Effect of macroalgal reduction on coral-reef fish in the Watamu Marine National Park, Kenya

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Abstract. The paper extends by five months the record of effects of reduction of leathery-macrophyte abundance in plots in a coral reef outcrop in the Watamu National Park, a site that had eliminated fishing for >20 years. After one year, leathery macrophytes had not recovered, but articulated green calcareous algae (*Halimeda*) had, and replaced leathery macrophytes as the dominant cover on the experimental plots. Of the 56 fish species studied, 20 were influenced by the algal reduction. There were increased numbers of individuals and species of herbivorous surgeonfish (4 species) and parrotfish (5 species), and increased population densities of invertebrate-eating fishes including angelfish (2 species), butterflyfish, emperors and snappers (not identified to species), wrasses (2 species), and a triggerfish. Negative effects were restricted to three damselfishes and one wrasse. Parrotfish, snappers and the total fish abundance showed a significant increase in size and biomass in the algal reduction plots over the year. No differences were found for macrophyte-feeding parrotfish (*Calotomus carolinus*). Increased herbivory was the likely cause of the slowness of the recovery of leathery macrophytes and the switch in dominance towards *Halimeda*.

Extra keywords: algae, herbivory, Kenya, phase shifts, marine protected areas, reef degradation

Introduction

The effect of erect leathery macrophytes on fish populations is variable and may differ with ecosystems and the composition and structure of their substratum. Studies from temperate regions, mostly from sandy bottoms, suggest that submerged aquatic vegetation (SAV) such as seagrasses can have a positive effect on fish populations by providing food and refuge to adults and recruits (Huh and Kitting 1985; Rozas and Odum 1988; Lubbers *et al.* 1990). High levels of SAV may, however, inhibit the success of predatory fish (Heck and Crowder 1991), which could reduce their populations while enhancing their prey populations. Further, late-successional algae may have lower levels of net production than early-successional algal communities (Littler 1980; Littler and Littler 1980; Birkeland *et al.* 1985; Steneck and Dethier 1994) and this could reduce the transfer of benthic production to higher trophic levels common to fish.

High levels of SAV in coral reefs have been considered a form of reef degradation (Hughes 1994). High frondose-algal cover has been shown to reduce the abundance and numbers of species of coral reef fishes (Chabanet *et al.* 1995;

McClanahan *et al.* 1999, 2000, 2001) and coral survival (Tanner 1995; Hughes and Tanner 2000). Short-term experimental reductions of abundant leathery macrophytes on coral reefs have generally shown positive effects on fishes, particularly herbivorous fishes, but also fishes that feed on invertebrates (McClanahan *et al.* 1999, 2000, 2001). Consequently, reducing erect algae could change the patterns of fish dominance in reefs where frondose algae have overgrown reefs previously dominated by corals. The effects may be short lived, however, if unpalatable algae quickly colonize and dominate the substratum. Frondose leathery macrophytes would be expected to colonize and recover after 2 to 6 months in the absence of high herbivory (McClanahan 1997; McClanahan *et al.* 2001).

Investigations were undertaken in lagoonal-reef carbonate outcrops within the Watamu Marine National Park (WMNP; 3°22′S,40°0′E), in an area where substratum cover has been monitored for 12 years. This park was established and largely eliminated resource extraction in 1978. The reef outcrops are ~2 km from Mida creek in a lagoonal area receiving high-nutrient groundwater runoff (Mwatha *et al.* 1998). Algae were reduced in experimental plots, and the response of the fish families was recorded for 3 months

(McClanahan *et al.* 1999). The present paper extends the record for a further 9 months. The aims of this study were to determine *(1)* whether the benthic taxa on the reduction plots differed from the control plots after one year, *(2)* whether the short-term responses of the fish would be maintained beyond the few months required for algae to colonize after a pulsed disturbance, and *(3)* whether, after 1 year, fish on the algal reduction plots had increased in size relative to control plots.

Materials and methods

Study site

The reef is a linear lagoonal coral reef with scattered outcrops of massive *Porites*, encrusting *Montipora* and scattered colonies of *Acropora* and species in the Faviidae. The area selected for manipulations was in shallow water (1 to 2.5 m deep at low tides; 4 m tidal range). The substratum is dead carbonate coral and algae, colonized by algae and hard corals, and surrounded by seagrass (*Thalassodendron ciliatum*) and sand. The dominant erect algae on these outcrops were *Sargassum duplicatum* and *Halimeda opuntia*. Other species of *Sargassum* and *Halimeda* were also present, as well as species in the genera *Turbinaria*, *Dictyota*, *Lobophora*, *Hypnea* and *Amansia*.

The establishment of eight 10 m × 10 m plots in January 1997 has been described (McClanahan *et al.* 1999). During 19–21 March 1997, erect algae were reduced in four of the plots as far as was possible while avoiding damage to living coral and other invertebrates. The remaining four plots served as controls. The benthos and fish fauna in these plots was studied twice two months before, and seven times during the year after the manipulation. Family-level taxonomic analyses of all surveys except the final four have already been reported (McClanahan *et al.* 1999).

Field measurements and data analysis

Benthic cover, fish abundance and species richness were studied in treatment and control plots. The linear contribution of each of nine substratum categories was measured along two haphazardly placed 10 m transects, although organisms <3 cm were not recorded. We present the data on benthic algae based on the nomenclature of gross functional groups as described by Steneck and Dethier (1994). The substratum categories were hard coral, soft coral, seagrass, sponge, sand, microalgae, crustose red algae, articulated calcareous green (*Halimeda*) algae and leathery macrophytes. We present findings for hard coral and the dominant algal groups. Immediate changes after the algal reduction were attributable to increased exposure of some organisms, such as hard coral, microalgae and crustose red algae, so statistical comparisons of substratum were restricted to the sampling periods after algal reduction.

