Biological Conservation 171 (2014) 186–194

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs

Fiorenza Micheli [a,*], Peter J. Mumby [b], Daniel R. Brumbaugh [c,d], Kenny Broad [e], Craig P. Dahlgren [f], Alastair R. Harborne [b], Katherine E. Holmes [c,g], Carrie V. Kappel [h], Steven Y. Litvin [a], James N. Sanchirico [i]

[a] Hopkins Marine Station, Stanford University, 120 Oceanview Blvd., Pacific Grove, CA 93950, USA
[b] Marine Spatial Ecology Lab, School of Biological Sciences, University of Queensland, St. Lucia Brisbane, Queensland 4072, Australia
[c] Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA
[d] Institute of Marine Science, Center for Ocean Health, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA
[e] Rosenstiel School of Marine & Atmospheric Science, Division of Marine Affairs & Policy, 1365 Memorial Drive, Ungar Building, Room 230-H, Coral Gables, FL 33146, USA
[f] Perry Institute for Marine Science, 100 N. US Highway 1, Suite 202, Jupiter, FL 33477, USA
[g] Global Conservation Program, Wildlife Conservation Society, 2300 Southern Blvd, Bronx, NY 10460, USA
[h] National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA
[i] Department of Environmental Science and Policy, University of California, Davis, Wickson Hall, 1 Shields Ave., Davis, CA 95616, USA

## ARTICLE INFO

*Article history:*
Received 17 May 2013
Received in revised form 12 December 2013
Accepted 19 December 2013

*Keywords:*
Biodiversity
Coral reef
Ecosystem functioning
Ecosystem services
Functional diversity
Functional redundancy
Marine reserve

## ABSTRACT

Determining how ecosystem function and services are related to diversity is necessary for predicting the consequences of diversity loss and for setting goals and priorities for marine conservation. The consequences of biodiversity loss for ecosystem functions and services depend on the level of functional redundancy – the number of species with similar ecological functional traits. Using field data on fish assemblages from 199 coral reef and lagoon sites from six islands, and on local fisheries from four islands in The Bahamas, we examined levels of functional diversity and redundancy within these assemblages and determined how fish biomass and local fisheries catches vary with local diversity. A majority of functional groups contain few species, suggesting that these assemblages have limited functional redundancy. Most also include species targeted by local fisheries, thus fishing has the potential to broadly impact food webs. Comparisons between a large marine reserve and fished reefs confirm that fishing significantly reduces functional redundancy and removes whole functional groups. Positive exponential relationships of fish biomass and fisheries catches with species and functional diversity highlight that even small declines in biodiversity may result in large reductions in secondary production and seafood provision. Taken together, these results indicate that Caribbean fish assemblages have low functional redundancy and high vulnerability of ecosystem functions and services to diversity loss, and that protection of multi-species assemblages is needed to maintain functions and services.

## 1. Introduction

The impacts of human activities on marine biodiversity are nearly ubiquitous (Halpern et al., 2008) – causing declines in ecosystem functions, such as productivity and resilience, and the loss of key services (Millennium Ecosystem Assessment, 2005; Worm et al., 2006). However, the generality of a relationship between diversity, functions, and services is still debated (Hooper et al., 2005; Stachowicz et al., 2007; Reich et al., 2012). In particular, the extent of diversity loss that can occur before functions and services are lost (e.g., Loreau et al., 2001; Micheli and Halpern, 2005; Danovaro et al., 2008) is unknown for most marine ecosystems. Determining how ecosystem function and services are related to diversity is necessary for predicting the consequences of diversity loss and for setting goals and priorities for marine conservation.

Functional redundancy within a community (defined as the number of taxonomically distinct species that exhibit similar ecological functions; Walker, 1992; Naeem, 1998) mediates the consequences of diversity loss because the loss of one species, and of its functional role, may be compensated by the persistence of other species with similar functional roles. Thus, a first step for linking

---

* Corresponding author. Tel.: +1 831 655 6250; fax: +1 831 375 0793.
*E-mail addresses:* micheli@stanford.edu (F. Micheli), p.j.mumby@uq.edu.au (P.J. Mumby), dbrumbaugh@amnh.org (D.R. Brumbaugh), kbroad@rsmas.miami.edu (K. Broad), cdahlgren@perryinstitute.org (C.P. Dahlgren), a.harborne@uq.edu.au (A.R. Harborne), kholmes@wcs.org (K.E. Holmes), kappel@nceas.ucsb.edu (C.V. Kappel), litvin@stanford.edu (S.Y. Litvin), jsanchirico@ucdavis.edu (J.N. Sanchirico).

http://dx.doi.org/10.1016/j.biocon.2013.12.029
0006-3207/© 2014 Elsevier Ltd. All rights reserved.

diversity and function is to examine the relationship between measures of diversity, such as species diversity, functional diversity and redundancy, and measures of ecosystem function and services.

The consequences of diversity loss for ecosystem functions and services are likely dependent on the shape of diversity-function or diversity-service relationships and on the range of diversity over which species are lost or added (Fig. 1). This relationship is expected to be linear with a slope of 1 if each species has a unique functional role (Fig. 1b), or greater if a subset of species can each perform multiple functions. In contrast, multiple species performing similar functions will result in a linear relationship with a shallower slope. Alternatively, measures of ecosystem functions or services may increase rapidly at low diversity levels if new species perform functions not already represented in the community while at higher diversity levels new species may be functionally redundant and the rate of addition slows down (Fig. 1a). Another biologically plausible scenario is where functions or services remain low at low levels of species diversity (Fig. 1c). This might occur, for example, if disturbance leads to the persistence of a subset of species sharing a limited number of functional traits. When conditions change, species addition leads to the addition of functions represented, but only at higher diversity levels. As in Fig. 1a, a plateau is eventually reached in 1c as it becomes increasingly likely that additional species at higher diversity levels are functionally similar to species already present in the community. Under all the scenarios above, species loss will ultimately result in decreasing ecosystem function but the rate and extent of this decrease is greatest for exponential relationships (Fig. 1c), least for saturating relationships (Fig. 1a), and intermediate in the linear case (Fig. 1b).

Few studies have addressed biodiversity-function relationships in marine ecosystems, and even fewer studies have addressed relationships between diversity and services (Raffaelli, 2007).

