

Factors Influencing Algal Community
Composition on the East Fore Reef,
Jama Discovery Bay, Jamaica,
West Indies.

Ian and Bill -

A very well designed study: good conceptual
start, good methodology, good presentation of
data, and good interpretation of
results.

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- Marine Ecology, Winter, 1980
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Introduction

One conspicuous feature of coral reef communities is their paucity of macrophytic algae, relative to ~~the~~ temperate marine ecosystems, which, in many cases, are comparatively glutted with macroalgae. The intertidal and shallow subtidal zones of the New Hampshire coast, for example, are often characterized by thick growths of *Fucus*, *Gracilaria*, *Laminaria* and numerous other algal genera. In the *Acropora palmata* zone of a Jamaican coral reef, on the other hand, one can snorkel quite a while and see very few macrophytic algae.

While they are not very conspicuous, algae are of great importance to coral reef ecosystems. Zooxanthellae, contained within the tissues of many reef invertebrates (most notably the hematypic corals), are involved in complex coelenterate-algal symbioses, which, while not fully understood, are of demonstrated importance to the process of reef growth. Nor are they the only important component of the primary production of the reef; on closer inspection, the sand, rocks, and corals of the reef are found to host a surprisingly great amount of red, green, brown, and blue-green algae.

These algae are of great importance to much of what goes on on the reef. They are important foodstuffs for fish, echinoderms, and numerous other invertebrates (c.f. Erlich, 1975).

They are an important structural component, providing settling and hiding places for a number of vertebrates and invertebrates.

Some, the blue-greens, are involved in nitrogen fixation on the reef, and, while the ~~topo~~ extent of their activity is not known (at least for completely submerged areas), it is likely to be an important part of the nitrogen, hence energy,

of the reef
energy

cycle of the ecosystem (Magne & Hilm-Hansen, 1975; Brawley & Adey, 1977). Finally, algae are important competitors with reef-building organisms. Van der Hock et al (1975) have shown that algal growth can prevent the settlement and growth of sessile ~~invertebrates~~ ^{organisms}, including hermatypic corals and crustose (calcareous) red algae.

The coral reef may be thought of as a grazer-dependent structure, exhibiting complicated relationships between its primary producers and its herbivores. The interplay of herbivory and the territoriality of pomacentrid fishes (which actively defend algal lawns) has been investigated from a number of aspects (Ogden and Buckman, 1973; Kaufman, date unknown; Buckman and Ogden, 1973; Brawley and Adey, 1971; numerous other studies). One of us (Carlson, unpublished data) has found depth-related differences in the abundances of pomacentrid species, and in the prevalence of herbivorous fish schools. In examining the submanne world of the coral reef, we have noticed a number of other trends which bespeak the importance of ^{the} interplay between other algal community-molding factors:

1. Algal growth is greatest in damselfish territories, scarce elsewhere.
2. The "quality" of this algal growth (a measure of the thickness and species makeup - some algae are more edible than others - of the lawn) is related to the species of damselfish.
3. The abundance of the various species of damselfish varies with depth. The Three-spot damselfish, Eupomacentrus planifrons, and the Bicolor damselfish,

Eupomacentrus partitus, are present across a wide depth range, but not in equal abundances (absolute or relative) at different depths.

¶

Given these observations, we hypothesized that characteristics of the algal community ~~are~~ in large part determined by the territorial behavior of reef damselfish, without whom the algae of reef areas ^{would be} ~~are~~ rapidly consumed by non-territorial herbivorous fishes, notably scarid parrotfishes and acanthurids.

However, we were aware that other alga-influencing factors also change with depth. Thus, predictions had to be made that would first distinguish between the factors, and, second, predict in some fashion the combined effect of the factors. A series of predictions based on the individual effects of light, sand settlement, and ~~the~~ schooling herbivorous fish and *Diadema* grazing were made and are symbolically summarized in Table 1, along with the hypothesized synergistic outcome.

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| Factor | 1 | 2 | 3 | 4 | 5 | |
|--------|-------------------------------------|--------------------------------|-------------------------|-----------------|--------------------------|-----------------|
| Depth | Effect of damselfish territoriality | Effect of schooling herbivores | Effect of sand settling | Effect of light | Effect of urchin grazing | Combined effect |
| 25' | ++ | ++ | + | +++ | + | + 9 |
| 45' | +++ | +++ | ++ | ++ | ++ | + 12 |
| 85' | + | + | +++ | + | +++ | + 9 |

Key:

+++ low algal growth

++ medium algal growth

+ high algal growth

Table 1. Algal depth-related model.

Table 1 merits some explanation. For each biotic or abiotic factor (e.g. damselfish territoriality) the three depths are ranked for predicted algal growth, if that factor alone were operating. Rankings are assigned ^{for} the following reasons:

Factor 1 Damselfish. In earlier work at these three depths at Discovery Bay, one of us (Carlson) found that large, aggressive Three-spot damselfish were most common at 45', and least common at 85'.

The Three-spot territories are characterized by lush algal growth, hence we rank factor 1 by order of their abundance.

Factor 2 Schooling herbivores. In the same study, it was found that schooling herbivorous fish (primarily parrotfish of the family Scaridae) were most numerous at 85', and least numerous at 45'.

Hence, we suggest that their consumptive effect on algae is greatest at the former depth, least at the latter depth.

Factor 3 . Sand settlement. The east fore-reef of Discovery Bay (where the study was conducted; see "Methods") is characterized by wide sand channels exposed to storm-generated surge, which periodically suspends a great deal of sand in the water. We believe that high sand deposition at the shallow site (where surge is greatest) would have a depressing effect on the growth of algae, and that this effect would become less important as depth increased (and surge decreased).

Factor 4. Light. Diminishing light limits the ability of algae to photosynthesize, hence to grow. ~~Between the~~ (t~~eam~~, Biehl, 1962) Between the depths of 25' and 85', we predict an inverse relationship between increasing depth and algal growth.

