

# Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure\*

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**ABSTRACT:** An experiment was performed on Britomart Reef (central region, Great Barrier Reef) to determine the effects of fish grazing and territoriality by the damselfish *Hemiglyphidodon plagiometopon* on benthic algal community structure. This pomacentrid excludes herbivorous fish from its territory, creating undergrazed patches with characteristic 'algal lawns' within coral reef lagoons. Pieces of natural coral substratum were placed at a depth of 10 m under 4 sets of treatments: within cages protected from fish grazing, within damselfish territories, within shaded damselfish territories, and outside territories exposed to natural levels of fish grazing. A reduction in grazing by herbivorous fish, caused by caging or by the territorial behaviour of *H. plagiometopon*, resulted in marked changes in algal community structure. After 3 to 4 mo, the response of algal abundance and community structure to the treatments was highly variable. After 11 to 12 mo, however, decreased fish grazing was found to cause a significant increase in algal biomass and percent-cover. Algal species diversity ( $H'_B$ ,  $J'_B$ , and number of species) was relatively high within damselfish territories, while diversity within cages and on substrate fully exposed to fish grazing was relatively low. Thus, species diversity was maximized at intermediate levels of accessibility to fish grazing. Algal species composition also shifted with accessibility to fish grazing. The algal community within cages was dominated by rhodophytes, particularly *Polysiphonia subtilissima*. Damselfish territories were dominated by a mixture of rhodophytes and cyanophytes, including *Centroceras clavulatum*, *Gracilariopsis rhodotricha*, and *Lyngbya aestuarii*. Species composition within shaded territories was intermediate between these 2 treatments, exhibiting affinities to both. The naturally grazed algal community outside the damselfish territory was dominated by filamentous cyanophytes such as *L. aestuarii* and *Symploca hydroides* and by the encrusting chlorophyte *Pseudendoclonium* sp. The interstices of the coral substratum were found to be riddled with *S. hydroides*, *L. convervroides*, *Oscillatoria* aff. *amphibia*, and *O. aff. nigroviridis*. Cyanophytes clearly dominated substratum exposed to natural levels of fish grazing. It is suggested that rates of nitrogen fixation on natural coral reef substratum are positively related to levels of fish grazing.

## INTRODUCTION

Marine grazers are known to exert strong control over the structure of benthic algal communities (reviews: Crisp, 1964; Lawrence, 1975; Ogden, 1976; Borowitzka, 1981; Lawrence and Sammarco, 1982; Hatcher, in press). Algal community structure is also affected by the behaviour of certain site-attached pomacentrid fish, particularly on coral reefs (Vine, 1974; Brawley and Adey, 1977; Potts, 1977; Ogden and Lobel, 1978; Mahoney, 1981). Some of these damselfish are themselves grazers (Montgomery, 1980a, b) and are interspecifically territorial, excluding other graz-

ing fish from their territories (Myrberg and Thresher, 1974; Thresher, 1976; Itzkowitz, 1977). In some cases, even grazers of other phyla are actively excluded from the territories (Albrecht, 1969; Clarke, 1970). For example, *Eupomacentrus planifrons* Cuvier in the Caribbean excludes both *Diadema antillarum* Philippi and *Echinometra viridis* A. Agassiz (Echinoidea: Echinoidea) from their territories (Williams, 1979, 1980, 1981; Sammarco and Williams, 1982), within which distinct algal 'lawns' develop. Territorial and feeding behaviours of such damselfish as *E. planifrons*, *Dischistodus perspicillatus* Cuvier, and *E. acapulcoensis* Fowler can be associated with adult coral mortality as a result of this lush algal growth (Kaufman, 1977; Potts, 1977; Wellington, 1982).

In the central region of the Great Barrier Reef,

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the pomacentrid *Hemiglyphidodon plagiometopon* Bleeker (Allen, 1975) is found in high abundance locally (Sammarco and Carleton, 1982) along with other territorial damselfish. This fish excludes grazing fish from its territories and maintains an algal lawn (Las-suy, 1980). Coral recruitment on natural primary substratum within the territories of *H. plagiometopon* is significantly higher (by 5 to 7 times) and more diverse than on similar substratum outside the territories or within enclosures, protected from fish grazing (Sammarco, 1980b; Sammarco and Carleton, 1982). Territoriality by *H. plagiometopon* is also believed to assist indirectly in accelerating internal bioerosion of dead coral (Risk and Sammarco, 1982). These indirect effects of *H. plagiometopon* on the benthic coral reef community support hypotheses proposed by Levin (1974), Levin and Paine (1974), and Paine and Levin (1981), that small-scale disturbance and patch-formation, in this case by a biological agent, can increase species diversity (Sammarco and Williams, 1982).

The present study is an extension of the above experiment involving *Hemiglyphidodon plagiometopon*,

concentrating on the effects of territoriality and reduced fish grazing on algal community structure. Here I demonstrate that the territorial activities of this fish cause an increase in algal biomass and species diversity. It is also shown that increased grazing by fish causes a shift in the benthic algal community from one dominated by red algae to one dominated by blue-greens and greens. Justification is shown for a hypothesis that increased fish grazing may lead to increased rates of nitrogen-fixation by the benthic algal community of a coral reef.

### MATERIALS AND METHODS

Many of the techniques used here are described in Sammarco and Carleton (1982), but pertinent details are presented below.

All experimentation was performed on Britomart Reef (18°14'S, 146°45'E) in the central region of the Great Barrier Reef (Figs. 1 and 2). The study site was a

