REPORT

Reduced density of the herbivorous urchin *Diadema antillarum* inside a Caribbean marine reserve linked to increased predation pressure by fishes

A. R. Harborne · P. G. Renaud · E. H. M. Tyler · P. J. Mumby

Abstract Disease has dramatically reduced populations of the herbivorous urchin *Diadema antillarum* Philippi on Caribbean reefs, contributing to an increased abundance of macroalgae and reduction of coral cover. Therefore, recovery of *D. antillarum* populations is critically important, but densities are still low on many reefs. Among the many potential factors limiting these densities, the focus of this study is on predation pressure by fishes. Marine reserves provide opportunities to examine large-scale manipulations of predator–prey interactions and, therefore, *D. antillarum* densities were compared inside and outside a reserve in The Bahamas (Exuma Cays Land and Sea Park; ECLSP). Urchins and their fish predators were surveyed at nine sites inside and outside the ECLSP. Because of lower fishing effort, the total biomass of urchin predators, weighted by their dietary preferences for urchins, was significantly higher inside the ECLSP. Furthermore, fish community structure was significantly different inside the Park because of the increased biomass of the majority of species. No urchins were seen inside the ECLSP and this was significantly lower than the density of 0.04 urchin m^{-2} outside the Park. Regression analysis indicated that the relationship between the biomass of urchin predators and the proportion of transects containing urchins was non-linear, suggesting that small increases in fish biomass dramatically reduce urchin abundances. The link between lower density of urchins and higher density of their predators inside the ECLSP is strengthened by discounting five alternative primary mechanisms (variations in macro-algal cover, larval supply, environmental setting, density of other urchin species and abundance of predators not surveyed). Caribbean marine reserves have an important conservation role, but increased fish predation appears to reduce densities of *D. antillarum*. Urchins currently have limited functional significance on Bahamian reefs, but any future recovery of *D. antillarum* is likely to be limited in reserves, with potentially important ecological consequences.

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Introduction

Sea urchins are important herbivores, and play a critical role in many of the documented trophic cascades in benthic marine ecosystems (Pinnegar et al. 2000). Their essential role was clearly demonstrated on Caribbean coral reefs when *Diadema antillarum* populations were decimated by a waterborne pathogen in 1983–1984. Urchin densities

were reduced by more than 93% across the entire Caribbean and tropical western Atlantic (Lessios 1988). Following *D. antillarum* mortality, reduced grazing pressure led to dramatic changes on reefs, including increased algal biomass, altered community composition of algae and decreased primary productivity (Carpenter 1990a). The indirect ecological effects of the loss of *D. antillarum* were profound because of its critical role, along with a range of fish species, in mediating coral–algal interactions and hence increasing reef resilience (Mumby et al. 2006a, 2007a). Macroalgae can inhibit the settlement, growth and survival of coral recruits (McCook et al. 2001; Box and Mumby 2007), and have detrimental competitive interactions with adult corals (Nugues and Bak 2006). Grazing fishes exhibited some positive compensatory responses after urchin mortality (Carpenter 1990b), but ecological models suggest that reefs are far more resilient when modest densities (>1 m^2) of urchins are present in addition to grazing fishes (Mumby et al. 2006a; 2007a). These models are supported by empirical studies that demonstrate where *D. antillarum* populations have increased, macroalgal cover has been reduced and coral recruitment has increased (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). Furthermore, urchins and grazing fishes have different algal feeding preferences and bioerosion rates (Ogden and Lobel 1978; Bellwood et al. 2004), so that optimal functioning of reefs may only occur in the presence of both taxa. The importance of algal grazing on reefs means that the functional extinction of *D. antillarum* has been implicated as a major cause of the increasing algal cover and decreasing coral cover on Caribbean reefs (Gardner et al. 2003).

