DEEP WATER CORAL REEF ALGAL TURFS: ANALYSIS OF COMMUNITY STRUCTURE AND BIOMASS

A Thesis by:

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DEEP WATER CORAL REEF ALGAL TURFS:

ANALYSIS OF

COMMUNITY STRUCTURE AND BIOMASS

A Thesis

Presented to the Faculty of the Biology Department

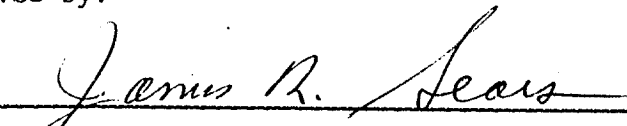of Southeastern Massachusetts University
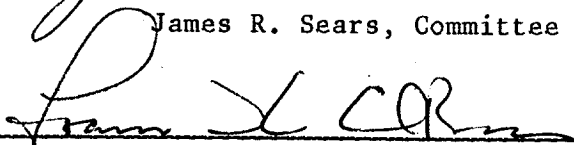
Master of Science

by

Marcia Louise Gilnack

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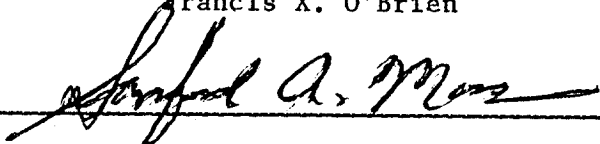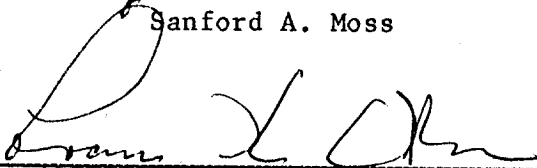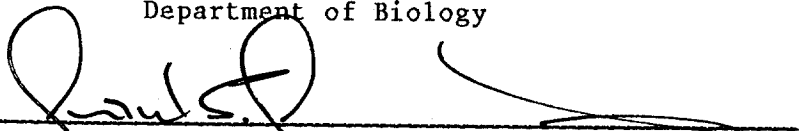Approved by:

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DEEP WATER CORAL REEF ALGAL TURFS:
ANALYSIS OF COMMUNITY STRUCTURE AND BIOMASS

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Southeastern Massachusetts University, 1987

Algal turf communities on deeper water (20 m) caged and uncaged artificial reefs were studied in Salt River Submarine Canyon, St. Croix. The use of NOAA's underwater habitat "Hydrolab" allowed for extensive sampling at 20 m depth. A detailed acccount of the relative abundance of algal species for each community was made. A total of 53 species was observed during the study, 43 occurring on uncaged reefs. Considerable spatial variability was observed in algal turf communities. The difference in the algal communities between caged and uncaged reefs indicated that grazing plays a significant role in structuring the plant community at this depth. Algal biomass and species composition were found to be significantly different on the caged and uncaged reefs. Caged communities contained a greater algal biomass, composed mostly of more structurally complex forms and their associated epiphytes. This is in contrast to the largely prostrate, fast growing, filamentous and fleshy forms found in the unprotected areas. Algal species diversity was not significantly affected by caging. It seems that grazing may enhance the productivity of the algal community by shifting the species composition towards the more highly productive species.

BIOGRAPHICAL SKETCH

Marcia Louise Gilnack was born in Manchester Connecticut on July 3, 1955. She graduated from the University of Connecticut in June 1977 with a Bachelor of Arts degree in biology. A certified diving instructor for nine years, she has worked as the Dive Supervisor for Fairleigh Dickinson University's West Indies Laboratory on St. Croix. Ms. Gilnack participated in three saturation diving missions in NOAA's underwater research habitat, the Hydrolab. She is currently employed by the Government of the Virgin Islands, Department of Conservation, as a Marine Biologist in charge of the Marine Water Monitoring Program. She also works at the University of the Virgin Islands as an Adjunct Professor teaching "Marine Plant Biology" and "Introduction to Oceanography". She has been employed as a private consultant on several environmental projects in the U.S. and British Virgin Islands, and is a member of the Phycological Society of America and the International Society for Reef Studies. Her publications in the primary literature include the following:

Rogers, C.S., Gilnack, M., and C.H. Fitz. 1983. Monitoring of coral reefs
    with linear transects: a study of storm damage. Journal of
    Experimental Marine Biology and Ecology. 6:285-300.

Rogers, C.S., Fitz, C.H., Gilnack, M., Beets, J. and J. Hardin. 1984.
    Scleractinian coral recruitment patterns at Salt River Canyon, St.
    Croix, U.S. Virgin Islands. Coral Reefs 3:69-76.

ACKNOWLEDGMENTS

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INTRODUCTION

Coral reefs, unlike near-shore temperate marine communities, are bathed in nutrient deficient waters and yet are one of the most productive and diverse communities known to man. They accomplish this by maintaining an efficient system of recycling essential nutrients through algae rather than a detritus food web which is typical of shallow marine communities (Hatcher 1983). A highly productive turf of benthic algae maintains a large biomass of herbivores on coral reefs.

The benthic algae associated with coral reefs vary in form, distribution, and importance to the trophodynamics of the coral reef. Zooxanthellae, unicellular algal symbionts, reside in the tissues of hermatypic corals (Odum and Odum 1955), and multicellular algae live inside and upon both living and dead calcified coral skeletons. Free-living benthic algae include crustose forms, macroalgal species (rare in the open reef environment) and algal turfs.

Algal turfs resemble a short fuzz, or mat, of often filamentous benthic algae growing on most non-living stable substrates. The turfs are multispecific with representatives from the major algal divisions: Rhodophyta, Phaeophyta, Chlorophyta and the Cyanobacteria. Turfs dominate the areal coverage on many reefs (Benayahu and Loya 1977, Wanders 1977, Rogers, Gilnack and Fitz 1983). Recent productivity studies on Caribbean reefs indicate that the algal turfs are the most productive component of shallow coral reefs and provide the majority of the energy for this complex ecosystem (Rogers and Salesky 1981, Carpenter 1984, 1985). Because of this high trophic contribution of turf algae to

the coral reef ecosystems, it is important to understand the composition, diversity and structuring agents of algal turfs.

Pioneering work on the benthic plants of the Virgin Islands was done by the Danish botanist F. Børgesen who published numerous papers on the algae of this area including the two volumes of "The Marine Algae of the Danish West Indies" (1913-1920). Since that time, additions to the Virgin Islands flora have been made by Taylor (1960), Earle (1972), Abbott (1976, 1979), and Sears and Brawley (1982). Turf communities of shallow reefs around St. Croix have been examined (Connor and Adey 1977, Rogers and Salesky 1981, Adey, Rogers and Steneck 1981, Carpenter 1981, 1983, 1984), but little work has been done on the turfs occurring in deeper water in this area.

Studying the algal turfs present special difficulties. Many turf species require microscopic examination for identification because of their small size. Grazing may affect plant form to a degree where the vegetative habit of grazed turf forms bears little resemblance to the ungrazed forms of the same species. Moreover, reproductive structures, often necessary for species identification in small filamentous algae, are often absent in these plants. These algae are opportunistic species and expand into available substrata via vegetative growth rather than expending their energy to reproduce sexually (Carpenter 1984). Abundance of the different algal taxa is also difficult to quantify because of their small size, difficulty of distinguishing between one plant from a colony of connected branches or upright fronds and because of their interweaving manner of growth. Separating species and weighing them individually is impossible. Because species identification requires

laboratory microscopy, it is necessary to collect samples in the field that can later be observed under the microscope to estimate the relative abundance of each species.

The algae of a turf community form a functional group rather than an assemblage representing any single taxonomic unit. An algal turf is a diminutive algal assemblage, and can be functionally defined as a dense aggregation of filamentous or foliose algae less than 1 cm in height. Filamentous forms are abundant in the turfs, but other forms such as parenchymatous, foliose, corticated, crustose and articulated calcareous are often important components. Many members of the turf algae have at least a partial basal creeping system in addition to their erect components.

The structure of turf communities vary according to environmental factors. Intertidal turfs with low grazing pressure tend to be composed of sparsely branched and loosely arranged algal forms (Hay 1981). An abundance of micrograzers can result in algae with larger thalli diameters with few filamentous forms (Brawley and Adey 1981). Territorial damselfish "farm" algal communities into specialized turf communities (Lobel 1980, Sammarco 1983). Subtidal, heavily grazed turfs are often shorter, more highly branched and compacted (Hay 1981). It was this compacted turf which occurs at 20 m in Salt River Canyon that was examined in this study.

The turf growth-form strategy has costs as well as benefits. Self-shading and nutrient limitation resulting from tightly packed uprights decrease productivity (Hay 1981, Carpenter 1986). The algae of the turf community often require more attachment space than individuals

or colonies with more loosely arranged uprights. On the other hand, the intertidal turf algae enjoy a reduction in desiccation stress due to the increased water-holding capacity (Hay 1981). Loss from grazing may also be decreased due to the shielding of basal attachments (Hay 1981). However the integrity of the turf functional form is maintained in many turfs, such as those examined in this study, by repeated grazing.

Plants of the turf community which are not grazed, lose their short, compact, turf structure and develop into a macroalgal community. This change may be accompanied by changes in species composition (Earle 1972, Lassuy 1980, Hixon and Brostoff 1981, 1983, Lewis 1986), an increase in biomass (Sammarco 1983, Carpenter 1984), and a decrease in productivity (Wanders 1977, Carpenter 1984, 1986). Similarly, areas inaccessible to reef grazers, such as cracks and crevices, have a more luxuriant growth of algae than surrounding exposed areas (Earle 1972). Likewise, in damselfish territories, where total grazing pressure is reduced by the aggressive territorial behavior of the damselfish, algal standing crop is higher than surrounding areas (Brawley and Adey 1977, Vine 1974).