Experimental manipulations rigorously testing effects of diversity on ecosystem function (e.g., Worm et al., 2006; Stachowicz et al., 2007) are limited because of logistical constraints, and therefore the consequences of diversity loss in high-diversity assemblages are generally unknown (e.g., Micheli and Halpern, 2005; Guillemot et al., 2011). Correlative analyses from natural ecosystems have highlighted both linear and non-linear saturating relationships between marine species and functional diversity (Micheli and Halpern, 2005; Halpern and Floeter, 2008). Exponential relationships between species diversity and ecosystem functions, including biomass, secondary production, and decomposition rates, were reported in the deep sea (Danovaro et al., 2008), and non-saturating relationships between fish biomass and functional diversity were found in a global analysis of coral reef fish assemblages (Mora et al., 2011). Furthermore, linear relationships between taxonomic diversity and variables describing the magnitude and variability of fisheries catches were found in a global analysis conducted at the scale of large marine regions (Worm et al., 2006).

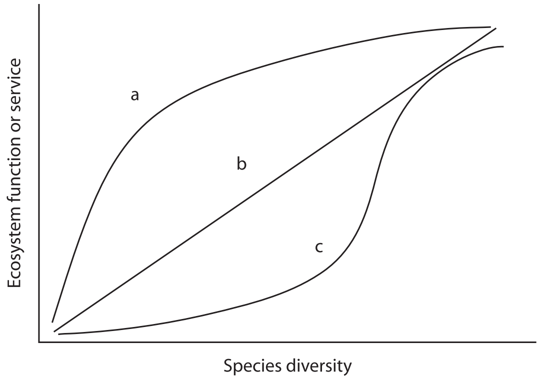

**Fig. 1.** Possible relationships of functional diversity, ecosystem function and/or services with species diversity (modified from Micheli and Halpern 2005). Depending on levels of functional redundancy within assemblages, functional diversity, ecosystem function or ecosystem services may increase linearly with increasing species diversity (b), or at declining (a), or increasing rates (c). These ecosystem properties are expected to reach a plateau at high diversity levels (a,c).

It is particularly important to examine the shape of diversity-function and diversity-service relationships in coral reefs because they are the most diverse and among the most threatened marine ecosystems (Bellwood et al., 2004; Hoegh-Guldberg et al., 2007; Halpern et al., 2008). Coral reef ecosystems worldwide have undergone significant decline and degradation due to combinations of anthropogenic and natural disturbances, including increases in water temperature and consequent coral bleaching, hurricanes, disease and direct impacts of fishing and coastal development on reef, mangrove, and seagrass habitats (Gardner et al., 2003; Pandolfi et al., 2005; Mora et al., 2011; De'ath et al., 2012). Such impacts have been particularly severe in the Caribbean (Gardner et al., 2003). Lower species diversity and limited functional redundancy of Caribbean reef assemblages, compared to Indo-Pacific reefs, may underlie low resilience in the face of increasing disturbance (Bellwood et al., 2004; Roff and Mumby, 2012). For example, mass mortality of a single sea urchin species, *Diadema antillarum,* and two coral species, the staghorn and elkhorn corals (*Acropora cervicornis* and *A. palmata*) from disease in the 1980s virtually eliminated entire ecological functions, namely the control of macroalgae by invertebrate grazers and the provision of complex three-dimensional habitat by live branching corals (Roff and Mumby, 2012). Under currently low sea urchin abundance, parrotfishes are the key remaining grazers that control macroalgae and allow for coral recovery (Mumby et al., 2006a, 2007), though functional effects of parrotfishes do not completely replace those of urchins across the range of environmental conditions (Mumby et al., 2006b; Korzen et al., 2011).

In this study, we examine levels of functional redundancy and relationships between total biomass, fisheries catches and diversity in fish assemblages of the Bahamian archipelago. Fish species perform critical ecosystem functions on coral reefs and provide key resources to local human communities (Moberg and Folke, 1999; Harborne et al., 2006; Broad and Sanchirico, 2008; Mumby et al., 2008). Because fishing and seafood provisioning are marine ecosystem services of primary interest to many people, and fish diversity, abundance, and biomass are relatively well understood ecological metrics, we utilize these variables as a first step in exploring the empirical relationships among diversity, function, and services in coral reef ecosystems. Specifically, we use data from field surveys of fish assemblages across a suite of habitats to examine (1) the distribution of species across different functional groups and the levels of functional redundancy within these assemblages, (2) the impacts of local extractive activities (i.e., small-scale food and ornamental fisheries) on functional diversity and redundancy, and (3) the significance and shape of the relationship between diversity and fish biomass or fisheries catches in these assemblages.

## 2. Materials and methods

### 2.1. Survey methods

We surveyed 199 sites, comprising a total of 12 different habitat types, within island regions of the Bahamian archipelago (Appendix Table A1). Nine to 15 habitat types (e.g., forereef, patch reef, gorgonian plains, seagrass, algal beds, mangrove stands; Table A1) were surveyed within the island systems of Abaco, Andros, Bimini, and San Salvador in The Bahamas and South Caicos in the Turks and

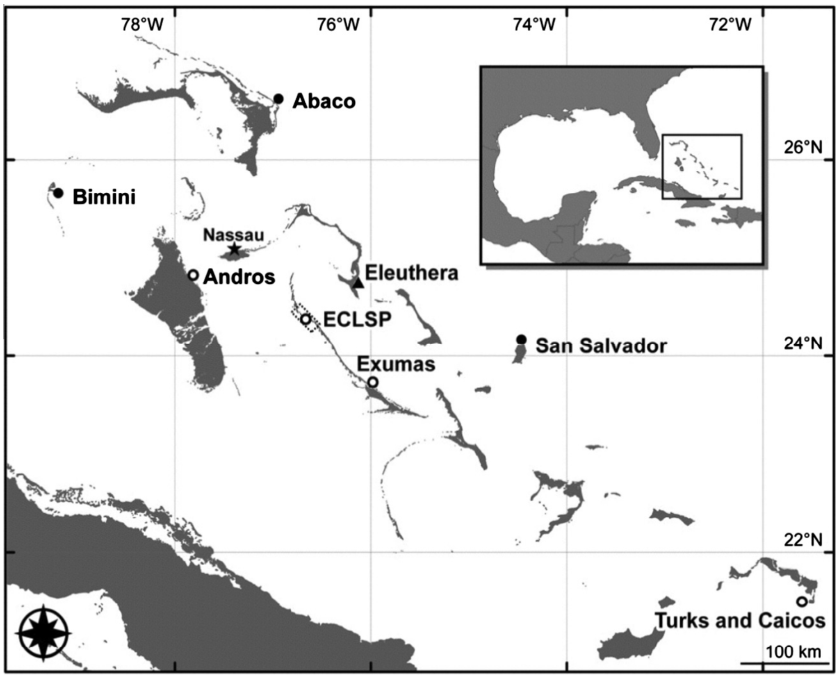

**Fig. 2.** Map of the Bahamian archipelago showing study locations. Circles indicate locations of fish surveys. Filled symbols indicate locations of ethnographic surveys. Filled circles reflect locations where both fish and ethnographic surveys were performed. Only ethnographic surveys were conducted on Eleuthera (filled triangle). Exuma Cays Land and Sea Park (ECLSP) boundaries are noted with a dashed line.

