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REPORT

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Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize

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Abstract Macroalgae were experimentally reduced by approximately 2.5 kg/m^2 on eight similar-sized patch reefs of Glovers Reef Atoll, Belize, in September 1998. Four of these reefs were in a protected "no-take" zone and four were in a "general use" fishing zone. Eight adjacent reefs (four in each management zone) were also studied as unmanipulated controls to determine the interactive effect of algal reduction and fisheries management on algae, coral, fish, and rates of herbivory. The 16 reefs were sampled five times for 1 year after the manipulation. We found that the no-fishing zone had greater population densities for 13 of 30 species of fish, including four herbivorous species, but lower herbivory levels by sea urchins. However, there was lower stony coral cover and higher macroalgal cover in the "no-take" zone, both prior to and after the experiment. There were no significant effects of management on the percent cover of fleshy macroalgae. The algal reduction resulted in an increase in six fish species, including four herbivores and two which feed on invertebrates. One species, *Lutjanus griseus*, declined in experimental reefs. Macroalgal biomass quickly recovered from the reduction in both management areas within a few months, and by species-level community measures within 1 year, while stony coral was reduced in all treatments. Coral bleaching and Hurricane Mitch disturbed the site at the beginning of the study period and may explain the loss of stony coral and rapid increase in erect algae. We suggest that reducing macroalgae, as a technique to restore turf and encrusting coralline algae and stony corals, may work best after reefs have been fully protected from fishing for a period long enough to allow herbivorous fish to recover (i.e. >5 years). Further ecological studies on Glovers Reef are required to understand the shift from coral to algal dominance that has occurred on this reef in the last 25 years.

Key words Algae · Coral reef fishes · Disturbance · Fishing · Herbivory · Marine protected areas

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Introduction

Caribbean coral reefs have experienced a number of ecological disturbances over the past two decades that have resulted in reefs being dominated by erect fleshy algae (Carpenter 1990; Hughes 1994; Ogden and Ogden 1994; Lapointe et al. 1990; Shulman and Robertson 1997; Szmant 1997; McClanahan and Muthiga 1998; McClanahan et al. 1999a). This change is frequently associated with the death of corals through diseases, bleaching or other disturbances (Aronson and Precht 1997; McField 1999) or through competition with erect algae that has increased with reduced herbivory (Carpenter 1990; Hughes 1994; McClanahan et al. 1996) or increased nutrient loads (Smith et al. 1981; Lapointe 1999). Changes appear to be persistent such that stony coral populations, particularly in the Caribbean, show little sign of recovery after disturbances and the establishment of erect algae (Connell 1997). The consequences of this change to algal-dominated reefs include: reduced recruitment of corals (Hughes and Tanner 2000), reduced abundance of herbivorous fishes and their rates of herbivory (McClanahan et al. 1999b, 2000), reduced abundance of coral-eating fishes, and variable responses for predators of other invertebrates (such as amphipods and crabs) attached to erect algae (Wahl and Hay 1995; Stachowicz and Hay 1996; McClanahan et al. 1999b). The potential to experimentally shift reef ecology back to coral dominance has only recently been explored (McClanahan et al. 1999b, 2000).

Feasible methods for controlling erect algae on a large scale include increasing the levels of herbivory on coral reefs and reducing nutrient run-off or waste discharges (Smith et al. 1981; Lapointe et al. 1990). On a smaller scale, algae can be physically reduced for experimental purposes or in order to increase survival of coral on small highly visited reef sites (Tanner 1995; McClanahan et al. 1999b, 2000). One possible method to increase herbivory is through the establishment of marine protected areas (MPAs) that include "no-take" zones that may result in increases in grazing herbivores such as surgeon and parrotfish (McClanahan et al. 1994; Roberts 1995). Erect algae can, however, dominate reefs in MPAs that protect herbivorous fish and, in these cases, direct intervention may be required to prevent a decline in corals and associated fishes (Tanner 1995; McClanahan et al. 1999b, 2000).

This study explores the dual and interactive role of MPAs and direct macroalgal reduction on patch reefs of Glovers Reef, Belize, to determine the responses of fish, herbivory, and benthic organisms to both of these potential management practices. The patch reefs in this atoll have changed over the past 30 years, with the coral:algal ratio changing from 4 to 0.25 between 1970 and 1996 (McClanahan and Muthiga 1998). One of the potential driving forces of this shift is reduced fish abundance and herbivory. Thus, this experiment was designed to test the hypothesis that reefs in the unfished zone would respond differently from reefs in the fished zone to the physical reduction of algae. Specific hypotheses were that the experimental reefs subjected to algal reduction would over time experience: (1) increased coral cover, (2) a shift in algal community composition to "turf" algal taxa that are more palatable to herbivores, (3) increased fish abundance and herbivory (McClanahan et al. 1999b, 2000), and (4) a subsequent reduction of fleshy algae, particularly the genera *Sargassum*, *Turbinaria* and *Lobophora* which were the most prevalent erect algae on these patch reefs (McClanahan and Muthiga 1998). These changes were hypothesized to occur in experimental versus control plots, and to a greater extent within the Wilderness Zone versus the General Use Zone of the Glovers Reef Marine Reserve.

Materials and methods

Study sites and experimental design

This study was undertaken in Glovers Reef, a coral-rimmed atoll 32 km long and 12 km wide located approximately 45 km off the coast of mainland Belize. The atoll was gazetted as a Marine Reserve in 1993 and intermittent management has been in effect since 1995. All forms of resource extraction are prohibited in the small Wilderness Zone, while only subsistence fishing for about 20 residents is permitted in the larger Conservation Zone. The remaining 75% of the atoll is zoned as General Use, with additional restrictions on fishing (Coastal Zone Management Authority and Institute 1999). Nearly 850 patch reefs exist in this atoll's lagoon and most of them have become dominated by erect algae over the past 20 years (see map in McClanahan and Muthiga 1998). Erect macroalgae, the focus of the reduction, largely included brown algae in the genera *Turbinaria*, *Sargassum* and *Lobophora* (McClanahan and Muthiga 1998), but also included other less common genera of brown, red and green algae (Appendix 1). The colonization of erect algae has blurred previous zones within the atoll based on coral species dominance (Wallace 1975; McClanahan and Muthiga 1998).

Sixteen patch reefs of moderate size (average ~1,000 m^2) and depth (maximum depth to the reef top was 1–2 m) were haphazardly selected in September 1998. Selected reefs were on the eastern side of the atoll among the first patch reefs encountered after the sand apron on the leeward side of the reef flat rim. Prevailing winds and currents and direction of approach of Hurricane Mitch were from the northeast, seasonally varying between north and east. Temperature measurements and current observations suggest that the General Use Zone is better mixed and cooler than the Wilderness Zone (M. McField, unpublished data).

Eight patch reefs were selected within both the Wilderness and General Use Zones, with four patch reefs in each zone subjected to the algal reduction treatment and four control patch reefs in each zone. Baseline data were collected on all patch reefs approximately 1 week prior to the algal reduction (September 1998). The next sampling period occurred immediately after the reduction (October 1998) and included only experimental patches, as controls were assumed to remain stable over this 2-week interval (McClanahan et al. 2000). The third sampling occurred in early December 1998, about 8 weeks after the reduction and 5 weeks after Hurricane Mitch battered the coast of Honduras approximately 100 km to the south. The remaining samples were taken in early April 1999 and finally in September 1999, 1 year after the experiment began. The study was terminated after 1 year as algae and fish abundance and species composition had, by then, returned to the pre-removal levels (see Results).

Erect macroalgae was cleared in two steps. First, the large fronds were clipped with hedge trimmers, and the remaining holdfasts were then cleared using wire brushes. Care was taken to minimize the damage to corals and other benthic invertebrates. An average of ~28 person-hours was allotted to the reduction for each patch reef. The total algae cleared per patch reef was estimated from algal biomass samples taken before and after the removal and was equivalent to about 1–2 tons per patch reef.

Benthic cover and algal biomass

Benthic cover on each patch reef was assessed by the line intercept method for three 10-m line transects per patch reef. Transects were laid parallel to the patch reef's windward northeast edge along three locations: on the edge (the transition from the sand to patch reef), shoulder (shallow windward edge) and center. Substrate cover was recorded by species for stony corals (Humann 1993), by genus for fleshy and calcareous algae (Littler et al. 1989), and by gross functional groups for encrusting coralline algae, branching coralline algae, algal turf, seagrass, sand, sponge, soft coral, zoo-anthids and "microalgae" (cyanobacteria and diatoms). All benthic organisms 3 cm or larger directly under the draped line were measured and recorded. An algal species list is provided in Appendix 1.