Marine grazers are abundant and diverse in tropical waters where they exert strong control over the structure of benthic algal communities (see reviews by Ogden 1976, and Hatcher 1983). The effects of specific grazer groups on turf community structure and productivity have been studied by several authors. Reef fish (Randall 1961, Vine 1974, Ogden and Lobel 1978, Sammarco 1983, Carpenter 1986) sea urchins (Ogden, Brown and Salesky 1973, Carpenter 1981, 1984, 1986) and micrograzers (Brawley and Adey 1981, Carpenter 1986) all affect algal community structure in

general and turfs in particular.

While many animals graze the algae growing on shallow coral reefs, herbivorous fish are major grazers on deeper reefs where sea urchins are less abundant (Ogden and Lobel 1978). Herbivorous fish constitute only a small proportion of taxa of Caribbean reef fishes, but predominate in numbers and biomass (Ogden and Lobel 1978). They are largely non-selective, opportunistic feeders (Hatcher 1983), with low assimilation efficencies and high and continuous ingestion rates (Ogden and Lobel 1978). Because herbivorous fishes are the most influential grazers in deep reef communities in general (Ogden and Lobel 1978) and in Salt River specifically (Rogers et al. 1983), their influence was examined in this study.

Most herbivorous reef fishes in the Caribbean are in four families: Pomacentridae (damselfish), Scaridae (parrotfish), Acanthuridae (surgeonfish), and Kyphosidae (chubs) (Ogden and Lobel 1978). Pomacentrids are largely territorial and are found in relatively shallow water. Scarids, acanthurids and kyphosids, common in deep water, often function as foraging groups, which heavily graze an area for a short time and then move on. It is the effect of this functional group of herbivores, with larger foraging ranges, that was examined in this study by the use of exclusion cages. Contrasting algal communities in caged and uncaged treatments reveals the effects of these grazers on the structure of deep water turf communities.

Exclusion cages have been used in many tropical grazing experiments (Stephenson and Searle 1960, Randall 1961, Earle 1972, Vine 1974, Wanders 1977, Sammarco 1983, Hixon and Brostoff 1981, 1983, Carpenter 1981,

1984, 1986). Although used widely, caging does not provide a perfect
experimental situation. For instance, the size of the cage mesh may
select for small fish while excluding larger ones. Even if all grazers
could be excluded, the cages may also affect other parameters important
to the caged community. Two major effects of the cages are the effects
on light intensity and water circulation within the enclosed area. In
this study, to examine the degree to which the cages affected these
parameters, a relative measure of light intensity and water circulation
was compared in both caged and uncaged conditions.

Grazing can affect the algal community in many ways, the most
obvious of which is algal abundance (biomass). The effect of grazing on
shallow reef algal biomass has been demonstrated (Carpenter 1984, 1986,
Wanders 1977, Sammarco 1983, and others), but rarely have deeper reefs
been closely examined. Earle (1972) qualitatively noted an increase in
biomass after caging at 17 m depth on a St. John algal community.
However Vine (1974), working at 20 m in the Red Sea, found no significant
difference between standing crops of algae on protected vs. exposed
settling plates. In this study, I have estimated the influence of
grazing by larger herbivorous fish on a deep water turf community.

Few investigators have examined the turfs for relative abundance of
all of the different algal taxa. Many studies of turf communities list
only dominant species (Dahl 1972, Earle 1972, Atkinson et al. 1973,
Carpenter 1981, 1983, Hixon and Brostoff 1983) without examining the
minor components. More detailed examination of turfs come only from
shallow reef areas (Wanders 1977, Adey et al. 1981). In this study I
have attempted to quantify the presence of all members of the turf

communities and have compared these turf communities to those which were protected from larger grazers. Moreover, I examined several samples from each area demonstrating the degree of spatial variability not examined in previous studies.

Results from earlier caging experiments in other environments have been inconsistant, some showing an increase (Montgomery 1980) or a decrease (Paine and Vadas 1969) in plant species diversity. According to the "intermediate-disturbance" hypothesis (Connell 1978), species diversity reaches a peak at moderate levels of disturbance. Hixon and Brostoff (1983) used this concept to explain high algal species diversity in shallow damelfish territories. The "intermediate-disturbance" hypothesis predicts that there will be a lower species diversity in areas where there are high levels of disturbance (such as grazing), due to the elimination of many species. The species diversity will also be low at low levels of disturbance due to the dominance of competitively superior species. At intermediate levels, competitively inferior species may persist, resulting in a higher species diversity. In this study species diversity for algal samples from caged and uncaged communities were examined. The application of the "intermediate-disturbance" principle as it relates to grazing in deeper reef communities was also examined.

MATERIALS AND METHODS

Study Site

This study was conducted in Salt River Submarine Canyon, St. Croix, (17° 47' N., 64° 47' W.). Ten artificial reefs made of cinderblocks were constructed on the sandy canyon floor in January 1981 (Reaka 1981). Each reef consisted of eleven cinderblocks arranged in a pyramid, lashed together, and anchored in place with reinforcement bars (Figure 1a). These reefs were arranged in a line parallel to the junction of the sandy floor and the east coral wall 15 m away. All reefs were at least 10 m from each other and at a depth of 20 m. Every second reef in the line had a cage enclosure composed of plastic mesh with 3.8 x 3.8 cm openings over a 1.5 x 3 x 1.5 m frame (Figure 1b). Cages were equipped with hinged doors for diver access. Cages were cleaned of algae and invertebrate growth bimonthly by brushing all surfaces of the cages.

The depth of the artifical reefs and their distance from the east slope coral community limited the kinds and numbers of herbivores which foraged there. One of the major grazers of algae on Caribbean reefs, Diadema antillarum Philippi was rare or absent on these artificial reefs. These sea urchins were abundant on the shallow Salt River reef but are rare at 20 m depth (Rogers et al. 1983). Their limited mobility makes it unlikely that they would have ventured 15 m from the protection of the natural reef. In contrast, many fish were observed on these artificial reefs (Reaka 1981, 1982a, 1982b, 1983). Although small fish (primarily carnivorous wrasses) were observed inside the caged reefs, larger fishes (mostly scarids, acanthurids and kyphosids) which foraged the uncaged reefs were excluded from the caged areas. Abundance

and diversity of herbivorous fish at various depths in Salt River Canyon can be found in Clavijo (1978) and Rogers et al. (1983).

All algal samples were collected during a one week mission (February 20-March 3, 1984, NUL-I #84-2) in NOAA's National Undersea Research Program "Hydrolab", an underwater laboratory and saturation diving facility (Figure 2). This made it possible to make all collections during a seven day period thus eliminating time as a major variable in this study. Seasonal changes in biomass and species composition were obviously not the focus of this short duration sampling.

Algal Standing Crop

Divers collected 25 cm^2 epilithic algal samples by scraping the substratum and airlifting all material recovered in an airlift vacuum (Figure 3). Samples were taken randomly from a horizontal surface of the reef. The coordinates of random sample areas were generated using a computer. When a sample location overlapped with a previously sampled area, this area was passed over and another random area sampled. The airlift consisted of a 2.5 cm diameter, 50 cm long piece of PVC pipe connected to high pressure plastic tubing. A numbered Nytex bag, to hold the vacuumed algae, was attached to the distal end of the tubing with a hose clamp. Low pressure air from a SCUBA regulator was blown in one end of the PVC pipe to create suction. A valve, added to control the flow of air in the pipe, regulated the strength of suction. While one diver scraped the biomass, the second diver collected the scrapings with the airlift. A sharpened paint scraper was used to scrape clean the substratum inside of the 5 x 5 cm template. When all epilithic algae were removed from the area (Figure 4a), the airflow was allowed to

continue for several seconds, assuring that all algae in the pipe and hose were flushed into the bag. When the air flow was turned off, the hose was immediately pulled down and the bag closed off with a twist tie. The bag number was recorded on an underwater slate and the next bag attached. Five areas on each of ten reefs were collected in this manner. See Figure 4b for an in situ photograph of this process.

Visible non-plant material was removed by careful examination using a dissecting microscope. Acid was added and allowed to sit until all calcified material was dissolved. The sample was filtered through pre-weighed and pre-rinsed Whatman #2 filters and rinsed repeatedly with deionized water to remove salts. The filters were weighed to constant mass at $65^{o}C$ before and after filtering the samples to determine net weight of the samples.

To determine the statistical difference in biomass means for each treatment, the single classification analysis of variance (ANOVA) was used. To assure equality of variances (an underlying assumption of ANOVA), the F_s-test (Sokal and Rohlf 1969) was first employed.

Cage Effects

Changes in light intensity and water circulation due to caging were examined. Submarine photon flux densities on caged and uncaged reefs were measured in situ using a Li-Cor model LI-185A photometer with a LI-192S underwater cosine quantum sensor. Readings were taken on two cloudless days, September 19, 1983 and February 16, 1984. All readings were taken within 30 min. of each other on both days. A diver held the sensor on each reef while a surface scientist recorded photon flux

densities. Photon flux densities on caged vs. uncaged reefs were compared using ANOVA.

Water motion inside and outside of the cages was determined using the dissolution rates of plaster of Paris balls, following the procedures of Muus (1968) and Doty (1971). Divers placed 5, dry weighed plaster of Paris balls on each caged and uncaged reef for six hours. These were then collected, dried at $65^{\circ}C$ for 48 hours and re-weighed to determine how much plaster had dissolved during this period. The dissolution rates of the plaster of Paris balls on each type of reef were compared using ANOVA.