Duplicate quadrats of 25 cm × 25 cm were placed randomly in all the plots and the erect algae within the quadrat area were cropped and transported to the laboratory in sealed plastic bags for identification (Jaasund 1976; Moorjani and Simpson 1988) and separation and weighing of genera. The algae were placed on absorbent towels to remove excess water before the wet weight of those in each genus was determined. Average wet weight per 0.065 m^2 per experimental plot (biomass) was used in the analyses. Biomass data were analysed by a two-way ANOVA with replication. The data on substratum cover were log-transformed before the two-way ANOVA. ANOVAs were used to determine the effects of treatment and time on both algal biomass and cover after the manipulation.

Fish were sampled at each survey interval by visual counts in each of the plots using the Discrete Groups Sampling (DGS) method (Greene and Alevizon 1989; McClanahan 1994); for details, see McClanahan *et al.* (1999). In the analysis, parrotfish were divided into browsers of macrophytes (*Calotomus*) and grazers (*Scarus* and *Hipposcarus*) (Bellwood 1990). Wet biomass was estimated from known length–weight relationships (McClanahan and Kaunda-Arara 1996).

Differences between fish abundance for individual species, species per plot and the wet weight and number of individuals per family were determined by a two-way ANOVA of the period after algal reduction to determine the effects of the treatment and time on fish populations. If statistically significant differences occurred for the individual species, a *t*-test was performed on the pre-reduction data to test whether differences occurred before the manipulation. Population count data estimated from the DGS method are more accurate than biomass estimates and were, therefore, relied on more heavily in making decisions concerning statistical significance. Statistical significance of $P < 0.05$ was used for decisions about significant changes but $P < 0.1$ are reported in the tables and figures in order to record borderline cases.

Results

Algal reduction and recovery

By the end of the year of sampling, total algal biomass in the experimental plots approached but did not reach the biomass in the controls, with greater recovery on a weight basis than in terms of cover (Table 1).

Water turbulence during the south-east monsoon (April–September) uprooted leathery macrophytes, particularly *Sargassum*, in the control plots. Neither control nor experimental plots had recovered to the original biomass levels at the end of the year (Fig. 1). The apparent rise in the cover of crustose red algae after reduction of the algal canopy was largely attributable to the increased visibility of the under storey to the line-transect survey.

There were significant differences in total biomass and absolute cover between control and experimental plots and with time (Table 1). There were also significant interactions between time and treatment.

The fish fauna

Effects of algal reduction on the fish included increases in total fish density, biomass and numbers of species (Table 2). On the basis of the total year of sampling, population densities of surgeonfish, triggerfish, butterflyfish, wrasses, angelfish and parrotfish were higher on the algal reduction plots. Browsing parrotfishes showed no effect from the treatment alone, but a significant interaction between time and treatment attributable to an increase in their numbers on the reduction plots and a decrease in the control plots after 150 days (Table 2).

Total fish wet weight estimates suggest a doubling in biomass in the algal reduction plots with the greatest increases in parrotfish and surgeonfish, and in emperor and snapper (Fig. 2), although this was not significant for parrotfish and surgeonfish when analysed separately. Biomass increased significantly over time in the experimental plots for the parrotfish and snappers and marginally so for the total fish group compared with control plots (*t*-test, Fig. 3). Size frequency analysis from the

Table 1. Differences in the gross categories of substratum after algal reduction and in control plots: *(a)* absolute cover for the dominant fleshy algal genera and *(b)* wet weight (g per 0.0625 m^2)

