
Lag Effects in the Impacts of Mass Coral Bleaching on Coral Reef Fish, Fisheries, and Ecosystems

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Abstract: *Recent episodes of coral bleaching have 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 assessed the long-term impacts of this event on fishery target species in the Seychelles, the overall size structure of the fish assemblage, and the effectiveness of two marine protected areas (MPAs) in protecting fish communities. The biomass of fished species above the size retained in fish traps changed little between 1994 and 2005, indicating no current effect on fishery yields. Biomass remained higher in MPAs, indicating they were effective in protecting fish stocks. Nevertheless, the size structure of the fish communities, as described with size-spectra analysis, changed in both fished areas and MPAs, with a decline in smaller fish (<30 cm) and an increase in larger fish (>45 cm). We believe this represents a time-lag response to a reduction in reef structural complexity brought about because fishes are being lost through natural mortality and fishing, and are not being replaced by juveniles. This effect is expected to be greater in terms of fisheries productivity and, because congruent patterns are observed for herbivores, suggests that MPAs do not offer coral reefs long-term resilience to bleaching events. Corallivores and planktivores declined strikingly in abundance, particularly in MPAs, and this decline was associated with a similar pattern of decline in their preferred corals. We suggest that climate-mediated disturbances, such as coral bleaching, be at the fore of conservation planning for coral reefs.*

Keywords: climate change, coral bleaching, coral reef ecosystems, coral reef fishes, coral reef resilience, marine protected areas, size spectra analysis

Efectos a Largo Plazo de los Impactos del Blanqueado Masivo de Corales sobre Peces de Arrecifes Coralinos, Pesquerías y Ecosistemas

Resumen: *Episodios recientes de blanqueado de corales han llevado a la pérdida extensiva de arrecifes de coral y han incrementado la preocupación sobre la efectividad de los esfuerzos actuales de conservación y manejo. El evento de blanqueado de 1998 fue más severo en el occidente del Océano Índico, donde el coral declinó hasta en 90% en algunas localidades. Utilizando datos independientes de pesquerías, evaluamos los impactos a largo plazo de este evento sobre especies importantes para las pesquerías en las Seychelles, sobre la estructura de tallas en el ensamble de peces y sobre la efectividad de dos áreas marinas protegidas (AMPs) en la protección de las comunidades de peces. La biomasa de peces capturados por arriba de la talla retenida en las trampas de peces cambió poco entre 1994 y 2005, lo que indica que no hay efectos actuales sobre la producción de las pesquerías. La biomasa fue mayor en las AMPs, lo que indica que fueron eficientes en la protección de*

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los peces. Sin embargo, la estructura de tallas de las comunidades de peces, descritas con el análisis del espectro de tallas, cambió tanto en las áreas con pesca como en las AMPs, con una declinación en peces pequeños (<30 cm) y un incremento en peces más grandes (>45 cm). Pensamos que esto representa una respuesta a largo plazo porque se están perdiendo peces debido a la mortalidad natural y no están siendo reemplazados por juveniles. Se espera que este efecto sea mayor en términos de la productividad de las pesquerías y, debido a que se observan patrones congruentes para herbívoros, sugiere que las AMPs no ofrecen resiliencia a largo plazo contra los eventos de blanqueado de arrecifes de coral. La abundancia de coralívoros y planktívoros declinó marcadamente, particularmente en AMPs, y esta declinación se asoció con un patrón de declinación similar en sus arrecifes preferidos. Sugerimos que las perturbaciones debido al clima, como el blanqueado de corales, estén en primer plano en la planificación de la conservación de arrecifes de coral.

Palabras Clave: análisis de espectro de tallas, áreas marinas protegidas, blanqueado de corales, cambio climático, ecosistemas coralinos, peces de arrecifes coralinos, resiliencia de arrecifes coralinos

Introduction

Coral reefs and their associated communities are threatened by anthropogenic and natural disturbances, including overharvesting, sedimentation, pollution, disease, and warming waters (Hughes et al. 2003; Bellwood et al. 2004; 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 (Hughes et al. 2003; Sheppard 2003). The 1998 bleaching event was the largest on record, and in the most heavily affected region, the western Indian Ocean, coral cover declined by up to 90% (Sheppard 2003). Recovery from such severe disturbances is likely to be slow and affect other reef-associated organisms.