Species Composition and Relative Abundance

Algal samples for species composition and relative abundance were sampled by airlifting as described above. After the samples were collected, they were sent to the surface where the scientific support staff added enough formalin to the seawater and sample to make a 5% solution. In the laboratory all visible invertebrates were removed before a weak acid ($<10\%$ HCL) solution was added. The acid dissolved the calcium carbonate, facilitating the identification of the calcified algae and dissolving the carbonate sediment. Several drops of aniline blue dye were added to increase the contrast of the cell walls when viewed microscopically. The fixed, stained, decalcified algae from each vial were mounted on microscope slides using a 60:40 filtered seawater/Karo syrup solution. The slides were air dried, adding additional Karo solution when necessary. The edges of the coverslips were sealed using clear fingernail polish. Between one and five slides were made for each sample according to the quantity of plant material present. A total of

one hundred and forty-five slides were prepared in this manner; 65 from uncaged reefs, and 80 from caged reefs.

The relative abundances of the dominant taxa were determined microscopically using the point-intercept method (Belk and Belk 1975, Jones 1968). Random mechanical stage coordinates (vernier scale gradations) were determined with the use of an Apple 2e computer. A program was developed to accept the limiting coordinates (vernier scales gradations) of each cover slide and to return random points within that area. Algae were viewed at 100x magnification. All plant tissue below any of the 121 intersects of the ocular grid were identified to species, when possible, and counted. Approximately 1000 points per sample were required to obtain 80 percent of the species present. Plants were identified to species using Taylor (1960), Børgesen (1913-1920), Humm (1980), Navarro (1981), Kapraun (1980), Kapraun and Norris (1982), Kapraun et al. (1983), Van den Hoek (1978), Díaz-Piferrer (1968), and personal communication with Dr. D. F. Kapraun (University of North Carolina), Dr. D. Ballantine (University of Puerto Rico), and Nancy Odgen (West Indies Laboratory).

The relative abundance of each species present was calculated for each 25 cm^2 scraped sample using the point intercept method. This set of species proportions was used to determine the species diversity for every algal sample using the Shannon formula for diversity (Shannon and Weaver 1949):

$$H' = -\sum_{i}^{S} p_i \ln p_i,$$

where p_i = the proportion of the total sample belonging to i^{th} species, S = the number of species, and H' = the index of species

diversity.

The analysis of similarity between sets of species abundances was carried out by applying Schoener's (1968) index of niche overlap:

$$d = 1 - (\sum_{i}^{S} | p_{ij} - p_{ik}|/ 2),$$

where p_{ij} is the proportion of species i in communities j and k, and S = the number of species. Indices between sets randomly paired within each treatment were compared to randomly paired sets between treatments using analysis of variance on transformed data.

Relative abundances of several species between treatments were compared using t or t' tests (Sokal and Rohlf 1969).

RESULTS

Algal Standing Crop

The mean values of algal biomass on caged turfs were significantly higher than those for the uncaged turfs ($p < 0.02$) (Table 1). Algal biomass values for all the reefs ranged from 26.3-76.6 g/m^2 (decalcified dry weight per area). The mean algal biomass for caged reefs was 53.5 g/m^2 (S.D.=13.2, n=25) and for uncaged reefs 44.7 g/m^2 (S.D.=11.9, n=25). Variances of means between reefs of each treatment were not significant.

Cage Effects

The mean photon flux densities of the reef surface inside of cages were not significantly different from the mean photon flux densities from adjacent uncaged reefs at the same depth (Table 2). Although the average photon flux density was higher on the uncaged reefs, 16 % in Sept. 1983 and 11 % in Feb. 1984, the variability in photon flux densities within treatments was so great that no significant difference between treatments was obtained. Variability in submarine photon flux densities can be caused by small changes in surface photon flux densities as well as by reflection, refraction and dispersion of light from particles suspended in the 20 m column of water through which the light passed. The degree of surface disturbance from waves also affect submarine photon flux densities. Although the reduction of light due to caging was real, it seems insignificant when compared to the naturally changing light conditions.

Dissolution rates for plaster of Paris balls as a way to compare

estimates of water motion are given in Table 3. ANOVA revealed no significant differences between dissolution rates on caged reefs and uncaged reefs for either sampling date. No significant difference in dissolution rates was found between reefs within treatments except in Sept. 1983 where caged reefs E and C were significantly greater than caged reefs A, B and D (Student-Newman-Keuls, $p < 0.05$). Dissolution rates in September were significantly larger than those taken in February $(p < 0.001)$.

Species Composition and Relative Abundance

A total of 53 species of benthic plants were identified in the scrapings of algal turfs from the experimental reefs studied (Table 4). Included were: one species of Spermatophyta, one species of Cyanophyta, one species of Chrysophyta, nine species of Chlorophyta, six species of Phaeophyta, and 35 species of Rhodophyta. The relative abundances of each taxa for each of 50 algal samples are given in Appendix I.

The relative abundances of algal taxa in samples from caged reefs were more similar to other caged algal samples than they were to those of the samples from the uncaged reefs (Table 5). Similarly, the relative abundances of the uncaged algal samples were more similar to other uncaged algal samples than to those of the caged samples. The mean degree of similarity among treatments (0.36) was significantly higher than that between treatments (0.14) (Table 5). Although the similarity within treatments was higher than between treatments, samples within treatments in general did not show a high degree of similarity (0.35), demonstrating the highly variable nature of the turf community.

The dominant species ($> 3\%$ relative abundance) and their average

percentages found on the uncaged and caged reefs (when all samples in each treatment were pooled) are given in Table 6. Species whose abundances differed significantly between treatments are marked with an asterisk. Of the 14 dominant species given in Table 6, seven were found to have a statistical difference of relative abundance between treatments ($p < 0.05$, one-way ANOVA).

Comparisons between samples from the caged and uncaged reefs revealed that species diversity (1.55 vs. 1.50) was nearly identical (Appendix I, $p > 0.01$, Mann-Whitney Test). Out of a total of 53 plants collected and identified, 43 occurred on uncaged reefs and 47 occurred on caged reefs. Those which were restricted to caged reefs numbered four and included : Caulerpa mexicana, Halophila decipiens, Dictyopteris divaricata, and Jania adherens. All species observed on uncaged reefs were observed on caged reefs.

DISCUSSION

This study examines in detail the morphology and composition of the algal turf community in deep water (20 m) within Salt River Canyon and the effect of grazers on the algal turfs. The grazing effects on the turfs will be compared with control, non-grazed areas, and these results will be analyzed vis-a-vis other studies on herbivore/algal interactions on tropical reefs. Finally, there will be a discussion on how fish foraging affects the species diversity and productivity of the algal turf community.

Algal Standing Crop

The higher biomass values for the deep turf algae found on caged reefs versus uncaged reefs during this study were not unexpected. Shallow water studies of algal turf biomass using cages for exclusion of grazers similar to those used in this study have reported similar effects (Wanders 1977, Sammarco 1983, Vine 1974). A decrease in grazing intensity by excluding grazers resulted in a larger, more luxuriant growth of algae than in exposed areas.

Although there have been many studies which have measured algal turf biomass (Vine 1974, Sammarco et al. 1974, Wanders 1977, Brawley and Adey 1977, Borowitzka et al. 1978, Adey et al. 1981, Carpenter 1981, 1985, Conner and Adey 1977, Sammarco 1983), differences in collecting and analyzing techiques made it impossible to compare much of the previous data to the biomass data presented here. Only values obtained from mature, subtidal, naturally grazed turfs which have been decalcified and dry weighed can be compared to the 40-50 g/m^2 range

found here for uncaged turfs: Vine (1974), 9-29 g/m^2; Borowitzka et al. (1978), 3-52 g/m^2; Carpenter (1981), 21-45 g/m^2; Carpenter (1985), 10-36 g/m^2; Sammarco (1983), 5-10 g/m^2. Although the ranges overlap, generally the biomass data given above, which were all taken from shallow reef areas, are lower than the 40-50 g/m^2 range found in this study. This is expected due to the lower grazing pressure usually found on deeper reefs (Ogden and Lobel 1978, Rogers et al. 1983).

Cage Effects

There are problems with the use of exclusion cages as a technique to evaluate grazer effects. The physical presence of the cages naturally decreases water circulation and light intensity over the caged areas. However, the data collected during this study show that irradiance levels and water circulation vary more over space and time than between caged and uncaged treatments. Despite the fact that cages do somewhat alter ambient conditions of the caged area, the data suggests that there are no significant differences between treatments with regard to irradiance or water circulation.

Other reseachers using exclusion cages have tried to evaluate the caging effect. Lewis (1986) measured water flow inside and outside of exclusion fences and concluded that the fences had no measurable effect on water flow. Hixon and Brostoff (1981) tested physical effects of caging with partially caged areas simulating light reduction and decrease in water motion but allowing access to grazers. They concluded that their cages did not significantly affect the caged community growing inside. Carpenter (1986) also showed that partially caged reefs did not differ in biomass or relative abundance of dominant algae. Wanders

(1977) concluded that changes in biomass and species diversity in caged versus uncaged areas was due to the exclusion of grazers, and not to the effect of the cages themselves. These studies, along with the data reported here, suggest that physical effects of caging on light and water movement are insignificant when compared with their exclusion of grazers.