Percent difference and two-way ANOVA statistics included. NS, not significant

| Genus	Control		Experiment		Change	Treatment		Time		Interaction	
	Mean	s.e.m.	Mean	s.e.m.	% ((e–c)/c)	F	P	F	P	F	P
(a) absolute cover (cm m^2)											
Sargassum	52.3	8.2	16.9	3.0	–67.6	29.6	0.00	3.1	0.01	6.2	0.00
Halimeda	79.4	13.3	24.6	6.2	–69.0	15.1	0.00	2.1	0.07	0.6	NS
Turbinaria	0.8	0.4	2.4	0.9	202.5	4.0	0.05	2.3	0.06	2.7	0.03
Amansia	0.7	0.3	0.4	0.2	–46.3	0.8	NS	0.5	NS	0.7	NS
Amphiroa	0.7	0.2	0.2	0.1	–69.3	6.1	0.02	1.3	NS	1.5	0.19
Pocokiella	1.1	0.6	0.9	0.6	–13.9	0.0	NS	1.4	NS	0.4	NS
Dictyota	0.2	0.1	0.3	0.2	76.5	0.3	NS	1.0	NS	1.5	0.19
Wet total	135.2	14.2	45.8	7.3	–66.1	48.9	0.00	3.0	0.02	4.1	0.00
(b) wet weight											
Sargassum	29.7	13.8	7.8	6.9	–73.7	90.8	0.00	5.3	0.00	4.9	0.00
Halimeda	20.6	8.7	10.5	7.4	–49.2	15.6	0.00	2.6	0.06	1.0	NS
Turbinaria	1.5	1.4	2.2	1.5	42.4	2.9	0.09	2.1	NS	1.9	NS
Amphiroa	0.7	2.0	0.3	0.7	–51.4	0.2	0.08	157.6	0.00	0.3	NS
Pocockiella	0.5	0.7	0.4	0.7	–25.7	0.9	NS	3.4	0.02	0.2	NS
Crustose red	13.3	6.9	21.5	9.1	62.1	28.4	0.00	7.7	0.00	12.0	0.00
Dictyota	3.0	2.8	4.0	2.9	34.4	3.2	0.08	4.3	0.01	0.4	NS
Total	69.2	9.8	46.9	10.3	–32.2	59.5	0.00	3.8	0.01	0.8	NS
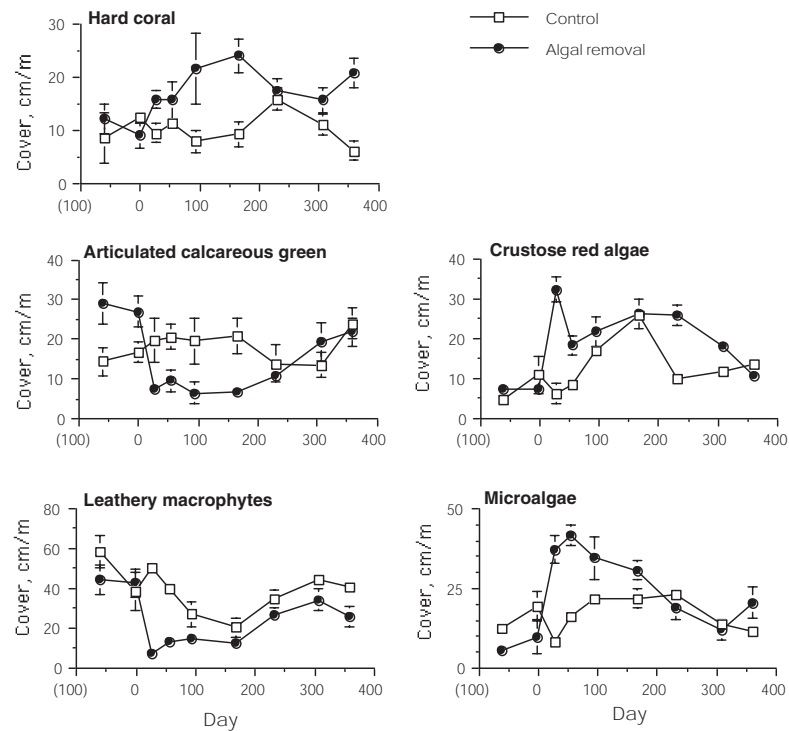
Fig. 1. Changes in hard coral and the dominant algal groups over time in the erect-algal-reduction experiment and control plots based on the line-transect data. Bars are s.e.m.

**Table 2.   Two-way ANOVA statistics for *(a)* fish biomass (kg 100 m^{-2}), *(b)* population density (individuals per 100 m^{-2}) and
(c) numbers of species per 100 m^2 in the algal reduction and control plots**

P values given if between 0.01 and 0.10; otherwise, NS is *P* >0.10. *P <0.01, **P <0.001, ***P <0.0001

Family	Control		Experiment		Change	Treatment		Time		Interaction	
	mean	s.e.m.	mean	s.e.m.	% ((*e–c*)/*c*)	F	*P*	F	*P*	F	*P*
(a) wet weight per plot											
Acanthuridae	0.6	0.1	1.2	0.1	98.0	22.4	***	1.0	NS	0.8	NS
Balistidae	0.1	0.1	0.2	0.1	172.6	2.4	NS	2.0	0.09	1.4	NS
Chaetodontidae	0.0	0.0	0.0	0.0	90.0	1.2	NS	0.4	NS	2.0	0.09
Labridae	0.8	0.1	1.0	0.1	32.3	2.8	0.10	0.3	NS	0.5	NS
Lutjanidae	0.5	0.1	2.0	0.3	291.7	36.2	***	0.9	NS	1.4	NS
Mullidae	0.0	0.0	0.1	0.0	88.9	1.2	NS	0.6	NS	1.1	NS
Others	0.9	0.2	2.1	0.3	125.7	7.7	**	1.0	NS	0.3	NS
Pomacanthidae	0.1	0.0	0.2	0.1	105.1	2.4	NS	2.1	0.07	1.6	NS
Pomacentridae	0.5	0.1	0.6	0.1	7.7	0.2	NS	2.1	0.08	0.1	NS
Scaridae	1.2	0.1	2.7	0.3	124.7	22.7	***	0.8	NS	1.0	NS
Siganidae	0.3	0.1	0.4	0.2	39.0	0.2	NS	0.8	NS	1.1	NS
Total	5.1	0.3	10.5	0.8	107.1	42.3	***	1.4	NS	0.9	NS
(b) individuals per plot											
Acanthuridae	6.5	0.4	11.5	0.5	76.0	29.5	***	0.3	NS	0.7	NS
Balistidae	0.2	0.0	0.5	0.1	180.0	6.9	*	0.9	NS	0.9	NS
Chaetodontidae	0.3	0.2	0.9	0.2	200.0	8.7	**	1.7	NS	1.3	NS
Labridae	17.5	1.3	22.4	1.8	28.4	8.9	**	3.0	*	0.6	NS
Pomacanthidae	0.8	0.1	2.5	0.3	200.0	36.9	***	1.1	NS	1.2	NS
Pomacentridae	19.0	1.3	24.3	1.7	27.6	3.6	0.07	0.8	NS	0.3	NS
Scaridae	3.3	0.4	7.2	0.6	119.6	38.7	***	0.7	NS	2.1	0.08
Scaridae-grazers	1.7	0.2	5.3	0.5	208.6	41.2	***	1.2	NS	2.5	0.02
Scaridae-browsers	1.6	0.3	1.9	0.3	22.7	1.1	NS	0.4	NS	2.1	0.05
Total	47.6	2.1	69.3	3.9	45.5	25.2	***	1.5	NS	0.6	NS
(c) species per plot											
Acanthuridae	2.8	0.2	3.4	0.2	23.1	5.1	*	0.7	NS	1.4	NS
Balistidae	0.2	0.0	0.5	0.1	180.0	6.9	*	0.9	NS	0.9	NS
Chaetodontidae	0.3	0.1	0.7	0.1	185.7	8.0	**	1.6	NS	0.7	NS
Labridae	8.1	0.3	8.3	0.4	3.1	0.2	NS	0.7	NS	0.9	NS
Pomacanthidae	0.6	0.1	1.4	0.2	123.5	21.7	***	1.5	NS	1.1	NS
Pomacentridae	4.6	0.2	3.8	0.2	−17.1	3.3	0.07	0.6	NS	0.3	NS
Scaridae	2.2	0.2	4.2	0.3	93.4	35.2	***	0.9	NS	0.9	NS
Total	18.7	0.5	22.4	0.9	19.7	11.9	**	0.8	NS	0.9	NS