Diadema antillarum has recovered towards pre-1983–1984 densities in parts of the Caribbean with densities from 1.7–8.9 m^{-2} recorded at particular sections of reefs in six countries (Carpenter and Edmunds 2006) and densities up to 12 m^{-2} documented in Jamaica (Edmunds and Carpenter 2001). However, urchin densities generally remain low with a regional mean density of 0.023 m^{-2} (Kramer 2003), particularly on the habitat considered here (forereefs at depths of ≈ 9–15 m). Limited recovery has been attributed to a range of factors including limited larval supply, Allee effects, poor larval survivorship, lack of conspecifics providing protection from predators, lack of suitable recruitment sites and interspecific competition (Lessios 1988, 1995; Chiappone et al. 2002; Carpenter and Edmunds 2006). This study examines the importance of predation pressure. A decreased abundance of predatory fishes, caused by fishing, increases *D. antillarum* populations (Hughes 1994), and grazing by urchins becomes more prominent on heavily fished reefs (Hay 1984). Furthermore, historical changes to *D. antillarum* morphology (larger feeding parts relative to body size) have been attributed to increasing fishing pressure that has

increased urchin population densities and reduced food availability (Levitan 1992). Controlling the abundance of predatory fishes is very difficult at scales larger than a few square metres, and such scales provide limited insight into the actual population dynamics of *D. antillarum* on reefs. Marine reserves can represent large-scale manipulations of predator abundance because of differential fishing pressure inside and outside the reserve. Furthermore, marine reserves are widely used as a conservation tool in tropical marine ecosystems, and understanding their effect on the density of ecologically important species such as *D. antillarum* is critical.

Despite the opportunities provided by marine reserves to examine the interaction of *D. antillarum* with its predators, data are currently scarce. In a Belizean marine reserve, urchin densities were lower and predator density was generally higher than outside the reserve (Brown-Saracino et al. 2007). However, this study surveyed a mix of patch reef and coral reef ridge habitats inside and outside a reserve. The study described here is habitat specific and considers the forereef habitat visually dominated by corals of the genus *Montastraea* that is particularly important because it typically supports the highest biomass and diversity of reef organisms (Mumby et al. 2008). Furthermore, urchins were surveyed inside and outside one of the oldest and best enforced reserves in the Caribbean (the Exuma Cays Land and Sea Park; ECLSP), so that any effect of marine reserves on *D. antillarum* populations should be clearly distinguishable. While there are few data on the abundance of urchin predators inside and outside the ECLSP, the biomass of piscivores has increased significantly (Chiappone and Sullivan Sealey 2000; Mumby et al. 2006b; Harborne et al. 2008). Major urchin predators such *Balistes vetula* and *Calamus* spp. are also commercially important and are regularly found in fish traps (Garrison et al. 2004), and should benefit from reduced fishing effort.

In summary, the Park is likely to have higher predation pressure than sites outside the Park, and the aim of this study is to examine the impacts of this differential predation pressure on *D. antillarum* density. If increased predation pressure from fishes appears to have reduced urchin density inside the Park, this will have implications for both the functioning of reserve areas relative to adjacent non-reserve areas and the likelihood of recovery of *D. antillarum* populations on reefs protected from fishing.

Materials and methods

Study site and sampling design

Surveys in and around the ECLSP were conducted in April and May 2007. The ECLSP lies near the centre of the

Bahamian archipelago, is large (442 km^2) and was established in 1958 (Chiappone and 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, and has been effective for maintaining larger populations of fish and invertebrates than found outside the reserve (e.g. Chiappone and Sullivan Sealey 2000). Poaching inside the ECLSP has been assessed as low (supporting material with Mora et al. 2006). Surveys were conducted in the forereef habitat visually dominated by corals of the genus *Montastraea* (subsequently '*Montastraea* reef'). *Montastraea* reef was sampled at three sites (≈ 150 m $\times \approx 150$ m) near the centre of the ECLSP, three sites between 5.8 and 18.1 km north of the Park and three sites around Lee Stocking Island (LSI), ≈ 70 km south of the Park (see Electronic Supplementary Material). Extensive 1 m^2 quadrat surveys at each site have demonstrated that rugosity, depth, and coral cover and species composition did not vary significantly at sites inside the ECLSP compared to sites outside the Park, but macroalgal cover is significantly lower inside the Park because of increased grazing rates (Mumby et al. 2006b; Harborne et al. 2008 and see Electronic Supplementary Material).