Species Composition and Relative Abundance

The Turf Community

Contrary to the uniform, carpet-like appearance of algal turfs, this study has demonstrated the complex and variable nature of this community. The number of species present in 25 cm^2 samples varied from as few as ten to as many as 24 (mean=15.6). The degree of variability in species composition and relative abundance is evident from the low average similarity between treatments (0.35). Despite the complex and variable nature of the community, some general observations about the natural (uncaged) turf community are discussed below.

The natural, uncaged turf community at Salt River Canyon was dominated by fast growing, structurally simple species. Many turf species are heterotrichous, having both a prostrate and an upright form. The prostrate section functions in lateral expansion, attachment, and as a resting stage with a low rate of respiration (Hay 1981). This creeping habit allows opportunistic lateral expansion into adjacent cleared patches opened by herbivores. The prostrate section is shielded from grazers by the more productive, heavily grazed, upright form (Hay 1981). In this study, of the 43 species found on uncaged reefs, 21 had a creeping or prostrate habit, with nine being simple polysiphonous reds.

The species richness found in this study for 25 cm^2 samples seems high compared to some reported in shallow tropical algal turfs. Hixon and Brostoff (1981) found an average of 3.8 species/50 cm^2 on shallow Hawaiian reefs and only 13 species throughout the entire study. Carpenter (1981) found 12 species of algae in turfs on shallow experimental plots on Teague Bay. Similarly, Brawley and Adey (1977) found 4-12 species per 0.05 m x 1 m transects on shallow Jamaican reefs. However, Borowitzka et al. (1978) found over 38 species on a shallow Australian reef. As this study only examined deep water algal turfs at one site, no generalizations on species richness relative to depth can be made.

Differences in species dominance also appears to be variable. Adey et al. (1981) reported that several algal turf communities on the south shore of St. Croix were dominated by bluegreen algae (Cyanobacteria). Atkinson et al. (1973) found greater than 90 percent relative abundance of Herposiphonia secunda in a shallow St. Croix algal turf community. Others found that crustose corallines dominated shallow algal turfs (Wanders 1977, Carpenter 1981). But diverse assemblages of species-rich algal communities have also been reported (Lassuy 1980, Montgomery 1980, Borowitzka et al. 1978).

From the data presented here and the limited data from shallow turf communities, we can see that species composition and relative abundance are variable among algal turf communities. In this study, a deep water algal turf community was described and was shown to be spatially variable and species rich.

Grazing Effects

The plant species distribution of caged and uncaged communities

differed in several ways. Simple polysiphonous reds (Polysiphonia,

Herposiphonia, Hetersiphonia) were more abundant on the uncaged than

on caged reefs where they were replaced by slower growing, more

structually complex forms such as calcified reds (Jania,

Peyssonnelia), macroscopic forms, and associated epiphytes, on the

caged reefs. These results suggest that plant communities on grazed

reefs represent a successional sere maintained by grazing.

Parallels can be made to terrestrial plant communities. Abandoned

farmland in North Carolina, for example, is quickly colonized by fast

growing opportunistic species such as herbs and grasses. If left

undisturbed, this community will eventually develop into a climax

community of more structually complex plants, in this case, hardwoods

(Keever 1950).

Shallow water reef turfs have been shown to have a similar response

to a decrease in grazing. Several investigators have shown an increase

in macroalgal abundance with a decrease in grazing: Sammarco et al.

(1974), Carpenter (1981, 1986), Wanders (1977), Hinds and Ballantine (in

press), Lassuy (1980).

In contrast, short-term exclusion studies have noted an increase in

structurally simple, fleshy algae. Vine (1974) found that a filamentous

green alga dominated caged substrates after three months. Others found

that simple reds (Polysiphonia, Ceramium, Taenioma, Centroceras)

dominated protected turfs after 4-10 weeks (Hixon and Brostoff 1981,

Wanders 1977). Wanders (1977) found that simple browns and greens

(Giffordia, Enteromorpha, Cladophora) were dominant after 6-8 weeks
but were replaced by larger, structurally more complex species
(Centroceras, Wrangelia, Jania, Dictyota, Laurencia,
Spyridia) after 10-15 weeks.

The response to grazer exclusion seems to affect not only the
distribution but the growth-form of a species. The following discussion
will examine several species whose relative abundance was significantly
different on caged versus uncaged reefs. A discussion on possible
reasons for this shift based on growth-form is also offered.

Lobophora variegata

This brown, parenchyamous, sheet-like alga, can be found growing in
a prostrate manner, attached by rhizoids from the lower surface (the only
form found in this study), or in an erect manner. Lobophora
variegata is known to be exceptionally productive among tropical marine
algae with net photosynthesis/dark respiration (P/R) values of 22.9
(Buesa 1977). This alga was one of the dominant algae in the uncaged
reefs and rare on the caged reefs. One explanation for this disparate
distribution is that Lobophora, in the absence of grazing, is overgrown
by competitively superior algae normally removed by grazing. This seems
probable because in the absence of grazing, the competitive erect forms
of other algae can more easily compete for available light by growing
above the prostrate form of Lobophora. In the presence of grazers, its
rapid growth and prostrate growth form allow it to expand rapidly into
newly opened substrate.

The greater amount of L. variegata on uncaged reefs as compared
to caged reefs could also have resulted from its greater resistance to

herbivory. However, there is no clear evidence that <u>L. variegata</u>

has any physical or chemical deterrents to herbivory. In fact, recent

algal susceptibility studies in Belize have clearly demonstrated that

<u>L. variegata</u> is highly susceptible to fish grazers, particularly

parrotfish (Lewis 1985, 1986). Experimental transplants of the prostrate

form of <u>L. variegata</u> from a low-herbivory habitat into a

high-herbivory habitat showed percentage weight losses of 99.8 percent

over an eight hour transplant period, compared to plants protected from

grazing by cages with a percentage weight loss of 13.5 (pers. comm. S.

Lewis). However, others have shown that <u>Lobophora</u> is less susceptible

to grazing (Hay and Göertemiller 1983, Paul and Hay 1986). It has been

suggested that differences in susceptibility may represent geographical,

habitat or individual variation in plant defenses (Lewis 1985). To

determine if chemical deterrents give <u>Lobophora</u> a competitive advantage

at 20 m in Salt River Canyon, chemical analyses and grazing

susceptibility studies would have to be performed.

<u>Polysiphonia</u> <u>ferulacea</u>

<u>Polysiphonia</u> <u>ferulacea</u> is a red, polysiphonous (four pericentral

cells) alga with a creeping habit. It was one of the dominant algal

species found on uncaged reefs but was an insignificant member of the

caged community. Although its creeping growth form is well suited for a

grazed environment, it is quickly overgrown in the absence of grazing by

competitively superior algae which grow on and above the substratum.

This follows the pattern of other creeping forms which, although less

abundant, occurred with greater frequency on uncaged versus caged reefs,

e.g. <u>P. subtilissima</u>, <u>P scopulorum</u>, <u>P. denudata</u>, <u>P.</u>

howei, _Herposiphonia_ _secunda_ (see Appendix I).

Wurdemannia _miniata_

This multiaxial, creeping red alga forms a low mat and is attached
to the substrate by basal haptera. This plant was significantly more
abundant on the uncaged grazed reefs, while being maintained by grazing,
and was found only in small abundance on caged reefs, where it was
presumably overgrown by competitively superior forms. It was noted
during microscopic examinations that the tips of many of these plants
found on uncaged reefs had been cropped.

Jania _capillacea_

This articulated coralline alga occurred in greater abundance on
caged reefs than on uncaged reefs. Its calcified thalli with flexible
joints make it able to withstand mechanical stress (Littler and Littler
1980). Its upright calcified form presumably give it a selective
advantage in interference competition for space and light (Littler and
Littler 1980). Littler and Littler (1980) described _Jania_ as belonging
to the growth form which was k-selected, of low calorific value,
stress-tolerant, and with a lower reproductive output. Where turf
species invest their energy to replace tissue lost to herbivory, these
forms use their energy for structural complexity.

Antithamnion _butleriae_

Antithamnion _butleriae_ was the second most abundant species
found on the caged reefs and was found significantly more abundant on the
caged vs. uncaged reefs. In contrast to the structurally complex
Jania, _Antithamnion_ _butleriae_ is a small, delicate, uniseriate red

alga. <u>Antithamnion butleriae</u> is often found, as in this study,
creeping epiphytically on other algae (B⌀rgesen 1913-1920). An increase
in epiphytic algae when grazing pressure was reduced was also noted in
other studies (Carpenter 1984, Lewis 1986, Hinds and Ballantine, in
press). The increase in larger, more persistant, algal forms in the
caged areas undoubtly increased the habitat for this alga, allowing it to
become one of the major plant constituents of the community. Lower
grazer pressure also allows fleshy, filmentous species to exist in this
habitat. Unlike other structually simple algae which have a
heterotrichous growth-form, epiphytic species do not require a hard
substratum and so can survive without being overgrown.

<u>Asparagopsis</u> <u>taxiformis</u>

The <u>Falkenbergia</u>-form (tetrasporic phase) of this red alga is a
small, irregularly branched filament which grows epiphytically on other
algae. As with <u>Antithamnion</u> <u>butleriae</u>, significantly more
of this was found on the caged reefs, probably due to the increase in
larger erect algae on which it grows, and the decrease in grazing
pressure..

<u>Caulerpa</u> <u>mexicana</u>

This macroscopic green was found significantly more abundant on
caged reefs compared to uncaged reefs. Although it was found on only two
of the five caged reefs, it was the fourth most abundant alga overall on
caged reefs. This alga was particularly conspicuous on the reefs due to
its great canopy height. It is, however, known to have particularly low
productivity among tropical marine algae with P/R values of 1.0 (Buesa

1977).

