

# Reserve effects and natural variation in coral reef communities

Alastair R. Harborne<sup>1\*</sup>, Peter J. Mumby<sup>1</sup>, Carrie V. Kappel<sup>2,3</sup>, Craig P. Dahlgren<sup>4</sup>, Fiorenza Micheli<sup>3</sup>, Katherine E. Holmes<sup>5</sup>, James N. Sanchirico<sup>6</sup>, Kenneth Broad<sup>7</sup>, Ian A. Elliott<sup>1</sup> and Daniel R. Brumbaugh<sup>5</sup>

<sup>1</sup>Marine Spatial Ecology Laboratory, School of Biosciences, Hatherly Laboratory, University of Exeter, Prince of Wales Road, Exeter, EX4 4PS, UK; <sup>2</sup>National Center for Ecological Analysis and Synthesis, University of California–Santa Barbara, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA; <sup>3</sup>Hopkins Marine Station, Stanford University, Oceanview Boulevard, Pacific Grove, CA 93950-3094, USA; <sup>4</sup>Perry Institute for Marine Science, 100 N. US Highway 1, Suite 202, Jupiter, FL 33477-5112, USA; <sup>5</sup>Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA; <sup>6</sup>Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, 2140 Wickson Hall, Davis, CA 95616, USA; and <sup>7</sup>Rosenstiel School of Marine and Atmospheric Science, Division of Marine Affairs and Policy, 4600 Rickenbacker, Causeway, Miami, FL 33149, USA

## Summary

1. No-take reserves are a common tool for fisheries management and biodiversity conservation in marine ecosystems. Despite much discussion of their benefits, data documenting many reserve effects are surprisingly scarce. Several studies have also been criticized for a lack of rigour so that changes within reserves cannot be separated from underlying natural variation and attributed unequivocally to protection.

2. We sampled both benthic (video quadrats) and associated fish communities (underwater visual censuses) in a well-enforced reserve in The Bahamas. Sampling was explicitly stratified by habitat ('*Montastraea* reef' and 'gorgonian plain'). To distinguish reserve effects from natural variation, we compared changes inside and outside the reserve with those seen at equivalent spatial scales in other reef systems in the Bahamian archipelago that lack reserves. Reserve-level differences in benthic or fish communities not documented in other reef systems are categorized as 'robust' effects.

3. Robust reserve effects were limited to *Montastraea* reefs. The reserve supported an average of  $\approx 15\%$  more fish species per site compared to outside the reserve. This pattern was particularly driven by more large-bodied grouper, damselfish, and butterflyfish species inside the reserve. Increases in fish biomass and differences in community structure inside the reserve were limited to large-bodied groupers. Increased grazing pressure by parrotfishes in the reserve has lowered macroalgal cover, and caused previously undocumented changes in benthic community structure compared to sites outside the reserve.

4. Some reserve-level differences in fish communities were categorized as 'misleading' because equivalent differences were seen in other reef systems, and are likely to be caused by natural intra-habitat variation. Separation of robust and misleading results was only possible because of archipelago-scale sampling.

5. *Synthesis and applications.* The Bahamas represents a relatively lightly fished system within the Caribbean. However, cessation of fishing has still increased the mean number of species, the abundance of the most highly prized fishes and, through trophic cascades, altered benthic community structure. In certain habitats, reserves are clearly important for conserving fisheries and biodiversity. However, reserve effects must be explicitly separated from confounding variables to ensure conservation benefits are accurately identified and reported, and not oversold to managers and local stakeholders.

**Key-words:** Exuma Cays Land and Sea Park, intra-habitat variation, marine reserves, reef-fish communities, sampling design, trophic cascades, The Bahamas

\*Correspondence author. E-mail: a.r.harborne@ex.ac.uk

## Introduction

Protected areas are a key conservation tool in a range of ecosystems, including marine environments where they are primarily used to conserve biodiversity and manage fisheries (e.g. Sale *et al.* 2005). In particular, no-take marine reserves are established with the aim of conserving fish diversity, facilitating recovery of depleted stocks, and causing spillover of individuals and larvae to fished areas (e.g. Lubchenco *et al.* 2003). The increasing number of marine reserves has facilitated numerous empirical studies and subsequent meta-analyses and reviews documenting the changes to fish communities, such as increases in abundance, biomass, size, and diversity, following the cessation of fishing (e.g. Côté, Mosqueira & Reynolds 2001; Halpern 2003; Micheli *et al.* 2004). Consequently, reserves are widely advocated to reverse trends of declining coral reef health where a range of factors, including over-exploitation of grazing fishes, has caused significant declines in coral cover and increases in macroalgal abundance (Gardner *et al.* 2003).

Despite an apparent wealth of data, evidence for some of the expected effects of marine reserves is still equivocal, and limited by a lack of definitive experiments at appropriate spatio-temporal scales (Russ 2002). Studies clearly demonstrating reserve effects should not be confounded by factors such as insufficient spatial or temporal replication or an absence of suitable control sites outside reserves (Willis *et al.* 2003). For example, 'habitat effects' (habitat differences inside and outside reserves) clearly need to be separated from 'reserve effects' (García-Charton & Pérez-Ruzafa 1999; Halpern 2003). In the absence of a 'BACI' (Before/After, Control/Impact) sampling design (Underwood 1994), even within relatively well-replicated studies, it is difficult to separate reserve effects from natural variability associated with intra-habitat abiotic and biotic gradients, but this should be an important consideration during sampling design (Fraschetti *et al.* 2002). Finally, studies addressing the effects of reserves should be limited to locations where protection has been effectively enforced for several years.