biomass sampling estimates suggests that there was an increase in the body sizes of these herbivorous groups and snappers and emperors over the 1-year of study (Fig. 4), but that there were no changes in the control plots.

There was a 20% increase in numbers of fish species on the algal reduction plots with elevated numbers for the surgeonfish, triggerfish, butterflyfish, angelfish and parrotfish families (Table 2). Of the 58 species sampled, 22 had significantly different population numbers on control *v.* experimental plots after reduction: 17 were higher and 5 were lower on the experimental plots (Table 3). However, one damselfish species had more individuals and one damselfish species had fewer, on experimental plots even before the manipulation. Hence, 20 of 56 species were influenced by the algal reduction; 16 were positive (including 4 herbivorous surgeonfish species and 5 parrotfish species) and 4 were negative population effects (with 3 being damselfish).

Discussion

Response of fishes

Twenty of the 56 studied species showed a population response to the algal reduction of which 80% were positive responses and of these 56% were among the grazing herbivores. In many cases the response was rapid and persisted over the year. Increased sizes of surgeonfish, parrotfish, scavengers and snappers after one year suggest either *(1)* increased growth rates on these plots or
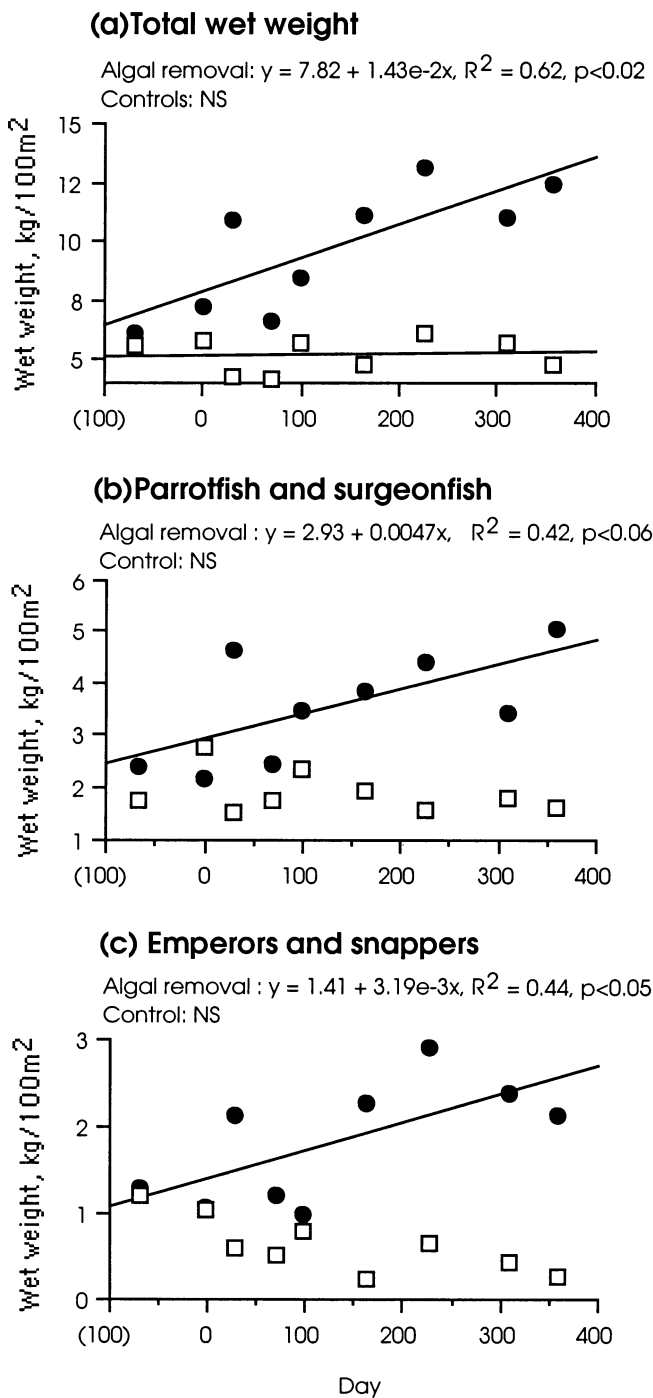
(a)Total wet weight