The short-term effects of bleaching on fish are mainly manifest in species that specialize on live coral for diet, shelter, or recruitment habitat (reviewed by Wilson et al. 2006). In the medium to long term declines in coral feeders can continue (Pratchett et al. 2006), but the greatest impacts occur if the physical matrix of the reef collapses, reducing overall species richness (Garpe et al. 2006; Glynn 2006; Graham et al. 2006). The medium to long-term impacts of bleaching on the size structure of fish populations and assemblages are currently 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 conservation measures that may have been proposed or implemented prior to a bleaching event.

Assessments of the impacts of mass bleaching on fisheries and associated socioeconomic factors 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). Nevertheless, such assessments have all been made within 5 years of bleaching events. Because loss in structural complexity of the reef framework, which can take over 5 years (Wilson et al. 2006), is likely to affect small individuals and because these may take some time to recruit to the fish-

ery, a lag effect may exist before the full impact of coral bleaching on reef fisheries is realized.

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 coral bleaching, the expected ecological communities in MPAs (e.g., a greater biomass, density, and size of herbivorous fishes in regions where herbivores are fished) should promote coral recovery, thus providing spatial resilience in the form of populations that can reseed depleted areas (Hughes et al. 2003). There is some evidence of an initial build up of fish biomass in MPAs even during habitat degradation (Hawkins et al. 2006); however, both abundance and diversity may subsequently 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 assessed the medium to long-term effects of mass coral bleaching on target reef fish above the size retained in fish traps, overall size structure of the whole assemblage and particular feeding groups, and 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 that reaches mean depths of 44–65 m. The fringing reefs of the islands are typically shallow; the reef slope terminates at 6–13 m (Jennings et al. 1995). The 1998 bleaching event reduced live coral cover from 27% to 3%, an overall reduction of approximately 90%. Furthermore, coral mortality extended throughout the depth range of the coral

reefs in this area. Recovery has been extremely slow, with collapse in the physical complexity of the reefs accelerating since 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 experienced relatively little change in other stressors over the study period (Graham et al. 2006).

We conducted reef surveys in seven areas, around Mahé, Praslin, and associated islands, that included most of the shallow fringing reef around the inner islands (for map see Jennings et al. 1995). Five fished areas were subject to similar levels of fishing intensity, whereas the other two areas were long-standing MPAs. Sainte Anne Marine National Park was gazetted by the Government of Seychelles in 1973 because it is suitably located for tourist use. Cousin Island Special Reserve was established by Birdlife International, who bought the island in 1968 to protect an endangered bird (Jennings et al. 1996). Both MPAs are within the same geographic area as the other sites and have similar bathymetry and habitat types. There are 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). Spatial studies of MPA effects are expected to reflect the outcome of temporal studies (Russ et al. 2005); therefore, we believe that the higher levels of diversity and biomass in the MPAs reflect the effect of protection from fishing. Studies conducted within other reef systems highlight the disproportionate effect of small amounts of fishing on fish communities and the more subtle impacts of further increases in fishing effort (Jennings & Polunin 1997; Hawkins & Roberts 2004). For these reasons we assessed the interaction between bleaching impacts and management by comparing the two MPAs with the five fished areas before and after coral bleaching in 1998.

Assessment of Fish Assemblage and Benthic Community Structure

We surveyed 21 sites, covering over 50,000 m² of coral reef habitat, at the same time of year in 1994 and 2005. Three sites were surveyed in each of the seven areas so that one site in each of three different habitat types (Jennings et al. 1995) would be included: carbonate fringing reefs; granitic rocky reefs with coral growth; and patch reef habitats on sand, rubble, or rock base. At each site 16 replicate 7-m radius point counts were completed with underwater visual censuses along the base of the reef slope. This technique maximized area coverage and replication, yet allowed for detailed searching for territorial species so that it provided a quantitative estimate of the number of fish of varying sizes and behavior. We separated replicates by a random number of fin kicks with the proviso that each count was separated by a minimum of 15 m; thus, an approximately 0.5-km stretch of reef was covered at each site.