To estimate the weight of erect algae, a 25 × 25 cm quadrat was randomly placed on a point along each transect and cleared of erect algae. All algae other than benthic-attached turf and encrusting coralline algae was collected in plastic bags. The algal samples (three per patch reef) were individually weighed with a triple-beam balance and then pooled per patch reef. Pooled algae samples were sorted according to the functional groups: brown fleshy, green fleshy, green calcareous, red fleshy, red coralline and other (seagrass), and each group was weighed separately. Initially half of the baseline algal samples were air-dried for 24 h before weighing. However, due to noted differential desiccation rates of various genera, we used wet weights for the remainder of the study. A representative 100-g sample of each functional group was weighed wet and after 24 h air-dried. The percent reduction for air drying was calculated for each functional group and applied to the air-dried samples as a conversion factor to adjust these eight original samples to wet weight.

Fish population estimates

The fish fauna of each patch reef was sampled once before and four times after the algal reduction. Visual counts were carried out using the discrete group sampling (DGS) method (Greene and Alevizon 1989; McClanahan 1994) where a limited number of species are sampled during a single sampling period. The shallowness and small size of patch reefs did not permit the use of standard belt transects and, therefore, a 5-min search interval was used to sample fish. During the total 35-min sampling period the investigator swam haphazardly over each patch reef, and recorded the number of species and individuals in each group for the 5-min interval. Individuals less than 3 cm were not counted. Species were separated into discrete groups based on their taxonomy and position in the reef or water column. Each of the following seven discrete groups were sampled separately: group 1 Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes); group 2 Acanthuridae (surgeonfishes); group 3 Haemulidae (grunts), Sparidae (porgies) and Lutjanidae (snappers); group 4 Scaridae (parrotfishes); group 5 Labridae (wrasses); group 6 Spyringnea, Balistidae, trumpetfish, Carangidae and *Chromis*; group 7 Serranidae (groupers) and territorial pomacentrids (damselfishes). During the first two sampling periods, all surgeonfish and parrotfish were assigned to one of eight 5-cm size class intervals. A prior study (McClanahan et al. 2000) presents a partial analysis of these and additional behavioral data based on only the before and first after removal period. This study presents the results of the longer sampling period and additional data, such as body sizes, not previously reported.

Herbivory assays

Herbivory on patch reefs was studied using assays of two plant species – the seagrass *Thalassia testudinum* and the brown alga *Lobophora variegata*. Seagrass blade tips and algae were collected and visually inspected to avoid pre-bitten or epiphyte-covered samples. Seagrass blades were cut to a standard length of 9 cm. Seagrass and algae clippings were held by weighted clothespins attached at approximately 2-m intervals to thin nylon lines (Hay 1981; McClanahan et al. 1994). Nine clippings of each species were positioned in each zone – edge, shoulder and center – for a total of 27 clippings per species per reef. Assays were left for 24 h before recovering for examination. Divers recorded whether or not the samples had been bitten, the amount of seagrass bitten (to the closest 0.5 cm), and based on bite scar characteristics which herbivores were responsible for the bites: fish or sea urchins (Hay 1981; Hay et al. 1983; McClanahan et al. 1994). This herbivory assay method is biased towards macroalgal feeding species and underestimates herbivory by some groups such as scrapping and excavating parrotfish and sea urchins and does not measure herbivory by some sucking and scrapping species such as most grazing surgeonfish (McClanahan et al. 1994).

Data analysis

The percent cover of benthic taxa for each patch reef was calculated from the pooled cover (in centimeters) of the three transects. Thus, the total area sampled per patch reef was 30 m, stratified into the three previously identified reef zones. The effects of the algal reduction were tested with three-way fixed factor ANOVA. There were four replicate patch reefs in each of the treatments (algal reduction and fisheries protection) with time (five sampling periods) as the third factor. Algal biomass samples were similarly pooled by patch reef, then converted to a meter-squared basis, and tested with the same procedure. Each benthic category was tested for normality and transformed as necessary prior to analysis of variance (Tables 1, 2 and 3) using JUMP 3.0.2 statistical software (Sall and Lehman 1996). Multidimensional scaling plots were created from square-root-transformed benthic community data (percent cover) using PRIMER ecological statistics as described in Clarke and Ainsworth (1993).

The effects of the algal reduction on the abundance of fish families, functional groups and individual species over time were examined with a three-way fixed factor ANOVA using Statistica 4.0 software package. The average of two to four repeated surveys was used in the analyses. Where necessary, fish abundance was $\log_{10}(X+1)$ transformed to meet the assumption of homogenous variances (Cochran's $C < 0.05$). Abundance data presented in the tables of this paper are based on non-transformed data. Species with < 30 individual total sightings throughout the entire sampling period were excluded from the analyses. Only the abundance of one species, *Chromis viridis*, differed significantly between treatments before the removal (Tukey's Honest Significant Difference test, $P > 0.05$).

The herbivory assay data were analyzed with a three-way fixed factor ANOVA using Statistica 4.0 software package based on the pooled samples for each reef. Herbivory data were normally distributed and did not require transformations based on the Cochran's test. There were no significant differences between management and pre-reduction data, and pre- and post-reduction data were analyzed together.

Results

Benthic cover and algal biomass

The algal reduction dramatically altered the benthic community (Tables 1 and 2), with brown fleshy algae, the dominant group, reduced from approximately 22 to 4% on experimental patch reefs. After removal of the canopy algae, often ~20 cm in height, the underlying substratum was exposed, resulting in increased cover values for coral, turf and encrusting coralline algae. The initial increase in turf quickly returned to baseline levels and stony coral subsequently declined in percent cover, due to a recovery of fleshy algae (Fig. 1). By the December 1998 sampling, brown fleshy algae had returned to 29% cover on the experimental reefs, although it increased from 24 to 40% cover on control reefs over this same time period. Brown fleshy algae continued to increase throughout the experiment and by September 1999 the experimental reefs had 33% cover versus 31% cover on control patch reefs. The immediate effect of the reduction was significant for turf, brown fleshy algae, red fleshy algae, branching coralline algae and sponges (Tables 1 and 2). Similarly, the effects of time were significant for all the dominant categories (groups having at least 10% initial cover), and several which had lower cover.

Table 1 Mean (SE) percent cover of community components over time, by management zones (*Ma*) (*G* General Use Zone, *W* Wilderness Zone) and treatment (*Tr*; *E* experimental reduction and *C* control patches); $n = 4$ for each mean. *Br fleshy* Brown fleshy algae; *Rd fleshy* red fleshy algae; *Gr fleshy* green fleshy algae; *Calcareous* green calcareous algae; *B coralline* branching coralline algae; *E coralline* encrusting coralline algae; *Rd coralline* red branching coralline algae; *ns* not significant

