

Phase shifts and the role of herbivory in the resilience of coral reefs

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Abstract Cousin Island marine reserve (Seychelles) has been an effectively protected no-take marine protected area (MPA) since 1968 and was shown in 1994 to support a healthy herbivorous fish assemblage. In 1998 Cousin Island reefs suffered extensive coral mortality following a coral bleaching event, and a phase shift from coral to algal dominance ensued. By 2005 mean coral cover was <1%, structural complexity had fallen and there had been a substantial increase in macroalgal cover, up to 40% in some areas. No clear trends were apparent in the overall numerical abundance and biomass of herbivorous fishes between 1994 and 2005, although smaller individuals became relatively scarce, most likely due to the loss of reef

structure. Analysis of the feeding habits of six abundant and representative herbivorous fish species around Cousin Island in 2006 demonstrated that epilithic algae were the preferred food resource of all species and that macroalgae were avoided. Given the current dominance of macroalgae and the apparent absence of macroalgal consumers, it is suggested that the increasing abundance of macroalgae is reducing the probability of the system reverting to a coral dominated state.

Keywords Recovery · Coral bleaching · Seychelles · Marine protected areas · Coral reef fishes · Feeding observations

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Introduction

The interaction between natural and anthropogenic disturbance has undermined the resilience of coral reefs and led to their worldwide degradation (Nyström et al. 2000; Gardner et al. 2003; Hughes et al. 2003). Coral bleaching is one such disturbance which, through potential enhancement by anthropogenic global warming (Reaser et al. 2000), poses a great challenge to coral reef management. While the immediate effects of coral bleaching on reef fish assemblages are largely restricted to species which depend on live coral for habitat or food (reviewed by Wilson et al. 2006), there is evidence that reefs can support abundant and diverse fish assemblages after bleaching as long as reef structure is maintained (Lindahl et al. 2001). However, the longer-term loss of structural complexity can affect recruitment, competition and predation (Buchheim and Hixon 1992; Hixon and Beets 1993; Öhman et al. 1998), leading to declines in species richness (Graham et al. 2006) and numerical abundance (Garpe et al. 2006).

The loss of live coral cover following disturbances such as bleaching is often accompanied by a proliferation of macroalgae (McClanahan et al. 2001; Graham et al. 2006). Although there has been some speculation regarding the causality and mechanisms of competitive interactions between algae and corals (McCook et al. 2001), high algal biomass has been demonstrated to have a detrimental effect on coral health (e.g. Birkeland 1977; Tanner 1995; Smith et al. 2006). Through their role in algal removal, herbivorous fishes are considered to play an important role in promoting reef resilience and in reef recovery to coral dominated states if disturbance has occurred (Nyström and Folke 2001; Bellwood et al. 2004).

The role of herbivorous fishes in promoting coral recovery and enhancing resilience suggests that relatively small-scale (km to 10s km) variation in the structure and abundance of their assemblages will contribute to small-scale variation in rates of reef recovery. Management measures that locally reduce fishing mortality and increase the abundance of herbivorous fishes, such as marine protected areas (MPAs), are therefore expected to play an important role in promoting recovery and resilience (Hughes et al. 2003). The extent to which different groups of herbivorous fishes promote recovery will depend on their functional role and the algae that they graze. Three functional groups have been recognised within the herbivorous fish guild—grazers, scrapers and bioeroders—and these have different and complementary roles in preconditioning reefs to permit coral recovery following disturbance (Bellwood et al. 2004). Furthermore, in terms of enhancing resilience it is not only the species diversity within functional groups which is important but the response diversity of these species to environmental change (Elmqvist et al. 2003).

Although MPAs may be an effective means of reducing local disturbance (Jennings et al. 1996; Halpern 2003), they are not immune to the effects of large-scale external disturbances such as bleaching (Reaser et al. 2000; Jones et al. 2004). The global bleaching event of 1998 led to the

greatest coral mortalities on record worldwide (Hoegh-Guldberg 1999; Goreau et al. 2000) but the Indian Ocean was most severely affected (Sheppard 2003). In the Cousin Island no-take MPA (Inner Seychelles), there was a massive decline in live coral cover in 1998, followed by an ongoing decline in structural complexity. The aim of this study was to describe changes in the composition of benthic communities following the 1998 bleaching event and to assess the potential role of herbivorous fishes in promoting reef recovery. This was achieved by (1) analysing benthic community and herbivorous fish biomass and numerical abundance data from before, immediately after and seven years after the bleaching event and (2) assessing the feeding habits of six abundant and representative herbivorous fish species to determine whether they had the potential to create suitable conditions for successful coral settlement.

Materials and methods

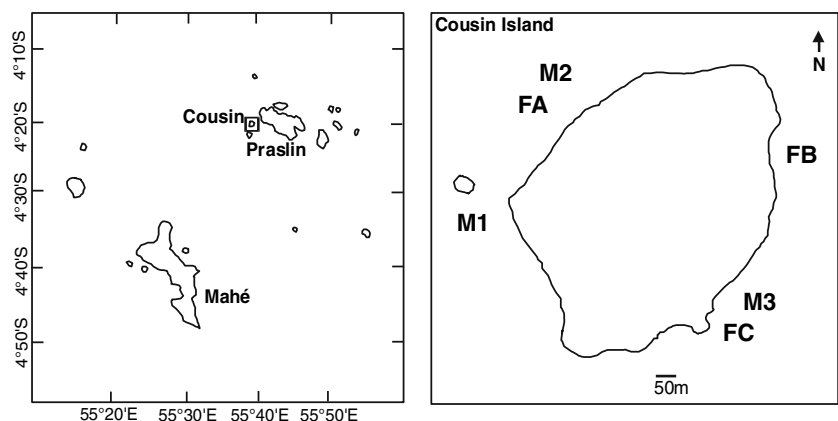
Study area

The small granitic island of Cousin is situated in the Inner Seychelles (Fig. 1) (4°20'S, 55°40'E). The entire island including the surrounding reef was declared a 'Special Reserve' in 1968 and 1.2 km² of sea, extending 400 m seaward from the high-water mark, is legally protected (Jennings et al. 1996). Effective and continuous policing by resident Seychellois wardens has ensured the reef has not been fished in recent years (Jennings 1998).