Surveys of *Diadema antillarum* predators

Randall (1967) found sea urchin body parts in 34 Caribbean fish species, but these include both predators and scavengers (Randall et al. 1964; McClanahan 1999). Fish surveys in this study were restricted to the 15 species listed as *D. antillarum* predators by Randall et al. (1964; Table 1), and exclude scavengers from genera such as *Halichoeres* and *Thalassoma*. The importance of *D. antillarum* in the diets of the different species varies significantly. Randall et al. (1964) includes data on the proportion of individuals of each species sampled that contained *D. antillarum* remains in their stomachs. For example, only 1 out of 50 *Haemulon sciurus* specimens contained urchin remains, compared to 53 out of 87 *B. vetula* specimens. In order to account for these established inter-specific differences in dietary preferences for urchins, the Randall et al. (1964) data are used here to weight the biomass of each species during analyses (Table 1). Note that we recognise that there are limitations in extrapolating the Randall et al. (1964) data to reefs that have changed considerably over the last 40 years, but we do feel that some degree of biomass weighting is necessary to reflect well-established diets of the species considered. For example, the fish

Table 1 Urchin predators surveyed inside and outside the Exuma Cays Land and Sea Park (ECLSP), and the percentage weightings used in multivariate analysis of fish community structure. Also shown are the mean unweighted and weighted biomasses (plus standard errors) of each species inside and outside the park ($n = 6$ outside ECLSP and 3 inside the park)

Species	% with *D. antillarum* remains (n)	Biomass weighting	Mean unweighted biomass (g 200 m^{-2})		Mean weighted biomass (g 200 m^{-2})	
			Outside ECLSP	Inside ECLSP	Outside ECLSP	Inside ECLSP
Haemulon sciurus	2.00 (50)	0.033	1368.21 (536.30)	2293.17 (1353.98)	44.92 (17.61)	75.29 (44.45)
Diodon hystrix	3.70 (27)	0.061	0.00 (0.00)	107.59 (107.59)	0.00 (0.00)	6.54 (6.54)
Spheroides spengleri	7.14 (14)	0.117	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Calamus calamus	7.69 (13)	0.126	11.49 (4.01)	22.71 (8.64)	1.45 (0.51)	2.87 (1.09)
Haemulon carbonarium	8.33 (24)	0.137	96.42 (50.79)	0.00 (0.00)	13.19 (6.95)	0.00 (0.00)
Haemulon plumieri	10.53 (19)	0.173	1088.65 (269.86)	8029.02 (5551.79)	191.77 (47.74)	1387.34 (959.30)
Trachinotus falcatus	12.50 (8)	0.205	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Lactophrys bicaudalis	14.29 (7)	0.235	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Bodianus rufus	19.23 (26)	0.316	0.45 (0.45)	16.77 (16.77)	0.14 (0.14)	5.29 (5.29)
Halichoeres radiatus	22.73 (22)	0.373	9.67 (6.59)	0.00 (0.00)	3.61 (2.46)	0.00 (0.00)
Canthidermis sufflamen	25.00 (4)	0.410	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Anisotremus surinamensis	38.89 (54)	0.638	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Calamus bajonado	40.00 (10)	0.657	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Haemulon macrostomum	48.15 (27)	0.790	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Balistes vetula	60.92 (87)	1.000	14.07 (14.07)	85.05 (85.05)	14.07 (14.07)	85.05 (85.05)
Total biomass	–	–	2588.96 (664.46)	10554.31 (6738.83)	269.14 (45.43)	1562.38 (947.16)

Weightings derived from the number of fishes containing *Diadema antillarum* remains as quantified by Randall et al. (1964). Biomass weightings are from the same data, and used in univariate analysis of total biomass of predators

surveyed varied from specialist urchin predators such as *B. vetula* to species that feed on a wide range of invertebrates.