The number and size of 134 species of reef-associated, diurnally active, noncryptic fish (>8 cm) were estimated within each count area. The time taken to complete a count varied depending on the number and diversity of fish present. Size estimation of fish was to the nearest centimeter, validated by estimating the lengths of a random selection of PVC pipes before the first count at each site. Length estimates were not consistently shorter or longer than actual lengths in both 1994 and 2005, with a mean error of 8- to 35-cm 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 is the smallest component of variation in fish counts (Williams et al. 2006; McClanahan et al. 2007). We converted data on fish counts to biomass with published length-weight relationships (Léotourneur et al. 1998; Froese & Pauly 2006). Species were assigned to feeding groups (herbivores, piscivores, coralivores, planktivores, and mixed-diet feeders [i.e., species consuming animal and plant material or fish and invertebrates]) based on dietary literature and Froese and Pauly (2006).

After a fish count was complete, we assessed the benthic composition and structural complexity of the count area. 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 was accurate when assessed against the line-intercept method (no significant difference, multivariate analysis of variance (MANOVA) $F_{6,35} = 0.56$, $p = 0.76$; Wilson et al. 2007). We assessed structural complexity of the benthos with a six-point visual scale and tested the accuracy of this method with the linear versus contour chain method. The two methods were highly 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 following Grandcourt (1999). There is a strong relationship between body depth of retained fish and the maximum width of trap meshes (Munro et al. 2003). In Seychelles the minimum legal hexagonal mesh diameter is 4 cm, but fishers often use trap meshes larger than this, 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 (S.F.A., unpublished data). Ninety-five percent of fish in the sample had a body depth of over 6.0 cm. Data on target fish species from the 1994 and 2005 reef surveys were filtered to

exclude individuals with a body depth of <6 cm for species level and aggregated feeding group analyses to assess the impact of the bleaching event on the dominant inshore trap fishery.

Data Analysis

Along with structural complexity, we categorized live corals into two groups: (1) complex corals that have branching, plating, or corymbose functional forms, which offer the most structure for other organisms to live in (Jones et al. 2004) and are generally the favored corals for diet and habitat specialists (Munday 2004; Pratchett 2005) and (2) simple corals that have massive and encrusting functional forms, which offer limited structure for other organisms to live within (Jones et al. 2004). We assessed differences between years, habitat types, and management status (fished vs. protected) with three-way, crossed fixed-effects orthogonal analysis of variances (ANOVAs). We assessed homogeneity of variances with Levene's test and normality of the data with histograms and normal probability plots of the residuals. Counts of complex corals were square-root transformed to meet assumptions. We used Tukey's post hoc test to identify where differences occurred among habitats.

Changes in the biomass of individual species and aggregated feeding groups of fishery targets above size at first capture were also assessed with the same ANOVA design. At the species level we used log transformation to meet the assumption of homogeneity of variances for a number of species. Ten species that failed to meet assumptions were not analyzed (see Supplementary Material).

The overall size structure of the assemblage at each site (including size below first capture) was described with the slope of the abundance-size relationships of the 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} midpoint of each length class. Centering the independent variable provides values of midpoint height (community abundance) that are comparable among spectra. 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. Change in the slope and midpoint height of the size spectra were assessed with the same ANOVA design described above.

To assess what was driving the observed trends in slopes of the size spectra, changes in the numerical abundance of fishes in individual size bins of 5 cm between 1994 and 2005 were assessed for the entire assemblage and for five key feeding groups: mixed-diet feeders, piscivores, herbivores, corallivores, and planktivores. To partition any effects of marine protection and habitat type, we plotted data separately by management status and within this by habitat type.