Temporal assessment of herbivorous fish assemblage and benthic composition

Three sites were used in the temporal monitoring of the herbivorous fish assemblage and benthic composition (Fig. 1). Site M1 was a fringing reef with a carbonate framework, site M2 was characterised by coral growth on a granitic substrate and site M3 was patch reef on a base of

Fig. 1 The Inner Seychelles and Cousin Island showing location of monitoring sites (M1, M2 and M3) and feeding study sites (FA, FB and FC) (adapted from Jennings et al. 1996)



sand, rock or rubble (Jennings et al. 1995). The sites were surveyed at the same time of year in 1994, 1998 (immediately after the bleaching event) and in 2005, although site M2 was not surveyed in 1998. At each site, fishes were counted in sixteen 7-m-radius point counts. Large mobile species were counted first, before the count area was actively searched for territorial species. Point counts were considered appropriate because spearfishing is banned in the Seychelles and recreational diving and fish feeding, which can result in fish gathering around divers, do not take place in Cousin MPA. The size and numerical abundance of herbivorous fishes were recorded as part of a larger study in which the individual size and numerical abundance of 134 reef-associated fish species were documented. The time taken to complete the census was not standardised and varied according to the number and diversity of species present. The accuracy of length estimation was maintained by practising with objects of known size (from 8–35 cm) throughout the survey period and mean errors were 2.2–3.1%. Size estimates of fishes were converted to biomass using published length-weight relationships (Letourneur 1998; Letourneur et al. 1998; Froese and Pauly 2006).

When a fish count was complete the percentage cover (based on plan view) of sand, rock, rubble, macroalgae, dead and live branching coral, massive, tabulate, encrusting and soft coral was estimated. The topographic structural complexity of the reef inside each count area was described using a six-point scale (Polunin and Roberts 1993). Visual estimates of these benthic parameters provide comparable values to line intercept transects for benthic composition (no significant difference $P = 0.639$) and linear versus contour chain distance for structural complexity (significantly correlated, $P < 0.001$) (Wilson et al. 2007).

Feeding habits

Data relating to the feeding habits of fishes were collected from 22 April to 31 May 2006. Three study sites (FA, FB and FC) were selected as representative of different reef habitats around the island (Fig. 1). These locations were slightly different from those used in monitoring of the fish assemblage and benthic composition and were therefore treated separately. Site FA (northern side of Cousin) was structurally non-complex and from 1–5 m depth was dominated by dense macroalgae growing on a granitic substrate with intermittent sand and coral rubble patches. Below 5 m macroalgal cover was sparse and sand was the abundant substrate type. Site FB (NE side of Cousin) was a reef slope environment ranging from 5–8 m in depth and consisting mainly of dead coral rubble covered in epilithic algae and sand patches. Site FC (SE side of Cousin) was a structurally complex reef consisting of large granitic

boulders covered with epilithic algae from 2–5 m and macroalgae and sand patches below 5 m.

Study animals

For the feeding study, species were chosen to represent the three functional groups of reef herbivores identified by Bellwood et al. (2004); bioeroders, scrapers and grazers. This study focused on the most abundant species in each functional group. *Chlorurus sordidus* and *Chlorurus strongylocephalus* were chosen to represent the bioeroders (e.g., Bellwood 1995). *C. sordidus* was abundant at all three sites but *C. strongylocephalus* was only observed at sites FB and FC. However, the scarcity of any other bioeroding fishes in the study area limited the choice of species. *Scarus niger* and *Scarus rubroviolaceus* were chosen to represent the scrapers (Bellwood and Choat 1990). Observations of scarids were restricted to terminal phase individuals. While it is possible that the feeding preferences of such individuals may have been influenced by reproductive activity, evidence from the Caribbean has indicated that the diet of initial and terminal phase scarids does not differ (Bruggemann et al. 1994; McAfee and Morgan 1996). *Acanthurus leucosternon* and *Acanthurus triostegus* were chosen to represent the grazers (e.g., Barlow 1974).

Behavioural observations

All feeding observations were undertaken whilst snorkelling. The prohibition of spearfishing in the Seychelles, and the fact that Cousin has been protected from any other fishing or tourist diving activity since 1968, meant that fishes generally did not show any obvious behavioural response to an observer at distances > 2 –3 m, and would often swim underneath the observer and continue feeding. However some species such as *A. triostegus* were more skittish, especially in shallow water, and observations could only be undertaken when visibility was sufficient to allow observations from a greater distance. In all cases observations were discontinued if the fishes appeared to have been disturbed by the observer.

Diet composition

Upon arrival at the site the observer swam in a rough zig-zag pattern from the reef flat to the reef slope (from depths of approximately 3–6 m) until a target individual was located (Bellwood 1995). After a short acclimation period the fish was followed for a period of 5 minutes during which the number of bites on different substrates was recorded, in addition to the time of day and depth.