	Ma Tr	Sep-98 G	Sep-98 W	Oct-98 G	Oct-98 W	Dec-98 G	Dec-98 W	Apr-99 G	Apr-99 W	Sep-99 G	Sep-99 W
Coral	C	22.0 (1.2)	19.3 (2.3)	22.0 (1.2)	19.3 (2.3)	18.4 (3.6)	14.0 (1.5)	17.9 (0.9)	16.0 (2.7)	16.6 (1.0)	11.3 (1.7)
	E	28.7 (2.8)	20.2 (2.1)	34.4 (2.3)	26.0 (2.8)	18.9 (2.2)	17.5 (4.3)	19.4 (2.3)	13.6 (2.5)	14.7 (1.0)	9.5 (1.6)
Turf	C	14.9 (3.5)	13.1 (4.3)	14.9 (3.5)	13.1 (4.3)	12.1 (2.5)	12.4 (1.3)	19.1 (3.3)	18.7 (4.2)	11.3 (2.3)	10.8 (1.5)
	E	18.9 (1.7)	12.4 (3.0)	36.1 (2.4)	43.4 (3.6)	15.3 (2.4)	20.4 (2.9)	17.0 (1.9)	15.1 (2.5)	8.6 (2.7)	15.9 (3.6)
Br fleshy	C	22.1 (3.3)	26.1 (5.2)	22.1 (3.3)	26.1 (5.2)	32.9 (4.6)	47.4 (3.5)	30.4 (1.0)	29.7 (7.0)	33.6 (1.7)	28.5 (5.1)
	E	19.1 (2.0)	23.9 (4.0)	6.7 (1.1)	1.9 (0.7)	29.9 (2.7)	28.9 (5.7)	35.2 (2.6)	30.6 (1.4)	36.0 (1.7)	30.0 (4.0)
Rd fleshy	C	8.9 (4.1)	5.6 (3.1)	8.9 (4.1)	5.6 (3.1)	8.2 (0.7)	7.2 (3.2)	8.6 (3.4)	6.3 (1.7)	8.2 (3.2)	7.5 (1.6)
	E	2.5 (1.1)	7.9 (3.3)	0.4 (0.3)	1.7 (0.8)	4.7 (1.9)	4.8 (2.7)	3.5 (1.1)	6.8 (3.2)	4.8 (1.4)	8.7 (4.3)
Gr fleshy	C	3.4 (0.4)	5.7 (1.1)	3.4 (0.4)	5.7 (1.1)	0.9 (0.4)	1.3 (0.6)	1.8 (0.5)	1.0 (0.4)	5.6 (1.3)	7.3 (1.5)
	E	3.4 (0.8)	5.9 (0.6)	1.3 (0.3)	0.9 (0.3)	1.5 (0.1)	0.5 (0.4)	1.8 (0.7)	1.8 (0.6)	5.4 (0.8)	5.4 (0.6)
Calcareous	C	5.5 (1.4)	10.8 (3.0)	5.5 (1.4)	10.8 (3.0)	3.1 (0.6)	4.0 (1.4)	2.1 (0.1)	5.2 (1.0)	3.6 (0.3)	7.3 (1.5)
	E	5.4 (0.5)	7.8 (2.3)	1.9 (0.4)	3.2 (0.8)	4.3 (1.0)	1.8 (0.7)	3.2 (0.6)	5.6 (1.0)	4.2 (1.0)	6.1 (0.4)
E coralline	C	2.8 (0.4)	3.2 (0.3)	2.8 (0.4)	3.2 (0.3)	5.2 (1.0)	1.8 (0.5)	3.0 (0.3)	2.1 (0.6)	4.1 (0.6)	4.3 (1.1)
	E	2.9 (0.6)	3.2 (1.1)	4.0 (0.6)	8.6 (3.7)	5.6 (0.7)	5.1 (3.0)	2.8 (0.3)	4.6 (1.5)	4.7 (0.5)	4.7 (0.9)
B coralline	C	5.3 (0.7)	2.8 (0.9)	5.3 (0.7)	2.8 (0.9)	6.2 (1.4)	2.7 (1.4)	9.1 (0.9)	10.9 (1.7)	4.4 (0.2)	7.9 (0.5)
	E	3.8 (1.0)	2.8 (0.8)	1.2 (0.5)	0.8 (0.3)	2.9 (0.7)	2.8 (1.3)	7.1 (1.2)	7.6 (1.2)	5.0 (1.2)	7.2 (1.0)
Gorgonia	C	7.0 (2.0)	5.0 (2.9)	7.0 (2.0)	5.0 (2.9)	6.5 (1.0)	4.8 (2.0)	2.7 (0.8)	5.2 (2.3)	3.9 (0.7)	3.7 (0.8)
	E	7.5 (2.3)	7.1 (2.2)	8.7 (3.0)	5.6 (2.0)	7.5 (1.6)	6.2 (1.6)	2.4 (0.6)	4.7 (1.5)	4.7 (1.8)	2.7 (0.9)
Sponge	C	2.3 (1.0)	3.7 (1.3)	2.3 (1.0)	3.7 (1.3)	2.2 (0.9)	1.2 (0.3)	2.6 (1.0)	3.1 (1.1)	3.1 (0.7)	4.9 (1.7)
	E	3.3 (0.7)	4.8 (1.8)	4.4 (0.7)	5.8 (2.0)	3.6 (1.5)	2.7 (1.5)	3.5 (0.9)	4.9 (1.9)	4.4 (1.1)	6.6 (1.8)
Microalga	C	1.3 (0.2)	1.9 (0.4)	1.3 (0.2)	1.9 (0.4)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	1.4 (0.7)	2.0 (0.6)
	E	1.5 (0.6)	1.3 (0.7)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	2.5 (1.1)	0.2 (0.1)
Other	C	4.7 (1.6)	3.1 (1.0)	4.7 (1.6)	3.1 (1.0)	4.5 (2.2)	3.2 (1.9)	2.7 (0.7)	1.9 (0.7)	4.3 (0.8)	4.6 (0.9)
	E	3.2 (0.5)	2.7 (0.5)	1.0 (0.6)	2.1 (0.6)	6.1 (2.4)	9.0 (4.5)	4.1 (1.9)	4.9 (1.6)	5.1 (1.3)	3.1 (1.1)

Fishing exclusion had little significant effect on benthic cover, with the exception of calcareous algae, which had higher cover, and stony coral, which had lower cover in the Wilderness Zone. The only significant interaction was between time and treatment for several of the benthic categories, but none was greater (lower *p* values) than the single factor effects. Responses of specific taxa varied over time (Fig. 1). Even within a functional group, such as brown fleshy algae, there was considerable variation in response. *Sargassum* spp. had increased cover in December 1998 on both control and experimental patches, while other genera had moderate increases or remained fairly stable. By September 1999, *Sargassum* spp. cover was approximately the same (~6%) as the initial survey. *Turbinaria* spp. was initially the dominant brown fleshy alga (~10%) and was effectively reduced on experimental patches. It had a slower recovery than *Sargassum*, but returned to initial levels by April 1999. The effect of the reduction was significant for turf, brown fleshy algae, red fleshy algae, branching coralline algae and sponges (Tables 1 and 2). There was a significant increase in branching coralline algae over time ($P = 0.01$; Tables 1 and 2), with significantly lower abundance in experimental patches ($P = 0.0008$; Tables 1 and 2).

Classification of the full multivariate benthic community composition using multidimensional scaling based on Bray-Curtis similarity coefficients (Fig. 2) illustrates the changes that took place over time for each

Table 2 Results of three-way ANOVAs, with data transformations. *Ma* Management zones; *Tr* treatment; E *Coralline* encrusting coralline algae; *B coralline* branching coralline algae; *ns* not significant

Category	Time	Ma	Tr	Time × Ma	Time × Tr	Ma × Tr	Time × Ma × Tr	Transformation
Coral	0	0	0.0134	ns	0.0078	ns	ns	None
Turf	0.001	ns	0.0012	ns	0.0003	ns	ns	Arc
Brown fleshy	0	ns	0.0012	ns	0.0002	ns	ns	None
Red fleshy	ns	ns	0.0083	ns	ns	0.0377	ns	Square root
Green fleshy	0	ns	0.0213	0.0377	0.0022	ns	ns	Square root
Calcareous	0.0003	0.0018	0.0332	0.0381	0.0082	ns	ns	Log(X + 1)
E coralline	ns	ns	0.0216	0.0382	ns	ns	ns	Arc
B coralline	0	ns	0.0008	0.0053	ns	ns	ns	Square root
Gorgonia	ns	ns	ns	ns	ns	ns	ns	Square root
Sponge	ns	ns	0.0122	ns	ns	ns	ns	None[a]
Microalga	0	ns	0.0455	ns	0.0421	0.0403	0.0523	None[a]
Other	ns	ns	ns	ns	ns	ns	ns	None[a]

[a] No transformations produced a normal distribution, so untransformed data tested, cautionary results

Table 3 Mean (SE) algal biomass (g/m^2) data over time and multiple factor ANOVA analysis. *Ma* Management (*G* General Use Zone; *W* Wilderness Zone); *Tr* treatment (*C* control; *E* experimental); *Br fleshy* brown fleshy algae; *Rd fleshy* red fleshy algae; *Gr fleshy* green fleshy algae; *Calcareous* green calcareous algae; *Rd coralline* red branching coralline algae

