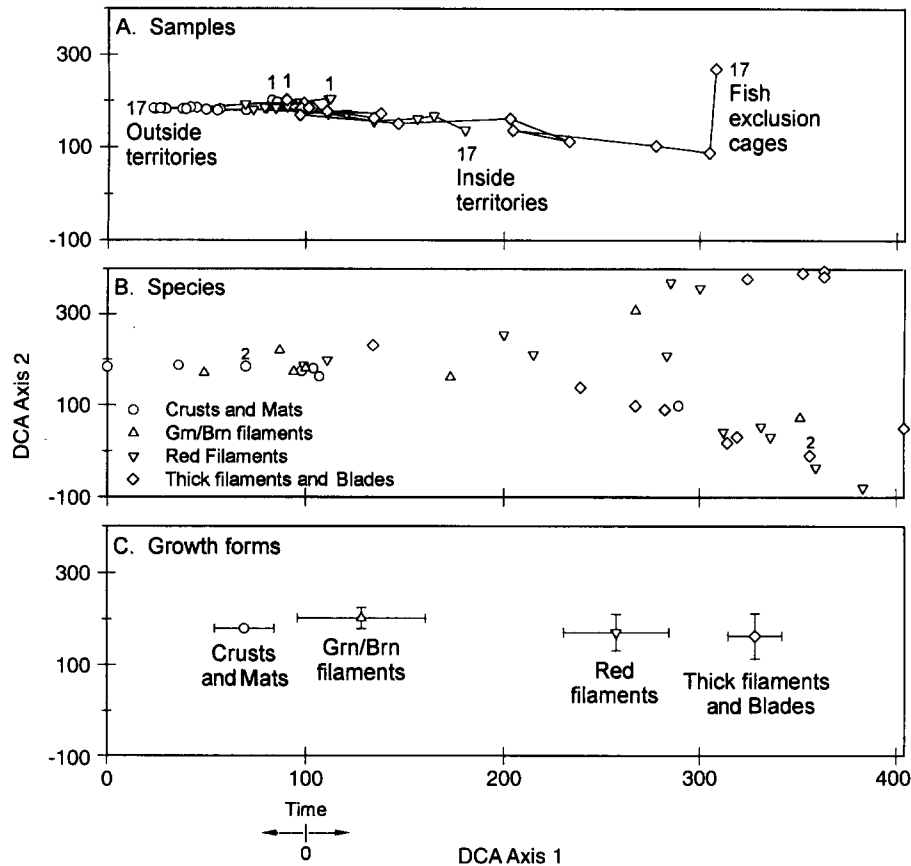
FIG. 6. Detrended correspondence analysis of succession. (A) Mean scores of 17 samples of settling plates over 1 yr for each of three grazing treatments ($n = 21$ plates per point, except $n = 12$–20 for the first three samples due to 36 plates supporting no detectable algae and five plates excluded because of outlier assemblages [Table 3], and $n = 19$–20 for three later points with four other plates excluded because of outlier assemblages [Table 3]). Standard error bars are about the same size as the symbols, and so were deleted for clarity. Connecting the 17 points for each treatment gives a mean trajectory of succession (see Fig. 1), starting from the first sample after 1 wk (symbols labelled "1" for each treatment, as indicated by "time 0" along the abscissa) and ending after 1 yr (labelled "17"). (B) Species scores corresponding to sample scores. Each point represents one species, except the two points labelled "2," indicating pairs of species with nearly identical coordinates. The proximity of each species to each sample in graph (A) reflects its average representation in that sample. (C) Average species scores pooled by growth form (± 1 SE), after excluding one outlier species from each group. Comparing graphs (A) and (C) indicates that succession within cages proceeded from green and brown filaments toward red filaments, and eventually, toward thick filaments and blades (left to right). Succession inside territories proceeded only partway down this trajectory. In contrast, succession outside territories proceeded from green and brown filaments directly to crusts and prostrate mats (right to left).

pared the reef samples with the last (day 365) sample of settling plates composed of naturally contoured coral rock.

As detailed in the two central columns of Table 4, comparisons *within* the natural reef samples *between* grazing treatments reflected the patterns found at the end of the main succession experiment for all settling plates combined: inside damselfish territories, herbivorous invertebrates were more abundant (cf. Fig. 3C), all algal growth forms were more abundant (except crusts and prostrate mats, which strongly dominated outside territories, cf. Figs. 4 and 5), and all measures of algal diversity were greater (cf. Fig. 8) than outside territories.