Caicos Islands (Fig. 2). Within the Exumas, we conducted more intensive surveys in the *Orbicella*/*Montastraea*-dominated forereefs (henceforth *Montastraea*-dominated forereefs) in and around the Exuma Cays Land and Sea Park (ECLSP), a 442 km$^2$ protected area established in 1958 and given no-take marine reserve status in 1986 (Fig. 2).

At each site all but nocturnal (e.g., Apogonidae) and highly cryptic (Clinidae and Gobiidae) fish species were surveyed using visual fish census techniques (Green and Alevizon, 1989). Species' densities and size (to nearest cm) were estimated along belt transects and biomass was calculated using published constants (Harborne et al., 2008a). Transects of different dimensions were surveyed to target species characterized by different density and mobility: 30 × 2 m ($n = 4$ transects/site) for Pomacentridae, Labridae, Holocentridae, and small Serranidae; 30 × 4 m ($n = 10$/site) for Scaridae, Acanthuridae, Pomacanthidae, Chaetodontidae, Diodontidae, and Monacanthidae; 50 × 4 m ($n = 5$/site) for Haemulidae, Lutjanidae, Carangidae, Balistidae, planktivorous Labridae, large Serranidae, and other large predators (Harborne et al., 2008a, 2008b).

### 2.2. Classification of species into functional groups

We assigned each of the 168 species in our database to functional groups (Appendix Table A2) based on three ecological traits – diet, size, and adult mobility/habitat use – selected because these characteristics are key for determining trophic role and have been used in other studies examining functional diversity and redundancy in fish assemblages (e.g., Micheli and Halpern, 2005; Halpern and Floeter, 2008; Guillemot et al., 2011). Similar to other studies (e.g., Guillemot et al., 2011) we conducted functional classifications at the scale of sites (100s m).

Because basic information on diet, size and mobility/habitat use is available for a majority of fish species, these data can serve as proxies or indicators for functional roles within communities, and the resulting functional classifications can be broadly applied across assemblages and ecosystems. This approach has limitations, however, such as low ability to discriminate subtle differences in the functional roles of species and account for possible ontogenetic shifts in functional traits (e.g., between juveniles and adults of the same species). More detailed quantifications of functional diversity based on continuous morpho-anatomical traits have been conducted in lower diversity fish assemblages (e.g., 62 species, Villeger et al., 2010; 37 species, Mouillot et al., 2008) and within target families (e.g., Labridae and Scaridae, Bellwood et al., 2006). Functional classification schemes based on continuous traits (e.g., Petchey et al., 2004), instead of the categories used here, were not applicable because detailed natural history and ecological information is not available for all life stages of the 168 species in this dataset. Finally, our approach to functional classification assumes that functions are simply based on species presence, whereas interactions among species may modulate functions (e.g., Willems and Hill, 2009; Madin et al., 2011). Future studies should attempt to link function to species' behaviors and interactions within assemblages, and across space.

Our categories (Appendix Table A2) comprised nine trophic groups (algal turf grazers, erect macroalgae grazers, omnivores, planktivores, predators of mobile macroinvertebrates, predators of sessile macroinvertebrates, predators of small invertebrates, macroinvertebrate feeders/piscivores, and piscivores), four size classes ($\leqslant$25 cm, 25–50 cm, 50–100 cm, and >100 cm, based on maximum reported standard lengths), and four mobility/habitat use categories (sedentary or territorial species closely associated with the seafloor, roving/demersal species, relatively sedentary midwater species, and mobile pelagic species). Information about the diets, reported maximum lengths, and habitat use and mobility was obtained for each species through literature review (Randall, 1967; Bohlke and Chaplin, 1993; Claro et al., 2001; Froese and Pauly, 2003).

To test the robustness of our conclusions, particularly how results may be affected by the number and combination of classification criteria used, we grouped species into functional categories using different classification criteria. First, we considered trophic group, size, and mobility/habitat use separately, and combinations of pairs of traits: trophic group and size (for a total of 22 groups) or trophic group and mobility/habitat use (25 groups) combinations. The total number of pair wise classification groups is lower than the theoretical maximum (for example 9 trophic groups × 4 size groups = 36 groups) because some combinations did not occur within these assemblages. Finally, we combined all three traits, and then aggregated some of the groups (e.g., size classes were combined when the size classes did not correspond to meaningful functional differences for some combinations of trophic mode and habitat association) and separated others (e.g., we separated invertebrate feeders foraging primarily on coral reefs *vs.* sandy bottom) based on additional information on the ecology of each species obtained through literature review (see references above and Appendix Table A2). This classification resulted in 33 detailed functional groups (henceforth ''functional groups'') in total.

Each of the 168 species in the database was also assigned to one of four exploitation categories – primary fishing target (for food), secondary fishing target (for food), potential aquarium trade target (ornamental fish), or non-target – based on data from ethnographic surveys (Broad and Sanchirico, 2008) conducted within four Bahamian islands, San Salvador, Eleuthera, Bimini, and Abaco (Fig. 2). Sixty-seven species or species groups were reported as targets of fishing in at least one of 72 ethnographic surveys from the four locations. Taxa were considered primary targets if they were reported in more than half of surveys and in at least two of the four islands. The other reported fished species were considered secondary targets. For the species that were not mentioned in interviews with fishers, we used information reported in *FishBase* (www.fishbase.org; Froese and Pauly, 2003) to assign them to one of three possible categories: secondary targets, aquarium-trade targets, or non-targets.

### 2.3. Measures of species and functional diversity

Fish diversity at each of the 199 sites was quantified as richness both in terms of species and functional groups (i.e., as the number of species or groups encountered). In addition, we calculated the Shannon–Wiener diversity index using number of species within each functional group as a measure of functional redundancy within fish assemblages at different sites (Stevens et al., 2003). Higher values of this index indicate a more even distribution of species among the functional groups observed at a site, and therefore greater functional redundancy on average within the assemblage. Conversely, low values indicate a skewed distribution of species among functional groups, with few groups containing many species and many groups represented by few species. At low values of the index a few groups would be characterized by high functional redundancy, but several functional trait combinations would have low redundancy and might be lost with species loss. Thus the assemblage would have lower functional redundancy overall.