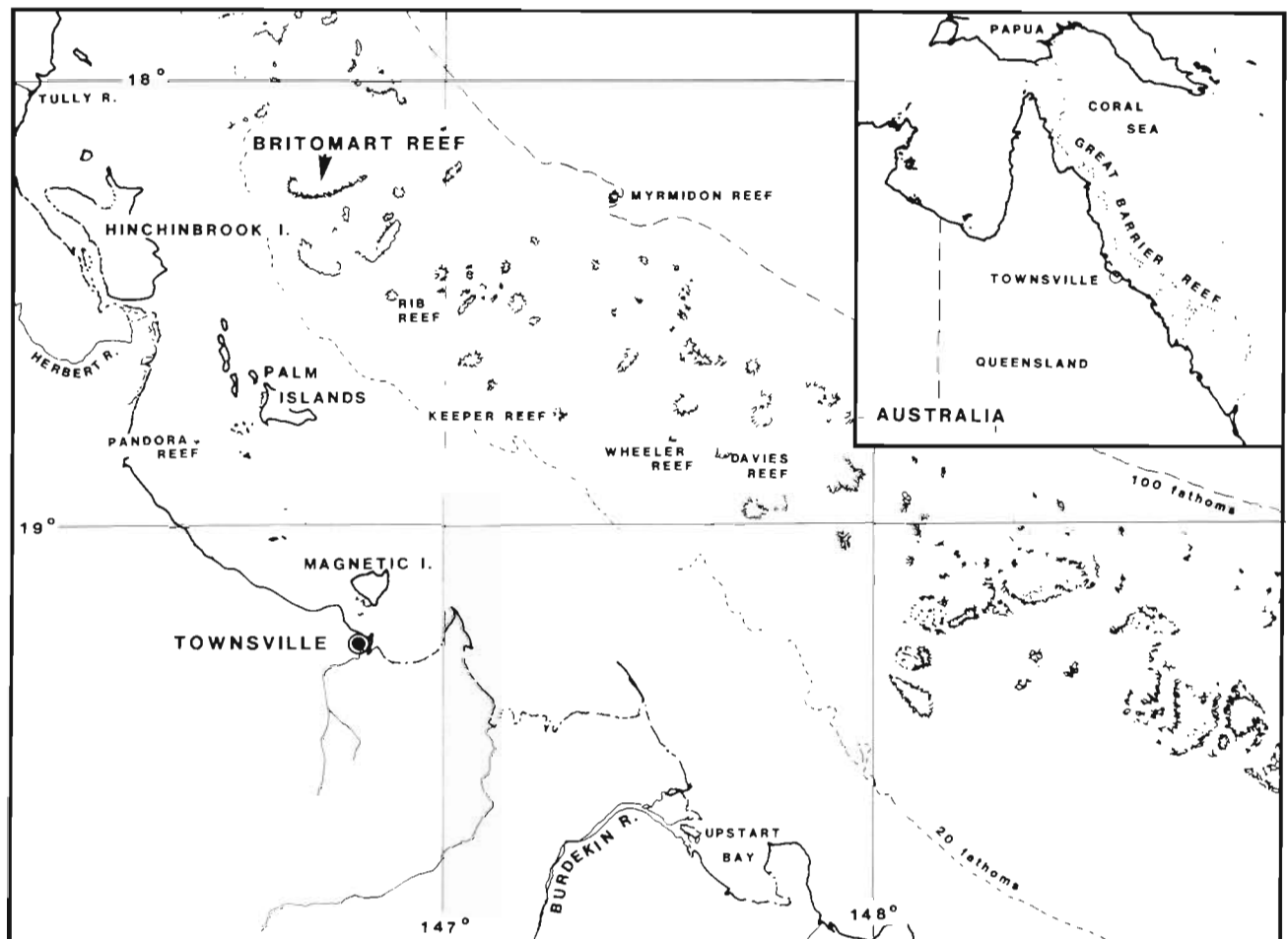


Fig. 1. Map of central region of the Great Barrier Reef off Townsville, Qld., Australia. Study area: Britomart Reef

depression (labeled Hole 1A) directly behind the reef crest, 50 to 60 m in diameter with a maximum depth of 11 m. The damselfish *Hemiglyphidodon plagiometopon* is abundant there, occurring in densities of  $2.9 (10 \text{ m}^2)^{-1}$  ( $s = 0.84$ ,  $n = 3$ , based on three  $30 \text{ m}^2$  belt transects; Sammarco and Carleton, 1982).

The experimental settling substratum utilized was *Pachyseris speciosa* Dana, a foliose scleractinian coral (Veron and Pichon, 1980). Natural coral works well as a settling substratum for algae as well as juvenile corals in experimental studies such as this (Sammarco et al., 1974; Sammarco, 1975, 1977, 1980a, b, 1982). In November 1979, colonies of this coral were collected, returned to the research vessel, deep-frozen overnight for  $\geq 12$  h, and then exposed to full sunlight for several hours. Plates  $\geq 200 \text{ cm}^2$  in size ( $10 \times 20 \text{ cm}$ ) were cut on shipboard from these freshly killed colonies using a diamond-bladed rocksaw. Seawater was used as a blade-collant to minimize contamination of the substratum. The substratum was deliberately not denuded of its dead tissue or associated epibiota in order to promote natural colonization by bacteria and blue-green algae in the earliest stages of exposure, simulating conditions of primary succession (Odum, 1971) as closely as possible. Settling plates were then attached to galvanized steel Arc-mesh® racks with nylon cable ties. Small plastic Ramset® tips placed over plate supports insulated the coral plates from direct contact with the steel.

The data considered in the present study follow a balanced, random blocks, three-way ANOVA design (Sokal and Rohlf, 1981). (They are drawn from a somewhat larger experiment – four-way ANOVA, the results of which will be published later.) The major treatment was an experimental gradient in fish grazing pressure. Twelve coral settling plates were placed on steel racks. Each rack was placed under one of 4 experimental conditions: (1) fully exposed to grazing by fish; (2) within the territories of *Hemiglyphidodon plagiometopon*; (3) within cages; and (4) beneath a shading top covered with mesh similar to that of the cages. Three complete sets of replicate treatments (A, B and C) were used, with each set or block (in statistical terminology; see Sokal and Rohlf, 1981) being implanted in a different area within the study site at a depth of 9 to 11 m.

The cages were  $100 \times 130 \times 25 \text{ cm}$  in size, constructed of  $5 \times 5 \text{ cm}$  galvanized steel Arc-mesh®. This cage structure was then covered with 2.54 cm square corrosion-resistant plastic mesh attached by small cable ties. Each cage or rack was in turn supported by four 1.27 cm solid steel reinforcement bars. All mesh structures were cleared of algae via brushing at monthly intervals.

The shading structure served as a control for

decreased light, a control additional to those used in similar experiments conducted by Lassuy (1980) and Hixon and Brostoff (1982, 1983, in press). Underwater irradiance within the treatments was measured *in situ* with a diver-operated P.A.R. radiometer, designed and constructed by Drew (1983), which measures light energy in the 400 to 700 nm wavelength range. Measurements were taken in mid-April (mid-Fall, southern hemisphere) between 1130 and 1230 h. Values were converted from mW to quantum flux density in  $\mu\text{Em}^{-2}\text{s}^{-1}$ , using spectral composition of irradiance at 11 m depth in Type II oceanic water calculated from the spectral transmission values of Jerlov (1976). Light levels were determined to be  $392.0 \mu\text{Em}^{-2}\text{s}^{-1}$  on exposed racks (23.9 % of surface illumination),  $\leq 169.7 \mu\text{Em}^{-2}\text{s}^{-1}$  under shading structures ( $\leq 10.4$  % surface), and  $\leq 245.0 \mu\text{Em}^{-2}\text{s}^{-1}$  within cages ( $\leq 15$  % surface).

Exposed and shaded racks were placed in areas of low habitat preference for the damselfish; nevertheless, all of the shading structures were colonized by adult *Hemiglyphidodon plagiometopon* within the first few months. These fish were not removed as it was believed that this would not deter recolonization by other adults. Although the shading control was confounded somewhat, the major effect of this colonization was to shift the treatment with respect to its ranking in relative accessibility to fish grazing as follows (treatments listed from most to least accessible): fully exposed, within territories, within shaded territories, and within cages.

Two plates per rack per sampling period were visually assessed for algal percent-cover and community structure using the non-destructive sampling techniques described by Sammarco (1982) (total = 48 plates). This was done 3 and 11 mo after initiation of the experiment (February and October, 1980). A grid ( $9.2 \times 18.5 \text{ cm}$ ) divided into 98 ( $7 \times 14$ ) equally sized squares was placed over each of the plates sampled. Each individual square possessing  $\geq 50$  % cover was considered to be fully covered by the flora or fauna in question; one with  $\leq 50$  % was considered to be bare of epilithic biota. Each square considered to possess algae was assessed for major representative species and its microassociates. This major representative species was initially characterized in the field with the naked eye. Small subsamples of the major species and its microassociates were then collected from the plates, placed in labeled plastic bags, deep-frozen on shipboard, and returned to the laboratory for identification with the aid of a compound microscope. Relative abundance was calculated simply as the number of squares containing a particular subdominant divided by the total number of squares for a given plate.

An attempt was also made to isolate and identify any algae present on portions of the substrate not bearing





Fig. 2. Composite aerial photograph of Britomart Reef

obvious epilithic algae. Samples of the plates were decalcified in 5 % HCl and the remains were examined with the aid of a compound microscope. Algal identifications were made with the aid of Dawson (1954) and Cribb (1973, 1981), although Chapman (1961, 1963), and Prescott (1968) were also useful in some cases.