However, there were differences *between* the natu-

rally contoured coral-rock settling plates and the reef samples *within* each grazing treatment, indicating that succession on the plates had not fully converged toward natural assemblages (Table 4). Inside damselfish territories, the reef samples supported significantly less early successional green and brown filaments and more late successional thick filaments and blades than the settling plates. These differences were accompanied by greater species richness on the settling plates, although evenness (J) and composite diversity (H') were not significantly different. Outside territories, the reef samples were more strongly dominated by crusts and prostrate mats than the settling plates, resulting in significantly lower algal diversity by all measures. Overall, it appeared that the natural substrata supported assem-
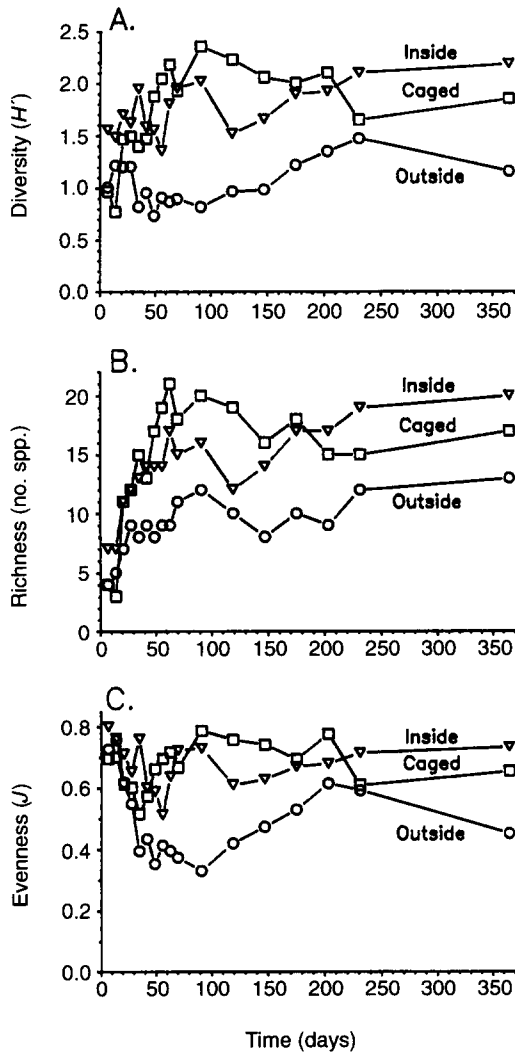
FIG. 7. Patterns of among-plate (global) algal species diversity during succession. Each point gives the pooled diversity of 21 settling plates in terms of (A) the Shannon-Wiener Index, (B) species richness, and (C) Pielou's Evenness. Grazing treatments are: caged = within fish-exclusion cage; inside = exposed inside damselfish territory; outside = exposed outside territory.
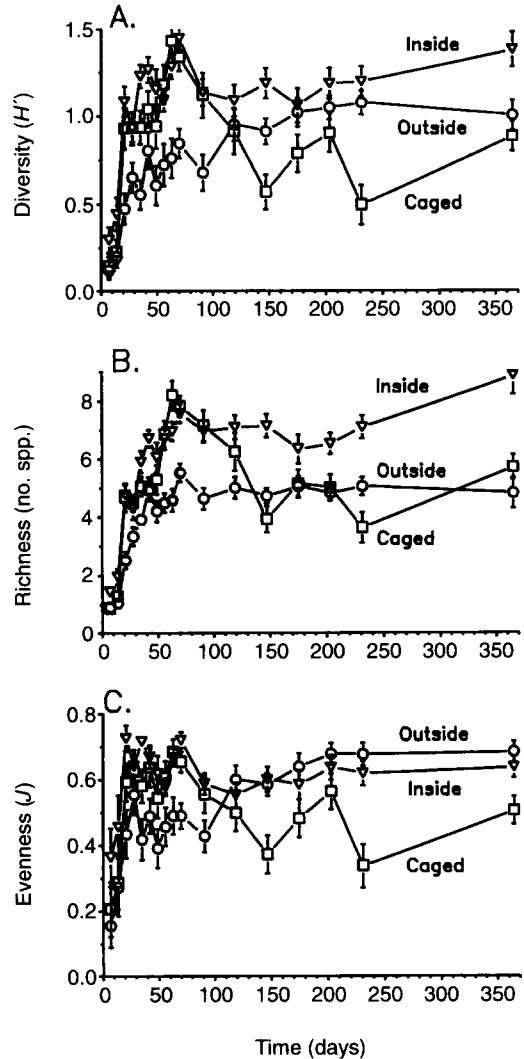
FIG. 8. Patterns of within-plate (local) algal species diversity during succession. Each point gives the mean (± 1 SE) diversity of 21 settling plates in terms of (A) the Shannon-Wiener Index, (B) species richness, and (C) Pielou's Evenness. Grazing treatments are: caged = within fish-exclusion cage; inside = exposed inside damselfish territory; outside = exposed outside territory.

blages that were similar to but successionally older than those on the year-old settling plates.

