Coral Reefs (1999) 18:195–203

REPORT

**T. R. McClanahan · V. Hendrick · M. J. Rodrigues**
**N. V. C. Polunin**

# Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef

Accepted: 2 February 1999

**Abstract** The consequences of macroalgal overgrowth on reef fishes and means to reverse this condition have been little explored. An experimental reduction of macroalgae was conducted at a site in the Watamu Marine National Park in Kenya, where a documented increase in macroalgal cover has occurred over the last nine years. In four experimental 10 m by 10 m plots, macroalgae were greatly reduced (fleshy algal cover reduced by 84%) by scrubbing and shearing, while four similar plots acted as controls. The numerical abundance in all fish groups except wrasses and macroalgal-feeding parrotfishes (species in the genera *Calotomus* and *Leptoscarus*) increased in experimental algal reduction plots. Algal (*Sargassum*) and seagrass (*Thalassia*) assays, susceptible to scraping and excavating parrotfishes, were bitten more frequently in the algal reduction plots one month after the manipulation. Further, surgeonfish (*Acanthurus leucosternon* and *A. nigrofuscus*) foraging intensity increased in these algal reduction plots. The abundance of triggerfishes increased significantly in experimental plots relative to control plots, but densities remained low, and an index of sea urchin predation using tethered juvenile and adult *Echinometra mathaei* showed no differences between treatments following macroalgal reduction. Dominance of reefs by macrofleshy algae appears to reduce the abundance of fishes, mostly herbivores and their rates of herbivory, but also other groups such as predators of invertebrates (triggerfishes, butterflyfishes and angelfishes).

**Key words** Algae · Carnivory · Coral reef fishes Herbivory · Restoration

## Introduction

Many tropical reefs have undergone substantial ecological changes, including losses in hard coral cover, during the last few decades, particularly in the Caribbean (Connell 1997). Long-term historical data inferred from geological cores suggest that this change is unusual (Aronson and Precht 1997) but may be persistent (Hughes 1994; Connell 1997). Investigators have attributed these changes variously to processes and events such as loss of herbivores (Hatcher 1983; Hughes 1994; McClanahan and Muthiga 1998), increased supply of inorganic nutrients (Smith et al. 1981; Pastorok and Bilyard 1985; Lapointe et al. 1997), coral bleaching (Porter and Meier 1992; Gleason 1993; Glynn 1993; Shulman and Robertson 1996) predation on corals (Moran 1986; Hayes 1990; Turner 1994), fishing (McClanahan and Mutere 1994), storm disturbance (Bythell et al. 1993); and diseases (Porter and Meier 1992; Aronson and Precht 1997). Hard coral is often replaced by turf-forming algae (Gleason 1993; Porter and Meier 1992; Bak and Nieuwland 1994) or erect and often unpalatable fleshy algae (Hughes et al. 1987; Carpenter 1990; Shulman and Robertson 1996; Aronson and Precht 1997; McClanahan and Muthiga 1998). The full implications of such shifts in reef communities are far from clear, and a major management question is what might be done to reverse the trend.

An increase in fleshy algae may be caused by or coincide with a loss of herbivores attributable to fishing (Ferry and Kohler 1987; Koslow et al. 1988; Hughes 1994; McClanahan et al. 1994; 1995) or diseases such as the disease that killed the important herbivore *Diadema antillarum* in the Caribbean (Lessios et al. 1984; Liddell and Ohlhorst 1986; de Ruyter van Steveninck and Bak 1986; Hughes et al. 1987; Levitan 1988; Hughes 1994).

T. R. McClanahan (✉)
The Wildlife Conservation Society, Coral Reef Conservation Project, P.O. Box 99470, Mombasa, Kenya
e-mail: crcp@africaonline.co.ke

V. Hendrick · N. V. C. Polunin
Department of Marine Sciences and Coastal Management, University of Newcastle, Newcastle upon Tyne NE1 7RU, UK

M. J. Rodrigues
Institute of Fisheries Research, Maputo, Mozambique

Experimental manipulations of herbivores suggest that a reduction of herbivores can result in an increase in fleshy algae (Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Foster 1987) and increases in algae can result in losses of hard coral cover (Hay and Taylor 1985; Lewis 1986; Tanner 1995; McClanahan et al. 1995). Two ways in which resource managers might intervene are through (1) enhancement of grazing and (2) macroalgal reduction. The former measure is conceivable through marine reserve establishment or fisheries regulations, where depletion of grazers has occurred through exploitation. The latter would be feasible at smaller scales, and might offer local foci for recovery from macroalgal dominance if grazing was able to maintain the lowered macroalgal coverage and if excluded components of the benthos, especially hard corals, were then able to recolonise.

Because most coral reef herbivores prefer palatable turf-forming algae (Choat 1991), many fishes such as scrapers, excavators, and suckers (Bellwood and Choat 1990; Purcell and Bellwood 1993) may effectively be excluded where unpalatable erect algae are abundant. Macroalgal reduction might therefore be expected to enhance the abundance and/or activity of such species, while macroalgal feeders such as parrotfishes in the genera *Calotomus* and *Leptoscarus* may not be affected.