Some have suggested that members of the Caulerpaceae produce unusual secondary compounds which act as chemical deterrents to grazers (Norris and Fenical 1982). However, recent studies show that even though these plants have "chemical defenses", they are nevertheless highly susceptible to fish grazing (Lewis 1985, Paul and Hay 1986).

Bryopsis plumosa

The coenocytic algal Bryopsis has a feather-like frond and an upright habit. Although this alga was not found in great abundance, it was found significantly more abundant on the ungrazed (caged) reefs than on the grazed (uncaged) reefs. This plant is not generally observed in algal turfs exposed to herbivory but can often be observed in cracks and crevices less accessible to grazers (personal observations). In the absence of grazing, characteristics to enhance substrate acquistion and retention are not as important as characteristics which allow more efficient utilization of light. In caged areas, Bryopsis, with its erect growth habit, is may be better able to compete with other algae. Because it does not have a creeping growth form to quickly recolonize opened spaces, it may not compete well with creeping turf forms. Bryopsis would seem to be particularly grazer-susceptible due to its erect form and delicate coenocytic thalli. A recent study on seaweed susceptibility to herbivory indicated that Bryopsis plumosa was consumed more readily than most plants tested. Thin layer chromatography showed no unusual secondary metabolites (Paul and Hay 1986).

The results given in this study, which show that grazed algal communities differ from protected communities, complement those of other

investigators on effects of tropical herbivory on the benthic algae
of coral reefs. As on shallow reefs, herbivorous fish grazing influences
benthic species distribution and abundance at 20 m in Salt River Canyon.
The macroalgal species distribution appears to be limited by herbivory
rather than lack of spore availability or unsuitable physical conditions.
Grazing maintains the algal community at an intermediate successional
sere preventing dominance by macroalgal species.

The algal turf maintained by grazing on the uncaged reefs was
composed largely of structually simple algae with a heterotrichous growth
habit. This form persists by maintaining a prostrate system, somewhat
shielded by the upright portion, which allows the plant to quickly expand
into newly opened substrata. When subjected to grazing, the ability to
acquire space quickly and grow rapidly gives these algae a competitive
advantage over slow growing erect plants. Constant grazing reduces the
erect forms which could potentially overgrow these heterotrichous forms.

In the absence of grazers, the algal communities are often dominated
by large, structurally complex, erect plants. The ability to expand
rapidly is less advantageous in protected areas than in exposed areas.
Structural complexity allows algae to withstand mechanical stress and
large erect forms are better able to compete for space and light.
Another growth-form not common on grazed turfs which also competes well
in the absence of grazing, is the small epiphytic species. The increase
in macroalgal forms creates a new habitat allowing epiphytic algae to
become dominant members of the community. This new habitat increases the
species diversity of the community.

Connell's intermediate-disturbance hypothesis would predict that

moderate grazing would enhance species at higher grazing intensities, or decrease species diversity by preventing the competitive dominance which occurs in mature communities. Hixon and Brostoff (1981, 1983) applied this hypothesis to shallow-water turf communities confirming a unimodal relationship between grazing intensity and species diversity.

To apply the intermediate-disturbance hypothesis to this study one would have to make an assumption of the level of grazing at 20 m in Salt River Canyon. I suggest that the grazing pressure here is comparable to the level of grazing designated as "moderate" in Hixon and Brostoff's (1981, 1983) study. Although the grazing pressure was not measured in this study, Steneck (1983) measured the intensity of fish grazing in Salt River Canyon at a depth of 60 feet. Steneck (1983) found that the fish grazing pressure at 60 feet was approximately six percent of that found in shallow well grazed areas. Hixon and Brostoff (1981) reported that the "moderate" level of grazing was also approximately six percent of the "intense" level of grazing. Additionally, the algal communities on unprotected reefs have a considerably greater species richness than the low diversity crustose community found on the areas designated as "intense grazing" by Hixon and Brostoff (1981) (3.8 species/50 cm^2). If we assume that there was moderate grazing pressure on the uncaged reefs, we would expect the caged communities to have a lower species diversity. Because there is no significant difference in species diversity between treatments, this study does not support this hypothesis.

The intermediate-disturbance hypothesis seems not to be applicable to algal communities examined in this study due to the creation of the

new epiphytic habitat which developed on the larger algal forms as a result of decreased grazing. This niche differentiation on caged reefs increased the species diversity in the caged community. This complements Hatcher's (1983) suggestion that the principles of tropical algal-herbivore relationships in terms of species diversity have not yet been established.

If we do not accept the above assumption but instead assume that the naturally grazed community represents "intense grazing", the intermediate-disturbance concept would predict that at an intermediate level of grazing (a level of grazing between that on uncaged and caged reefs), a community with a higher species diversity would develop. More field work would need to be performed to prove this application of the intermediate-disturbance hypothesis.

Grazing has been shown to increase plant productivity in both terrestrial and aquatic environments (Mattson and Addy 1975, Dyer and Bokhari 1976, Porter 1976, Carpenter 1981, 1985, 1986). One example of this was the recent mass-mortality of the Caribbean sea urchin which resulted in the immediate decrease in algal community production (Carpenter 1985). This decrease in productivity was attributed to either the decrease in urchin excretions which provided nutrients for the algae or an increase in algal self-shading (Carpenter 1985). I suggest, from the differences in species distribution noted in this study, that grazing can also decrease the community productivity by a change in species distribution.

Although no productivity data were collected in this study, it seems likely, based on species specific production rates given in previous

reports (Buesa 1977, Littler and Arnold 1982), that grazing increases community productivity at 20 m in Salt River Canyon. The most dominant alga on grazed reefs, Lobophora variegata, has been shown to be exceptionally productive among tropical marine algae (Buesa 1977). In contrast, the dominant alga on protected areas, Jania, has been shown to have very low productivity rates in comparison to other algae (Littler and Arnold 1982). The limited productivity data available for tropical algae prevents a complete analysis for all species. But, based on the limited species-specific production rates, and generalizations made from algal functional-form groupings (Littler and Arnold 1982), it seems that grazing can be seen as a mechanism for increasing productivity in a nutrient deficient environment by shifting species composition towards the more highly productive species.

TABLE 1

Mean algal biomass data (decalcified dry wt.) per 25 cm^2 (+/- S.D., n=5) for caged and uncaged reefs.

Reef	Uncaged reefs g/m^2	Reef	Caged reefs g/m^2
A	45.9 (11.7)	F	54.4 (16.4)
B	40.4 (7.7)	G	44.0 (8.3)
C	50.3 (12.7)	H	62.3 (13.3)
D	41.8 (13.9)	I	54.0 (16.3)
E	45.1 (15.2)	J	52.6 (7.0)
Mean for all reefs	44.7 (11.9)		53.5 (13.2)

TABLE 2

Photon flux densities ($uEm^{-2}s^{-1}$) of caged and uncaged reefs at 20 m depth in Salt River Canyon on Sept. 19 and Feb. 4, 1984. Readings were taken at the surface of the cinderblock substrate using a Li-Cor underwater photon sensor.

	Uncaged reefs			Caged reefs	
	Sept. 19, 1983	Feb. 4, 1984		Sept. 19, 1983	Feb. 4, 1984
A	151	123	F	108	115
B	143	115	G	125	91
C	132	140	H	128	126
D	120	137	I	96	140
E	196	112	J	167	84
Mean	148	125		125	111
(S.D)	(29.1)	(12.7)		(26.9)	(23.5)

TABLE 3

Comparisons of water motion in caged and uncaged reefs using dissolution rates (mg/hr) of plaster of Paris balls during Sept. 1983 and Feb. 1984. There are 5 replicates for each treatment of each reef.

| | Sept. 1983 | | | Feb. 1984 | |
	Uncaged reefs	Caged reefs		Uncaged reefs	Caged reefs
A	474	426	F	401	347
	472	440		355	288
	468	353		346	314
	453	443		371	295
	397	466		331	371
B	475	351	G	253	285
	440	359		342	255
	470	369		363	364
	488	352		349	373
	421	427		291	319
C	402	459	H	221	308
	416	383		315	364
	350	386		357	328
	394	396		279	318
	389	421		309	295
D	455	388	I	281	254
	479	459		266	293
	397	366		365	273
	435	372		378	356
	433	384		251	341
E	356	464	J	338	352
	301	345		311	350
	422	346		254	267
	325	358		314	328
	401	450		356	219
Mean	421	399		320	314
(S.D.)	(50)	(42)		(47)	(41)

TABLE 4

Plant species found on uncaged and caged reefs.