In this study, we compared fish and benthic communities inside and outside a Caribbean coral reef reserve (Exuma Cays Land and Sea Park [ECLSP], The Bahamas), stratified by habitat type, with data collected at equivalent spatial scales on reefs without reserves throughout the Bahamian archipelago. The latter data provide insights into the natural spatial variability of community structure where data before reserve establishment are not available, which is the case here and in many marine reserve studies (an 'ACI' sampling design). If differences observed between reefs inside and outside the reserve are not evident elsewhere, we can conclude that such variation can be attributed to reserve establishment. In the present study, fish data were collected to examine any direct effects of cessation of fishing, and also indirect effects caused by predator-prey relationships (Micheli *et al.* 2004). We used benthic community data to examine the effects of any trophic cascades caused by alterations in fish communities. For example, the reduction in fishing pressure has led to a net increase in

grazing by parrotfishes, and a reduction in macroalgal cover inside the ECLSP (Mumby *et al.* 2006). However, Mumby *et al.* (2006) did not analyse benthic community structure inside and outside the reserve. Documenting changes in benthic community structure is important because of, for example, species-specific differences in the abilities of algae to compete with corals for space (McCook, Jompa & Diaz-Pulido 2001).

Effects of the reserve on fish and benthic communities were documented in two hard-bottom habitat types: 'Montastraea reef' (coral-rich areas visually dominated by *Montastraea* spp.) and 'gorgonian plain' (low-relief areas visually dominated by fleshy brown algae and sparse gorgonians). We hypothesized that changes in fish communities would be more pronounced on *Montastraea* reefs because it is the favoured habitat of adults of many commercially important species (e.g. the large-bodied grouper *Mycteroperca bonaci*, *M. tigris*, *M. venenosa*, *M. interstitialis*, and *Epinephelus striatus*; Sluka *et al.* 1998) and, when fishing pressure is low, the higher topographical complexity of this habitat will support a greater biomass and number of species of fishes (Gratwicke & Speight 2005). Furthermore, because of higher densities of parrotfishes on *Montastraea* reefs (Harborne *et al.* 2006), we expected grazing-mediated changes in benthic communities to be clearer in this habitat type.

## Materials and methods

### STUDY SITES AND SAMPLING DESIGN

Surveys in and around the ECLSP were conducted in October 2004. The ECLSP lies near the centre of the Bahamian archipelago (see Supplementary material Appendix S1), is large (442 km<sup>2</sup>) and was established in 1958 (Chiappone & Sullivan Sealey 2000). There is no evidence of the reserve containing especially healthy or diverse reefs before its establishment (Ray 1958). A ban on fishing has been enforced by warden patrols since 1986. Poaching inside the ECLSP has been assessed as low (supporting material associated with Mora *et al.* 2006).

*Montastraea* forereef was sampled at three sites ( $\approx 150 \times \approx 150$  m) near the centre of the ECLSP, three sites between 5.8 km and 18.1 km north of the Park and three sites around Lee Stocking Island (LSI)  $\approx 70$  km south of the Park (see Supplementary material Appendix S1). Gorgonian plain (the predominant forereef habitat in the area) in the ECLSP was sampled at nine sites centred on the middle of the reserve. Gorgonian plain was also sampled at six sites between 1 km and 10 km both south and north of the reserve ( $9 + 6 + 6 = 21$  sites in total). Data from these sites were used for comparisons of communities inside and outside the ECLSP, stratified by habitat type.

To assess natural variation, we sampled five additional island systems (July 2002–November 2003). These additional data facilitated intra-island comparisons at the same spatial scale (tens of kilometres) as in the Exumas, but on reefs without reserves. The additional island systems were Andros, San Salvador, and South Caicos (Turks and Caicos Islands) (*Montastraea* reef and gorgonian plain) and Bimini and Abaco (gorgonian plain only; see Supplementary material Appendix S1). In each island system, we sampled three groups of sites 5–10 km apart, equivalent to the group of sites inside, and the two groups of sites outside, the ECLSP. Each group of sites consisted of three (two on three occasions) replicate *Montastraea* reefs and/or a minimum of two gorgonian plain sites.

Fishing effort at each site was estimated, and varied among islands (see Supplementary material Appendix S2). Critically, because of the presence of the ECLSP, the Exumas appeared to be the only reef system where fishing pressure varies at the scale of tens of kilometres. Any significant results within any of the other reef systems can, therefore, be attributed to natural variation rather than variable fishing pressure.