Feeding selectivity of fishes

It was clear from the results of the succession experiment that the schooling parrotfishes and surgeon-fishes in this system, treated as a group, consumed all erect algae exposed to them. This conclusion is based on two observations. First, only grazer-resistant crusts and prostrate mats persisted on settling plates exposed outside territories (Fig. 4C), where these fishes were the only abundant herbivores. Second, several times during the experiment, we removed extra settling plates from inside territories and fish-exclusion cages, and

placed them outside territories. Within a day, these plates were invariably grazed bare with numerous fish bite marks evident, as happens to natural territories when the resident damselfish are removed (Lobel 1980, Mahoney 1981, see also Low 1971, Ogden and Lobel 1978, Hourigan 1986).

The feeding selectivity of territorial damselfish defending mature algal mats was determined directly from paired samples of gut contents and the algal mats from which the fish (17 males and 13 females) had been feeding. The 30 samples yielded 22 species of algae, all but two of which were found on settling plates during the succession experiment (see Appendix). Two species (Struvea anastomosans and Spirulina subsalsa)

TABLE 4. Mean parameter values for the last sample (day 365) of settling plates composed of naturally contoured coral rock ($n = 7$ each) and samples of natural coral rock removed directly from the reef ($n = 24$ each), both exposed inside damselfish territories and outside territories. Symbols between adjacent means give significance of each comparison. Unpaired comparisons between settling plates and reef samples within each grazing treatment were by Mann–Whitney U tests; paired comparisons between reef samples inside vs. outside territories were by Wilcoxon signed-ranks tests.

| | Grazing treatment/substratum | | | | | | |
| | Inside territories | | | | Outside territories | | |
Parameter	Settling plates		Reef samples		Reef samples		Settling plates
Herbivorous invertebrates (no./50 cm^2)	0.43	NS	1.58	*	0.71	NS	0.57
Percent relative abundance by growth form							
Simple green/brown filaments	16.74	**	4.76	***	0.00	***	16.86
Complex red filaments	42.55	NS	59.01	***	0.04	***	1.70
Thick filaments and blades	4.68	*	24.31	***	0.42	NS	0.43
Crusts and blue-green mats	36.03	NS	11.92	***	99.54	***	81.01
Algal species diversity							
Richness (no. species/50 cm^2)	8.86	*	5.96	***	3.00	***	7.71
Evenness (J)	0.63	NS	0.56	**	0.35	***	0.71
Composite diversity (H')	1.39	NS	1.05	***	0.36	***	1.43

* $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$, NS not significant ($P > 0.05$).

each occurred in a single mat sample, but were not found in damselfish guts. Only one alga (*Nostoc spumigena*) was found in a fish but not in any algal mat.

Overall, Johnson's (1980) method rejected the null hypothesis that all algae were equally preferred by the damselfish ($F = 7.58$, $P < 0.01$). However, Waller–Duncan multiple comparisons revealed few significant differences in average "preference" ($-\bar{t}$) among most algal species (Fig. 9). In addition, considering the preference ranks of the algal species, there was little indication that the damselfish preferred one algal growth form over another. For example, the five most preferred species (ranks 1–5 in Fig. 9) comprised two green filaments, one brown filament, one red filament, and one blue-green mat (see Appendix). Similarly, the five least preferred species (ranks 18–22) comprised one brown filament, two red filaments, one green crust, and one blue-green mat.

In summary, *Stegastes fasciolatus* in our system grazed their *mature* algal mats in a fairly nonselective way. Note that "preference" here is a purely statistical phenomenon and does not necessarily imply active selection. In similar previous studies of territorial dam-

selfish, nonselective grazing was also demonstrated for *Microspathodon chrysurus* in the Gulf of California (Montgomery 1980) and *Stegastes planifrons* in the Caribbean (Hinds and Ballantine 1987). However, another study of the latter species indicated that it specialized on blue-green epiphytes (Lobel 1980), yet when it was presented algal monocultures, this fish showed preferences for thin red filaments (Irvine 1982).