Species composition and abundance matrices were constructed for each set of treatments and blocks. Species diversity indices ( $H'_B$ ,  $J'_B$ , and  $S$  – Brillouin's Index, species evenness, and number of species, respectively; Pielou, 1969) were calculated from these data. Number of species ( $S$ ) was calculated for the number of algal associations characterizable by a major species in the field.  $S$  is known to be highly significantly correlated with  $S_t$  – the total number of species encountered within a treatment – and is considered to be a fair although conservative estimate of  $S_t$  (Sammarco, 1982).  $S$  has been used in all calculations of  $H'_B$  and  $J'_B$ .

Four and 12 mo after initiation of the experiment (in March and November, 1980), estimates of algal biomass (standing crop) were made via destructive sampling of certain plates. A set of 4 plates from each treatment within each block were retrieved, deep-frozen in labeled plastic bags, and returned to the laboratory. They were later thawed and examined with a dissecting microscope, and all epibenthic algae (excluding encrusting coralline algae) were removed with the aid of a fine pair of dissecting forceps. The algae were then placed in labeled, pre-weighed Petri dishes, decalcified in dilute (5 %) HCl, and dried in a drying oven at 55 °C for  $\geq 24$  h. Samples were weighed on a Sartorius balance to an accuracy of  $1 \times 10^{-4}$ g.

## RESULTS

### Abundance

After 3 mo, there were significant differences in percent-cover of filamentous algae and corallines between treatments (Table 1), but there was no distinct gradient of response to the different experimental levels of grazing pressure. Algal cover, although highest within damselfish territories, was highly variable between other treatments. Even in this early sere, percent-cover of endolithic and cryptic micro-algae was highest within the open or naturally grazed treatment.

As time progressed, a gradient of response in percent-cover became apparent (Fig. 3). After approximately 1 yr, cover of filamentous algae and corallines decreased significantly from 85 % to 44 % as accessibility to grazing by herbivorous fish increased (Fig. 4). Concomitantly, there was an increase in the amount of 'bare substrate' and endolithic algae from an average of 0 to 51 %. Unstable sediment primarily accounted for the remainder of substratum not covered by epibenthic or cryptic algae in all treatments.

Algal biomass exhibited a highly variable response to all treatments after 4 mo (Table 2). Variability was also found between replicate blocks. Variances between blocks and treatments were highly uneven or heteroscedastic (despite logarithmic transformation of the data). Algal biomass was significantly higher within damselfish territories than under any other treatment at this time and was also less variable there. Algal biomass varied significantly between replicate blocks as well at this time.

Table 1. Percent-cover of (a) epibenthic filamentous and coralline algae; (b) endolithic algae, cryptic algae, and 'bare substrate'; (c) sediment on primary coral substrate. Data collected after 3 mo exposure, respectively, to 4 experimental treatments: (a) within cages; (b) within experimentally shaded damselfish territories; (c) within natural damselfish territories; (d) exposed to natural levels of fish grazing. Data also shown for sediment after 11 mo. Data pooled over blocks, presented with 95 % confidence intervals. (\* Data for percent-cover of filamentous and cryptic algae after 11 mo shown in Fig. 4)

Sampling period			Treatment			
			closed	shaded	territory	open
3 mo	Filamentous algae and corallines	Cumulative percentage	84.0 %	67.3	99.8	75.5
		95 % conf. limits	80.8–86.9 %	63.4–71.1	99.1–100.0	71.8–78.9
	'Bare substrate' and endolithic algae	Cum. percentage	2.8	0.8	0	20.4
		95 % conf. limits	1.7–4.4	0.3–1.9	0–0.6	17.2–23.9
	Sediment	Cum. percentage	13.0	31.6	0.2	4.0
		95 % conf. limits	10.4–16.0	27.9–35.5	0.07–0.9	2.6–5.9
11 mo*	Sediment	Cum. percentage	14.1	13.9	27.9	3.2
		95 % conf. limits	11.3–17.3	11.2–17.0	24.3–31.7	2.0–5.0



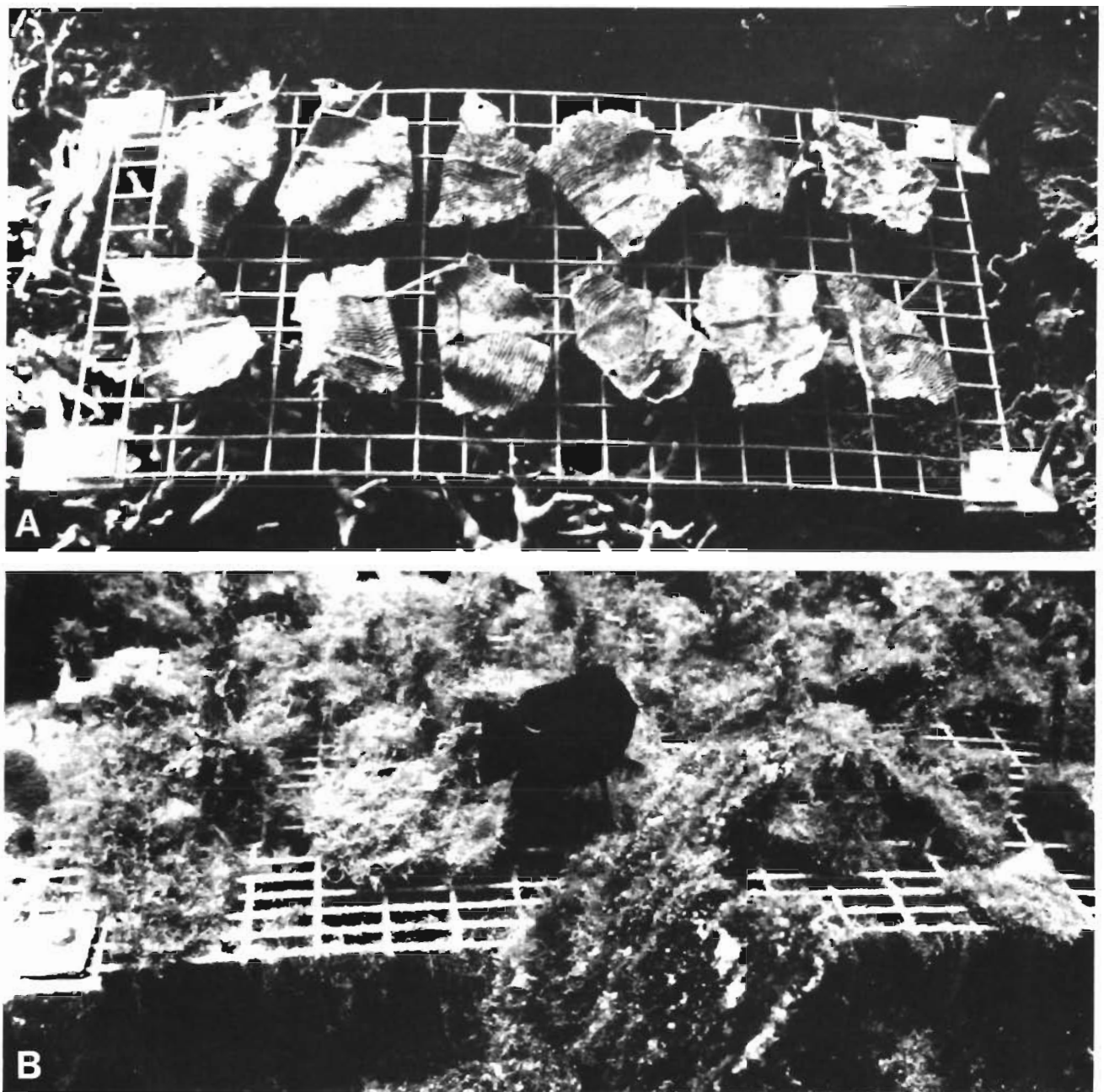


Fig. 3. Settling plates composed of dead coral (*Pachyseris speciosa*) mounted on galvanized steel mesh racks (A) after several months under conditions of full exposure to fish grazing; (B) after the same period of time within a territory of the damselfish *Hemiglyphidodon plagiometopon*, restricted from fish grazing

After 1 yr, the highly variable response of algal biomass to the treatments disappeared (Fig. 5). The standing crop of algae was highest within the cages and lowest on substratum exposed to grazing by herbivorous fish. Plates within territories and within shaded territories were intermediate in algal biomass (Fig. 5), and those within territories possessed almost as high an abundance of algae as those within cages. There was also a highly significant difference between

replicate blocks; but the differences between treatments described above was generally consistent within blocks, as the interaction term between treatments and blocks was only barely significant.

