Evidence for protection of targeted reef fish on the largest marine reserve in the Caribbean

Effective marine reserves can restore fish abundance and diversity in areas impacted by overfishing, but the outcomes of some reserves in developing countries where resources for enforcement are limited have seldom been evaluated. Here we assess whether the establishment of the largest marine reserve in the Caribbean has had a positive effect on the abundance of commercially valuable reef fish species in relation to neighboring unprotected areas. We surveyed 25 sites including two reef habitats (reef crest and reef slope) inside and outside the marine reserve Gardens of the Queen in Cuba over a 1.5-year period. Densities of the most targeted reef fish species were significantly higher inside than outside the reserve in both habitats. This trend was mostly consistent over time. Supporting evidence from previously published studies in the area indicates that habitat complexity, benthic communities, and the intensity of fishing pressure were similar inside and outside the reserve before reserve establishment. Additionally, reported differential fish behavior towards divers inside and outside the reserve and relative low poaching inside the reserve supported our results. Therefore, the differences observed during the study in the density of targeted reef fish among non-reserve and reserve sites have likely resulted from protection.

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Fabián Pina-Amargós[1], Gaspar González-Sansón[2], Félix Martín-Blanco[3] and Abel Valdivia[4*]

[1]Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, Morón, Ciego de Ávila, CP 69 400, Cuba,

[2]Department of Studies for Sustainable Development of the Coastal Zone, University of Guadalajara, Jalisco, Mexico

[3] Tropical Research and Education Center, University of Florida, Homestead, FL 33031, USA

[4]Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599 USA

*Correspondence author email: abel.valdivia@unc.edu

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INTRODUCTION

Marine reserves have been largely beneficial for the recovery of fish density, biomass, and diversity (Côté *et al.* 2001; Halpern 2003; Molloy *et al.* 2009). Studies have shown an increase in abundance of targeted species, families, and even functional groups after the establishment of no-take marine reserves (Russ *et al.* 2003; Alcala *et al.* 2005; Claudet *et al.* 2008). Positive effects have been observed in average size (20-30% increase), species richness (11-23% increase), and reproductive capacity (Mosquera *et al.* 2000; Côté *et al.* 2001; Russ & Alcala 2003; Palumbi 2004). The benefits of protection have been detected as early as one to five years following fishing bans (Gell & Roberts 2003; Halpern 2003; Russ *et al.* 2003; Palumbi 2004) with positive effects increasing over time (Halpern & Warner 2002; Maypa *et al.* 2002; Alcala *et al.* 2005; Claudet *et al.* 2008). Although marine reserves are presumed to restore several species from exploitation, not all species respond positively to protection due to their ecological characteristics (Claudet *et al.* 2010).

The response to protection is greatly variable among fish taxa depending on their commercial value, body size, mobility and other life-history and ecological traits. Overall, strongly exploited species of larger body size tend to respond significantly better and faster than unexploited and relatively smaller species (Mosquera *et al.* 2000; Russ *et al.* 2003; Claudet *et al.* 2008, 2010). Furthermore, relative long-lived species with great mobility and variable recruitment may respond slower to fishing closures than short-lived species with narrow spatial requirements and steady recruitment (Gell & Roberts 2003; Russ *et al.* 2003; Palumbi 2004). In fact, beneficial effects could take decades to detect in very mobile species. For instance, pelagic fish species, which movement patterns expand beyond reserve boundaries, respond slower than less vagile coastal species (Roberts & Sargant 2002; Micheli *et al.* 2004). Nonetheless, exploited mobile species with wide home ranges still benefited from protection (Claudet *et al.* 2010). In contrast, non-commercial bycath and unexploited species rarely respond to protection and may

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even show declines after fishing has ended due to different life-history and ecological traits such as body size, habitat preferences and schooling behavior (Palumbi 2004; Claudet *et al.* 2010).

Several factors can hinder the detection of positive effects in marine reserves. Dissimilarities in habitat structural complexity and benthic community composition can lead to differences in fish assemblages that are independent of protection status, as the abundance of a number of fish species is correlated with substratum characteristics (McClanahan 1994; Roberts & Sargant 2002; Friedlander *et al.* 2003; Harborne *et al.* 2012). Similarly, the acquired behavior of target fish species towards divers (e.g. due to feeding practices in some areas) could lead to overestimation of fish abundances (Kulbicki 1998; Hawkins *et al.* 1999). Additionally, lack of appropriate spatial and temporal replication in some studies (Halpern & Warner 2002; Halpern 2003; Alcala *et al.* 2005), the use of different methods to compare fish abundances (Maypa *et al.* 2002; Ward-Paige *et al.* 2010), temporal fluctuations in population abundance (Babcock *et al.* 2010), and ineffective enforcement (Pomeroy *et al.* 2005; Mora *et al.* 2006) can thwart the detections of beneficial effects of marine reserves.

Most studies addressing the effects of marine reserves on fish assemblages in the Caribbean have focused on relative small protected areas (Polunin & Roberts 1993; Roberts 1995; Roberts & Hawkins 1997; Roberts *et al.* 2001). This is because few relative large and continuous marine reserves exist in the region and their fish communities can be highly variable due to natural intra habitat differences (Chiappone & Sullivan-Sealey 2000; Harborne *et al.* 2008). Relative larger marine reserves, however, may have more implications for the recovery of large and mobile reef fish populations than smaller reserves at scales necessary for conservation and fisheries management (Halpern 2003; Claudet *et al.* 2008; Gaines *et al.* 2010). But effective enforcement and management in relative large marine reserves is difficult to achieve, especially in developing countries where there is limited amount of resources for conservation (Mora *et al.* 2006; Guidetti *et al.* 2008). Thus, understanding the dynamics of relative large marine reserves in

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protecting fish populations where enforcement may be a problem will provide crucial insights into reserve design and management needs.