DISCUSSION

From the perspective of either growth forms or individual species of algae, grazing by different groups of fishes had substantial but very different effects on the rate and trajectory of benthic algal succession on a Hawaiian coral reef. These results bolster an increasingly general caveat that any model of succession ignoring herbivory may miss a major determinant of community change, as recently emphasized by Bach (1994). Additionally, we know of only one other study that investigated how different kinds of herbivores can affect successional rates and trajectories within the same system. Brown and Gange (1992) showed that
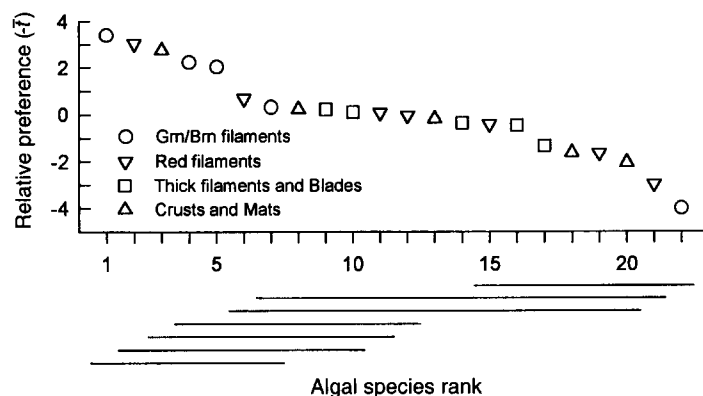

FIG. 9. Mean relative "preference" (Johnson's [1980] $-\bar{t}$) of 30 damselfish for each of 22 species of algae, listed from most preferred (rank 1) to least preferred (rank 22). Preference values near zero indicate nonselective grazing, and values with the same underline are not significantly different ($P > 0.05$, Waller–Duncan multiple comparison). Symbols identify growth forms and rank numbers identify species, as listed in the Appendix.

early secondary terrestrial succession was decelerated by foliar-feeding insects, but accelerated by root-feeding insects.

In the absence of grazing fishes in our system, early green and brown filaments were replaced by a diverse midsuccessional assemblage of mostly thin and finely branched red filaments, which in turn were replaced by thick and coarsely branched filaments and blades by the end of a year. This general pattern of structurally simple algae being replaced by more complex species is common among seaweeds (reviews by Lubchenco and Gaines 1981, Connell 1987, Sousa and Connell 1992).

On exposed surfaces subjected to intense grazing by parrotfishes and surgeonfishes outside damselfish territories, succession was deflected onto a new trajectory: early successional forms were quickly replaced by crusts and prostrate blue-green mats, which persisted until the end of the experiment and which strongly dominated exposed natural substrata outside territories.

Inside damselfish territories, succession was decelerated, such that the early and midsuccessional stages were protracted and late successional forms were still rare by the end of the year. Natural substrata inside territories supported algal stands similar to those on settling plates at the end of the succession experiment, although the presence of fewer early successional forms and more later successional forms indicated that the natural assemblages were somewhat older. These patterns corroborate previous studies indicating the general importance of herbivorous fishes in structuring algal assemblages on coral reefs (reviews by Steneck 1988, Glynn 1990, Hay 1991, Steneck and Dethier 1994, Hixon 1996).

Herbivory and succession

In marine systems, the most commonly documented effect of predation on benthic succession is acceleration (Farrell 1991, Sousa and Connell 1992). The mechanism is that predators differentially consume early successional species that could otherwise prevent later species from dominating (the inhibition model of Connell and Slatyer 1977). Our study provides examples of the two other ways consumers can alter succession: deflection and deceleration.

Deflection.—Of the possible effects of herbivores on succession, deflection is the least documented. The concept of "deflected" succession was introduced by Godwin (1929*a*), who described how agricultural cutting changed the trajectory of succession on English fenland from sedges replaced by bushes to sedges replaced by grasses (Godwin 1929*b*). Recently, Gibson and Brown (1992) showed experimentally that intense grazing by sheep deflects succession on English grasslands. Comparable data for marine algae are rare, however, because successional processes under different grazing regimes in the same system are seldom examined. Nonetheless, erect algae are commonly re-

placed by crustose algae in areas where there is intensive grazing by sea urchins (e.g., Kitching and Ebling 1961, Paine and Vadas 1969, Dayton 1975, Harrold and Reed 1985, Morrison 1988) or fishes (e.g., John and Pople 1973, Vine 1974, Wanders 1977, Carpenter 1986, Lewis 1986, reviews by Steneck 1988, Steneck and Dethier 1994). The underlying assumption is that there is a trade-off between competitive ability and resistance to grazing (reviews by Gaines and Lubchenco 1982, Steneck 1988, Huntly 1991). For marine algae, this trade-off has been documented for competitively superior erect forms vs. grazer-resistant crusts (Lubchenco and Cubit 1980, Dethier 1981, Littler et al. 1983, Steneck 1983, Lewis et al. 1987).