#### Species diversity

There was no particular gradient of response to the treatments evident in species diversity of epibenthic

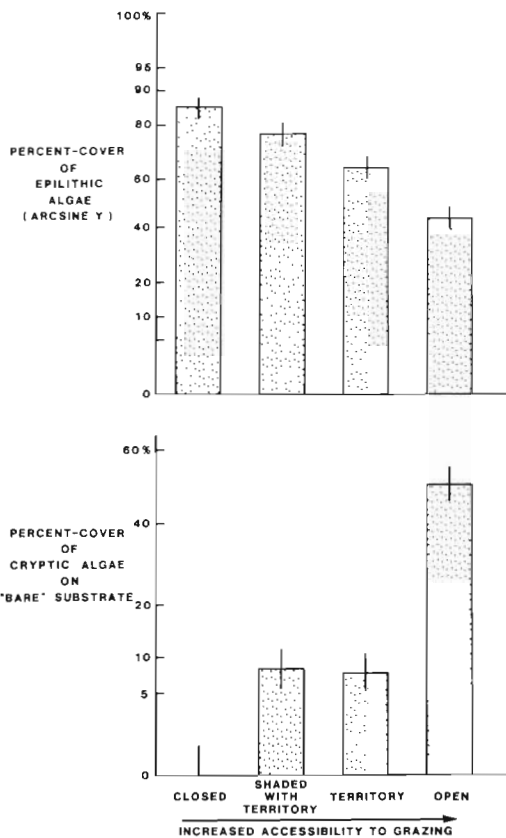


Fig. 4. (Upper) Percent-cover of epilithic and coralline algae on primary coral substrate after 11 mo of exposure to 4 sets of experimental conditions: (1) within cages, protected from fish grazing; (2) within territories of *Hemiglyphidodon plagiometopon*; (3) within shaded damselfish territories to control for decreases in light; and (4) fully exposed to fish grazing. Treatments ranked with respect to accessibility to grazing. Data pooled from all blocks; 95 % confidence intervals also shown. (Lower) Percent-cover of substratum lacking epilithic algae but including cryptic blue-green algae after 11 mo of exposure to the same treatments. (Arcsine transformation used for purposes of normalization; see Sokal and Rohlf, 1981)

filamentous and coralline algae in the earlier samples (Table 3). Diversity as measured by  $H'_B$  and  $S$  (number of species) appeared to be maximal within cages, but this trend was indistinct. Species evenness as measured by  $J'_B$  showed no interpretable pattern of response at this time.

After 1 yr, species diversity of benthic algae exhibited a clear response to the experimental gradient of grazing pressure. Diversity appeared to be maximized within damselfish territories under conditions of reduced grazing, while it was relatively low both within cages and on plates exposed to fish grazing. This trend was consistent, irrespective of the diversity index considered; Brillouin's Diversity Index ( $H'_B$ ), species evenness ( $J'_B$ ), and number of species ( $S$ ) all exhibited precisely the same pattern of response

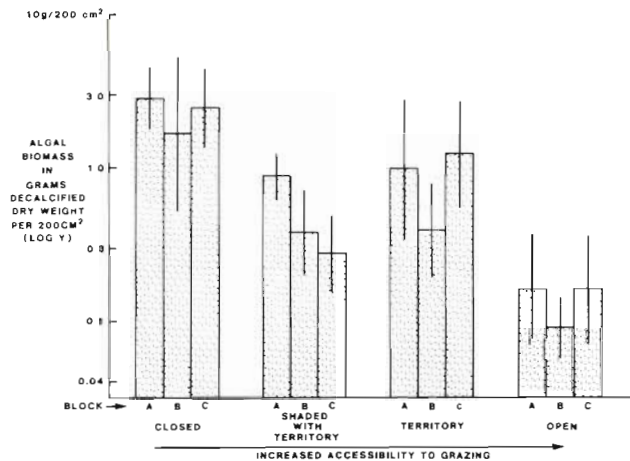


Fig. 5. Biomass of algae in decalcified dry wt. per 200 cm<sup>2</sup> of primary coral substrate after 12 mo under 4 conditions, representing a gradient of grazing pressure (see text and legend of Fig. 4 for details). 95 % confidence intervals also shown. Data shown for replicate blocks. Significant difference between treatments ( $p < 0.001$ , two-way ANOVA) and between blocks ( $p < 0.001$ ); barely significant interaction between treatments and blocks ( $p = \sim 0.05$ , Bartlett's test)

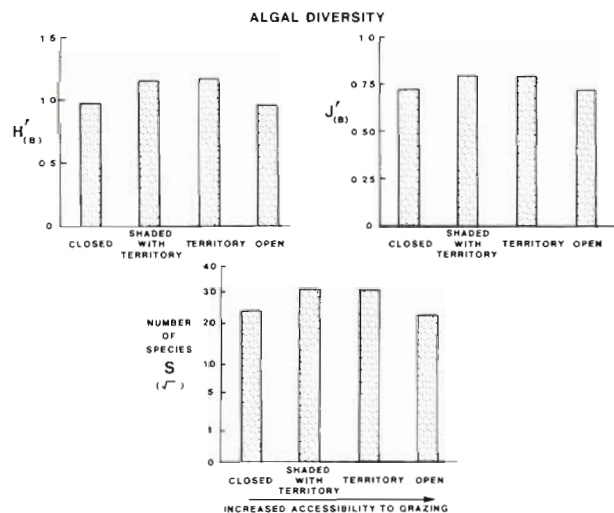


Fig. 6. Species diversity of algae on natural primary coral substrate after 11 mo of exposure to 4 experimental conditions representing a gradient of fish grazing pressure (see text and legend of Fig. 4 for details). Indices are Brillouin's diversity index ( $H'_B$ , using  $\log_{10}$ ), species evenness ( $J'_B$ ), and total number of major representative algal species ( $S$ ). Data pooled over blocks. ( $S$  transformed by square root for purposes of normalization; see Sokal and Rohlf, 1981)

(Fig. 6). Algal species diversity within shaded territories was similar to that within unshaded territories.