Complex interactions among food availability, structural complexity, and composition of the benthos make it difficult to predict the results of experimental manipulations of coral reefs (Pimm 1991; Polunin and Klumpp 1992a,b; Jennings et al. 1996; McClanahan et al. 1995; Szmant 1997). Thus, because erect algae such as *Sargassum* can provide refuge for small invertebrates (Duffy and Hay 1991; Wahl and Hay 1995; Stachowicz and Hay 1996), the abundance and/or activity of fishes which feed extensively on invertebrates (e.g., Balistidae, Labridae, Lethrinidae, Lutjanidae and Haemulidae) may be reduced when macroalgae are removed because of the invertebrate epifauna associated with such plants. Conversely, late successional algal species, such as *Sargassum*, will frequently have lower net production than early successional turfs and lower net production could result in lower consumer abundance.

Monitoring of reefs in the protected Watamu Marine National Park (WMNP) of Kenya over a nine-year period has indicated that while herbivorous fish populations have fluctuated about a mean level, a regular increase in the cover of fleshy algae has occurred compared to another enforced marine protected area at Malindi about 20 km north of the WMNP (McClanahan and Obura 1997; T.R. McClanahan unpublished data). Further enhancement of grazing through reduction in fishing effort is inconceivable, because the WMNP is already fully enforced, but physical macroalgal reduction might be a means to reverse the shift in reef community structure at affected sites. We, therefore, experimentally reduced erect fleshy brown, red, and green, algae, and hypothesised that abundance and feeding rates of herbivorous fishes would increase, while those of invertebrate-feeders such as wrasses and triggerfishes would either decrease or be unaffected by the reduction of macroalgae.

## Materials and methods

### Study area and macroalgal reduction

The algal reduction experiment was undertaken on lagoonal reef carbonate outcrops within the WMNP (40°0′E 3°22′S), from which all forms of resource extraction have been eliminated. The reef is a linear lagoonal coral reef with scattered outcrops of coral of about 400 m long and 20 m wide with dead carbonate surfaces colonised by algae and hard corals and surrounded by seagrass (*Thalassodendron ciliatum*) and sand (Fig. 1; Table 1). For the algal reduction study we chose an area about 100 m wide where the nearest plot was 100 m from the monitoring study site. The cover of hard coral was lower and erect algae were more abundant in the experimental than monitoring site; in fact, this experimental site had the highest algal cover observed in the marine parks of Kenya (T. R. McClanahan unpublished data). The dominant macroalgae were *Sargassum duplicatum* and *Halimeda opuntia*, but there were other species of *Sargassum* and *Halimeda* as well as species in the genera *Turbinaria*, *Dictyota*, *Lobophora*, *Hypnea* and *Neurymenia*.

Eight $10 \times 10$ m plots were established by the placement of markers (PVC pipe cemented to the bottom) along this reef strip at low-water depths of 1 to 2.5 m in early January 1997 such that there were 5–20 m between adjacent plots. During 19–21 March 1997, four plots were selected for reducing the erect algae, and the reduction was effected by a group of six divers. One diver removed the canopy macroalgae using gardening shears, while the five others cleared the subcanopy algae from the carbonate surface with wire brushes while avoiding living coral and other invertebrates. Effort was made to remove all macroalgae including holdfasts in order that all experimental plots started at the same initial conditions (Fig. 1). Continuous reduction of algae was not undertaken because we were interested in determining if herbivores would be able to maintain a low-algal community after this initial pulsed disturbance.

### Field measurements and data analysis

The benthos and fish fauna were sampled in each of the plots during January–June 1997, twice before the algal reduction (survey 1, 9 and 17 January; survey 2, 17–18 March) and three times after the reduction (survey 3, 15 and 17 April; survey 4, 13 May and 2 June; survey 5, 21 and 25 June). Individual plots were considered replicates and data used in the statistical analyses were calculated from the appropriate surveys. We compared samples using repeated measures ANOVAs (a) before the reduction (treatment $df = 1$, plot nested within treatment $df = 6$, and time $df = 1$), (b) straight $t$-test comparisons between sampling times 2 and 3, and (c) repeated measures ANOVA after macroalgal reduction (treatment $df = 1$, plot nested within treatment $df = 6$, and time $df = 2$). If data were percentages we performed an arcsin transformation on the proportions before conducting the statistical tests (Zar 1996), but we present the untransformed data in the tables and figures for ease in interpretation.

The projected canopy area of the benthos was sampled by two draped 10 m line transects run diagonally across each plot (McClanahan and Shafir 1990), and these were used to measure the distance that each of nine substratum categories contributed to the total measured length; organisms $< 3$ cm were not recorded. The substratum categories were hard coral, soft coral, seagrass, sponge,

**Fig. 1** Photo of the study sites a preremoval plot, left and a plot after the reduction, right (Credit, T.R. McClanahan)

**Table 1** Characterization of algal/plant categories used in this study

| Category | Genera/Species |
|---|---|
| Calcareous algae | *Halimeda* |
| Coralline algae | *Amphiroa*, *Jania* and encrusting red algae |
| Fleshy algae | *Caulerpa*, *Codium*, *Cystoseria*, *Dictyospheria*, *Dictyota*, *Hypnea*, *Neurymenia*, *Padina*, *Pocockiella*, *Sargassum*, *Turbinaria*, *Ulva* and red filamentous species |
| Turf algae | Frondose and filamentous algae (Chlorophyta, Phaeophyta and Rhodophyta) grazed to a height of 1–2 cm above the substratum with a tight compact appearance (Borowitzka 1983) |
| Seagrass | *Thalassodendron ciliatum* |

sand, and fleshy, turf, coralline, and calcareous algae (Table 1). Hard corals and fleshy algae were identified to genus. This method only measures the abundance of the categories forming the canopy and, therefore, after the reduction the immediate changes were attributable to some categories, such as hard coral, algal turf and coralline algae, being more exposed and not due to an absolute change in their abundance.

