

## LETTER

# Structure of Caribbean coral reef communities across a large gradient of fish biomass

Marah J. H. Newman,<sup>1\*</sup> Gustavo A. Paredes,<sup>1</sup> Enric Sala<sup>1</sup> and Jeremy B. C. Jackson<sup>1,2</sup>

<sup>1</sup>Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, La Jolla, CA 92093-0202, USA

<sup>2</sup>Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Box 2072 Balboa, Republic of Panama

\*Correspondence: E-mail: mjnewman@ucsd.edu

## Abstract

The collapse of Caribbean coral reefs has been attributed in part to historic overfishing, but whether fish assemblages can recover and how such recovery might affect the benthic reef community has not been tested across appropriate scales. We surveyed the biomass of reef communities across a range in fish abundance from 14 to 593 g m<sup>-2</sup>, a gradient exceeding that of any previously reported for coral reefs. Increased fish biomass was correlated with an increased proportion of apex predators, which were abundant only inside large marine reserves. Increased herbivorous fish biomass was correlated with a decrease in fleshy algal biomass but corals have not yet recovered.

## Keywords

Algal biomass, coral reefs, fish biomass, fishing impacts, marine reserves, reef degradation.

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## INTRODUCTION

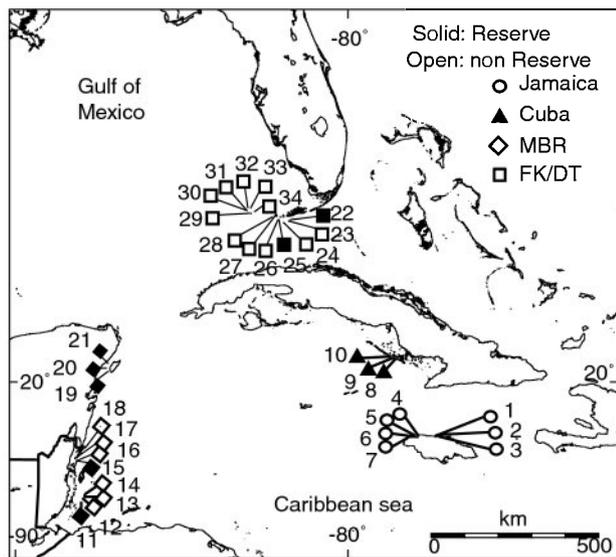
Overfishing, compounded by disease, bleaching, and the almost complete loss of the sea urchin *Diadema antillarum* in 1983, has been implicated in the collapse of coral populations on Caribbean reefs (Hughes 1994; Jackson *et al.* 2001; Knowlton 2001; Pandolfi *et al.* 2003). The recovery of fishes and sea urchins, and the subsequent restoration of increased levels of herbivory, is widely believed to be necessary for coral recovery (Pandolfi *et al.* 2005; Carpenter & Edmunds 2006; Mumby *et al.* 2006). Numerous studies have demonstrated the importance of fish and sea urchins as major grazers on Caribbean reefs prior to 1983 (Ogden & Lobel 1978; Sammarco 1982). Moreover, recent work highlights a concomitant decrease of fleshy algae and increase in coral recruitment in areas with small populations of *Diadema* that show early signs of recovery (Edmunds & Carpenter 2001; Carpenter & Edmunds 2006). However, changes within reef fish assemblages and their consequent impact on the benthic community remain untested across appropriately large ecosystem and geographical scales. While multiple factors currently contribute to the declining health of coral reefs, we set out to establish a geographically broad and quantitative baseline to evaluate the effects of changes in fish biomass on coral reef communities. Here we report how the biomass of major components of coral reef ecosystems differs among

reefs across a 19- to 37-fold gradient of total fish biomass. Biomass represents a common currency among all marine organisms, allowing for simultaneous analysis across the major taxonomic groups of coral reefs, an approach not possible with traditional numerical abundance and cover data.

## MATERIALS AND METHODS

### Site selection

We surveyed the fore reef at 5 and 15 m depths at 34 sites across the north-western Caribbean in Belize, Yucatan (Mexico), Jamaica, Cuba, and the Florida Keys (USA) (Fig. 1). Due to natural variability in habitat, not all sites contained comparable reef formations at both depths (see Table S1). We selected sites to maximize the range of total fish biomass, from fully protected, no-take marine reserves to reefs that are currently and have been historically extremely overfished (Munro 1983; Jackson *et al.* 2001; Pandolfi *et al.* 2003). All sites marked as marine reserves in this study meet these criteria of full protection. To account for spatial variability, we sampled reefs at three different scales: (i) transects within sites (tens of metres); (ii) sites within areas (kilometres); and (iii) areas within regions (tens to hundreds of kilometres).



**Figure 1** Map of the Caribbean showing the location of all survey sites. Detailed depth and location information for each site can be found in Table S1. MBR, Mesoamerican Barrier Reef; FK/DT, Florida Keys/Dry Tortugas. Only no-take, well-enforced marine reserves were considered in this study (solid symbols). Map created using Generic Mapping Tools (GMT).

### Surveys of reef flora and fauna

At each site, we conducted standard underwater visual surveys of the abundance and size of fishes and invertebrates, and the abundance and per cent cover of the sessile benthic community (Table S2). Underwater fish surveys were carried out using visual belt transect survey methods (Harmelin-Vivien *et al.* 1985) and were conducted in daylight at least 2 h after sunrise and 2 h before sunset. We surveyed both conspicuous and more cryptic species, and pilot surveys showed no significant differences in fish biomass throughout the day. The authors were experienced at visually surveying fish assemblages and estimating fish lengths. Several replicate 50 × 5 m transects were placed randomly on the substratum at each site (Table S1). A diver swam each transect at constant speed (*c.* 15 min per transect), counting all fishes belonging to all species and estimating their size within 2.5 m to either side of the centre line and 2.5 m height above the line. Species larger than 20 cm (total length, TL) were recorded on an initial swim, and smaller, more cryptic species were recorded on a second swim of the transect line.

The benthic community was surveyed by recording each organism touching the transect line at every 20 cm (point-intercept method) along replicate 30 m long transects. Overlapping organisms were all recorded (thus the total point count for each transect varied depending on the degree of overlap). The 20 cm interval was determined by

calculating species diversity (Shannon–Wiener index,  $H'$ ) and species richness curves for different intervals (1, 5, 10, 20, 25, 30, 50 cm) and determining the minimum number of points needed for saturation of the curves. All scleractinian corals were identified to species, while algae and octocorals were identified to genera whenever possible. Other organisms such as sponges, anemones and zoanths were grouped into more general categories. For erect fleshy algae, height was also measured to the nearest 5 cm. See Table S2 for species list and group identification.