### Species composition and dominance shifts

Differences in species composition were evident between treatments early on in the experiment (Table

Table 2. Biomass of algae on natural primary substrate after 4 mo exposure to an experimental gradient of fish grazing pressure (see text and legend of Table 1 for details). Individual and transformed means shown for all blocks and treatments; grand means also presented. Data highly heteroscedastic ( $p < 0.001$ , Bartlett's test). Treatments significantly different ( $p < 0.001$ , Kruskal-Wallis test); blocks also significantly different ( $p < 0.05$ ). (Data transformed by  $\log_{10}$  to help normalize data and facilitate comparison of means; see Sokal and Rohlf, 1981)

Block		Algal biomass (g decalcified dry wt)				$\bar{Y}$
		closed	shaded	territory	open	
A	$\bar{Y}$	0.0784 g	0.0918	1.1947	0.0427	0.4298
	$\bar{Y}_{\log}$	-1.5008	-1.3920	0.1455	-1.5762	
	$S_{\log}$	0.7450	0.6180	0.1289	0.5857	
	n	4	4	4	3	
B	$\bar{Y}$	0.3750	0.0968	1.5703	0.2834	0.5814
	$\bar{Y}_{\log}$	-0.9440	-1.7710	0.1579	-0.6138	
	$S_{\log}$	1.2522	1.5228	0.2064	0.2747	
	n	4	4	4	4	
C	$\bar{Y}$	0.0046	0.4586	0.2663	0.8449	0.3549
	$\bar{Y}_{\log}$	-2.7573	-0.3440	-0.6627	-0.4774	
	$S_{\log}$	0.8920	0.0977	0.3296	0.7256	
	n	4	2	3	3	
	$\bar{Y}$	0.1527 g	0.1672	1.0781	0.3796	

Table 3. Species diversity of algae on natural primary coral substratum. Data collected after 3 mo of exposure to an experimental gradient of fish grazing pressure (see text and legend of Table 1 for details). Indices shown are Brillouin's diversity index ( $H'_B$ , using  $\log_{10}$ ), species evenness ( $J'_B$ ), and number of major representative algal species (S)

Species diversity index	Cumulative species diversity after 3 mo			
	closed	shaded	territory	open
$H'_B$	0.8110	0.7922	0.6832	0.7801
$J'_B$	0.7280	0.7922	0.6832	0.7801
S	13	10	10	10

4). The caged treatment was dominated by the rhodophyte *Ceramium procumbens* Setchell and Gardner and the cyanophyte *Entophysalis conferta* Drouet and Daily. Chlorophytes such as *Derbesia attenuata* Dawson, *Rhizoclonium kochianum* Kützinger, and *Enteromorpha clathrata* Roth were also present but usually constituted only micro-associates. Various other rhodophytes were recorded such as *Polysiphonia tongatensis* Harvey and *Centroceras clavulatum* C. Agardh. The only cyanophytes found in the caged treatment at this time were 3 species of *Lyngbya*, at times being represented as major species. Sedimentation was consistently high in this treatment.

After approximately 1 yr, *Polysiphonia subtilissima* Montagne, a rhodophyte, clearly dominated the plates within cages. *Entophysalis conferta*, a cyanophyte, and the rhodophyte *Lophosiphonia villum* J. Agardh were

also important (Table 5). These filamentous algae were commonly observed to be covered with a thick but light epiphytic film of *Oscillatoria salinarum* Collins (entered separately in Table 5).

The shaded-territory treatment was dominated by the cyanophytes *Oscillatoria* aff. *amphibia* Agardh and *Hydrocoleum lyngbyaceum* Gomont as well as *Lyngbya* sp. in the earlier samples. The delicate rhodophyte *Acrochaetium subseriatum* Børgesen was also an important component of the community. After approximately 1 yr, the shading treatment was still dominated mainly by cyanophytes *Symploca hydroides* Gomont, *L. majuscula* Gomont and *L. aestuarii* Gomont. *Polysiphonia subtilissima* also accounted for a reasonable percentage of the cover in this treatment.

Within damselfish territories (unshaded), the community was dominated by *Enteromorpha kylinii* Bliding (Chlorophyta), *Centroceras clavulatum* (Rhodophyta), and *Lyngbya* sp. (Cyanophyta) in the earlier samples. After 1 yr, however, *Lyngbya aestuarii*, *Centroceras clavulatum*, and *Gracilariopsis rhodotricha* Dawson were dominant. The encrusting chlorophyte *Pseudendoclonium* sp. (Nielsen, 1980) also accounted for a small proportion of the algal cover.

On substratum exposed to natural levels of fish-grazing, the algal community was dominated by the cyanophyte *Lyngbya confervoides* Gomont and the rhodophyte *Neomonospora pedicellata* var. *tenuis* Feldmann-Mazoyer in the earlier samples. *Pseudendoclonium* sp., *Enteromorpha kylinii*, and *Phormidium* spp. were also important at this time. After approxi-



Table 4. Species composition and relative abundances (in %) of major representative algal species algae and their microassociates on natural primary coral substratum. Data collected after 3 mo under 4 experimental conditions, listed in order of accessibility to fish grazing. Data shown for groups generally constituting  $\geq 10\%$  cover. Cyanophytes, encrusting coralline algae, and *Peyssonnelia* sp. also included. n = ~175 for each column. Data pooled within blocks. (1) Closed-C only; (2) closed-A only; (3) shaded-A only; (4) shaded-A, B only; (5) territory-C only; (6) territory-B only

Major representative algae and micro-associates	Percent-cover after 3 mo Treatment												
	Closed				Shaded territory			Territory			Open		
	Block	A	B	C	A	B	C	A	B	C	A	B	C
<i>Acrochaetium subseriatum</i>					8.9	14.6							
<i>Centroceras clavulatum</i>			290					35.7	36.2	25			
<i>Ceramium procumbens</i>													
<i>Cladophora albida</i>													
<i>Cladophora perpusilla</i> (5)													
<i>Enteromorpha clathrata</i> (5)													
<i>Gracilariopsis rhodotricha</i>													
<i>Lyngbya majuscula</i>													
<i>Ceramium procumbens</i>		3.1 %		50									
<i>Derbesia attenuata</i> (1)													
<i>Lyngbya aestuarii</i> (2)													
<i>L. confervoides</i> (1)													
<i>L. majuscula</i> (1)													
<i>Polysiphonia tongatensis</i> (1)													
<i>Rhizoclonium kochianum</i> (1)													
Corallines (all)		0.5		1	1.6						1.1	1	
<i>Enteromorpha kylinii</i>								49.5	33.2	40.8			
<i>Centroceras clavulatum</i>													
<i>Ceramium procumbens</i>													
<i>Falkenbergia hillebrandii</i> (6)													
<i>Gracilariopsis rhodotricha</i>													
<i>Entophysalis conferta</i>		57.1	71.4	21.4	5.7		0.5						
<i>Gracilariopsis rhodotricha</i>		0.5	0.5		5.2	4.7	11.2						
<i>Cladophora perpusilla</i> (4)													
<i>Ceramium procumbens</i> (4)													
(c) <i>Cladophora</i> sp. (4)													
<i>Hydrocoleum lyngbyaceum</i>							29.1						
<i>Lophosiphonia villum</i>												15.7	
<i>Cladophora perpusilla</i>													
<i>Enteromorpha kylinii</i>													
<i>Gracilariopsis rhodotricha</i>													
<i>Lyngbya confervoides</i>													
<i>Lyngbya confervoides</i>		5.1	8.3	14.8							13.5	22.7	34.5
<i>Centroceras clavulatum</i>													
<i>Enteromorpha clathrata</i>													
<i>Lyngbya</i> sp.				1.5		9.4	14.8	13.3	27.6	33.2			
<i>Centroceras clavulatum</i>													
<i>Neomonospora pedicellata</i>													21.3
var. <i>tanius</i>													
<i>Enteromorpha clathrata</i>													
<i>Falkenbergia hillebrandii</i>													
<i>Lyngbya majuscula</i>													
<i>Oscillatoria</i> aff. <i>amphibia</i>					7.8	31.2	39.8		2.6				
<i>Enteromorpha klyinii</i>													
<i>Peysonnellia</i> sp.		1.0		1.5	4.2	1.6		0.5				0.5	
<i>Phormidium weissii</i> /											1.1	10.6	4.6
<i>Phormidium</i> sp.													
<i>Lyngbya confervoides</i>													
<i>Pseudendoclonium</i> sp.				4.2						20.1	3.5	14.7	
<i>Lophosiphonia villum</i>													
<i>Lyngbya confervoides</i>													
<i>Rhizoclonium</i> sp.													
Unidentified membranous red alga (aff. <i>Kallymenia</i> )													
<i>Rhizoclonium kochianum</i>		2.6								32.0	27.8		
<i>Cladophora heteronema</i> (3)													
<i>Lyngbya majuscula</i> (3)													
<i>Polysiphonia tongatensis</i> (3)													
Unidentified rhodophyte 830 (3)													
Other algae		5.1	0.5	1.5	8.9	1	1	0.5	0.5	1.0	0.6		
Epifauna					1								