Species #

Cyanophyta
1.   _Microcoleus lyngbyaceus_ (Kützing) Crouan

Bacillaripohyta
2.   _Biddulphia reticulata_ Roper

Chlorophyta
3.   _Bryopsis plumosa_ (Hudson) C. Agardh
4.   _Caulerpa mexicana_ (Sonder) J. Agardh
5.   _Cladophora delicatula_ Montagne
6.   _Cladophoropsis membranacea_ (Agardh) Børgesen
7.   _Cladophora_ sp.
8.   _Entermorpha chaetomorphoider_ Børgesen
9.   _Neomeris annulata_ Dickie
10.   _Ostreobium quekettii_ Bornet and Flahault
11.   _Rhizoclonium kerneri_ Stockmayer

Spermatophyta
12.   _Halophila decipiens_ Ostenfeld

Phaeophyta
13.   _Giffordia rallsiae_ (Vickers) Taylor
14.   _Dictyopteris delicatula_ Lamouroux
15.   _Dictyota divaricata_ Lamouroux
16.   _Lobophora variegata_ (Lamouroux) Womersley
17.   _Sphacelaria novae-hollandine_ Sonder
18.   _Sphacelaria tribuloides_ Meneghini

Rhodophyta
19.   _Acrochaetium seriatum_ Børgesen
20.   _Antithamnion antillarum_ Børgesen
21.   _Antithamnion butleriae_ Collins
22.   _Asparagopsis taxiformis_ (Delile) Collins and Harvey
            (_Falkenbergia hillebrandii_ form)
23.   _Callithamnion byssoides_ Arnott
24.   _Centroceras clavulatum_ (C. Agardh) Montagne
25.   _Ceramiella jolyi_ Díaz-Piferrer
26.   _Ceramium cruciatum_ Collins and Hervey
27.   _Ceramium fastigiatum_ (Roth) Harvey
28.   _Ceramium strictum_ (Kützing) Harvey
29.   _Ceramium subtile_ J. Agardh
30.   _Chondria littoralis_ Harvey

TABLE 4 cont.

31. <u>Digenia simplex</u> (Wulfen) C.Agardh
32. <u>Diplothamnion jolyi</u> Van den Hoek
33. <u>Fosliella farinosa</u> (Lamouroux) Howe
34. <u>Gelidium pusillum</u> (Stackhouse) LeJolis
35. <u>Griffithsia globulifera</u> Harvey
36. <u>Griffithsia</u> sp.
37. <u>Herposiphonia secunda</u> (C. Agardh) Ambronn
38. <u>Heterosiphonia wurdemanni</u> (Bailey <u>ex</u> Harvey) Falkenberg
39. <u>Hypnea cervicornis</u> J. Agardh
40. <u>Jania adherens</u> Lamouroux
41. <u>Jania capillacea</u> Harvey
42. <u>Laurencia chondrioides</u> Børgesen
43. <u>Peyssonnelia simulans</u> Weber-van Bosse
44. <u>Polysiphonia atlantica</u> Kapraun and Norris
45. <u>Polysiphonia denudata</u> (Dillwyn) Greville <u>ex</u> Harvey
46. <u>Polysiphonia ferulacea</u> Suhr
47. <u>Polysiphonia havanensis</u> Montagne
48. <u>Polysiphonia howei</u> Hollenberg
49. <u>Polysiphonia scopulorum</u> v. villum (J. Agardh) Hollenberg
50. <u>Polysiphonia subtilissima</u> Montagne
51. <u>Spermothamnion investiens</u> (Crouan) Vickers
52. <u>Wrangelia argus</u> Montagne
53. <u>Wurdemannia miniata</u> (Draparnaud) Feldmann and Hamel

TABLE 5

Schoener's (1968) similarity indices among and between caged and uncaged reefs. The reef letter and type that each sample number represents is given in Appendix I. Sets were randomly paired.

Uncaged Reefs		Caged Reefs		Between Treatments	
Sample # Compared	Similarity Index	Sample # Compared	Similarity Index	Sample # Compared	Similarity Index
1,11	0.46	26,35	0.29	1,38	0.20
2,25	0.46	27,37	0.52	2,41	0.04
3,14	0.35	28,36	0.78	3,32	0.36
4,23	0.34	29,43	0.55	4,44	0.09
5,10	0.14	30,49	0.19	5,41	0.02
6,18	0.44	31,40	0.47	6,37	0.17
7,13	0.39	32,46	0.18	7,29	0.22
8,19	0.40	33,45	0.33	8,43	0.17
9,15	0.52	34,50	0.16	9,47	0.18
1,21	0.36	38,47	0.13	10,40	0.29
16,20	0.17	39,44	0.45	11,26	0.08
17,12	0.17	41,42	0.27	12,36	0.14
				13,34	0.13
				14,49	0.14
				15,28	0.05
				16,27	0.10
				17,48	0.13
				18,39	0.24
				19,45	0.07
				20,31	0.09
				21,31	0.14
				22,42	0.04
				23,33	0.09
				24,35	0.06
Mean	0.35		0.36		0.14

TABLE 6

Dominant Algal Species found on caged and uncaged reefs. The percentages given represent the proportional occurrence found in pooled data for each treatment.

Uncaged Reefs	percentage	Caged Reefs	percentage
Lobophora variegata*	25.9	Jania capillacea*	20.0
Polysiphonia ferulacea*	22.6	Antithamnion butleriae*	13.7
Laurencia chondrioides	5.2	Peyssonnelia simulans	10.4
Wurdemannia miniata*	4.8	Caulerpa mexicana*	9.5
Sphacelaria novae-hollandiae	4.6	Fosliella farinosa	5.2
Fosliella farinosa	4.1	Dictyota divaricata	5.0
Jania capillacea	3.4	Sphacelaria novae-hollandiae	4.4
Dictyota divaricata	3.4	Asparagopsis taxiformis*	4.2
Cladophoropsis membranacea	3.3	Bryopsis plumosa*	3.4
Peyssonnelia simulans	3.3	Cladophoropsis membranacea	3.3

* Indicates that there is a significant difference in the abundance of this species between the caged and uncaged reefs.

Labels on figure:
- vacuumed algae
- Nytex bag
- tygon tubing
- 3 m
- low pressure air
- 0.5 m
- 2.5 cm pvc pipe
- flow valve
- alum. template
- turf
- 5 cm
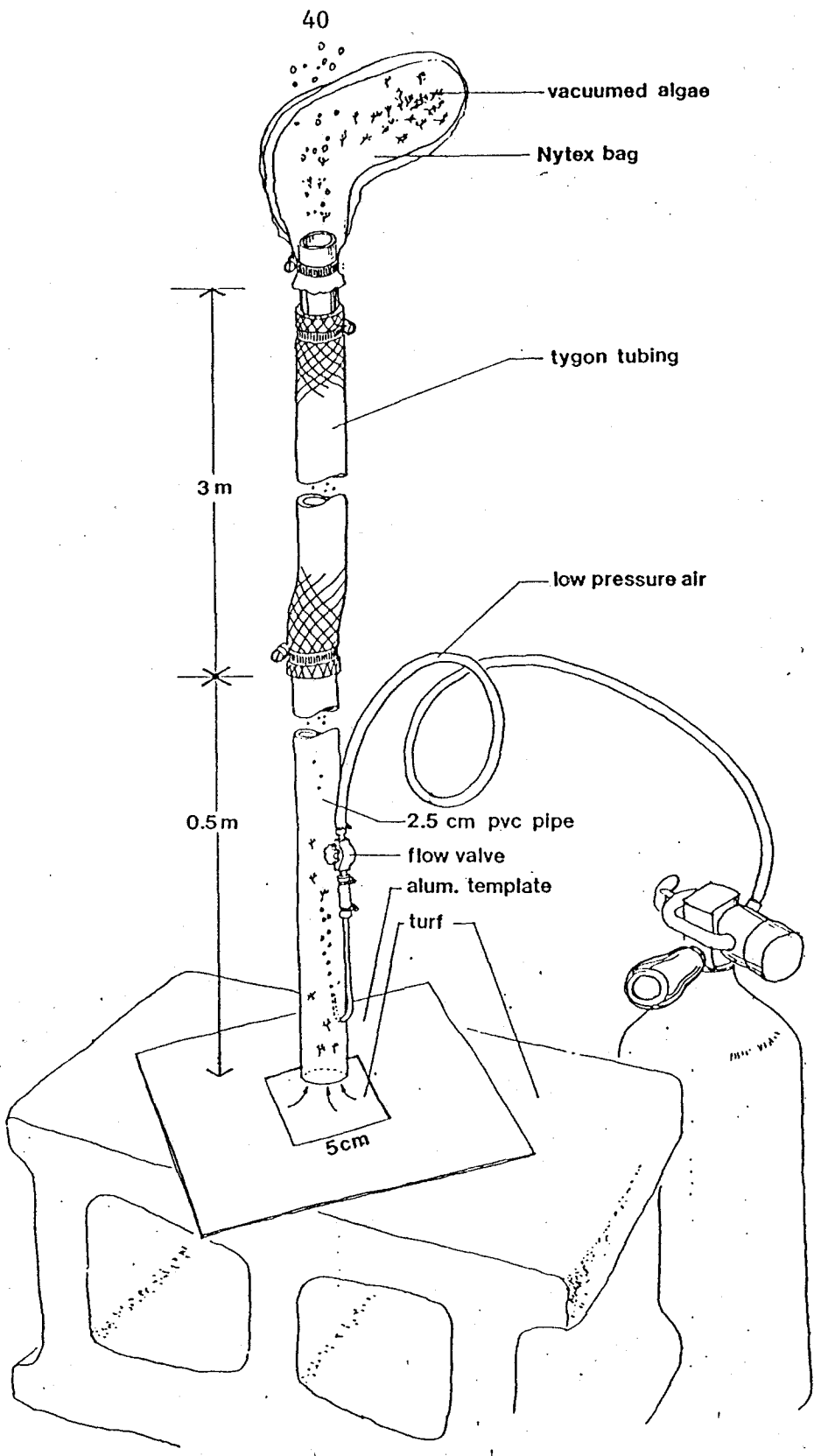
FIGURE 3   Diagram of the airlift used to collect algal samples

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APPENDIX I

Tables A, B, C, D, E, and F give the relative abundances, as expressed by a species proportional occurrence in each sample, and the species diversities, calculated using the Shannon formula for diversity (Shannon and Weaver 1949), found on caged and uncaged reefs.

TABLE A

The relative abundance and species diversity of plants found on uncaged reefs A and B.