Results

Structural complexity of the benthos declined between years ($F_{1,30} = 19.94, p < 0.001$), but 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 in MPAs than in 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, irrespective of whether the site was in an MPA or fished. Cover of simple corals remained relatively stable

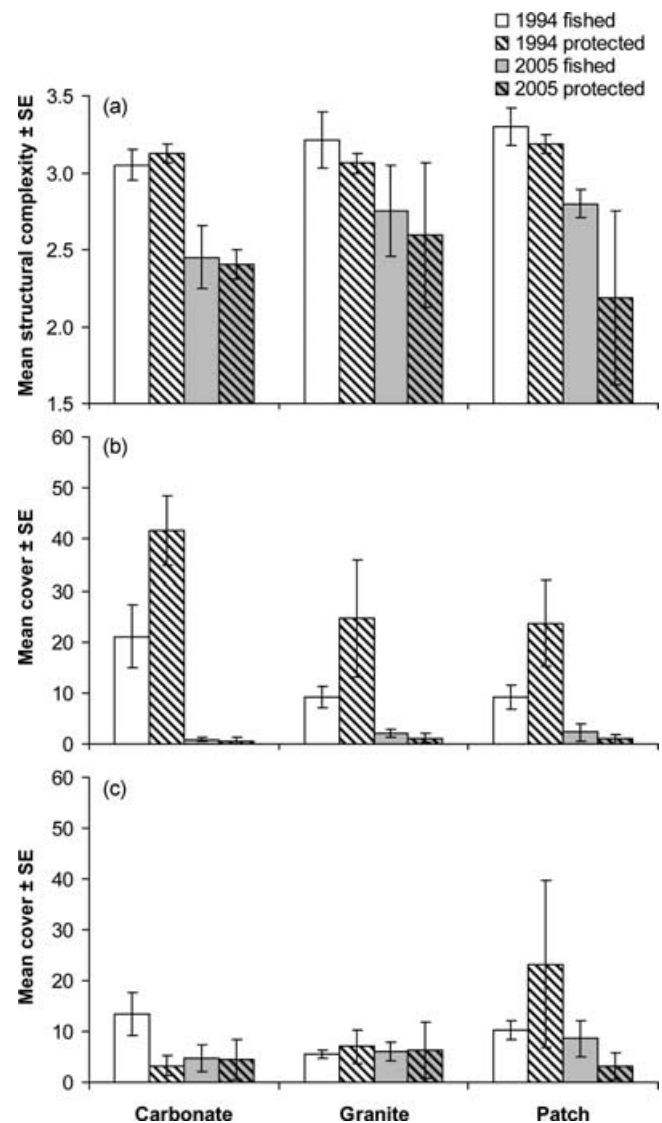


Figure 1. Change in (a) structural complexity, (b) complex corals (coral cover), and (c) simple corals (coral cover) between 1994 and 2005 for three habitat types (carbonate, granite, patch) and two management scenarios (fished, protected).