Algal removal: y = 7.82 + 1.43e-2x, R^2 = 0.62, p<0.02
Controls: NS

(b)Parrotfish and surgeonfish

Algal removal : y = 2.93 + 0.0047x, R^2 = 0.42, p<0.06
Control: NS

(c) Emperors and snappers

Algal removal : y = 1.41 + 3.19e-3x, R^2 = 0.44, p<0.05
Control: NS

Fig. 2. Time-series plot of the estimated wet weight of fish on (●) algal reduction and (□) control plots: *(a)* all fish *(b)* grazing parrotfish and surgeonfish (genus *Scarus* and *Hipposcarus*), and *(c)* snappers and emperors. Bars are s.e.m.

(2) occupation by competitive dominants, and both suggest better resource conditions on the algal-reduction than on the control plots. Previous studies have found increased feeding and aggression rates on algal reduction plots for herbivorous

fishes (McClanahan *et al.* 1999, 2000). Negative effects were largely restricted to the wrasse *Cheilio inermis* and three small-bodied damselfish species (*Amphiprion allardi*, *Stegastes fasciolatus* and *Plectroglyphidodon dicki*). Perhaps these smaller species lacked protective cover or appropriate food without erect algae.

Some of these changes were expected and others were not. Most herbivorous fish feed on turf or microscopic algae (Choat 1991), which is likely to be more accessible once the less palatable algal canopy is reduced. Our study indicates that in established marine parks such as Watamu, the effect persists for at least one year, in contrast to a newly established marine park where the effect persisted for only a few months (McClanahan *et al.* 2001). The positive population response in many of the invertebrate-feeding species was unexpected because we had predicted that their prey might decrease (Duffy and Hay 1991). This may depend, however, on the particular food and cover requirements of the individual species. For example, there were more butterflyfishes in the experimental plots, and this may be attributed to the higher coral cover or increased accessibility to coral on these plots. Less easy to explain are population increases on the experimental plots of the two ornate wrasses (*Thalassoma lunare* and *Gomphosus caeruleus*), which are generalized pickers of small-bodied invertebrates and ubiquitous to reef environments in this region. A comparable study in the Caribbean found an increase in a similar wrasse, *Thalassoma bifasciatum*, with the algal reduction (McClanahan *et al.* 2001). Both studies indicate that these wrasses prefer reduced algal abundance. In the Caribbean study, two snappers were affected by the algal reduction, one positively (*Lutjanus apodos*) and one negatively (*L. griseus*). Sano (2001) found higher numbers of the emperor *Lethrinus harak* in an algae-dominated than in a rubble-dominated reef area. Consequently, it is hard to generalize about the response of snappers and emperors to algal abundance. They are, however, likely to be influenced by the history of fishing at the sites (McClanahan *et al.* 2001). The one wrasse that decreased in the experimental plots in Watamu was the cryptically coloured and thin-bodied *C. inermis*. Sano (2001), too, found higher numbers of this species in algae-dominated than in rubble-dominated areas. Tolerance of species to different cover environments could play a more influential role than food availability in explaining the differences found for wrasses and, perhaps, snappers and emperors.

The differences reported here for coral reefs compared with other studies of SAV largely associated with seagrass and sandy bottom ecosystems suggest differences for tropical hard bottom and soft bottoms. In hard-bottom ecosystems the reef or rock structure may largely provide the refuge that fishes require (Hixon 1993), whereas in sandy-bottom ecosystems the plants themselves are critical for structure (Rozas and Odum 1988). In tropical hard-bottom
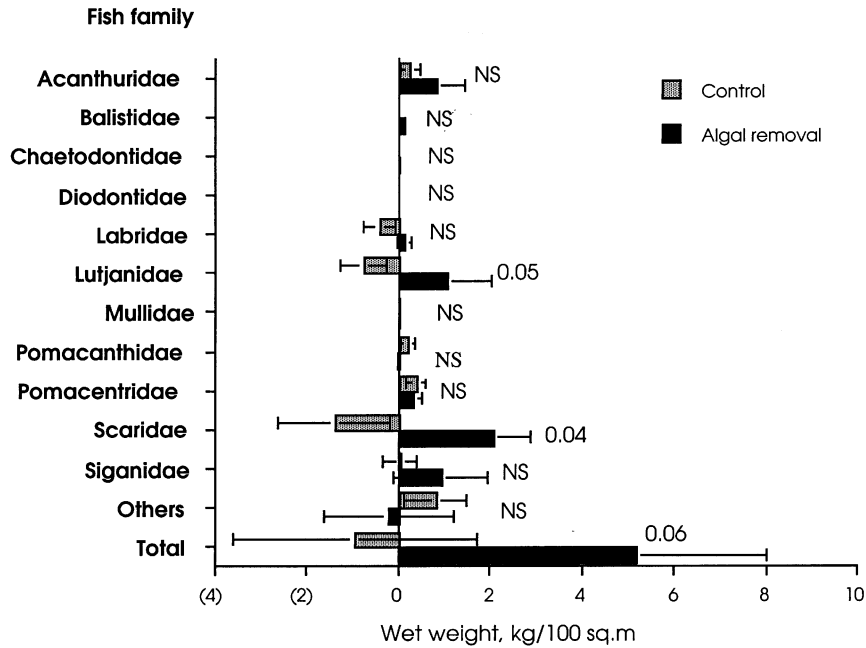
Fish family

Fig. 3. Change in wet weight of fish one year after the reduction of erect algae. *t*-test results presented for comparisons of control and experimental plots. Bars are s.e.m.

ecosystems, erect algae may, however, be a slightly more preferred habitat for some tropical fishes than coral rubble that lacks the complexity of undisturbed reefs (Sano 2001).