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). Water clarity exceeded 5 m during each of the sampling intervals. A single observer (T. R. McClanahan) swam around the borders of all plots and recorded the species and number of individuals inhabiting each. Each plot was circumnavigated five times, counting each of four groups separately: group 1 Scaridae (parrotfishes) and Acanthuridae (surgeonfishes); group 2 Labridae (wrasses); group 3 herbivorous and omnivorous Pomacentridae (damselfishes); and group 4 Pomacanthidae (angelfishes), Chaetodontidae (butterflyfishes) and Balistidae (triggerfishes). Differences between fish abundance were determined by repeated measures ANOVA as described.

After the algal reduction, indices of herbivory and carnivory were derived using unbitten and epiphyte-free tethered fronds of a brown alga (*Sargassum latifolium*) and two seagrasses (*Thalassia hemprichii*, *Thalassodendron ciliatum*), and juvenile and adult sea urchins (*Echinometra mathaei*), respectively, in each of the plots in April and May (surveys 3–4). The particular herbivory assays were chosen because bites are easily recognised on the entire margins of these species and because they are intermediate in their susceptibility to herbivory; highly susceptible species will not last, while highly resistant species will not be bitten over the soaking interval. For the herbivory assay, a nylon line with loops at 1.5 m intervals was haphazardly placed in each of the plots. Individual blades of *S. latifolium*, *T. hemprichii* and *Thalassodendron ciliatum* were clipped to each loop with a weighted clothes pin (Hay 1981; McClanahan et al. 1994) and left on the reef for 24 h, after which the number of blades bitten was recorded and used to calculate relative herbivory in control and experimental plots. Sea urchins were tethered by piercing their body wall with a hypodermic needle, threading them with monofilament line, and tying them to the loops on the nylon lines for 24 h. The number of missing urchins was recorded and the percent mortality calculated across the four replicate treatment and control plots and tested for significance with a t-test ($df = 1$, $n = 4$). Because predation may be affected by the size of the animals (Sala and Zabala 1996) one experiment used only adult urchins (test diameter $> 3$ cm; 22 May) while a second experiment used juveniles ( $< 2.5$ cm; 23 May).

Herbivory assays used in areas with abundant fish are most sensitive to feeding by parrotfishes and are not correlated with the feeding of surgeonfishes (McClanahan et al. 1994). Consequently, feeding rates were quantified by direct observation of four species of surgeonfishes, namely *Acanthurus leucosternon*, *A. nigrofuscus*, *Ctenochaetus striatus*, and *C. strigosus*, for comparison between experimental and control plots. Observations were carried out during periods of low tide from 8 June to 5 July 1997 (just after survey 4 to after survey 5), while snorkeling or using SCUBA equipment. The observer moved haphazardly between plots at intervals of approximately half an hour. Individuals were selected at random and observed for 1-min observation periods, which were initiated at the onset of a feeding foray. A foray was defined as a feeding event of successive bites without a discernible interval, other than that necessary to reapply the jaws to the substratum (Bellwood and Choat 1990). The total number of bites and the number of forays initiated within the time period were recorded. Only observations in which the focal individual remained in clear view and within the study plot throughout the observation period were included in the analysis. Situations in which no recordings were made were due to the absence of the species in the plot.

## Results

Prior to the reduction of macroalgae, there were no significant differences among plots within treatments or between treatments (control and experimental plots) in cover of any of the substratum categories except calcareous algae, the mean percentage cover of which was significantly higher in the experimental plots than in the control plots (ANOVA $P < 0.05$) (Fig. 2). Experimental reduction of macroalgae significantly reduced the cover of fleshy and calcareous algae by 84% and 71%, respectively, in the experimental plots between surveys 2 and 3 (Table 2). Cover of fleshy and calcareous algae increased in the control plots over the same period by 10% and 3%, respectively (Fig. 2). Fleshy algae was reduced in the control plots during surveys 4 and 5 due to seasonally intense waves and currents.

After the macroalgal reduction, hard coral (repeated measures ANOVA $P < 0.01$), algal turf ($P < 0.001$) and coralline algae ($P < 0.001$), covered more of the canopy, while fleshy algae ($P < 0.001$), calcareous algae ($P < 0.001$) and sand ($P < 0.001$) covered significantly less, in experimental plots than in control plots (Fig. 2). Much of this change, particularly for corals, coralline algae and algal turf occured during sample intervals 2 and 3, and is due to the change in canopy associated with the reduction of fleshy and calcareous algae rather than a change in absolute abundance of these three categories. Consequently, the absolute increase in coral due to the algal reduction is probably around 5% over this study period. There were no significant differences in the other substratum categories between treatments.

### Fish abundance

Prior to the reduction of macroalgae (surveys 1–2), there were no significant differences between control and experimental plots in fish numerical abundance and biomass, except for the damselfishes, which were more abundant ($P < 0.05$) in control than experimental plots (Fig. 3). Following macroalgal reduction (surveys 3–5), the mean numerical abundance of fish was greater in the experimental plots than in the control plots for all families, but the differences were not significant for wrasses, or the macroalgal-feeding parrotfishes (repeated measures ANOVA $P < 0.01$) (Fig. 3). The fish biomass was significantly greater in the experimental plots than in the control plots only for the surgeonfishes ($P < 0.001$) and parrotfishes ($P < 0.05$), and for all families combined ($P < 0.01$).