Within each survey period every effort was made to select different individuals for observation; for some

species their abundance ensured a degree of independence but for those which were less abundant the size and any distinctive markings were noted to ensure that the same individual was not observed twice. All observations of feeding behaviour were conducted by the same observer (M.H.L.) between 09.00 and 16.00. A total of 168 fishes were observed and as time of day has previously been shown to affect the feeding rates of herbivorous fishes (Polunin and Klumpp 1989) observations were split as evenly as possible between morning and afternoon.

Substratum availability

To determine whether feeding preferences were influenced by the availability of potential food resources, substratum availability was quantified in situ. This was possible only at sites FA and FB as adverse sea conditions restricted access to site FC at the end of the study period. At sites FA and FB twenty randomly placed replicate 5 m transects were surveyed using the line point intercept method. Substrate type was recorded at 20 cm intercepts. For site FC, analysis of digital photographs was used to quantify substratum availability by estimating the percentage cover of the different substrates beneath lines ≈ 5 m overlain on the photographs. Algal vegetation was categorised as: epilithic algae [multispecies assemblage of diminutive algae with a canopy height of less than 1 cm (Steneck 1988)], macroalgae [large fleshy algae with canopy heights greater than 1 cm (Steneck 1988), in this case dominated by *Sargassum* and *Turbinaria*], crustose coralline algae (encrusting calcareous algae occurring as a hard, smooth pavement on the substratum) and other algae (predominantly *Chlorodesmis*). Non-algal categories were live coral, sand and dead coral (coral which had recently died and had not been colonised by algae).

Data analysis

Temporal benthic data

Changes in benthic composition were analysed using a correlation-based principal components analysis. Draftsman plots were used to indicate any skewness in the data and variables were $\log_{10}$ transformed in order to improve the spread. In order to place the data on a common scale they were normalised by subtracting the mean and dividing by the standard deviation (Clarke and Gorley 2006). Changes in live coral and macroalgal cover between 1994, 1998 and 2005 were assessed using a 2-way ANOVA with year and monitoring site as fixed factors. Since monitoring sites were located in different reef habitats they could not be pooled for analysis and as site M3 had not been surveyed in 1998, subsets of the data

that had observations for all factors were analysed separately (Quinn and Keough 2002). This involved one ANOVA with data from 1994 and 2005 at sites M1, M2 and M3 and one with data from 1994, 1998 and 2005 at sites M1 and M2. Normality of data was examined using probability plots of the residuals and homogeneity of variances was tested using Levene's test ($P < 0.05$). Data required $\log_{10}$ transformation to meet the assumptions of the analysis. In the case of macroalgal cover the assumption of homogeneity of variance could not be met due to the presence of outliers. The removal of these outliers allowed the assumption of homogeneity of variance to be met but did not affect the inference of the test and the original results are reported. Where differences were significant, Tukey's test was used to identify significant pairwise differences.

Temporal fish numerical abundance and biomass data

A 2-way ANOVA, with year and monitoring site as fixed factors, was used to assess changes in numerical abundance and biomass of the whole herbivorous fish assemblage and of the three functional groups of herbivorous fishes. The absence of data for site M3 in 1998 was overcome using the approach described for benthic data. Probability plots of residuals were used to assess normality of the data and homogeneity of variances were tested using Levene's test ($P < 0.05$). Numerical abundance data were $\log_{10}$ transformed and biomass data were square root transformed to meet the assumptions of normality and homogeneity of variance. In several cases the assumption of homogeneity of variance could not be met due to the presence of outliers. Again, the removal of these outliers allowed the assumption of homogeneity of variance to be met but did not affect the inference of the tests and the original results are reported. Where differences were significant, Tukey's test was used to identify significant pairwise differences.

Feeding selectivity

Two separate 2-way crossed ANOSIMs with site and species, and with site and functional group, based on Bray-Curtis similarity matrices were undertaken in PRIMER (Plymouth Routines in Multivariate Ecological Research) to assess differences in the proportion of bites on different substrates (Clarke and Gorley 2006). As most bites were on epilithic algae, data were square root transformed to give greater relative weighting to bites on other substrates.

Ivlev's electivity index was used to quantify feeding selectivity, by comparing the proportion of bites taken on different substrates with respect to their availability (Ivlev 1961). The index is defined as

$$E = (r_i - p_i) / (r_i + p_i)$$

where r_i is the proportion of bites taken on food type i and p_i is the average percent occurrence of food type i in the environment. The index ranges from +1.0 to −1.0 with a positive value indicating preference, a negative value indicating avoidance and zero representing no selection (Ivlev 1961).

Results

Changes in benthic composition 1994–2005

In 1994 the reefs were dominated by live (massive and branching) coral and were structurally complex (Fig. 2). The bleaching event of 1998 resulted in a massive reduction in live coral cover but the structural complexity was maintained (Fig. 2). By 2005 this complexity had been lost and the reefs were dominated by macroalgae (mainly