Where shelter is available, such as topographically complex reefs, factors of food availability, its palatability and net production may be more limiting to fish populations. Food
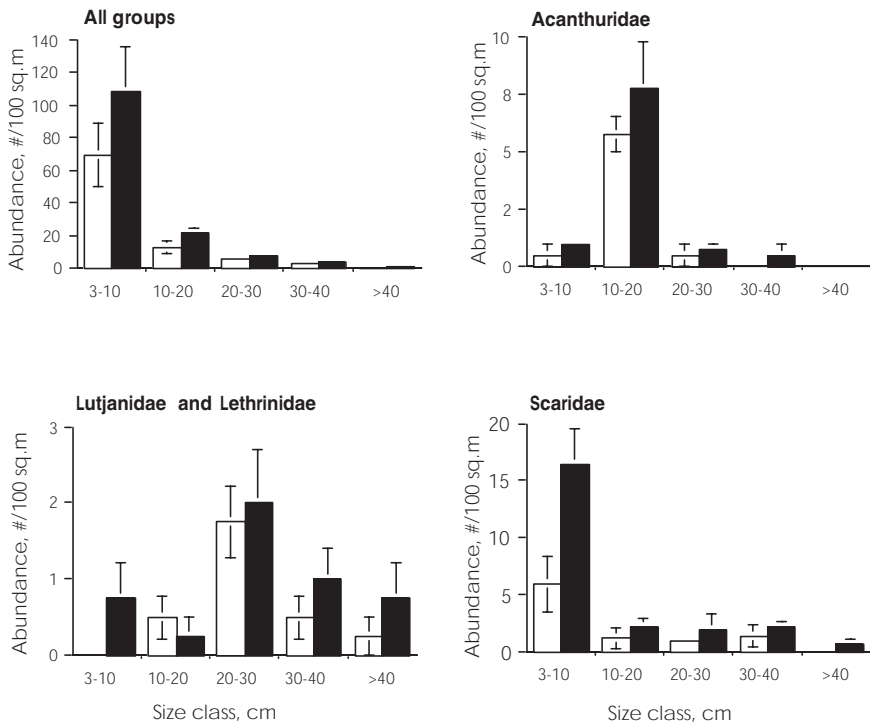

Fig. 4. Size frequency distributions of fishes showing size responses to algal reduction. White columns: March 1997, before algal reduction. Black columns: March 1998, 1 year after reduction. Bars are s.e.m.

Table 3. Effects of time and algal removal on fish species

Results of two-way ANOVA. If ANOVA was significant, a *t*-test was performed on the pre-removal data. NS, not significant; n.e., not encountered