Reef	A					B				
	1	2	3	4	5	6	7	8	9	10
Species number										
1	0.38	0.10	1.50	3.36	0.10	0.53	–	–	0.54	–
2	–	–	–	–	–	–	–	–	–	–
3	2.18	0.20	–	–	–	–	–	2.13	–	–
4	–	–	–	–	–	–	–	–	–	–
5	–	–	–	2.10	–	2.13	–	–	–	1.41
6	0.26	–	–	3.78	–	–	–	–	2.96	4.39
7	1.80	–	–	7.98	2.04	6.38	3.36	8.53	2.70	4.86
8	–	–	–	–	–	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–
11	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–
14	2.82	1.71	0.37	8.40	5.18	2.93	1.81	8.00	17.79	14.42
15	–	–	–	–	–	–	–	–	–	–
16	52.47	83.33	–	–	80.71	–	–	–	–	–
17	1.67	0.24	4.68	15.55	0.26	3.99	0.52	5.87	–	4.39
18	0.13	0.05	0.75	3.78	1.41	1.33	0.52	–	–	0.47
19	–	–	2.43	–	–	0.27	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–
21	–	–	–	–	0.26	–	–	–	–	–
22	–	–	–	–	–	–	1.29	–	–	–
23	–	–	–	–	–	–	–	3.20	–	–
24	0.71	–	–	–	–	–	–	–	–	–
25	0.26	–	–	–	–	1.06	–	–	–	–
26	–	–	–	–	–	–	–	–	1.08	1.25
27	0.45	–	–	–	–	–	–	–	2.70	–
28	0.13	–	–	.84	–	–	–	–	–	–
29	–	–	–	–	–	–	–	–	–	–
30	5.77	–	2.43	6.72	–	–	–	–	–	–
31	–	–	–	1.26	1.36	–	7.49	–	–	2.04
32	5.45	0.88	3.00	5.04	0.89	1.6	–	–	–	–
33	–	–	4.68	–	–	32.18	25.84	13.33	–	–
34	–	–	–	–	–	–	–	–	–	–
35	–	–	–	–	–	–	–	–	–	–
36	0.96	0.24	0.37	–	–	–	–	–	–	–
37	0.13	–	–	–	–	–	–	–	–	7.99
38	4.75	–	2.06	2.94	0.42	–	–	–	2.70	0.78
39	–	–	–	–	–	–	–	–	–	5.96

TABLE A cont.

	A					B				
	1	2	3	4	5	6	7	8	9	10
40	–	–	–	–	–	–	–	–	–	–
41	3.59	0.54	11.05	4.20	1.20	–	6.98	5.07	32.61	4.08
42	–	1.32	2.81	10.08	0.58	11.17	11.37	13.60	5.12	5.96
43	–	–	47.57	–	–	–	5.43	–	–	–
44	0.38	–	–	–	0.31	–	–	–	–	–
45	–	1.46	0.75	–	–	1.06	17.83	–	–	–
46	–	7.95	6.93	12.61	1.78	30.05	17.57	21.87	21.02	38.09
47	–	–	–	–	–	–	–	–	–	–
48	0.32	–	–	–	–	–	–	–	–	–
49	0.90	0.34	5.99	9.24	1.83	–	–	10.13	–	2.19
50	13.28	0.93	2.43	–	–	–	–	–	–	1.72
51	0.32	–	0.19	–	–	–	–	–	–	–
52	–	–	–	–	0.78	–	–	–	–	–
53	0.90	0.73	–	2.10	0.89	5.32	–	8.27	10.78	–
Species diversity	1.84	0.76	1.98	2.60	0.95	1.88	2.05	2.23	1.87	2.15

TABLE B

The relative abundance and species diversity of plants found on uncaged reefs C and D.

Reef	C					D				
	11	12	13	14	15	16	17	18	19	20
Species number										
1	1.38	0.48	1.12	–	1.07	1.13	–	0.53	0.80	0.17
2	–	–	–	–	–	–	–	–	–	–
3	–	–	–	1.24	–	–	–	–	–	–
4	–	–	–	–	–	–	–	–	–	–
5	2.76	–	–	–	2.59	–	1.51	–	–	–
6	3.21	3.84	1.68	–	3.05	2.27	–	1.77	3.03	0.34
7	3.90	7.67	9.68	3.23	3.96	2.27	–	–	3.50	0.76
8	–	–	–	–	–	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	0.16	1.34
11	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	4.06	5.57	–
15	–	–	–	–	–	–	–	–	–	–
16	39.27	–	–	45.52	18.45	–	59.79	28.45	–	66.89
17	5.28	4.08	9.68	4.23	3.51	7.08	–	6.18	13.38	2.35
18	2.64	7.91	1.86	–	0.76	0.57	1.60	1.77	3.50	0.34
19	2.64	8.39	0.93	–	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–
21	–	–	–	–	–	–	–	–	–	–
22	–	–	–	–	–	–	–	–	–	–
23	–	–	–	–	–	–	–	–	–	–
24	–	–	–	–	–	–	–	–	–	–
25	–	–	–	–	–	–	–	–	1.11	–
26	–	–	–	–	–	1.70	–	–	–	–
27	0.34	2.40	–	1.00	–	3.40	–	–	1.11	–
28	–	–	–	1.00	–	–	–	0.88	–	–
29	–	–	–	–	–	–	–	–	–	–
30	–	–	–	–	–	4.25	0.36	–	15.61	–
31	0.57	–	–	–	1.07	7.37	0.18	1.41	–	–
32	–	–	–	–	–	–	–	6.36	3.66	–
33	–	–	10.61	–	10.82	–	–	2.83	–	–
34	–	–	–	–	–	–	–	–	–	–
35	–	–	–	–	–	–	0.71	–	2.23	–
36	–	–	1.30	–	–	–	–	–	–	–
37	–	–	0.74	–	–	–	–	–	–	–
38	–	–	–	–	–	–	–	–	–	–
39	1.61	–	–	–	–	–	10.14	–	4.78	1.26

TABLE B cont.

	C						D			
	11	12	13	14	15	16	17	18	19	20
40	–	–	–	–	–	–	–	–	–	–
41	0.92	1.44	–	–	0.46	–	0.18	2.47	2.23	2.94
42	0.46	3.12	6.52	6.22	1.83	27.76	1.25	1.06	–	1.26
43	–	–	–	20.90	–	–	9.16	–	–	–
44	–	–	–	–	–	–	–	–	–	–
45	–	–	–	–	2.13	–	–	–	–	–
46	19.86	18.47	41.53	15.42	46.04	42.21	10.85	34.81	38.54	11.85
47	–	–	–	–	–	–	–	–	–	–
48	–	–	–	–	–	–	–	–	–	–
49	–	–	–	–	3.51	–	–	7.42	0.80	5.63
50	–	–	–	–	–	–	–	–	–	1.76
51	–	0.24	–	–	–	–	–	–	–	0.92
52	–	–	–	–	–	–	–	–	–	–
53	15.15	41.97	14.34	1.24	0.76	–	4.27	–	–	2.18
Species diversity	1.90	1.84	1.84	1.59	1.82	1.67	1.40	1.91	2.05	1.33

TABLE C

The relative abundance and species diversity of plants found on uncaged reef E.

Reef	E				
	21	22	23	24	25
Species number					
1	1.27	0.96	2.19	0.07	0.70
2	–	–	–	–	–
3	7.19	3.65	–	–	–
4	–	–	–	–	–
5	1.27	1.92	0.26	–	1.05
6	–	5.95	5.24	0.55	5.34
7	3.17	–	1.92	–	5.51
8	–	–	–	–	–
9	–	2.69	–	–	–
10	–	2.88	0.61	0.34	11.90
11	–	–	–	–	–
12	–	–	–	–	–
13	–	–	–	–	–
14	5.29	6.91	0.17	–	–
15	0.21	–	–	–	–
16	–	–	50.44	87.66	34.73
17	–	13.63	–	1.30	6.56
18	4.02	6.53	4.11	0.55	1.84
19	–	1.34	5.42	–	1.31
20	–	–	–	–	–
21	–	–	–	–	–
22	–	1.34	–	0.07	–
23	–	–	–	–	–
24	–	–	–	–	–
25	1.69	–	–	–	–
26	–	0.38	–	–	–
27	–	–	0.09	0.20	0.09
28	–	–	–	–	–
29	–	–	–	–	–
30	0.42	0.77	–	–	0.35
31	–	–	–	1.16	–
32	–	0.58	1.14	–	0.87
33	–	–	–	2.52	–
34	–	3.26	–	–	–
35	–	0.58	–	–	–
36	–	–	–	–	–
37	–	–	–	–	–
38	–	–	–	–	–
39	2.33	–	2.97	1.36	0.96

TABLE C cont.

	E				
	21	22	23	24	25
40	–	–	–	–	–
41	1.48	–	2.01	0.20	2.01
42	5.92	–	11.28	–	–
43	–	–	–	–	–
44	–	0.38	0.44	–	0.35
45	–	–	–	–	0.79
46	49.26	43.95	7.26	2.66	24.76
47	–	–	–	–	–
48	–	–	–	–	–
49	5.50	–	–	–	–
50	5.50	–	–	–	–
51	0.63	–	3.32	–	0.61
52	–	–	–	–	–
53	4.86	2.30	1.14	1.36	0.26
Species diversity	1.96	2.06	1.87	0.64	1.97

TABLE D

The relative abundance and species diversity of plants found on caged reefs F and G.