Here we analyzed for the first time the spatial and temporal variability of the density of relative large-bodied and commercially important reef fish species inside and outside the largest marine reserve of the Caribbean, the Gardens of the Queen ("*Jardines de la Reina*") national park in Cuba (Appeldoorn & Lindeman 2002). Some reef sites in the park are known to support one the highest fish biomass of the entire region (Newman *et al.* 2006), however, no comprehensive study has analyzed the effectiveness of this protected area in enhancing reef fish populations. Our study focused in the response of fish species of high commercial values that were historically targeted in the region before the reserve establishment and that are still targeted outside the reserve (Pina-Amargós *et al.* 2008a). We hypothesized that fish densities of these species were significantly higher inside the reserve than in neighboring unprotected areas due to protection from fishing. We discussed whether these differences were independent of modulating factors such as habitat heterogeneity or the structure of benthic communities (coral and algae assemblages). Furthermore, we analyzed whether fish density differences were related to differential protection level, fishing pressure before protection, alteration of fish behavior, or spatial recruitment variability across the park. Our study provides useful information about the implications that relative large marine reserves have in developing countries with very limited resources for appropriate enforcement and effective reserve management.

MATERIAL AND METHODS

Study sites and survey design

The Jardines de la Reina archipelago (hereafter JDLR) consists of ~661 keys and covers ~360 km in south-central Cuba (Fig. 1). In 1996, approximately 950 km^2 of the archipelago, that includes a variety of coral reef, seagrass and mangrove systems, was proclaimed by the Cuban Ministry of

Fisheries as "zone under special regime of use and protection". This management category is equivalent to the internationally recognized "Marine Reserve", terminology that will be used in this manuscript. This park is considered the largest continuous marine reserve of the Caribbean (Appeldoorn & Lindeman 2002) with an area more than twice that of the Exuma Cays Land and Sea Park (442 km^2) in the Bahamas (Chiappone & Sullivan-Sealey 2000).

There is no quantitative data describing the reef fish and benthic community structure before reserve establishment. Few studies indicated, however, that catch and fishing pressure were homogeneously distributed across the entire JDLR archipelago before protection, suggesting similar abundance of economic valuable species across the region (Pina-Amargós *et al.* 2008a; Claro *et al.* 2009). Although after the declaration of the reserve fishing efforts were relocated to outside the reserve, poaching is still present towards the boundaries of the protected area (Claro *et al.* 2001; Pina-Amargós *et al.* 2008a). In fact, due to park resources limitation there is a gradient of effective protection from the center of the reserve (with higher enforcement) to the boundaries of the reserves (with lower enforcement) that may affect fish communities (Pina-Amargós *et al.* 2008a).

We estimated the spatial and temporal variability in density of relatively large and commercially valuable reef fish species inside and outside of the JDLR marine reserve. To analyze intra habitat variability, we sampled two distinct reef habitats; reef slope (depths 8-15m) and reef crest (depths 1-3m). We accounted for location effects by surveying sites at both ends of the marine reserve. To stratify our survey methodology, we divided the study area into five zones (Fig. 1), identified as Non-Reserve West (NRW), Reserve West (RW), Reserve Center (RC), Reserve East (RE) and Non-Reserve East (NRE). Thus, for reef slope habitats, we sampled 15 sites within the reserve (five sites equally distanced in each of the three reserve zones) and 10 sites outside the reserve (five sites in each of the two non-reserve zones) (Fig. 1, Table S1). Reef crest habitats were only surveyed in NRW, RW and RC because the reef crest in RE and NRE

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were shorter in length (<500m) than as required for our survey method (see below). Thus, for reef crests we surveyed eight sites within the reserve (four sites in RW and four sites in RC) and four sites outside the reserve in NRW. To account for temporal variability, we surveyed all sites five times, during June of 2004 and January, April, September and December of 2005. Based on Pina-Amargós *et al*. (2008a), reserve enforcement follows this pattern by zones RC>RW>RE>NRW>NRE, where RC had high protection, RW and RE moderated protection, and NRW and NRE showed no protection.

Fish densities

Underwater visual census for large mobile reef fish was used for fish counts (methods modified from Richards *et al.* 2011). That is, instead of towed divers, swimming divers performed the surveys. We randomly deployed two permanent belt transects (800x10 m) at each slope site and two (500x10 m) at each crest site. Shorter transects were used on the latest because continuous crest were never longer that this length. During each survey, divers counted only individual fish in a 10x10 m area in front of them for ~1-2 minutes moving consecutively along the transect when all fish were recorded. Each transect was surveyed in ~40-50 minutes. This approach was useful to avoid recording the same fish more than once, ensuring a near instantaneous sampling design, and minimizing changes in fish behavior due to diver presence (Ward-Paige *et al.* 2010). A power analysis performed in a previous pilot survey showed values of 0.8 for the analysis of variances indicating relative high power for this type of survey. During this previous pilot study, each permanent belt transect was marked with bottom buoys, underwater reference points were photographed, and their coordinates were registered using a GPS unit. Before beginning every survey the observers became acquainted with the belt transects width (10 m) using a metric tape.