### Carnivory, herbivory and herbivore feeding activity

No significant differences were observed between the control and experimental plots in the inferred mortality of adult (55 ± 8% ± SE, for both controls and experiments) or juvenile sea urchins (controls = 40 ± 9%, experiments = 30 ± 12%). There was significantly more feeding on seagrass blades in experimental plots compared to the control plots for both *Sargassum latifolium* and *Thalassia hemprichii* in April, but grazing did not differ significantly between treatments for *Thalassia hemprichii* in May or for *Thalassodendron ciliatum* on either occasion (Table 3).

There were significant differences between treatments in surgeonfish feeding. The number of forays per minute was reduced (*Acanthurus leucosternon* and *Ctenochaetus striatus*; Fig. 4a), and the number of bites per foray (*Acanthurus leucosternon*, *A. nigrofuscus*, *Ctenochaetus striatus* and *C. strigosus*; Fig. 4b), and overall bites per minute (*A. leucosternon* and *A. nigrofuscus*; Fig. 4c) were higher in the experimental plots. In particular, the combined bite rate of *A. leucosternon* and *A. nigrofuscus* was 40% greater in experimental than in control plots.

## Discussion

Prior to reduction of the macroalgae, with one exception, there were no significant differences in fish numbers between plots intended for treatment and plots designated as controls. Damselfish were the exception, being more abundant in control than experimental plots, although this pattern was reversed following the reduction. Following the macroalgae reduction, the mean number of fish was greater in the experimental plots than in the control plots for all fish families surveyed except wrasses. This was as expected for herbivorous species such as the grazing acanthurids, pomacentrids and scraping/excavating parrotfishes, which are likely to have responded to the relative abundance or accessibility of algal turf in these plots. More surprising was the lack of change in the abundance of macroalgal-feeding parrotfishes following algal reduction, because their food presumably decreased in experimental plots. Also unexpected was the increase in predators of small invertebrates, because their prey was predicted to become less abundant in the experimental plots. The observed differences were generally most pronounced soon after the algal reduction and decreased over time as algae recolonised the experimental plots and was reduced in the control plots by a seasonal increase in waves and water motion.

