# Response of fishes to algae reduction on Glovers Reef, Belize

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ABSTRACT: Many Caribbean coral reefs have experienced an increase in erect brown algae (species of *Sargassum*, *Turbinaria* and *Lobophora*) over the past 18 yr. We explored the effects of fleshy algal overgrowth on coral reef fishes by reducing erect algae by ~2.5 kg(wet) m$^{-2}$ on 8 patch reefs (average size ~1000 m$^2$) whereby half were in a new no-fishing zone and half in an unrestricted fishing zone. Another 8 reefs were left as unmanipulated controls in the respective zones. Multivariate ordination indicated that the algal removal had marginal effect on whole-fish assemblages but that effect was highly significant on the biomass of common herbivores. The reduction of erect algae resulted in a rapid increase in the abundance of the blue-headed wrasse *Thalassoma bifasciatum* (Labridae), in the biomass of the blue tang *Acanthurus coeruleus* (Acanthuridae), and in both the abundance and biomass of the spotlight parrotfish *Sparisoma viride* (Scaridae). Bite rates and intra- and inter-specific aggressive encounters were used as measures of resource quality, and we found that these measures increased for surgeonfishes and damselfishes after the algal reduction, particularly in the center of the patch reefs, where most erect algae was originally located. Increased accessibility, net production and palatability of the early successional turf algae on the manipulated reefs are likely to account for the increased numbers, biomass and feeding rates of the dominant herbivorous fishes.

KEY WORDS: Acanthuridae · Algal-fish interactions · Brown algae · Herbivory · Labridae · Management interactions · *Sargassum* · Scaridae · *Turbinaria*

## INTRODUCTION

Coral reefs in the Caribbean have experienced a large-scale change in their ecology over the past 2 decades resulting in the loss of hard coral cover and reefs dominated by various forms of fleshy algae (Carpenter 1990, Hughes 1994, Connell 1997, Shulman & Robertson 1997, McClanahan & Muthiga 1998, McClanahan et al. 1999a). This ecological change has been associated with the disease-induced die-offs of corals

(Aronson et al. 1998) and of an important grazing sea urchin (*Diadema antillarum*) (Lessios 1988, Hughes et al. 1999), coral bleaching (Porter & Meier 1992, Glynn 1993, Shulman & Robertson 1997, Winter et al. 1998), cyclones (Woodley et al. 1981, Done 1992, Rogers 1993, Mumby 1999), and increased fishing pressure (Koslow et al. 1988, Hughes 1994) and seawater nutrient concentrations (Cockey et al. 1996, LaPointe 1999). The consequences of this large-scale macroalgal overgrowth for coral reef fishes have been poorly explored, apart from a study in the Watamu Marine National Park, a 25 yr-old unfished park in a Kenyan reef lagoon, which found that increased abundances of her-

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bivorous and invertebrate-eating fishes followed the experimental reduction of fleshy algae (McClanahan et al. 1999b). The considerable age of the Watamu Park assured sufficient time for the recovery of fishes from fishing disturbances, and the response may differ in areas more recently closed to fishing. The recovery of herbivore populations could help restore reefs dominated by fleshy algae to coral domination. Therefore, studies of the interaction between fishing, reduction of macroalgae, and time since initiation of management should be useful in planning restoration of reefs dominated by macroalgae.

Ecological interactions combined with fishing may produce complex responses to ecological changes or perturbations (Knowlton 1992, McClanahan 1995, 1999, McClanahan et al. 1995). For example, increases in late successional macroalgae may increase the structural refuge for small invertebrates (Duffy & Hay 1991, Wahl & Hay 1995, Stachowicz & Hay 1996), which could enhance resources for invertebrate-feeding fishes if fishing is not strongly influencing their populations. Late successional algae may, however, have lower photosynthetic rates and net production, as well as a reduced nutritive content and increased chemical defences, resulting in lower palatability than early successional opportunistic turf algae (Littler & Littler 1980, Birkeland et al. 1985, Steneck & Dethier 1994). Late successional algae could, therefore, reduce the benthic production available to consumers directly (to herbivorous) and indirectly (to invertebrate-consumers) (McClanahan et al. 1999b). The immediate response of fishes to a reduction in late successional algae is likely to be manifested first in herbivorous fishes, as these are most likely to respond to an increase in their preferred turf algal food (Choat 1991, van Rooij et al. 1996a, Lawson et al. 1999). The response may, however, depend on the species' feeding behavior and the morphology of the feeding apparatus (Bellwood 1990, Bruggemann et al. 1994b, Polunin et al. 1995). Therefore, the successional state of algae is likely to influence the distribution and abundance of herbivorous species according to their feeding behavior (e.g. browsing, scraping, excavating) (McClanahan et al. 1999b).