#### COMMUNITY CHARACTERIZATION

At each site, 30–40 randomly placed 1 m<sup>2</sup> quadrats were used to quantify the species composition of the benthic community. Content of quadrats was filmed in 20-cm swathes, using a high-resolution digital video camera. Following completion of all the swathes within a given quadrat, cryptic organisms and areas of high relief (e.g. under ledges) were filmed in more detail. Depth and rugosity (maximum vertical relief inside quadrat assigned to one category from 0–10 cm, 10–50 cm, 50–100 cm, 100–200 cm, and > 200 cm) were also measured for each quadrat *in situ*. This measure of rugosity was found to correlate well to more labour-intensive chain-transect methods ( $r = 0.67$ ,  $P < 0.001$ ). The digital video of each quadrat was projected onto a large monitor for identification (presence/absence) of species of scleractinian corals (minimum diameter, 1 cm), and macroalgae, macroscopic mobile invertebrates, sponges, and gorgonians to the highest taxonomic resolution possible. Data were then converted to frequency of occurrences (number of times present divided by number of quadrats) for each taxon at each site. Coral and macroalgal cover were assessed from a mean of 14.1 (*Montastraea* reef) or 9.4 (gorgonian plain) of the 1 m<sup>2</sup> quadrats used for characterization of benthic communities. Coral and macroalgal cover in each 1 m<sup>2</sup> quadrat was recorded as the mean of five randomly sub-sampled areas of 20 × 20 cm (0.04 m<sup>2</sup>). Note that we measured macroalgal cover rather than the cover of all parrotfish food items (macroalgae and large turfs) measured by Mumby *et al.* (2006). Presenting data on percentage cover of macroalgae (rather than macro and turf algae; cf. Mumby *et al.* 2006) is consistent with other patterns documented in this study.

All but nocturnal (e.g. Apogonidae) and highly cryptic (Clinidae and Gobiidae) fish species were surveyed using discrete group visual fish censuses (Green & Alevizon 1989) at the same time as the benthic sampling. Species were divided into three groups and their density and size (to the nearest centimetre) estimated along belt transects at each island system. Transect size and number were optimized using data from equivalent surveys within the Caribbean (Mumby *et al.* 2004). Four 30 × 2 m transects were surveyed for small demersal families such as Pomacentridae; ten 30 × 4 m transects were surveyed for mid-sized demersal families such as Scaridae, and five 50 × 4 m transects were used for large demersal and pelagic fish such as Serranidae. All subsequent fish analyses (undertaken at transect-level resolution, with the exception of tests on the entire community) consider biomass; fish lengths were converted to biomass using allometric relationships (Bohnsack & Harper 1988).

#### DATA ANALYSES

Percentage cover data were arcsine-transformed (Zar 1996), and other variables were square root, cube root or Box-Cox-transformed to ensure normality where possible. Differences in univariate parameters inside the ECLSP compared to sites to the north and south were tested using ANOVA (plus Tukey's HSD pairwise comparisons), Kruskal–Wallis or Mann–Whitney tests as appropriate.

Effects of the ECLSP on coral and algal cover were tested by ANCOVA with the percentage cover of sand as a covariate to control for any variation in hard substratum area among sites. Tests for significant variation in community structure (repeated for the entire benthic and fish communities and also individual fish families) were conducted using ANOSIM (Clarke 1993), with fish data square root transformed. The discriminating taxa were determined using Similarity Percentage (SIMPER) analysis (Clarke 1993) to examine significant ANOSIM results further. Parrotfishes in the *Montastraea* reef habitat are described in detail elsewhere (Mumby *et al.* 2006), and are not reanalysed here. Parrotfish grazing in the gorgonian plain habitat was calculated using the model described in Mumby *et al.* (2006).

Wherever significant reserve-level effects were detected, analogous tests were conducted on data from the other island systems to assess natural variation. Including tests involving the ECLSP, a total of 12 comparisons were possible for the *Montastraea* reef habitat (three groups of sites in four reef systems; Table 1), and 18 were possible for gorgonian plains (three groups of sites in six reef systems).

#### CATEGORIZATION OF RESULTS

Results for differences in fish and benthic communities inside the ECLSP were defined as 'robust', 'potential', 'misleading' or 'absent' (Table 1). Benthic community structure data had to be calculated for an entire site (frequency of occurrence data are the number of times a taxon was seen divided by total number of quadrats) while individual fish transects at a site were treated as replicates. This additional statistical power allowed pairwise comparisons for fish community structure between communities inside the ECLSP and sites to the north and sites to the south. In contrast, benthic communities inside the ECLSP were compared to all sites outside the Park combined, and then, two further comparisons were made between sites to the north vs. sites in the ECLSP and to the south combined, and between sites to the south vs. sites in the ECLSP and to the north combined. For this reason, fish results could be robust, potential, misleading or absent. Effects on benthic communities could only be robust, misleading or absent. Justification of these categories can be made using the probability theory (see Supplementary material Appendix S3).

#### Results

A total of 142 fish species and 218 benthic taxa were recorded at the *Montastraea* reef and gorgonian plain sites. Within the Exuma Cays, there were no differences in mean depth or vertical relief in either habitat inside compared to outside the reserve (ANOVA:  $P > 0.05$ ). *Montastraea* reefs were found at mean depths of ≈ 9–12 m with mean vertical relief of ≈ 65–72 cm. Gorgonian plains were found at mean depths of ≈ 7–10 m with mean vertical relief of ≈ 10–27 cm. Effects of the ECLSP on the biological communities are summarized (Table 2), described in the subsequent text, and documented in full in Supplementary material Appendix S4.