The abundance of mobile macroinvertebrates was surveyed along replicate 30 × 1 m transects. Urchins were identified to species while all other organisms were categorized according to the groups listed in Table S2. Due to obvious logistical constraints, all sites were not surveyed simultaneously. Sites within areas were all surveyed during the same month, but different regions were surveyed during different months from April 2004 through August 2005 (see list of dates of surveys in Table S1).

### Biomass calculations

All data were converted to biomass per unit area of reef ( $\text{g m}^{-2}$ ) using conversion factors from the literature for fish and most mobile invertebrates, and our own determinations of coral and macroalgal biomass per unit surface area (Newman, unpublished data, 2006). Length estimates (TL) of fish from surveys were converted to weight by using the allometric length–weight conversion:  $W = aTL^b$ , where  $W$  is weight in grams, parameters  $a$  and  $b$  are constants obtained from the literature (Froese & Pauly 2005), and TL is total length in cm. Where the weight–length equation required standard or fork lengths, conversions from total length to the required lengths were obtained from Fishbase (Froese & Pauly 2005). Where values for  $a$  and  $b$  were unavailable, the parameters from a congeneric species with similar shape and maximum total length were used.

Biomass conversions for coral, algae, gorgonians and sponges were determined from separate measurements conducted at the Smithsonian Tropical Research Institute field station in Bocas del Toro, Panama. For algae, we collected samples from measured surface areas of reef, and for corals, gorgonians and sponges, we collected samples from multiple colonies/individuals. We then calculated the surface area for each sample, and determined wet and dry weights. For the most abundant erect algae we also measured their height in the area sampled to take into account the varying height of *Sargassum* and other erect genera. Wet weights were calculated after drip-drying samples for *c.* 1 h in the laboratory. Dry weights were determined by drying samples in an oven at 60 °C until no further change in weight was recorded. For calcified algae (such as *Halimeda*) and corals, samples were collected,

surface areas calculated, and wet and dry weights recorded before and after bleaching (Newman, unpublished data). Bleaching successfully removed all living tissue without dissolving calcified structures. We then used linear regressions to determine the relationship between surface area and weight for each species or species group collected and applied this conversion value to our survey data (Newman, unpublished data). For species that were not collected in the biomass surveys, we used the conversion factor from a congener or species with similar growth morphology. For *Sargassum* sp. we used a regression of volume and weight and applied this value for *Sargassum* and *Styopodium* spp. Conversion factors incorporated the average height of the most abundant erect algae. For final analyses, we used wet weight conversion values for all species. In addition, weight conversions for some algal species and other benthic groups were determined by using values from the literature (Vinogradov 1953; Ballesteros 1992; Opitz 1996). Sea urchin biomass was determined by taking the average weight of individuals weighed at the Discovery Bay Marine Lab, Jamaica. All data was then standardized to  $\text{g m}^{-2}$  for each species or species group.

### Data analysis

Species were assigned to functional groups based on published data on diet and trophic level (Froese & Pauly 2005; Opitz 1996; Table S2) or basic morphology. The total biomass of all fish was calculated for each site, creating a gradient in fish biomass along which all sites were ranked. Correlations among the biomass of large functional groups of fish, sea urchins and fleshy algae were determined using Spearman's rank order test (Table 1). We conducted correlations between the different groups and total algal biomass and also just fleshy algal biomass, and found there were no differences in the patterns observed. The results for only fleshy algae are presented in Table 1.

To explore the structure of the fish community across all sites we conducted a principal components analysis (PCA) on the biomass of nine functional groups of fish: herbivores, large omnivores, small omnivores, planktivores, microinvertebrates, macroinvertebrates, piscivore-invertebrates, piscivores and apex predators (Tables S2 and S4). Data were centred by functional group and scaled using inter-group correlations. Functional group scores were divided by the standard deviation of the groups.

To test for differences in overall benthic community composition among sites, we conducted a PCA using the average biomass values for 10 benthic taxonomic or functional groups at each site and depth. The groups were: hard corals (all scleractinian species), fleshy algae (fleshy), turf algae (turf), calcareous erect algae (CalErect), crustose coralline algae, sponges, zoanthids, octocorals, cyanobac-

teria (cyano) and other (see Table S2 for group list). Data were centred by taxonomic group and scaled using inter-group correlations. Taxonomic group scores were divided by the standard deviation of the groups.

To determine the influence of the fish community on the overall benthic community structure, we regressed the site scores of PC1 and PC2 from the benthic PCA analysis against the biomass of the fish functional groups for each site and depth using the linear model function in the program R (R Development Core Team 2005). We then bootstrapped the calculated slopes of these regressions, and determined the fraction of bootstrapped slopes that were greater than zero ( $f$ ). By chance,  $f$  is expected to be equal to 0.5 (50% positive slopes and 50% negative). The two tailed  $P$ -value was calculated as:  $[1 - 2 \times \text{absolute value}(0.5 - f)]$ .