For the surveys, we selected only 28 reef fish species that are often targeted and of high commercial value (Claro *et al.* 2009) (Table 1 and Table S2). Body size (fork length in

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133 centimeters) of each individual was estimated in 10 cm intervals, as recommended by Westera *et*
134 *al.* (2003). We chose these species based on information obtained from semi-structured
135 interviews of local fishermen to determine the most common targeted fish species and their
136 minimum catch size ("trophy size"). Semi-structure interviews consisted in a limited and formal
137 set of questions, but new questions were added as a result of what fishermen were stating. The
138 results of the interviews indicated that these 28 relatively large species (Table 1) were of high
139 commercial value and the most targeted by local fishermen (F. Pina-Armargós, unpublished data).
140 The term "trophy species" was used for these targeted species.

141 For all comparative analyses among zones and time, we selected the most frequent fish
142 species (f >50%) from the 28 trophy species surveyed across sites (Table 1). Frequency (f) was
143 defined as the proportion of occurrence of a given species across all sites and time within the
144 same reef habitat. The rest of the species with frequencies <50% were not included in the
145 analyses because the likelihood to detect differences among reserves and non-reserves sites was
146 small and the results could lead to misleading conclusions. Additionally, to increase the
147 probability of detecting differences due to fishing, we only used individuals larger than the
148 species-specific trophy size in the analyses (Table 1). This approach made comparison between
149 non-reserve and reserve sites more meaningful as fishermen mostly target individuals above the
150 trophy size. Of the most frequent species, we analyzed the data including and excluding the
151 schoolmaster (*Lutjanus apodus*). This species shows strong schooling behavior (Claro *et al.*
152 2001), was the most abundant in most sites, and it is the least commercially attractive based on
153 the semi-structured interviews.

154 Spatial and temporal variation of fish biomass among reserve and non-reserve was not
155 analyzed in this study and it is beyond the scope of our objectives. This was because we were
156 only interested in analyzing differences of fish densities of the most targeted and commercially
157 valuable species above a certain trophy size to determine the effectiveness of reserve protection.

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Reef structural complexity and benthic communities

A previous study characterized in detail the reef architectural complexity and benthic communities structure (mainly corals and algae) during the same time and of the reef sites analyzed in this study (Pina-Amargós *et al.* 2008c). They found no significant differences of reef structural complexity, corals, and algae assemblages among reserve and non-reserve within the same reef habitat. Specifically, most of the values of reef structural complexity, coral cover, density of coral colonies, coral bleaching prevalence, coral mortality percentage, density of coral recruits, algae cover (divided in six functional groups) were statistically similar across all zones within the same reef habitat independently of protection status. For detailed information refer to (Table S3).

Data analysis

Statistical significant differences in mean density were assessed using a two-factorial fixed-effects analysis of variance (ANOVA), considering levels of protection (five zones) and sampling time (five months) as factors. We tested the assumptions for the ANOVA following the criteria suggested by Underwood (1996) and Quinn and Keough (2002). When the assumptions of the ANOVA were not met, we perfomed the analysis on log-transformed data. Habitat structural complexity and benthic community composition were no included in the models because no differences were found in these confounding factors among reserves and non-reserves sites within the same reef habitat (Pina-Amargós *et al.* 2008c, Table S3). For graphical representation, we constructed bubble scatterplots, where the circle diameter was proportional to mean density of trophy fish in each combination of zone and sampling time. Using a Welch's *t* test (i.e., modified Student's t test for two samples having possibly unequal variances), we also analyzed the

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differences between protection levels based on the pooled mean density for each trophy species. Data was analyzed using the STATISTICA 8.0 program (StatSoft 2007).

RESULTS

The JDLR archipelago showed relative high frequency and density of commercially valuable fish species. Out the 28 species surveyed, 10 were present in at least 50% of all transects and were categorized as frequent (Table 1). Of this group, schoolmaster was the most frequent and abundant species in both reef habitats (slope and crest), with mean densities by one or two order of magnitude higher than the rest of the species. Schoolmaster was also three-times more abundant on reef crests than on reef slopes due to the schooling behavior of the species. Overall, these 10 species, except dog snapper, were more frequent on the slope than on the reef crest (Table 1). Hogfish and mutton snapper followed in density on reef slopes and reef crests, respectively. Although we did not test statistically the differences of fish body-size between habitats, most species in reef slope showed broader size ranges than in reef crest (Table 1). Cubera snapper, black grouper and great barracuda had the broadest body-size ranges in reef slopes, while dog snapper, black grouper and great barracuda showed similar trends in reef crest. Schoolmaster had the smallest body-size ranges from all the most frequent species in both habitats (Table 1).

Less frequent species (i.e. those present in less than 50% of all transects) showed different distribution patterns between habitat types than the most frequent ones (Table 1). From this group, nurse shark was the most frequent species on both reef slopes and crests. After nurse shark, Cero was more frequent on reef slopes while rainbow parrotfish had higher frequency on reef crests. However, horse-eye jack was the most abundant species in both habitats due to its gregarious behavior (Table 1). Jacks and tarpons were more abundant on reef slopes than on reef crest while rainbow and midnight parrotfishes had higher densities on the reef crest. In terms of

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sizes ranges, spotted eagle ray, southern stingray, goliath grouper and nurse shark showed relatively broader body size ranges on reef slopes than on reef crests (Table 1).