Target fishes were counted and sized (to nearest cm) along eight to ten 30×4 m belt transects at each site. Transect size and number were optimised using data from equivalent surveys within the Caribbean (Mumby et al. 2004). Fish lengths were converted to biomass using allometric relationships (Bohnsack and Harper 1988), and all subsequent fish analyses consider biomass. Biomass data are most appropriate for the consideration of ecosystem structure, trophic relationships, and fisheries exploitation (Bohnsack and Harper 1988). Replicate transects were combined to provide a mean biomass per species per site, which was standardised to an area of 200 m².

Analysis of fish data

The total weighted biomass of urchin predators at each site inside and outside the ECLSP was calculated by multiplying the weighting factor in Table 1 with the biomass of each species. Total biomasses of predator communities were then compared using a Mann–Whitney test. Variation in community structure inside versus outside the Park was conducted using Analysis of Similarity (ANOSIM) (Clarke 1993). ANOSIM uses similarity coefficients between each pair of samples to return a statistic R, which is a measure of separation among groups where 0 indicates complete mixing and 1 represents full clustering in which all samples within groups are more similar to one another than to any sample in another group. In order to incorporate species weightings (Table 1) into the multivariate analysis, ANOSIM was conducted on weighted Bray–Curtis similarity coefficients using the method proposed by Mumby et al. (1996), shown in Eq. 1.

$$S_{jk} = \left[1 - \frac{\sum_{i=1}^{p} w_i |X_{ij} - X_{ik}|}{\sum_{i=1}^{p} w_i (X_{ij} + X_{ik})} \right] \quad (1)$$

where S_{jk} is the weighted Bray–Curtis similarity between samples j and k, X_{ij} and X_{ik} are the biomasses of the ith species in the jth and kth samples, respectively, and there are p species overall, and w_i is the percentage of fish specimens containing *D. antillarum* remains in the ith species as reported by Randall et al. (1964) (Table 1).

In order to examine the ANOSIM result further, the discriminating species driving the differences inside versus outside the Park were determined using Similarity Percentage (SIMPER) analysis (Clarke 1993) on weighted biomass data.

Diadema antillarum surveys

Diadema antillarum were counted on between 7 and 21 randomly placed, 10×1 m transects at each survey site. All the surveys were conducted in the daytime, but were assisted by torchlight to ensure that any urchins present within holes and crevices on the reef were also recorded. Numbers of *Echinometra* spp. were also recorded during the *D. antillarum* transects.

Analysis of *Diadema antillarum* data

Only 6.6% of *D. antillarum* survey transects contained more than one urchin (6 out of 91, maximum number of urchins on a single transect was 3). It was, therefore, appropriate to transform the data set to presence/absence of urchins per transect, and use binomial probability distributions. The analytical model used had a null hypothesis that the binomial probability of finding an urchin on transects outside the ECLSP was identical to that within the Park. Rather than pooling data from sites outside the ECLSP for a comparison with sites inside the Park, the model used each of the six site-level probabilities of finding an urchin on a transect outside the Park to calculate a 'mean' probability of recording the observed number of transects with urchins at each site within the Park (Eq. 2).

$$P(n_j) = \frac{1}{6} \sum_{i=1}^{6} B(n_j | N_j, p_i) \quad (2)$$

where n_j is the number of transects with urchins present at site j inside the ECLSP, N_j is the total number of transects surveyed at site j, and p_i is the probability of an urchin being present on a transect at the ith site outside the ECLSP.

The total probability of recording the observed number of urchins on transects inside the ECLSP, if the probability of finding an urchin on a transect was the same inside and outside the Park, was the product of the three values of $P(n_j)$ (one calculated for each site inside the ECLSP). The null hypothesis of the probability of finding an urchin on a transect being the same inside and outside the Park was rejected if the total probability across all three sites was <0.05.

The focus of this study was the factorial comparison of *D. antillarum* populations inside and outside the ECLSP, but to further examine the relationship between weighted predator biomass and urchin abundances regression analysis was also conducted. Because of the nature of the *D. antillarum* data (proportions of transects containing urchins) generalised linear models with binomial error structures and the logit link function were used.