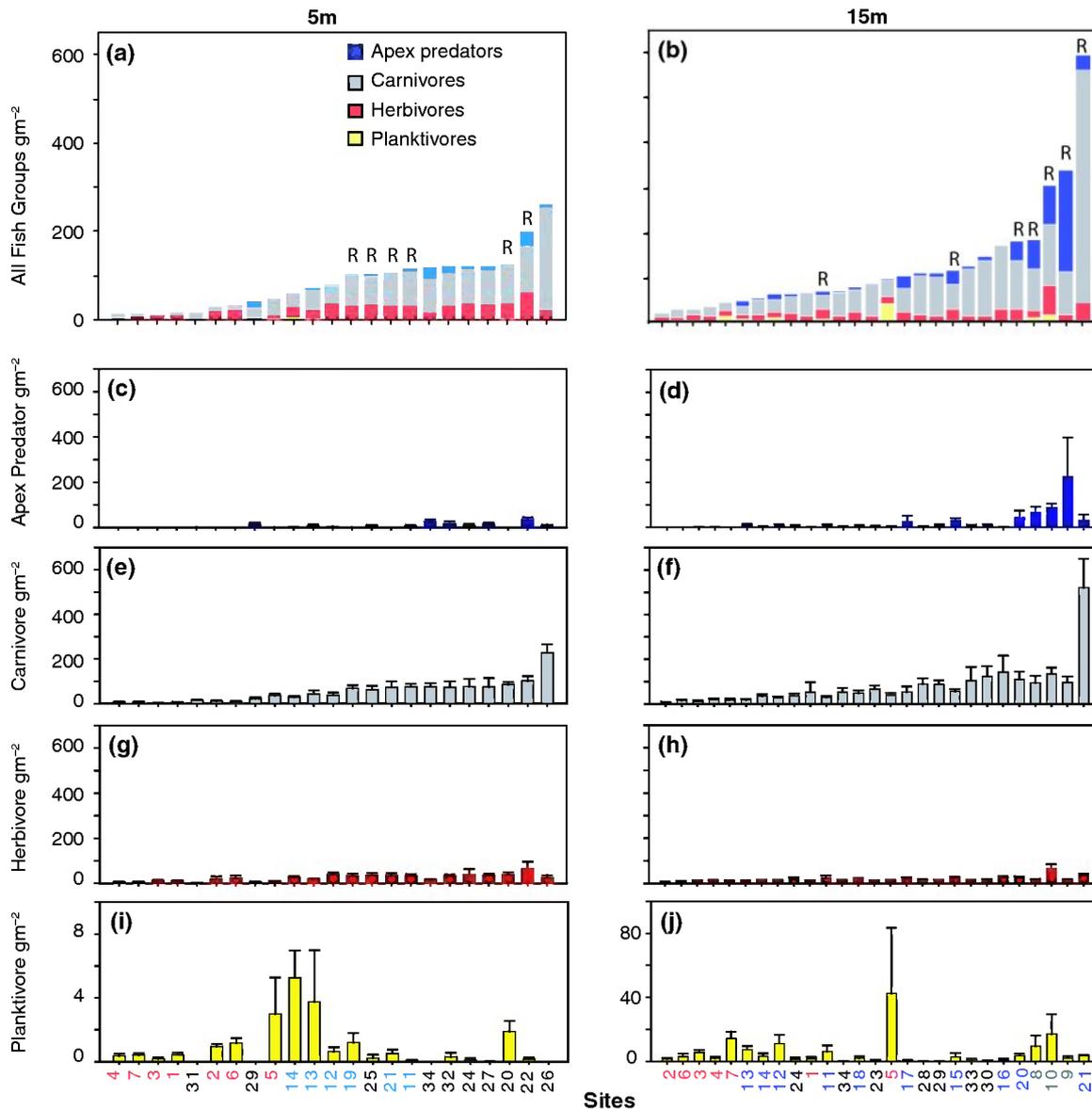
### RESULTS

Total fish biomass ranged from 14.0 to 263  $\text{g m}^{-2}$  for the 23 sites at 5 m and from 15.6 to 593  $\text{g m}^{-2}$  for the 27 sites at 15 m (Fig. 2). This gradient is larger than any previously reported including that observed between the north-western and main Hawaiian Islands (Friedlander & DeMartini 2002). The biomasses of herbivores, carnivores other than apex predators, and apex predators were all positively correlated with each other (Table 1A). Planktivore biomass was positively correlated with top predators at 5 m but not with any other group at either depth (Table 1A). The differential changes in absolute biomass among functional groups (Fig. 2) resulted in changes in the proportion of functional groups within the fish community. The proportion of apex predators increased with increased total fish biomass from a low of 0% to 25.5% at 5 m and from 0.1% to 45.7% at 15 m (Fig. 2, Fig. S1, and Table 1B). Similar increases in the proportion of apex predators inside marine reserves have been reported previously (Friedlander & DeMartini 2002; Micheli *et al.* 2004), but very few studies include benthic analyses (but see Dulvy *et al.* 2002). The disproportionate loss of apex predators with decreasing total fish biomass strongly suggests that the gradient in Fig. 2 reflects a gradient of fishing pressure (Pauly *et al.* 1998) and corroborates earlier studies that provided qualitative and quantitative estimates of fishing pressure at the same or nearby site locations (Munro 1983; Polunin & Roberts 1993; Koslow *et al.* 1994; Williams & Polunin 2001). The proportion of carnivores increased with total fish biomass at 5 m whereas the proportion of herbivores and planktivores decreased with total fish biomass at both depths (Fig. S1 and Table 1B).

Principal components analysis (PCA) of 10 functional groups of fish (Table S4) revealed similar patterns of linear positive correlations between most functional groups except planktivores and small omnivores (Fig. 3, species arrows in

**Table 1** Spearman's rank order correlation values for fish, urchins and algae (A, B, D). Results for 5 m in upper half, 15 m in lower half.  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ . PCA loadings for largest contributors (C).