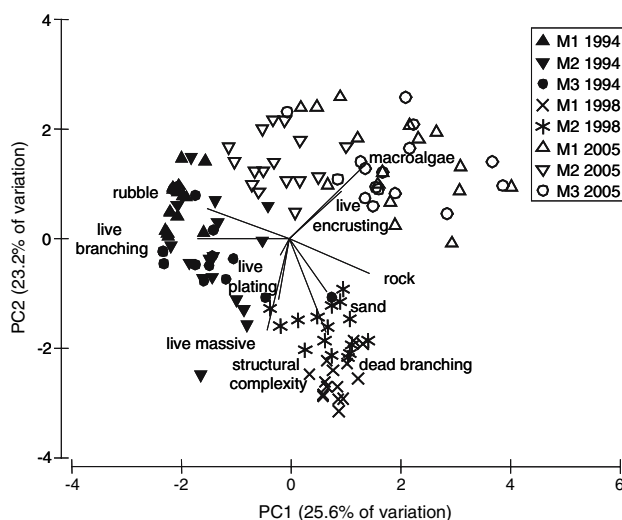


Fig. 2 Principal components analysis of change in benthic composition and structure of Cousin reefs over period 1994–1998–2005. Eigenvectors of each benthic variable are overlaid

Phaeophyta from the genera *Sargassum* and *Turbinaria*, with some *Padina*) and bare rock (Fig. 2). Coral cover declined from 1994 to 1998 and again from 1998 to 2005 with similarly low levels at all three sites in 2005 (Fig. 3a). Although there was no increase in macroalgal cover between 1994 and 1998, there had been a substantial increase by 2005 (Fig. 3b). However there were marked differences in macroalgal cover among monitoring sites in 2005, with site M2 having much lower cover than sites M1 and M3 (Fig. 3b). There was a significant interaction between year and monitoring site, due to smaller declines in coral cover and smaller increases in macroalgal cover at site M2 than at the other sites over time. There was also a significant difference in coral and macroalgal cover among years and, in most cases, among monitoring sites (Table 1).

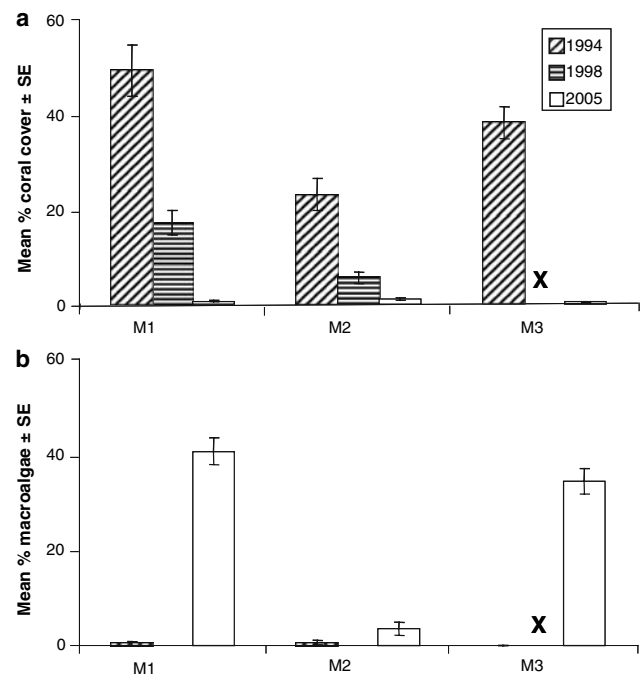


Fig. 3 a Mean percent coral cover, and **b** mean percent macroalgal cover at monitoring sites in Cousin Marine Protected Area in 1994, 1998 and 2005. X indicates a lack of data for site M3 in 1998

Table 1 Results of two-way ANOVAs on percentage cover of coral and macroalgae

Variate	Year			Monitoring site			Year × monitoring site		
	df	F ratio	P value	df	F ratio	P value	df	F ratio	P value
Comparison of 1994 and 2005 at monitoring sites M1, M2 and M3									
Coral cover	1,90	1131.87	<0.001	2,90	3.02	0.054	2,90	11.72	<0.001
Macroalgal cover	1,90	575.85	<0.001	2,90	55.77	<0.001	2,90	68.75	<0.001
Comparison of 1994, 1998 and 2005 at monitoring sites M1 and M2									
Coral cover	2,90	188.48	<0.001	1,90	18.43	<0.001	2,90	9.93	<0.001
Macroalgal cover	2,90	210.89	<0.001	1,90	68.52	<0.001	2,90	74.88	<0.001

Numerical abundance and biomass of herbivorous fishes

No consistent trends were apparent in numerical abundance or biomass of grazers, scrapers or bioeroders among monitoring sites or years (Fig. 4; Table 2). Total numerical abundance remained stable from 1994–1998–2005 at site M1 but decreased at sites M2 and M3, while total biomass increased at site M1 but showed little change at sites M2 and M3 (Fig. 4). Changes in the numerical abundance and biomass of the three functional groups were very variable and differed among monitoring sites but in the majority of cases numerical abundance declined or remained stable whereas biomass increased or declined to a lesser extent (Fig. 4). This trend reflects a change in the size structure of the fish assemblage due to a decline in the numerical

abundance of smaller individuals and an increase in larger individuals (Graham et al. 2007). It is likely to have been driven by a combination of increased growth and/or survivorship of larger fishes due to improved dietary resources and an increase in the mortality of smaller fishes due to a loss of reef structure (Graham et al. 2007). Such changes were especially notable in the case of grazers and scrapers whereas the numerical abundance and biomass of the bioeroders remained relatively more stable over time (Fig. 4). There were significant interactions between year and monitoring site for both numerical abundance and biomass (Table 2); in many cases this was due to greater declines in numerical abundance at sites M2 and M3 than at site M1. Numerical abundance of grazers and bioeroders differed significantly among years, as did biomass of bioeroders (Table 2). There was also a significant difference

Fig. 4 **a** Numerical abundance, and **b** biomass of herbivorous fishes at monitoring sites in Cousin Marine Protected Area in 1994, 1998 and 2005