Results

Diadema antillarum predator communities

Only 8 out of the 15 urchin predators were seen during fish surveys, and the communities were dominated by *Haemulon plumieri*, *B. vetula* and *Haemulon sciurus* (Table 1; Fig. 1). Weighted biomasses of each of these species were >75 and >14 g 200 m^{-2} inside and outside the Park, respectively (Table 1; see Electronic Supplementary Material for site-specific fish biomasses). With the exception of *Haemulon carbonarium* and *Halichoeres radiatus*, all the species were more abundant inside the Park (Table 1; Fig. 1). Weighted total biomass of predatory species was nearly six times greater inside the ECLSP, and was significantly higher inside the Park than outside the reserve (one-tailed Mann–Whitney test $P = 0.014$). Furthermore, community structure of urchin predators was significantly different inside, compared to outside, the Park (ANOSIM: Global $R = 0.494$; $P = 0.036$). The higher biomass of *H. plumieri* and *B. vetula* inside the ECLSP accounted for over 89% of the multivariate difference between communities inside and outside the Park (Fig. 1).

Diadema antillarum populations

No *D. antillarum* individuals were seen along the 35 transects inside the ECLSP, covering 350 m^2 of reef. Outside the Park, 17 out of 56 transects contained

D. antillarum (Fig. 2). A total of 25 urchins were seen at sites outside the ECLSP, with a mean density of 0.04 m^{-2} (densities at each site are given in the Electronic Supplementary Material). The majority (68%) of urchins seen on transects were mature adults (>3 cm test diameter; Randall et al. 1964), although individuals with a test diameter <3 cm were recorded from five out of the six sites outside the Park. The probability of finding 0 urchin at each of the two sites inside the Park that were surveyed with seven transects, given the probabilities of finding an urchin on a transect at each of the sites outside the Park, was 0.271. The equivalent probability of finding 0 urchin at the site inside the ECLSP surveyed with 21 transects was 0.174. Therefore, the probability of finding 0 urchin at each of the three sites was $0.271 \times 0.271 \times 0.174 = 0.013$. This analysis confirmed that the absence of *D. antillarum* in the Park was significantly lower than would be expected if there was no reserve influence ($P < 0.05$). No *Echinometra* spp. was seen on any transect.

Regression analysis

The relationship between weighted predator biomass and the proportion of transects containing *D. antillarum* was non-linear (Fig. 3) and, therefore, models were fitted using a generalised non-linear regression model tool within the gnlm package [James Lindsey. gnlm: Generalized Nonlinear Regression Models. R package version 1.0. http://popgen.unimaas.nl/~jlindsey/rcode.html] in R
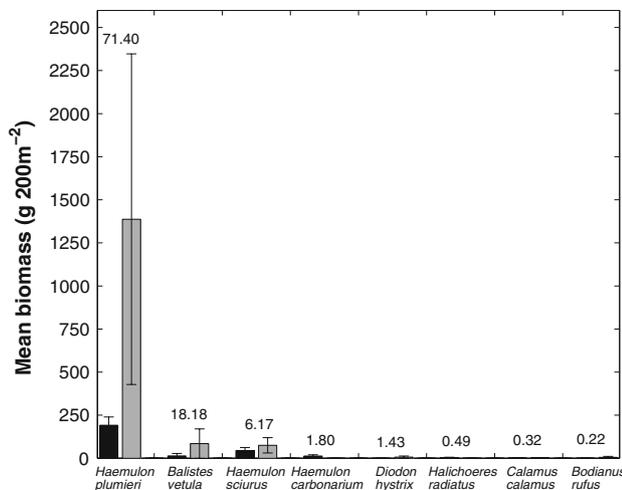