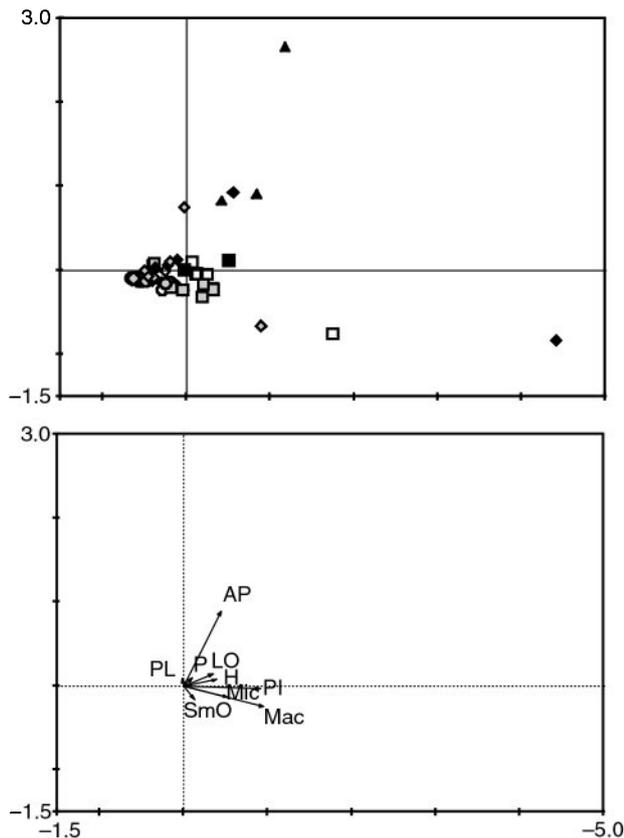
A. Fish biomass ( $\text{gm}^{-2}$ )				
	Herbivore	Carnivore	Apex predator	Planktivore
Herbivore	—	0.690***	0.3	0.117
Carnivore	0.719***	—	0.600**	-0.267
Apex predator	0.651***	0.625***	—	-0.511**
Planktivore	-0.001	0.265	0.141	—
B. Proportion of fish groups				
	Herbivore/Total fish	Carnivore/Total fish	Apex pred/Total fish	Planktivore/Total fish
Total fish 5 m	-0.561**	0.580**	0.441*	-0.488*
Total fish 15 m	-0.778***	0.375	0.491**	-0.587**
C. Cumulative fit per species as fraction of variance of select species				
	5 m PC1	5 m PC2	15 m PC1	15 m PC2
Fleshy algae	0.9382	0.9433	0.9484	0.9584
Coral	0.1247	0.7750	0.4061	0.9432
Octocoral	0.0113	0.4014	0.2513	0.3189
Sponge	0.3460	0.5947	0.4943	0.8251
Zoanthid	0.3829	0.9258	0.0166	0.0245
D. Fish, sea urchins, and fleshy algae correlations				
	Fleshy algae	Sea urchin/ Diadema	Total fish	Herbivorous fish
Fleshy algae	—	0.03/ -0.022	-0.488*	-0.451*
Sea urchin/ Diadema	-0.202/ 0.0108	—	-0.547**	-0.344
Total fish	-0.351	-0.162	—	—
Herbivorous fish	-0.453*	-0.194	—	—
E. Slope of regression between benthic site scores from PC1 and fish functional groups				
Significant Bonferroni correction results at $P < 0.005$ shown in bold.				
	Original slope	Mean	Standard error	$P$ value
5 m				
Herbivore	-8.08412519	-7.999994318	3.0645703	0.0108
Large omnivore	-0.52254987	-0.455983791	1.711123	0.7038
Macroinvert	-16.97912792	-17.26870364	8.7425066	0.016
Microinv	-0.45541688	-0.45881606	0.2022601	0.0096
Pisc-inv	-6.35028839	-6.563068568	3.5618857	0.0676
Piscivore	1.63536839	1.561987152	1.2587541	0.2056
Plank	-0.09420932	-0.086403601	0.2118737	0.6096
Small omnivore	-0.87144402	-0.898236649	0.3850021	0.007
Apex predator	-3.53935752	-3.545962102	2.490866	0.1602
Total fish	-34.33602352	-34.74137282	14.2285739	0.0168
15 m				
Herbivore	-2.2454815	-2.210035855	1.50792023	0.1202
Large omnivore	-4.0659618	-4.088898979	1.24359005	<b>0.0006</b>
Macroinvert	-20.0200617	-20.31283216	12.10244178	0.007
Microinv	-1.0820836	-1.097509054	0.32427379	<b>0</b>
Pisc-inv	-10.2586391	-10.48159914	9.86882429	0.2746
Piscivore	-0.7556338	-0.770692949	0.44165393	0.049
Plank	1.2325633	1.331926273	1.16480661	0.1562
Small omnivore	-0.1400905	-0.142013299	0.05449083	0.0066
Apex predator	-5.9442859	-5.743818225	5.57931445	0.2580
Total fish	-43.7408768	-44.02555438	24.39918533	0.0134



**Figure 2** Distribution of biomass among major reef fish groups at 5 and 15 m (a, b) and the mean and standard error for each group (c–j). Fish were categorized based on published diet information (Froese & Pauly 2005). Apex predators are piscivores, trophic level 4.5 or higher; carnivores have trophic levels between 2.1 and 4.5; herbivores are primarily plant eaters, trophic level 2.0; and planktivores eat predominantly plankton, trophic level 3. See Table S2 for species lists in each group. Site numbers correspond to those in Fig. 1. ‘R’ indicates marine reserves. Colours for sites along the x-axis are as follows: Red, Jamaica; Black, Florida/Dry Tortugas; Blue, Mesoamerican Barrier Reef; Gray, Cuba.

the same direction). The first axis (PC1) explained 64.6% of the total variability in the data set and PC2 explained another 24.6%. Macroinvertivores and piscivore–invertivores were most strongly correlated with PC1 and apex predators were most strongly correlated with PC2 (Table S3). In the combined depth analysis, there was no clear distinction in the ordination of sites between 5 and 15 m. Separate analyses by depth (not shown) revealed the same patterns as the combined depth analysis.

Principal components analysis also effectively described patterns in overall benthic community structure wherein PC1 explained 51.1% of the variability at 5 m and 64.8% at 15 m (Fig. 4 and Table S5). Despite the large number of benthic groups surveyed, over 93% of the variability among sites along PC1 was explained by the biomass of fleshy algae at both depths (Fig. 4b,d, Table 1C). None of the other macroalgal groups made major contributions to the site locations in the ordination (Table S3). The few sites with



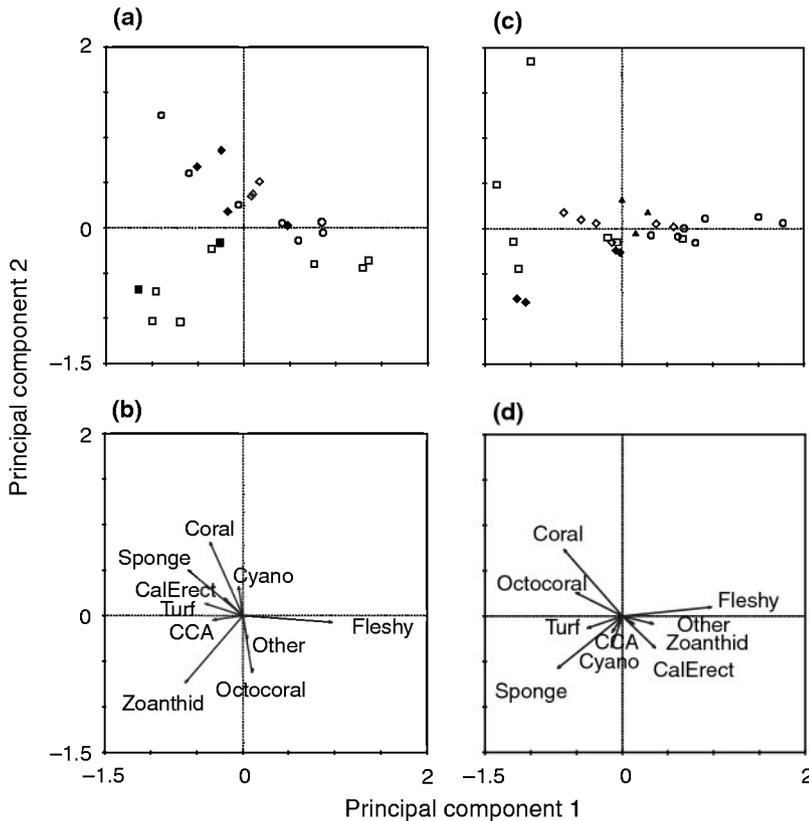
**Figure 3** Principal components analysis (PCA) of nine functional groups of fish based on average biomass for each site (see Table S4). The values of descriptors (functional groups) along the principal components (shown by arrows) represent the relative contribution to the position of sites along the principal components. See Materials and methods for details on analysis, Table S2 for lists of species in each group and abbreviations, Table S3 for species loadings, and Table S4 for biomass values of each group per site. Open symbols are 5 m and solid grey symbols are 15 m. Reserves at 5 m are patterned, 15 m reserves are black. Shapes are as in Fig. 1. Abbreviated functional groups: AP, apex predators; H, herbivores; LO, large omnivores; Mac, macroinvertebrates; Mic, microinvertebrates; PI, piscivore–invertebrate; P, piscivore; PL, planktivores; SmO, small omnivores.

