

Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries and ecosystems

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Abstract

The increased frequency and intensity of bleaching episodes has led to wide-scale loss of reef corals and raised concerns over the effectiveness of existing conservation and management efforts. The 1998 bleaching event was most severe in the western Indian Ocean where coral declined by up to 90% in some locations. Using fisheries independent data, we assess the long-term impacts of this event in the Seychelles on fishery target species, the overall size structure of the fish assemblage and assess the effectiveness of two marine protected areas (MPAs) in offering resilience. Fishery target species above size at first capture showed little change in biomass between 1994 and 2005, corroborating studies that suggest fisheries yields are currently not affected. Biomass remained higher in protected areas, indicating they are still effective in protecting fish stocks. However, the size structure of the fish communities, as described with size-spectra, changed in both fished and protected areas, with a decline in smaller fish (<30 cm) and an increase in larger fish (>45 cm). This is likely to represent a time lag response; with the larger fish that are lost to natural mortality and fishing no longer being replaced by juveniles. This effect is expected to be even greater in terms of productivity, affect fisheries and, as congruent patterns are observed for herbivores, suggests no long term resilience in the MPAs. Corallivores and planktivores demonstrate striking declines in numerical abundance which are greatest in MPAs, and associated with a similar pattern of decline in their preferred corals. There is an urgent need for climate mediated disturbance to be at the fore of conservation and management planning for coral reefs, which should include MPAs placed in areas of resistance and resilience to bleaching, and a greater emphasis on reducing other stressors to the system as a whole.

Introduction

Coral reefs and associated communities are threatened by anthropogenic and natural disturbance. Substantial declines in coral cover, fish abundance and changes in ecosystem function have been attributed to multiple stressors including overharvesting, sedimentation, pollution, disease and warming waters (Hughes et al. 2003; Bellwood et al. 2004; Jones et al. 2004; Graham et al. 2006; Wilson et al. 2006). Although multiple stressors often act in synergy, climate driven coral bleaching has emerged as one of the greatest threats to coral reef ecosystems (Hoegh-Guldberg 1999; Hughes et al. 2003; Sheppard 2003). The 1998 bleaching event was the largest on record, and in the most heavily impacted region, the western Indian Ocean, coral cover declined by up to 90% (Goreau et al. 2000; Sheppard 2003). Recovery from such severe disturbances is likely to be slow, particularly for isolated systems when brood stocks become severely depleted and replenishment from external sources are expected to be rare events (Hughes et al. 2003; Graham et al. 2006). Disturbance at this scale is expected to have significant, yet little understood, ramifications for other reef associated organisms (Walther et al. 2002).

The short-term impacts of bleaching on fish are mainly manifest in species that specialise on live coral for diet, shelter or as a recruitment habitat (reviewed by Wilson *et al.* 2006) with greater impacts in proportion to the degree of specialisation (Munday 2004). In the medium- to long-term, if there is little coral recovery, declines in coral feeders can continue, due to reduced fitness associated with unfavourable food resources (Pratchett et al. 2006). However, the greatest impacts are realised if the physical matrix of the reef collapses, reducing topographic complexity and associated refuge space, and in such scenarios species richness of the community falls (Garpe et al. 2006; Graham et al. 2006). However the medium to long-term impacts of

bleaching on the size structure of fish populations and assemblages, particularly those of species that do not specialise on live coral, are unknown (Wilson et al. 2006).

These impacts are important because they determine the future viability of populations and assemblages and thus interact with fisheries management and other conservation measures that may have been proposed or implemented prior to any bleaching event.

Assessments of the impacts of mass bleaching on fisheries and associated socio-economics are currently limited to fisheries-dependant data and are considered small in relation to the direct impacts of fishing (McClanahan et al. 2002; Grandcourt & Cesar 2003). However, such assessments have all been made within 5 years of bleaching events. Since a loss in structural complexity of the reef framework, which can take >5 years (Wilson et al. 2006), is likely to affect small individuals, and since these may take some time to recruit to the fishery, a lag effect may exist before the full impact of coral bleaching on reef fisheries is realised.

In order to conserve and manage reefs in the face of unpredictable disturbance, scientists and managers are increasingly proposing that no-take marine protected areas (MPAs) can increase resilience of the reef ecosystem (Hughes et al. 2003; Bellwood et al. 2004). Although it is clear that MPAs cannot prevent the influx of warm water that can cause widespread coral mortality, theory predicts that maintenance of greater biomass, density and size of herbivorous fishes by MPAs (in regions where herbivores are fished) should promote coral recovery, thus providing spatial resilience in the form of populations that can re-seed depleted areas (Nystrom & Folke 2001; Hughes et al. 2003). There is evidence of an initial build up of fish biomass in MPAs even during habitat degradation (Hawkins et al. 2006), however biodiversity may

decline (Jones et al. 2004) and it is unclear how the size-structure of the fish assemblage may respond.

Using fisheries independent data, collected across the inner granitic islands of the Seychelles, we assess the medium to long-term effects of mass coral bleaching on 1) target reef fish above size at first capture in the fishery, 2) the overall size structure of the assemblage and that of aggregated feeding groups and 3) the effectiveness of existing no-take MPAs in offering spatial resilience to the disturbance.

Methods

Study sites

The inner granitic islands of the Seychelles lie on the Mahé Plateau, a shallow, extensive submarine platform which reaches mean depths of 44-65m. The fringing reefs of the islands are typically shallow, the reef slope terminating at 6-13m, and consist of a carbonate or granitic rock framework (Jennings et al. 1995, Graham et al. 2006). The 1998 bleaching event reduced live coral cover from 27 to 3%, an overall reduction of approximately 90%. Furthermore, there was no apparent depth refuge; coral mortality extended throughout the depth range of the coral reefs in this area (Linden et al. 2002; Sheppard 2003). Recovery has been extremely slow, with collapse in the physical complexity of the reefs accelerating from 2003 (Engelhardt 2004) and mean coral cover attaining only 7.5% by 2005 (Graham et al. 2006).

Other than climate-mediated bleaching mortality of corals, Seychelles reefs have experienced relatively little change in other stressors over the study period (Graham et al. 2006). A small crown-of-thorns starfish outbreak in 1996 has not been repeated (Linden et al. 2002). Sedimentation is a chronic problem in the wet season (December-February) at particular sheltered locations, and sedimentation resulting

from land reclamation has been effectively mitigated in recent years (J. R., unpublished data). The December 2004 tsunami exerted negligible impacts on Seychelles reefs (Abdulla et al. 2006). There has been very little change in relative fishing pressure on inshore artisanal fishing grounds (Seychelles Fishing Authority technical reports from 1989 to 2004).