Species	Experiment mean	s.d.	Control mean	s.d.	Change (%) [(e–c)/c]*100	ANOVA Treatment F	P	Time F	P	*t*-test, two tail Before, *c* v. *e*
Acanthurus leucosternon	4.6	0.6	3.7	0.6	23.1	13.1	0.01	2.6	NS	NS
Ctenochaetus striatus	4.2	1.0	1.1	0.4	268.8	123.3	0.01	3.0	NS	NS
Ctenochaetus strigosus	1.0	0.4	0.8	0.5	33.3	0.8	NS	0.3	NS	
Acanthurus xanthopterus	0.7	0.3	0.1	0.1	375.0	13.0	0.01	0.8	NS	NS
Acanthurus nigrofuscus	0.5	0.4	0.2	0.3	133.3	1.5	NS	0.3	NS	
Acanthurus dussumieri	0.3	0.4	0.1	0.3	75.0	1.4	NS	6.6	0.02	
Naso annulatus	0.0	0.1	0.2	0.5	−80.0	0.6	NS	0.9	NS	
Zebrasoma scopas	0.0	0.1	0.2	0.3	−80.0	1.8	NS	1.1	NS	
Zebrasoma veliferum	0.2	0.2	0.0	0.0		6.3	0.05	1.0	NS	n.e.
Balistapus undulatus	0.5	0.3	0.2	0.1	180.0	7.4	0.03	1.0	NS	NS
Chaetodon trifascialis	0.8	0.3	0.0	0.0		4.5	0.08	1.0	NS	n.e.
Chaetodon auriga	0.5	0.4	0.2	0.3	180.0	3.6	NS	1.4	NS	
Chaetodon trifasciatus	0.1	0.1	0.0	0.1	200.0	2.4	NS	2.6	NS	
Chaetodon guttatissimus	0.1	0.1	0.0	0.1	100.0	0.3	NS	0.6	NS	
Thalassoma hebraicum	6.1	1.8	5.0	1.5	22.1	5.6	0.06	6.4	0.02	NS
Halichoeres hortulanus	2.9	1.3	2.1	0.2	36.7	2.9	NS	1.2	NS	
Labroides dimidiatus	2.4	1.0	2.2	0.4	8.1	0.2	NS	0.8	NS	
Gomphosus caeruleus	2.9	0.9	1.3	0.4	128.6	15.0	0.01	0.6	NS	NS
Thalassoma hardwicke	1.5	0.6	1.2	0.6	23.5	0.9	NS	1.6	NS	
Stethojulis albovittata	1.4	1.2	1.2	1.0	14.7	0.6	NS	11.0	0.01	
Thalassoma amblycephalum	1.1	1.4	0.9	0.6	23.1	0.2	NS	2.4	NS	
Cheilinus trilobatus	0.5	0.3	0.6	0.4	−22.2	0.4	NS	0.4	NS	
Thalassoma lunare	0.8	0.4	0.3	0.2	214.3	13.0	0.01	1.8	NS	NS
Pseudocheilinus hexataenia	0.5	0.7	0.3	0.3	100.0	0.8	NS	1.2	NS	
Labrichthys unilineatus	0.4	0.5	0.4	0.4	0.0	0.0	NS	1.1	NS	
Anampses caeruleopunctatus	0.4	0.3	0.3	0.2	42.9	0.8	NS	1.8	NS	
Cheilio inermis	0.1	0.2	0.5	0.5	−76.9	7.3	0.04	3.5	0.07	NS
Coris caudimacula	0.1	0.1	0.3	0.3	−50.0	1.8	NS	1.2	NS	
Epibulus insidiator	0.3	0.3	0.1	0.2	100.0	1.2	NS	0.8	NS	
Hemigymnus melapterus	0.1	0.1	0.2	0.1	−20.0	0.3	NS	1.2	NS	
Bodianus axillaris	0.1	0.1	0.1	0.2	−25.0	0.1	NS	0.6	NS	
Labroides bicolor	0.1	0.2	0.1	0.2	33.3	0.1	NS	0.4	NS	
Coris frerei	0.2	0.2	0.0	0.0		10.8	NS	1.0	NS	
Coris aygula	0.0	0.0	0.1	0.2	−100.0	3.7	0.10	1.0	NS	n.e.
Oxycheilinus mentalis	0.0	0.1	0.1	0.1	−50.0	1.0	NS	4.3	0.05	
Anampses twisti	0.1	0.1	0.0	0.1	100.0	1.0	NS	4.3	0.05	
Diproctacanthus xanthurus	0.1	0.3	0.0	0.0		1.0	NS	1.0	NS	
Centropyge multispinis	2.0	0.7	0.7	0.3	175.0	20.2	0.01	1.1	NS	NS
Pomacanthus semicirculatus	0.5	0.4	0.1	0.2	550.0	13.4	0.01	4.3	0.05	NS
Plectroglyphidodon lacrymatus	12.9	1.8	3.3	1.4	289.2	126.7	0.01	1.0	NS	0.03
Pomacentrus sulfureus	5.3	1.4	4.0	0.8	32.4	14.8	0.01	5.5	0.03	NS
Chrysiptera unimaculata	2.1	1.1	3.3	1.9	−34.8	1.6	NS	0.8	NS	
Amphiprion akallopisos	1.0	0.2	4.1	0.7	−74.8	76.0	0.01	0.4	NS	0.02
Abudefduf sexfasciatus	1.7	2.1	2.1	1.8	−19.0	0.6	NS	7.9	0.01	
Pomacentrus caeruleus	0.7	0.7	0.2	0.3	280.0	3.0	NS	0.8	NS	
Plectroglyphidodon dickii	0.0	0.0	0.8	0.2	−100.0	85.4	0.01	1.0	NS	NS
Plectroglyphidodon johnstonianus	0.5	0.4	0.1	0.1	275.0	4.8	0.07	0.9	NS	NS
Amphiprion allardi	0.0	0.0	0.6	0.1	−100.0	153.6	0.01	1.0	NS	NS
Stegastes fasciolatus	0.0	0.0	0.5	0.3	−100.0	21.1	0.01	1.0	NS	NS
Scarus niger	1.9	0.6	0.8	0.3	134.8	37.9	0.01	2.9	NS	NS
Chlorurus sordidus	1.6	0.6	0.5	0.4	253.8	13.1	0.01	0.3	NS	NS
Scarus frenatus	0.5	0.2	0.3	0.1	114.3	8.0	0.03	1.0	NS	NS
Chlorurus strongylocephalus	0.4	0.4	0.0	0.0		9.2	0.02	1.0	NS	NS
Hipposcarus harid	0.3	0.2	0.0	0.1	700.0	10.5	0.02	1.9	NS	n.e.
Scarus ghobban	0.1	0.2	0.1	0.2	100.0	0.4	NS	0.5	NS	
Scarus russelii	0.1	0.3	0.0	0.1	300.0	1.0	NS	1.2	NS	
Grazers	5.3	1.3	1.7	0.4	208.3	37.7	0.01	0.7	NS	NS
Calotomus carolinus	1.9	0.7	1.6	0.9	20.5	0.3	NS	0.2	NS	
Browser	1.9	0.7	1.6	0.9	22.7	0.4	NS	0.2	NS	
All species	70.3	12.8	48.0	5.9	46.5	34.3	0.00	2.9	NS	NS

is likely to be of secondary importance to cover but significant where cover is already available, as in the topographically complex sites we studied.

A possible restoration method?