This study reports the results of an experiment whereby macroalgae were reduced on patch reefs in the lagoon of the remote Glovers Reef atoll (Belize, Central America). These patch reefs have experienced a large increase in macroalgae over the past ~20 yr, particularly by late successional brown algae (McClanahan & Muthiga 1998). The southern end of this atoll was closed to fishing in 1996. Our study focused on the immediate response of fishes to the algal reduction with particular focus on the response of herbivorous surgeon (Acanthuridae), damsel (Pomacentridae) and parrotfishes (Scaridae). Our working hypotheses

were that macroalgae inhibit the feeding rates of herbivorous fishes, while invertebrate-feeders, such as wrasses (Labridae), grunts (Haemulidae) and snappers (Lutjanidae), would have variable or delayed responses (McClanahan et al. 1999b). The greater net production and palatability of early successional turfs (Choat 1991, Steneck & Dethier 1994) was hypothesized to increase accessible algal resources, which in turn should lead to greater feeding rates and aggression between ecologically similar individuals (Carpenter & MacMillen 1976, Eakin 1987, van Rooij et al. 1996a). This study was undertaken to determine if the generally positive response of fishes to the reduction of algae in the Kenyan study is also applicable to the Caribbean, where the largest recent increases in fleshy brown algae have been reported (Connell 1997).

## METHODS

**Study sites and management.** Glovers Reef is a 260 km$^2$ atoll located approximately 15 km east of the Belizean Barrier reef — the largest reef in the Atlantic (see Stoddart 1962, Wallace & Schafersmann 1977, Gischler 1994 for further geologic descriptions). The atoll is an almost continuous reef, with 3 large tidal channels and ~850 patch reefs within the lagoon. The outer edge of the atoll drops into deep water (>500 m), while the central lagoon seldom exceeds 20 m in depth. Patch reefs, the focus of the study, occur in the lagoon and vary in size from ~25 to ~10 000 m$^2$. The patch reefs are separated by sand and seagrass beds at a depth of 4 to 20 m, with the distance between the nearest-neighbor patch reef seldom exceeding 30 m. Patch reefs consist of massive coral species (the genera *Montastrea*, *Diploria*, *Siderastrea*, *Porites*) with occasional thickets of *Agaricia agaricites* and *A. cervicornis*. Sea fans (*Gorgonia ventalina*), sea whips (genera *Eunicea*, *Plexaurella*, *Pseudoplexaura*) and brown algae (genera *Lobophora*, *Dictyota*, *Turbinaria*, *Sargassum*) are abundant on most patch reefs (McClanahan & Muthiga 1998).

Despite the remoteness of the atoll, fishing is practiced by a small number of residents and a larger number of transient fishers. Fishers collect lobsters, conches and finfishes using spear, hook and line. The Belizean Fisheries Department zoned the atoll into 4 fisheries management zones and began management in June 1996. The southern half of the atoll is divided into 3 zones: 'wilderness', 'conservation' and 'general use' zones. The wilderness and conservation zones exclude all forms of fishing except by a small number (<10) of residents who can fish only for personal consumption in the conservation zone. The general use zone allows the controlled continuation of existing

fisheries practices. The fourth zone is a seasonal closure area of a grouper spawning ground on the northeast end of the atoll.

**Experimental design and algal reduction logistics.** We haphazardly selected 16 patch reefs of moderate size (985 ± 173 m$^2$) such that 8 were located in the wilderness and general use zones respectively. We used a balanced design, whereby 4 patch reefs in each of the 2 management zones were selected for the macroalgae reduction (experimental patch reefs) and 4 were left unmanipulated as controls (a small portion of the largest experimental patch reefs was not cleared on the leeward side). Water depth to the bottom of the patch reefs did not exceed 4 m, and the distance between reefs used for the algal reduction was >15 m (although some control reefs were <10 m from experimental reefs). All patch reefs were studied approximately 1 wk prior to and 1 wk after algae reduction in September and October 1998, respectively. Algae was removed in 2 steps. First, the large fronds were cleared with hedge-trimmers, and the remaining holdfasts were then cleared using wire brushes. An average of ~28 person-hours was allotted to the clearing of each patch reef. Algae were scraped from 3 replicate 0.0625 m$^2$ plots on each patch reef before and after the clearance to estimate the change in the wet weight of macroalgae. From these measurements we roughly estimated a wet weight algal reduction of ~2.5 kg m$^{-2}$ or ~1250 kg$^{-1}$ patch reef.