Date	Ma	Tr	*n*	Br fleshy	Rd fleshy	Gr fleshy	Calcareous	Rd coralline	Other	Total
Sep-98	G	C	4	1,010.8 (426.7)	379.9 (233.4)	284.9 (128.0)	172.0 (54.1)	115.1 (64.2)	0.4 (0.4)	1963.1 (692.1)
Sep-98	G	E	4	1,147.7 (308.5)	191.6 (71.6)	88.7 (23.0)	283.3 (49.6)	71.8 (12.6)	84.0 (84.0)	1867.1 (238.8)
Sep-98	W	C	4	719.9 (223.1)	230.4 (90.4)	214.0 (179.5)	234.7 (111.8)	140.0 (59.5)	8.3 (7.1)	1547.2 (376.5)
Sep-98	W	E	4	554.9 (190.3)	171.5 (105.3)	213.4 (91.4)	562.8 (225.2)	60.9 (22.8)	12.3 (12.3)	1575.7 (243.3)
Oct-98	G	C	4	1,010.8 (426.7)	379.9 (233.4)	284.9 (128.0)	172.0 (54.1)	115.1 (64.2)	0.4 (0.4)	1963.1 (692.1)
Oct-98	G	E	4	215.7 (75.2)	43.5 (37.2)	11.6 (2.3)	162.9 (96.0)	24.3 (13.0)	26.2 (17.7)	484.1 (157.7)
Oct-98	W	C	4	719.9 (223.1)	230.4 (90.4)	214.0 (179.5)	234.7 (111.8)	140.0 (59.5)	8.3 (7.1)	1547.2 (376.5)
Oct-98	W	E	4	129.9 (35.5)	86.8 (34.8)	53.7 (43.3)	599.6 (310.1)	68.7 (23.3)	4.1 (4.1)	942.8 (280.5)
Dec-98	G	C	4	2,627.3 (390.2)	355.4 (68.5)	76.0 (50.1)	58.0 (17.5)	81.3 (31.2)	0.0 (0.0)	3,198.0 (351.6)
Dec-98	G	E	4	1,426.0 (145.8)	530.0 (80.9)	104.7 (23.7)	111.4 (43.6)	132.0 (35.3)	0.0 (0.0)	2,304.0 (252.2)
Dec-98	W	C	4	3,370.7 (340.4)	450.7 (158.3)	61.4 (23.5)	128.7 (48.9)	152.7 (112.1)	0.0 (0.0)	4,164.0 (293.9)
Dec-98	W	E	4	1,002.7 (255.3)	333.4 (170.5)	140.0 (108.6)	284.7 (131.8)	43.4 (13.3)	0.0 (0.0)	1,804.0 (517.4)
Apr-99	G	C	4	1,257.5 (533.4)	829.9 (403.7)	96.4 (47.1)	53.8 (21.5)	214.5 (86.7)	0.0 (0.0)	2,452.0 (499.5)
Apr-99	G	E	4	915.6 (106.8)	254.3 (60.3)	43.7 (12.5)	157.3 (84.7)	365.3 (93.4)	0.0 (0.0)	1,736.3 (206.4)
Apr-99	W	C	4	636.7 (219.3)	199.2 (66.5)	121.1 (55.0)	370.1 (155.5)	355.2 (110.8)	28.9 (28.9)	1,711.2 (504.4)
Apr-99	W	E	4	598.4 (183.8)	175.8 (82.9)	13.7 (7.2)	97.5 (41.6)	203.2 (63.9)	0.0 (0.0)	1,088.5 (285.2)
Sep-99	G	C	4	1,461.0 (185.5)	338.4 (130.4)	599.4 (182.2)	158.4 (81.6)	185.6 (57.3)	31.1 (18.6)	2,773.7 (385.5)
Sep-99	G	E	4	1,396.1 (383.2)	433.5 (307.8)	202.2 (88.9)	234.5 (127.4)	225.2 (128.6)	19.6 (11.4)	2,511.1 (512.8)
Sep-99	W	C	4	1,650.3 (334.6)	427.6 (202.2)	264.7 (121.0)	552.0 (107.6)	206.8 (132.2)	1.2 (1.2)	3,102.6 (596.1)
Sep-99	W	E	4	1,166.6 (148.4)	77.5 (12.8)	110.3 (55.4)	516.9 (158.5)	143.5 (82.6)	88.6 (34.9)	2,103.2 (243.2)
Multiple factor ANOVA (*P*)										
Time				0.0000	ns	0.0053	0.0327	0.0008	0.0078	0.0000
Ma				0.0547	ns	ns	0.0015	ns	ns	ns
Tr				0.0001	0.0147	0.0053	ns	ns	ns	0.0001
Time × Ma				ns	ns	ns	ns	ns	ns	ns
Ma × Tr				ns	ns	ns	ns	ns	ns	ns
Tr × Time				0.0045	ns	ns	ns	ns	ns	ns
Tr × Ma × Time				ns	ns	ns	ns	ns	0.0253	ns

of the four treatment combinations. The three main clusters separate the initial and final samples from the post-reduction samples (experimental treatments only), and the transitional third and fourth samples. Seasonality, or a response to natural disturbances, is evident in the changes experienced by control reefs. Throughout the study, the two management zones are distinguishable within the main temporal clusters. It is notable that despite the clear effect of the removal, both experimental groups re-cluster into their respective management zones by December 1999 (sample 3), although this effect is greater by April 1999 (sample 4). The September 1999 communities closely resembled the initial September 1998 communities, although the similarity was greater in controls versus experimental reefs.

There were, however, several significant changes in the benthic community between September 1998 and September 1999, based on 2-tailed t-tests of patch reef data ($n = 16$) assuming unequal variances. These net changes (% cover September 1999 to September 1998) included: increases in *Lobophora* 5.8% ($P \leq 0.003$), branching coralline 2.5% ($P \leq 0.001$), encrusting coralline 1.4% ($P \leq 0.006$), *Amphiroa* 1.6%($P \leq 0.03$), *Dictyota* 2.9% ($P \leq 0.0001$), *Padina* 1.1% ($P \leq 0.002$), fleshy algae (grouped taxa) 12.3% ($P \leq 0.008$), and decreases in stony coral 9.5% ($P \leq 0.0001$), gorgonians 2.9% ($P \leq 0.03$), and calcareous green algae 2.4% ($P \leq 0.05$).

Algal biomass sampling (three 25 × 25 cm samples/patch reef) was at a small scale and subject to greater variability than the line transect data. Despite this, there were significant effects of time ($P = 0.00001$) and treatment ($P = 0.0001$) for the total algal biomass (Table 3) with lower algal biomass in the experimental versus control reefs and increased algal biomass over time after the reduction. While benthic cover of fleshy algae was higher in the Wilderness Zone, the biomass was lower, both initially and in April 1998 (by September 1999 they were approximately equivalent). T-test analysis found a significant ($P = 0.006$) increase in total algal biomass between September 1998 (1,738.3 g/m^2, SE = 790.1) and September 1999 (2,633.7 g/m^2, SE = 896.5).

Fish population estimates

For ease of interpretation, the fish population estimates are presented as the pooled averages of the four post-removal sampling periods (Table 4). Half of the 30 species presented were significantly affected by management, and of these, 13 were more abundant in the Wilderness Zone (Table 4). Only the wrasse, *Halichoeres garnoti*, and the angelfish, *Pomacanthus arcuatus*, were more abundant in the General Use Zone. Six species increased in abundance on the experimental patch reefs. These were *Lutjanus apodus*, *Sparisoma viride*,

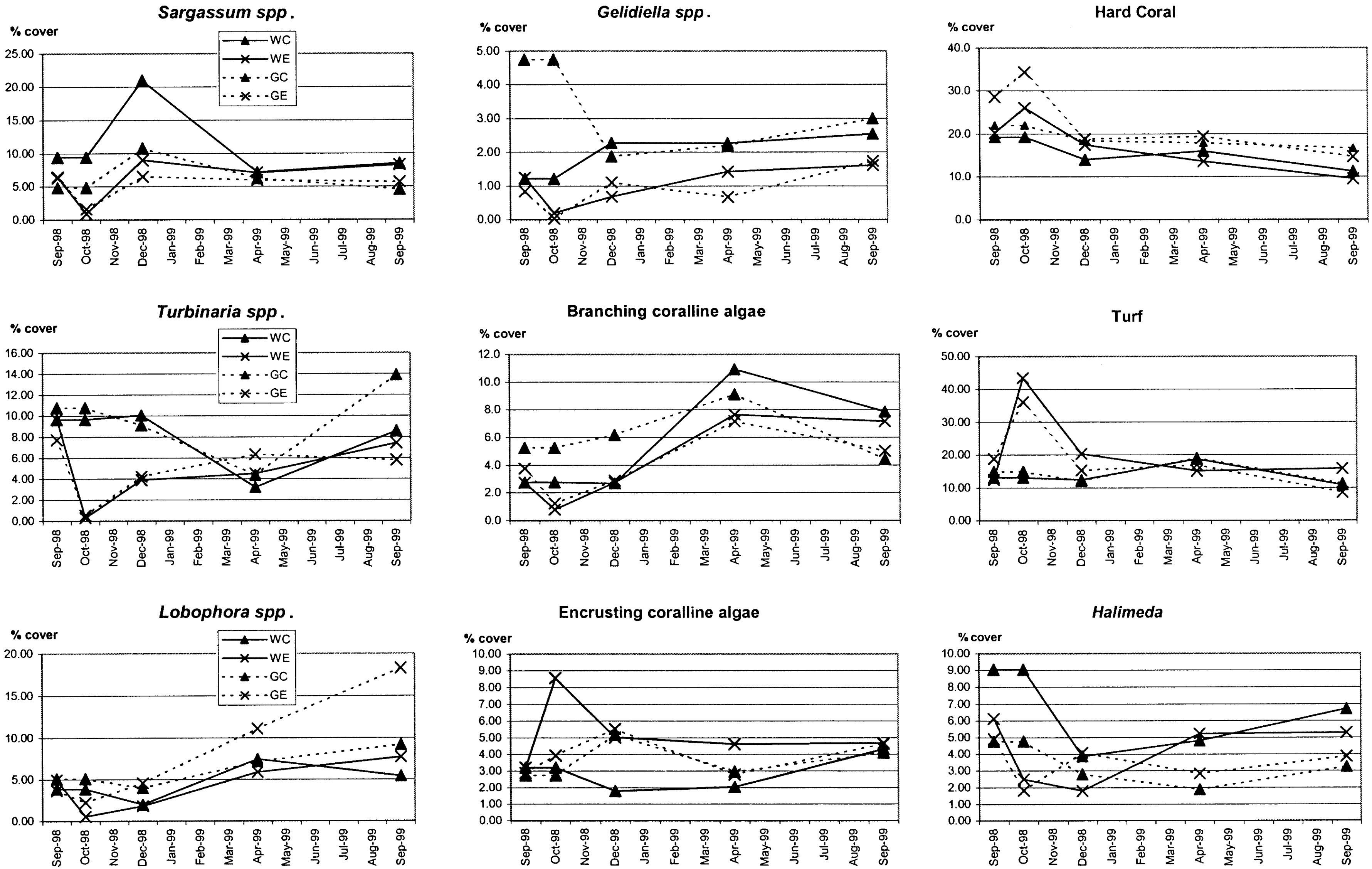

Fig. 1 Percent cover of various algal genera and stony corals by treatment over time

Acanthurus coeruleus, *A. bahianus*, *Thalassoma bifasciatum* and *Stegastes* spp. *Lutjanus griseus* increased, however, on the control patch reefs and decreased on the experimental patch reefs.