The factorial analysis of variance within habitats indicated that in reef slopes the interaction between reef zones and time was significant for all the 10 most frequent trophy species (Table 2a, Fig. 2). This indicates that the spatial distribution patterns in average density of these species varied across zones in the archipelago during the study (Fig. 2). For example, dog snapper had the highest densities on January in RC but by September the highest density was found outside the reserve in NRE (Fig. 2). Although we found a great degree of variability among trophy species, for most of them the highest average density per zone tended to be in September while December appeared to show the lowest values (Fig. 2). Overall, with few exceptions, all these species showed a trend towards higher densities inside than outside the marine reserve during the study, especially in RC (Fig. 2). The pooled mean densities within the reef slope habitat and by protection level (combining all transects during the survey) showed the same trend, however, only the densities of three out of ten species (i.e., mutton snapper, black grouper, and hogfish) were significantly higher inside than outside the reserve (Fig. 3a, Table 2b). This is because the pooled mean density was influenced by the spatial and temporal variability among zones within the reserve. Within the reserve hogfish and schoolmaster had the highest densities and the later with one or two order of magnitude higher than the rest of the species (Fig. 3a).

The analysis of variance for the reef crests showed that six out of the ten most frequent fish species (i.e. mutton snapper, cubera snapper, dog snapper, Nassau grouper, yellowfin grouper and hogfish) showed significant interactions between zones and time (Fig 4, Table 2a). This also indicates that fish densities within reef crest varied spatially during the study. Overall, these six species tended to have higher densities inside than outside the reserve during the study, especially in RW (Fig. 4). In contrast, the density of the rest of the species (i.e. black grouper, tiger grouper, schoolmaster, and great barracuda) showed no interactions among zones and time. Density of

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229 black grouper differed among zones with higher values inside than outside the reserve
230 ($F_{(2,105)*}$=6.35, p=0.002, *degree of freedom of the effect and residuals), but showed no difference
231 among months. Tiger grouper and schoolmaster showed no spatial and temporal variation in
232 densities distribution (Table 2a), while great barracuda only showed seasonality ($F_{(4,105)}$=3.24,
233 p=0.015) but no difference among zones (Table 2a). As with reef slopes, the pooled mean density
234 within the reef crest showed a trend towards higher densities of trophy species inside the reserve
235 (Fig. 3b). Yet only four out of the ten most frequent trophy species (i.e. mutton snapper, cubera
236 snapper, yellowfin grouper, and hogfish) had statistically significant differences (Fig. 3b, Table
237 2b). Within the reserve reef crest, schoolmaster had the highest density with one order of
238 magnitude higher than the rest, followed by mutton snapper (Fig. 3b).

239 Finally, densities of the 10 most frequent trophy species were combined as a group
240 (trophy species density) and significant interactions between zones and time were detected on
241 both reef slopes and reef crest, including or excluding schoolmaster (Table 2). Overall, higher
242 densities of total trophy species were found inside than outside the reserve (Fig. 5). On reef
243 slopes the trend was similar with and without schoolmaster. On this habitat, the highest density of
244 trophy species was found on Jun'04 in RW followed by Jan'05 in RW and RC. In contrast, on
245 reef crests, total trophy density was higher for Jul'04, Jan'05 and Apr'05 in RC, but by Sep'05
246 higher densities were observed in RW and NRW. By Dec'05, the three reef crest zones had
247 comparable densities of total trophy species (Fig. 5). However, the density of trophy species on
248 reef crest zones when schoolmaster was excluded from the analysis, tended to be higher inside
249 than outside the marine reserve overtime (Fig. 5). This indicated that on the reef crest
250 schoolmasters had a strong effect in the total trophy species density among zones and time (Table
251 2)

252 **DISCUSSION**

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Our results support the hypothesis that the implementation of the JDLR marine reserve has promoted higher densities of commercially valuable and relative large reef fish species. This is consistent with previous meta-analyses that found that the greatest benefits of reserves are the recovery of exploited species, especially large ones (Côté *et al.* 2001). The relative larger size of this reserve (over 900 km^2) may have provided greater benefits to species, such as top predators, that have large area requirements and that are not effectively protected in small reserves (Halpern 2003). There is no long-term data set addressing changes in the fish communities before and after this reserve establishment, therefore evidence of protection based on a before and after approach is impossible to demonstrate. Nonetheless, the patterns observed in the density of trophy species are unlikely the response to several confounding factors such as, within reef type heterogeneity, spatially different fishing efforts before the reserve establishment, lack of appropriate replication, alteration of fish behavior due to observers, differential recruitment, or a combination of them. By surveying multiple control sites outside the reserve, replicating our study in space and time, and critically analyzing these aforementioned cofactors we can demonstrate that protection from fishing and a gradient of enforcement, from the center to outside the reserve, is the most plausible explanation for the differences observed.