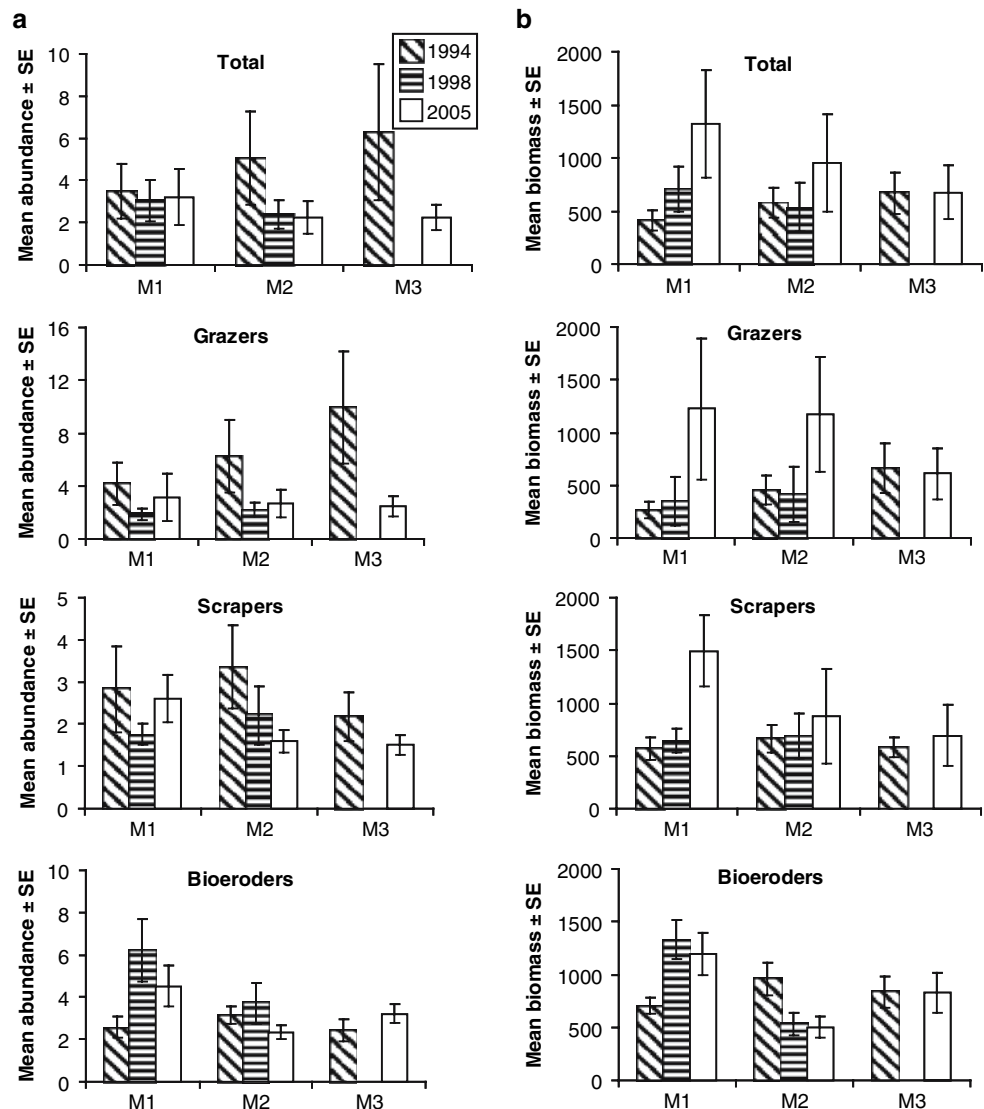


Table 2 Results of two-way ANOVAs on numerical abundance and biomass of herbivorous fish species

Variate	Year			Monitoring site			Year $\times$ monitoring site		
	df	F ratio	P value	df	F ratio	P value	df	F ratio	P value
Comparison of 1994 and 2005 at monitoring sites M1, M2 and M3									
Numerical abundance									
Grazers	1,83	32.65	<0.001*	2,83	0.96	0.387	2,83	2.56	0.083
Scrapers	1,76	1.30	0.259	2,76	3.97	0.023*	2,76	3.20	0.046*
Bioeroders	1,65	0.78	0.381	2,65	1.45	0.243	2,65	2.16	0.123
All	1,87	29.17	<0.001*	2,87	1.64	0.199	2,87	7.70	0.001*
Biomass									
Grazers	1,90	0.00	0.986	2,90	0.26	0.769	2,90	3.20	0.046*
Scrapers	1,90	1.17	0.282	2,90	9.12	<0.001*	2,90	6.35	0.003*
Bioeroders	1,90	0.12	0.733	2,90	3.76	0.027*	2,90	6.23	0.003*
All	1,90	1.13	0.290	2,90	5.13	0.008*	2,90	10.51	<0.001*
Comparison of 1994, 1998 and 2005 at monitoring sites M1 and M2									
Numerical abundance									
Grazers	2,85	12.95	<0.001*	1,85	2.51	0.117	2,85	4.71	0.012*
Scrapers	2,79	0.75	0.475	1,79	0.08	0.774	2,79	13.47	<0.001*
Bioeroders	2,70	4.91	0.010*	1,70	10.04	0.002*	2,70	4.65	0.013*
All	2,87	8.93	<0.001*	1,87	1.34	0.250	2,87	10.52	<0.001*
Biomass									
Grazers	2,90	1.33	0.269	1,90	0.04	0.833	2,90	3.07	0.051
Scrapers	2,90	1.36	0.261	1,90	3.98	0.049*	2,90	16.12	<0.001*
Bioeroders	2,90	6.11	0.003*	1,90	29.99	<0.001*	2,90	10.66	<0.001*
All	2,90	2.91	0.060	1,90	5.78	0.018*	2,90	13.04	<0.001*

* Indicate statistically significant results at a significance level of 0.05

among monitoring sites in numerical abundance and biomass of bioeroders and scrapers (Table 2).