Reef surveys were conducted in seven areas, around Mahé, Praslin and associated islands, which included most of the shallow fringing reef around the inner islands (for map of sites see Jennings et al. 1995). Five fished areas were subject to similar levels of fishing intensity, while the other two areas were long-standing MPAs. Sainte Anne Marine National Park was gazetted by the Government of Seychelles in 1973 as it is suitably located for tourist use, whereas Cousin Island Special Reserve was established by Birdlife International who bought the island in 1968 to protect an endangered species of bird (Jennings et al. 1996). Both MPAs are within the same geographic area as the other sites and have similar bathymetry and habitat types. Spatial studies of MPA effects are expected to reflect the outcome of temporal studies (Russ et al. 2005) and in Seychelles previous work has shown significant differences in the diversity and biomass of fish between the two MPAs and the five fished areas but not within the MPAs or fished areas *per se* (Jennings et al. 1995). Studies conducted within other reef systems have also highlighted the disproportionate effect of small amounts of fishing on fish communities and the low statistical power to detect more subtle additional impacts of further increases in fishing pressure (Jennings & Polunin 1997; Hawkins & Roberts 2004). For these reasons, we assess the interaction between bleaching impacts and management by comparing the two MPAs to the five fished areas, before and after coral bleaching in 1998.

Comment [TMD1]: The text begged the question “what is a ‘medium’ fishing pressure”

Assessment of fish assemblage and benthic community structure

Twenty one sites, covering over 50,000m² of coral reef habitat, were surveyed at the same time of year in both 1994 and 2005. Three sites were surveyed in each of the seven areas of coast described above. One site in each of three statistically different habitat types (Jennings et al. 1995); carbonate fringing reefs, granitic rocky reefs with coral growth and patch reef habitats on a sand, rubble or rock base, were surveyed. At each site 16 replicate 7m radius point counts were completed using underwater visual census along the base of the reef slope. This technique maximised area coverage and replication, yet allowed for detailed searching for territorial species providing a quantitative estimate of fish of varying size and behaviour. Replicates were separated by a random number of fin kicks with the proviso that each count was separated by a minimum of 15 m; thus ~1/2 km stretch of reef was covered at each site. The numerical abundance and size of 134 species of reef-associated, diurnally-active, non-cryptic fish (>8cm) was estimated within each count area, with the most mobile species surveyed first. The time taken to complete a count varied and depended on the number and diversity of fish present. Size estimation of fish was to the nearest centimetre, validated at each site by estimating the lengths of a random selection of PVC pipes. Length estimates were not consistently shorter or longer than actual lengths in both 1994 and 2005, with a mean error associated with estimates of 8 to 35cm pipes of 3.1% and 2.2% respectively. Fish counts in 1994 were conducted by S.J. and in 2005 by N.A.J.G. Although small errors can exist among observers (Thompson & Mapstone 1997), bias among experienced divers has been shown to be the smallest component of variation in fish counts (Williams et al. 2006; McClanahan et al. in press). Fish count data was converted to biomass using published length-

weight relationships (Letourneur 1998; Letourneur et al. 1998; Froese & Pauly 2006). Species were assigned to feeding groups (herbivores, piscivores and mixed diet feeders; those species that consume either animal and plant material or fish and invertebrates and can not be easily classified to a distinct feeding group) based on regional fish identification guides, dietary literature and Froese and Pauly (2006).

After a fish count was complete the benthic composition and structural complexity of the count area was assessed. Percent cover of benthic categories (live branching, plating, massive, corymbose and encrusting coral, soft coral, macroalgae, rock, rubble, sand and dead branching coral) was estimated visually and found to be accurate when compared with results obtained from the line-intercept method (no significant difference, MANOVA $F_{6,35} = 0.56$, $P = 0.76$) (Wilson et al. 2007). Structural complexity of the benthos was assessed using a 6 point visual scale and assessed for accuracy using the linear verses contour chain method; the two methods being highly correlated (significantly correlated, linear regression $r = 0.85$ $P < 0.001$)(Wilson et al. 2007).

Establishment of fishery target species and size of first capture

Fish species that are targeted by the local artisanal fishery were assigned to three groups: primary targets, important targets and occasional targets (Grandcourt 1999). To assess the impact of the bleaching event on the fish that were likely to be accessible to capture fisheries, data were filtered by size to exclude fish too small to be caught by the dominant inshore trap fishery. There is a strong relationship between body depth of retained fish and the maximum width of trap meshes (Munro et al. 2003). In Seychelles minimum legal trap hexagonal mesh diameter is 4cm, but fishers often use trap meshes larger than this size and fish are able to squeeze through meshes

smaller than their specific body depth (Robichaud et al. 1999). We calculated size at first capture from length frequency data of 5651 trap-caught fish between January 1992 and June 1994 (SFA, unpublished data). Ninety five percent of fish in the sample had a body depth of over 6.0 cm. Target fish species data from both the 1994 and 2005 reef surveys were therefore filtered to exclude individuals with a body depth of less than 6 cm for species level and aggregated feeding group analyses.

Data analysis

Since structural complexity may affect the availability of refuges for small individuals and species, we assessed changes in structural complexity between 1994 and 2005. Furthermore, live corals were categorised into two groups, 1) complex; branching, plating and corymbose functional forms which offer the most structure for other organisms to live in (Bellwood et al. 2004; Jones et al. 2004) and are generally the favoured corals for diet and habitat specialists (Munday 2004; Pratchett 2005; Wilson et al. 2006) and 2) non-complex; massive and encrusting functional forms which offer limited structure for other organisms to live in (Jones et al. 2004). Three-way crossed fixed-effects orthogonal analysis of variances (ANOVAs) were used to assess differences between years, habitat types and management status (fished versus protected) of structural complexity and the two coral cover categories. Homogeneity of variances were assessed using Levene's test and normality of the data was assessed with histograms and normal probability plots of the residuals. Due to the very low cover of complex corals in 2005, data had to be square root transformed to meet assumptions. Tukeys post-hoc test was used to identify where differences occurred among habitats when significant.

Changes in the biomass of individual species and aggregated feeding groups of fishery targets above size at first capture were also assessed using the same three-way crossed fixed-effects orthogonal ANOVA design. At the species level, log transformation was necessary to meet the assumption of homogeneity of variances for a number of species and ten species that still failed to meet assumptions could not be analysed. Details of species requiring transformation are given in the footnote of Table S1.

The overall size structure of the assemblage (including size below first capture) was described with size spectra; slopes of abundance-size relationships of the whole assemblage (Dulvy et al. 2004; Graham et al. 2005). Slopes of the size-spectra were calculated from linear regressions of $\log_{10}(x + 1)$ numbers per size class (5 cm) on the rescaled \log_{10} mid-point of each length class. Centering the independent variable gives values of mid-point height that are comparable among spectra (Daan et al. 2005). A steepening of the slope can be the result of a decrease in the number of large fish, an increase in the number of small fish, or both. Mid-point height is a measure of community abundance. Change in the slope and mid-point height of the size spectra were also assessed using the three-way crossed fixed-effects orthogonal ANOVA design. All assumptions of the analysis were met.