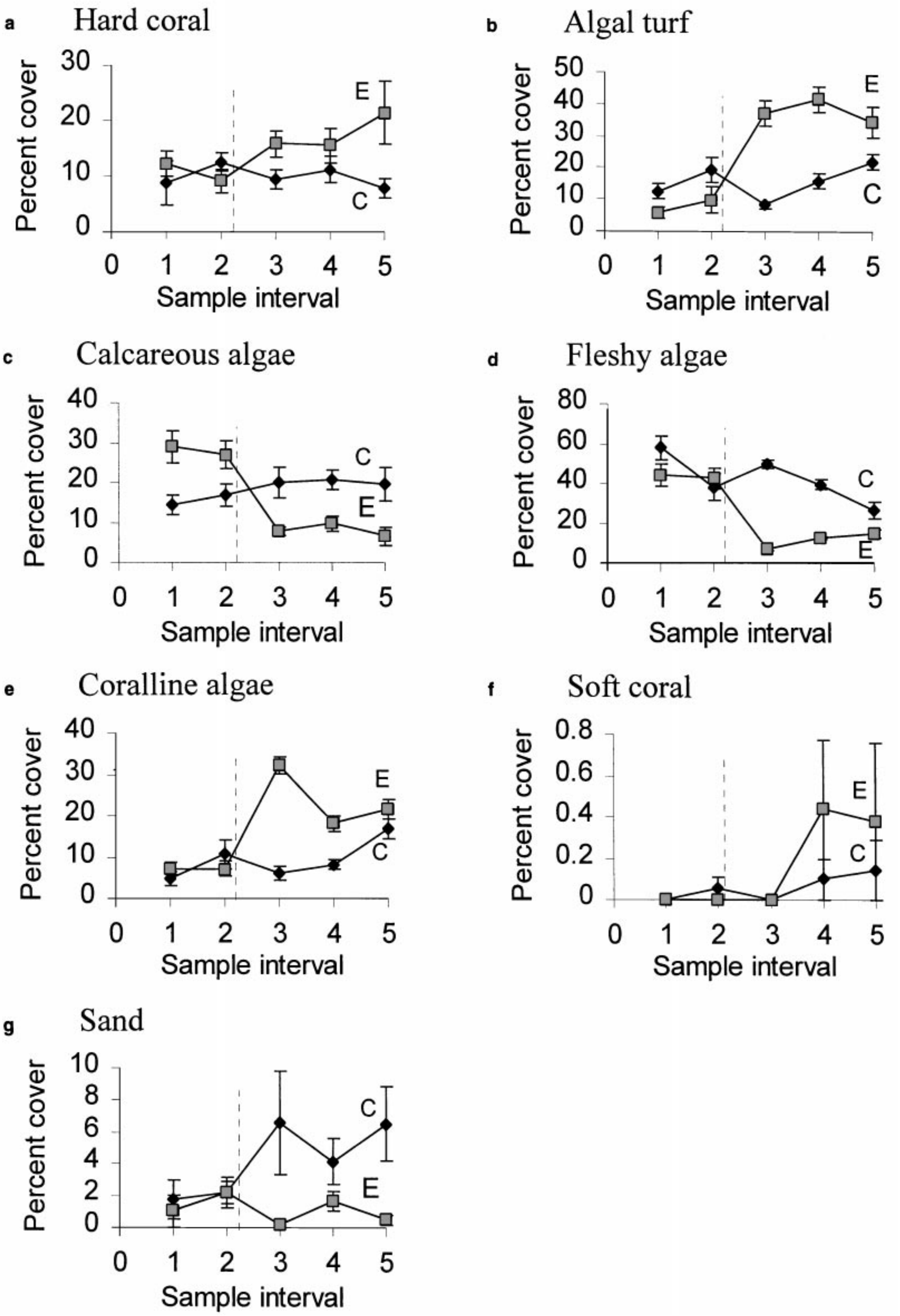

**Fig. 2a–g** The mean ( ± SE) percentage cover of the different substratum categories in the control (C) and experimental (E) plots. The dotted line indicates the point of experimental reduction of macroalgae

The high susceptibility of *Echinometra mathaei* to predation relative to other common sea urchin species (McClanahan 1988) makes it a useful indicator species of predation intensity on invertebrates (McClanahan and Muthiga 1989). However, tethering restricts the urchins' ability to avoid predation by hiding in burrows (Bernstein et al. 1981; Carpenter 1984). Consequently the carnivory assay technique can only be considered a relative index of predation intensity, not an absolute measure. Regardless, there was no indication that feeding

**Table 2** Comparison of the mean percentage cover of fleshy and calcareous algae in the experimental plots before (survey 2) and after (survey 3) experimental reduction of macroalgae

| Substratum Category | Survey 2 Mean (%) ± SE | Survey 3 Mean (%) ± SE | Change (%) | *P* |
|---|---|---|---|---|
| Fleshy algae | 42.47 ± 4.94 | 6.86 ± 0.89 | − 84 | ** |
| Calcareous algae | 27.03 ± 3.40 | 7.77 ± 1.13 | − 71 | ** |

** $P < 0.01$

rates on *Echinometra mathaei* differed in the experimental and control plots.

The implication of our findings is that macroalgal reduction had no effect on the level of carnivory. This is surprising considering the significantly higher numbers of triggerfishes in experimental relative to control plots (Fig. 2e), triggerfishes (*Balistapus undulatus*) being dominant sea-urchin predators in the area (McClanahan and Muthiga 1989; McClanahan and Shafir 1990). Population densities were, however, low in both treatments, and triggerfish may forage over larger areas than the experimental plots. Consequently, it is possible that these plots were too small to determine the foraging effects of large carnivores, like triggerfish. Triggerfish may prefer to establish their dens in algal reduction plots but probably forage more widely. The smaller bodied wrasses, which may also prey on urchins, particularly juveniles, did not differ significantly in population density between treatments, which may explain the lack of a difference in mortality of juvenile *Echinometra mathaei* in these plots.

The significantly greater predation on *S. latifolium* and *T. hemprichii* assays in April is suggestive of a rapid increase in scraping/excavating scarid herbivory following the macroalgae reduction (McClanahan et al. 1994). This was expected considering the significantly higher populations of all parrotfishes, particularly scraping and excavating species, observed to feed on these assays in the experimental plots (T.R. McClanahan personal observation). The subsequent lack of differences between treatments is partially attributable to the lower abundance of parrotfishes in the experimental plots by the time of survey 4 (Fig. 2b,d); in the case of the *Thalassodendron hemprichii* assays in May the data in the experimental plots were very variable (Table 3). The *T. ciliatum* assay was probably mostly eaten by the macroalgal feeding parrotfishes (*Calotomus* and *Leptoscarus;* T.R. McClanahan personal observation) which did not differ between treatments, which probably explains the lack of difference between treatments for this particular herbivory assay. The data indicate that scraping/excavating scarid abundance and their herbivory increased temporarily in experimental plots after macroalgal reduction. Another explanation for increased grazing on assays is that the assays were more conspicuous to the fishes foraging in plots where macroalgae had been reduced, but this would not explain differences in scarid numbers. The greater similarity in fleshy- and turf-algal cover by survey 4 may explain why assay results differed between deployment times. These data suggest that scraping/excavating parrotfishes are sensitive to changes in macroalgae abundance while macroalgal feeders are not.

Although the investigation of acanthurid feeding behaviour was undertaken three months after the macroalgal reduction, significant differences were found between the experimental and control plots in the foraging patterns of the four studied species. This implies that these fish altered their feeding behaviour in response to the experimental manipulation of macroalgal cover. In experimental plots, acanthurids had fewer forays but more bites per foray, and this resulted in an overall increase in the number of bites made to the substratum. Fewer forays and more bites per foray suggests improved grazing conditions for these species. Diet composition and ingestion rates were not determined during this study because destructive sampling was illegal in the WMNP but some of these species probably feed on detritus as well as algae (Choat 1991).