**Benthic cover estimates.** Benthic cover was estimated on each patch reef using the line-intercept method (McClanahan & Shafir 1990). A 10 m transect line was haphazardly laid in 3 locations on the growing front (NE compass direction) of the patch reef. The 3 locations were the patch reef edge (transition from sand to patch reef), shoulder and center. Substrate cover was separated into functional groups: hard corals, fleshy algae, algal turf, calcareous algae, encrusting coralline algae, branching coralline algae, gorgonians, sponges, zoanthids, seagrasses, sand and 'microalgae', the latter including diatoms and cyanobacteria. All groups covering a distance of 3 cm or more were measured to the nearest 1 cm, recorded on a plastic slate, and used for calculating percentage cover for each functional group. It should be noted that this method only measures groups composing the canopy, and the results therefore represent relative canopy-cover abundances. Sand and seagrass areas were avoided when laying out the transect lines, and therefore their estimated abundances do not necessarily represent their true cover on these patch reefs.

**Fish counts.** Visual counts were carried out using the discrete groups sampling (DGS) method (Greene & Alevizon 1989, McClanahan 1994), whereby a limited number of species are sampled during a single search-sampling period of 5 min. During the total 35 min sampling period, the investigator swam haphazardly over each patch reef, and recorded the number of species and individuals of 7 groups, each allotted a 5 min observation interval. Individuals of <3 cm were not counted. Each of the following 7 discrete groups were sampled separately: Group 1: Chaetodontidae (butterflyfishes) and Pomacanthidae (angelfishes); Group 2: Acanthuridae (surgeonfishes); Group 3; Haemulidae (grunts); Lutjanidae (snappers) and Sparidae (porgies); Group 4: Scaridae (parrotfishes); Group 5: Labridae (wrasses); Group 6: Sphyraenidae (barracuda), Balistidae (triggerfishes), Carangidae (jacks), Aulostomidae (trumpetfishes) and Fistulariidae (cornetfishes), and *Chromis cyanea*; Group 7: Serranidae (groupers, of which graysby comprised >95% of the observations) and territorial pomacentrids (damselfishes). All surgeonfishes and parrotfishes were assigned to 8 different 5 cm size-class intervals. Size-frequency data was converted to biomass, using length-weight relationships from an NOAA technical paper (Bohnsack & Harper 1998).

**Herbivore bite and aggression rates.** In order to estimate the potential effects of algal reduction on feeding of herbivorous fishes, direct observations of feeding were carried out on patch reefs where the algae had been cleared as well as on control reefs. Observations on bite rates and aggression were carried out on the 2 most common species of surgeonfish, *Acanthurus coeruleus* (blue tang) and *A. bahianus* (ocean surgeonfish), 2 species of territorial damselfishes (*Stegastes fuscus* and *S. planifrons*), and on the dominant parrotfish, *Sparisoma viride* (spotlight parrotfish). Fish foraging behavior on the edge and shoulder of the patch reef was compared to that of the center of the reef. The observer followed each haphazardly selected individual for a 1 min observation period, during which all bites on substrate were recorded as well as all interactions or attack rates on other fishes (McClanahan et al. 1999b).

**Data analyses.** The percentage cover of each functional group was calculated for each patch reef based on the pooled transect data. We only present benthic cover data for the experimental patch reefs, as no significant differences were found between control and experimental patch reefs prior to the treatment (Student's *t*-tests, p > 0.05). Two-way ANOVAs were used to determine the effects of time, management and their interaction on the relative cover of the functional groups.

In order to confirm uniformity in fish assemblages among patch reefs in each respective management zone prior to algal removal, independent *t*-tests were conducted. To investigate the effects of algal removal on the structure of fish assemblages, data were sub-

jected to non-metric multidimensional scaling (MDS) using the Bray-Curtis similarity measure (Clarke 1993). The average of 2 repeated surveys on each reef was used in all fish analyses. Prior to the multivariate analyses, both fish numbers and biomass of selected species were double square-root-transformed to enhance the contribution of less abundant species. Differences in fish assemblages between the 2 management zones, as well as between treatments, were examined using a 2-way crossed ANOSIM, which is an analogue of multivariate analysis of variance with a randomization test for significance (Clarke 1988). Where the ANOSIM revealed significant differences among groups of samples, similarity percentage analysis (SIMPER) was used to identify the percentage contribution of individual species ($i$), to the average among-group dissimilarity $\bar{\delta}$ (Warwick et al. 1990). The Bray-Curtis measure of dissimilarity $\bar{\delta}$ (Bray & Curtis 1957) takes on values in the range 0 to 100, with $\bar{\delta} = 100$ representing the case of no species in common and $\bar{\delta} = 0$ being 2 samples with identical species patterns. When the mean species-specific contribution to $\bar{\delta}$ ($\bar{\delta}_i$) is large and the standard deviation ($\bar{\delta}_i/SD[\delta_i]$) is low, the $i$th species constitutes a good discriminating species because of its consistent contribution to the dissimilarity (Clarke 1993). Finally, the effect of the algae reduction on individual species abundance and biomass was examined with a 2-way fixed factor ANOVA.