The physical reduction of canopy algae with sheers and wire brushes could be useful to restore coral on the small scale of highly visited sites in parks. The low abundance of erect algae may persist if herbivory increases after the reduction. Our study indicated increased herbivory after the reduction and this is likely to have slowed recovery of leathery macrophytes, because one year is sufficient time for canopy algae to recover (McClanahan 1997; McClanahan *et al.* 2001). There was also a switch in algal dominance on these plots from leathery macrophytes to *Halimeda*. This indicates that herbivory arrested the algal succession (McClanahan 1997) because most articulated calcareous green algae are more herbivore resistant than leathery macrophytes (Littler *et al.* 1983; Hay 1984; Lewis 1986).

The success of coral reef restoration methods relies on other factors affecting coral and fish mortality. For example, we abandoned this restoration experiment after March 1998 when corals in the plots bleached and died at the end of the north-east monsoon. This was associated with the 1998 El-Niño warming and coral bleaching (McPhaden 1999; Goreau *et al.* 2000). Additionally, if nutrification is a factor contributing to algal dominance, continued or increasing nutrification will make restoration programmes difficult. Consequently, regional or global-level phenomena have the potential to interfere with local restoration programmes, and their potential influence needs to be considered before restoration is attempted.

Acknowledgments

References

Bellwood, D. R. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**, 189–214.

Birkeland, C., Nelson, S. G., Wilkins, S., and Gates, P. (1985). Effects of grazing on herbivorous fishes on coral reef community metabolism. Proceedings of the 5th International Coral Reef Congress **4**, 47–51.

Chabanet, P., Dufour, V., and Galzin, R. (1995). Disturbance impact on reef fish communities in Reunion Island (Indian Ocean). *Journal of Experimental Marine Biology and Ecology* **188**, 29–48.

Choat, J. H. (1991). The biology of herbivorous fishes on coral reefs. In 'The Ecology of Fishes on Coral Reefs'. (Ed. P. F. Sale.) pp. 120–55. (Academic Press: New York.)

Duffy, J. E., and Hay, M. E. (1991). Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* **72**, 1286–98.

Goreau, T., McClanahan, T., Hayes, R., and Strong, A. (2000). Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**, 5–15.

Greene, L. E., and Alevizon, W. S. (1989). Comparative accuracies of visual assessment methods for coral reef fishes. *Bulletin of Marine Science* **44**, 899–912.

Hay, M. E. (1984). Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* **64**, 396–407.

Heck, K. L., and Crowder, L. V. (1991). Habitat structure and predator–prey interactions in vegetated aquatic systems. In ' Habitat complexity: the physical arrangement of objects in space. (Eds S. S. Bell, E. D. McCoy and H. R. Mushinsky.) pp. 281–9. (Chapman & Hall: New York.)

Hixon, M. A. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63**, 77–101.

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–51.

Hughes, T. P., and Tanner, J. E. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250–63.

Huh, S.-H., and Kitting, C. L. (1985). Trophic relationships among concentrated populations of small fishes in seagrass meadows. *Journal of Experimental Marine Biology and Ecology* **92**, 29–43.

Jaasund, E. (1976). 'Seaweeds in Tanzania.' (University of Tromsø: Norway.)

Lewis, S. A. (1986). The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* **56**, 183–200.

Lieske, E., and Myers, R. (1994). 'Coral Reef Fishes: Indo-Pacific & Caribbean.' (Harper Collins: London.)

Littler, M. M. (1980). Morphological form and photosynthetic performances of marine macroalgae: tests of a funtional/form hypothesis. *Botanica Marina* **22**, 161–5.

Littler, M. M., and Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *The American Naturalist* **116**, 25–44.

Littler, M. M., Taylor, P. R., and Littler, D. S. (1983). Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* **2**, 111–18.

Lubbers, L., Boynton, W. R., and Kemp, W. M. (1990). Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* **65**, 1–14.

McClanahan, T. R. (1994). Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* **13**, 231–41.

McClanahan, T. R. (1997). Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* **218**, 77–102.

McClanahan, T. R., and Kaunda-Arara, B. (1996). Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* **10**, 1187–99.

McClanahan, T. R., Hendrick, V., Rodrigues, M. J., and Polunin, N. V. C. (1999). Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. *Coral Reefs* **18**, 195–203.

McClanahan, T. R., Bergman, K., Huitric, M., McField, M., Elfwing, T., Nystrom, M., and Nordemar, I. (2000). Response of fishes to algal reductions on Glovers Reef, Belize. *Marine Ecology Progress Series* **206**, 273–82.

McClanahan, T. R., McField, M., Huitric, M., Bergman, K., Sala, E., Nystrom, M., Nordemer, I., Elfwing, T., and Muthiga, N. A. (2001). Responses of algae, corals and fish to the reduction of macro algae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* **19**, 367–79.

McPhaden, M. J. (1999). Genesis and evolution of the 1997–98 El Niño. *Science* **283**, 950–4.

Moorjani, S., and Simpson, B. (1988). 'Seaweeds of the Kenya Coast.' (Oxford University Press: Nairobi.)

Mwatha, G. K., Fondo, E., Uku, J., and Kitheka, J. U. (1998). Biodiversity of Mida Creek, Kenya. Final Technical Report. KWS/KMFRI. (Mombasa, Kenya.) pp. 197.

Rozas, L. P., and Odum, W. E. (1988). Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* **77**, 101–6.

Sano, M. (2001). Short-term responses of fishes to macroalgal overgrowth on coral rubble on a degraded reef at Iriomote island, Japan. *Bulletin of Marine Science* **68,** 543–56.

Steneck, R. S., and Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos* **69**, 476–98.

Tanner, J. E. (1995). Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* **190**, 151–68.