#### 2.3.1. Levels of functional redundancy and fishing impacts

To examine the effects of fishing on fish diversity and functional redundancy, we used two approaches. First, we determined the number of species assigned to different functional groups and exploitation categories for each functional classification scheme (single traits, pairs of traits, or combinations of all three traits, see above) to examine the distribution of species subject to different exploitation levels across functional groups. Second, we compared species and functional diversity and redundancy between fish communities within the ECLSP and in adjacent, fished waters. We compared functional diversity and redundancy among Montastraea-dominated forereefs within the no-take reserve (the ECLSP) and fished reefs to the north and south of the park using one-way Analysis of Variance (ANOVA). We used asymmetric ANOVA models comparing diversity between the no-take reserve and the two fished areas, with $N = 3$ reefs surveyed within each area.

### 2.4. Relationships between diversity, biomass and fisheries catch

We examined the significance and shape of relationships of species diversity with functional diversity and then between these measures of diversity and both fish biomass and estimated fisheries catch. We used the standing biomass of fish assemblages as a metric of ecosystem functioning. There is a strong relationship between body mass and energy requirements in fishes, thus standing biomass is an accurate surrogate for energy fluxes in fish assemblages (Mora et al., 2011). Total fish biomass for each site (per unit area) was calculated by summing individual biomass estimated from all transects (Harborne et al., 2008b).

The provisioning service of seafood production was estimated from a simple model of fisheries production. Fisheries catch statistics do not exist at the scale of individual locations and were estimated, for each field site, by combining estimates of fishing effort (Harborne et al., 2008a) with quantification of the biomass of primary fishing targets at the site (this study). Harborne et al. (2008a) combined a predictive model of travel costs for fishing with a spatially explicit dataset of human population sizes to estimate the total fishing pressure from local small-scale fisheries at each site. Fishing effort at each *Montastraea* reef and gorgonian plain site surveyed in this study was estimated as the inverse of the predicted travel cost, weighted by local human population size. This measure assumes that fishing will be higher near sites of large populations and that sites further from a given population will be fished less heavily than a closer site.

We multiplied total estimated fishing effort by the total biomass of fish species that are primary targets for local small-scale fisheries. Thus, total catch (TC) at each location *i* was estimated as:

$$TC_i = q \times FE_i \times B_i$$

where *FE* is fishing effort, and *B* the total biomass of all species targeted by local fisheries. We assumed a catchability coefficient ($q$) of 0.02, although other constants could be used and the magnitude of this constant does not influence the shape and significance of the relationship between catch and species diversity. This approach to estimating catches accounts for variation in fish biomass, species composition, distance from settlements, and local human population density among field sites. This measure of catch captures the fact that some sites supporting high fish biomass cannot be easily accessed and thus may not provide high levels of services (benefits) (Fig. A1). Catches were estimated, rather than directly measured, and values should be considered as a relative index of fisheries production, not actual catch amounts.

To determine whether measures of functional diversity, fish biomass, and fisheries catch are associated with the species diversity of fish assemblages, and if so, whether relationships are linear, saturating, or exponential (non-saturating) within the observed diversity ranges (Fig. 1), we fitted linear, logarithmic, and exponential models to the data. In each case we retained the relationship that explained the most variation (all models contain the same number of terms, and so can be compared directly using $R^2$ values). We did not fit logistic models (Fig. 1) because visual inspection of data revealed that this distribution was never observed.

## 3. Results

### 3.1. Levels of functional redundancy and fishing impacts

The average number of species per functional group varied across the functional classification schemes (Fig. 3). Trophic groups

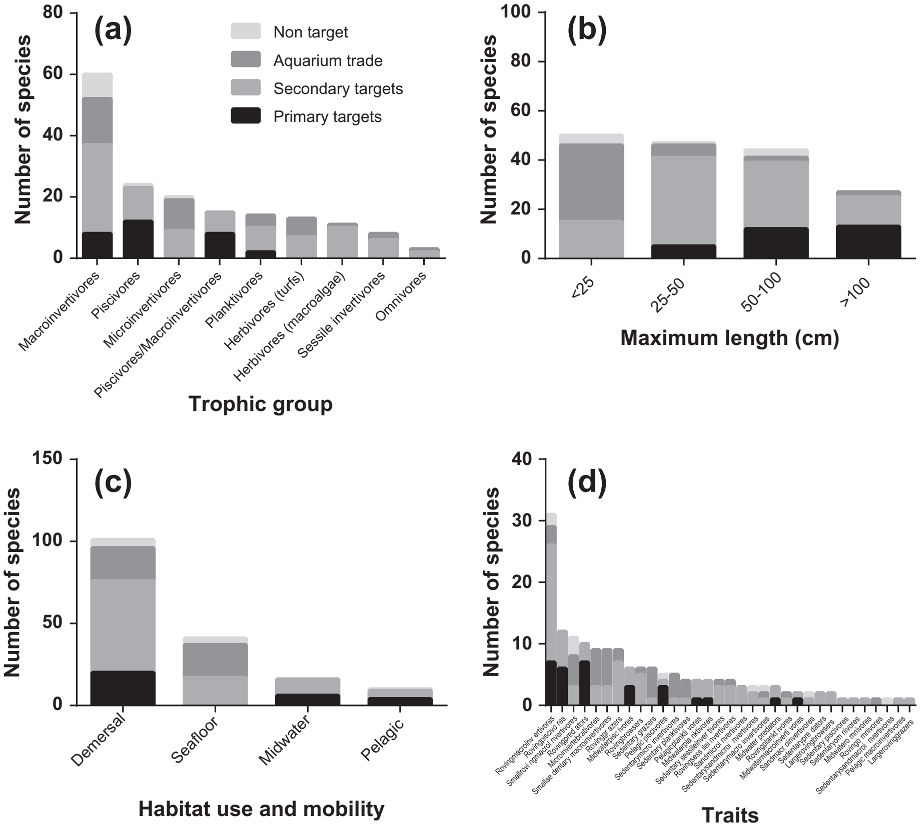

**Fig. 3.** Functional group composition of Bahamian fish assemblages. Distribution of fish species ($N = 168$ in total) subject to different exploitation levels (primary and secondary fishing targets, aquarium-trade targets, and non-target species) across functional groups determined based on different functional classification criteria: diet (nine trophic groups, a); size (four size groups, b); habitat use and mobility (four habitat use groups, c); and combinations of these traits (33 functional groups, d).

include between 3–60 species (*av.* = 18.7 species/group), size groups 27–50 species (*av.* = 42 species/group), habitat use groups 10–101 species (*av.* = 42 species/group), and detailed functional groups 1–31 species/group (*av.* = 5.1 species/group). Despite variation among different functional classification schemes, in most cases the distribution of species among functional groups is skewed with one or a few groups containing a large number of species while the majority of groups containing relatively few (Fig. 3a,c,d). Only for size is there a similar number of species per functional group (Fig. 3b). In particular, the macroinvertebrate feeder group comprises over one third of species (35.7%; Fig. 3a) and nearly two thirds of species are demersal (60.1%, Fig. 3c). In the most detailed functional classification, half of the species (48.8%) are contained in just 6 of the 33 functional groups, while 23 groups contain fewer than 5 species (Fig. 3d).