#### ROBUST PARK EFFECTS

*Montastraea* reef sites inside the ECLSP had significantly more fish species than those outside the Park (mean 48.67 vs. 42.33; one-tailed Mann–Whitney:  $P = 0.035$ ). None of the

**Table 1.** Definition and diagrammatic representation of terms used to categorize the effects of the Exuma Cays Land and Sea Park (ECLSP) on fish and benthic communities. Diagrammatic representation is for fish communities on *Montastraea* reefs. Solid circles represent replicate sites sampled. Solid arrows represent significant comparisons ( $P < 0.05$ ); dotted arrows represent non-significant comparisons

Reserve effect category	Definition	Diagrammatic representation
Robust	Within the Exuma Cays, only significant pairwise comparisons between the ECLSP and sites to <i>both</i> the north and south (fishes) <i>or</i> only a significant difference in the comparison between sites inside the ECLSP with those outside (benthos) <i>and</i> no differences at the same scale on reefs around any other island	
Potential*	Within the Exuma Cays, only a significant pairwise comparison between the ECLSP and sites to <i>either</i> the north <i>or</i> the south <i>and</i> no differences at the same scale on reefs around any other island	
Misleading	Within the Exuma Cays, only one or two significant pairwise comparisons between the ECLSP and sites to the north and south (fishes) <i>or</i> only a significant difference in the comparison between sites inside the ECLSP with those outside (benthos) <i>but</i> differences at the same scale on reefs around any other island	
Absent	Within the Exuma Cays, no significant pairwise comparisons between the ECLSP and sites to the north and south (fishes) <i>or</i> no significant difference in the comparison between sites inside the ECLSP with those outside (benthos)	

\*not possible for tests of benthic communities.

other 11 comparisons within the four reef systems showed a significantly higher number of species at the same spatial scale (one-tailed Mann–Whitney:  $P > 0.05$ ). To investigate whether species in particular fish families were driving the high number of species seen in the ECLSP, we conducted Monte Carlo simulations with the data set from all four reef systems (a conservative approach incorporating any large-scale variations in species richness). We calculated whether removing individual families reduced the difference between sites inside the ECLSP compared to those outside by a significantly ( $P < 0.05$ ) greater amount than removing an equal number of species at random (10 000 permutations). Significant results were obtained for: (i) large-bodied, commercially important serranids (*Mycteroperca bonaci*, *M. tigris*, *M. venenosa*, *M. interstitialis* and *E. striatus*;  $P = 0.008$ ); (ii) territorial pomacentrids (six *Stegastes* species and *Microspathodon chrysurus*;  $P = 0.042$ ); and (iii) chaetodontids (five species;  $P = 0.048$ ). Furthermore, the ECLSP has had a clear effect on mean large serranid biomass on *Montastraea* reefs (4750.96 g 200 m<sup>-2</sup>

inside vs. 472.47 and 1585.58 for north of the ECLSP and LSI respectively; ANOVA:  $F_{(2,33)} = 10.93$ ,  $P < 0.001$ ). Large serranid community structure was also significantly different inside the ECLSP (ANOSIM: Global  $R = 0.220$ ;  $P = 0.003$ ), primarily caused by the increased abundance of *E. striatus* and *Mycteroperca tigris* (Fig. 1).

Only macroalgal cover on *Montastraea* reefs was significantly different (lower) inside the ECLSP (2.8% inside vs. 15.32% and 17.98% to the north and south, respectively; ANCOVA:  $F_{(2,125)} = 58.05$ ,  $P < 0.001$ ). Analysis of benthic community structure on *Montastraea* reefs inside compared to those outside the Park showed significant differences (ANOSIM:  $R = 0.377$ ,  $P = 0.048$ ). The taxa driving such differences included a decrease in the frequency of occurrence of the brown macroalgae *Sargassum* spp. (not including *S. hystrix*) and *Dictyota*, and an increase in the abundance of *S. hystrix*, *Lobophora variegata*, and red coralline algae in the ECLSP (Table 3). Three species of corals (*Montastraea franksi*, *Agaricia agaricites*, and *Millepora alcicornis*) had higher frequency of occurrences within the ECLSP.

**Table 2.** Summary of the effects of the ECLSP on fish and benthic communities. Reserve effect categories defined in Table 1. Effects on fishes are presented first in each category. CS, community structure; BM, biomass

Habitat	Reserve effect			
	Robust	Potential	Misleading	None
Montastraea reef	<ul style="list-style-type: none"> <li>• Mean number of fish species</li> <li>• Number of large serranid*, territorial pomacentrid† and chaetodontid species</li> <li>• CS and BM of large serranids</li> <li>• CS of scarids, and grazing by scarids (Mumby <i>et al.</i> 2006)</li> <li>• Macroalgal percentage cover</li> <li>• Benthic CS</li> </ul>	<ul style="list-style-type: none"> <li>• CS of lutjanids</li> </ul>	<ul style="list-style-type: none"> <li>• CS of chaetodontids and territorial pomacentrids†</li> <li>• BM of haemulids</li> </ul>	<ul style="list-style-type: none"> <li>• Shannon diversity of the entire fish community</li> <li>• CS or BM of the entire fish community</li> <li>• CS or BM of acanthurids and small serranids‡</li> <li>• CS of haemulids</li> <li>• BM of chaetodontids, lutjanids, and territorial pomacentrids†</li> <li>• Number of benthic species or benthic Shannon diversity</li> <li>• Coral percentage cover</li> </ul>
Gorgonian plain	–	<ul style="list-style-type: none"> <li>• BM of large serranids* and lutjanids</li> </ul>	<ul style="list-style-type: none"> <li>• CS of chaetodontids</li> </ul>	<ul style="list-style-type: none"> <li>• Mean number of fish species and Shannon diversity of the entire fish community</li> <li>• CS or BM of the entire fish community</li> <li>• CS or BM of acanthurids, haemulids, territorial pomacentrids†, scarids, and small serranids‡</li> <li>• CS of lutjanids and large serranids*</li> <li>• BM of chaetodontids</li> <li>• Parrotfish grazing pressure</li> <li>• Number of benthic species or benthic Shannon diversity</li> <li>• Coral and algal percentage cover</li> <li>• Benthic CS</li> </ul>

\*large-bodied, commercially important only (*Mycteroperca bonaci*, *M. tigris*, *M. venosa*, *M. interstitialis* and *Epinephelus striatus*).