Where necessary, benthic data was arcsine-transformed and fish data was $\log_{10}(x + 1)$ or square-root-transformed to meet the assumption of homogeneity of variances (Cochran's $C$, p > 0.05). Repeated testing (e.g. ANOVA and $t$-tests) can lead to decision errors, particularly at the p < 0.05 to 0.01 levels. In this study both benthic and fish data consisted of numerous variables, and therefore the sequential Bonferroni technique, which adjusts the α-value according to the number of variables included, was applied (Holm 1979). In order to relate the adjusted α-values to their unadjusted counterparts we use the symbols *p < 0.05, **p < 0.01 and ***p < 0.001. Bite and aggression rates of herbivorous fish were analyzed with the Kruskal-Wallis non-parametric test.

## RESULTS

### Benthic cover

Algae reduction targeted macroalgae, which led to an expected decrease in fleshy algae (ANOVA, p < 0.00008***), and a significant decrease in both calcareous and branching coralline algae (ANOVA, p < 0.006*; Table 1). As a result of the reduction in the macroalgae, turf algae became more visible and therefore appeared more abundant in the canopy (ANOVA, p < 0.00009***). This was however an artifact resulting from the opened canopy following macroalgae reduction. Management did not affect benthic cover (ANOVA, p > 0.05) exept that coral cover was higher in the general use zone (p < 0.05). However, the interaction of management and algae reduction was significant for fleshy algae (ANOVA, p < 0.004*). This may have been due to the fact that algae cover prior to the removal was higher in the wilderness zone and hence the removal in this zone had a stronger effect (Table 1).

### Fish response

Prior to the algal reduction, fish assemblages on the patch reefs were similar within each management zone (ANOSIM, p > 0.05), as was the abundance and biomass of individual species ($t$-tests, p > 0.008*). The

Table 1. Mean % (±SE) cover of the functional groups in the 2 management areas: wilderness zone and general use zone

| Functional groups | Wilderness zone | | General use zone | |
| --- | --- | --- | --- | --- |
| | Pre-removal | Post-removal | Pre-removal | Post-removal |
| Hard coral | 20.2 (2.1) | 26.0 (2.8) | 28.7 (2.8) | 34.4 (2.3) |
| Turf | 12.4 (3.0) | 43.4 (3.6) | 18.9 (1.7) | 36.1 (2.4) |
| Calcareous algae | 7.8 (2.3) | 3.2 (0.8) | 5.4 (0.5) | 1.9 (0.4) |
| Fleshy algae | 37.7 (2.1) | 4.4 (0.8) | 25.0 (2.6) | 8.5 (0.8) |
| Encrusting coralline algae | 3.2 (1.1) | 8.6 (3.7) | 2.9 (0.6) | 4.0 (0.6) |
| Branching coralline algae | 2.8 (0.8) | 0.8 (0.3) | 3.8 (1.1) | 1.2 (0.5) |
| Seagrass | 1.0 (0.6) | 0.1 (0.1) | 0.2 (0.2) | 0.0 (0.0) |
| Sand | 1.6 (0.3) | 1.8 (0.5) | 2.5 (0.3) | 0.8 (0.5) |
| Gorgonia | 7.1 (2.2) | 5.6 (2.0) | 7.5 (2.3) | 8.7 (3.1) |
| Sponge | 4.8 (1.8) | 5.8 (2.0) | 3.3 (0.7) | 4.4 (0.7) |
| Zoanthid | 0.1 (0.1) | 0.1 (0.1) | 0.6 (0.1) | 0.1 (0.1) |
| Microalgae | 1.3 (0.7) | 0.1 (0.1) | 1.5 (0.6) | 0.0 (0.0) |
| Patch reefs (n) | 4 | 4 | 4 | 4 |

reduction of algae influenced whole-fish assemblages and caused significant change in the biomass of common herbivores. Multivariate scaling ordination (MDS) illustrated certain dissimilarity in whole-fish assemblages between control and experimental reefs (ANOSIM, p = 0.056; SIMPER, $\bar{\delta}$ = 24.26; Fig. 1). The responses of individual species and families are presented in Table 2. Species and family-wise analyses of variance revealed a highly significant effect of the algae removal on *Sparisoma viride* (p < 0.0005**) and a significant effect on *Thalassoma bifasciatum* (p < 0.003*). The effect of the algae removal on herbivore biomass could be determined by subjecting the biomass of common surgeon- and parrotfishes to MDS (Fig. 2). The difference in biomass of parrot- and surgeonfishes between control and experimental patch reefs was highly significant (ANOSIM, p < 0.01). The Bray-Curtis average dissimilarity ($\bar{\delta}$) between control and experimental reefs was 19.57, a relatively low value, attributable to the fact that the ordination was carried out on a small part of the fish assemblages, i.e. on the biomass of common herbivores. The almost 6 times higher biomass of *S. viride* on experimental reefs explained almost 30% of the Bray-Curtis dissimilarity, and its contribution to the overall dissimilarity between control and experimental reefs was also the most consistent (SIMPER, $\bar{\delta}_i/SD[\delta_i]$ = 2.49; Table 3). Univariate analyses of species-specific effects of algae removal on biomass support the conclusions from the SIMPER procedure, as they were significant for 2 individual species, *S. viride* and *Acanthurus coeruleus*
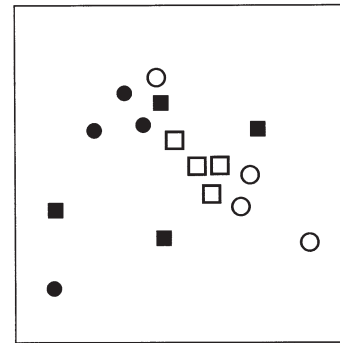