There was apparently no significant difference in the foraging behavior of the four species of surgeonfishes in the control plots. However, the number of bites to the substratum per minute, and the average number of bites per foray, did differ significantly among the species in the experimental plots, suggesting that the four species responded differently to the experimental manipulation. The data on foraging by each of the four species (Fig. 4) suggest that the greatest response to the macroalgal reduction was shown by *Acanthurus leucosternon*. Considering that some degree of resource partitioning is likely to exist among these surgeonfishes (Robertson et al. 1979; Choat 1991), some differences in response to a disruption of benthic composition were expected.

The findings presented here indicate that the reduction of macroalgae from a coral reef may have a number of short-term ecological effects. The abundance and foraging activity of herbivores such as parrotfishes, damselfishes and surgeonfishes, which feed on turf, coralline, calcareous algae, and detritus can increase. This increase in herbivory could assist in suppressing or slowing the recovery of algae depending on the balance between algal growth and mortality. Some invertebrate-feeding fishes (e.g. angelfishes, butterflyfishes and triggerfishes) may increase in abundance as well, while others may not, but the evidence from the sea-urchin assays is that carnivore feeding may not

**Fig. 3a–j** Mean number of fish counted per plot, over time, in the control (C) and experimental (E) plots. The dotted line indicates the point of experimental reduction of macroalgae, and error bars are SE

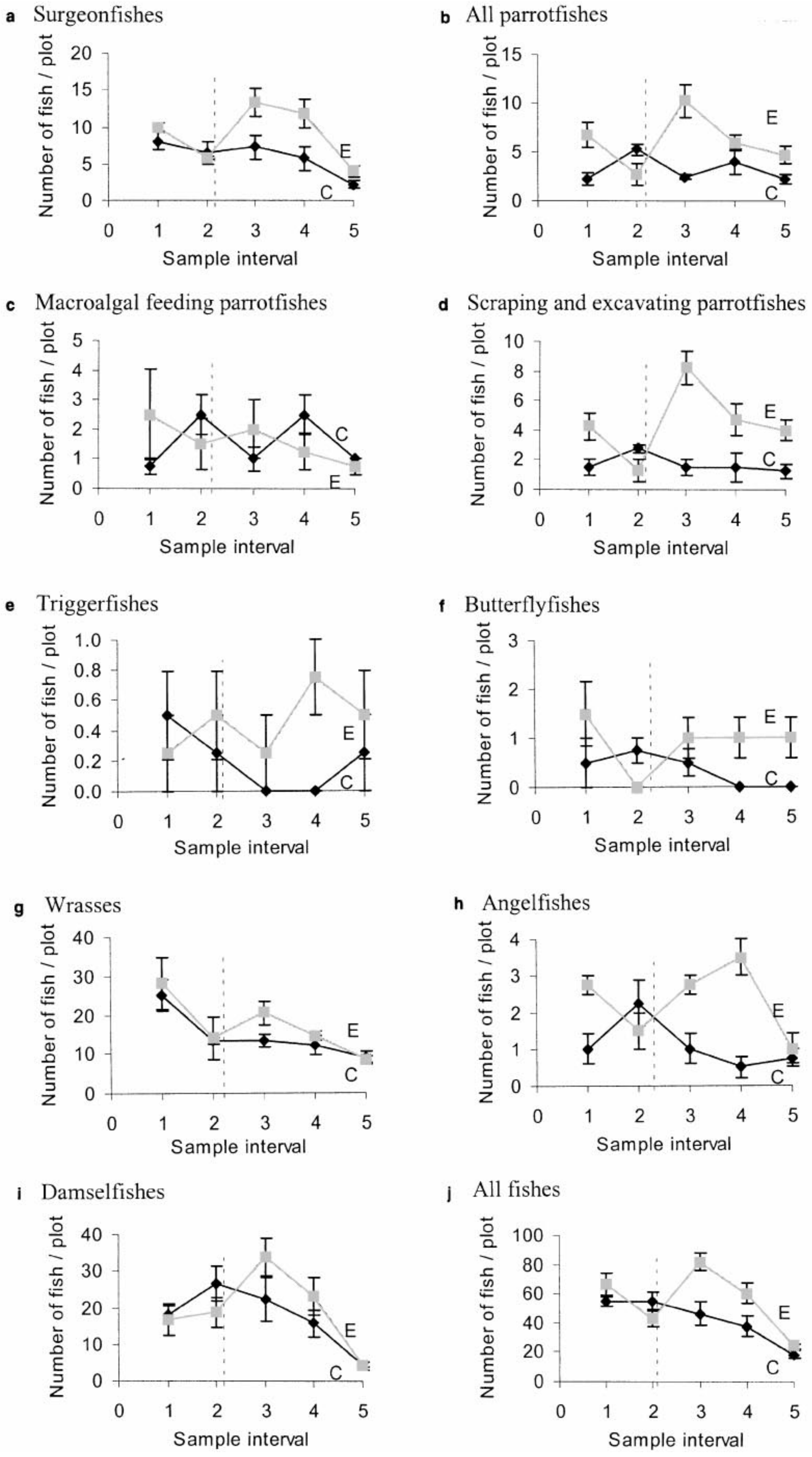

**Table 3** Summary of the indices of herbivory on *S. latifolium*, *T. hemprichii* and *T. ciliatum* in the experimental and control plots

| Sampling Period | *Sargassum latifolium* Control (% bitten) | *Sargassum latifolium* Experiment (% bitten) | *Thalassia hemprichii* Control (% bitten) | *Thalassia hemprichii* Experiment (% bitten) | *Thalassodendron ciliatum* Control (% bitten) | *Thalassodendron ciliatum* Experiment (% bitten) |
|---|---|---|---|---|---|---|
| April | 7.5 ± 2.5 | 35.0 ± 6.5* | 56.7 ± 8.8 | 87.5 ± 4.8* | 55.0 ± 11.9 | 55.0 ± 20.2 |
| May | — | — | 84.4 ± 4.8 | 72.5 ± 24.3 | 75.0 ± 8.7 | 72.5 ± 6.3 |