What, then, is the mechanism by which successional change occurs during deflection? In our system, there were only two successional stages outside damselfish territories: a short early stage dominated by simple green and brown filaments, which also occurs in the absence of fish grazing, and a persistent late stage dominated by crusts, which does not. In the absence of grazing, the early stage is replaced by other erect algae; crusts never dominate (see also Carpenter 1986, Lewis 1986, Morrison 1988, and references therein). This pattern suggests that erect algae normally inhibit crusts from becoming successional dominants, corresponding to Connell and Slatyer's (1977) "inhibition" model of successional change: later stages (crusts) can dominate only when disturbance (grazing) removes earlier stages (filaments).

Clearly, the high intensity of destructive (i.e., holdfast-removing) grazing by parrotfishes and surgeonfishes in our system allows only crusts to persist. Intensive grazing thus shifts algal succession from a sequence of "low-disturbance" erect species to a succession of "high-disturbance" crustose forms (sensu Connell 1987). Note that this pattern has ramifications for coral reefs in general. Given that erect algae can often outcompete corals, Glynn (1990:391) concluded that the "maintenance of modern coral reefs may be due largely to the activities of fish and invertebrate herbivores that prevent competitively superior algal populations from dominating open, sunlit substrates."

Deceleration.—Herbivores have been shown to decelerate succession in both terrestrial and aquatic systems (reviews by Lubchenco and Gaines 1981, Crawley 1983, Brown 1984, Farrell 1991, Sousa and Connell 1992). On land, both insects (e.g., Brown 1982, 1985, McBrien et al. 1983, Bach 1994) and mammals (e.g., Hope-Simpson 1940, Watt 1981*a, b,* Marrs et al. 1988) commonly slow the rate of succession. Considering marine algae, Sousa et al. (1981) showed that sea urchins off southern California preferred late successional seaweeds, and consequently early successional species persisted longer in areas where urchins were abundant (see also Dayton 1975). Similarly, Farrell (1991) demonstrated that grazing by limpets on the

Oregon coast delayed the successional transition from barnacles to macroalgae.

How do territorial damselfish decelerate succession in our system? There are three possible classes of mechanisms: (1) nonconsumptive inhibition of late successional species, including "weeding" behavior; (2) differential consumption of late successional species; or (3) nonselective grazing that differentially inhibits late successional species. Several lines of evidence are less consistent with the first two mechanisms than the third possibility. First, although other species of damselfish have been shown to literally "weed" their territories by removing individual thalli of undesirable species without consuming them (Lassuy 1980, Irvine 1982), many hours of activity budgets of *Stegastes fasciolatus* at our site revealed no incidents of weeding during our experiment (M. A. Hixon, *unpublished data*). The rarity of weeding may have been due to the algae being of generally similar filamentous forms and growing in mixed-species stands, thereby inhibiting visual selection. Second, the relative abundance of late successional thick filamentous and frondose algae inside territories was very low throughout our succession experiment, and had reached only ≈2% by the end of our study. This low relative abundance may have comprised too low a standing crop for the damselfish to discern individual thalli. Indeed, our feeding-preference analysis suggested that the damselfish were fairly nonselective grazers. Combined, these observations suggest that damselfish were neither differentially removing nor differentially consuming late successional species, at least at a level that could alter successional patterns.

We hypothesize that generalized grazing by the damselfish, evident from our paired gut–mat samples from mature territories, slows the rate of succession by inhibiting the competitive displacement of early successional species by late successional forms, as originally proposed by Montgomery (1980). Theoretically, if prey species show some differences in resource use, a modification of MacArthur's (1970) consumer–resource model is relevant (P. Chesson and N. Huntly, *unpublished manuscript*). This model predicts that moderate levels of equal proportional consumption of prey species will promote coexistence of slow-growing, late successional competitive dominants and faster growing, early successional competitive subordinates by differentially inhibiting the dominants. In our system, both early and late dominants were present throughout the succession experiment. Late successional, slower growing, thick filaments and blades appeared eventually to outcompete earlier species inside grazer-exclusion cages, but not inside damselfish territories. In the Gulf of California, very intensive nonselective grazing by the damselfish *Microspathodon dorsalis* also appeared to stop succession at an early stage (Montgomery 1980). In contrast, a combination of selective grazing and weeding behavior appeared to accelerate early

succession inside the territories of *Stegastes planifrons* in the Caribbean (Irvine 1982).