Table 5. Species composition and relative abundances (in %) of major representative algal species and their microassociates on natural primary coral substrate. Data collected after 11 mo under the 4 experimental conditions listed in order of accessibility to fish grazing. Data shown for groups generally constituting  $\geq 10\%$  cover. Cyanophytes, encrusting coralline algae, and *Peyssonnelia* sp. also included. n = ~175 in all cases. (1) Closed-B only; (2) closed-C only; (3) territory-C only; (4) territory-A and shaded-A only; (5) shaded-A only

Major representative algae and micro-associates	Percent-cover after 11 mo Treatment												
	Closed				Shaded territory			Territory			Open		
	Block	A	B	C	A	B	C	A	B	C	A	B	C
<i>Centroceras clavulatum</i>					1.7 %			36.2	1.1	2.2			
<i>Ectocarpus mitchellae</i> (4)													
<i>Gelidiopsis intricata</i> (4)													
<i>Gracilariopsis rhodotricha</i> (5)													
<i>Polysiphonia subtilissima</i> (4)													
Corallines (all)					4.6		1.2	0.5	0.5		2.7		
<i>Ectocarpus irregularis</i>												14.2	
<i>E. mitchellae</i>								4.5	0.5	18			
<i>Lophosiphonia obscura</i>													
<i>Centroceras clavulatum</i> (3)													
<i>Entophysalis conferta</i>			26.7 %										
<i>Gracilariopsis rhodotricha</i>									32.3	7.7			
<i>Centroceras clavulatum</i>													
<i>Lophosiphonia villum</i>			21.5										
<i>Lyngbya aestuarii</i>	2.4					40			20.3	29.6	17.5	8.7	20.8
<i>Centroceras clavulatum</i>													
<i>Gracilariopsis rhodotricha</i>													
<i>Ectocarpus mitchellae</i> (3)													
<i>Microcoleus chthonoplastes</i>													
<i>Polysiphonia subtilissima</i>													
<i>L. majuscula</i>						46.2							
<i>L. meneghiniana</i>				2.7									4.8
<i>Ecotocarpus mitchellae</i>													
<i>Oscillatria salinarum</i>	15.4	2.6											
<i>Polysiphonia subtilissima</i>													
<i>Peyssonnelia gunniana</i>	0.6		1.1		9		1.1			1.1	2		
<i>Polysiphonia subtilissima</i>	55	40.8	81.2		31.1	4.6							
<i>Symploca hydroides</i> (1)													
<i>Pseudendoclonium</i> sp.							1.7	3.5		3.3	23.3	11.5	21.4
<i>Symploca hydroides</i>							63.3						19.3
<i>Lyngbya confervoides</i>													
<i>Oscillatoria</i> aff. <i>amphibia</i>													
<i>O. aff. nigro-viridis</i>													
<i>Wurdemannia miniata</i>	4.7		0.5		19.2				1.1				
<i>Polysiphonia subtilissima</i>													
<i>Peyssonnelia gunniana</i> (2)													
Other algae	1.2				9			4.5	4.2	4.9		2.2	
Epifauna (Porifera 518)	0.6												

mately 1 yr, however, the algal community was dominated by *Pseudendoclonium*, *L. aestuarii*, and *Symploca hydroides*.

Substratum devoid of obvious epilithic algae actually accounted for the largest proportion of the surface on grazed plates. Microscopic examination of the decalcified substratum, however, revealed a considerable concentration of cyanophytes growing cryptically

between septa of the coral substratum. These algae included *Symploca hydroides*, *Lyngbya confervoides*, *Oscillatoria* aff. *amphibia*, and *O. aff. nigro-viridis* Gomont. Substratum bearing cryptic algae but lacking visible epilithic algae constituted > 50 % of the cover on the naturally grazed plates. Therefore, these 4 cyanophytes constituted the true dominants of the algal community under natural levels of fish grazing.

Red coralline algae and *Peyssonnelia gunniana* J. Agardh (an encrusting, partially calcified rhodophyte) were present in all treatments, but the latter was slightly more abundant in the shaded treatment.

## DISCUSSION

### Algal abundance and species diversity

Reduction in grazing by herbivorous fish caused by experimental cages or by the territorial behaviour of this damselfish significantly altered epibenthic algal community structure, as has also been shown in related studies (Vine, 1974; Brawley and Adey, 1977; Montgomery, 1980a, b). The responses of the algal community (particularly in abundance) resulting from experimental alteration of grazing pressure decreased in variability with time. After 3 to 4 mo, estimates of both percent-cover and biomass of algae, but especially the latter, were highly variable between treatments and blocks. Even after this short period of time, however, the standing crop of algae within damselfish territories was relatively high and exhibited a low variance.

After 12 mo, a clearer pattern of response in algal biomass and percent-cover emerged which suggested that the damselfish were effectively excluding herbivorous grazing fish from their territories. Algal percent-cover was observed to decrease predictably with increased fish grazing. This agrees with the results of Lassuy (1980) concerning *Hemiglyphidodon plagiometopon*, Hixon and Brostoff (1982, 1983, in press) with *Stegastes fasciatus*, and Brawley and Adey (1977) with *Eupomacentrus planifrons*. The response was also similar to that of algal percent-cover to experimental reduction of densities of *Diadema antillarum* in Jamaica, W. I. (Sammarco, 1977, 1980a).

A period of 3 mo appeared to be too short for species diversity to exhibit any graded response to the treatments. Species diversity reached a relative maximum within damselfish territories after ca. 1 yr, while levels of diversity under natural levels of grazing and within enclosures were low and indistinguishable from each other. These results support the hypothesis originally proposed by Vadas (1968) and Paine and Vadas (1969) that species diversity of algae should be maximized at intermediate levels of grazing. The low diversity observed at the 2 extremes of accessibility to fish grazing apparently occurred for the reasons originally suggested by Paine and Vadas (1969): strong dominance and near monopolization of substratum by a single dominant within the cages, and 'overgrazing' and cropping of most fleshy algal species in the grazed treatment. These results again support the hypotheses proposed by Grassle (1973), Levin (1974), Levin and

Paine (1974), Whittaker and Levin (1977), and Paine and Levin (1981) that small-scale disturbance and patch-formation can increase species diversity on a local scale. These 'local' effects can be substantial, as in this case, the territories of *Hemiglyphidodon plagiometopon* account for ~15 % of the hard-bottom in the study area (Sammarco and Carleton, 1982).