Feeding selectivity

There was a significant difference among species (ANO-SIM, $P = 0.024$) in terms of proportion of bites on different substrates but not among feeding study sites and the only significant pairwise difference was between *A. triostegus* and *C. sordidus* ($P = 0.001$).

Epilithic algae and macroalgae (predominantly *Sargassum* and *Turbinaria*) were the most abundant substrate types at the feeding study sites although more than 80% of bites for all fish species were from epilithic algae (Table 3). Only *A. triostegus* and *S. rubroviolaceus* consumed macroalgae in any notable proportion although bites from this substrate represented less than 10% of their total bites (Table 3). Electivity indices confirmed that most fishes consumed only epilithic algae and avoided macroalgae and other substrata (Fig. 5). There was no significant difference overall in the proportion of bites taken on different substrates among functional groups although there

was a significant pairwise difference between grazers and bioeroders ($P = 0.029$).

Discussion

The three functional groups of herbivores studied here all appeared to prefer epilithic algae over other algal resources and frequently avoided macroalgae. Such preferences have also been noted for Caribbean herbivores (Bruggemann et al. 1994; Paddock et al. 2006), for Indo-Pacific scarids (Bellwood and Choat 1990) and for herbivorous reef fishes in general (Russ and St. John 1988; Choat 1991; Bellwood et al. 2006). Furthermore, analysis of the gut contents of some of the species studied here support the finding that macroalgae are rarely consumed by these fishes (Hiatt and Strasburg 1960; Robertson et al. 1979; Sano et al. 1984; Choat et al. 2002). The avoidance of macroalgae has been attributed to the presence of chemical and physical deterrents which renders macroalgae less palatable and digestible to herbivores (e.g., Hay et al. 1987), although intense herbivorous grazing of epilithic algal turfs has been shown

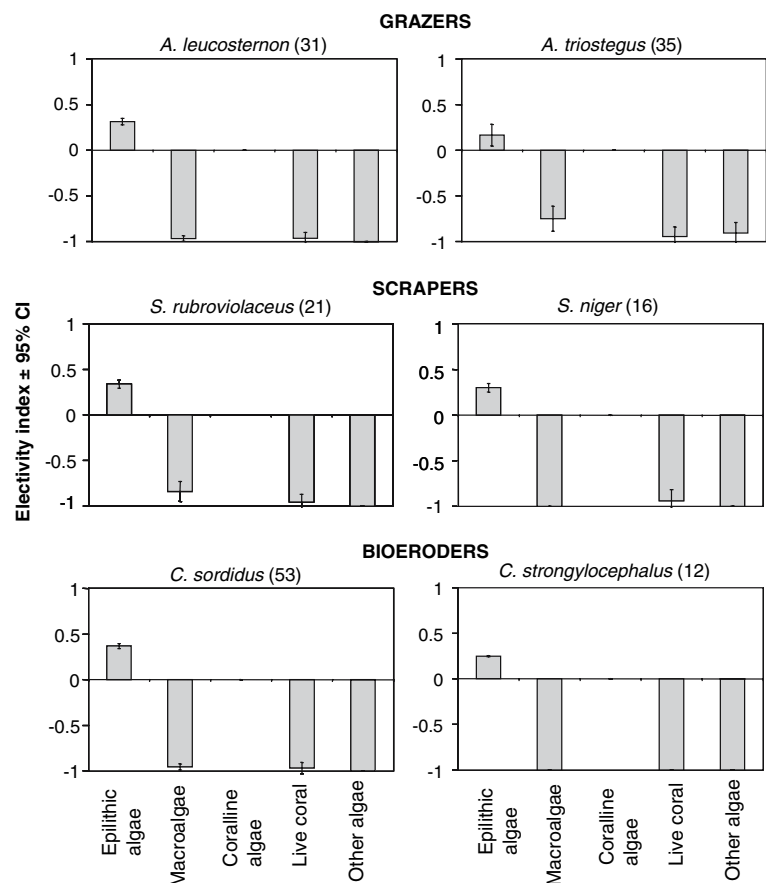
Table 3 Availability of substrate types averaged over all three feeding study sites and mean percentage of bites taken on these substrates by each fish species

Substrate	Epilithic algae	Macro-algae	Crustose coralline algae	Live coral	Other algae	Sand	Dead coral
Mean availability (%)	53.00	27.58	0.28	1.06	0.98	17.00	0.08
Mean percentage of bites							
<i>Chlorurus sordidus</i>	98.16	1.46	0.03	0.12	0.00	0.12	0.12
<i>Chlorurus strongylocephalus</i>	100	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acanthurus leucosternon</i>	98.79	1.00	0.17	0.03	0.00	0.00	0.00
<i>Acanthurus triostegus</i>	85.08	7.96	0.00	0.50	0.13	0.61	0.00
<i>Scarus rubroviolaceus</i>	95.26	4.69	0.00	0.05	0.00	0.00	0.00
<i>Scarus niger</i>	98.01	0.00	1.91	0.08	0.00	0.00	0.00

to limit the establishment and growth of macroalgae (Lewis 1986; Williams et al. 2001; Paddock et al. 2006).