†*Stegastes* and *Microspathodon* only.

‡*Cephalopholis fulvus*, *C. cruentatus*, *Epinephelus guttatus*, *E. adscensionis*.

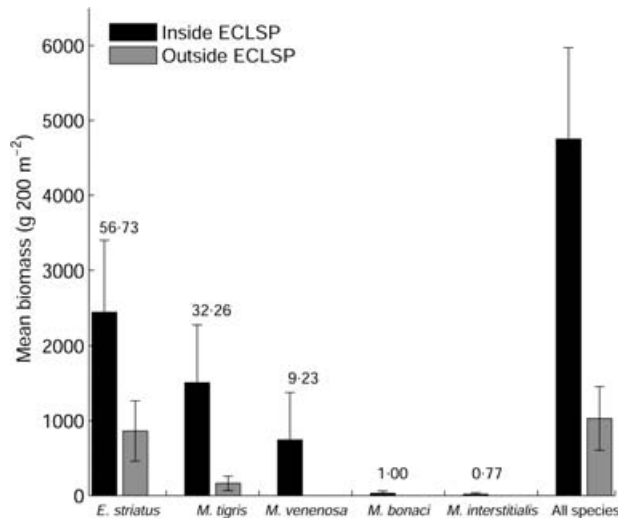
Taxon	Mean frequency of occurrence (%) (SE)		Percentage contribution
	Outside ECLSP	Inside ECLSP	
<i>Sargassum</i> spp.	72.97 (10.93)	12.80 (7.82)	4.14
<i>Sargassum hystrix</i>	36.97 (13.15)	91.60 (7.09)	3.83
<i>Pseudopterogorgia</i> spp.	41.24 (12.56)	69.06 (24.81)	2.96
<i>Dictyota</i> spp.	78.26 (12.08)	51.54 (14.04)	2.70
<i>Montastraea franksi</i>	13.02 (5.53)	49.37 (14.09)	2.65
<i>Ircinia felix/strobilina</i>	31.81 (9.93)	62.61 (13.41)	2.54
<i>Lobophora variegata</i>	33.14 (11.18)	48.50 (22.05)	2.41
<i>Agaricia agaricites</i>	39.51 (6.97)	74.23 (5.17)	2.39
Red coralline algae	43.52 (8.52)	75.23 (7.68)	2.17
<i>Millepora alcicornis</i>	38.29 (4.57)	46.69 (22.86)	2.09

**Table 3.** SIMPER analysis of the top 10 taxa characterising the dissimilarity between benthic communities inside and outside the Exuma Cays Land and Sea Park (ECLSP). Percentage contribution = average contribution/average dissimilarity between sites inside and outside the reserve (= 34.73%).  $n = 6$  outside ECLSP and 3 inside the reserve

#### POTENTIAL PARK EFFECTS

The community structure of lutjanids on *Montastraea* reefs varied between the ECLSP and LSI (ANOSIM:  $R = 0.173$ ,  $P = 0.021$ ), but not between the ECLSP and sites to the north of the Park. There was significant variation in the biomass of

large serranids and lutjanids on gorgonian plains between the ECLSP and sites to the north (Tukey's HSD:  $P < 0.05$ ; 88.38 g 200 m<sup>-2</sup> to the north vs. 1801.42 in the Park, and 00.00 g 200 m<sup>-2</sup> to the north vs. 2160.22 in the Park, respectively), but not between the Park and sites to the south (Tukey's HSD:  $P > 0.05$ ).



**Fig. 1.** Mean biomass of each large-bodied grouper species (*E.*, *Epinephelus*; *M.*, *Mycteroperca*) inside and outside the Exuma Cays Land and Sea Park (ECLSP). Values represent percentage contribution of each species to SIMPER analysis of the dissimilarity between inside and outside the ECLSP [percentage contribution = average contribution/average dissimilarity between sites inside and outside the reserve (= 75.39%)].  $n = 24$  outside ECLSP and 12 inside.

#### MISLEADING PARK EFFECTS

Territorial pomacentrid community structure on *Montastraea* reefs inside the ECLSP differed significantly from both locations outside the reserve, but six out of nine equivalent comparisons in other reef systems lacking reserves were also significant (ANOSIM:  $P < 0.05$ ). Also on *Montastraea* reefs, significant differences in community structure of chaetodontids were found between ECLSP and LSI sites (ANOSIM:  $R = 0.064$ ;  $P = 0.010$ ) and the biomass of haemulids between the ECLSP and north of the Park (Tukey's HSD:  $P < 0.05$ ), but equivalent differences were seen in other reef systems (one and four comparisons respectively). Chaetodontid community structure differed between the ECLSP and sites to the north of the Park on gorgonian plains (ANOSIM:  $R = 0.045$ ;  $P = 0.025$ ), but natural variation was also seen in one comparison in another reef system.