The responses of diversity to fish grazing observed here vary greatly in their agreement with related studies on territorial damselfish. For example, Hixon and Brostoff (1982, 1983, in press) found that algal diversity, as in this study, is maximized within territories of the damselfish *Stegastes fasciatus*, irrespective of the numerical index used for estimation. By contrast, Lassuy (1980) worked in Guam with the same damselfish examined here, *Hemiglyphidodon plagiometopon*, and obtained opposite results, i.e. algal species diversity was minimized within territories. Explanatory hypotheses accounting for this contrast may involve the algae, the fish, or both. With respect to the algae, different responses could be due to lack of a dominant alga in the Guam community (Yodzis, 1976), or, if present, lack of its successful recruitment during the study (Sammarco, 1975, 1977, 1982; Lawrence and Sammarco, 1982). It could also be attributable to differences in food preferences of the major grazers (Lubchenco, 1978; Lubchenco and Gaines, 1981) or in feeding and 'weeding' behaviours of the damselfish (Lassuy, 1980; Montgomery, 1980a).

I believe it is possible to state that many site-attached territorial damselfish are effective at reducing grazing pressure by fish and altering algal community structure. One cannot, however, generalize about the effects of these pomacentrids as a group on specific directions of change in algal species diversity due to the many factors of influence potentially operating in a given situation.

### Algal species composition and implications for nitrogen fixation rates

The substratum inaccessible to grazing fish was initially colonized by a wide variety of algal species but eventually became dominated by the rhodophyte *Polysiphonia subtilissima*. In addition, almost all of the chlorophytes disappeared from this community within 1 yr. Because of these changes, species diversity declined to a relatively low level and has continued to decline since that time (unpubl.). Encrusting coralline algae and *Peyssonnelia gunniana* seemed to colonize under any level of fish grazing, but corallines did not survive well in the absence of grazing.

The coral substratum within damselfish territories was initially colonized by a wide variety of chloro-



phytes, rhodophytes, and cyanophytes, despite the relatively low numerical diversity observed. The algal community eventually shifted to one dominated by rhodophytes and cyanophytes as chlorophytes disappeared.

Shaded territories exhibited affinities to both the caged and territory treatments, since they were co-dominated by cyanophytes as well as *Polysiphonia subtilissima*. The response of the 'shaded' community may well be a function of both increased deterrence to fish grazing as well as increased shading. In this case, the fish's behavior (habitat preference for the shading structure) unfortunately hindered the complete partitioning of these 2 factors.

Natural levels of fish grazing caused a shift in the algal community from one dominated by a variety of algae to one heavily dominated by epilithic filamentous cyanophytes. In addition, over one half of the substratum seemed to be dominated by cryptic cyanophytes (e.g. *Symploca*, *Lyngbya*, and *Oscillatoria*) living within the porous and somewhat corrugated coral substratum. Tsuda and Kami (1973) also found that selective browsing by herbivorous fishes in lagoonal waters resulted in dominance by such blue-greens as *Calothrix crustacea* Thuret, Bornet & Flahault and *Micrococcus lyngbyaceus* Kützinger.

Of the cyanophyte genera encountered in this study, most have been reported to fix nitrogen (Stewart, 1980). Therefore, I hereby suggest that rates of nitrogen-fixation within the calcium carbonate on a coral reef are most likely enhanced by natural levels of fish grazing and inhibited by reduced grazing. Preliminary experimental evidence lends support to this hypothesis (Wilkinson and Sammarco, 1982, 1983). These results contradict Lobel's (1980) hypothesis that rates of nitrogen-fixation should be comparatively higher within damselfish territories under conditions of reduced grazing.

### CONCLUSIONS

The major findings of this study may be summarized as follows:

- (1) Benthic algal community structure on a coral reef was altered greatly under an experimental gradient of fish grazing pressure.
- (2) Algal abundance (in percent-cover and biomass) increased significantly as accessibility of substratum to grazers was decreased, particularly after 1 yr.
- (3) Territoriality by the damselfish *Hemiglyphidodon plagiometopon* increased algal species diversity, while natural levels of fish grazing and exclusion of grazing fish resulted in low algal diversity; therefore, species diversity was maximal at intermediate levels of

grazing, supporting Vadas' (1968) and Paine and Vadas' (1969) hypothesis.

(4) As accessibility of substratum to fish grazing was increased, algal species composition shifted from dominance by rhodophytes within cages through rhodophytes and cyanophytes inside damselfish territories, to cyanophytes under natural levels of fish grazing. Many cyanophytes in the last case occurred cryptically in the interstices of the coral substratum.

(5) It is hypothesized that rates of nitrogen-fixation will be higher on primary coral substratum fully exposed to natural levels of fish grazing than under conditions of reduced fish-grazing (Wilkinson and Sammarco, 1982, 1983).

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### LITERATURE CITED

- Albrecht, H. (1969). Behavior of four species of Atlantic damselfish from Columbia, South America (*Abudefduf saxatilis*, *A. taurus*, *Chromis multilineata*, *C. cyanea*; Pisces, Pomacentridae). Z. Tierpsychol. 26: 622-676
- Allen, G. R. (1975). Damselfishes of the South Seas. T. F. H. Publ., Neptune City, New Jersey
- Borowitzka, M. (1981). Algae and grazing in coral reef ecosystems. Endeavour (New Series) 5: 99-106
- Brawley, S. H., Adey, W. H. (1977). Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Environ. Biol. Fish. 2: 45-51
- Chapman, V. J. (1961). The marine algae of Jamaica, Part 1, Myxophyceae and Chlorophyceae. Bull. Inst. Jam. Sci. Ser. 12: 1-159
- Chapman, V. J. (1963). The marine algae of Jamaica, Part 2, Phaeophyceae and Rhodophyceae. Bull. Inst. Jam. Sci. Ser. 12: 1-201
- Clarke, T. A. (1970). Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda* (Pomacentridae). Ecol. Monogr. 40: 189-212
- Cribb, A. B. (1973). The algae of the Great Barrier Reefs. In: Jones, O. A., Endean, R. (ed.) Biology and geology of coral reefs, Vol. 2, Biology. Academic Press, New York, p. 47-75
- Cribb, A. B. (1981). Coral reefs. In: Clayton, M. N., King, R. J. (eds.) Marine botany: an Australasian perspective. Longman Cheshire, Melbourne, p. 329-345
- Crisp, D. J. (Ed.) (1964). Grazing in terrestrial and marine environments: a symposium of the British Ecological Society. Blackwell, Oxford
- Dawson, E. Y. (1954). Marine plants in the vicinity of the