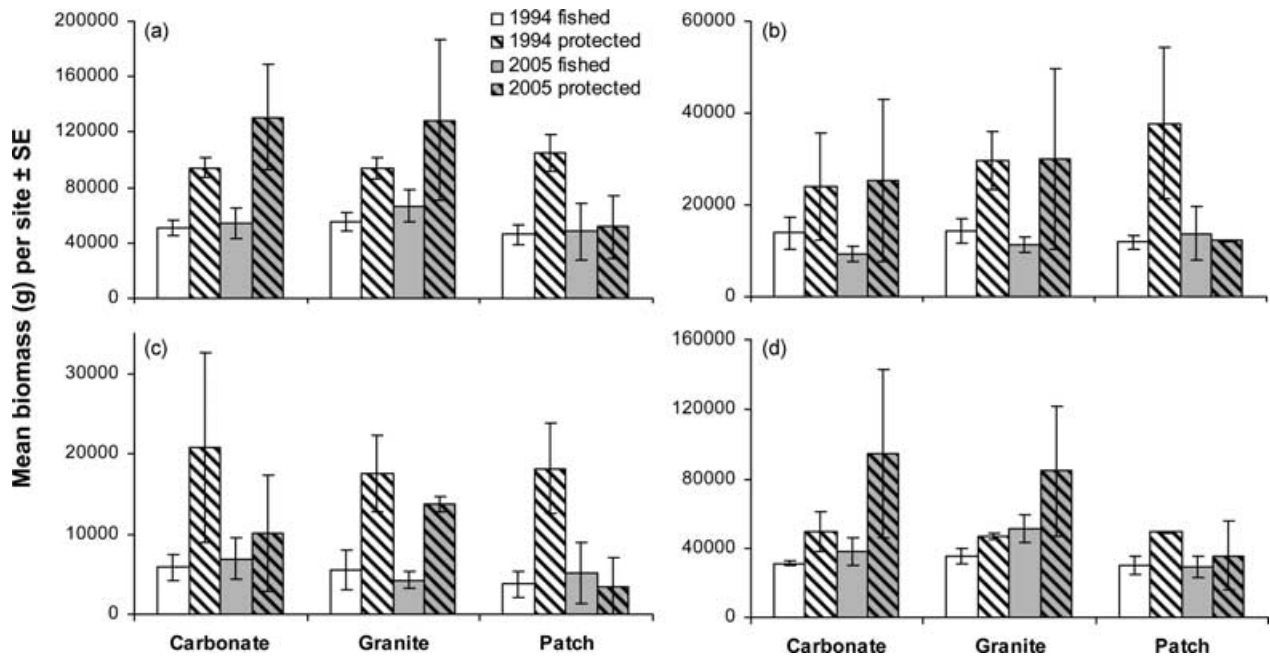


Figure 2. Change in biomass of fishery target species above size at first capture between 1994 and 2005 for (a) entire assemblage of fishery target species, (b) mixed-diet feeders, (c) piscivores, and (d) herbivores in three habitat types (carbonate, granite, patch) and under two types of management (fished, protected).

between 1994 and 2005, with no significant factors in the model (Fig. 1c).

The biomass of individual target fish species above size at first capture varied between years; some increased, some decreased, and over 70% did not change significantly (see Supplementary Material). The entire target assemblage and mixed-diet feeders showed greater biomass in MPAs than in fished areas ($F_{1,30} = 28.29, p < 0.001$ and $F_{1,30} = 14.44, p = 0.001$, respectively), but no trends between years or among habitat types (Fig. 2a-b). Piscivore biomass did not differ among habitats, but differed between years ($F_{1,30} = 4.69, p < 0.05$) and with protection ($F_{1,30} = 16.65, p < 0.001$). A significant year-protection interaction term ($F_{1,30} = 5.49, P < 0.05$) showed that the main change between years was 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 ($F_{1,30} = 11.65, p = 0.002$), and had no interaction or 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 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 an effect of management status ($F_{1,30} = 17.53, p < 0.001$) that showed a greater abundance of fish in 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

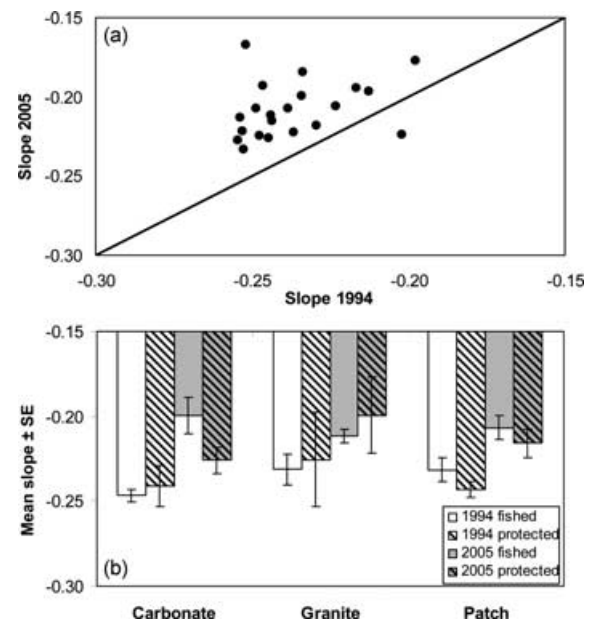


Figure 3. (a) Change in the slope of size spectra of the fish assemblage for individual survey sites. Sites falling above the 1:1 trend line had a lower slope value in 2005. (b) Mean change in slope of size spectra of the fish assemblage by habitat type (carbonate, granite, patch) and management status (fished, protected).