Habitat structural complexity and benthic community structure was unlikely a driver for the differences observed in trophy fish densities within the same habitat across sites in our study. Structural complexity is often a significant factor influencing reef fish assemblages in coral reefs (Sale 1991; Harborne *et al.* 2012). For instance, the three dimensional structure of corals can affect fish recruitment patterns (Sale 1991), provide refuge by reducing predation risk (Hixon & Beets 1993), and increase sheltering in high-flow environments (Johansen *et al.* 2008). In fact, there is a long recognized positive correlation between coral cover and the abundance and diversity of reef fish (Jones *et al.* 2004). Moreover, coral loss due to bleaching events has considerably altered the population dynamics of reef fish species that rely on live coral for food

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or shelter (Jones *et al.* 2004; Graham 2007). Thus the benthic structure and composition in reserves sites may foster more fish abundance, regardless of local protection. However, a previous study showed no significant differences in reef structural complexity, benthic community composition, coral and algae cover, or bleaching prevalence among reserve and non-reserve sites within the same reef habitats (Pina-Amargós *et al.* 2008c) (see Table S3). Therefore, based on the homogeneity of the benthic community and reef structural complexity, the differences observed in fish assemblages among zones were independent of these factors.

Understating fishing pressure before the establishment of marine reserves is important to determine the potential effects of protection after fishing has ended (Russ & Alcala 1998; Halpern 2003; Alcala *et al.* 2005; Osenberg *et al.* 2006). This approach is fundamental to avoid confounding factors such as spatial differences in fishing activities. In JDLR, for both reef habitats on all zones, except NWR, catch and fishing effort were homogeneously distributed along the archipelago before the reserve establishment, suggesting similar spatial abundance of finfishes before protection (Pina-Amargós *et al.* 2008a; Claro *et al.* 2009). With the declaration of the marine reserve in 1996, catch and fishing effort were relocated to outside the reserve (Claro *et al.* 2001; Pina-Amargós *et al.* 2008a). After ten years of protection, Pina-Armagós *et al.* (2008a) found strong negative association between landings and fish abundance of most commercially important species across the JDLR archipelago. This suggests that fishing pressure has been lower inside the reserve where fish were more abundant (Pina-Amargós *et al.* 2008a). Thus, the fish abundance distribution in JDLR (greater inside the reserve) was unlikely related to uneven fishing pressure before the establishment of the protected area.

Lack of appropriate replication or control sites in studies that detected the effects of marine reserves could also lead to misleading conclusions and unsound management policies (Willis *et al.* 2003). We consider, however, that our analysis was based on strong experimental design as recommended by others studies (Halpern 2003; Willis *et al.* 2003). Our patterns were

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robust in both habitats and across the five sampling periods, thus we can state that the differences inside and outside the marine reserve prevail at spatial and temporal scales and they were not a response to random instant surveys.

Observations of fish behavior in JDLR archipelago showed that species of most commercial value tended to flee from divers, when closely approached, more often in non-reserve sites than reserve sites (Pina-Amargós *et al.* 2008b). Comparisons of flight distance (i.e. *distance at which an organism begins to flee an approaching threat*) inside and outside long-established reserves indicate fish behavior can be modified by the presence/absence of fishing (Gotanda *et al.* 2009; Feary *et al.* 2011). For example, fish respond to divers in fished areas by fleeing or swimming away, while in protected areas they are less afraid and more curious (Gotanda *et al.* 2009; Feary *et al.* 2011). Thus, this modified behavior can be used as a metric of fishing intensity. The previously reported contrasting behavior of trophy species between outside and inside the JDLR (Pina-Amargós *et al.* 2008b) support our hypothesis of stronger protection in the reserve.

Furthermore, differences in fish behavior towards diver inside and outside the reserve may have influenced our results. If divers were significantly altering fish behavior, and flight distance of trophy species was sufficiently greater outside than inside the marine reserve, we may have underestimated fish densities outside the reserve. This is due to lower fish detectability where individual fishes are fleeing from observers (Gotanda *et al.* 2009; Feary *et al.* 2011). However, our sampling methodology minimized the interaction between fish and observer, hence reducing the possibility of changes in fish behavior due to the diver presence (McClanahan *et al.* 2007; Ward-Paige *et al.* 2010; Richards *et al.* 2011). Thus, it is unlikely that the differences in fish density between protected and not protected zones were influenced by the observers.

Potential net movement of adult fish towards outside the marine reserve could also be evidence of effective protection within the reserve. After years of protection, fish and larvae tend to migrate from areas of higher abundance (e.g. inside reserves) to areas of lower abundance (e.g.

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outside reserves). This is also known as spillover effect and has been reported in several long-established and well functional protected areas (Russ & Alcala 2003; Alcala *et al.* 2005; Francini-Filho & Moura 2008; Halpern *et al.* 2009). Spillover effects within the JDLR archipelago have been experimentally confirmed through density manipulation of large-size and commercially valuable reef fish species through tagging methods and visual census (Pina-Amargós *et al.* 2010). Although the study was performed at a relatively small scale, the authors found that net emigration rates of tagged fish were two-fold higher than control sites when a sharp fish density was established (Pina-Amargós *et al.* 2010). In addition, anecdotal accounts of spillover effects of adult fish from the JDLR reserve reported by fishers (*"fish leave the reserve and for that reason we catch more fish now than we did before"*), supports the scientific findings. Thus, if the evidence of net movement of adult fish in the JDLR archipelago towards the exterior of the reserve is true, then protection might explain a fish density gradient.