- Institut Oceanographique de Nha Trang, Viet Nam. Pacif. Sci. 8: 372-481
- Drew, E. A. (in press). Light. In: Earll, R., Erwin, D. (ed.) The sublittoral environment of the British Isles - in perspective. Oxford University Press, London
- Grassle, J. F. (1973). Variety in coral reef communities. In: Jones, O. A., Endean, R. (ed.) Biology and geology of coral reefs, Vol. 2, Biology. Academic Press, New York, p. 247-270
- Hatcher, B. G. (in press). Grazing in coral reef ecosystems. In: Barnes, D. J. (ed.) Perspectives on coral reefs, Proc. of Workshop, Aug. 1979, Austral. Inst. Mar. Sci., Townsville, Qld., Australia
- Hixon, M. A., Brostoff, W. N. (1982). Fish grazing and community structure of Hawaiian reef algae. In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh, J. A., Jr., Tsuda, R. T. (ed.) Proceedings of the fourth international coral reef symposium, May 1981, Vol. 2. Marine Sciences Center, University of the Philippines, Diliman, Quezon City, p. 507-514
- Hixon, M. A., Brostoff W. N. (1983). Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science, N. Y. 220: 511-513
- Hixon, M. A., Brostoff W. N. (in press). Differential fish grazing and benthic community structure on Hawaiian reefs. In: Caillet, G. M., Simenstad, C. A. (ed.) Fish food habit studies, Proc. 3rd Pacif. Workshop, Univ. Wash. Sea Grant Program
- Itzkowitz, M. (1977). Spatial organization of the Jamaican damselfish community. J. exp. mar. Biol. Ecol. 28: 217-241
- Jerlov, N. C. (1976). Marine optics (2nd ed.). Elsevier Scientific Publishing Co., Amsterdam
- Kaufman, L. (1977). The threespot damselfish: effects on benthic biota of Caribbean coral reefs. In: Taylor, D. L. (ed.) Proceedings of the third international coral reef symposium, Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, Miami, Florida, p. 559-564
- Lassuy, D. R. (1980). Effects of 'farming' behavior by *Eupomacentrus lividus* and *Hemiglyphidodon plagiometopon* on algal community structure. Bull. mar. Sci. 30: 304-312
- Lawrence, J. M. (1975). On the relationships between marine plants and sea urchins. Oceanogr. mar. Biol. A. Rev. 13: 213-286
- Lawrence, J. M., Sammarco, P. W. (1982). Effect of feeding on the environment: Echinoidea. In: Jangoux, M., Lawrence, J. M. (ed.) Echinoderm nutrition. A. A. Balkema Press, Rotterdam, p. 499-519
- Levin, S. A. (1974). Dispersion and population interaction. Am. Nat. 108: 207-228
- Levin, S. A., Paine, R. T. (1974). Disturbance, patch formation, and community structure. Proc. natn. Acad. Sci. U.S.A. 71: 2744-2747
- Lobel, P. S. (1980). Herbivory by damselfishes and their role in coral reef community ecology. Bull. mar. Sci. 30: 273-289
- Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112: 23-29
- Lubchenco, J., Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. 12: 405-437
- Mahoney, B. M. (1981). An examination of interspecific territoriality in the dusky damselfish, *Eupomacentrus dorsopunicans*. Bull. mar. Sci. 31 (1): 141-146
- Montgomery, W. L. (1980a). Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. J. exp. mar. Biol. Ecol. 30: 290-303
- Montgomery, W. L. (1980b). The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. Bull. mar. Sci. 47: 9-24
- Myrberg, A. A., Jr., Thresher, R. E. (1974). Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Am. Zool. 14: 81-96
- Nielsen, R. (1980). A comparative study of five marine Chaetophoraceae. Br. phycol. J. 15: 131-138
- Odum, E. (1971). Fundamentals of ecology. Saunders, Philadelphia
- Ogden, J. C. (1976). Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. 2: 103-116
- Ogden, J. C., Lobel P. S. (1978). The role of herbivorous fishes and urchins in coral reef communities. Environ Biol. Fish. 3: 49-63
- Paine, R. T., Levin, S. A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51(2): 145-178
- Paine, R. T., Vadas, R. L. (1969). The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14: 710-719
- Pielou, E. C. (1969). An introduction to mathematical ecology. Wiley, New York
- Potts, D. C. (1977). Suppression of coral populations by filamentous algae within damselfish territories. J. exp. mar. Biol. Ecol. 28: 207-216
- Prescott, G. W. (1968). The algae: a review. Houghton-Mifflin Co., Boston
- Risk, M. J., Sammarco, P. W. (1982). Bioerosion of corals and the influence of damselfish territoriality: a preliminary study. Oecologia (Berl.) 52: 376-380
- Sammarco, P. W. (1975). Grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): density-dependent effects on coral and algal community structure. Proc. Ass. Isl. Mar. Labs. Caribb., Christiansted, St. Croix, U. S. V. I. 11: 19
- Sammarco, P. W. (1977). The effects of grazing by *Diadema antillarum* Philippi on a shallow-water coral reef community. Ph. D. dissertation, Department of Ecology and Evolution, State University of New York at Stony Brook.
- Sammarco, P. W. (1980a). *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. exp. mar. Biol. Ecol. 45: 245-272
- Sammarco, P. W. (1980b). The effects of damselfish territoriality on coral diversity and community structure. Aust. mar. Sci. Bull. 71: 22-23
- Sammarco, P. W. (1982). Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. J. exp. mar. Biol. Ecol. 65: 83-105
- Sammarco, P. W., Carleton, J. H. (1982). Damselfish territoriality and coral community structure: reduced grazing, coral recruitment, and effects on coral spat. In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh, J. A. Jr., Tsuda, R. T. (ed.) Proceedings of the fourth international coral reef symposium, May, 1981, Manila, Vol. 2. Marine Sciences Center, University of the Philippines, Diliman, Quezon City, p. 525-535
- Sammarco, P. W., Levinton, J. S., Ogden J. C. (1974). Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. mar. Res. 32: 47-53

- Sammarco, P. W., Williams, A. H. (1982). Damselfish territoriality: influence on *Diadema* distribution and implications for coral community structure. Mar. Ecol. Prog. Ser. 8: 53-59
- Sokal, R. R., Rohlf, F. J. (1981). Biometry. Freeman, San Francisco
- Stewart, W. D. P. (1980). Systems involving blue-green algae (Cyanobacteria). In: Bergersen, F. J. (ed.) Methods for evaluating biological nitrogen fixation. Wiley, New York, p. 583-635
- Thresher, R. E. (1976). Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia 1976 (2): 266-276
- Tsuda, R. T., Kami, H. (1973). Algal succession on artificial reefs in a marine lagoon environment in Guam. J. Phycol. 9: 260-264
- Vadas, R. L. (1968). The ecology of *Agarum* and the kelp bed community. Ph. D. dissertation, Univ. Washington, Seattle
- Veron, J. E. N., Pichon, M. (1980). Scleractinia of eastern Australia, Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae. Aust. Inst. mar. Sci. monogr. Ser. 4: 1-442
- Vine, P. J. (1974). Effect of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. Mar. Biol. 24: 131-136
- Wellington, G. M. (1982). Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. Ecol. Monogr. 52(3): 223-241
- Whittaker, R. H., Levin, S. A. (1977). The role of mosaic phenomena in natural communities. Theor. Populat. Biol. 12: 117-139
- Williams, A. H. (1979). Interference behavior and ecology of the threespot damselfish (*Eupomacentrus planifrons*). Oecologia 38: 223-230
- Williams, A. H. (1980). The threespot damselfish: a non-carnivorous keystone species. Am. Nat. 116: 138-142
- Williams, A. H. (1981). An analysis of competitive interactions in a patchy back-reef environment. Ecology 62: 1107-1120
- Wilkinson, C. R., Sammarco, P. W. (1982). Nitrogen fixation on a coral reef: effects of fish grazing and damselfish territoriality. In: Gomez, E. D., Birkeland, C. E., Buddemeier, R. W., Johannes, R. E., Marsh, J. A. Jr., Tsuda, R. T. (ed.) Proceedings of the fourth international coral reef symposium, May, 1981, Manila, Vol. 2. Marine Sciences Center, University of the Philippines, Diliman, Quezon City, p. 589 (abstract)
- Wilkinson, C. R., Sammarco, P. W. (1983). Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. Mar. Ecol. Prog. Ser. 13: 15-19
- Yodzis, P. (1976). The effects of harvesting on competitive systems. Bull. math. Biol. 38: 97-109

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