Fig. 1. Multidimensional scaling plots based on population densities of 46 fish species on patch reefs in Glovers Reef lagoon. Of the fish assemblages observed, 8 were sampled on patch reefs in the wilderness zone, and 8 were sampled in the general use zone. The fish fauna was examined after macroalgae had been removed from half of the reefs in each zone. A stress value of 0.13 indicated that the 2-dimensional ordination constituted a good representation of a relationship in multidimensional space. (O) wilderness zone control, (●) wilderness zone experiment, (□) general use zone control, (■) general use zone experiment

(ANOVA, p < 0.008* and p < 0.01* respectively). The biomass of *A. coeruleus* on experimental reefs was 2-fold that on control reefs. For 2 species, *A. chirurgus* and *Scarus croicensis*, biomass decreased on reefs from which algae had been removed (Table 3).

In contrast, management had no effect on whole-fish assemblages (ANOSIM, p = 0.57). Only adult *Acanthu-*

Table 2. Mean (± SE) fish abundance per 5 min count in the 2 management zones and in the 2 treatments. Total of 46 species of fish were recorded on the 16 examined patch reefs in Glovers Reef lagoon. Many of the species were uncommon and/or displayed erratic distribution and were therefore pooled into families in order to facilitate interpretation of results

| Family/species | Wilderness zone | | General use zone | |
|---|---|---|---|---|
| | Control | Removal | Control | Removal |
| Serranidae | 1.8 (0.7) | 0.5 (0.4) | 0.3 (0.3) | 1.0 (0.3) |
| Haemulidae | 65.8 (22.0) | 69.8 (4.6) | 71.2 (62.8) | 48.3 (15.2) |
| Lutjanidae | 13.1 (5.0) | 6.5 (2.0) | 12.4 (6.6) | 6.6 (2.7) |
| Mullidae | 0.1 (0.1) | 0.8 (0.6) | 0.8 (0.3) | 0.6 (0.1) |
| Pomacanthidae | 0.9 (0.2) | 0.4 (0.1) | 1.3 (0.9) | 1.8 (0.5) |
| Chaetodontidae | 2.8 (0.8) | 2.6 (0.8) | 4.3 (1.1) | 4.4 (1.6) |
| *Chromis cyanea* | 5.1 (1.8) | 12.1 (7.1) | 1.8 (1.8) | 5.4 (1.8) |
| *Stegastes* sp. | 89.5 (17.1) | 104.3 (3.9) | 87.3 (8.1) | 126.9 (19.2) |
| *Bodianus rufus* | 1.1 (1.0) | 4.5 (1.5) | 0.5 (0.5) | 22.3 (2.5) |
| *Halichoeres bivittatus* | 2.0 (1.5) | 1.8 (0.8) | 0.9 (0.6) | 1.4 (0.8) |
| *Halichoeres garnoti* | 12.5 (3.3) | 15.4 (3.1) | 17.8 (5.1) | 22.3 (2.5) |
| *Thalassoma bifasciatum* | 27.8 (6.4) | 55.4 (8.4) | 32.6 (3.8) | 66.8 (10.0) |
| *Scarus croicensis* | 50.6 (6.8) | 44.8 (4.9) | 30.8 (4.5) | 38.1 (10.8) |
| *Sparisoma aurofrenatum* | 25.4 (8.8) | 27.5 (8.8) | 27.6 (6.4) | 29.3 (6.7) |