Results of *t*-test: * = $P < 0.05$, $n = 4$.
Values are expressed as the mean percentage of blades bitten ± 95% CL, for each assay

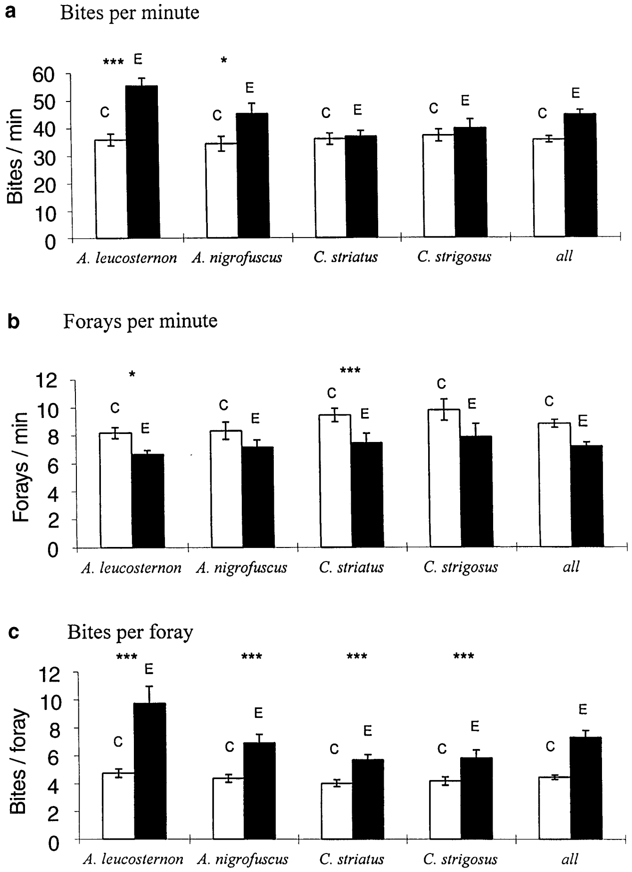

**Fig. 4a–c** Histograms of mean ( ± SE) **a** number of bites per minute, **b** number of forays per minute, and **c** number of bites per foray, in control (open bars) and experimental (closed bars) plots for the four species of surgeonfishes, individually and combined. Results of the Mann-Whitney test for comparisons of medians between control and experimental plots: * = $P < 0.05$, *** = $P < 0.001$

necessarily increase. In the present instance, the effect of macroalgal reduction on fishes was short-lived, because seasonal monsoons reduced the macroalgae in the control plots and algae recovered somewhat in the experimental plots.

The long-term effects of this algal reduction on other substratum groups will require longer term field studies but the present study suggests that many herbivorous species respond quickly to the abundance of macroalgae. The implication of this study is that many of the reefs experiencing large increases in macroalgae cover may be suppressing the abundance of many fish groups and not just corals (Hughes 1994; Tanner 1995). Manual reduction of macroalgae remains one option for restoring reefs on a small scale, such as highly visited marine protected areas, but is unlikely to be undertaken or succeed on the larger scale of fisheries grounds that may require restrictions on the catch of herbivores. In many reefs, such as the one studied here, seasonal waves and currents remove algae. Therefore manual removal may be best undertaken at times offset from the seasons when waves and currents naturally remove macroalgae.

**Acknowledgements** This research was supported by The Wildlife Conservation Society with financial assistance of the Pew Scholars in the Environment Program (T.R. McClanahan and M.J. Rodrigues) and the University of Newcastle-upon-Tyne, Department of Marine Sciences and Coastal Management (V. Hendricks and N.V.C. Polunin). Permission to undertake the work was provided by Kenya's Office of the President and Kenya Wildlife Service. We are grateful for the logistic support provided by the Warden, D. Macharia, and staff of the Watamu MNP who assisted with the algal reduction and monitoring.

## References

Aronson RB, Precht WF (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. Paleobiology 23:336–346

Bak RPM, Nieuwland G (1994) Twenty years of change in coral communities over deep reef slopes along leeward coasts in the Netherlands Antillies. In: Ginsburg RN (ed) Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History. Rosentiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, pp 54–159

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. Environ Biol Fish 28:189–214

Bernstein BB, Williams BE, Mann KH (1981) The role of behavioural responses to predators in modifying urchins (*Stronglocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. Mar Biol 63:39–49

Borowitzka MA (1983) Calcium carbonate deposition by reef algae: morphological and physiological aspects. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouster Publisher, Manuka, Australia, pp 16–28

Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common caribbean reef corals. Coral Reefs 12:143–152

Carpenter RC (1984) Predator and population density control of homing behaviour in the Caribbean echinoid *Diadema antillarum*. Mar Biol 82:101–108

Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56:345–363

Carpenter RC (1990) Mass mortality of *Diadema antillarum I*. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Mar Biol 104:67–77