Differential recruitment inside and outside the reserve is also unlikely at the spatial scale of our study and may not influence the differences observed. To our knowledge, only two studies have addressed fish larvae transport in Cuba (Lindeman *et al.* 1999; Paris *et al.* 2005). Both studies modeled larval transport through simulations from spawning aggregation sites for grunts and snappers in the southwest region (Lindeman *et al.* 1999) and for five snapper species (all of them included in our study) around the Cuban shelf (Paris *et al.* 2005). In the simulations, Paris *et al.* (2005) included two spawning aggregation sites in or near JDLR and suggested that significant levels of self-recruitment (up to 80%) structure the snapper populations, especially in this region. Based on these studies, it is not possible to make strong inferences about the distribution of larval recruitment at the relatively small spatial scales of JDRL archipelago (~350km). However, the species in our study have monthly spawning aggregations (Lindeman *et al.* 2000; Claro & Lindeman 2003; Claro *et al.* 2009) and several spawning aggregations sites for snapper and grouper have been reported in the southeast region of the island (Claro & Lindeman

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2003). In fact, a grouper spawning hot spot has been confirmed inside the reserve (in RC) (Pina–Amargós *personal observation*). Therefore, several potential spawning aggregation sites could be producing larvae and being dispersed homogeneously along the entire JDLR archipelago.

Out of the ten trophy species analyzed in our study, six showed significantly higher densities in both reef habitats (slope and crest) inside the marine reserve at some time during the study. Differences between reserves and non-reserves may be stronger for the reef slope than the crest habitat where fishes are naturally more abundant. These species (yellowfin grouper, Nassau grouper, cubera snapper, dog snapper, mutton snapper and hogfish) are also among the most commercially valuable and targeted in the region (Claro & Lindeman 2003; Pina-Amargós *et al.* 2008a; Claro *et al.* 2009). Therefore, as expected, these species have benefited the most from protection when fishing stopped or was drastically reduced (Côté *et al.* 2001; Micheli *et al.* 2004; Russ *et al.* 2008). Tiger grouper and schoolmaster did not clearly respond to protection and positive effects were not consistent between reef habitats for black grouper and great barracuda. These last four species are less targeted by recreational fisheries in the JDLR archipelago (Pina-Amargós *et al.* 2008a; Claro *et al.* 2009). The main reasons, based on the semi-structure interviews, were that schoolmaster was regarded as low quality for consumption in the region, which support prior finding that less targeted species are generally unaffected by reserve establishment (Micheli *et al.* 2004; Claudet *et al.* 2010). Similarly, tiger grouper, black grouper and great barracuda are prone to "ciguatera" (i.e. fish poisoning) in the region and fishers may avoid them (Claro *et al.* 2001). In contrast, fishing regulations in Cuba have limited catch allowances for larger specimens of black grouper, cubera snapper and dog snapper around the island (Claro *et al.* 2009) and although they are also prone to ciguatera (Claro *et al.* 2001) they may still caught and consumed. Nonetheless, our results support that commercially valuable species has increased in abundance after the establishment of marine reserves, hence responding better to protection.

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Finally, effective management is essential for the success of marine reserves (Pomeroy *et al.* 2005; Mora *et al.* 2006). Ultimately, the positive response of fish to protection is indicative of good compliance with fishing restrictions (Smith *et al.* 2006; Guidetti *et al.* 2008). Thus, fish responses to protection can be indirectly used to evaluate the effectiveness of fully no-take areas (Smith *et al.* 2006; Guidetti *et al.* 2008). According to Pina-Amargós et al. (2008a), effective protection decreases from RC, with the least human impact, to RW and RE with moderate protection, and NRW and NRE with the highest human activity. Although the JDLR marine reserve is not formally enforced by any national entity (Pina-Amargós *et al.* 2008a), the area has mostly escaped the high fishing pressure recorded in the rest of the Caribbean (Hawkins & Roberts 2004). This seems related to the relative remoteness of the archipelago, the economic situation of the country, restricted accessibility, and the limited amount of resources (e.g. boats, fuel, ice) that local recreational and commercial fishermen have faced for decades (Claro *et al.* 2009). Enforcement in the park is achieved indirectly by the reserve users. For example, former fishermen have become tour operators for the small resort that operates within the park (within the RC zone), where only ~1000 divers and fly-fishers (catch and release) are allowed every year. This model have indirectly promoted a reduction of illegal fishing by fostering protection (Pina-Amargós *et al.* 2008a) since the revenue from local tourism is highly more profitable than fishing (Figueredo-Martín *et al.* 2010). Yet adequate protection in JDLR marine reserve closer to the boundaries of the park might be an issue (as reflected in relative lower trophy fish densities) because most of the touristic activities, thus indirect enforcement, occur at the center of the reserve (Pina-Armargós, *personal observations*).

In summary, our study supports the findings that Caribbean reserves can work and effectively restore populations of highly valued fish species on different reef habitats. The density of six out of ten highly target and frequent species in the JDLR archipelago were greater inside the marine reserve – a pattern that was consistent in reef slope and reef crest over time. Although

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poaching may occur within the reserve, especially at the boundaries, effective protection from fishing was the most plausible explanation for the patterns observed. Relative large marine reserves in the Caribbean are necessary to ensure the protection of valuable fish species at scales necessary for conservation and fisheries management. The JDLR marine reserve is the largest in the region and could function as a source area for species that has been extensively depleted Caribbean wide.