#### PARK EFFECTS ABSENT

The ECLSP did not have a significant effect on fish Shannon diversity in either habitat or number of species on gorgonian plains (one-tailed Mann–Whitney:  $P > 0.05$ ). Insignificant results for comparisons of the biomass and community structure of the entire fish community and individual fish families inside vs. outside the ECLSP are summarized in Table 2. In addition to the absence of community structure or biomass differences of parrotfishes on gorgonian plains, grazing intensity was not significantly higher inside compared to outside the Park (Kruskal–Wallis:  $P > 0.05$ ). The ECLSP did not have a significant effect on coral or algal cover on gorgonian plains or coral cover on *Montastraea* reefs. There

was no difference in the number of benthic species or Shannon diversity inside the Park compared to sites outside the Park in either habitat (one-tailed Mann–Whitney:  $P > 0.05$ ). No reserve-level differences were found in benthic community structure in gorgonian plain sites (ANOSIM:  $P > 0.05$ ).

## Discussion

### SPATIAL VS. TEMPORAL REPLICATION IN MARINE RESERVE STUDIES

There are few long-term data sets addressing ecological changes in marine reserves, and researchers typically have to use data from reserves established for different lengths of times to examine temporal recovery after cessation of fishing (e.g. Micheli *et al.* 2004; McClanahan *et al.* 2007). Such space-for-time substitutions are inferior to BACI experiments in an individual reserve, particularly for examining the mechanisms of changes, but do provide useful insights into rates of recovery in marine reserves that are generally consistent with long-term monitoring (Russ, Stockwell & Alcala 2005). Here we use an analogous approach by surveying multiple control sites to quantify natural variation at the scale of tens of kilometres. The controls are effectively a proxy of potential reef states, and hence natural variation, in the Exuma Cays over time in the absence of a reserve. While a BACI design would be preferable, this is clearly better than simply assuming that the reefs inside and outside the ECLSP would be indistinguishable if the Park had not been established. Ideally, our study would have also included multiple reserves, but there are few other comparable reserves in the archipelago. However, there is little reason to suggest that the effects of the ECLSP are any different from those that would occur in another well-enforced reserve of the same age in the region. The ECLSP is larger than most reserves in the Caribbean, but meta-analyses suggest that the difference in effects of large and small reserves may be limited (Halpern 2003). An exception may be changes in taxa, such as apex predators, that have large area requirements and are not adequately protected in small reserves (McClanahan *et al.* 2007).

### ROBUST RESERVE EFFECTS

As hypothesized, robust effects of the ECLSP were limited to the *Montastraea* reef habitat. Perhaps the most striking impact was the increased mean number of species per site in the Park. Meta-analyses have previously shown that reserves increase species richness by 11–23% (here 15%), either directly through reduction in fishing or indirectly through habitat improvement (Côté *et al.* 2001; Halpern 2003). Our simulations indicated that number of species particularly increased among large-bodied serranids, territorial pomacentrids, and chaetodontids. The direct effects of reduction in fishing appear the most likely cause of the increase in the number of serranid species. Pomacentrids and chaetodontids are not target fish species. Both families are prey for fishes such as serranids (Randall 1967), and some species may

benefit indirectly from reduced inter-specific competition caused by increased predation in the reserve (Robertson 1996). Both taxa are also intimately linked to the benthos through requirements for territories and food (e.g. Emery 1973), and may be affected by grazer-mediated changes in benthic community structure.

Reserve effects on fish biomass and community structure were limited to large serranids with a high fisheries value. This is consistent with meta-analyses that conclude that the greatest benefits of reserves are seen in the most exploited species (often large predators) and large-bodied species in general (Côté *et al.* 2001). Biomass of large serranids was nearly five times higher inside the ECLSP, and this ratio is in the middle of the range (0.91–7.6) reported by Russ (2002) in a review of studies of large predatory reef fishes inside reserves. The efficacy of the ECLSP for protecting grouper is also consistent with previous studies (Chiappone & Sullivan Sealey 2000). In contrast, non-target species are generally unaffected by the establishment of reserves (Micheli *et al.* 2004). Despite the increase in predator biomass, there appears limited potential for trophic cascades in the reef-fish communities because of strong omnivory and the patterns of food chain interactions (Bascompte, Melián & Sala 2005).

Grazing by parrotfishes on *Montastraea* reefs is twice as intense inside the ECLSP compared to sites outside the Park (Mumby *et al.* 2006), and this was reflected in significantly reduced macroalgal cover, which we attribute to the differences in parrotfish grazing (see also Mumby *et al.* 2006). Other grazing fishes (acanthurids and pomacentrids) did not have greater biomasses inside the Park, and the urchin *Diadema antillarum* is functionally extinct in the area. Furthermore, when all sites inside and outside the Park were resurveyed using identical methods in May 2007, macroalgal cover was still significantly lower inside the ECLSP compared to the sites outside the Park (A.R. Harborne and P.J. Mumby, unpublished data). This temporally consistent pattern is strong evidence that differential grazing pressure, rather than spatially variable disturbances such as hurricanes, is driving benthic community changes inside the ECLSP.