| *Sparisoma viride* | 10.3 (0.9) | 17.8 (2.8) | 6.5 (1.0) | 15.9 (0.8) |
| *Acanthurus bahianus* | 2.6 (0.7) | 6.3 (2.3) | 3.0 (1.4) | 1.8 (0.3) |
| *Acanthurus chirurgus* | 2.5 (1.1) | 2.5 (0.8) | 1.6 (1.0) | 0.9 (0.6) |
| *Acanthurus coeruleus* | 25.0 (6.8) | 46.5 (6.9) | 17.4 (3.0) | 24.3 (1.5) |
| Species richness | 20.6 (0.7) | 19.6 (0.9) | 17.9 (1.5) | 20.8 (0.8) |
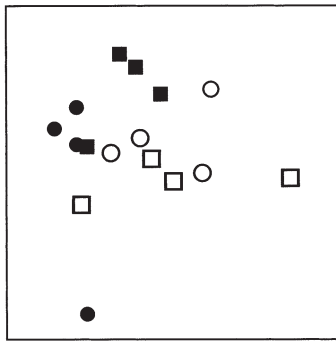
Fig. 2. Multidimensional scaling plots of biomass of 6 common surgeonfishes and parrotfishes on patch reefs in Glovers Reef lagoon. Of the fish assemblages observed, 8 were sampled on patch reefs in the wilderness zone, and 8 were sampled in the general use zone. The fish fauna was examined after macroalgae had been removed from half of the reefs in each zone. A stress value of 0.09 indicated that the 2-dimensional ordination constituted a good representation of a relationship in multidimensional space. Symbols as in Fig. 1
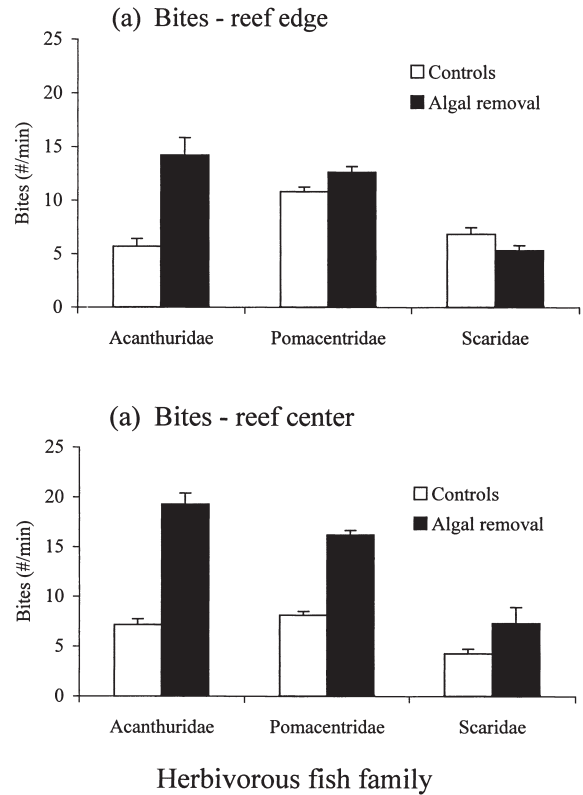


Fig. 3. Bite rates per 1 min observation in control and experimental algal reduction patch reefs for Acanthuridae, Pomacentridae (*Stegastes* spp.) and Scaridae in the patch reef edge (a) and patch reef center (b) positions. Bars are standard errors of the mean

*rus coeruleus* (>18 cm) appeared influenced by management, and therefore the biomass of this surgeonfish was significantly higher in the wilderness zone than in the general use zone (ANOVA, p = 0.01*). Fish-species richness did not differ between manipulated and unmanipulated reefs, nor did it differ between management zones (ANOVA, p > 0.05).

Comparisons of bite and aggression rates of herbivorous fishes on shoulder/edge and the center of patch reefs pooled data for the 3 *Acanthurus* species as well as those for the 2 *Stegastes* species, as they exhibited no intra-generic difference in patterns. On reefs from which algae had been removed, the bite rate on both shoulder/edge and center sites increased significantly for *Acanthurus* spp. (Kruskal-Wallis test, p < 0.001, n = 320 and n = 307 for shoulder/edge and center respectively) and *Stegastes* spp. (p < 0.05, n = 240 and p <

0.001, n = 399 respectively; Fig. 3). Similarly, aggression rates increased for *Acanthurus* spp. (p < 0.05, p < 0.001), *Stegastes* spp. (p < 0.001), and *Sparisoma viride* (p < 0.05, n = 136 and p < 0.001, n = 57 for shoulder/edge and center respectively; Fig. 4).