To assess what was driving the trends in size spectra slope, changes in the numerical abundance of fishes in individual size bins of 5cm between 1994 and 2005 were assessed (1) for the assemblage as a whole and (2) for 5 key feeding groups: mixed diet feeders, piscivores, herbivores, corallivores and planktivores. To partition any effects of marine protection and habitat type, data were plotted separately by management status and within this by habitat type.

Results

Structural complexity declined significantly between years ($F_{1,30} = 19.94$, $P < 0.001$) and did not vary with habitat or protection (Fig. 1a). The cover of live complex corals fell by over 95% (Fig. 1b) ($F_{1,30} = 100.22$, $P < 0.001$), with the greatest reductions on carbonate habitats (significant interaction: $F_{2,30} = 3.71$, $P < 0.05$) and greater reductions on reefs within protected than fished areas ($F_{1,30} = 7.30$, $P < 0.05$). The greater impact in MPAs resulted from a higher initial cover of complex corals within MPAs in 1994, which declined to a similar base level (<1%) in 2005 as in fished sites. Cover of non-complex corals remained relatively stable between 1994 and 2005, with no significant factors in the model (Fig. 1c).

Fish target species above size at first capture showed variable trends in biomass between years, with some species increasing, some decreasing, and over 70% showing no significant change (Table S1). Combined, target species above size at first capture showed significantly greater biomass in MPAs than in fished areas for the whole assemblage and mixed diet feeders ($F_{1,30} = 28.29$, $P < 0.001$ and $F_{1,30} = 14.44$, $P = 0.001$ respectively), but no significant trends between years or among habitat types (Fig. 2a, b). Piscivore biomass did not differ among habitats, but responded significantly to year ($F_{1,30} = 4.69$, $P < 0.05$) and protection ($F_{1,30} = 16.65$, $P < 0.001$). The significant year-protection interaction term ($F_{1,30} = 5.49$, $P < 0.05$) showed that the main change between years is associated with a decreased biomass in MPAs (Fig. 2c). Herbivore biomass was greater in 2005 ($F_{1,30} = 4.67$, $P < 0.05$) and in MPAs ($F_{1,30} = 11.65$, $P = 0.002$) with no interaction and no habitat effect (Fig. 2d). These results indicate that although there were some small changes between years for certain groups, MPAs continued to support a higher biomass of targeted reef fish than fished areas (Fig. 2).

The slope of the size spectra became less steep from 1994 to 2005 in all but one, fished, granite site (Fig. 3a). This significant trend between years ($F_{1,30} = 18.90$, $P < 0.001$) did not vary among habitats and was not affected by management status (Fig. 3b). The height of the size spectra did not differ between years or among habitats, however there was a significant effect of management status ($F_{1,30} = 17.53$, $P < 0.001$), highlighting the greater abundance of fish within the MPAs.

The decreasing steepness of the size spectra slope was a result of a relative decline in smaller fish (<30 cm) and increase in larger fish (>45 cm) in the assemblage. This trend was consistent for both fished areas and MPAs (Fig. 4a). Different size classes in the mixed diet feeding group showed various trends with no common patterns apparent (Fig. 4b). The piscivores also showed a variable response, however there was a fairly consistent decline in medium size classes (20-50cm), which was most apparent in MPAs (Fig. 4c). The herbivores showed a decline in smaller size classes (<30 cm) and an increase in larger size classes (>40 cm) in both fished areas and MPAs (Fig. 4d). Corallivores and planktivores showed a consistent and marked decline, which was greatest in MPAs (Fig. 4e, f). Although there was some variation, particularly for the mixed diet feeders and piscivores, the trends were generally similar among habitat types.

Discussion

We demonstrate an impending recruitment failure to fishery size classes in the Seychelles following a major bleaching event. The decline in juveniles (<30 cm) in the assemblage can be expected to extend into adult stocks and cause overall declines, as is frequently shown in fisheries (XXXX 19XX). Although our data predict this effect will happen, the lack of time series data prevent us from projecting the likely

time-span over which this effect will start to impact larger size classes and reduce the overall biomass of the fishery target assemblage. Our data also highlight a lack of resilience within MPAs, as the decline in smaller size classes, including herbivores, is also apparent in these management areas. We support the proposal that MPAs should increasingly be placed in areas of resistance and resilience to climate mediated coral bleaching events.

There were minor changes in the biomass of target species available to the Seychelles artisanal trap fishery following the 1998 mass bleaching event. However, this belies apparent system-wide failures of recruitment to the fished size-classes which are expected to have long-term impacts on the viability of populations, assemblages and the fishery. Our results suggest that the current biomass and reef fishery are maintained primarily by the growth of fishes that had already recruited to the reefs at the time of the bleaching event, and/ or before topographic structure was reduced, and have now grown sufficiently to reach fishable size. The results lend support to studies in the Seychelles and elsewhere using fishery catch data that suggest no short-term change in yield associated with mass bleaching (McClanahan et al. 2002; Grandcourt & Cesar 2003). However, our results also suggest that the short-term maintenance of yield cannot be assumed to reflect medium and long-term expectations, and a decline in yield is likely if the reefs fail to recover.

The surveyed MPAs still supported a higher biomass of target species above size of first capture than fished areas. However, the reduction in slopes of the size spectra was consistent across all but one site and similar for fished and protected locations. The greater size-spectra height in the Seychelles protected areas is consistent with the expected effects of reduced fishing mortality on abundance (McClanahan & Graham, 2005), but the shallowing of the slope in both the fished

areas and MPAs suggests the same drivers are affecting the size distribution of fish in these areas and are unrelated to fishing pressure.

Plotting each individual size class bin by its change in numerical abundance highlights that the change in the slope of the size spectra was driven by both an increase in large individuals (>45 cm) and a decrease in smaller individuals (<30 cm). As fishing pressure has not changed, the most likely drivers for the increase in larger-bodied fish are increased growth and/or survivorship related to increases in dietary resources associated with the change in benthic composition. The decline in smaller-bodied individuals could be driven by various processes. We consider consistently high mortality of small and juvenile fish in the years since the bleaching event to be the most likely explanation, based on the expectation that the larger fishes have retained their abundance and have good feeding conditions, that successful spawning is unlikely to be affected by changes in the reef habitat and that many smaller species and individuals are most dependent on refuge availability and live coral (Munday & Jones 1998; Dulvy et al. 2004; Munday 2004; Pratchett 2005; Graham et al. 2006). Furthermore, the diversity and numerical abundance of fish 10-30cm in length was correlated with structural complexity in 2005 (Wilson et al. 2007), and showed marked decline between 1994 and 2005 following a loss in structure. While the existence of several years of high larval supply prior to the bleaching event and several years of poor larval supply post-bleaching could also account for the patterns we observed, the latter possibly as a result of reduced live coral as a settlement cue, we consider this unlikely when the effects are manifest for all species and at a large spatial scale. Based on the size-based analyses, we predict a time lag effect whereby the full effects of the bleaching on the fringing reef fishery species and the fish

Comment [TMD2]: Most decline between 94 & 05. These are the only two points. 'the most' compared to what?

assemblage as a whole are yet to be realised, as declines in smaller sized fish suggest impending recruitment failure to larger size classes.