Factor 5. Urchin grazing. Since the abundance of Diadema antillarum, an important algivore, decreases with depth, its depressing effect on algal growth will diminish with depth.

Thus, on the admittedly fallacious assumption of equal factor ~~to~~ importance, we predicted the occurrence of maximum algal growth at the intermediate depth (Its assumptions aside, this relatively simple model enables one to more easily visualize the inter-factor interactions which are probably occurring in this system).

In order to distinguish between the abiotic and biotic controlling factors influencing algal growth, we designed an experiment which would separate the effects of herbivory and territoriality, both from each other and from abiotic factors (e.g. sand settlement).

In this experiment, we addressed two questions. First of all, how do territoriality and herbivory affect reef algal composition? Second, how do abiotic depth-related changes in the ~~p~~ growth and survival of algae affect territory-defending herbivores? Abiotic factors, such as light, are not controllable by the herbivore farmer, and their effects

on algal growth are expected to have behavioral implications for the damselfish.

Materials and Methods

This study was conducted on the east fore reef of Discovery Bay, Jamaica, West Indies, a gradually sloping reef which is exposed to considerable wind and storm-generated surge. Three sites were chosen at depths with permanent moonrugs, 25 ft, 45 ft, and 85 ft (corresponding to approximate distances of 100 m, 225 m, and 500 m from the reef crest, respectively). The shallow site is characterized by small coral blocks of a number of species, jutting up from a basement of well-consolidated limestone, and overlain by 0-5 cm. of limestone sand.

The middle site is characterized by a thick cover of mixed-zone corals, including abundant Acropora cervicornis (almost totally absent at 25'). A wide sand channel was located roughly 50 ft. to the west, running roughly N-S.

The deep site is characterized by scattered clumps of a number of corals, separated by sand. The terrain slopes here more than at the other 2 sites, although the particular area we worked on was quite flat. A sand channel runs N-S approximately 25 m east of the site.

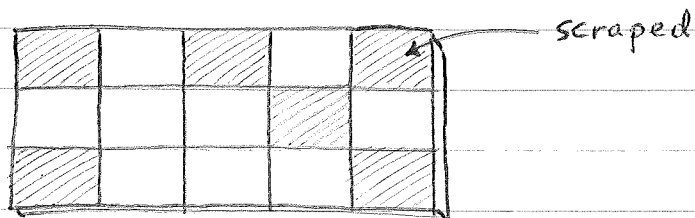
At each site, the following information was collected using SCUBA: size, algal abundance, ~~and~~ density and ~~the~~ species composition (when we could determine species) of macroalgae at five randomly-chosen Three-spot damselfish (Eupomacentrus planifrons) territories, five Bicolor damselfish (Eupomacentrus partitus) territories, and five 24 x 24" plots, not located within territories of any damselfish species. Territory sizes were measured

with a meter stick, and algal abundances were visually estimated using the Braun-Blanquet abundance-dominance scale (Stoddart and Johannes, 1978; see "results" section this paper).

Between one and five pieces of substrate (Acropora cervicornis pieces, coral rubble, etc) were collected at each site, and returned to the lab, where measurements of epiphytic algae species diversity and abundance were made. A dissecting microscope was used to determine percent cover of the substrate; a higher-magnification compound microscope was used for species identification. A census of Diadema antillarum (a common herbivorous sea urchin) was made along a 7 m² strip transect at each depth.

The effect of herbivory on algal colonization and growth with respect to the influence of damselfish territories was studied with the use of wire cage enclosures and asbestos-cement plates. 7cm by 10cm asbestos plates were enclosed in 15x20x10 cm. wire mesh cages (mesh size 11mm and 7mm) to exclude herbivores, and the cages were secured to the bottom with string. Uncaged plates were also left; the following were positioned at each of the 3 experimental sites: 2 caged and 2 uncaged plates in E. planifrons territories, and 2 caged and 2 uncaged plates outside all damselfish territories. The plates were left in place for ten days. They were then carefully transported to the laboratory in black plastic bags (Glad heavy-duty trash bags).

In the lab, plates were scored into ≈ 15 4 cm^2 squares, and 6 squares were scraped completely clean with a razor, and the scrapings transferred to slides, where they were suspended in a drop of water and covered with a $30 \text{ mm} \times 23 \text{ mm}$ cover slip. The initial scraping pattern (see diagram below) was chosen randomly and used for all plates.



Under the compound microscope, five $30 \text{ mm} \times 1.5 \text{ mm}$ horizontal sweeps were made ($\frac{5}{13}$ of the total area of the cover slip), counting all algae seen during each sweep. A total of 144 slides were examined, six slides for each of the 24 plates.

With ~~tes~~ these methods we measured two things:

1. Algal characteristics of damselfish territories and undefended areas at three depths.
2. Colonization and growth of algae on settling plates under a variety of depth, territorial, and exclusion conditions, in an effort to separate out the principal factors of the previously-discussed algal growth model.

Results and Discussion

In the non-manipulative part of our experiment, two measurements of algal abundances were made. The first, in situ characterizations, were made using the Braun-Blanquet index, a generalized percent cover index by which algal growth is rated on the following scale: + = algae present but less than 5% cover of the substrate, 1 = 5-10% cover of the substrate, 2 = ~~10~~ 10-25% cover, 3 = 25-50% cover, 4 = 50-75%, and 5 = 75-100% substrate cover. Braun-Blanquet scores for the 30 damselfish territories sampled, as well as the 15 non-territorial areas, are recorded in Table 2. The most striking aspect of these numbers is the consistently greater lushness of Eupomacentrus planifrons territories than E. partitus territories. E. planifrons defends thick algal carpets at 45' and 85', while E. partitus sports its Persian best at 85'.

The second measurement involved a much more detailed analysis of the algal composition and distribution in 3-spot and bicolored territories and non-territorial areas. The data are presented in Table 3 and Table 4. Table 3 presents algal species on a presence/absence basis, and Table 4 presents only data on filamentous algae, in terms of percent cover of substrate.