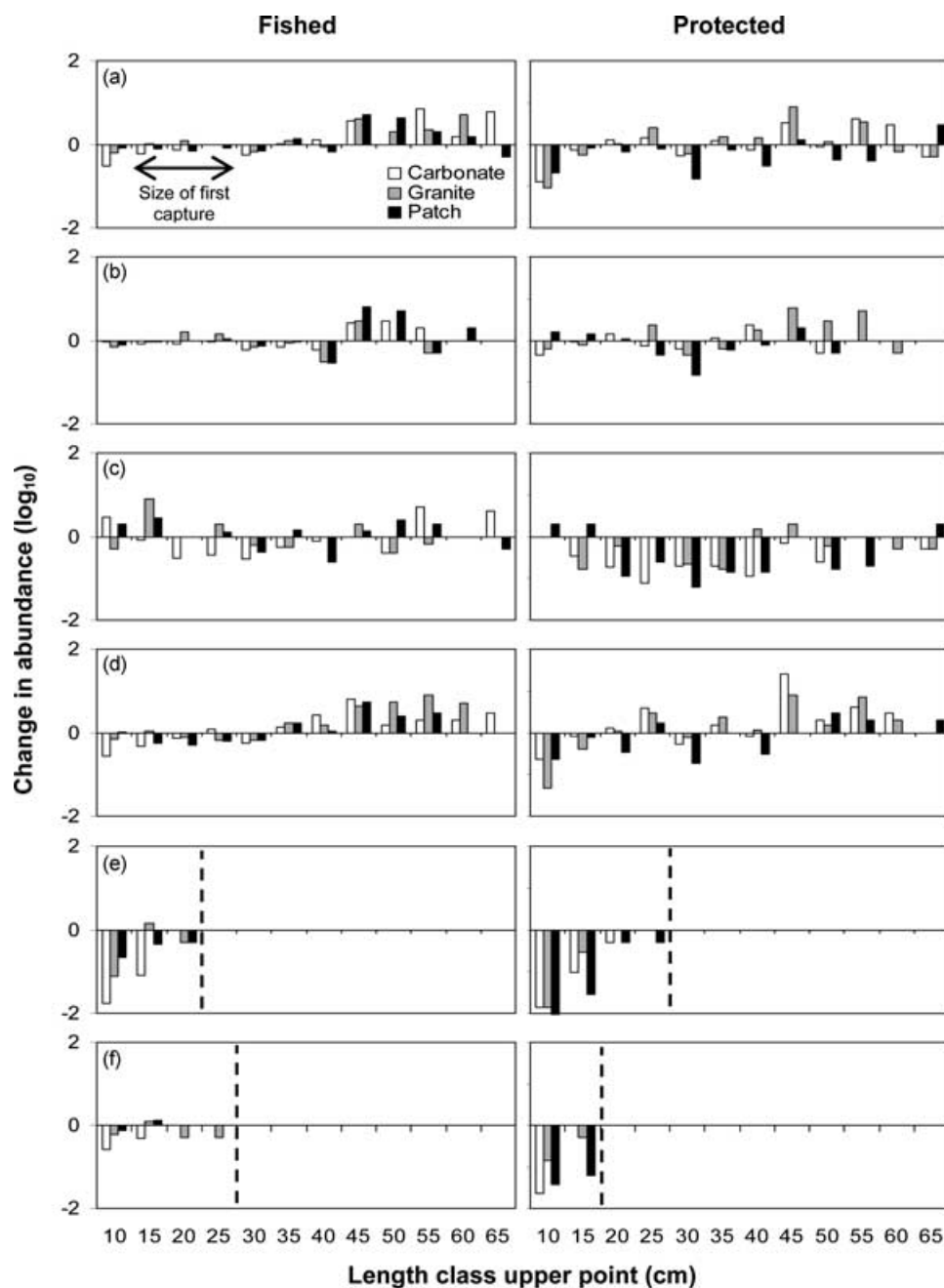


Figure 4. Change in log abundance of individual size classes of fish for (a) the entire assemblage, (b) mixed-diet feeders, (c) piscivores, (d) herbivores, (e) corallivores, and (f) planktivores by habitat type (carbonate, granite, patch). Plots in the left-hand column are fished sites, and plots in 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).

(Fig. 4a). Different size classes in the mixed-diet group showed various trends, and there was no common pattern apparent (Fig. 4b). The piscivores also responded variably; however, medium size classes (20–50 cm) tended to decline, especially in MPAs (Fig. 4c). The herbivores declined in smaller size classes (<30 cm) and increased in larger size classes (>40 cm) in both fished areas and MPAs (Fig. 4d). Corallivores and planktivores consistently and markedly declined, with the greatest decline in the 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

Based on our results an impending recruitment failure to reef-fishery size classes is likely in the Seychelles following a major coral bleaching event. Our results show a decline in juvenile abundance (<30 cm) in the reef-fishery assemblage that will ultimately lead to declines in adult abundance, as has been shown consistently in fisheries (Hilborn & Walters 1992). Although our data predict this effect will happen, the lack of time-series data and knowledge of the growth trajectories of individual species prevent us from projecting the likely time span over which

larger size classes will be affected. Our data also highlight a potential decline in the resilience of MPAs due to the decline in smaller size classes of herbivorous fishes in these management areas.

There were only minor changes in the biomass of target species available to the Seychelles artisanal trap fishery following the 1998 mass bleaching event. Nevertheless, these small changes belie apparent system-wide failures of recruitment to fished size classes that 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. This corroborates other evidence that shows there is no short-term change in yield associated with mass bleaching (McClanahan et al. 2002; Grandcourt & Cesar 2003).