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, New York, pp 120–155

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16:S101-S113

de Ruyter van Steveninck ED, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. Mar Ecol Prog Ser 34:87–94

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286–1298

Ferry RE, Kohler CC (1987) Effects of trap fishing on fish populations inhabiting a fringing coral reef. N Am J Fish Mang 7:580–588

Foster SA (1987) The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*:effects of habitat and surge. J Exp Mar Biol Ecol 105:1–20

Gleason MG (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. Coral Reefs 12:193–201

Glynn PW (1993) Coral reef bleaching:Ecological perspectives. Coral Reefs 12:1–17

Greene LE, Alevizon WS (1989) Comparative accuracies of visual assessment methods for coral reef fishes. Bull Mar Sci 44:899–912

Hatcher BG (1983) Grazing in coral reef ecosystems. In:Barnes DJ (ed) Perspectives on coral reefs. Brian Clouster Publishers, Manuka, Australia, pp 164–179

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the ephilitic algal community on a coral reef. J Exp Mar Biol Ecol 69:61–84

Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: Herbivory and algal disturbution. Aquat Bot 11:97–109

Hay ME, Taylor PR (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia 65:591–598

Hayes JA (1990) Distribution, movement and impact of the corallivorous gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian patch reef. J Exp Mar Biol Ecol 142:25–42

Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. Science 265:1547–1551

Hughes TP, Reed DC, Boyle M (1987) Herbivory on coral reefs:community structure following mass mortalities of sea urchins. J Exp Mar Biol Ecol 113:39–59

Jennings S, Boulle DP, Polunin NVC (1996) Habitat correlates of the distribution and biomass of Seychelles' reef fishes. Environ Biol Fish 46:15–25

Koslow JA, Hanley F, Wicklund R (1988) Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. Mar Ecol Prog Ser 43:201–212

Lapointe BE, Littler MM, Littler DS (1997) Macroalgal overgrowth of fringing coral reefs at Discovery Bay, Jamaica: Bottom-up versus top- down control. Proc 8th Int Coral Reef Symp 1:927–932

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337

Levitan DR (1988) Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, US Virgin Islands. J Exp Mar Biol Ecol 119:167–178

Lewis SA (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. J Exp Mar Biol Ecol 95:271–278

McClanahan TR (1988) Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. Oecologia 77:210–218

McClanahan TR (1994) Kenyan coral reef lagoon fish: Effects of fishing, substrate complexity, and sea urchins. Coral Reefs 13:231–241

McClanahan TR, Muthiga NA (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. J Exp Mar Biol Ecol 126:77–94

McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia 83:362–370

McClanahan TR, Mutere JC (1994) Coral and sea urchin assemblage structure and interrelationships in Kenyan reef lagoons. Hydrobiologia 286:109–124

McClanahan TR, Obura D (1997) Sediment effects on shallow coral communities in Kenya. J Exp Mar Biol Ecol 209:103–122

McClanahan, TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. Environ Cons 25:122–130

McClanahan TR, Nugues M, Mwachireya S (1994) Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons-the role of reef management. J Exp Mar Biol Ecol 184:237–254

McClanahan TR, Kamukuru AT, Muthiga NA, Gilagabher Yebio M, Obura D (1995) Effect of sea urchin reductions on algae, coral and fish populations. Cons Biol 10:136–154

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanogr Mar Biol Ann Rev 24:379–480

Pastorek RA, Bilyard GR (1985) Effects of sewage pollution on coral reef communities. Mar Ecol Prog Ser 21:175–189

Pimm SL (1991) The balance of nature? Ecological issues in the conservation of species and communities. The University of Chicago Press, Chicago

Polunin, NVC, Klumpp DW (1992a) Algal food supply and grazer demand in a very productive coral-reef zone. J Exp Mar Biol Ecol 164:1–15

Polunin, NVC, Klumpp DW (1992b) A trophodynamic model of fish production on a windward reef tract. In:John DM, Hawkins SJ, Price JH (eds) Plant-animal interactions in the marine benthos. Clarendon Press, Oxford (Systematics Ass Spec Publ 46), pp 213–233

Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. Am Zool 32:625–640

Purcell SW, Bellwood DR (1993) A functional-analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). Env Biol Fish 37:139–159

Robertson DR, Polunin NVC, Leighton K (1979) The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucostenum*, and *Zebrasoma scopas*): Their feeding strategies, and social and mating systems. Env Biol. Fish 4:125–170

Sala E, Zabala M (1996) Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. Mar Ecol Prog Ser 140:71–81

Shulman MJ, Robertson DR (1996) Changes in the coral reefs of San Blas, Caribbean Panama:1983 to 1990. Coral Reefs 15:231–236

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. Pac Sci 35: 279–402

Stachowicz JJ, Hay ME (1996) Facultative mutualism between an herbivorous crab and a coralline alga: Advantages of eating noxious seaweeds. Oecologia 105:377–387

Szmant AM (1997) Nutrient effects on coral reefs: A hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. Proc 8th Int Coral Reef Symp 2:1527–1532

Tanner JE (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. J Exp Mar Biol Ecol 190:151–168

Turner SJ (1994) The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs. Oceanogr Mar Biol Ann Rev 32:461–530

Wahl M, Hay ME (1995) Associational resistance and shared doom: Effects of epibiosis on herbivory. Oecologia 102:329–340

Zar JH (1996) Biostatistical analysis. Prentice Hall, New Jersey, USA