If successional deceleration is indeed the result of nonselective grazing by damselfish, then the conceptual models of Farrell (1991) provide some insight on the mechanisms of succession inside territories. However, to apply Farrell's models in this context, one must assume that the predictions are correct before an underlying mechanism can be inferred (Sousa and Connell 1992). Connell and Slatyer (1977) proposed that the effect of early successional species on later species is positive (the "facilitation" model), neutral (the "tolerance" model), or negative (the "inhibition" model). Although this formulation has been criticized as being too simplistic (e.g., Finegan 1984, Breitberg 1985, Pickett et al. 1987, Walker and Chapin 1987, McCook 1994), it nonetheless is useful for understanding net effects between successional stages (Connell et al. 1987, Sousa and Connell 1992).

Farrell (1991) predicted that nonselective ("equivalent") grazing will decelerate succession only in the tolerance and facilitation models. When tolerance occurs, the removal of early species by herbivores will have no effect and the removal of late successional forms will slow species replacement. When facilitation occurs, equivalent grazing will greatly decelerate succession by both decreasing the facilitation provided by early species and by removing late successional species. Although our study was not designed to test these alternatives, the fact that algae of all successional stages were present throughout our experiment leads us to hypothesize that tolerance was the prevailing mechanism; it appeared that early species did not have to modify the local environment before later species could become established.

By whatever means succession is decelerated inside territories, the result appears to be nutritionally beneficial to the resident damselfish. First, earlier successional green and red filaments have a greater nutritional content and are more digestible than later successional algae (Montgomery and Gerking 1980, see also Horn 1989). Second, because algal productivity tends to decrease late in succession as biomass accumulates (Birkeland et al. 1985, Carpenter 1986), damselfish could maintain a system of relatively high productivity compared to ungrazed areas. Additionally, damselfish territories exhibit greater algal productivity than more intensively grazed areas outside territories (Brawley and Adey 1977, Montgomery 1980, Russ 1987, Klumpp et al. 1987).

Ramifications for species diversity on coral reefs

Coral reefs are the marine analogs of tropical rain forests, supporting more species than any other aquatic system (Paulay 1996). The mechanisms maintaining this diversity have been the subject of much interest (e.g., Connell 1978, Hay 1985, Huston 1985), es-

pecially given recent anthropogenic threats to coral reefs (Ginsburg et al. 1993). Recent research suggests that herbivorous fishes can maintain high diversity of benthic algae on and near coral reefs at several spatial scales, both between and within habitats (Hay 1985). Between habitats, schooling herbivores may prevent competitively dominant but highly palatable algae inhabiting sand plains (Hay 1981) and low-relief beachrock (Lewis 1985, 1986) from displacing competitively subordinate but grazer-resistant algae on adjacent reefs. The herbivores do not forage extensively over sand and flat rock apparently because the lack of physical refuges increases the risk of predation (review by Hixon 1991).

Within habitats, our data suggest that herbivorous fishes may enhance local algal diversity in two ways: first, by causing between-patch differences in algal species composition, and second, by maintaining high local diversity within one kind of patch, i.e., damselfish territories. Between patches defended by damselfish and areas outside these territories, differential grazing causes different successional trajectories leading to algal assemblages of very different species composition. The resulting dominance by filamentous species inside territories and crustose species outside enhances local species diversity overall.

Within a patch in the absence of disturbance, local species diversity commonly peaks midway during succession (Connell 1978). The mechanism underlying this pattern is that a few late successional forms competitively exclude the greater variety of species found earlier in succession (Connell 1978, Paine 1984). This pattern occurred within fish-exclusion cages during our study: both species richness and composite diversity (H') peaked ≈ 2–3 mo into the succession experiment and then declined as thick filaments and blades apparently excluded thinner filaments (considering diversity both within and among settling plates). By decelerating succession inside their territories, *Stegastes fasciolatus* prolonged the high-diversity midsuccessional stage, such that diversity was greater inside territories than within cages by the end of the year. Diversity inside territories was also greater than that on exposed surfaces outside territories.