Fig. 1 Mean biomass of each urchin predator species (±1 standard error) inside (*grey bars*) and outside (*black bars*) the Exuma Cays Land and Sea Park (ECLSP). Biomasses weighted using the data in Table 1. Values represent percentage contribution of each species to SIMPER analysis of the dissimilarity between communities inside and outside the ECLSP (percent contribution = average contribution/average dissimilarity between sites inside and outside the reserve (=71.59%); $n = 3$ inside ECLSP and 6 outside
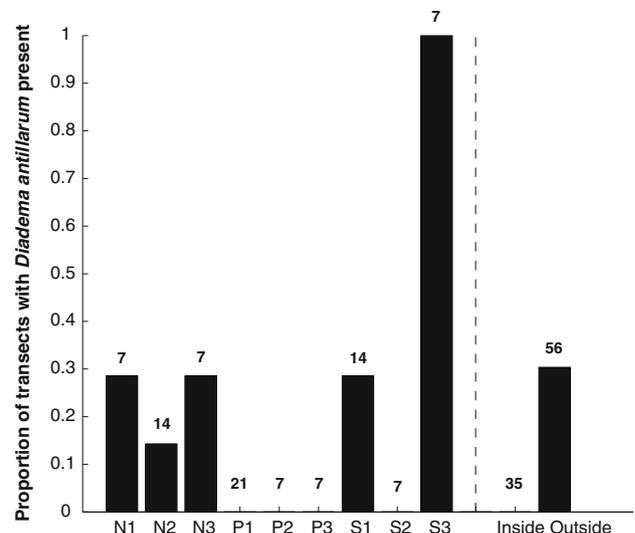

Fig. 2 The proportion of transects containing *Diadema antillarum* at each of the nine survey sites, and all pooled sites inside and outside the Exuma Cays Land and Sea Park (ECLSP). *N* sites north of the ECLSP; *P* sites inside the ECLSP; *S* southern sites at Lee Stocking Island. Values give the number of transects at each site
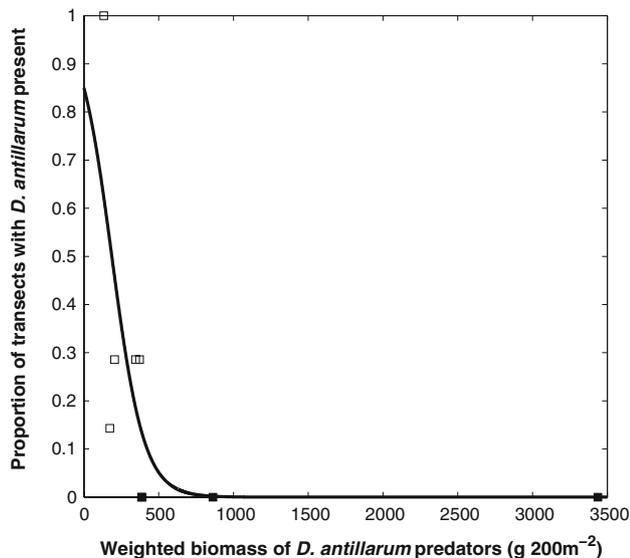
Fig. 3 Relationship between the weighted biomass of urchin predators and proportion of transects containing *Diadema antillarum*. Sites inside the Exuma Cays Land and Sea Park (ECLSP) represented by filled squares, sites outside the ECLSP as open squares. Fitted line generated from non-linear regression with a beta-binomial distribution (proportion of transects = $1/(1 + e^{(-1.7351+0.0093*biomass)})$)

(R Development Core Team 2008). We fitted the inverse of the logistic transformation (Proportion of transects containing *D. antillarum* = $1/(1 + e^{(-a-b*biomass)})$) as a function with a beta-binomial distribution, and estimates of 1.7351 for a and −0.0093 for b were derived (Fig. 3). Although it is not possible to quantify the fit of this model, it is clear that the weighted biomass of predators is needed in the model (χ^2-test, 1 d.f., $P < 0.05$) and that the model fit is better than a binomial generalised linear model (Akaike's information criterion reduced from 18.43 to 15.93). Therefore, the model can be considered a good indication of the relationship between the two variables, and provides evidence that small increases in the biomass of predatory fishes may lead to dramatic decreases in the abundance of urchins.