Among the species pooled into families, the Lutjanidae and Acanthuridae were both significantly more abundant in the Wilderness than General Use Zone ($P < 0.01$ and < 0.001 respectively, df = 4). Acanthuridae and Labridae both exhibited highly significant effects of treatment ($P < 0.001$) as well as time ($P < 0.001$). Interaction terms were significant for the Acanthuridae due to a larger response in the Wilderness than General Use Zone ($P < 0.05$). The Scaridae, combining all species, were not affected by any of the factors considered. However, large parrotfishes (*Sparisoma aurofrenatum* and *S. viride*), which have a similar foraging behavior (scraping and excavating turf algae), were affected by both treatment ($P < 0.05$) and time ($P < 0.001$) (Table 4).

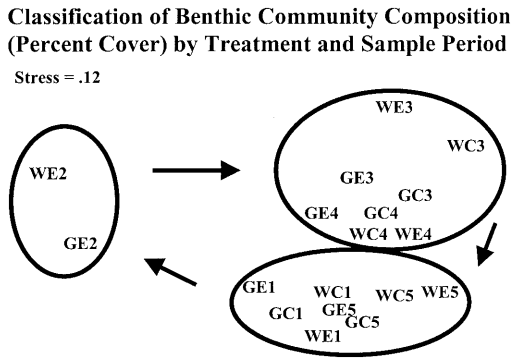

Fig. 2 Classification of benthic community composition (percent cover) by treatment and sample period using multiple dimensional scaling of Bray-Curtis similarities. *W* Wilderness Zone; *G* General Use Zone; *E* experimental reduction; *C* control; *1* September 1998 sample; *2* October 1998 sample; *3* December 1998 sample; *4* April 1999 sample; *5* September 1999 sample

Table 4 Average abundances of most common fish species are pooled for four sampling occasions after reduction of erect macroalgae. Species with < 30 sightings throughout entire study period were excluded from analyses. Effects of management (*Ma*) (Wilderness and General Use Zones), treatment (*Tr*) (control and experiment) and time (post-removal, time 1–4) were analyzed with three-way fixed factor ANOVA. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Species	Pooled mean (SE) for all post-removal sampling				Ma	Tr	Time	Ma× Tr	Ma× Time	Tr× Time	Ma× Tr× Time
	Wilderness Zone		General Use Zone								
	Control	Experiment	Control	Experiment							
Chaetodon capistratus	2.3 (0.3)	3.3 (0.6)	2.9 (0.5)	3.6 (0.5)							
C. ocellatus	0.6 (0.2)	1.2 (0.3)	0.3 (0.1)	0.3 (0.1)	**						
Chaetodontidae	3.3 (0.4)	4.6 (0.7)	3.2 (0.5)	3.8 (0.5)							
Holocanthus ciliaris	0.4 (0.1)	0.3 (0.1)	0.0 (0.0)	0.3 (0.1)	*		**	**			**
Pomacanthus arcuatus	0.0 (0.0)	0.2 (0.1)	0.5 (0.2)	0.5 (0.2)	*						
Pomacanthidae	0.5 (0.1)	0.6 (0.3)	0.6 (0.3)	0.8 (0.2)							
Haemulon aurolineatum	7.8 (5.5)	4.7 (2.8)	0.2 (0.1)	0.8 (0.3)	*						
H. flavolineatum	30.6 (6.1)	23.8 (4.7)	16.7 (6.5)	29.3 (6.3)							
H. plumieri	8.6 (1.5)	6.0 (1.0)	10.1 (4.3)	12.7 (3.1)							
H. sciurus	24.9 (6.4)	16.6 (3.8)	10.7 (5.9)	7.2 (1.6)	*						
Haemulidae	71.9 (7.9)	52.9 (5.0)	38.1 (16.0)	50.5 (8.8)							
Lutjanus apodus	1.8 (0.3)	2.1 (0.3)	0.9 (0.2)	2.4 (0.6)		*					
L. griseus	7.3 (2.3)	0.7 (0.5)	1.2 (0.5)	0.0 (0.0)	*	**		*			
L. synagris	3.8 (1.0)	3.7 (1.0)	2.1 (0.9)	0.4 (0.1)	**		*				
Ocyurus chrysurus	3.5 (1.0)	5.0 (1.2)	4.7 (1.6)	2.4 (0.6)							
Lutjanidae	16.3 (3.2)	11.7 (1.7)	8.9 (2.2)	5.2 (1.0)	**						
Scarus croicensis	60.8 (5.2)	61.4 (7.6)	54.0 (6.1)	61.9 (7.5)			***		*		
Sparisoma aurofrenatum	13.3 (3.0)	15.9 (2.9)	12.5 (2.8)	15.4 (2.6)			***				
S. viride	7.2 (0.8)	10.8 (1.5)	5.0 (0.7)	9.3 (1.1)	*	***	***			***	
Scaridae	155.4 (10.1)	165.6 (17.2)	138.8 (10.2)	164.0 (14.8)							
Acanthurus bahianus	2.5 (0.4)	5.3 (0.6)	2.0 (0.6)	2.2 (0.7)	**	*		*			
A. chirurgus	1.8 (0.4)	1.7 (0.5)	0.6 (0.3)	0.5 (0.2)	**		*				
A. coeruleus	15.1 (2.4)	23.0 (4.1)	10.3 (1.5)	13.1 (1.9)	***	**	***			*	
Acanthuridae	19.3 (2.7)	30.0 (4.4)	12.8 (1.8)	15.7 (1.9)	***	***	***	*		*	*
Bodianus rufus	0.6 (0.3)	1.3 (0.6)	0.1 (0.1)	0.7 (0.3)			***			*	
Halichoeres bivittatus	1.8 (0.5)	2.5 (1.0)	1.3 (0.4)	1.2 (0.4)							
H. garnoti	13.2 (1.7)	15.9 (1.2)	16.1 (1.8)	19.0 (1.6)	*		***				
Thalassoma bifasciatum	30.3 (3.5)	52.1 (8.0)	32.2 (5.0)	44.3 (6.0)		***	***				
Labridae	45.9 (4.0)	71.8 (9.0)	50.0 (5.7)	65.3 (7.1)		***	***				
Calamus bajonado	0.9 (0.3)	1.4 (0.4)	0.7 (0.3)	0.2 (0.1)	*						
Caranx ruber	3.6 (1.2)	4.8 (1.9)	1.7 (0.9)	4.8 (1.8)							
Sphyraena barracuda	1.1 (0.3)	1.1 (0.4)	0.1 (0.0)	0.2 (0.1)	**						
Mulloidichthys martinicus	0.3 (0.2)	1.5 (0.6)	0.3 (0.1)	0.5 (0.3)							
Epinephelus cruentatus	1.0 (0.2)	0.9 (0.2)	0.5 (0.2)	0.7 (0.2)							
Chromis cyanea	8.0 (1.6)	10.3 (2.6)	2.5 (0.9)	6.3 (1.0)	*						
Stegastes sp.	72.3 (6.7)	84.4 (5.8)	79.5 (4.2)	98.4 (7.6)		*	**				
Total	659.6 (19.2)	712.2 (45.9)	539.5 (52.4)	668.4 (36.8)	*	*	**				

The Acanthuridae and Labridae also exhibited a significant effect of time ($P < 0.001$, df = 4). Both families increased in abundance immediately after the clearing of erect macroalgae and progressively decreased to a level below that of the pre-removal population (Fig. 3). For Acanthuridae, the positive response to the algal manipulation was only observed in the Wilderness Zone (Fig. 3). The reduction resulted in an immediate increase in the size frequency distributions for the Acanthuridae and the three common species of parrotfish (*Scarus croicensis*, *Sparisoma aurofrenatum* and *S. viride*; Fig. 4).