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Table 1 (on next page)

Overall descriptive statistics of targeted trophy fish species by reef habitat.

Trophy size, average density (number of individuals per 1000 m^{-2} ± 1 standard error) above trophy size, and entire body-size range are shown. Trophy size for each species was determined based on semi-structure interviews and was defined as the minimum fish-size that fishermen would catch for that species. Frequency (*f* %) was defined as the proportion of occurrence of the species above trophy size across sites within reef habitat. Sample size was 250 (5 months x 5 zones x 5 sites x 2 transects) and 120 (5 months x 3 zones x 4 sites x 2 transects) transects for reef slope and reef crest, respectively. For taxonomic information of each species see Table S2.

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1 Table 1

Common name	Trophy (cm)	Reef slope			Reef crest		
		f (%	Mean ± SE	Size (cm)	*f* (%	Mean ± SE	Size (cm)
Nassau grouper	55	96	0.48 ± 0.03	15-85	58	0.15 ± 0.02	15-65
Hogfish	45	100	1.96 ± 0.08	10-65	84	0.63 ± 0.06	10-55
Schoolmaster	35	100	17.57 ± 0.84	10-55	100	53.17 ± 2.16	10-55
Cubera snapper	65	95	0.53 ± 0.05	25-125	66	0.22 ± 0.03	25-85
Dog snapper	55	87	0.40 ± 0.05	15-85	97	0.78 ± 0.06	15-85
Mutton snapper	45	94	0.38 ± 0.03	15-75	82	1.06 ± 0.15	15-65
Yellowfin grouper	55	94	0.47 ± 0.03	15-75	69	0.25 ± 0.03	15-65
Tiger grouper	55	96	0.47 ± 0.03	15-75	89	0.35 ± 0.04	15-75
Black grouper	65	83	0.24 ± 0.02	15-105	79	0.24 ± 0.02	15-95
Great barracuda	85	94	0.31 ± 0.02	35-135	78	0.31 ± 0.03	25-105
Spotted eagle ray	150	9	0.03 ± 0.002	105-235	2	0.01 ± 0.001	95-165
Yellow jack	55	14	0.11 ± 0.05	35-75	20	0.06 ± 0.001	25-75
Crevalle jack	55	11	0.39 ± 0.04	35-85	5	0.12 ± 0.01	25-75
Horse-Eye jack	55	37	0.43 ± 0.02	25-75	26	0.28 ± 0.03	25-85
Reef shark	150	3	0.01 ± 0.001	95-205	10	0.03 ± 0.003	105-215
Silky shark	150	14	0.03 ± 0.001	135-255	0	-	-
Southern stingray	150	35	0.10 ± 0.03	65-175	21	0.07 ± 0.002	75-135
Goliath grouper	75	15	0.05 ± 0.003	65-255	4	0.03 ± 0.001	55-135
Nurse shark	150	43	0.10 ± 0.02	75-255	36	0.12 ± 0.01	85-205
Margate	45	23	0.06 ± 0.002	25-65	0	-	-
Tarpon	100	19	0.36 ± 0.03	95-205	26	0.16 ± 0.02	85-195
Lemon shark	150	0	-	-	10	0.03 ± 0.002	155-205
Rainbow parrotfish	55	18	0.05 ± 0.002	45-115	37	0.12 ± 0.02	45-115
Midnight parrotfish	55	5	0.04 ± 0.002	35-95	19	0.08 ± 0.003	35-105
King mackerel	75	9	0.03 ± 0.002	65-135	0	-	-
Spanish mackerel	55	11	0.03 ± 0.001	55-95	0	-	-
Cero	55	42	0.13 ± 0.02	25-65	7	0.03 ± 0.001	25-55
Permit	55	4	0.01 ± 0.000	35-75	8	0.01 ± 0.001	45-85

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Table 2(on next page)

Summary statistics from the factorial ANOVAs and Welch's t test performed on density data for the ten most frequent species (f >50%).

A) Values of F-ratio and p-values are for the interaction term (zone x time) within habitats for the two-factorial ANOVA. Degrees of freedom for the interaction and residual are in parenthesis. B) Values of T_{welch} and p-values are for the comparison between reserve and non-reserve. Values with star (*) indicate significance at a level of $\alpha 0.05$. For the ANOVA, only the results of the interaction are showing for brevity, see main text for other significant factors.

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1 Table 2

A. ANOVA	Reef slope x Time		Reef crest x Time	
Species/groups	$F_{(16, 215)}$	p	$F_{(8,105)}$	p
Black grouper	4.05	<0.001*	1.09	0.378
Yellowfin grouper	2.38	0.003*	5.52	<0.001*
Tiger grouper	2.54	0.001*	1.18	0.321
Schoolmaster	2.24	0.005*	1.69	0.109
Nassau grouper	3.37	<0.001*	2.14	0.038*
Cubera snapper	1.95	0.018*	3.54	0.001*
Dog snapper	3.52	<0.001*	3.52	0.001*
Mutton snapper	3.38	<0.001*	2.37	0.022*
Hogfish	2.08	0.010*	2.36	0.023*
Great barracuda	2.20	0.006*	0.67	0.716
Total trophy	25.67	<0.001*	12.61	<0.001*
Total trophy (no schoolmaster)	20.81	<0.001*	7.55	<0.001*