Potential fishing impacts are broadly distributed within nearshore fish assemblages of the Bahamas. Of the 168 fish species observed in the field, 30 (17.9%) are primary fishing targets, and 88 (52.4%) are secondary fishing targets. Thus, 70.2% of fish species in shallow (<25 m depth) coastal habitats may be caught in fisheries. An additional 40 (23.8%) species are reported as targets of the aquarium trade, leaving only 6% of species not targeted by any extractive activity (Fig. 3).

The majority of species within all trophic groups, except predators of small invertebrates and grazers of algal turfs (Fig. 3a), are primary or secondary fisheries targets. In addition, all species in the largest size category (>1 m maximum length; Fig. 3b) and in midwater and pelagic groups (Fig. 3c) are fisheries targets.

Our most detailed functional classification further suggests that fishing may cause functional loss throughout the food web (Fig. 3d). In particular: (1) in nearly half of the groups (15 of 33, 45.5%), all the included species are fishing targets; (2) all groups except one (species feeding on small invertebrates on sandy bottom) include species targeted by fishing; and (3) over one third of groups (12 groups, 36.4%) contain only 1–2 species, almost all targeted by fisheries (Fig. 3d).

Previous studies have shown that species richness is significantly lower in fished areas compared to the unfished reefs inside the ECLSP (a 15% decrease) (Harborne et al., 2008b). Here we found that fishing impacts on species richness also result in decreased functional diversity and redundancy in fished areas (Table 1; Appendix Fig. A2). Unfished reefs have significantly more functional groups (1.7–3.6 more groups within the park than fished reefs, on average; Table 1) and significantly greater functional redundancy (Table 1), with fished reefs having a subset of functional groups (midwater piscivores, omnivores, and invertebrate feeders, demersal piscivores, pelagic and sedentary planktivores, and large roving browsers) with a disproportionately high number of species which were not seen in our surveys, thereby decreasing functional redundancy within these groups (Table 1 and Fig. A2).

**Table 1**
Results of ANOVAs comparing measures of functional richness and redundancy between unfished reefs within the ECLSP (Fig. 2) and fished reefs north and south of the park. Species were assigned to each of 33 functional groups based on information on diet, maximum size and habitat use and mobility (Fig. A2 and Table A2 in Supplementary materials). Averages (+1*SE*, $N = 3$ reefs) of each diversity measure are reported for each area. Degrees of freedom are 1 and 7 in both cases.

| Variable | North | ECLSP | South | *F* | *P* |
|---|---|---|---|---|---|
| No. functional groups | 15.7(0.9) | 19.3(1.5) | 17.7(0.3) | 9.3 | 0.02 |
| Functional redundancy | 2.4(0.0) | 2.7(0.1) | 2.5(0.0) | 8.3 | 0.02 |

Lower numbers of piscivorous and planktivorous species were seen in fished compared to protected reefs, particularly demersal and midwater piscivores and pelagic and sedentary planktivores (Fig. A2). Moreover, some key functional groups, such as the large roving browsers of turf and macroalgae (i.e., the largest parrotfish species, *Scarus coeruleus* and *S. guacamaia*), were seen inside the reserve but not at the adjacent fished sites north and south of the ECLSP (Fig. A2).

### 3.2. Relationships between diversity, biomass and fisheries productivity

All measures of functional diversity, as well as fish biomass and fisheries catch were significantly and positively correlated with species richness (Table 2 and Figs. 4 and A3). Comparison of the fit of different models (linear, saturating, or exponential) showed that, within the species richness ranges we observed at our field sites, measures of functional diversity have non-linear saturating (Table 2 and Fig. A3) or linear (Table 2 and Figs. 4a and A3) relationships with species richness, depending on the functional classification scheme.

Fish biomass and estimated total catch both increase exponentially with increasing species and functional richness (Table 2). Biomass and catches do not reach a plateau for the range of species richness observed at our sites (Fig. 4b and c). Relatively low biomass and catch levels are evident at sites with fewer than 30 observed species (Fig. 4b,c). Separate analyses conducted for the gorgonian plains – the habitat type for which we have the greatest number of replicate sites – indicated that significant positive relationships between functional diversity or fish biomass and species richness exist even within a single habitat type ($R^2 = 0.34–0.77$, $p < 0.01$). Within the gorgonian plain habitat, the relationship of estimated catch with functional richness is also significant ($R^2 = 0.18$, $p < 0.05$), but not with species richness ($R^2 = 0.06$, $p > 0.05$).

## 4. Discussion

Fish assemblages across the Bahamian archipelago are characterized by low levels of functional redundancy, high exposure of multiple functional groups to fishing, and positive, exponential relationships between diversity, a measure of ecosystem function (total biomass), and an ecosystem service (seafood provision). A few groups contained large numbers of species. In particular, a majority of species are demersal predators of benthic invertebrates, consistent with the classic role played by tropical coral reefs in supporting demersal fish diversity through the (1) creation of complex three-dimensional habitat structure and (2) substantial primary production in otherwise oligotrophic environments. In contrast, a large fraction of functional groups in these assemblages included only 1–2 species (12 of 33 groups, 36.4%, in our most detailed classification), a majority less than 5 species (23 groups, 69.7%), indicating that multiple functional trait combinations may be lost with relatively small declines in species diversity. These low levels of functional redundancy are similar to what previously reported by Micheli and Halpern (2005) for a suite of tropical and temperate reefs, and by Guillemot et al. (2011) for highly diverse fish assemblages from coral reef sites in New Caledonia. Only at the greatest species-richness levels (50–70 species encountered in 50 m long transects) does redundancy appear to increase, though only for some functions (Guillemot et al., 2011). Results of our analyses and these previous studies suggest that low functional redundancy may broadly characterize fish assemblages, except for the most diverse systems.