low fleshy algal biomass separated along PC2 according to the biomass of corals, sponges and octocorals. At 5 m, zoanthid biomass also contributed to location of sites along PC2 (Fig. 4b, Table 1D). In particular, 5 m sites in the Florida region clustered separately due to comparatively low algal and high zoanthid biomass. Overall, PC2 explained 32.3% of benthic community variability at 5 m and 20.9% at 15 m. Sites from different regions overlapped broadly within the ordination space, indicating that biomass of benthic organisms, not geographical factors *per se*, are of primary importance (Fig. 4a,c).

There were few significant correlations between the composition of benthic community biomass and the different functional groups of fish. At 5 m, using a Bonferroni correction value based on 10 compared tests, the PC1 site scores were not significantly correlated with any functional group (Table 1E). However, apex predators and planktivores were negatively correlated with PC2. At 15 m, PC1 scores for benthic sites were negatively correlated with large omnivores and microinvertebrates (Table 1E). Site scores for PC2 were not correlated with any of the fish groups at 15 m.

In any large natural data set, spurious correlations are inevitable, thus we only evaluate importance in the context of well-established hypotheses of functional and ecological relationships. Based upon several decades of experimental work (Sammarco 1982; Edmunds & Carpenter 2001) and the overwhelming signal of fleshy algae as the main contributor to benthic community variability in our surveys, we explored in more detail the association among fish, fleshy algae and sea urchins (Fig. 5, Table 1D). Consistent with these earlier experiments, herbivorous fish biomass was negatively correlated with fleshy algal biomass at both depths (Spearman's rank correlation,  $P < 0.02$ ). Sea urchin biomass remained extremely low at most sites across our gradient, especially at 15 m (Fig. 5e,f), compared with their abundance prior to 1983 (Lessios *et al.* 1984). The average density of *Diadema* was only 0.368 and 0.019 individuals  $m^{-2}$  at 5 and 15 m, respectively, compared with densities ranging from 1 to 10 individuals  $m^{-2}$  before the 1983 die-off of this species (Lessios *et al.* 1984). We found no correlation between sea urchin biomass and algal biomass at either depth (Table 1D). Because of the unique role of *Diadema* as major grazers on the reef, we also looked at the correlation between *Diadema* and fleshy algae specifically. There was no significant relationship at either depth (Table 1D). Only four sites had more than one individual  $m^{-2}$  and these were all at 5 m.

Finally, we found that coral biomass was not correlated with herbivorous fish biomass at either depth (Spearman's rank correlation,  $P > 0.05$ ). Coral biomass was positively correlated with total fish biomass at 15 m (Spearman's rank correlation,  $P < 0.02$ ). This correlation was driven by just one site in the Dry Tortugas, USA (Fig. 5d, #21) where the coral community was dominated by very large ( $> 0.45$  m) heads of *Montastrea faveolata/franksi*. Given the size of these colonies and the long generation times of corals (Jackson 1991), there is no doubt that these corals are relics, at least several decades old, and do not represent a response of corals to recent changes in fish biomass. Excluding the data from this site, there was no relationship between coral and total fish biomass (Fig. 5c,d).



**Figure 4** Principal components analysis (PCA) of benthic community structure of Caribbean coral reefs. The ordination was based on the biomass of major community components at 5 m (a, b) and 15 m (c, d). The values of descriptors (species groups) along the principal components (shown by arrows) represent the relative contribution to the position of sites along the principal components (b, d). See Materials and methods for details on analysis, Table S2 for lists of species in each group and abbreviations, Table S3 for species loadings, and Table S5 for biomass values of each group per site. Solid symbols are reserves. Shapes are as in Figs 1 and 3.