Table 3. Average Scaridae and Acanthuridae biomass (g), calculated from observations of fish abundance per 5 cm size class per 5 min count, on control reefs (n = 8) and reefs subjected to algal removal (n = 8). Species were ranked according to their mean contribution to the Bray-Curtis dissimilarity between control and experimental reefs. $\bar{\delta}_i$ is the contribution of the *i*th species to the average Bray-Curtis dissimilarity ($\bar{\delta}$), also expressed as percentage contribution ($\bar{\delta}_i\%$) and cumulative percentage ($\sum\bar{\delta}_i\%$). $\bar{\delta}$ = 19.57 between control and experimental reefs following the algae reduction. Ratio between the average contribution to between-group dissimilarity and its standard deviation ($\bar{\delta}_i/\text{SD}[\delta_i]$) is a predictor of how consistently the *i*th species is contributing to the overall dissimilarity

|  | Control | Removal | $\bar{\delta}_i$ | $\bar{\delta}_i/\text{SD}(\delta_i)$ | $\bar{\delta}_i\%$ | $\sum\bar{\delta}_i\%$ |
|---|---|---|---|---|---|---|
| *Sparisoma viride* | 1120 | 6327 | 5.56 | 2.49 | 28.42 | 28.42 |
| *Acanthurus chirurgus* | 392 | 331 | 3.84 | 1.47 | 19.62 | 48.04 |
| *Acanthurus coeruleus* | 2042 | 4900 | 3.22 | 1.35 | 16.46 | 64.50 |
| *Sparisoma aurofrenatum* | 804 | 2044 | 3.08 | 1.79 | 15.74 | 80.23 |
| *Acanthurus bahianus* | 259 | 681 | 2.65 | 1.15 | 13.54 | 93.77 |
| *Scarus croicensis* | 248 | 232 | 1.22 | 1.35 | 6.23 | 100.00 |

## (a) Aggression - reef edge



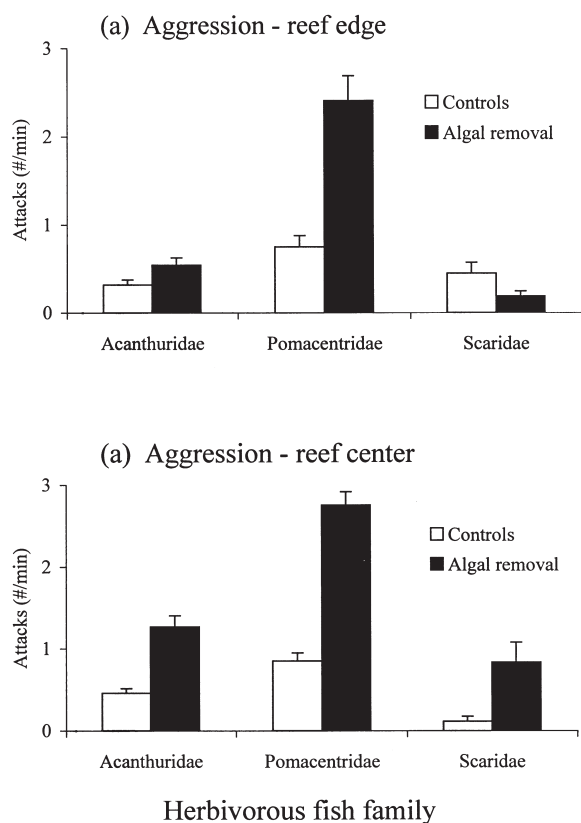## (a) Aggression - reef center



Herbivorous fish family

Fig. 4. Aggression rates per 1 min observation in control and experimental algal reduction patch reefs for Acanthuridae, Pomacentridae (*Stegastes* spp.) and Scaridae in the patch reef edge (a) and patch reef center (b) positions. Bars are standard errors of the mean

## DISCUSSION

The experimental algae-reduction technique was successful in reducing macroalgae (fleshy, calcareous and branching coralline algae) and increasing relative algae turf and coral canopy cover. The manipulation was expected to change the substratum from dominance by late successional macroalgae (McClanahan 1997, McClanahan et al. 1999b) towards early successional species of turf-forming and encrusting-coralline algae, which frequently dominate heavily grazed coral reefs (Klumpp & McKinnon 1989, 1992, Steneck 1989, McClanahan 1997). Prior to the reduction, these patch reefs were dominated by fleshy brown algae of the genera *Turbinaria*, *Sargassum* and *Lobophora* (McClanahan & Muthiga 1998). Consequently, the manipulation should have increased both the net production and palatability of the algal assemblage on these reefs as well as the exposure of turf and encrusting-coralline algae (Birkeland et al. 1985). In essence, we reversed an algal succession which has been occurring in many Caribbean reefs in the last 18 yr (Carpenter 1990,

Hughes 1994, Shulman & Robertson 1997, McClanahan & Muthiga 1998). This succession has been associated with reduced herbivory (Hughes et al. 1999), increased nutrient concentration (LaPointe 1999) and coral death through diseases and bleaching (McClanahan et al. 1999a). Our study allowed us to determine some of the consequences of this fleshy algae proliferation on coral-reef fishes and its possible interaction with fisheries management. We also intended to compare the findings of this study with those of a similar manipulation undertaken in a 25 yr-old coral reef park in Kenya (McClanahan et al. 1999b).