Because the trends in relative abundance of large and small fishes are similar in both fished and protected areas, MPAs seem to be offering no long-term resilience to the populations and assemblages. Although the MPAs may meet short-term conservation objectives by reducing fishing mortality on larger fish, future replacement by small fish may be insufficient to maintain abundance in the longer-term. The collapse of the physical structure of Seychelles reefs accelerated as recently as 2003 (Engelhardt 2004) and so the longer-term consequences of this process are yet to manifest in larger size classes. The lag effect of reduced replenishment will likely be longer in MPAs than in fished areas since mortality rates are likely to be lower and the age structure of the populations therefore extended. Greater predator biomass inside the MPAs (Jennings et al. 1995) could also result in higher rates of predation mortality on smaller individuals (Graham et al. 2003; Mumby et al. 2006), further reducing the number of recruits and severity of the lag impact.

Comment [TMD3]: Fishing mortality should be 0! It's the total mortality that would be lower leading to extended age structure

The effects on assemblage productivity and hence on fishery yield are expected to be even more substantial than the effects on biomass because the production to biomass (P/B) ratios of smaller individuals and species are higher and therefore a community of a given biomass that is dominated by larger species will be relatively less productive (Kerr & Dickie 2001). The observed changes in the size-spectra therefore suggest that total production will fall faster than biomass, owing to a decline in abundance of smaller fish and smaller size classes.

When changes in size composition are broken down by feeding groups it is possible to assess the causes for these changes with more certainty. Both mixed diet feeders and piscivores displayed variable responses among size classes between 1994

and 2005. Some of the families that make up these groups, for example lethrinids and lutjanids, are quite generalist in their juvenile habitat use and often associate with soft bottom habitats (Dorenbosch et al. 2005). Therefore, they may not be so reliant on the physical structure of the reef to evade predators. Within the piscivores there was a decline in numbers for medium size classes (20-50 cm) which was most pronounced for the protected areas. Although there may be various reasons for such a decline, the consistent nature of the decline among habitats suggests it is a **deterministic driver**. As piscivores on coral reefs tend to select prey according to their gape size (Mumby et al. 2006), and reef fish predator-prey dynamics are highly size structured (Dulvy et al. 2004), it is likely that the substantial decline in smaller size classes of the assemblage, which is most evident for the protected areas, may have reduced prey availability for medium sized piscivores, causing an indirect decline in their numbers.

Comment [TMD4]: What kind of drivers aren't 'deterministic'?

Of the indirect effects of bleaching that we have identified, the most significant for the reef ecosystem is likely to be the substantial decline in smaller size classes of the herbivorous fish assemblage in both fished and protected areas. This assemblage consists mainly of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), but also some rabbitfishes (Siganidae) and two species of damselfishes (Pomacentridae). When the changes in numerical abundance of acanthurids, scarids or species which span a large number of size classes are examined separately, the same patterns of reduction in small size classes (<30 cm) are prevalent. Many of these species use the reef for habitat as juveniles (Bellwood & Choat 1989; Dorenbosch et al. 2005) and as the trend is consistent among habitats and management strategies, it is likely that habitat degradation, leading to greater competition and predation, is the cause of decline. Many species of acanthurids have longevities of over 25 years and scarids 5-20 years (Choat & Robertson **2002**), so many of the individuals currently

Comment [TMD5]: Could cite Edwin's 13-29 year old Scarids to show they get old in Seychelles (grandcourt 2002)

contributing to the increase in numerical abundance of large size classes likely recruited prior to the 1998 bleaching event, and certainly prior to the collapse of the reef framework in 2003 (Engelhardt 2004). Previous studies have indicated that herbivores may increase in abundance following disturbance due to the increased algal resources that become available (Wilson et al. 2006). When disturbances are extensive and occur over large spatial scales, increased abundance of large herbivores is a result of both faster growth rates (Hart & Russ 1996) and of potentially higher survivorship associated with greater food abundance. However, fewer fish in smaller size classes are surviving to replace adults and a subsequent decline in overall biomass of herbivores seems likely. Herbivores are common targets of the trap fishery in the Seychelles (Grandcourt 1999) and yields have remained stable through the bleaching event (Grandcourt et al. 2003) despite the increase in larger fish we identify here. This is consistent because the decline in small-sized fish extends up to 30 cm, resulting in no substantial increase in biomass above size at first capture.

Herbivores are reported to be key to the resilience of coral reefs, controlling algae and promoting coral recovery (Bellwood et al. 2004; Mumby et al. 2006). Our results suggest that mass bleaching and the loss in structural complexity may ultimately lead to a reduction in the abundance of herbivores, including larger size classes, and as such, recovery rates may decline in the long-term. As the trend is also apparent in the sampled MPAs, our data suggest the MPAs offer no long-term resilience to bleaching.

What are the consequences for reef fisheries? In Seychelles, 50-60% of trap fishing effort occurs close to the shore and within the depth range of the UVC data collected in this study (T.D., unpublished data, A. Christophe, personal communication), suggesting that any future decline in biomass of target species will

impact the trap fisheries. However, given that a substantial portion of trap fishing grounds lie beyond the fringing reefs, on the deeper shoals and submerged reefs of the Mahé Plateau, there is potential for a degree of spatial mobility in the fishery if declines in target species biomass are restricted to the shallow fringing reefs. As the majority of reef fisheries are multi-species, our results suggest that if other locations suffer coral mortality and collapse on the scale of the Seychelles, target species assemblages will likely respond in the same way. In locations where the topography does not allow for a diversity of demersal fishery habitats and depths, and the entire demersal fishery is restricted to the inshore reef (e.g. Fiji, Jennings & Polunin 1997), the long-term impacts of bleaching on fishers could be more substantial.

Comment [TMD6]: I don't understand why the multi-species nature of fisheries is relevant here.