Taken together these results indicate that Caribbean reef-fish assemblages and a critical services they provide – seafood provision – may be highly vulnerable to human impacts and that even small declines in biodiversity may result in reduced biomass and fisheries catches. A majority of functional groups include species targeted by local fisheries, suggesting that fishing impacts may be broadly distributed through these food webs. In fact, only 6% of species are not caught in any current or anticipated fishery, highlighting that fishing has the potential to affect nearly all functional trait combinations within these assemblages. Moreover, regardless of the functional classification scheme used, all species within some groups are targeted (e.g. all species larger than 1 m in maximum size, all midwater species, and several groups of predators, omnivores, and herbivores; Fig. 3), indicating that fishing may eliminate whole functions. Multi-species small-scale fisheries are common in coral reef ecosystems and, although our analysis was limited to Caribbean reefs, the result of broadly distributed potential impacts of fishing on functional diversity may apply to a suite of tropical coastal assemblages.

This, to our knowledge, is the first empirical analysis showing a positive, exponential association between diversity and a key service (fisheries production) in a tropical marine ecosystem. The implications of these results are profound because they highlight that functional diversity affects seafood provisioning, and in turn, fishing depletes functional diversity. Thus, maintaining seafood production requires reducing the impacts of fishing on whole assemblages. Here we focused on a single service, but other functions and services, such as nutrient cycling, maintenance of reef structures protecting the coast (through net carbonate accretion), sediment production, and resilience to climatic impacts (e.g., through grazing and removal of algal competitors of corals) all depend on multiple species (Harborne et al., 2006) and might be negatively impacted by the loss of functional diversity. Exploring the

**Table 2**

Relationships between measures of species (species richness, S) and functional diversity (No. of trophic groups, NT, size groups, NS, habitat use groups, NH, pairwise combinations of these traits, NTS and NTH, and combinations of all traits, F), total fish biomass (B), and estimated fisheries catch (C) across the sites surveyed throughout the Bahamas (Fig. 2). $N = 199$ sites in all cases except for catch ($N = 66$ sites). Relationships are significant at $\alpha = 0.05$ in all cases.

| Response variable | Explanatory variable | Relationship | $R^2$ | Best-fit |
|---|---|---|---|---|
| No. trophic groups (NT) | Species richness (S) | NT = 1.9 Ln(S) + 1.1 | 0.88 | Saturating |
| No. size groups (NS) | Species richness (S) | NS = 0.7 Ln(S) + 1.6 | 0.78 | Saturating |
| No. habitat use groups (NH) | Species richness (S) | NH = 0.6 Ln(S) + 1.1 | 0.55 | Saturating |
| No. trophic by size groups (NTS) | Species richness (S) | NTS = 0.3 S + 3.1 | 0.87 | Linear |
| No. trophic by habitat groups (NTH) | Species richness (S) | NTH = 0.3 S + 2.2 | 0.89 | Linear |
| Functional Richness (F) | Species richness (S) | NF = 0.3 S + 2.6 | 0.90 | Linear |
| Total biomass (B) | Species richness (S) | $B = 787.5e^{0.07\ S}$ | 0.46 | Exponential |
| Total biomass (B) | Functional richness (F) | $B = 246.8e^{0.25\ F}$ | 0.48 | Exponential |
| Estimated catch (C) | Species richness (S) | $C = 2310.2e^{0.09\ S}$ | 0.12 | Exponential |
| Estimated catch (C) | Functional richness (F) | $C = 105.9e^{0.41\ F}$ | 0.19 | Exponential |

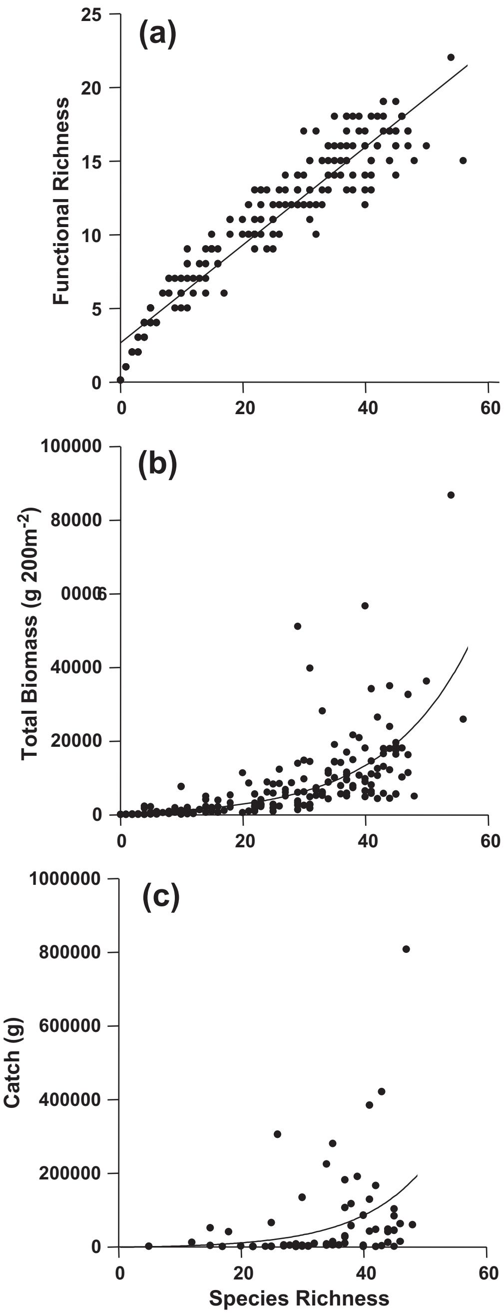

**Fig. 4.** Relationships of functional richness (a), total fish biomass (b), and estimated fisheries catch (c) with species richness. Functional richness was based on combination of three traits: diet, maximum body size, and habitat use and mobility (33 groups in total). $N = 199$ sites in all cases except for catch estimates ($N = 66$ sites). Best-fitting relationships are linear for functional richness (a), and exponential for fish biomass (b) and estimated catch (c) (Table 2).

relationships among diversity, functions, and services in coral reefs therefore remains an important priority.