Reef	F					G				
	26	27	28	29	30	31	32	33	34	35
Species number										
1	0.43	0.91	0.09	1.86	0.51	3.87	0.39	2.64	4.08	2.42
2	–	–	–	–	–	–	–	–	–	–
3	5.39	3.81	4.19	0.99	0.51	–	0.39	–	–	6.58
4	–	–	–	–	–	–	–	–	–	–
5	–	–	–	–	–	–	–	–	–	–
6	0.86	8.52	1.11	0.25	–	5.51	7.14	0.88	–	–
7	0.86	1.52	0.94	7.19	4.42	2.83	5.21	8.80	11.30	10.47
8	–	–	–	–	0.42	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–
11	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–
14	13.79	30.59	0.60	0.50	0.93	13.99	4.44	4.99	25.10	6.31
15	–	–	–	–	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–
17	1.94	1.07	0.26	1.49	1.19	0.89	5.41	5.28	0.21	1.07
18	0.65	–	0.09	3.47	0.51	2.08	3.67	–	1.67	1.07
19	–	–	–	–	–	6.55	–	–	–	0.27
20	–	0.46	–	–	–	–	–	–	–	–
21	1.29	3.50	5.81	39.41	59.13	6.10	0.39	4.69	–	2.82
22	3.02	3.65	4.44	2.60	5.27	2.08	5.98	9.68	10.77	4.03
23	–	–	–	–	–	–	–	–	0.21	–
24	–	–	–	–	–	–	–	–	–	–
25	–	–	–	0.37	–	–	–	–	–	–
26	–	–	–	–	0.34	–	–	0.29	–	–
27	–	–	0.17	0.62	–	0.89	1.54	–	0.21	0.27
28	–	–	–	–	–	–	–	–	–	0.40
29	–	–	–	–	–	–	–	–	–	–
30	3.23	1.37	–	2.48	0.51	–	–	–	–	–
31	–	–	–	–	2.89	–	–	–	–	–
32	1.29	2.89	0.77	0.25	–	–	0.19	–	–	3.36
33	–	0.30	–	0.62	–	8.33	–	2.35	–	20.13
34	–	–	–	–	–	–	–	–	–	–
35	–	–	–	–	–	–	–	–	–	–
36	–	–	–	–	–	–	–	–	–	–
37	–	–	–	0.62	–	–	–	–	–	–
38	–	1.83	2.05	0.99	–	1.64	2.51	1.47	–	1.34
39	20.91	–	–	–	1.95	0.89	–	–	2.62	–

TABLE D cont.

	F					G				
	26	27	28	29	30	31	32	33	34	35
40	–	–	–	–	–	–	–	–	–	–
41	8.19	35.31	18.63	25.40	11.72	41.67	41.89	53.08	41.11	36.91
42	2.59	1.98	1.37	1.73	8.41	–	2.51	0.59	0.42	–
43	33.41	–	54.44	–	–	–	13.32	–	–	–
44	–	0.15	0.34	1.73	–	–	3.28	0.59	–	–
45	1.51	–	–	4.71	–	–	–	–	–	–
46	–	0.61	0.77	1.36	0.17	2.23	–	–	–	1.34
47	–	–	–	–	0.34	–	–	–	–	–
48	–	–	–	–	–	–	–	–	–	–
49	–	0.61	–	0.37	0.08	–	–	3.52	2.20	1.21
50	–	–	1.11	–	–	–	0.58	–	–	–
51	–	0.61	0.26	0.99	–	0.45	1.16	0.88	0.10	–
52	–	–	–	–	–	–	–	–	–	–
53	0.65	0.30	2.56	–	0.68	–	–	0.29	–	–
Species diversity	2.06	1.93	1.64	2.02	1.56	2.05	2.08	1.77	1.65	2.03

TABLE E

The relative abundance and species diversity of plants found on caged reefs H and I.

Reef	H					I				
	36	37	38	39	40	41	42	43	44	45
Species number										
1	5.85	1.27	–	0.79	1.32	–	0.24	0.63	0.04	0.09
2	–	–	–	–	–	0.52	–	–	–	–
3	3.27	1.27	9.79	7.41	3.21	2.19	–	5.29	0.42	1.27
4	–	8.89	37.01	39.42	13.99	2.99	34.82	35.83	32.97	35.26
5	–	0.76	0.25	1.19	2.30	0.46	–	–	–	–
6	–	5.46	–	1.59	4.53	0.46	–	–	–	–
7	2.31	8.64	4.39	–	1.40	0.86	–	8.98	0.76	2.72
8	–	–	–	–	–	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–
11	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	14.16	–	–	–	–	–
14	0.82	0.13	2.63	–	14.81	5.53	–	–	–	0.85
15	–	–	–	–	–	–	–	–	–	–
16	–	–	6.27	12.70	–	–	–	–	–	–
17	4.90	5.46	0.88	2.25	0.66	1.32	–	0.73	1.22	0.66
18	0.82	1.52	1.76	1.98	1.15	0.06	0.05	0.24	–	0.09
19	–	–	–	–	0.16	–	–	–	–	–
20	–	–	–	–	–	–	–	–	–	–
21	3.40	–	6.15	–	–	70.01	15.67	26.21	51.96	33.76
22	9.39	13.34	6.78	8.60	14.81	–	–	–	–	0.38
23	–	–	–	0.66	–	–	–	–	–	–
24	–	–	–	–	–	–	–	–	–	–
25	–	–	–	–	–	–	–	0.05	–	–
26	–	–	–	–	–	–	–	–	–	–
27	0.95	–	0.75	0.40	0.25	–	–	–	–	–
28	–	–	–	–	1.98	–	–	–	–	0.14
29	–	–	–	–	–	–	–	–	0.21	–
30	–	–	0.75	–	–	0.35	1.18	–	–	–
31	–	–	–	–	–	–	–	–	–	–
32	–	–	1.00	–	–	–	0.28	–	–	–
33	–	0.25	1.63	2.25	1.81	–	39.20	–	–	–
34	–	–	–	–	–	–	–	–	–	–
35	–	–	–	–	1.15	–	–	–	0.46	–
36	–	–	–	–	–	–	–	–	–	–
37	–	–	–	–	–	–	–	–	–	–
38	1.50	–	–	0.40	2.47	–	–	–	–	–
39	–	–	–	–	0.91	–	–	0.83	–	–

TABLE E cont.

Species number	H					I				
	36	37	38	39	40	41	42	43	44	45
40	–	–	–	–	–	–	–	2.57	–	–
41	17.14	35.96	17.57	19.58	17.28	12.15	5.98	17.52	9.35	23.76
42	3.27	4.07	–	–	–	–	–	–	–	–
43	44.49	12.71	–	–	–	–	–	–	–	0.89
44	–	–	0.88	–	0.49	–	–	0.29	–	–
45	–	–	–	–	0.99	–	–	–	–	–
46	0.27	–	1.13	0.79	0.16	0.35	1.08	0.34	0.80	0.14
47	–	–	–	–	–	–	–	–	–	–
48	–	–	–	–	–	–	–	–	–	–
49	0.68	0.25	0.38	–	–	–	0.09	–	–	–
50	–	–	–	–	–	0.35	–	–	–	–
51	0.95	–	–	–	–	–	–	0.49	–	–
52	–	–	–	–	–	–	–	–	–	–
53	–	–	–	–	–	2.42	1.41	–	1.81	–
Species diversity	1.90	2.02	2.09	1.87	2.40	1.18	1.40	1.68	1.19	1.40

TABLE F

The relative abundance and species diversity of plants found on caged reef J.

Reef			J		
	46	47	48	49	50
Species number					
1	0.24	–	–	2.33	–
2	–	–	–	–	–
3	16.14	0.62	4.19	2.33	6.70
4	–	–	–	–	–
5	–	–	0.24	0.26	–
6	9.05	9.54	4.31	8.53	4.07
7	–	–	–	–	–
8	–	–	–	–	–
9	–	–	–	–	–
10	–	–	7.78	–	–
11	–	0.21	–	–	6.78
12	–	–	–	–	33.89
13	–	–	–	–	–
14	–	–	–	–	–
15	–	1.04	–	–	1.20
16	–	–	–	–	–
17	10.51	26.76	3.71	27.39	4.78
18	–	0.41	1.08	5.17	0.32
19	–	1.24	7.90	–	–
20	–	–	–	–	–
21	–	3.53	0.84	5.43	2.71
22	–	0.41	–	–	0.16
23	–	–	–	–	–
24	–	–	–	–	–
25	–	–	–	–	–
26	–	–	–	–	–
27	0.24	1.04	0.36	0.78	–
28	1.47	–	–	–	–
29	–	1.24	–	1.29	0.16
30	52.57	1.66	–	–	0.64
31	–	–	–	–	–
32	2.93	–	3.35	10.34	2.31
33	–	31.74	–	20.16	–
34	–	–	–	–	–
35	–	–	–	–	–
36	–	–	–	–	–
37	–	–	–	–	–
38	–	–	–	–	–
39	–	–	–	–	–

TABLE F cont.

	J				
	46	47	48	49	50
Species number					
40	–	–	–	–	–
41	–	3.32	1.20	3.62	1.59
42	–	–	–	6.46	0.88
43	3.67	5.60	62.16	–	30.30
44	–	–	–	–	–
45	–	–	–	–	–
46	0.49	1.66	2.51	–	2.31
47	–	–	–	–	–
48	–	–	–	–	–
49	–	–	–	–	–
50	–	–	–	–	–
51	2.69	1.45	0.36	2.58	0.32
52	–	–	–	–	–
53	–	8.51	–	3.36	0.88
Species diversity	1.53	2.03	1.49	2.22	1.93