Comment [TMD7]: We don't yet know if it is substantial in the Seychelles

The corallivores and planktivores demonstrated very large and consistent declines between years. Corallivores are well known to suffer declines and even local extinctions as a result of mass mortality of corals (Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2006). The planktivores in our study were principally coral dwelling damselfish, which suffer large declines through coral mortality (Wilson et al. 2006). Furthermore, both groups have small body size, suggesting they are more reliant on the reef matrix to avoid predation pressures (Munday & Jones 1998). Interestingly, the decline in both cases was greatest for the protected areas. Corallivores declined in numbers from a mean of 31.7 to 5.3 per site in fished areas and from 74.5 to 2.7 in protected areas. Similarly, planktivores declined in numbers from a mean of 90.3 to 44.4 per site in fished areas and 279.8 to 11.2 per site in protected areas. This is associated with the greater cover of the complex coral category in the protected areas prior to the bleaching event, which is the preferred habitat of many specialist fish (Munday 2004; Pratchett 2005) and offers greater structure to the assemblage as a whole (Bellwood et al. 2004; Jones et al. 2004). The

result is a subsequent homogenisation of the MPAs and fished areas in terms of both benthic cover and composition and the numerical abundance of small specialised fish species post bleaching.

In recent decades conservation of marine resources on coral reefs has focussed on the use of protected areas, such that most modern management strategies incorporate MPAs. Previous studies have highlighted that reef fish diversity can be compromised in MPAs following coral mortality (Jones et al. 2004), and here we provide evidence that the size structure of fish assemblages in MPAs are subject to the same long term lag effects as those in fished areas following coral bleaching and that these effects will likely compromise the ability of the ecosystem to recover. As future bleaching events seem inevitable (Sheppard 2003), the implementation of methods to ameliorate climate mediated disturbance should be treated as a priority in conservation and management plans for coral reefs. We recognise that some areas are less susceptible to climate induced disturbance and some show greater recovery, and therefore support the notion that MPAs should increasingly be sited in areas of resistance or resilience to bleaching to build up spatial resilience in the system (West & Salm 2003). In Seychelles the reefs north of Praslin and south of Mahé, and the granitic habitats in general, are currently displaying the most recovery and the most stable fish populations (Graham et al. 2006) and would be suitable locations to site future MPAs. MPAs are not the only management tool available, however, and it is important to manage areas outside MPAs to minimise other stressors, such as overfishing and nutrient enrichment, to create conditions where a recovery may be possible if brood stocks are available.

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Figure 1. Change in (a) Structural complexity, (b) Complex corals and (c) Non-complex corals between 1994 and 2005, for three different habitat types and two different management scenarios.

Figure 2. Change in biomass of fishery target species above size at first capture between 1994 and 2005 for (a) Whole fishery target species assemblage, (b) Mixed

diet feeders, (c) Piscivores, and (d) Herbivores. Each plotted by three different habitat types and two different types of management.

Figure 3. (a) Change in the slope of size-spectra for individual sites. Sites falling above the 1:1 trend line had a lower slope value in 2005. (b) Mean change in size-spectra slope by habitat type and management status.

Figure 4. Change in log abundance of individual size classes for (a) Whole assemblage, (b) Mixed diet feeders, (c) Piscivores, (d) Herbivores, (e) Corallivores and (f) Planktivores. Habitat type is plotted separately. Plots in left hand column are fished sites, plots on right hand column are protected sites. Size of first capture range indicated on plot a for fishery target species. Maximum size detected indicated with vertical dashed line on plots e and f.