We suggest that this pattern corroborates Connell's (1978) general version of the "intermediate disturbance hypothesis" (Hixon and Brostoff 1983, see Bowers 1993 for a recent example in a terrestrial grazing system). The critical question in applying this hypothesis is whether damselfish territories truly undergo an intermediate level of disturbance relative to both ungrazed patches and areas outside territories. Because grazing was clearly least intense within exclusion cages, this question boils down to whether grazing was less intense inside territories than outside. Because the standing crop of algae was greater inside territories than outside, each bite by a damselfish inside may have removed more biomass than each bite by a similarly sized or smaller schooling herbivore outside. Thus, the

biomass removal rate could conceivably be at least as high inside territories as outside (Russ 1987). However, the aspect of herbivory having the greatest effect on the relative abundance of algal species is destructive grazing that removes algal holdfasts, clearly a form of "disturbance" (Grime 1981). In our system, the intensity of nonselective destructive grazing on exposed surfaces was much greater outside damselfish territories than inside (see also Brock 1979, Carpenter 1986, Steneck and Dethier 1994). This difference was due to the high density outside territories of schooling parrotfishes and surgeonfishes (see Brock et al. 1979). Although feeding morphology and behavior differs among species of schooling herbivores, the scraping dentition of benthic-feeding surgeonfishes, and especially, the fused "beak" of parrotfishes make these the most destructive grazers among reef fishes (Bellwood and Choat 1990, Choat 1991, Horn 1992). In any case, because all fish bites are not the same, both within and between species, any general measure of grazing intensity must be interpreted with caution.

Given the available data, we conclude that damselfish territories in our system experienced an intermediate level of disturbance relative to both exposed areas outside territories and ungrazed surfaces. Note, however, that "intermediate-disturbance" effects caused by predation can occur by different mechanisms than those caused by physical disturbance (Menge and Sutherland 1987). This conclusion led Menge and Sutherland (1987) to restrict the label of "intermediate disturbance" to situations involving only physical disturbances, such that what occurred in our system is more accurately described as predator-mediated coexistence of prey species.

Because the diversity-enhancing effect manifested within territories depends on the presence of damselfish defending these areas, thereby preventing "overgrazing" by other fishes, damselfish provide a coral-reef example of Paine's (1969) "keystone species" concept (Hixon and Brostoff 1983). Given that damselfish territories can cover well over 50% of shallow reef tracts (Sammarco and Williams 1982, Klumpp et al. 1987), can account for 70–80% of the primary productivity on fore-reefs (Brawley and Adey 1977), and have numerous indirect effects on local reef benthos disproportionate to the abundance of damselfish (review by Hixon 1996), the keystone label seems particularly appropriate.

In summary, herbivorous fishes are capable of maintaining the diversity of tropical benthic algae at three scales: between habitats, between patches, and within patches. How general are these patterns geographically? Between-habitat patterns similar to those demonstrated by Hay (1981) off the Caribbean coast of Panama and Lewis (1986) off Belize were also documented on the Great Barrier Reef by Scott and Russ (1987). The between-patch pattern of different species composition inside vs. outside territories has been docu-

mented for a variety of damselfish species worldwide (e.g., Vine 1974, Brawley and Adey 1977, Lassuy 1980, Lobel 1980, Montgomery 1980, Sammarco 1983, Ruyter Van Steveninck 1984). Finally, the within-patch pattern of higher diversity inside damselfish territories compared to both ungrazed surfaces and areas exposed outside territories has also been demonstrated experimentally for *Hemiglyphidodon plagiometopon* on the Great Barrier Reef (Sammarco 1983), and implicated for *Stegastes planifrons* in the Caribbean (Hinds and Ballantine 1987). However, this pattern is not universal in that *Microspathodon dorsalis* in the Gulf of California maintained a near monoculture of a single species of *Polysiphonia* (Montgomery 1980), and the algal mats defended by both *Hemiglyphidodon plagiometopon* at Yap Island and *Stegastes lividus* at Guam were less diverse than caged assemblages adjacent to territories (Lassuy 1980). Yet, Lassuy's cages were in place only 2 mo, so his results may have represented early successional stages similar to initial patterns during both Sammarco's (1983) and our studies.

In conclusion, our data suggest that herbivorous fishes can differentially affect succession of benthic algae over small spatial scales. These effects, especially those of some territorial damselfishes, may partially explain the maintenance of high species diversity on coral reefs. In a broader perspective, our results both demonstrate the importance of herbivores in determining the rate and trajectory of succession, and corroborate Paine's (1966) general hypothesis that predation is a major factor maintaining high diversity in tropical systems.