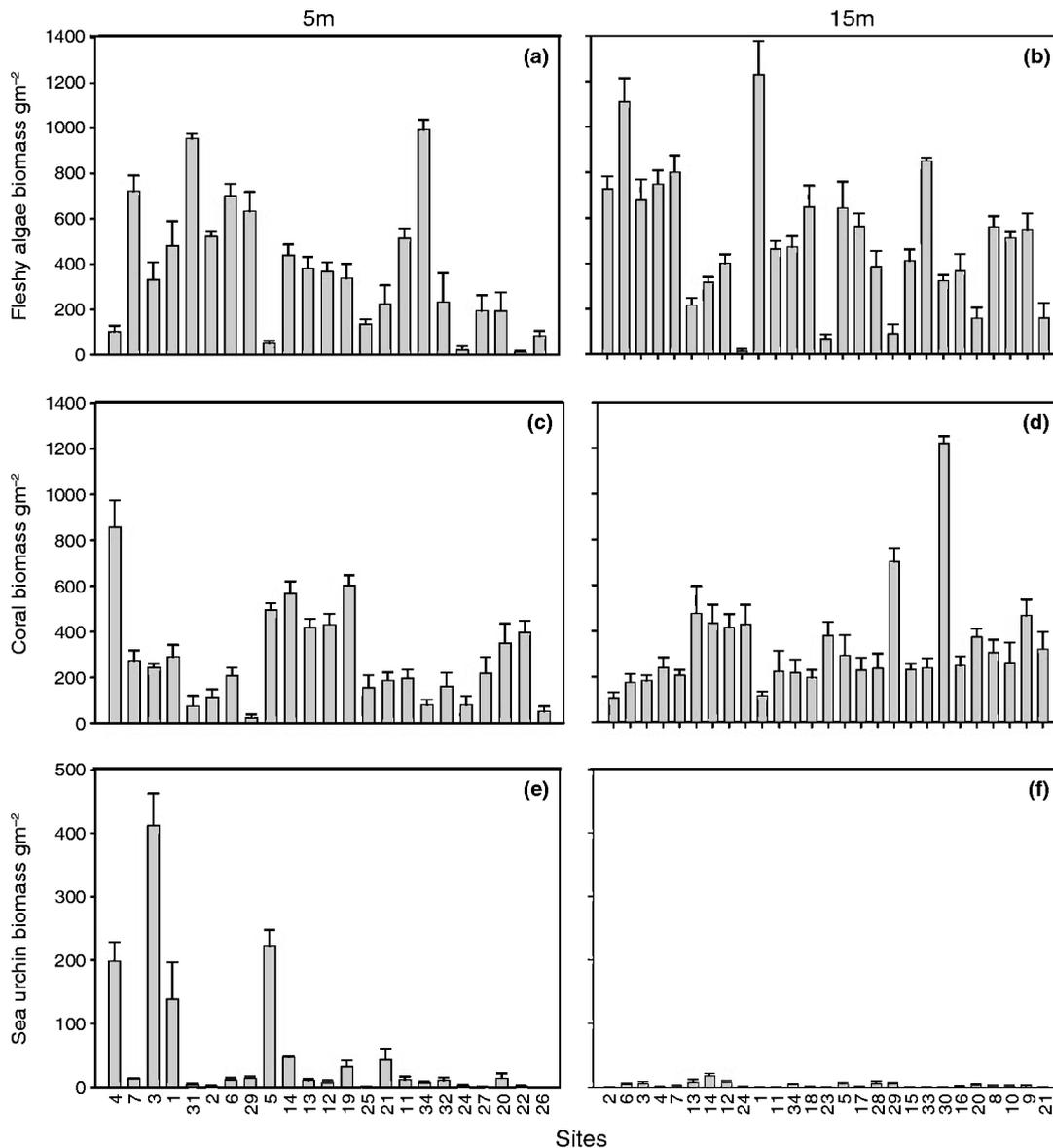
## DISCUSSION

During the past decade, a shift in the traditional approach to coral reef ecology has resulted in a handful of large-scale studies designed to address the regional to global-scale nature of both natural and anthropogenic processes that affect coral reef community structure (Jennings & Polunin 1997; Hughes *et al.* 1999; Dulvy *et al.* 2002; Friedlander & DeMartini 2002). This approach is powerful, but the large spatial scale may result in confounding geography and time (Dulvy *et al.* 2002). But such effects appear to have been small in our data as we found broad overlap of sites from different regions based on benthic community biomass and close clustering of all sites except reserves based on fish biomass. These results indicate that geographical effects were of minimal importance to community structure. The same argument applies to seasonal effects. Without enormous teams of surveyors collecting data simultaneously across locations (Hughes *et al.* 1999), it would be impossible to account for some temporal variation, but this effect is clearly second-order, given the results of the PCA analyses.

We found a remarkable 40-fold range in total fish biomass on fore reef environments across the north-western Caribbean. It is hardly surprising that the highest levels of fish biomass recorded were found only inside well-enforced marine reserves larger than 100 km<sup>2</sup>, and which have existed

for at least a decade (Claro *et al.* 2001; Spalding *et al.* 2001). Under such strict protection, fish assemblages are approaching recovery, with total fish biomass and trophic structure resembling relatively healthy reef fish populations in the Pacific (Friedlander & DeMartini 2002). The high end of our gradient therefore provides a useful baseline against which managers can compare recovery trends for fish assemblages in reef habitats across the Caribbean.

It is critical to understand the fundamental difference between subsistence fishing on Caribbean coral reefs and industrial-scale fishing in temperate waters. Unlike the practice of fishing down the food web, which has been documented in other marine ecosystems (Pauly *et al.* 1998), fishing on coral reefs in the Caribbean has been defined by intense over-harvesting of reef species from all trophic levels simultaneously (Jackson *et al.* 2001; Pandolfi *et al.* 2005). This is due to the widespread use of non-selective fishing gear in the form of fish traps and dynamite, compounded by the high densities of fishermen on small reef areas (Munro 1983; Hughes 1994). While large-bodied species, particularly predators, are expected to be the most vulnerable to fishing impacts (Jennings *et al.* 1999), almost all species are subjected to a relatively strong level of fishing pressure in the majority of sites we surveyed (Munro 1983; Polunin & Roberts 1993; Koslow *et al.* 1994; Williams & Polunin 2001).



**Figure 5** Mean and standard error for fleshy algae (a, b), corals (c, d) and sea urchins (e, f) for all sites. Sites are ordered from lowest to highest total fish biomass (same rank as Fig. 2). Note change of y-axis scale for sea urchins (e, f).

It has been argued that the lack of a strong effect of predator removal on reefs may in part be due to the high diversity of species and multiple omnivory links (Jennings & Kaiser 1998). While this may be true in relatively intact systems, in the majority of our sites the absence of response is most reasonably explained by the reduction of all fish trophic groups due to extreme overfishing. Under these circumstances it is not surprising that evidence for prey release on coral reefs is often not detected (Jennings & Polunin 1997; Russ & Alcala 1998; Dulvy *et al.* 2002) and we found no signs of trophic cascades in fished sites across our

gradient. Instead, sites from all areas clustered near each other in the fish PCA, indicating little difference in fish community structure across the gradient. The only sites to separate out in the ordination were reserve sites with comparatively high biomass of apex predators, and in one case, macroinvertebrates. Otherwise, the fish community was largely homogenized across the entire surveyed region and across both depths.

Given this history of fishing pressure, we also do not expect to find evidence for trophic cascades within the reserves studied. Instead, where fishing is eliminated, fish

biomass is expected to increase simultaneously across all trophic levels. This pattern of recovery is supported by our findings in the fish PCA, where the majority of functional groups are positively correlated (arrows point in the same direction) and in the positive correlations among herbivores, carnivores and apex predators. The recovery of multiple functional groups allows for restoration of functions such as grazing, while also permitting increased predator biomass inside of reserves (Mumby *et al.* 2006). Until the fish community begins to approach the carrying capacity of the system, predator–prey dynamics will not have as large an effect on the community as the reduction of fishing pressure, and therefore, trophic cascades inside the reserves will not be apparent.