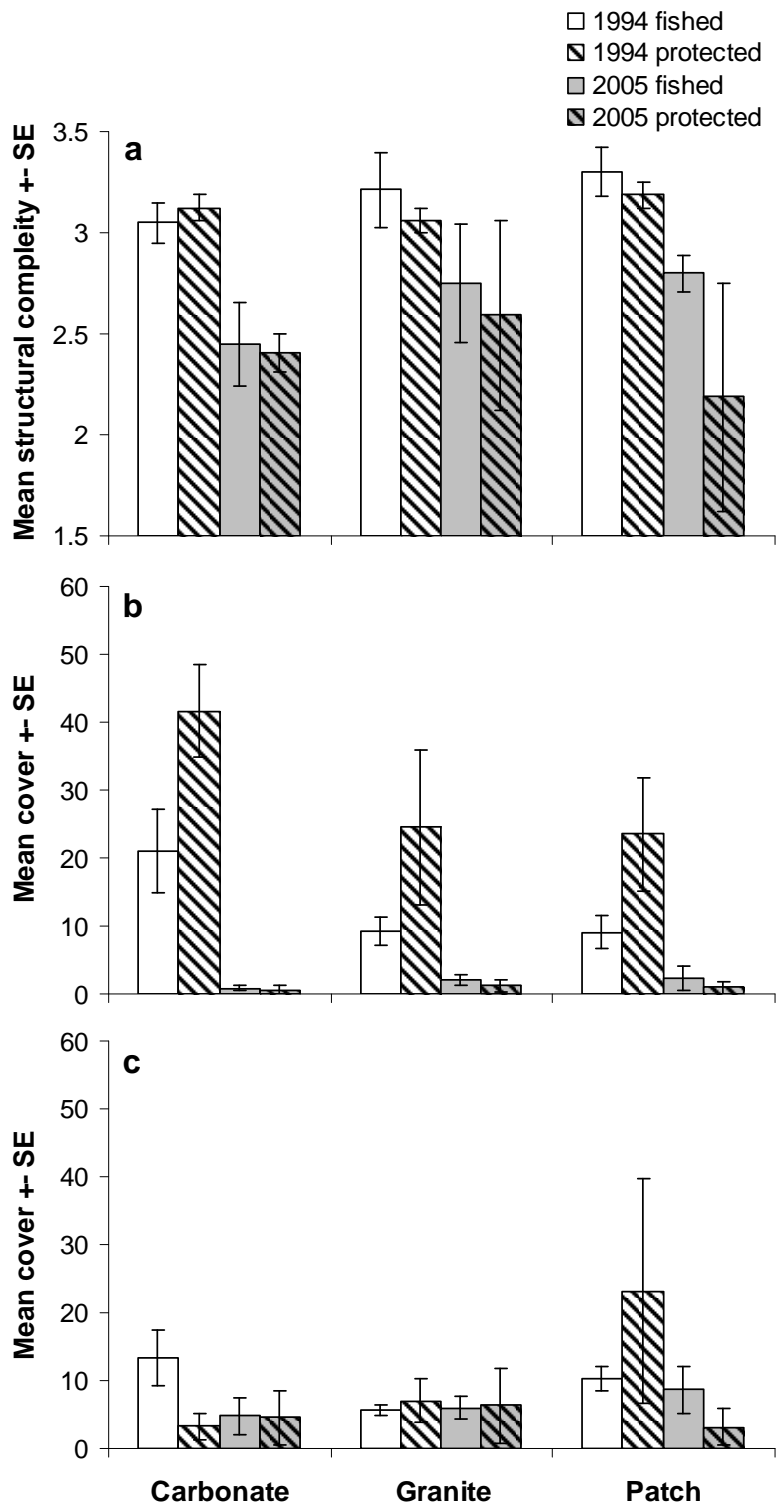


Figure 1

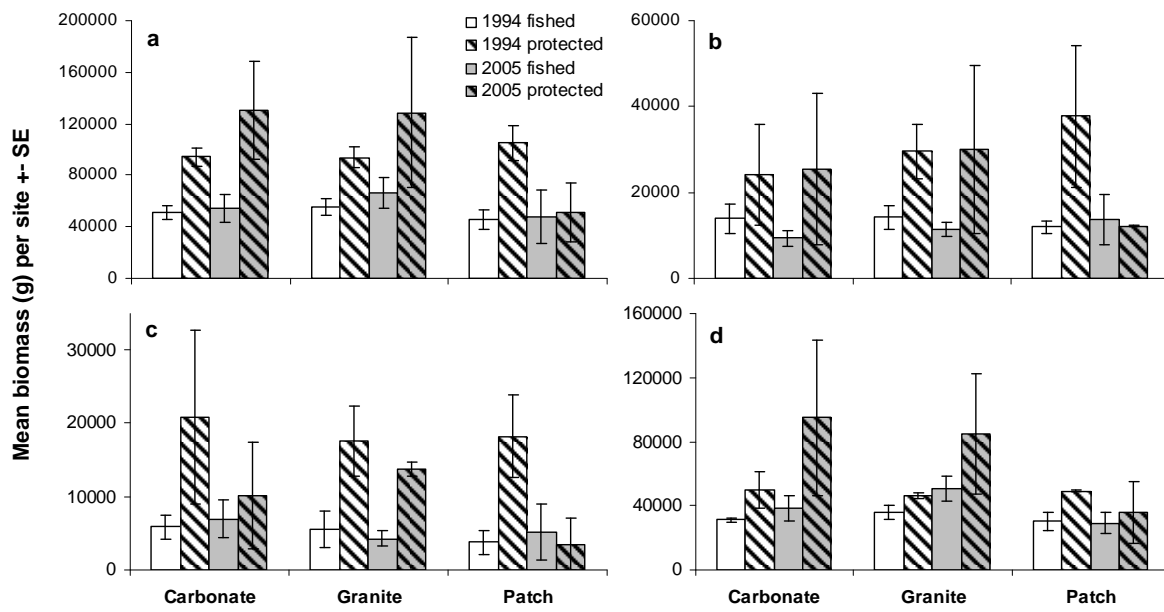


Figure 2

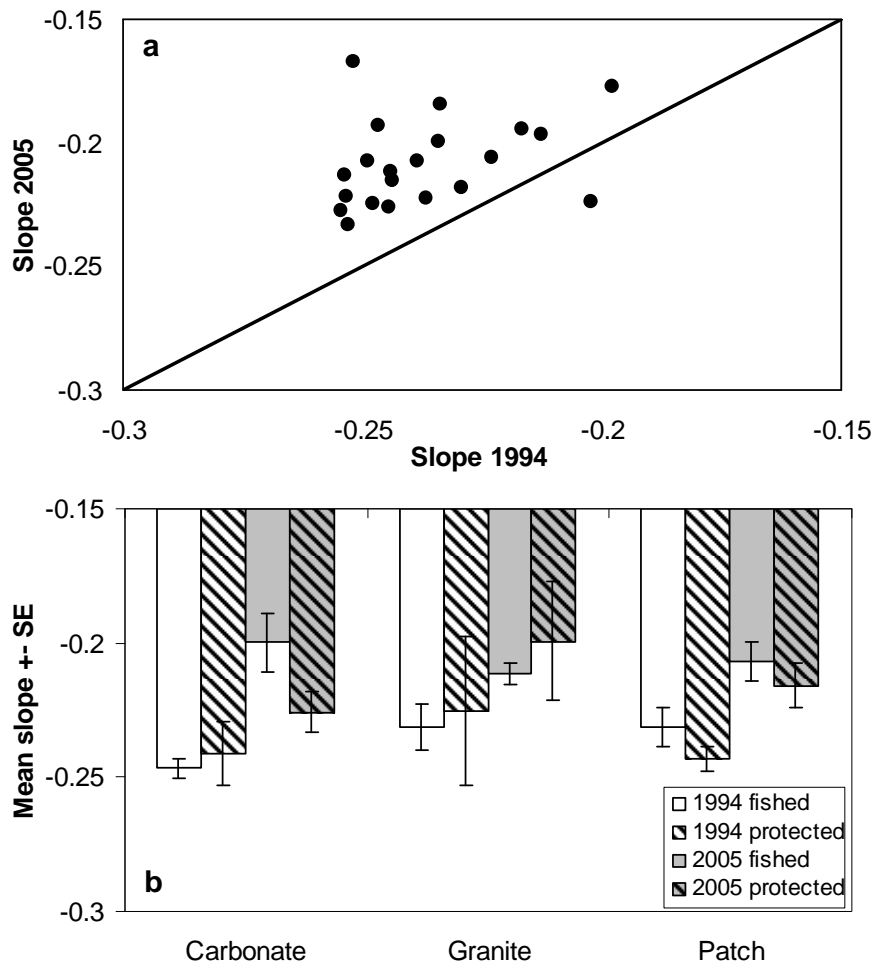


Figure 3

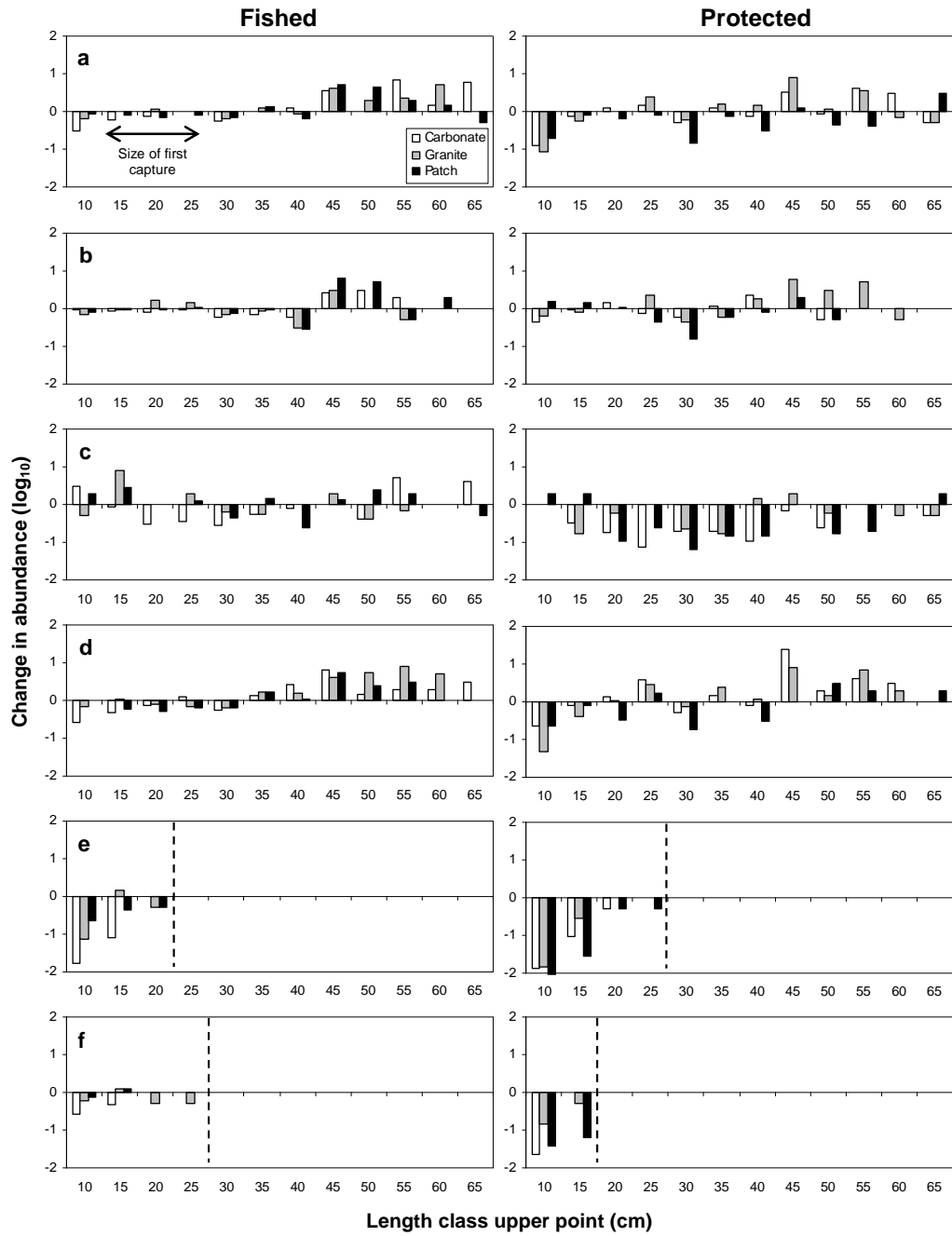


Figure 4

Supplementary Material

Table S1. Change in biomass and results of univariate three-factor crossed analysis of variance for primary, important and occasional target species above size at first capture. Values given for year, habitat and protection are *F* ratios (probability results given in brackets). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant.

Species	Size at	Biomass (g) 1994	Biomass (g) 2005	Δ	Year (1,30 <i>df</i>)	Habitat (2,30 <i>df</i>)	Protection (1,30 <i>df</i>)
	first capture						
Primary Targets							
<i>Aprion virescens</i>	25.5cm	4141	3497	-	0.75 (ns)	2.01 (ns)	11.30 (***)
<i>Cephalopholis leopardus</i> ^a	20.1cm	100	0	-	2.10 (ns)	0.65 (ns)	0.17 (ns)
<i>Chlorurus sordidus</i>	19.2cm	7073	7369	+	0.11 (ns)	0.75 (ns)	0.03 (ns)