One trend seen in Table 4 is a switch of substrate from predominantly bare rock and filamentous and encrusting algae to predominantly macrophytic algae at 85'. The switch is due to two factors: ~~the~~ reduction of filamentous-algae-supporting substrates (esp. dead Acropora cervicornis), and ^{a considerable} increase in macrophytic algae at 85'. We have noted a preference by E. planifrons for areas with A. cervicornis; at 85',

| Type of Sample Area | 25' | | | 45' | | | 85' | | | Total |
|---|-----------------------|--|-----------------|-----------------------|-------------------------|--------------|-----------------------|-------------------------|--------------|-------|
| | Patch dimensions (in) | Area (cm ²) | Algal Abund. | Patch dimensions (in) | Area (cm ²) | Algal Abund. | Patch Dimensions (in) | Area (cm ²) | Algal Abund. | |
| <u>Eupomacentrus planifrons</u> territory | No. 1 | 36 x 14 | 3252 | 3 | 76 x 27.5 | 4613 | 5 | 36 x 26 | 6039 | 5 |
| | 2 | 15 x 17 | 1645 | 2 | 27.5 x 11 | 1955 | 5 | 36 x 26 | 6039 | 5 |
| | 3 | 20 x 21 | 2710 | 2 | 26.5 x 25 | 4277 | 4 | 27 x 36 | 6271 | 3 |
| | 4 | 36 x 23 | 5342 | 2 | 21 x 20 | 2710 | 4 | 36 x 27 | 6271 | 3 |
| | 5 | 16 x 16 | 1652 | 3 | 24 x 20 | 3097 | 3 | 20 x 28 | 3613 | 2 |
| | Mean | | 2920 | 2.4 | | 3330 | 4.2 | | 5646 | 3.6 |
| | S.D. | | 1521 | | | 1104 | | | 1173 | |
| <u>Eupomacentrus parvus</u> territories | | | | | | | | | | |
| | No. 1 | 9.5 x 6.5 | 400 | + | 8 x 10 | 516 | 1 | 9.5 x 6.5 | 400 | 1-2 |
| | 2 | 15 x 18.5 | 1794 | + | 18 x 8 | 929 | 1 | 15 x 18.5 | 1794 | 2 |
| | 3 | 11 x 26 | 1845 | + | 9 x 15 | 871 | 2 | 11 x 26 | 1845 | 2 |
| | 4 | 18 x 17 | 1974 | + | 13 x 36 | 3019 | 2 | 18 x 17 | 1974 | 3 |
| | 5 | 19 x 17 | 2094 | + | 12 x 11.5 | 890 | 1 | 19 x 17 | 2084 | 1 |
| | Mean | Territory boundaries not easily observed. NO site measurements | | + | | 1245 | 1.4 | | 1609 | 1.9 |
| | S.D. | taken | | | | 1006 | | | 688 | |
| Undefended patch (no dam self fish) | Standardized All | All + | | | | All + | | | All 2 | |

Table 2. Characteristics of sample areas.

TABLE 3.
Presence/absence algae in
sampled areas

| Three-Spot | | | | | Bicolor | | | | | Non tern | | | | | p. (12) | | | | | | | | | |
|------------|-----|-----|---|---|---------|-----|-----|---|---|----------|-----|-----|---|---|---------|-----|-----|---|---|-----|-----|-----|--|--|
| 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | | | | | |
| 25' | | | | | 25' | | | | | 25' | | | | | 45' | | | | | 85' | | | | |
| | 45' | | | | | 45' | | | | | 45' | | | | | 45' | | | | | 45' | | | |
| | | 85' | | | | | 85' | | | | | 85' | | | | | 85' | | | | | 85' | | |

[illegible]

The Composition of Epiphyte Cover

13

| | 25' | | | 45' | | | 85' | | |
|-----------------------------------|---------------|---------------|---------------|-----------|------------|-------------|--------------|--------------|---------------|
| | 3-spot | Bicol | non-teen | 3-spot | Bicol | non-teen | Bicol | 3-spot | non-teen |
| Uncolonized Rock Substrate | 40± (3.6) | 22.4± 32.4 | 15± 13 | 0 | 14± 3.1 | 2.2± 8.9 | | | |
| Uncolonized Macro-phyte Substrate | | | | | | | 67.2± 20 | 48.7± ±39 | 50.2± ±5 |
| Filamentous greens | 25± (5) | 2± 4.4 | 10± 8.6 | 16± 25 | 3± 6.7 | 7.9± 10 | .5± 1 | 1.2± 2.5 | 3.33± 5.77 |
| Filamentous reds | 17.5± (2) | 1.2± 2.1 | | 39± 28 | 7± 10 | 9.6± 13 | 6± 5.3 | 21.5± 22 | 1.6± 2.8 |
| Algae Encrusting REDS | 15± (23) | 43.6± ±31 | 43± 31 | 18± 17 | 56± 22 | 34± 21 | 87± 4.7 | 8.3± 2.8 | 5± 1.3 |
| Dead Encrusting REDS | 5± 10 | | 18.3± ±153 | 10± 14 | 19± 18 | 30± 25 | | 5± 7 | |
| Bluegreens | 7.5± (6.4) | 10± 7.9 | | .4± .9 | | 1± 2.2 | 5± 5.7 | 16.2± 11 | 33± 41% |
| Diatom Tabellaria | | | | | | | 12.5± ±25 | | |
| Detritus | | | 6.6± ±11 | 15± 13 | 2± 4.4 | 6± 10.8 | | | |
| Encrusting Sponge | | | 5± 8 | .4± .9 | | | | | |

Table 4.
Percent cover by
selected species
(sampled areas).