These results are in contrast to temperate ecosystems, where fishing selectively targets upper trophic level species, and fishing-induced trophic cascades follow theoretical predictions of top-down effects (Pace *et al.* 1999) that have been well-documented (Estes *et al.* 1998; Sala *et al.* 1998; Frank *et al.* 2005). Strictly speaking, trophic cascades have been observed twice on coral reefs, in both cases involving invertebrate-mediated benthic community changes (McClanahan *et al.* 1994; Dulvy *et al.* 2004). In Kenya, experimental work showed a negative correlation between fish and sea urchins, and corresponding changes in algal communities (McClanahan *et al.* 1994; McClanahan 1997). Surveys in Fiji documented increased densities of starfish and reduced coral cover with decreased fish biomass (Dulvy *et al.* 2004). However, the range of fish biomass for both studies was small, with a maximum fish biomass of less than 175 g m<sup>-2</sup> in Kenya and less than 30 g m<sup>-2</sup> in Fiji, despite several years/decades of protection in reserve sites (McClanahan & Obura 1995; Jennings & Polunin 1996). Clearly, the dynamics of trophic cascades in degraded ecosystems must be interpreted with caution; in Fiji, direct grazing of fish on starfish was not observed and for both studies the impact of intact fish communities on invertebrate consumers, and consequent grazing activity, remains unknown. Other factors such as nutrients, sedimentation and recruitment may also play a large role in the observed dynamics (McClanahan 1997; Dulvy *et al.* 2004).

Although we did not find evidence for trophic cascades across the gradient surveyed, we did observe changes in the proportion of fish functional groups. These differences are likely a result of differential impacts of fishing on species with different life-history characteristics. Apex predators and large consumers tend to have slower population growth rates and increased vulnerability to fishing effects (Jennings *et al.* 1999). Therefore, recovery rates of different functional groups will vary under the same level of protection. Both the age and size of the reserves should also have a significant impact on the level of recovery for these organisms (Russ *et al.* 2005). We

found apex predators only in those reserves which are big enough to accommodate highly mobile species and that have been enforced for over a decade.

Marine reserves have been shown to effectively increase the biomass of fish assemblages over time (e.g. Russ *et al.* 2005). It is therefore likely that the high levels of fish biomass found inside of marine reserves in our study are due to increases in fish populations within reserve boundaries since inception of the reserve. These results suggest that in the Caribbean, areas protected from fishing for only a decade can successfully promote large quantities of fish, especially at higher trophic levels.

Our results support previous conclusions of smaller scale studies and meta-analyses of the impact of reserves on reef fish populations (Polunin & Roberts 1993; Micheli *et al.* 2004). In addition, our work demonstrates that these changes influence the benthic community via reduction of fleshy algae. While the direct relationship between fish and algae has been documented primarily at small spatial scales, our study links the role of reserves in influencing the benthic community and demonstrates that these patterns can be generalized across a large geographical area and very wide range of fish biomass. However, the recovery of fish populations alone may not be sufficient to restore coral dominance, at least over the short time period since protection began. Recent work on the effectiveness of marine reserves at regional- and global-scales determined that overall, coral reefs remain extremely vulnerable due to ineffective reserve size, spacing and enforcement (Mora *et al.* 2006). This ineffectiveness of reserves is reflected in the lack of significant correlation between the benthic community biomass and most fish functional groups or total fish biomass.

More specifically, coral biomass remains low across our gradient at all but a few sites and fleshy algae dominate most reefs. Consistent with recent findings of very restricted areas of high coral cover (Idjadi *et al.* 2006), we observed high coral biomass (and correspondingly high coral cover) at very few sites and these contained large colonies from remnant populations of predominantly *Montastraea annularis* (5 m) and *Montastraea faveolata/franki* (15 m), likely many decades old. The relatively long generation times of corals, compared with fish and algae, requires a long-term perspective with which to evaluate coral response. Fleshy algae are not only among the strongest competitors of corals for space (Knowlton 2001) but also can indirectly affect coral health. Recent work highlights the important role of increased organic carbon in disrupting the balance between the coral host and its symbiotic microbial community (Kuntz *et al.* 2005). Fleshy algae serve as a direct carbon source, stimulating increased growth of coral-associated microbes, which leads to increased coral mortality (Smith *et al.* 2006). Grazing by

both fish and sea urchins is therefore even more important than previously thought to reduce fleshy algal overgrowth on reefs in the long-term (Hughes 1994; Jackson *et al.* 2001; Hughes *et al.* 2003; Smith *et al.* 2006).

Additionally, the recent report of decreased macroalgal abundance and increased coral recruitment with increased *Diadema* (Carpenter & Edmunds 2006) implies that coral recovery may finally be beginning, at least at small spatial scales. However, the negative correlation between fish and sea urchin abundance at 5 m suggests that recovery of fishes may slow down recovery of sea urchins in areas protected from fishing, leading to potential changes in the benthic community (McClanahan *et al.* 1994). Other factors, such as rates of recruitment, nutrient loading and bleaching are also important variables that currently affect coral survival and recovery and must be included in any assessment of the dynamics of Caribbean coral reef health (Knowlton 2001; Gardner *et al.* 2003; Hughes *et al.* 2003; Pandolfi *et al.* 2003, 2005; Aronson & Precht 2006).

Regardless of these important complicating factors, the results of this study are encouraging. We found that increased fish biomass suppresses fleshy algal abundance on reefs across large geographical scales. This pattern emerges despite the various threats and different histories of the many sites surveyed and occurs consistently across the two depth habitats. If calls for improved marine reserve design at effective scales are met (Mora *et al.* 2006), then significant progress towards restoration of Caribbean reef ecosystems is still eminently possible.