Discussion

Not a single *D. antillarum* was found within the ECLSP, compared to the 25 individuals seen at the sites outside the reserve. This significant pattern is consistent with the higher abundance of predators inside the Park causing a high post-settlement mortality of urchins and reducing their densities. In addition, the non-linear relationship between predator biomass and the proportion of transects containing urchins indicates that urchins may remain rare on reefs with even relatively low numbers of predators. The

regression analysis should be interpreted with caution given the low number of sites and the difficulties of inferring causation from regression, but it does indicate a hypothesis for future research. Predation pressure reducing *D. antillarum* densities inside the ECLSP is similar to results in a reserve in Belize, but links the reduced urchin densities to a wider range of predatory fishes than just the labrids that dominated the Belizean fish censuses (Brown-Saracino et al. 2007). Furthermore, the results support suggestions that the highest densities of *D. antillarum* are found on heavily fished reefs with few predators. For example, the recovery of urchins in Jamaica is well documented (Edmunds and Carpenter 2001; Bechtel et al. 2006), and these reefs are perhaps the most exploited in the Caribbean. Large predatory fishes, including key urchin predators such as triggerfishes, were reported as being virtually absent by the mid-1990s, and populations had been steadily declining much before that time (Hughes 1994).

While the increased biomass of urchin predators is consistent with a top-down reduction of urchin densities inside the ECLSP, in the absence of data from manipulative experiments, it is necessary to discount alternative primary mechanisms. Five alternative mechanisms can be postulated. Firstly, reduced fishing inside the ECLSP has increased grazing by parrotfishes, and led to a significant reduction of macroalgal cover (Mumby et al. 2006b; Harborne et al. 2008 and Electronic Supplementary Material). Although the settlement preferences of *D. antillarum* are poorly known, there is some evidence using artificial substrata that larvae prefer to settle on grazed surfaces (Bak 1985), possibly because macroalgal mats are inhabited by a range of micro-predators (Bechtel et al. 2006). The possibility that settlement rates are higher on reefs with less macroalgal cover inside the ECLSP cannot be discounted, but it can be concluded that any increased settlement is less important than increased predation pressure in urchin population dynamics. If settlement rates were critical and were increased by lower macroalgal cover, *D. antillarum* densities would be higher inside the reserve. Conversely, it is possible that the benefit of macroalgal refuges from macro-predators outweighs any mortality from micro-predators, and settling urchins may have lower mortality rates outside the Park. However, this is highly speculative and requires further research. Similarly, it seems highly unlikely that densities of urchins inside the Park are limited by food availability, given that parrotfishes and urchins occupy different niches, and the taxa coexisted before the mortality of *D. antillarum* when macroalgae was less abundant on reefs (Hughes 1994). In the absence of any empirical data to the contrary, the increased predation by fishes inside the Park reducing *D. antillarum* densities remains the most parsimonious explanation for the

observed pattern. Secondly, *D. antillarum* larval supply might be greater to sites outside the Park. Islands in the Bahamas archipelago are highly interconnected with little larval subsidy from elsewhere in the region (Cowen et al. 2006). Given the low density of urchins throughout The Bahamas (Kramer 2003), larval production is almost certainly very low and it seems likely that larval settlement on all the reefs may also be low. It is, therefore, highly unlikely that there is demographically significant variation in larval settlement between sites inside and outside the Park. Furthermore, although not explicitly parameterised for *D. antillarum*, a recent biophysical model of larval dispersal parameterised for a range of taxa from passive coral planulae to mobile parrotfish larvae found no evidence of systematic differences in potential larval supply between the reserve and its non-reserve borders (Mumby et al. 2007b).