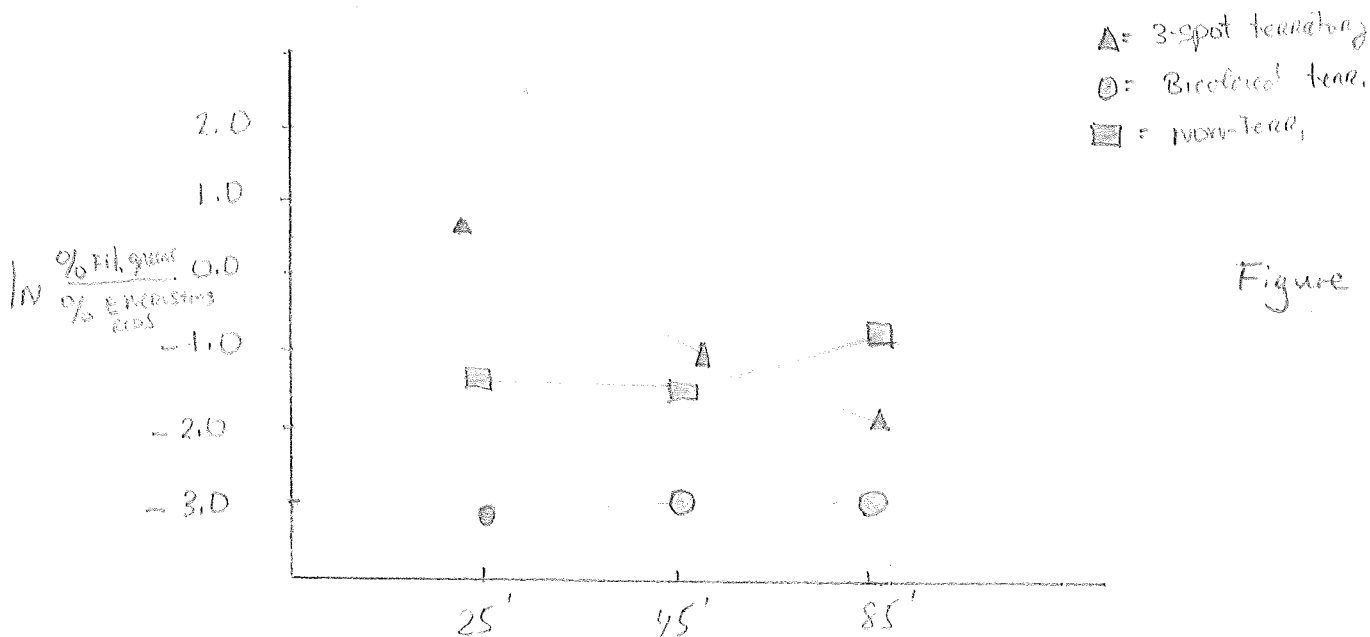


Figure 1.

this framework is densely overgrown by macrophytes (esp. genera Sargassum and Pocockiella). Hence, the actual substrate for filamentous algae is a sheet of macroalgae covering the A. cervicornis framework. Concurrent with this switch of substrate comes a marked decrease in percent cover by algal filaments and encrusting red algae. In other words, A. cervicornis seems to support a ~~greater~~ lusher growth of non-macrophytic algae than do macrophytes. This is not surprising, for a couple of reasons. First, the rock substrate is much more permanent than the macrophyte: it is not likely to grow, break off and float away, or be gulped down by a passing herbivore. Nor is it likely to have active defenses against epiphytes, which restrict macrophyte photosynthetic ability and hence might be defended against (in some way) by macroalgae.

Another notable trend is that corals tend to be more fully covered at 45' than at 25' (see our initial prediction).

The algae species ^{make-up} changes in important ways with depth: the % cover of filamentous greens and blue-greens decreases with depth; the filamentous reds and encrusting reds show peak cover at 45' depth.

Differences in algal species distribution within the different territories quantify the inherent higher quality of the E. planifrons territories than the E. parvulus territories or the no-man's (no-fish's?) land. E. planifrons territories contained the largest percentages of filamentous green and filamentous red algae, and the lowest cover

by encrusting calcareous reds. A number of other workers (Earle, 1972; Randall, 1967; ~~and~~ Doussard, 1979; and Atkinson et al, 1973) have shown that filamentous greens and reds are preferred food items over the crustose corallines, and that crustose corallines are dependent on heavy grazing pressure for their existence, due to their inferior competitive abilities. If one divides the values for % cover by filamentous greens by the % cover by encrusting reds, one obtains a rough index of territory palatability.

A log transformation was done on the index (to facilitate graphing); the results are presented in graphical form in Figure 1. Note from this graph that E. planifrons territory palatability is highest at 25' and decreases with depth, largely due to a decrease in filamentous greens. E. partides and non-territorial areas maintain approximately equivalent palatabilities with depth (the increase of the former at 85' is due to a decrease in encrusting reds, rather than an increase in the more edible greens).

The decrease in palatability of algae within E. planifrons territories could be explained in ~~two~~^{three} ways: 1) These fish graze their territories more heavily with increasing depth, or 2) Light-related factors favor non-green algae (Blebl, 1962), ~~Algae~~ or 3) Heavier grazing occurs within territories by other herbivores.

If the palatability index truly measures the quality of the algal lawn, perhaps the damselfish are under metabolic limitation at depth, despite the lush appearance of their mats. If the nutritive value of the algal mat is low, one might expect the damselfish to respond

with depth-related behavioral modifications, such as increasing territory size. This is exactly what appears to be occurring, the territory size (see Table 2) of *E. planifrons* increases with depth, from 2920 cm^2 at 25', to 3330 cm^2 at 45', to 5646 cm^2 at 85'.

It is interesting to note in passing that, from a look at ~~Table~~ Figure 1, it appears that the quality of *E. partitus* territories is actually lower, on this scale, than the quality of the no-man's land! Perhaps this decrease in quality is offset by the higher algal abundances found in ~~the~~ *E. partitus* territories at 45 and 85' (Table 2). It is also interesting to note that at 25', *E. partitus* territories ^{boundaries} could not be differentiated; there were no visible algal differences between places where Bicolored damselfish were and where they were not. This presents an interesting (sidelight) quandary, "Why defend territories if you are not growing an algal lawn?" Without dwelling on the question, we make a couple of observations: First, the *E. partitus* seen here are all very small, implying both that they are young (although care must be exercised when equating length with age in fishes) and that there is a high turnover of individuals, perhaps by starvation (there ain't much growing there) or by predation. If predation is indeed important, and algal lawn defense is simply not feasible for some reason, *E. partitus* may simply be defending shelter, a resource which like algae, is in short supply in some parts of the 25' site.