The composition of the fish fauna on patch reefs in the Glovers Reef atoll appeared to be influenced by the removal of macroalgae, as illustrated by multidimensional scaling ordination. The effect was, however, only significant when applied to a limited assemblage of common herbivores, using biomass estimates instead of abundance data. Juvenile surgeonfish (Acanthuridae) and parrotfish (Scaridae) were common on the examined reefs and constituted a large part of these families' numbers. Classification of individuals according to size classes revealed that the difference in abundance between control and experimental reefs was more pronounced in adult fishes, presumably because of their increased mobility. Adult surgeonfishes and parrotfishes often move in mixed schools among patches of reef and areas of seagrass, exploring available resources (Robertson et al. 1979), and are often found in proportion to these resources (van Rooij et al. 1996b, Lawson et al. 1999). Hence, for herbivorous fishes, biomass estimates produced the most relevant description of the immediate response to algae reduction.

Species-specific responses to the reduction of algae were evident for 2 of the dominant herbivores, *Sparisoma viride* and *Acanthurus coeruleus*. The former species also contributed most to the observed dissimilarities between manipulated and unmanipulated reefs. These species would appear to be most dependent on early successional turfs, as determined by this and other studies (Bruggemann et al. 1994a,b, van Rooij et al. 1996b, Lawson et al. 1999). A population increase was also found for the invertebrate-feeding wrasse *Thalassoma bifasciatum* (Labridae). While the response of herbivores to the algae reduction could be related to the movement of larger fishes, the response of *T. bifasciatum* may have been due to increased activity or visibility after the reduction. This species has, however, been observed to move over large distances of as much as 1.5 km for the purpose of participating in mating aggregations (Warner 1995) and could, therefore, have migrated from other patch reefs. *T. bifasciatum* appeared to be actively feeding and mating (McClanahan pers. obs.) on the algae-reduc-

tion reefs, and disturbance to the algae may have increased access to its prey.

Herbivorous surgeonfishes and damselfishes fed at faster rates and were more aggressive on experimental reefs, suggesting improved feeding conditions and, therefore, increased resource defense following the manipulation (Carpenter & MacMillen 1976, Eakin 1987). The algal reduction study in a Kenyan park found a similar response of increased abundance and feeding rates for many herbivorous species, but notably not for macrophyte-feeding parrotfishes of the genera *Leptoscarus* and *Calotomus* (McClanahan et al. 1999b), which are genera not found in the Caribbean fauna. In our Caribbean study, bite and aggression rates were more pronounced on the reef center, which originally contained the most algae and exhibited the lowest levels of herbivory, than on the edge positions of the reef (McClanahan & Muthiga 1998, McClanahan 1999).

Fisheries management was a weak factor in this study in relation to benthic cover and numbers of fishes. Fish assemblages did not differ in composition nor in species richness between the restricted and non-restricted zones. In the wilderness zone, however, a few species, particularly large size classes, were more abundant or exhibited a proportionally higher increase following algae reduction. The difference was however only significant for *Acanthurus coeruleus* biomass, which prior to manipulation was 30% higher in the wilderness zone than in the general use zone, and almost 3 times as high in the wilderness zone following the reduction of macroalgae. Consequently, either fishing was having only a small influence on reef fishes in this remote atoll (but see McClanahan & Muthiga 1998 and McClanahan 1999), or perhaps management is still of too recent or ineffective. Small differences were not likely to be detected by our sampling effort and an alternative sampling design and effort may be required to determine the effects of management in these early stages of closure from fishing. The Kenyan study (McClanahan et al. 1999b) was undertaken in a park that has been protected from fishing for 25 yr (Watamu Marine National Park, WMNP), and it is notable that the response of fishes to algae reduction was greater in this older park in terms of numbers, specific diversity, and feeding habits than in the study reported here. Beyond increases in parrot and surgeonfish numbers and feeding rates in the WMNP, there were also increases in angelfish, butterflyfish, and triggerfish numbers, although it is not known whether this was a response to changes in resources or simply a multispecies schooling behavior catalyzed by herbivorous fishes.

The implication of these 2 studies is that domination of coral reefs by macroalgae (i.e. >2 kg wet wt m$^{-2}$ or 40% of the substrate) reduces the abundance and feeding rates of a number of herbivorous fishes, but also of invertebrate feeders. This may seem counter intuitive, as it is arguable if herbivores would respond positively to additional plant and algal resources. However, most herbivorous fishes, with the exception of a small guild of macrophyte feeders, prefer turf algae (Choat 1991), and the overgrowth of turf algae and encrusting corallines by fleshy algae appears to suppress many herbivorous fishes. Previous studies have focused on the effects of macroalgal overgrowth on corals (Hughes 1994, McClanahan et al. 1995, Tanner 1995), but our composite studies of reefs from 2 oceans suggest that the ecological degradation of reefs by macroalgal overgrowth is also suppressing some species of fishes, particularily herbivores.

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