The third alternative mechanism to predatory fish abundances explaining why urchins were absent inside the Park is that reefs inside and outside the Park are in a different environmental setting. *D. antillarum* density can be correlated to reef complexity (Lee 2006) and depth (Morrison 1988), but neither varied significantly inside versus outside the ECLSP. Fourthly, *D. antillarum* populations might be correlated with the abundance of another urchin species that happens to be more abundant outside the Park. For example, *Echinometra viridis* may facilitate the recruitment of *D. antillarum* (Lessios 1995), and the recovery of both species are strongly associated in Jamaica (Bechtel et al. 2006). However, no *Echinometra* spp. were seen at any of the survey sites, indicating that there is no evidence that the abundance of this species is an important factor explaining the differential abundance of *D. antillarum* inside and outside the ECLSP. Finally, important urchin predators that were not surveyed during this study might actually be more abundant outside the ECLSP, and the suggestion that predators are more abundant inside the Park is spurious. There are additional predators of *D. antillarum* not considered by this study, notably two *Cassius* (helmet shell) species and the lobster *Panulirus argus* (Randall et al. 1964), and the toadfish species *Amphichthys cryptocentrus* and *Sanopus barbatus* (Hoffman and Robertson 1983). These species require specialist sampling techniques (e.g. nocturnal surveys), but would be expected to further increase predation pressure inside the reserve because of the fishing pressure on species such as lobsters outside the Park. Discounting these alternative mechanisms allows for a robust conclusion that the increased predation pressure in the ECLSP has reduced *D. antillarum* abundances and limits the potential for the recovery of the species. However, we cannot rule out the possibility that urchin populations are more comparable inside and outside the Park in shallow water habitats where *D. antillarum* is historically more abundant (Bauer 1980).

The indication that Caribbean marine reserves can reduce the functional role of urchins by limiting their density contrasts with results from other ecosystems. Typically, marine reserves restore populations of urchin predators and reduce the detrimental effects of unregulated urchin populations. Urchins are particularly susceptible to unregulated 'plagues' because only a few specialist predators can overcome their defensive spines, and food webs containing specialists are more susceptible to perturbations because other species cannot fill the ecological niche if a predator is over-exploited (Pinnegar et al. 2000). Furthermore, urchins have the ability to change body size rapidly with changing resource availability or the varying density of conspecifics, and unchecked population growth may be a consequence of this ability to regulate their size (Levitan 1989). For example, in the Indian Ocean, fishing has reduced densities of urchin predators, particularly two triggerfish species, and increased urchin populations (McClanahan and Shafir 1990). The increased urchin populations have led to changes in key reef processes, such as increased bioerosion rates, which can have detrimental effects on reef dynamics. These changes may be reversed inside marine reserves where reduced fishing pressure restores trophic interactions among urchins and their predators (McClanahan and Shafir 1990; McClanahan et al. 1999).

Even though the density of *D. antillarum* populations may be reduced inside the ECLSP, urchin densities were still relatively low outside the Park compared to pre-mortality densities on comparable *Montastraea* reefs habitats of $0.1–1.7 \ m^{-2}$ (Bauer 1980). Furthermore, the lower abundance of macroalgal cover inside the Park indicates that grazing on these reefs is dominated by fishes that benefit significantly from the ECLSP being in place, and there currently appears to be a limited functional significance of differing urchin densities at protected and non-protected *Montastraea* reef sites. Predation rates are likely to contribute to this lack of recovery throughout The Bahamas but clearly other factors, such as limited larval supply, are important. However, future recovery of urchin populations towards pre-mortality densities is possible, perhaps when the Allee effects of low adult populations are overcome when episodic conditions permit high recruitment and the establishment of numerous individuals on one or more reefs, and a subsequent increase in fertilisation success (Karlson and Levitan 1990). Equally, urchins may become established in shallower water habitats, as has occurred in Jamaica (Edmunds and Carpenter 2001), and then populate deeper reefs. Even under such circumstances, this study suggests that any recovery may be limited by high predator biomass in reserves, with potentially important ecological consequences. This is in contrast to the implicit aims of the ECLSP and other marine reserves.

Caribbean marine reserves are an important tool in biodiversity conservation, but the trophic cascade between urchins and their predators demonstrates the complexities of restoring key processes in disturbed ecosystems.

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