<i>Lutjanus bohar</i> ^a	18.9cm	966	1308	+	1.63 (ns)	1.74 (ns)	1.83 (ns)
<i>Scarus ghobban</i>	16.7cm	1137	2708	+	4.79 (*)	2.73 (ns)	6.93 (*)
<i>Scarus rubroviolaceus</i> ^a	18.7cm	871	5079	+	4.16 (*)	0.35 (ns)	0.32 (ns)
<i>Siganus sutor</i> ^a	15.4cm	338	0	-	2.79 (ns)	1.12 (ns)	0.56 (ns)
Important targets							
<i>Acanthurus tennentii</i> ^a	15.3cm	332	2307	+	1.06 (ns)	0.34 (ns)	0.08 (ns)
<i>Anyperodon leucogrammicus</i> ^a	24.2cm	287	37	-	3.64 (ns)	0.27 (ns)	0.09 (ns)
<i>Calotomus carolinus</i> ^a	16.0cm	79	1211	+	3.78 (ns)	0.03 (ns)	2.67 (ns)
<i>Cephalopholis argus</i> ^a	20.9cm	3063	988	-	9.44 (**)	0.32 (ns)	1.32 (ns)
<i>Cephalopholis miniata</i>	21.4cm	75	259	+	2.50 (ns)	1.39 (ns)	0.03 (ns)
<i>Cetoscarus bicolor</i> ^a	17.3cm	410	0	-	15.45 (***)	0.20 (ns)	4.14 (ns)
<i>Cheilinus fasciatus</i> ^a	19.0cm	219	66	-	4.95 (*)	0.13 (ns)	0.05 (ns)
<i>Cheilinus trilobatus</i>	17.7cm	1963	1281	-	1.67 (ns)	0.55 (ns)	2.91 (ns)