Previous studies in this and other systems have shown that fishing reduces species diversity (Worm et al., 2006; Harborne et al., 2008b; Lester et al., 2009). Our comparison between reefs protected within a large no-take marine reserve and adjacent fished reefs shows that fishing also significantly reduces functional diversity and redundancy, including the removal of entire functional groups. Fishing depletes species below detectable levels disproportionately more often within a subset of functional groups (mid-water piscivores, omnivores, and invertebrate feeders, demersal piscivores, pelagic and sedentary planktivores, and large roving browsers), thereby decreasing functional redundancy within these groups. Thus, fishing preferentially decreases predator and planktivore diversity, and may remove whole functional groups such as large roving browsers of macroalgae. The effects of such removals have been shown to be ecologically important for a subset of functional groups (predators, Stallings, 2008; herbivores, Mumby et al., 2007; corallivores, Bellwood et al., 2003) and ecological processes (algal grazing, bioerosion, and coral recruitment; references above). In particular, the effects of grazing have been studied extensively in coral reefs (Mumby et al., 2006, 2007; Burkepile and Hay, 2008; Korzen et al., 2011). However, a more comprehensive understanding of the ecological roles played by species within multiple functional groups is needed in order to make predictions about how their decline may affect dynamics of coral reef ecosystems. In particular, the lower piscivore diversity we documented in fished reefs may have important consequences for these assemblages through the removal of predator control of populations and communities (Mumby et al., 2006a). In addition, planktivores play an important ecological role by trophically linking coral reef and open-water communities (Hobson, 1991), and decline in their diversity may affect this function.

Unsurprisingly, the level of functional redundancy and the resulting shape of the relationship between species and functional diversity depend on the classification scheme used (Micheli and Halpern, 2005; Halpern and Floeter, 2008). However, high levels of functional redundancy within groups and saturating relationships were found only when species were assigned to the broadest (single) categories, such as trophic groups or habitat use categories. In contrast, empirical evidence shows high variation in effects within trophic guilds (e.g., Burkepile and Hay, 2008). Here we find that adding even just one trait to further subdivide these broad categories always results in linear relationships between species and functional diversity without saturation, even at the highest levels of species richness in our system. Although it is reasonable to expect that an asymptote would eventually be reached, a plateau was never reached within our observed diversity range. This result indicates that species additions result in the addition of new functional roles throughout the species diversity gradient in our study region, supporting the conclusion of low functional redundancy in these and other marine assemblages (e.g., Micheli and Halpern, 2005).

Total biomass and fisheries catches are exponentially related to measures of diversity; we would therefore expect to observe the greatest loss of function or service provision when species are lost from the most diverse systems. The positive exponential relationship of fish biomass and estimated fisheries catches with diversity suggests that even small declines in biodiversity may result in large reductions in secondary production and seafood provision in Caribbean fish assemblages. In general, small decreases in species diversity might lead to loss of ecosystem function and services in these and other highly diverse marine ecosystems.

The positive exponential relationship of biomass and catch with diversity is likely partly related to the selective removal of large-bodied species by fisheries (Fig. 3b). Depletion of large consumers from human impact has been documented in coral reef systems worldwide (Gell and Roberts 2003; Bellwood et al., 2004; Pandolfi et al., 2005; Stevenson et al., 2007) and would result in rapid loss of biomass due to the disproportionate contribution of large individuals to total biomass. However, our results suggest that rapid declines in biomass and catch may also occur in high diversity systems under fishing pressure because multiple species are simultaneously depleted throughout the food web (Fig. 3d). Thus, low functional redundancy and widespread impacts of fishing across functional groups may be an important additional mechanism underlying rapid loss of function and services in high diversity coral reef ecosystems.

Overall, these results indicate that conserving and re-building species and functional diversity and functional redundancy is important for maintaining the functions and services provided by coral reef seascapes in the Bahamas and other regions. This study provides additional evidence that marine reserves are an effective means of achieving multi-species protection and restoring function (Gell and Roberts, 2003; Micheli et al., 2004; Russ et al., 2004; Lester et al., 2009). In particular, protection in the ECLSP has resulted in greater abundances of large parrotfishes, with corresponding increased grazing rates, reduced macroalgal cover, and increased coral recovery (Mumby and Harborne, 2010), increased species richness (Harborne et al., 2008b), and increased functional diversity and redundancy (this study). These results demonstrate that implementation of management approaches such as marine protected areas that simultaneously target multiple species and functional groups, and the inclusion of ecosystem-level indicators, such as diversity measures, as performance metrics for fisheries management (Sainsbury and Sumaila, 2003; Link, 2005) are particularly important in coral reef ecosystems.

Experimental manipulations are unfeasible when dealing with large spatial scales (across seascapes) and hundreds of species, but the descriptive and comparative analytic approach used herein also has limitations. First, correlations between measures of functions or services and diversity do not imply causal relationships but instead could be due to other processes simultaneously influencing these variables. Second, we did not measure ecosystem function and services directly, but instead used proxies (i.e., total fish biomass and estimated fisheries catch). Additional future work directly quantifying ecosystem function and services will be critical for understanding the role of diversity in maintaining the suite of ecosystem functions and services provided by coral reefs and other marine ecosystems (e.g. Moberg and Folke, 1999; Harborne et al., 2006; 2008a; McClanahan, 2007; McClanahan et al., 2008).

## 5. Conclusions

Our analyses provide evidence of limited functional redundancy and a positive exponential relationship between diversity and measures of ecosystem function and services of fish assemblages across Caribbean coral reef seascapes. These results contribute to the ongoing debate on the relationship between diversity and function in marine ecosystems (Cardinale et al., 2006; Worm et al., 2006; Danovaro et al., 2008; Mora et al., 2011; Reich et al., 2012). These findings highlight the high vulnerability of diversity, function, and ecosystem services to human impacts, and the need to conserve whole species assemblages, in addition to focal taxa of known ecological and economic importance, through ecosystem-based management approaches.

## Acknowledgements

This work was supported by grants from the National Science Foundation's Biocomplexity in the Environment Program (OCE-0119976); the National Oceanic and Atmospheric Administration's National Undersea Research Program, administered by the Caribbean Marine Research Center (CMRC-03-NRDH-01-04A, under awards NA06RU0228 and NA16RU1496); and the U.S. Environmental Protection Agency (R832223).

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.12.029.

## References

Bellwood, D.R., Hoey, A., Choat, J.H., 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol. Lett. 6, 281–285.

Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J., Hoey, A.S., 2006. Functional versatility supports coral reef biodiversity. Proc. Roy. Soc. B 273, 101–107.

Bohlke, J.E., Chaplin, C.C.G., 1993. Fishes of the Bahamas and Adjacent Tropical Waters. University of Texas Press, Austin.

Broad, K., Sanchirico, J.N., 2008. Local perspectives on marine reserve creation in the Bahamas. Ocean Coast. Manag. 51, 763–771.

Burkepile, D.E., Hay, M.E., 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci. USA 105, 16201–16206.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., et al., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.