The surveyed MPAs supported a higher biomass of target species above size of first capture than fished areas. The greater size-spectra height in the Seychelles MPAs is consistent with the expected effects of reduced fishing mortality on abundance (McClanahan & Graham 2005). Nevertheless, the reduction in slope of the size spectra was consistent across all but one site and similar for both the fished areas and MPAs, which suggests that the same drivers are affecting the size distribution of fish in these areas and that they 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). Because fishing pressure has not changed, the most likely drivers for the increase in larger-bodied fishes are increased growth and/or survivorship. The decline in smaller-bodied individuals could be driven by various processes. We consider consistently high mortality of small and juvenile fish following the years because the bleaching event the most likely explanation, based on the expectation that the larger fishes have retained their abundance and have good feeding conditions, and that many smaller species and individuals are most dependent on refuge availability and live coral (Munday & Jones 1998; Dulvy et al. 2004; Graham et al. 2006). Furthermore, the diversity and numerical abundance of fish 10–30 cm 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. Although the existence of several years of high larval supply prior to the bleaching event and several years of poor larval supply after 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 event on the fringing-reef fishery species and the fish assemblage as a whole are yet to be realized.

The MPAs seem to offer 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 over the long term. The collapse of the physical structure of Seychelles reefs accelerated as recently as 2003 (Engelhardt 2004), 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 because mortality rates are likely to be lower and therefore age structures of the populations will be extended. Nevertheless, greater predator biomass inside the MPAs could result in higher rates of predation on smaller individuals (Graham et al. 2003; Mumby et al. 2006), ultimately increasing the severity of the lag effect.

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 ratios of smaller individuals and species are higher. 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.