Several sites on Cousin are dominated by macroalgae and macroalgal cover has increased through time. This highlights the limited capacity of the herbivorous fish guild to exclude macroalgae. Unfished herbivorous fish guilds in the Caribbean could only maintain 40–60% of reef substratum in a cropped state (Williams and Polunin 2001) and in the Florida Keys the high biomass of herbivorous fishes restricted macroalgal spread, but did not entirely exclude

these algae (Paddock et al. 2006). Coral cover has been implicated as an important factor in determining the impact of herbivorous fishes on algae, and on high coral-cover reefs the impact of herbivorous fishes on algae will be greater since there will be stronger competition for the limited algal resources. Conversely, on low coral cover reefs the large amount of space occupied by algae limits the ability of herbivorous fishes to keep it cropped down (Williams et al. 2001). On Cousin Island coral cover declined dramatically and algal cover increased, yet the

Fig. 5 Mean values of Ivlev (1961)'s electivity indices for *Acanthurus leucosternon*, *Acanthurus triostegus*, *Scarus rubroviolaceus*, *Scarus niger*, *Chlorurus sordidus* and *Chlorurus strongylocephalus*, averaged over all feeding study sites. Numbers in brackets after species refer to number of individuals observed

numerical abundance and biomass of algal feeding fishes generally did not increase sufficiently to control and restrict macroalgal development.

The recovery of coral reefs following disturbance is complex and there is evidence to suggest that once a phase shift has been initiated, hysteresis effects can inhibit reversal (Scheffer and Carpenter 2003). Around Cousin, it is likely that following the decline in coral cover in 1998, epilithic algae became dominant and colonised the available space. Not only can epilithic algal turfs reduce coral settlement in their own right (Birrell et al. 2005) but once they develop into macroalgae they become increasingly resistant to perturbations (McManus and Polsenberg 2004) and the community becomes more stable. High algal biomass has been shown to negatively affect coral recruitment (Birkeland 1977; Kuffner et al. 2006) and growth rates (Tanner 1995) and algae may also have an indirect effect on corals through the release of dissolved compounds which have been shown to enhance microbial activity and lead to an increased occurrence of coral mortality (Smith et al. 2006). Mumby (2006) described this cycle of events based on the results of model simulations of Caribbean reefs, whereby coral mortality led to an increase in the amount of space available for algae and a decrease in the grazing intensity on any given patch of reef. Reduced grazing intensity resulted in an increase in macroalgal cover and therefore an increase in juvenile coral mortality (Mumby 2006). The changes on Cousin probably provide evidence for a similar positive feedback loop in which an initial decline in coral cover due to bleaching provided more space for epilithic algae, which developed into macroalgae and dominated the benthos due to insufficient herbivory.

There are several other factors which may also have impeded coral recovery on Cousin and caused further declines in coral cover noted from 1998 to 2005. While Seychelles' reefs are located on a shallow continental plateau, they are relatively isolated from other reef systems, suggesting coral populations are largely reliant on self-recruitment. The small and disconnected nature of many coral brood stocks post-1998 is likely to have reduced the supply of coral larvae (Hughes and Tanner 2000; Ayre and Hughes 2004). In addition, while the role of coral-feeding fishes in reef recovery is largely unknown, they have been implicated in undermining reef resilience (West and Salm 2003). While some reef fishes are obligate coral feeders (Kokita and Nakazono 2001; Pratchett et al. 2004) others, notably several species of scarids, consume live coral in addition to other resources (Bellwood and Choat 1990; Bythell et al. 1993; Rotjan and Lewis 2005). Rotjan et al. (2006) demonstrated that scarid grazing had the potential to reduce coral fitness and retard the recovery of coral colonies following bleaching. McClanahan et al.

(2005) also indicated that predation by scarids may have retarded post-bleaching recovery of coral transplants in Kenya. One of the most prolific feeders on live coral is *Bolbometopon muricatum*, which take nearly half of all their bites from this substrate on the Great Barrier Reef (Bellwood et al. 2003). Schools of *B. muricatum* can often be seen around Cousin (Jennings 1998; M. H. Ledlie, personal observation) although their role in reef recovery is largely undefined, as the feeding response of this species when coral cover is low is unknown.

The role of herbivorous fishes in promoting reef recovery and resilience is likely to depend not only on their feeding preferences but also on their numerical abundance and biomass, which may be affected by changes in the benthos. With an increase in algal availability, the numerical abundance and biomass of herbivorous fishes might be expected to increase and to control algal proliferation. However, no consistent positive or negative trends were detected in the numerical abundance or biomass of herbivores on Cousin, over time, or at the different monitoring sites. Other studies have also found little evidence to indicate that the numerical abundance and biomass of herbivorous fishes increased following increases in turf algae (Hart et al. 1996; Spalding and Jarvis 2002). However, Russ (2003) found a significant positive correlation between grazer biomass and algal productivity on the Great Barrier Reef, and other studies have shown that an increase in the abundance and productivity of algal resources may result in an increase in grazing rates and in the numerical abundance and biomass of herbivores if they were formerly food limited (Carpenter 1990; Robertson 1991; McClanahan et al. 2000; Lindahl et al. 2001; Williams et al. 2001; Sheppard et al. 2002; Mumby et al. 2005; Garpe et al. 2006). Clearly not all herbivorous fish populations will be food limited and other changes in the reef benthos, such as the loss of habitat complexity following coral mortality can also influence the numerical abundance and biomass of fishes. This has certainly been the case on Cousin and may help to explain why herbivores have not increased in numerical abundance, despite the observed increase in epilithic algae.