Claro, R.K., Lyndeman, C., Parenti, L.R., 2001. Ecology of Marine Fishes of Cuba. Smithsonian Institution Press, Washington, DC, London.

Danovaro, R., Gambi, C., dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., 2008. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr. Biol. 18, 1–8.

De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. In: Proceedings of the National Academy of Science USA, October 1, 2012, published online before print. DOI: http://dx.doi.org/10.1073/pnas.1208909109.

Froese, R., Pauly, D., 2003. FishBase. <http://www.fishbase.org> (Last accessed 22.11.11).

Gardner, T.A., Cote', I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region wide declines in Caribbean corals. Science 301, 958–960.

Gell, F.R., Roberts, C.M., 2003. The Fishery Effects of Marine Reserves and Fishery Closures. WWF-US, Washington, DC.

Green, L.E., Alevizon, W.S., 1989. Comparative accuracies of visual assessment methods for coral reef fishes. Bull. Mar. Sci. 44, 899–912.

Guillemot, N., Kulbicki, M., Chabanet, P., Vigliola, L., 2011. Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. PLoS ONE 6 (10), e26735. http://dx.doi.org/10.1371/journal.pone.0026735.

Halpern, B.S., Floeter, S.R., 2008. Functional diversity responses to changing species richness in reef fish communities. Mar. Ecol. Prog. Ser. 364, 147–156.

Halpern, B.S., Waldbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Harborne, A.R., Mumby, P.J., Micheli, F., Perry, C.T., Dahlgren, C.P., Holmes, K.E., et al., 2006. The functional value of Caribbean reef habitats to ecosystem processes. Adv. Mar. Biol. 50, 57–189.

Harborne, A.R., Mumby, P.J., Kappel, C.V., Dahlgren, C.P., Micheli, F., Holmes, K.E., et al., 2008a. Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. Ecol. Appl. 18, 1689–1701.

Harborne, A.R., Mumby, P.J., Kappel, C.V., Dahlgren, C.P., Micheli, F., Holmes, K.E., et al., 2008b. Reserve effects and natural variation in coral reef communities. J. Appl. Ecol. 45, 1010–1018.

Hobson, E.S., 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press Limited, London, pp. 69–95.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., et al., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Korzen, L., Israel, A., Abelson, A., 2011. Grazing effects of fish versus sea urchins on turf algae and coral recruits: possible implications for coral reef resilience and restoration. J. Mar. Biol. 2011, 960207. http://dx.doi.org/10.1155/2011/960207.

Lester, S.E., Halpern, B.S., Grorud-Covert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., et al., 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser. 384, 33–46.

Link, J.S., 2005. Translating ecosystem indicators into decision criteria. ICES J. Mar. Sci. 62, 569–576.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., et al., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

Madin, E.M.P., Madin, J.S., Booth, D.J., 2011. Landscape of fear visible from space. Sci. Reports 1, 14. http://dx.doi.org/10.1038/srep00014.

McClanahan, T.R., 2007. Achieving sustainability in East African coral reefs. J. Mar. Sci. Environ. C5, 1–4.

McClanahan, T.R., Hicks, C.C., Darling, E.S., 2008. Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecol. Appl. 18, 1516–1529.

Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. Ecol. Appl. 14, 1709–1723.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8, 391–400.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Current State and Trends. Island Press, Washington, DC.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233.

Mora, C., Aburto-Oropeza, O., Ayala Bocos, A., Ayotte, P.M., Banks, S., Bauman, A.G., et al., 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biol. 9 (4), e1000606. http://dx.doi.org/10.1371/journal.pbio.1000606.

Mouillot, D., Culioli, J.M., Pelletier, D., Tomasini, J.A., 2008. Do we protect biological originality in protected areas? a new index and an application to the Bonifacio Strait Natural Reserve. Biol. Conserv. 141, 1569–1580.

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., et al., 2006a. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311, 98–101.

Mumby, P.J., Hedley, J.D., Zychaluk, K., Harborne, A.R., Blackwell, P.G., 2006b. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. Ecol. Model. 196 (1–2), 131–148.

Mumby, P.J., Harborne, A.R., Williams, J., Kappel, C.V., Brumbaugh, D.R., Micheli, F., et al., 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proc. Natl. Acad. Sci. USA 104, 8362–8367.

Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., et al., 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conserv. Biol. 22, 941–951.

Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS ONE 5 (1), e8657. http://dx.doi.org/10.1371/journal.pone.0008657.

Naeem, S., 1998. Species redundancy and ecosystem reliability. Conserv. Biol. 12, 39–45.

Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzmán, H.M., Hughes, T.P., et al., 2005. Are US coral reefs on the slippery slope to slime? Science 307, 1725–1726.

Petchey, O.L., Hector, A., Gaston, K.J., 2004. How do different measures of functional diversity perform? Ecology 85, 847–857.

Raffaelli, D., 2007. Food webs, body size and the curse of the Latin binomial. In: Rooney, N., McCann, K.S., Noakes, D.L.G. (Eds.), From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems. Springer, Dordrecht, pp. 53–64.

Randall, J.E., 1967. Food habits of reef fishes of the West Indies, in: Studies in Tropical Oceanography No. 5. University of Miami Institute of Marine Science, Miami Beach, pp. 665–847.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336, 589–592.

Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. Trends Ecol. Evol. 27, 404–413.

Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. Ecol. Appl. 14, 597–606.

Sainsbury, K., Sumaila, U.R., 2003. Incorporating ecosystem objectives into management of sustainable marine fisheries, including 'best practice' reference points and use of marine protected areas. In: Sinclair, M., Valdimarson, G. (Eds.), Responsible Fisheries in the Marine Ecosystem. CAB International, UK, pp. 343–361.

Stachowicz, J.J., Bruno, J.F., Duffy, J.E., 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annu. Rev. Ecol. Syst. 38, 739–766.

Stallings, C.D., 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes. Ecology 89, 2090–2095.

Stevens, R.D., Cox, S.B., Strauss, R.E., Willing, M.R., 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. Ecol. Lett. 6, 1099–1108.

Stevenson, C., Katz, L.S., Micheli, F., Block, B., Heiman, K.W., Perle, C., et al., 2007. High apex predator biomass on remote Pacific islands. Coral Reefs 26, 47–51.

Villeger, S., Ramos Miranda, J., Flores Hernandez, D., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20, 1512–1522.

Walker, B., 1992. Biological diversity and ecological redundancy. Conserv. Biol. 6, 18–23.

Willems, E.P., Hill, R.A., 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology 90, 546–555.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., et al., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.