At any rate, the dramatically different strategies

played by the two species of damselfish should be underscored. The Three-spot (*E. planifrons*) cultivates a thick, highly palatable lawn, while the Bicolor (*E. portus*) defends only a minor peach fuzz investment. Thus, the species composition of the damselfish guild occurring in an area will have a profound impact on the composition of the algal community.

Table 3 presents presence/absence data for the 46 algae types for both damselfish species' territories and non-territorial areas. It appears that algal species, on a presence/absence basis, are uniformly distributed across territorial boundaries. Yet, palatability does vary across territorial boundaries. Evidently, species-specific behavior regulates relative abundances of the various algal species, but presence/absence is a function of depth more than species-specific characteristics.

Two other trends are apparent from Table 3.

First, green algae, as a group, occur more consistently over a depth gradient inside damselfish territories than outside, further indication of the influence of territoriality on algal composition.

The second trend is one which we are at a loss to explain: the abundance of macroalgae explodes at 85'. At that depth, territories and non-territories alike are characterized by considerable growth of *Halimeda* spp., *Ceramium*, *Galaxaura*, *Dictyota*, *Sargassum*, and *Pocockiella*. It is interesting to note that, while she says very little about preferences, Earle (1972) lists all these genera as algae which are eaten by herbivorous

Fishes. Why aren't they completely eaten here, as (supposedly) occurs at different places on the reef? One possible explanation is that decreased structural complexity of the coral framework makes the area predation-susceptible to herbivorous fishes. This explanation is lent support by parrotfish data for the east fore-reef (Carlson, unpublished data), which indicate that, of all three depths, schooling is the most preferred mode of social behavior at 85'. And, while structural complexity is also low at 25', at that depth, storm-generated surge may well prevent growth of large algae like Pocockiella and Sargassum.

The Diadema censuses indicate that this urchin's density decreases with depth:

| 25 ' Depth | Density <u>Diadema</u> |
|-----------------------|------------------------|
| 25' | 20.8 /m ² |
| 45' | 6.5 /m ² |
| 85' | 0 /m ² |

Atkinson et al (1973) have indicated that, like the damselfish, Diadema show culinary leanings toward the filamentous greens and reds. It is quite possible that they may, in the shallow waters, be having a significant impact on the algae of damselfish territories, for they move and feed at night, when the territories are not defended. It is tempting to draw ~~an~~ a point ~~to~~ ^a causative finger at the concurrent trends of decreasing Diadema densities and increasing macrophytes with depth, but Atkinson et al (1973) give food preference

information that indicates that even where macrophytes like Halimeda, Penicillus^{and} Sargassum are common, they are eaten in relatively small amounts; a much larger percentage of the echinoid's diet is composed of algae like Herposiphonia, Jania, Coelothrix, Polysiphonia, Cladophora, and Dictyota. It is useful to note that the latter ~~spe~~ genera are characteristic of pomacentrid territories, while the former are found ubiquitously at 85'.

Plate colonization experiment

Table #5 tabulates the raw data for this part of the experiment. We differentiated 27 distinct taxonomic classes. Lacking good keys for microalgae, we were able to identify less than half to genus; however, we include here drawings of all species which we could not identify (Figures 4-14). The furthest column to the left in Table 5 is a code for broader taxonomic categories: BG = blue-green alga, G = green alga, D = diatom, P = brown alga, C = Chrysophyta, and R = red alga.

"Green #1" is a blue-green alga which was found on all plates, and was abundant on many. Since it was by far the most abundant alga on the plates (60.1% of the observed algae), we decided to compare its abundance on plates subjected to different environmental conditions. Figures 2 and 3 show trends related to depth, cage protection, and placement within or outside territories.

There are two notable features of these graphs. The first is that, with the exception of the plates within 25' deep E. planifrons territories, there are no apparent differences

65'

45'

25'