<i>Chlorurus gibbus</i>	17.5cm	1282	1138	-	0.07 (ns)	2.59 (ns)	0.96 (ns)
<i>Ctenochaetus striatus</i>	13.8cm	3703	1035	-	6.57 (*)	0.25 (ns)	5.24 (*)
<i>Epinephelus fasciatus</i>	22.3cm	59	159	+	1.46 (ns)	0.18 (ns)	0.07 (ns)
<i>Epinephelus merra</i> ^a	22.1cm	58	32	-	0.27 (ns)	2.36 (ns)	2.00 (ns)
<i>Leptoscarus vaigiensis</i>	21.8cm	77	478	+	1.45 (ns)	4.01 (*)	0.70 (ns)
<i>Lethrinus enigmaticus</i>	16.7cm	13	52	+	0.52 (ns)	0.96 (ns)	0.36 (ns)
<i>Lethrinus harak</i>	18.4cm	2594	2659	+	0.03 (ns)	0.67 (ns)	2.90 (ns)
<i>Lethrinus lentjan</i> ^c	16.7cm	27	93	+	3.03 (ns)	^b 3.36 (*)	7.61 (**)
<i>Lethrinus mahsena</i>	15.9cm	119	68	-	0.70 (ns)	0.18 (ns)	0.02 (ns)
<i>Lethrinus nebulosus</i> ^a	17.2cm	139	734	+	8.43 (**)	1.62 (ns)	3.52 (ns)
<i>Lethrinus obsoletus</i> ^a	18.3cm	1381	421	-	4.20 (*)	0.08 (ns)	12.71 (***)
<i>Lethrinus olivaceus</i> ^a	20.8cm	70	254	+	0.92 (ns)	0.11 (ns)	1.64 (ns)
<i>Lutjanus fulviflamma</i> ^a	20.2cm	1206	692	-	1.31 (ns)	3.19 (ns)	5.45 (*)
<i>Lutjanus gibbus</i> ^a	16.2cm	1257	684	-	0.28 (ns)	1.07 (ns)	0.31 (ns)
<i>Lutjanus kasmira</i>	18.5cm	29	9	-	0.02 (ns)	1.07 (ns)	0.02 (ns)
<i>Lutjanus rivulatus</i>	16.1cm	133	51	-	0.00 (ns)	0.31 (ns)	0.00 (ns)
<i>Macolor niger</i> ^f	16.6cm	478	158	-	3.93 (ns)	^b 4.02 (*)	0.09 (ns)
<i>Monotaxis grandoculis</i>	15.7cm	325	723	+	0.93 (ns)	0.43 (ns)	0.07 (ns)
<i>Mulloidichthys flavolineatus</i> ^a	25.5cm	366	31	-	1.82 (ns)	0.26 (ns)	3.43 (ns)
<i>Parupeneus barberinus</i> ^a	21.9cm	1200	529	-	0.64 (ns)	1.05 (ns)	1.57 (ns)
<i>Parupeneus ciliatus</i> ^a	21.8cm	1006	797	-	0.37 (ns)	0.43 (ns)	0.11 (ns)
<i>Parupeneus cyclostomus</i> ^a	22.7cm	196	50	-	1.69 (ns)	1.13 (ns)	0.00 (ns)
<i>Parupeneus macronemus</i>	21.4cm	410	139	-	2.46 (ns)	1.52 (ns)	0.10 (ns)
<i>Parupeneus rubescens</i> ^a	20.2cm	17	25	+	0.24 (ns)	0.40 (ns)	1.57 (ns)
<i>Plectorhinchus orientalis</i>	20.8cm	823	610	-	0.70 (ns)	1.21 (ns)	1.44 (ns)
<i>Plectorhinchus schotaf</i> ^a	18.7cm	397	721	+	0.14 (ns)	0.06 (ns)	0.14 (ns)
<i>Scarus caudofasciatus</i>	17.2cm	117	642	+	1.92 (ns)	1.07 (ns)	0.19 (ns)
<i>Scarus falcipinnis</i> ^a	17.4cm	200	291	+	0.01 (ns)	0.49 (ns)	0.50 (ns)
<i>Scarus frenatus</i> ^g	19.1cm	1882	660	-	15.66 (***)	1.17 (ns)	13.57 (***)
<i>Scarus globiceps</i>	18.3cm	189	667	+	0.74 (ns)	0.34 (ns)	0.07 (ns)
<i>Scarus niger</i> ^{h,i}	17.6cm	3692	5583	+	3.67 (ns)	2.45 (ns)	3.16 (ns)

<i>Scarus prasiognathos</i>	17.8cm	1080	4357	+	5.43 (*)	2.54 (ns)	0.46 (ns)
<i>Scarus psittacus</i>	19.4cm	574	840	+	0.42 (ns)	0.75 (ns)	3.72 (ns)
<i>Scarus scaber</i> ^a	19.4cm	784	192	-	4.92 (*)	^c 4.90 (**)	0.02 (ns)
<i>Scarus tricolour</i>	20.5cm	570	338	-	0.47 (ns)	0.70 (ns)	4.50 (*)
<i>Scarus viridifucatus</i>	17.5cm	48	42	-	0.00 (ns)	0.15 (ns)	1.10 (ns)
<i>Siganus argenteus</i> ^a	18.1cm	1482	3238	+	2.63 (ns)	0.33 (ns)	3.46 (ns)
<i>Siganus puelloides</i> ^{a, g}	16.4cm	2114	922	-	17.93 (***)	0.84 (ns)	1.78 (ns)
<i>Siganus stellatus</i> ^j	14.9cm	477	589	+	0.09 (ns)	4.33 (*)	9.82 (**)
Occasional targets							
<i>Acanthurus leucosternon</i>	12.1cm	886	393	-	0.45 (ns)	1.96 (ns)	0.43 (ns)
<i>Acanthurus lineatus</i> ^a	14.1cm	247	278	+	0.28 (ns)	^d 3.43 (*)	1.69 (ns)
<i>Acanthurus nigrofuscus</i>	15.1cm	511	484	-	0.06 (ns)	0.43 (ns)	0.02 (ns)
<i>Aethaloperca rogae</i> ^a	17.3cm	210	784	+	0.61 (ns)	0.35 (ns)	4.68 (*)
<i>Chlorurus atrilunula</i> ^a	18.4cm	731	2187	+	4.01 (ns)	1.37 (ns)	1.40 (ns)
<i>Ctenochaetus binotatus</i>	13.2cm	20	42	+	0.40 (ns)	0.24 (ns)	0.72 (ns)
<i>Ctenochaetus strigosus</i> ^a	12.8cm	1045	382	-	7.51 (**)	1.41 (ns)	3.01 (ns)
<i>Epinephelus caeruleopunctatus</i>	23.2cm	110	227	+	2.51 (ns)	1.60 (ns)	2.07 (ns)
<i>Hipposcarus harid</i> ^a	18.9cm	3621	3160	-	2.91 (ns)	0.31 (ns)	2.38 (ns)
<i>Scolopsis frenatus</i> ^{a, g}	20.7cm	2922	2303	-	7.70 (**)	1.22 (ns)	0.76 (ns)

^a Log10 transformation necessary, ^b Tukey's output: Co>Gr, ^c Tukey's output: (Co=Gr)>Pa, ^d Tukey's output: Gr>(Co=Pa), ^e Significant year*habitat interaction due to higher biomass in carbonate reefs in 2005, but lower biomass in granite and patch reefs, ^f Significant year*habitat interaction due to a greater biomass in granite reefs than carbonate and patch reefs in 1994, but similar in 2005. ^g Significant year*protection interaction due to a greater decline in biomass in protected than fished areas between years, ^h Significant three-way interaction due to greater changes in carbonate reefs than granite and patch reefs for both year and protection, ⁱ Levene's test could only be passed at 0.036, and so the significance was set at 0.03 for this species. ^j Significant three-way interaction due to a greater biomass in granite and patch reefs than carbonate reefs in protected areas, particularly in 2005. *Cephalopholis urodeta*, *Diagramma pictum*, *Epinephelus*

hexagonatus, *E. spilotoceps*, *E. tukula*, *Lethrinus rubrioperculatus*, *L. argentimaculatus*, *Lutjanus monostigma*, *Oxycheilinus diagrammus* and *Paracanthurus hepatus* were not analysed as assumptions could not be met due to too many zero's in counts.