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## REFERENCES

- Aronson, R.B. & Precht, W.F. (2006). Conservation, precaution, and Caribbean reefs. *Coral Reefs*, 25, 441–450.
- Ballesteros, E. (1992). *Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució*. Arxius de la Secció de Ciències CI, Institut d'Estudis Catalans, Barcelona.
- Carpenter, R.C. & Edmunds, P.J. (2006). Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecol. Lett.*, 9, 271–280.
- Claro, R., Lindeman, K.C. & Parenti, L.R. (eds) (2001). *Ecology of the Marine Fishes of Cuba*. Smithsonian Institution Press, Washington, DC.
- Dulvy, N.K., Mitchell, R.E., Watson, D., Sweeting, G. & Polunin, N.V.C. (2002). Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient. *J. Exp. Mar. Biol. Ecol.*, 278, 1–29.
- Dulvy, N.K., Freckleton, R.P. & Polunin, N.V.C. (2004). Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol. Lett.*, 7, 410–416.
- Edmunds, P.J. & Carpenter, R.C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases coral abundance of juvenile corals on a Caribbean reef. *Proc. Natl. Acad. Sci. U.S.A.*, 98, 5067–5077.
- Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998). Killer whale predation on sea otters linking oceanic and near-shore ecosystems. *Science*, 282, 473–476.
- Frank, K.T., Petrie, B. Choi, J.S. & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.
- Friedlander, A.M. & DeMartini, E.E. (2002). Contrasts in density size and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol. Prog. Ser.*, 230, 253–264.
- Froese, R. & Pauly, D. (2005) Fishbase World Wide Web electronic publication. <http://www.fishbase.org>.
- Gardner, T.A., Côte, I.M., Gill, J.A., Grant, A. & Watkinson, A. (2003). Long-term Regional-wide declining in Caribbean corals. *Science*, 301, 958–960.
- Harmelin-Vivien, M.L. *et al.* (1985). Visual evaluation of fish abundance and populations: methods and problems. *Rev. Ecol. Terre Vie*, 40, 467–539.
- Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschanivskyj, N.A., Pratchett, M.S., Tanner, J.E., *et al.* (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature*, 397 59–63.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C. *et al.* (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.

- Idjadi, J.A., Lee, S.C., Bruno, J.F., Precht, W.F., Allen-Requa, L. & Edmunds, P.J. (2006). Rapid phase-shifts reversal on a Jamaican coral reef. *Coral Reefs*, 25, 209–211.
- Jackson, J.B.C. (1991). Adaptation and diversity of reef corals. *BioScience*, 41, 475–482.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., *et al.* (2001). Historical overfishing and the collapse of coastal ecosystems. *Science*, 293, 629–638.
- Jennings, S. & Kaiser, M.J. (1998). The effects of fishing on marine ecosystems. *Adv. Mar. Biol.*, 34, 201–352.
- Jennings, S. & Polunin, N.V.C. (1996). Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *J. Appl. Ecol.*, 33, 400–412.
- Jennings, S. & Polunin, N.V.C. (1997). Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs*, 16, 71–82.
- Jennings, S., Greenstreet, P.R. & Reynolds, J.D. (1999). Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.*, 68, 617–627.
- Knowlton, N. (2001). The future of coral reefs. *Proc. Natl. Acad. Sci. U.S.A.*, 98, 5419–5425.
- Koslow, J.A., Aiken, K., Auil, S. & Clementson, A. (1994). Catch and effort analysis of the reef fisheries of Jamaica and Belize. *Fishery Bull.*, 92, 737–747.
- Kuntz, N.M., Kline, D.I., Sandin, S.A. & Rohwer, F. (2005). Pathologies and mortality rates caused by organic carbon and nutrient stressors in three Caribbean coral species. *Mar. Ecol. Prog. Ser.*, 294, 173–180.
- Lessios, H.A., Robertson, D.R. & Cubit, J.D. (1984). Spread of *Diadema* mass mortality through the Caribbean. *Science*, 226, 335–337 and references therein.
- McClanahan, T.R. (1997). Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. *J. Exp. Mar. Biol. Ecol.*, 218, 77–102.
- McClanahan, T.R. & Obura, D. (1995). Status of Kenyan coral reefs. *Coastal Manage.*, 23, 57–76.
- McClanahan, T.R., Nugues, M. & Mwachireya, S. (1994). Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J. Exp. Mar. Biol. Ecol.*, 184, 237–254.
- Micheli, F., Halpern, B.S., Botsford, L.W. & Warner, R.R. (2004). Trajectories and correlations of community no-take marine reserves. *Ecol. Appl.*, 14, 1709–1723.
- Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J. *et al.* (2006). Coral reefs and the global network of marine protected areas. *Science*, 312, 1750–1751.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R. *et al.* (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, 311, 98–101.
- Munro, J.L. (1983). Caribbean coral reef fishery resources. *ICLARM Stud. Rev.*, 7, 1–276.
- Ogden, J.C. & Lobel, P.S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.*, 3, 49–63.
- Opitz, S. (1996). *Trophic Interactions in Caribbean Coral Reefs*. Tech. Rep. 43, International Center for Living Aquatic Resources, Manila, Philippines.
- Pace, M.L., Cole, J.L., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *TREE*, 14, 483–488.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G. *et al.* (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301, 955–958.
- Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M. *et al.* (2005). Are U.S. coral reefs on the slippery slope to slime? *Science*, 307, 1725–1726.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F., Jr (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Polunin, N.V.C. & Roberts, C.M. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar. Ecol. Prog. Ser.*, 100, 167.
- R Development Core Team (2005). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Russ, G.R. & Alcala, A. (1998). Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs*, 17, 383–397.
- Russ, G.R., Stockwell, B. & Alcala, A. (2005). Inferring versus measuring rates of recovery in no-take marine reserves. *Mar. Ecol. Prog. Ser.*, 292, 1–12.
- Sala, E., Boudouresque, C.F. & Harmelin-Vivien, M. (1998). Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos*, 83, 425–439.
- Sammarco, P.W. (1982). Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. *J. Exp. Mar. Biol. Ecol.*, 61, 31–55.
- Smith, J.E., Shaw, M., Edwards, R.A., Obura, D., Pantos, O. *et al.* (2006). Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecol. Lett.*, 9, 835.
- Spalding, M.D., Ravilious, C. & Green, E.P. (2001). *World Atlas of Coral Reefs*. University of California Press, Berkeley, CA.
- Vinogradov, A.P. (1953). *The Elementary Chemical Composition of Marine Organisms*. Sears Foundation for Marine Research, Yale University, New Haven, CT (Translated by J. Efron & J. K. Setlow from original Russian).
- Williams, I.D. & Polunin, N.V.C. (2001). Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs*, 19, 358–366.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Figure S1** Mean biomass of fish functional groups as a proportion of total fish biomass plotted against the mean total fish biomass.

**Table S1** List of site names, location, depth, and number of transects conducted at each site and depth.

**Table S2** Species list for all taxonomic groups mentioned in text.

**Table S3** Cumulative fit per species as fraction of variance of benthic species groups in Benthic PCA from Fig. 4 and the Fish PCA in Fig. 3.

**Table S4** Mean values ( $\text{g m}^{-2}$ ) of transects for each fish functional group surveyed for all sites.

**Table S5** Mean values ( $\text{g m}^{-2}$ ) of transects for each benthic group surveyed for all sites.

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