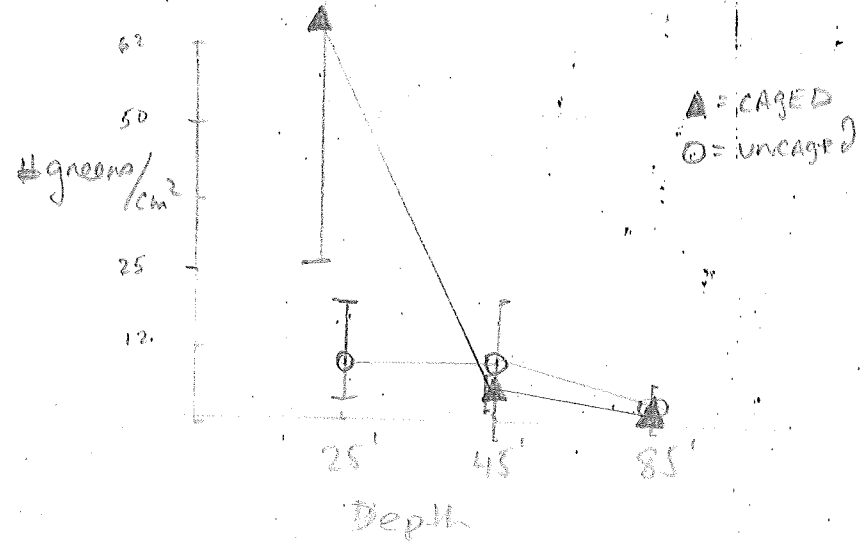
| | Three-spot | | | Non-territory | | | Three-spot | | | Non-territory | | | Three-spot | | | Non-territory | | | Totals | | |
|---------------------------|------------|------|-----|---------------|------|----|------------|------|-------|---------------|------|-----|------------|------|-------|---------------|------|-----|--------|----|------|
| | CAGE | OPEN | | CAGE | OPEN | | CAGE | OPEN | | CAGE | OPEN | | CAGE | OPEN | | CAGE | OPEN | | | | |
| 1. Green 1 | 235 | 020 | 400 | 134 | 113 | 86 | 86 | 67 | 55 | 509 | 162 | 184 | 73 | 158 | 4 | 8 | 7 | 75 | 46 | 10 | 5616 |
| 2. Green 2 | 125 | 30 | 15 | 3 | 1 | 4 | 2 | 4 | 13 | 2 | 1 | 6 | 3 | 13 | 5 | 2 | 7 | 4 | 5 | - | 266 |
| 3. Longbow | 240 | 85 | 25 | 9 | 2 | 8 | 19 | 26 | - | 7 | 5 | 37 | 14 | 56 | 1 | - | 2 | 36 | 14 | 1 | 627 |
| 4. Baseball net | 280 | 160 | 42 | - | - | 7 | 29 | 24 | - | - | - | 22 | 3 | 36 | 0 | 5 | 1 | 8 | 0 | 6 | 736 |
| 5. Straight fat | 85 | 20 | 14 | 2 | 3 | 3 | 25 | 56 | - | 14 | 8 | 25 | 7 | 26 | 5 | 1 | 0 | 5 | 0 | 2 | 321 |
| 6. Nitzschia | ++ | + | + | - | - | - | spurs | + | spurs | + | - | - | spurs | + | spurs | - | 4 | - | - | - | - |
| 8. Slider | 20 | 20 | 2 | 1 | - | - | - | 9 | - | - | - | 27 | - | 9 | - | - | - | - | 0 | 1 | 90 |
| 9. BD #2 | 15 | 5 | 2 | - | - | - | 7 | 15 | - | 1 | - | 9 | 2 | - | 9 | 1 | - | 5 | 0 | 3 | 74 |
| 10. Fragillaria | 25 | 25 | 5 | - | - | - | 3 | 1 | - | 2 | - | 1 | - | - | 2 | - | - | 2 | - | 2 | 68 |
| 11. Oscillatoria | 5 | - | - | - | 1 | - | 6 | - | 2 | - | 1 | 31 | 3 | - | 1 | - | - | 1 | - | 4 | 58 |
| 12. Lyngbya | 15 | 10 | 2 | - | 3 | 3 | 5 | 9 | - | 1 | - | 8 | 9 | - | 3 | - | 5 | - | - | 2 | 80 |
| 13. Fox | 5 | 15 | 4 | - | - | - | 7 | 2 | 1 | 2 | 3 | 8 | 4 | - | - | 4 | - | - | - | 1 | 57 |
| 14. BD #1 | - | - | - | - | - | - | - | - | 1 | 10 | 1 | - | - | - | 4 | - | - | - | - | - | 17 |
| 15. Abundant branching | 1 | - | - | - | 1 | 3 | 1 | - | - | 7 | - | - | - | - | 437 | 3 | 7 | 480 | 4 | 4 | 940 |
| 16. Red sausage | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 5 | 2 | - | 1 | - | - | 10 |
| 17. Cladophora | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | 1 | 2 |
| 18. Green dirt | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 16 | - | - | - | 9 | - | 30 |
| 19. Polysiphonia | 5 | 2 | 1 | - | 5 | 5 | 10 | 3 | - | 5 | - | 2 | - | - | 1 | 2 | - | - | 3 | 1 | 40 |
| 20. Coenocytic | - | - | - | - | - | - | - | - | 1 | 1 | - | - | 11 | - | - | - | 5 | 43 | - | - | 69 |
| 21. BQ (no cells visible) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 3 | - | - | - | 8 |
| 22. Encr. red | - | - | - | - | - | - | - | 1 | - | - | - | - | 7 | - | - | 1 | - | - | - | - | 10 |
| 23. Tabellaria | - | 5 | 4 | - | - | - | 1 | - | - | - | - | - | 1 | - | - | - | - | - | 2 | - | 14 |
| 24. Ceramium | - | - | - | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | 1 | - | 9 |
| 25. Red mussels | 5 | 3 | 2 | 1 | 2 | 2 | 2 | 12 | - | - | - | 2 | 1 | - | - | - | - | - | - | - | 35 |
| 26. Filamentous algae | - | - | - | - | - | - | - | 1 | - | - | - | 1 | 2 | - | - | - | - | - | 1 | - | 6 |
| 27. Helvetia | 45 | 15 | 2 | - | 1 | 1 | 2 | - | 1 | 2 | 4 | 4 | 1 | 2 | 7 | 1 | 1 | - | - | 1 | 92 |

Algae settled on plates after 10 days.

Table 5

$\bar{x} \pm SD$ of plant/cm²

| | 25' | 45' | 85' |
|---------|----------------|----------------|---------------|
| caged | 67.1 \pm 40. | 3.1 \pm .55 | .25 \pm .11 |
| uncaged | 11.1 \pm 7.8 | 11.7 \pm 13. | 1.7 \pm 2.0 |