Habitat complexity can reduce competition and predation (Buchheim and Hixon 1992; Hixon and Beets 1993) and there are locations where the maintenance of reef structure following coral mortality has sustained abundant and diverse fish populations (Lindahl et al. 2001; Riegl 2002). Yet other studies have been less conclusive; Almany (2004) found the effect of habitat complexity on predation and competition was more variable and depended on factors such as the availability of appropriate shelter sites and the behavioural attributes of predators. Habitat complexity can also affect recruitment (Öhman et al. 1998) and the loss of complexity may have contributed to the increased

dominance of larger fishes on Cousin as smaller size classes were limited by the availability of recruitment sites. This trend is concerning as it is likely to result in declines in numerical abundance and biomass of herbivorous fishes in the future, and further restrain their role in algal removal (Graham et al. 2006, 2007).

That the dramatic phase shift from coral to macroalgal dominance on Cousin took place in an established and well enforced MPA with a fully protected herbivorous fish guild highlights some questions regarding the role of spatial closures in buffering the effects of external disturbance events. Several studies have highlighted the fact that grazing by herbivorous fishes influences competitive interactions between corals and macroalgae (Lirman 2001; Williams and Polunin 2001; Mumby et al. 2006a; Paddock et al. 2006) and Mumby et al. (2006b) demonstrated that MPAs can enhance grazing and reduce macroalgal cover. However, the complexity of trophic interactions on coral reefs and the variable role of predation in structuring reef fish communities mean that spatial closures do not have a consistent effect on the numerical abundance and biomass of herbivores (Jennings and Polunin 1997; Graham et al. 2003, 2005; Dulvy et al. 2004; Mumby et al. 2006b). The size of MPAs is likely to be an important factor determining their role in the promotion of resilience, although the numerical abundance and biomass of herbivorous fishes has been shown to be enhanced even in very small MPAs (Halpern 2003), probably reflecting the strong site attachment of many herbivorous fishes (Chapman and Kramer 2000). Indeed, surveys in 1994 indicated that the effective protection of Cousin MPA from fishing had maintained a higher biomass and diversity of herbivores than in fished areas (Jennings et al. 1996).

The phase shift observed in the 1.2 km² Cousin MPA must be considered in the context of concurrent declines in coral reef resilience in the Seychelles as a whole (Graham et al. 2006). Even if the protection of Cousin had afforded more resilience to this small area by maintaining a healthy herbivorous fish guild, the degradation of other reef habitats within the Seychelles may have caused declines once a critical threshold was passed (Hughes et al. 2005). Furthermore, it is naïve to assume that the protection of herbivorous species which can prevent phase shifts by keeping epilithic algae cropped down will result in the reversal of a phase shift once macroalgae have become established (Bellwood et al. 2006). Most herbivorous fishes avoid macroalgae and a recent study on the Great Barrier Reef found a 'sleeping functional group', represented by a single species of batfish, that usually consumes benthic invertebrates or plankton, was almost solely responsible for removing macroalgae and facilitating reef recovery (Bellwood et al. 2006). It is possible that other functional groups may be present in the Seychelles, imparting an additional

dimension to the complexity of coral reef recovery and resilience following phase shifts.

While the importance of MPA networks and connectivity has been recognised (Lubchenco et al. 2003; Palumbi 2003; Ayre and Hughes 2004) the applicability of these concepts to remote reefs has yet to be determined. Moreover, the global scale of disturbance events such as climate change, and the large dispersal distances of many larvae, mean that even the largest MPAs may not be self-sustaining (Nyström and Folke 2001; Bellwood et al. 2004). Consequently, the localised benefits of small MPAs may become ineffective if such areas do not have the resilience to recover from global disturbance events. As a means of mitigating biodiversity losses from coral bleaching, West and Salm (2003) suggest that areas where environmental conditions enhance resistance and resilience to bleaching are incorporated into MPA networks. Indeed, coral recovery in the Seychelles has been shown to be highly site specific and influenced by local factors such as water quality and upwelling (Engelhardt 2004). In the Seychelles as a whole, granitic reef habitats appear to have recovered most successfully from the 1998 bleaching (Graham et al. 2006) and the protection of such areas may represent a means of preserving coral biodiversity (Engelhardt 2004) and enhancing resilience at a local scale.

With the frequency of coral bleaching in the Indian Ocean predicted to increase in the future (Sheppard 2003) the prospects for reef recovery to a coral dominated state on Cousin are not encouraging. Reef recovery following disturbance can no longer be taken for granted (Nyström et al. 2000) and hypothesised outcomes of increases in the occurrence of coral bleaching include changes in coral community structure or set backs to early successional stages or alternate states (Done 1999; Hoegh-Guldberg 1999). The lack of resilience in Cousin MPA and the consequent phase shift from coral to macroalgal dominated reefs would appear to support such predictions and even if coral recruitment does increase, the abundance of algae in this community may retard coral recovery. The MPA adhered to many of the current paradigms regarding effective coral reef management; local anthropogenic stressors were virtually non-existent and effective enforcement of the MPA had led to healthy populations of herbivorous fishes (Jennings et al. 1996). The fact that a dramatic phase shift accompanied by a collapse in reef structure still took place could be taken as an indication that such small-scale protected areas may not be successful on their own. Perhaps a larger scale approach involving networks of appropriately located MPAs (Lubchenco et al. 2003) based on an appreciation of the complexities inherent in the dynamics of coral reef recovery following disturbance (Bellwood et al. 2006) would be more appropriate.

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