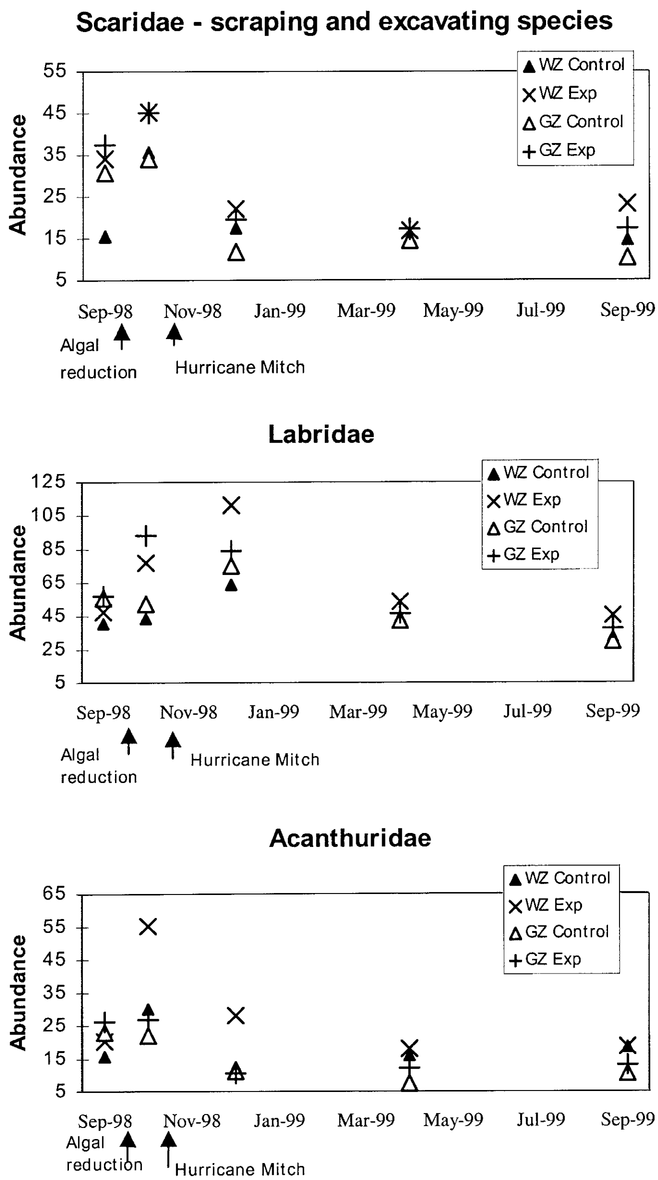

Fig. 3 Reduction of erect algae had a significant effect over time on one functional group and two families of fish ($P < 0.001$). Figures present average abundances of scraping and excavating parrotfish, Labridae and Acanthuridae before reduction as well as at four sampling occasions after reduction. Hurricane Mitch passed near Glovers Reef shortly after the first post-removal sampling occasion. Error bars are not included to clarify differences, but statistical comparisons are given in Table 4

MDS classification of treatments using the fish abundance data produced no clearly discernable patterns.

Herbivory assays

Fishing exclusion had a significant ($P < 0.01$) influence on herbivory, except for the sea urchin bite rate on *Lobophora* (Table 5). A post-hoc analysis [Tukey Honest Significant Difference (HSD) test] showed that the Wilderness Zone had a significantly higher grazing intensity for fish ($P < 0.001$) and total grazing ($P < 0.04$) for both assays over the year. On average, fish grazing was 52 and 43% higher in the Wilderness Zone than in the General Use Zone based on the *Thalassia* and *Lobophora* assays, respectively. On the other hand, the General Use Zone had a significantly ($P < 0.01$) higher intensity of sea urchin grazing on the *Thalassia* assay, being around 83% higher in the General Use Zone than in the Wilderness Zone. Time had a significant ($P < 0.05$) influence on all herbivory assays except for fish bites on *Lobophora*. *Thalassia* assays showed that fish grazing was significantly higher in September 1998 compared to April 1999 and September 1999 (Tukey HSD test; $P < 0.05$). Grazing from sea urchins was significantly higher in October 1998, i.e. before the Hurricane Mitch event, compared to periods between December 1998 and September 1999 ($P < 0.05$). In summary, total grazing was significantly higher in September 1998 and October 1998 compared to April 1999 and September 1999 ($P < 0.05$), suggesting an overall decrease in herbivory attributable to fishes during this 1-year period. Based on *Lobophora* assays, sea urchin grazing was higher in October 1998 than in September 1999. The algal reduction treatment alone had no effect on the herbivory assays. However, for the *Lobophora* assay there were significant effects of the interaction between fishing exclusion and the algal reduction treatment for total and fish herbivory ($P < 0.05$). A post-hoc comparison (Tukey HSD test) of the interaction showed that the control reefs in the General Use Zone were less grazed than control reefs in the Wilderness Zone (by 40 and 50%) for both total and fish-bitten assays, respectively ($P < 0.001$).

Discussion

Overall, the hypotheses proposed for coral and algal response to this manipulation were largely not supported. Instead of the predicted increase in stony coral cover, there was a significant decline in coral cover throughout this study. This can primarily be attributed to a coral bleaching event at the beginning of this study that led to some coral mortality (McField and McClanahan, personal observations). The effects of fisheries management and the algal reduction treatment did not alleviate the general declines in coral cover or the increases in macroalgae experienced during this study.

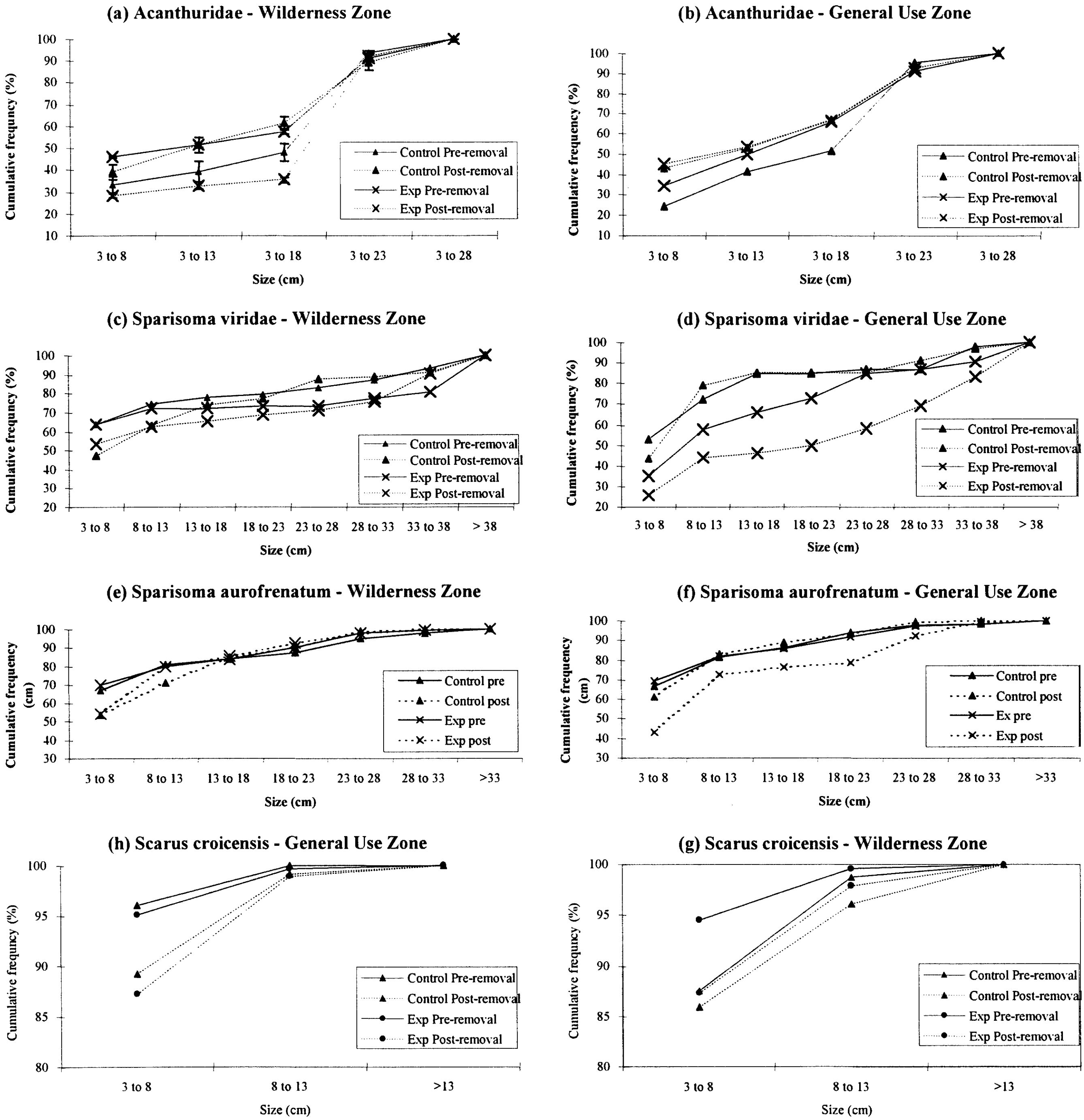

Fig. 4 Size-frequency distributions before and at first sampling occasion after reduction of (**a**, **b**) Acanthuridae, (**c**, **d**) *Sparisoma viride*, (**e**,**f**) *Sparisoma aurofrenatum* and (**g**, **h**) *Scarus croicensis* in Wilderness and General Use Zones, respectively. Individuals < 3 cm were not counted

However, the bleaching event and Hurricane Mitch likely influenced the outcome of our experiment. While this hurricane devastated some shallow exposed reefs in Belize, the patch reefs we studied appeared largely unaffected by physical damage. The water runoff and mixing from Mitch produced a phytoplankton bloom detectable in Sea WiFS satellite imagery. The bloom lasted 6–8 weeks in Belize, extending from the Gulf of Honduras through the southern half of Glovers Reef (Andréfouët et al., unpublished data). The large decrease in fleshy algae and increase in turf algae resulting from the manipulation reverted to near initial levels approximately 8 weeks after the removal. The control reefs also experienced algal increases, with brown fleshy algae increasing by 66% in 8 weeks.