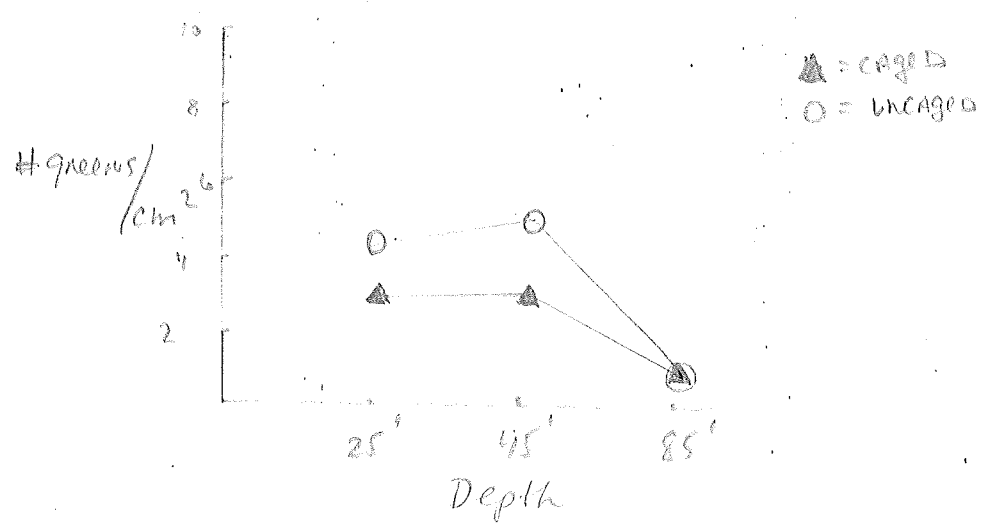


Growth of alga
"Green #1" on asbestos
plates within damselfish
territories

Fig. 2

| | 25' | 45' | 85' |
|---------|----------------|---------------|-----------------|
| CAGED | 2.89 \pm 2.6 | 3.1 \pm .55 | 1.3 \pm .73 |
| uncaged | 4.1 \pm .8 | 4.8 \pm 2.5 | 1.16 \pm 1.06 |

$\bar{x} \pm SD$



Growth of alga
"Green #1" on plates
outside of
damselfish territories

Fig. 3

between caged and uncaged plates. This suggests that herbivory was important in modifying abundances of Green #1 only at our shallow site. We suspect that herbivory differences would become apparent at other depths with time, but after ten days, colonization on these plates was almost entirely restricted to extremely small algae. Inspection of Figures 2 and 3 reveal that colonization decreased with depth for Green #1. Hence, at 85', for example, colonization by algae was so sparse that there are no caged/uncaged differences; the plates probably didn't even warrant inspection by passing herbivores.

Within 25' damselfish territories, however, we found strong differences in the predicted fashion between caged and uncaged plates; plates protected from herbivory showed a great deal more of the alga Green #1.

The second notable feature of this graph is that algal biomass of caged plates at 25' outside of damselfish territories was very low, not significantly different from growth on uncaged plates in the same area. This points out the probable importance of another factor controlling algal colonization, seed source. The comparatively algal-rich *E. planifrons* territories (relative to bicolor territories and non-territorial areas) are, according to Brawley and Adey (1977), areas of comparatively high bluegreen algae abundance. Thus, it seems likely that proximity to spore sources would be important in colonization.

The right-most column of Table 5 gives values for total abundances of our 27 plate-colonizer taxonomic units. Table 6 gives absolute abundances (per cm^2

| Taxonomic Unit | Relative Abundance (%) | Absolute Abundance (cm ⁻²) |
|----------------|------------------------|--|
| 1. | 60.9% | 23.35 |
| 2. | 2.8 | 1.20 |
| 3. | 6.7 | 2.83 |
| 4. | 8.3 | 3.50 |
| 5. | 3.4 | 1.45 |
| 6. | | |
| 7. | | |
| 8. | 0.8 | 0.41 |
| 9. | 0.7 | 0.33 |
| 10. | 0.7 | 0.31 |
| 11. | 0.6 | 0.26 |
| 12. | 0.9 | 0.36 |
| 13. | 0.6 | 0.26 |
| 14. | 0.2 | 0.08 |
| 15. | 10.1 | 4.28 |
| 16. | 0.1 | 0.05 |
| 17. | <.1 | 0.01 |
| 18. | 0.4 | 0.16 |
| 19. | 0.5 | 0.22 |
| 20. | 0.7 | 0.31 |
| 21. | <.1 | 0.04 |
| 22. | 0.1 | 0.05 |
| 23. | 0.1 | 0.06 |
| 24. | 0.1 | 0.04 |
| 25. | 0.4 | 0.16 |
| 26. | <.1 | 0.03 |
| 27. | 1.0 | 0.42 |

Table 6. Abundance of algae on experimental plates.

Although many algal species are represented, their distribution is skewed heavily toward high abundances of a very few species: the 5 most common species (#1, 3, 4, 5, and 15) account for nearly 90% of the algae found on our plates. Although the distribution of the algae presents a very complex picture, we note here a couple of interesting features of Table .

While Green #1 decreases in abundance with depth, another blue-green is fairly common at 85', and was seen infrequently elsewhere. Other bluegreens (*Oscillatoria*, *Lyngbya*, and #21) do not show obvious depth "preferences."

We had hoped, with the use of caged and uncaged plates to isolate the herbivory effects of damselfishes from those of other piscine herbivores. Due to the limited time available for the project, however, sufficient algal colonization and growth to differentiate herbivore effects occurred only in shallow damselfish territories.

Returning to our initial set of predictions concerning the factors predicted to affect algal abundance with depth, we can simplify the model somewhat with what we have learned. The effect of sand settlement can be disregarded as a consideration, because the accumulation of sand on the plates did not vary with depth.

The effect of Diadema grazing is limited to its depth distribution, and thus should only affect the 25 and 45 foot sites, the former more than the latter.

The predictive effects of light and damselfish territoriality were substantiated by this study. The effect of other (schooling) herbivorous fish was not differentiated, because in the short time our plates were out, colonization did not occur on caged non-territorial plates to any appreciable extent.

It is tempting to derive a model predicting the abundance of filamentous algae based solely on an index of the abundance of damselfish territories, corrected for species-specific behaviors which affect algal abundance. Such a measure may approximate normal algal distribution in cases where most of the area of study was within damselfish territories, and the effects of Diadema and other herbivorous fish were negligible. Such an area might well exist, at depths between our medium and deep sites.