The responses of mixed-diet feeders and piscivores varied among size classes. Some of the families that make up these groups, for example, lethrinids and lutjanids, are generalist in their juvenile habitat use and often associate with soft-bottom habitats (Dorenbosch et al. 2005). Therefore, they may not be as reliant on the reef structure for predator evasion. Within the piscivores there was a decline in the number of fishes in medium size classes (20–50 cm), which was most pronounced in the MPAs. The consistent nature of this decline among habitats suggests a deterministic driver. 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). Thus, it is likely that the substantial decline in smaller size classes of the assemblage, which was most evident in the MPAs, may have reduced prey availability for medium-sized piscivores and thus caused an indirect decline in their numbers.

Of the indirect effects of bleaching that we have identified, one of the most significant for the reef ecosystem as a whole is likely to be the substantial decline in smaller size classes of herbivorous fishes in both fished and protected areas. The surveyed assemblage consisted mainly of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), but also contained some rabbitfishes (Siganidae) and two species of damselfishes (Pomacentridae). Separate plots of the changes in size classes over time of

acanthurids, scarids, or species that span a large number of size classes showed the same patterns of reduction in small size classes. Many of these species use the reef for habitat as juveniles (Dorenbosch et al. 2005), and because the trend was consistent among habitats and management strategies, it is likely that habitat degradation, which leads to greater competition and predation (Hixon & Jones 2005), is the cause of decline in smaller sizes.

Acanthurids can live over 25 years and scarids live 5–20 years (Choat & Robertson 2002), so individuals currently contributing to the increase in numerical abundance of large size classes likely recruited prior to the 1998 bleaching event or the collapse of the reef framework in 2003 (Engelhardt 2004). When disturbances are extensive and occur over large spatial scales, increased abundance of large herbivores can result from faster growth rates (Hart & Russ 1996) and potentially higher survivorship associated with greater food abundance. Nevertheless, 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 throughout the bleaching event (Grandcourt & Cesar 2003), despite the increase in larger fish we identified. Yields were stable despite increases in larger fish because the decline in small-sized fish extended up to 30 cm, resulting in no substantial increase in biomass above size at first capture.

Herbivores are important to the resilience of coral reefs because they control algae and promote coral recovery (Bellwood et al. 2004; Mumby et al. 2006). Our results suggest that mass bleaching and the loss of structural complexity may ultimately lead to a reduction in the abundance of herbivores, including larger size classes and thus, resilience of reefs may decline over the long term. Because the trend is also apparent in the sampled MPAs, our data suggest the MPAs offer no long-term refuge from the impacts of coral 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 data collected in this study (T.D., unpublished data), which suggests that a future decline in biomass of target species will affect the trap fisheries. Nevertheless, given that a substantial portion of trap fishing grounds lie on 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. 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.

The corallivores and planktivores demonstrated very large and consistent declines between years. Declines in corallivores, and even local extinctions, as a result of mass mortality of corals have been documented previously (Graham et al. 2006; Pratchett et al. 2006; Wilson 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 (Munday & Jones 1998). The decline in both cases was greatest in the MPAs. Corallivore numbers declined from a mean of 31.7 to 5.3/site in fished areas and from 74.5 to 2.7/site in MPAs. Similarly, planktivore numbers declined from a mean of 90.3 to 44.4/site in fished areas and from 279.8 to 11.2/site in MPAs. These declines are associated with the greater cover of the complex coral category in the MPAs prior to the bleaching event, which is the preferred habitat of many specialist fish (Munday 2004; Pratchett 2005). The result is a subsequent homogenization of the MPAs and fished areas in terms of benthic cover and composition and the numerical abundance of small specialized fish species after bleaching.

In recent decades conservation of marine resources on coral reefs has focused on the use of MPAs. Results of previous studies show that reef fish diversity and abundance can be compromised in MPAs following coral mortality (Jones et al. 2004). Here we provide evidence that the size structure of fish assemblages is subject to the same long-term effects in MPAs and fished areas. Because 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 recognize 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 (Engelhardt 2004; Graham et al. 2006), and would be suitable locations for future MPAs. Marine protected areas are not the only management tool available, however, and it is important to manage areas outside MPAs to minimize 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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Supplementary Material

Change in biomass and results of univariate, three-factor crossed analysis of variance for primary, important, and occasional target fish species above size at first capture (Appendix S1) are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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