At the end of the year-long experiment, there were no significant changes in *Sargassum* or *Turbinaria* abundance and, against prediction, *Lobophora* increased. These data and our observations on bleaching and subsequent coral

Table 5 Mean (SEM) eaten and bitten of herbivory assays of *Thalassia testudinum* and *Lobophora variegata*. *Eaten* is percentage of *Thalassia* that was removed; *bitten* is frequency of bitten assays (i.e. bitten/not bitten). *Total* includes both fish and sea urchin herbivory. Sept-98 is pre-algal removal, and Oct-98 to Sept-99 are post-removal. *All post-removal* is mean average (SEM) from Oct-98 to Sep-99. Significant effects of analysis of variance (three-way ANOVA): $n=4$ for each treatment in both zones

Assay	Category	Period	Wilderness Zone		General Use Zone	
			Control	Experiment	Control	Experiment
Thalassia	Total eaten[a]	Sep-98	24.7 (4.5)	23.4 (6.1)	8.4 (3.9)	20.7 (6.9)
		Oct-98	25.9 (7.3)	20.9 (6.4)	19.6 (6.1)	28.7 (6.6)
		Dec-98	17.4 (3.3)	13.8 (4.4)	9.2 (2.7)	9.9 (2.8)
		Apr-99	16.5 (4.3)	20.8 (7.6)	5.2 (1.1)	14.7 (5.7)
		Sep-99	12.1 (2.6)	24.3 (7.6)	10.4 (2.6)	6.8 (2.6)
	All post-removal		18.0 (2.9)	20.0 (2.2)	11.1 (3.0)	15.0 (4.8)
	Total bitten[b]	Sep-98	0.6 (0.1)	0.5 (0.1)	0.4 (0.0)	0.4 (0.1)
		Oct-98	0.4 (0.1)	0.5 (0.1)	0.3 (0.1)	0.5 (0.1)
		Dec-98	0.3 (0.0)	0.3 (0.0)	0.3 (0.1)	0.3 (0.1)
		Apr-99	0.3 (0.0)	0.4 (0.1)	0.2 (0.0)	0.3 (0.1)
		Sep-99	0.3 (0.0)	0.4 (0.1)	0.3 (0.1)	0.2 (0.0)
	All post-removal		0.3 (0.0)	0.4 (0.0)	0.3 (0.0)	0.3 (0.1)
	Urchin bitten[c]	Sep-98	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
		Oct-98	0.1 (0.0)	0.1 (0.1)	0.2 (0.0)	0.2 (0.1)
		Dec-98	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)
		Apr-99	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)
		Sep-99	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)	0.0 (0.0)
	All post-removal		0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
	Fish bitten[d]	Sep-98	0.5 (0.1)	0.4 (0.1)	0.3 (0.0)	0.3 (0.1)
		Oct-98	0.3 (0.1)	0.3 (0.1)	0.2 (0.0)	0.4 (0.1)
		Dec-98	0.3 (0.1)	0.3 (0.1)	0.2 (0.1)	0.2 (0.1)
		Apr-99	0.2 (0.0)	0.3 (0.1)	0.1 (0.0)	0.2 (0.1)
		Sep-99	0.2 (0.0)	0.4 (0.1)	0.1 (0.1)	0.1 (0.0)
	All post-removal		0.3 (0.0)	0.3 (0.0)	0.1 (0.0)	0.2 (0.1)
Lobophora	Total bitten[e]	Sep-98	0.6 (0.1)	0.5 (0.0)	0.4 (0.0)	0.5 (0.1)
		Oct-98	0.6 (0.0)	0.5 (0.0)	0.3 (0.1)	0.5 (0.1)
		Dec-98	0.5 (0.0)	0.5 (0.1)	0.4 (0.0)	0.4 (0.1)
		Apr-99	0.4 (0.1)	0.4 (0.1)	0.3 (0.1)	0.3 (0.0)
		Sep-99	0.4 (0.1)	0.5 (0.1)	0.3 (0.0)	0.3 (0.1)
	All post-removal		0.5 (0.0)	0.5 (0.0)	0.3 (0.0)	0.4 (0.0)
	Urchin bitten[f]	Sep-98	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	0.1 (0.0)
		Oct-98	0.2 (0.0)	0.2 (0.0)	0.1 (0.1)	0.1 (0.0)
		Dec-98	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	0.2 (0.0)
		Apr-99	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
		Sep-99	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
	All post-removal		0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
	Fish bitten[g]	Sep-98	0.5 (0.1)	0.4 (0.0)	0.3 (0.0)	0.4 (0.1)
		Oct-98	0.4 (0.0)	0.4 (0.0)	0.2 (0.1)	0.4 (0.1)
		Dec-98	0.5 (0.0)	0.4 (0.1)	0.2 (0.0)	0.3 (0.1)
		Apr-99	0.3 (0.1)	0.3 (0.1)	0.2 (0.0)	0.3 (0.1)
		Sep-99	0.4 (0.0)	0.4 (0.1)	0.2 (0.0)	0.3 (0.1)
	All post-removal		0.4 (0.0)	0.4 (0.0)	0.2 (0.0)	0.3 (0.0)

[a] Time ($P=0.004$, F = 4.3), Management ($P=0.02$, F = 5.7)
[b] Time ($P=0.0005$, F = 5.8), Management ($P=0.04$, F = 4.6)
[c] Time ($P=0.005$, F = 4.1), Management ($P=0.007$, F = 7.7)
[d] Time ($P=0.006$, F = 4.0), Management ($P=0.0003$, F = 14.5)
[e] Time ($P=0.048$, F = 2.6), Management ($P=0.0006$, F = 13.1), Management:Treatment ($P=0.036$, F = 4.6)
[f] Time ($P=0.019$, F = 3.2)
[g] Management ($P=0.0003$, F = 14.7), Management:Treatment ($P=0.036$, F = 4.6)

mortality suggest that coral bleaching may be one factor causing declines in coral cover on these patch reefs. Nutrification resulting from Hurricane Mitch may have influenced our results, given the rapid increase in algal cover and biomass after the hurricane and the observed changes in water quality (Andréfouët et al., unpublished data). Because nutrient concentrations and algal growth as a function of nutrient concentration were not monitored over the study period we can only speculate as to their potential role. Background nutrient concentrations were measured in a preliminary study on Glovers Reefs (before Hurricane Mitch) at levels up to 0.3 μM for nitrates and 0.35–0.39 μM for soluble reactive phosphate (SRP) phosphates (Mumby 1999), which some investigators suggest is sufficient for maximum algal growth (Lapointe 1999). The design of our study does not, however, allow us to conclude that hurricane-induced mixing and nutrient concentrations influenced the rapid recover of algae.

Management effects could be confounded by differences in wave energy, water temperature or some other geographically influenced environmental factor between the two zones, which were separated by approximately

7 km. Initial differences between the two management zones were largely maintained throughout the study. Initially, the General Use Zone was significantly different from the Wilderness Zone, with a higher stony coral cover and a lower fleshy algae cover. This trend largely persisted throughout the study. This may be a result of better physical and chemical conditions for corals in this area of the atoll due to greater water exchange. The Wilderness Zone is more confined by islands than the General Use Zone, and this may result in reduced water flow. Preliminary water temperature measurements taken hourly over an approximately 1-month period found that the Wilderness Zone had somewhat greater variation in temperature than the General Use Zone (McField, unpublished data), which may make corals more susceptible to environmental stresses and coral bleaching. Clearly, there are other confounding environmental factors in our study that make it difficult to conclude about the role of fisheries and intervention management on the ecology of these patch reefs.