The trophic cascade driven by increased grazing pressure has also changed benthic community structure to an extent previously undocumented in a Caribbean marine reserve. *Sargassum polyceratum* (included within our *Sargassum* spp. taxon) and *Dictyota* species are both susceptible to parrotfish grazing (Lewis 1985, 1986). *Lobophora* was seen more frequently inside the Park, and is often the dominant brown algal species in highly grazed habitats (Arnold & Targett 2000). The palatability of *S. hystrix*, which was also seen more frequently in the ECLSP, is poorly understood but some evidence suggests the species is mildly toxic to herbivores (De Lara-Isassi, Álvarez-Hernandez & Collado-Vides 2000). *Lobophora* and *S. hystrix* may benefit from the reduced competition with other more palatable species as grazing increases. Increased abundance of red coralline algae is a well-established response to the reduction in macroalgae by grazing (Lewis 1986), and may be particularly important because of its role as a settlement substratum for coral larvae

(Morse *et al.* 1988). Additional studies are required to assess the effects of changing algal communities on coral population dynamics, and whether the increases in some coral species in the ECLSP can be attributed to the reserve. However, increased grazing and reduced macroalgal cover has increased the number of coral recruits in the Park (Mumby *et al.* 2007).

In contrast to *Montastraea* reefs, grazing pressure did not increase significantly on gorgonian plains inside the ECLSP, presumably because this habitat is less favoured by parrotfishes and more lightly fished. Consequently, benthic community structure did not vary in this habitat.

#### POTENTIAL RESERVE EFFECTS

There was some evidence that the ECLSP affected the community structure of lutjanids on *Montastraea* reefs, and the biomass of large-bodied serranids and lutjanids on gorgonian plains. Although the comparisons inside and outside the Park were equivocal, we believe that the reserve is likely to be driving the observed differences. It might be expected that the effects of the ECLSP would be weaker on habitats where fishes are naturally less abundant (gorgonian plains compared to *Montastraea* reefs) or for less valuable species (lutjanids have a lower market price compared to serranids). Furthermore, significant comparisons in only one direction (the Park vs. sites located to the north or south) may reflect asymmetric fishing effort, and potential effects would become robust for a reserve in an area where fishing pressure is more homogeneous. Fishing pressure may be greater to the north of the ECLSP than to the south because of large commercial boats travelling from the highly populous New Providence Island (particularly Nassau; see Supplementary material Appendix S2). It is possible that there were fewer grouper and snapper on gorgonian plains to the north of the ECLSP than the south because fisherfolk from Nassau are unwilling to travel around the Park to fish. Such de facto reserve extensions could be a significant additional conservation benefit when no-take areas are located in areas of heterogeneous fishing pressure.

#### MISLEADING RESERVE EFFECTS

Viewed without data on natural variation, some fish families in both habitats appeared to exhibit reserve-level effects, but natural variability at this spatial scale appeared a more parsimonious explanation. Results for territorial pomacentrid community structure on *Montastraea* reefs are a good example: within the Exuma Cays, only comparisons involving the Park were significant, but equivalent differences were seen several times in reef systems on islands lacking reserves. The number of potentially misleading reserve effects emphasizes the importance of adequate control sites, the lack of which has been a major criticism of marine reserve studies (Russ 2002; Willis *et al.* 2003). However, we recognize that it is possible that factors causing natural variation in the other reef systems are not present in the Exumas, and we are incorrectly labelling actual reserve effects as misleading results. Our

results, therefore, should be considered conservative, but there is no reason to believe that reefs in the Exuma Cays are more homogenous than elsewhere in The Bahamas. Natural variation seen in reef fish communities can be attributed to a range of factors. For example, mangroves locally enrich the biomass of haemulids (Mumby *et al.* 2004), and may explain some of the variation seen in this family in reef systems around multiple islands. Consideration of such potentially confounding factors is important when designing marine reserve studies.

#### THE ROLE OF MARINE RESERVES ON CARIBBEAN REEFS

This study supports the prediction that Caribbean reserves increase the biomass of highly valued fish species and the mean number of fish species, but only in specific habitats such as *Montastraea* reefs. Changes in parrotfish grazing pressure in those habitats can also significantly change benthic community structure, suggesting that reserves may have far-reaching consequences on the functioning of the ecosystem. There are also likely to be further benefits of the reserve that are not quantified here, such as the net export of adult and larval fishes to surrounding reefs (reviewed by Chiappone & Sullivan Sealey 2000). Furthermore, The Bahamas represents a lightly fished Caribbean reef system (Kramer 2003), and the impacts of marine reserves on fishes are likely to be more dramatic in more heavily fished systems (as demonstrated in studies such as Polunin & Roberts 1993). However, despite the urgent need to conserve reefs, our findings demonstrate that research on the effects of reserves needs to ensure the effects are separated from natural inter- and intra-habitat variability. Only rigorous studies can accurately predict changes expected in reserves, and avoid the benefits of this important management tool being oversold to local stakeholders.

#### Acknowledgements

This work was supported by grants from NSF, NURP, the US EPA, NERC, and the NFWF. LandScan data were courtesy of ORNL LandScan 2005/UT-Battelle, LLC. We thank the Bahamas Department of Marine Resources. Kevin Buch, Philip Kramer, Sandy Voegeli, Erin Rechisky, Ole Shelton, Kimberly Heiman, Liz Hemond, Steven Phillips, Everton Joseph, Linda Hammerton, and Jacqueline Chisolm helped with data collection. The comments of three referees significantly improved the manuscript.