Conclusions

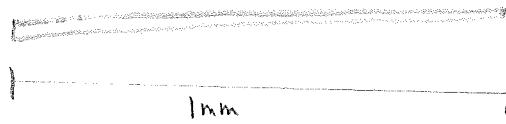
The territorial behavior of E. planifrons on this coral reef seems to be an extremely important factor regulating the algal community. Territoriality seems to be

most important with respect to the filamentous algae, increasing not only their absolute abundance, but changing the relative contributions of various species within the community, frequently favoring the more palatable and productive algae.

The exclusion of grazers was found to increase the biomass of algae colonizing plates. Since territoriality is simply a limited form of herbivory mitigation, it is not surprising ~~that~~ to find that territoriality increases algal biomass.

Territoriality may actually be increasing the primary productivity of the system; ^{in a further way} ~~for~~ faster growing (filamentous) species were favored in the territories. We found evidence that a good deal of blue-green algae grow within territories, and may very well be significantly contributing to nitrogen-fixation ⁱⁿ ~~at~~ this marine community.

① clean Filament: (Cyanophyta)



matrix is either light green or pink

Fig. 4

② Strait-FAT: (Diatom)

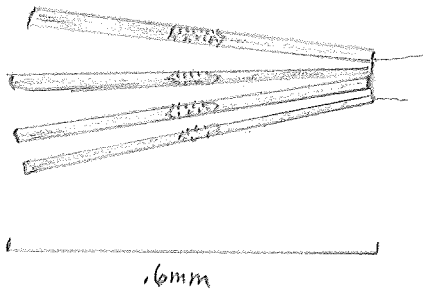
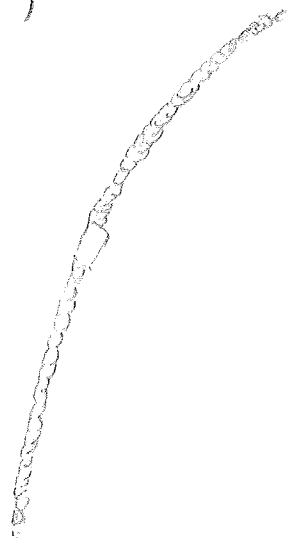


Fig. 5

③ long Bow (Diatom)

=.9mm Fig. 6

④ BASEBALL BAT - (chlorophyta)

APPENDIX 1

27

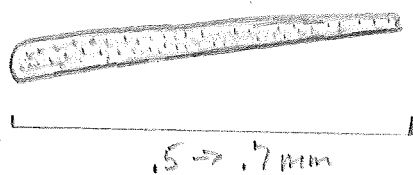


Fig. 7

⑤ SLIDERS - (Diatoms)

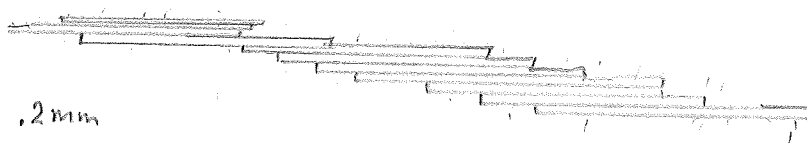
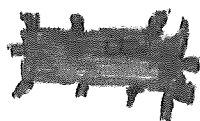


Fig. 8

compact size = .2 mm
Extended size up to 2 mm

⑥ Nubs - (Rhodophyta)



very plastic growth form

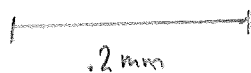
Fig. 9



⑦ B-D #2



Fig. 10



⑧ RED SAUSAGE

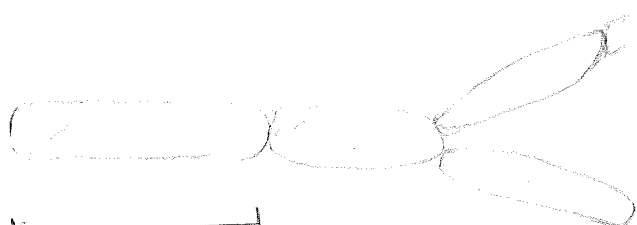
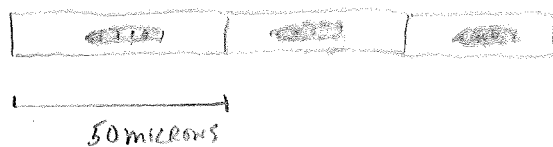


Fig. 11

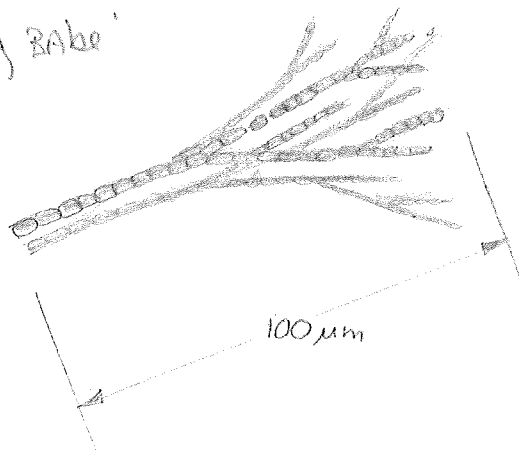


⑨ green type 2 - (chlorophyta)



Dichotomously branching Fig. 12

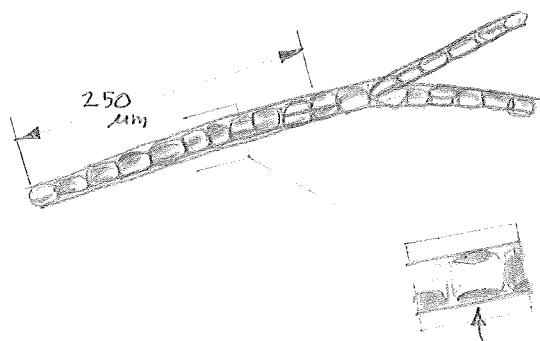
⑩ Branching Bacteria



A bluegreen
Color varies (as cells die?) between
green and reddish-brown.

Fig. 13

⑪



A bluegreen
Color usually light green. Much
larger

Fig. 14

Green often up against cell edges but
distinct chloroplasts are not visible. What
appears to be a sheath is visible at times.

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