Our findings support previous evidence that increased protection from fishing, such as in the Glovers Reef Wilderness Zone, promotes fish abundance (McClanahan et al. 1994; Roberts 1995) and decreased sea urchin abundance and grazing (Hay 1984; McClanahan et al. 1994). The effect of protection was apparent for more than half of the fish species examined, among which all but two were more abundant in the Wilderness Zone. A number of these species were herbivores, including the scraping parrotfish, *Scarus viride*. Only *Pomacanthus arcuatus* and *Halichoeres bivittatus* were more abundant in the General Use Zone. Among the families, snappers (Lutjanidae) and surgeonfish (Acanthuride) were both more common in the Wilderness Zone. At least the former category constitutes a sought-after source of food and may experience high fishing pressure in the General Use Zone.

The manual reduction of macroalgae caused a significant, although largely temporary, increase in the total fish abundance. Prior to the removal of algae, with the exception of the damselfish *Chromis cyanea*, there were no significant differences in fish densities between patch reefs assigned to control and those designated to the experimental treatment. Results of this manipulation support previous studies, where the reduction of erect macroalgae has promoted the availability of palatable turf and hence increased abundance and grazing pressure by herbivorous fish (Jones 1992; McClanahan et al. 1999b, 2000). We observed increased feeding and aggression by herbivorous fishes (McClanahan et al. 2000), but the results of our herbivory assays did not reflect these observations. It may be that herbivores were avoiding the large assay algal species in favor of turf algae (McClanahan et al. 1994). A previous study in East Africa had similar results in that macrophyte-feeding herbivores, such as *Calotomus* and *Leptoscarus*, fed more frequently on seagrass assays compared to other herbivores (McClanahan et al. 1999b). There are fewer herbivorous fish specialized to feed on macrophytes in the Caribbean than in the Indian Ocean.

Of seven species affected by the treatment, six exhibited a higher mean abundance on experimental reefs. Among them were the three most common herbivores (*Acanthurus bahianus*, *A. coeruleus* and *Stegastes* spp.) as well as the most common scraper/excavator *Sparisoma viride*. As hypothesized, the reduction of macroalgae, which previously obstructed the turf may attract feeding schools of herbivorous fishes. Territorial damselfish are dependent on the availability of turf algae (Choat 1991) and the reduction of macroalgae may hence have promoted their abundance. On temperate rock reefs, areas cleared of kelp attracted territorial damselfishes (Jones 1992). *Stegastes* spp. exhibited an initial response to the clearing by increased feeding and aggression rates (McClanahan et al. 2000). The clearing of macroalgae could have made damselfishes more conspicuous and the increase in numbers could be an artifact of visual sampling, but we also found increased bite rates and aggression for these species (McClanahan et al. 2000), which is unlikely to be a sampling artifact.

Size-frequency distributions suggest that an increase in larger individuals took place among herbivores and scrapers/excavators after the removal. The small-bodied parrotfish *Scarus croicensis* showed a clear response to the algal reduction in the Wilderness Zone where the abundance of large individuals increased significantly after the reduction. However, in the General Use Zone, larger individuals increased on both experimental and control patch reefs. Similarly, the population of *Sparisoma aurofrenatum* showed a tendency towards larger individuals after the removal in both Wilderness and General Use Zone.

Our prediction that the abundance of invertebrate feeders would decrease or be unaffected by the algal reduction was largely supported for most species, but the response was more complicated for some species. Seventeen of the sampled species can be classified as invertebrate feeders, and of these species, only three were affected. Many of the unaffected species are nocturnally active (Burke 1995), often feeding away from the reef at night while schooling on the reef during the day. Therefore, these species may not respond to changes in the reef or, if responding, may not be measurable from diurnal sampling. The algal reduction appeared, however, to improve conditions, at least temporarily, for *Thalassoma bifasciatum*. This species was observed to be active in feeding and reproductive behavior shortly after the reduction. It is possible that the mechanical cutting and scraping stirred up invertebrates or made them more susceptible to predation (Wahl and Hay 1995; Stachowicz and Hay 1996). Only *Lutjanus griseus* decreased on experimental reefs after the removal of algae, a response that was especially noticeable in the Wilderness Zone. A cogener, *Lutjanus apodus*, had nearly the opposite response, and there may be some ecological partitioning or competition between these two species that was influenced by the manipulation.

The aim of this study was to determine if the fisheries restrictions in combination with the physical reduction in erect algae could increase herbivorous fish populations to the level that they would suppress the recovery of macroalgae (McClanahan et al. 1999b) and lead to increased stony coral abundance (Tanner 1995). Benthic and algal biomass data suggest that neither factor had an appreciable long-term effect on the studied patch reefs. Physical conditions of water movement, temperature fluctuations and nutrient concentrations probably confounded the factors we studied. In contrast, there is evidence that fisheries restrictions and the algal reduction influenced the abundance of a number of fish species, including herbivores. These findings suggest that management is having an effect on fish populations, but that it may require additional time before this effect cascades down to the benthos. In addition to the length of time since protection, the extent of enforcement of ''no-take'' zones may be an important factor in this study. Enforcement activities were intermittent throughout this period and poaching may have prevented fish populations from achieving their maximum levels. A similar study in a reef protected from fishing for ~25 years found a larger increase in herbivorous fish and stony coral and a slower recovery of macroalgae than reported here (McClanahan et al. 1999b). Consequently, the age and effectiveness of fisheries protection may influence the outcome of these types of algal reduction and recovery experiments. Overall, we believe further testing of the combination of algal reduction and ''no fishing'' zones is warranted. Hopefully, future studies will not be confounded by two major ecological disturbances, as occurred during the course of this experiment.

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Appendix 1

Taxonomic list of species found in the transects and quadrats of the studied patch reefs

- Rhodophyta
  - *Acantophora spicifera* (Lamouroux) J. Agardh
  - *Amphiroa fragilissima* (Linnaeus) Lamouroux
  - *Amphiroa rigida* var. *antillana* Børgesen
  - *Amphiroa tribulus* (Ellis and Solander) Lamouroux
  - *Botryocladia shanksii* Dawson
  - *Centroceras clavulatum* (C. Agardh) Montagne
  - *Ceramium flaccidum** (Kützing) Ardissone
  - *Ceramium nitens* (C. Agardh) J. Agardh
  - *Champia parvula* (C. Agardh) Harvey
  - *Chondria littoralis* Harvey
  - *Coelothrix irregularis* (Harvey) Børgesen
  - *Digenia simplex* (Wulfen) C. Agardh
  - *Falkenbergia* sp.*
  - *Fosliella* sp.
  - *Galaxaura subverticillata* Kjellman
  - *Gelidiella acerosa* (Forsskål) J. Feldmann
  - *Herposiphonia pecten-veneris** (Harvey) Falkenberg
  - *Hypnea musciformis* (Wulfen *in* Jacquin) Lamouroux
  - *Hypnea spinella* (C. Agardh) Kützing
  - *Jania adhaerens* Lamouroux
  - *Jania capillacea* Harvey
  - *Laurencia collariopsis* (Montagne) Howe
  - *Laurencia intrincata* Lamouroux
  - *Laurencia obtusa* (Hudson) Lamouroux
  - *Laurencia papillosa* (C. Agardh) Greville
  - *Lejolisia* sp.
  - *Liagora dendroidea* (P. Crouan & H. Crouan in Mazé & Schramm) Abbott
  - *Stylonema* sp.*
  - *Titanoderma pustulatum** (Lamouroux) Nägeli
  - *Polysiphonia* spp.*
- Phaeophyta
  - *Dictyota divaricata* Lamouroux
  - *Dictyota humifusa* Hörnig, Schnetter & Coppejans *in* Höring et al.
  - *Dictyota menstrualis* (Hoyt) Schnetter
  - *Lobophora variegata* (Lamouroux) Womersley *ex* Oliveira
  - *Padina sanctae-crucis* Børgesen
  - *Sargassum vulgare* C. Agardh
  - *Turbinaria turbinata* (Linnaeus) Kuntze
- Chlorophyta
  - *Anadyomene stellata* (Wulfen) C. Agardh
  - *Caulerpa cupressoides* var. *cupressoides* (West *in* Vahl) C. Agardh
  - *Caulerpa racemosa* (Forsskål) J. Agardh
  - *Chateomorpha crassa* (C. Agardh) Kuetzing
  - *Cladophora* sp.*
  - *Cladophoropsis membranacea* (Hofman Bang *ex* C. Agardh) Børgesen
  - *Derbesia* sp.*
  - *Dictyosphaeria cavernosa* (Forsskål) Børgesen
  - *Halimeda opuntia* (Linnaeus) Lamouroux
  - *Halimeda* sp.*
  - *Penicillus pyriformis* A. Gepp
  - *Rhizoclonium riparium** (Roth)
  - *Udotea flabellum* (Ellis & Solander) Howe
  - *Valonia macrophysa* Kützing
  - *Valonia utricularis* (Roth) C. Agardh
  - *Ventricaria ventricosa* (J. Agardh) Olsen & West

Asterisk (*) denotes species included in the ''turf algae'' complex in the transects

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