ACKNOWLEDGMENTS

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APPENDIX

Overall percent relative abundance of each algal species in each grazing treatment over 1 yr, pooled over all samples, and listed by growth form and division. Treatments are: caged = within fish-exclusion cages; inside = exposed inside damselfish territories; outside = exposed outside damselfish territories. Relative abundances indicated by "tr" were <0.005%. Numbers before species indicate the rank dietary "preference" of that species by damselfish in a separate analysis (see Fig. 9).

		Grazing treatment		
Algal growth form/division/species		Caged	Inside	Outside
Simple green and brown filaments				
Chlorophyta				
1 *Bryopsis* sp. Lamouroux		1.04	0.03	0
5 *Cladophora* sp. Kützing		2.75	1.61	0.45
7 *Enteromorpha rhizoidea* J. Agardh		11.82	10.98	6.02
Ulothrix flacca Kützing		0.01	0	0
Unknown siphonous green filament		1.07	1.04	0.15
Phaeophyta				
4 *Ectocarpus indicus* Sonder in Zollinger		32.90	31.02	13.03
22 *Sphacelaria novaehollandiae* Sonder		0.59	1.68	0.33
	Total	50.18	46.36	19.98
Thin and finely branched red filaments				
Rhodophyta				
Acanthophora spicifera (Vahl) Børgesen		1.02	0	0
Acrochaetium sp. Nägeli		0.29	0.05	0.01
21 *Anotrichum tenue* (C. Agardh) Nägeli		0.01	0.12	0
6 *Antithamnion* sp. Nägeli		1.37	0.73	0.01
19 *Centroceras clavulatum* (C. Agardh) Montagne		10.53	5.52	0.02
11 *Ceramium fimbriatum* Setchell & Gardner		5.32	3.71	0.04
Gelidiella acerosa (Forsskål) Feldman & Hammel		0.14	0.28	0
Herposiphonia parca Setchell		0.04	0.15	0.03
15 *Jania* sp. Lamouroux		†	†	†
12 *Polysiphonia rhizoidea* Meñez		3.60	6.17	1.09
Spyridia filamentosa (Wulfen) Harvey		0.96	0	0
2 *Taenioma perpusillum* J. Agardh		0	0.45	0
Unknown ceramioid		1.15	0	0
	Total	24.43	17.18	1.20
Thick and coarsely branched filaments and blades				
Chlorophyta				
Microdictyon setchellianum Howe		0.33	0	0
16 *Struvea anastomosans* (Harvey) Piccone		0.01	0	0
17 *Udotea abbreviata* Gilbert		†	†	†
Phaeophyta				
Dictyota friabilis Setchell		0.06	0	0
Hydroclathrus clathratus (C. Agardh) Howe		0.17	0	0
Padina thivyi Doty & Newhouse		0.43	0	0
Rhodophyta				
14 *Champia parvula* (C. Agardh) Harvey		0.20	0.08	0.01
Chrysymenia sp. J. Agardh		0.14	0	0
Gelidium sp. Lamouroux		0.80	0.43	0
Gracilaria coronopifolia J. Agardh		0.26	0	0
9 *Hypnea cervicornis* J. Agardh		5.38	0.13	0
Laurencia clathratus (C. Agardh) Howe		0.02	0	0
10 *Pterocladia capillaceae* (Gmelin) Bornet & Thuret		0.23	0.14	0.02
Tolypiocladia glomerulata (C. Agardh) Schmitz		2.88	tr	0
	Total	10.91	0.78	0.03
Crusts and prostrate blue-green mats				
Chlorophyta				
Dictyosphaeria versluysii Weber-van Bosse		0	tr	0
20 Green crust*		8.09	18.09	54.23
Cyanophyta				
Anabaina oscillarioides Kützing		0	0.06	0
18 *Calothrix crustacea* Schousboe & Thuret		1.79	5.58	4.20
3 *Oscillatoria lutea* C. Agardh		2.75	5.98	7.05
8 *Nostoc spumigena* (Mertens) Drouet		0.71	1.04	0.64
13 *Spirulina subsalsa* Oersted		0	0.29	0.04
Rhodophyta				
Hydrolithon reinboldii (Weber-van Bosse & Foslie) Foslie		1.14	4.64	12.63
	Total	14.48	35.68	78.79

* Appeared to be anastomosing basal holdfasts of *Enteromorpha* and *Cladophora*.

† Denotes two species not encountered during the succession experiment, but sampled during the feeding selectivity analyses on a neighboring reef.