#### References

- Arnold, T.M. & Targett, N.M. (2000) Evidence for metabolic turnover of polyphenolics in tropical brown algae. *Journal of Chemical Ecology*, **26**, 1393–1410.
- Bascompte, J., Melián, C.J. & Sala, E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 5443–5447.
- Bohnsack, J.A. & Harper, D.E. (1988) *Length–Weight Relationships of Selected Marine Reef Fishes from the Southeastern United States and the Caribbean*. NOAA Technical Memorandum NMFS-SEFC-215, National Oceanographic and Atmospheric Administration, Miami, FL.
- Chiappone, M. & Sullivan Sealey, K.M. (2000) Marine reserve design criteria and measures of success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. *Bulletin of Marine Science*, **66**, 691–705.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Côté, I.M., Mosqueira, I. & Reynolds, J.D. (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, **59**, 178–189.
- De Lara-Isassi, G., Álvarez-Hernandez, S. & Collado-Vides, L. (2000) Ichthyotoxic activity of extracts from Mexican marine macroalgae. *Journal of Applied Phycology*, **12**, 45–52.
- Emery, A.R. (1973) Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bulletin of Marine Science*, **23**, 649–770.
- Fraschetti, S., Terlizzi, A., Micheli, F., Benedetti-Cecchi, L. & Boero, F. (2002) Marine protected areas in the Mediterranean Sea: objectives, effectiveness and monitoring. *Marine Ecology*, **23**, 190–200.
- García-Charton, J.A. & Pérez-Ruzafa, A. (1999) Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fisheries Research*, **42**, 1–20.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.
- Gratwicke, B. & Speight, M.R. (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, **66**, 650–667.
- Green, L.E. & Alevizon, W.S. (1989) Comparative accuracies of visual assessment methods for coral reef fishes. *Bulletin of Marine Science*, **44**, 899–912.
- Halpern, B.S. (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications*, **13**, S117–S137.
- Harborne, A.R., Mumby, P.J., Micheli, F., Perry, C.T., Dahlgren, C.P., Holmes, K.E. & Brumbaugh, D.R. (2006) The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in Marine Biology*, **50**, 57–189.
- Kramer, P.A. (2003) Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997–2000). *Atoll Research Bulletin*, **496**, 1–57.
- Lewis, S.M. (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia*, **65**, 370–375.
- Lewis, S.M. (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs*, **56**, 183–200.
- Lubchenco, J., Palumbi, S.R., Gaines, S.D. & Andelman, S. (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications*, **13**, S3–S7.
- McClanahan, T.R., Graham, N.A.J., Calnan, J.M. & MacNeil, M.A. (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications*, **17**, 1055–1067.
- McCook, L.J., Jompa, J. & Diaz-Pulido, G. (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, **19**, 400–417.
- Micheli, F., Halpern, B.S., Botsford, L.W. & Warner, R.R. (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*, **14**, 1709–1723.
- Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K.J. & Myers, R.A. (2006) Coral reefs and the global network of marine protected areas. *Science*, **312**, 1750–1751.
- Morse, D.E., Hooker, N., Morse, A.N.C. & Jensen, R.A. (1988) Control of larval metamorphosis and recruitment in sympatric agaricid corals. *Journal of Experimental Marine Biology and Ecology*, **116**, 193–217.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W. & Gill, A.B. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, **311**, 98–101.
- Mumby, P.J., Edwards, A.J., Arias-González, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczyńska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C. & Llewellyn, G. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533–536.
- Mumby, P.J., Harborne, A.R., Williams, J., Kappel, C.V., Brumbaugh, D.R., Micheli, F., Holmes, K.E., Dahlgren, C.P., Paris, C.B. & Blackwell, P.G. (2007) Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 8362–8367.
- Polunin, N.V.C. & Roberts, C.M. (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series*, **100**, 167–176.
- Randall, J.E. (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, **5**, 665–847.



- Ray, C., ed. (1958) *Report of the Exuma Cays Park Project* (revised edition of 1961). Submitted to the Government of The Bahamas, Nassau, The Bahamas.
- Robertson, D.R. (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology*, **77**, 885–899.
- Russ, G.R. (2002) Yet another review of marine reserves as reef fishery management tools. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. P.F. Sale), pp. 421–443. Academic Press, San Diego, CA.
- Russ, G.R., Stockwell, B. & Alcala, A.C. (2005) Inferring versus measuring rates of recovery in no-take marine reserves. *Marine Ecology Progress Series*, **292**, 1–12.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Ruse, G.R., Sadovy, Y.J. & Steneck, R.S. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, **20**, 74–80.
- Sluka, R., Chiappone, M., Sullivan, K.M., Potts, T.A., Levy, J.M., Schmitt, E.F. & Meester, G. (1998) Density, species and size distribution of groupers (Serranidae) in three habitats at Elbow Reef, Florida Keys. *Bulletin of Marine Science*, **62**, 219–228.
- Underwood, A.J. (1994) On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications*, **4**, 3–15.
- Willis, T.J., Millar, R.B., Babcock, R.C. & Tolimieri, N. (2003) Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation*, **30**, 97–103.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.

Received 24 June 2007; accepted 19 March 2008  
Handling Editor: Andre Punt

## Supplementary material

The following supplementary material is available for this article:

**Appendix S1.** Location of survey sites

**Appendix S2.** Estimation of fishing pressure

**Appendix S3.** Probability of each category of result occurring

**Appendix S4.** Full results for tests conducted

This material is available as part of the online article from:  
<http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01490.x>

(This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.