B. Welch's *t* test	Reef Slope		Reef Crest	
Species/groups	T_{welch}	p	T_{welch}	p
Black grouper	2.23	0.027*	1.33	0.188
Yellowfin grouper	1.28	0.201	2.11	0.037*
Tiger grouper	0.48	0.632	0.46	0.648
Schoolmaster	0.24	0.804	0.38	0.706
Nassau grouper	0.96	0.340	0.79	0.429
Cubera snapper	0.85	0.393	2.26	0.026*
Dog snapper	0.79	0.429	0.82	0.415
Mutton snapper	2.71	0.007*	3.26	0.001*
Hogfish	2.96	0.003*	3.49	0.001*
Great barracuda	1.41	0.159	0.83	0.372
Total trophy	0.18	0.854	0.14	0.886
Total trophy (no schoolmaster)	1.44	0.151	2.06	0.041*

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Figure 1

Location of survey sites across Gardens of the Queen (*Jardines de la Reina*) archipelago

Solid black circles are sites where reef slope and reef crest were surveyed. White circles represent sites where only reef slope was sampled. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center; RE, Reserve East; NRE, Non-Reserve East.

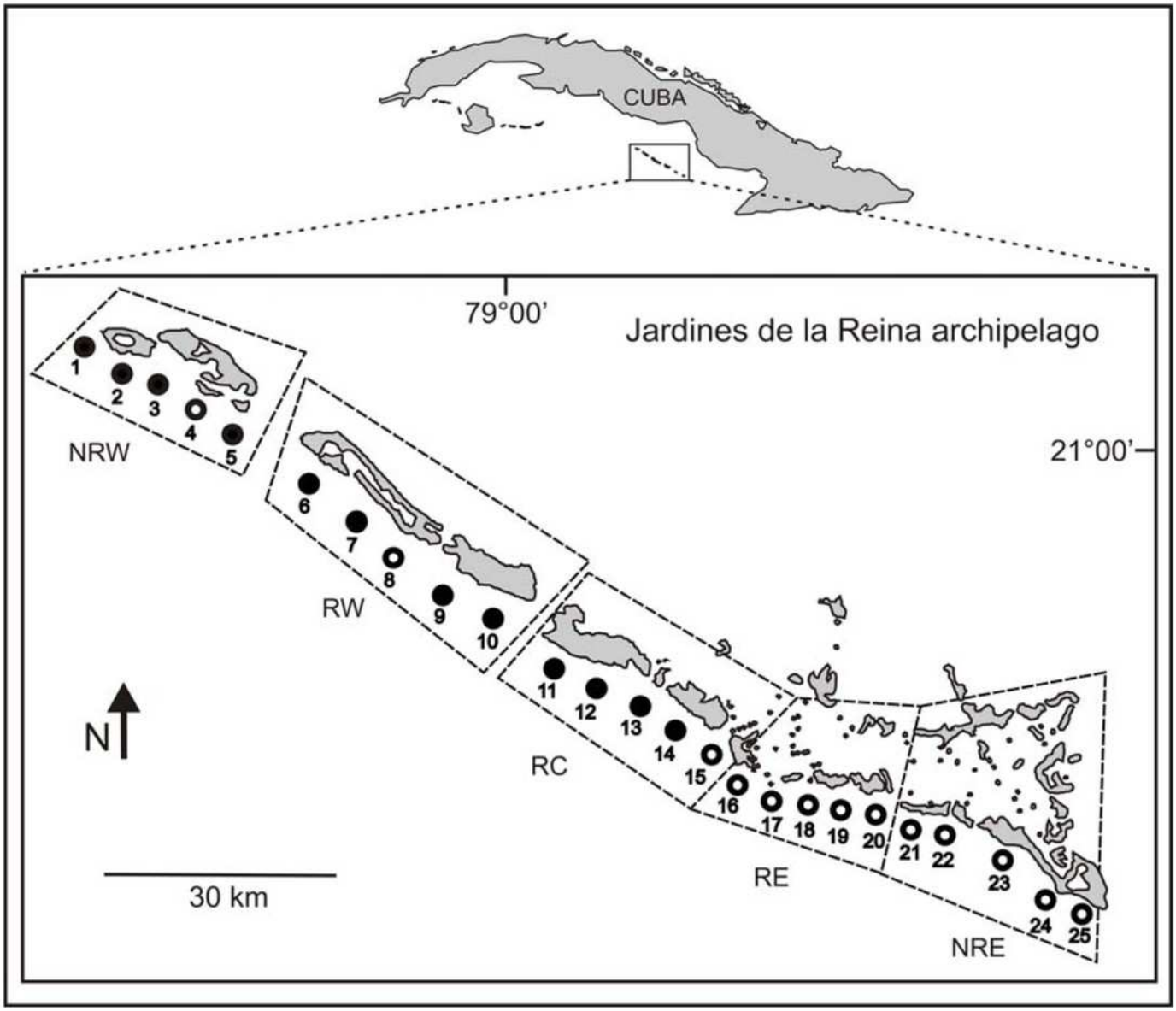

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Figure 2

Relative comparisons of mean densities of targeted trophy species (above trophy size) per zones and survey time on reef slope habitats.

Circle diameters are proportional to the mean density of each species at each combination of surveyed site and time. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center; RE, Reserve East; NRE, Non-Reserve East. Survey date labels show month (first two letters) and year (last two digits).

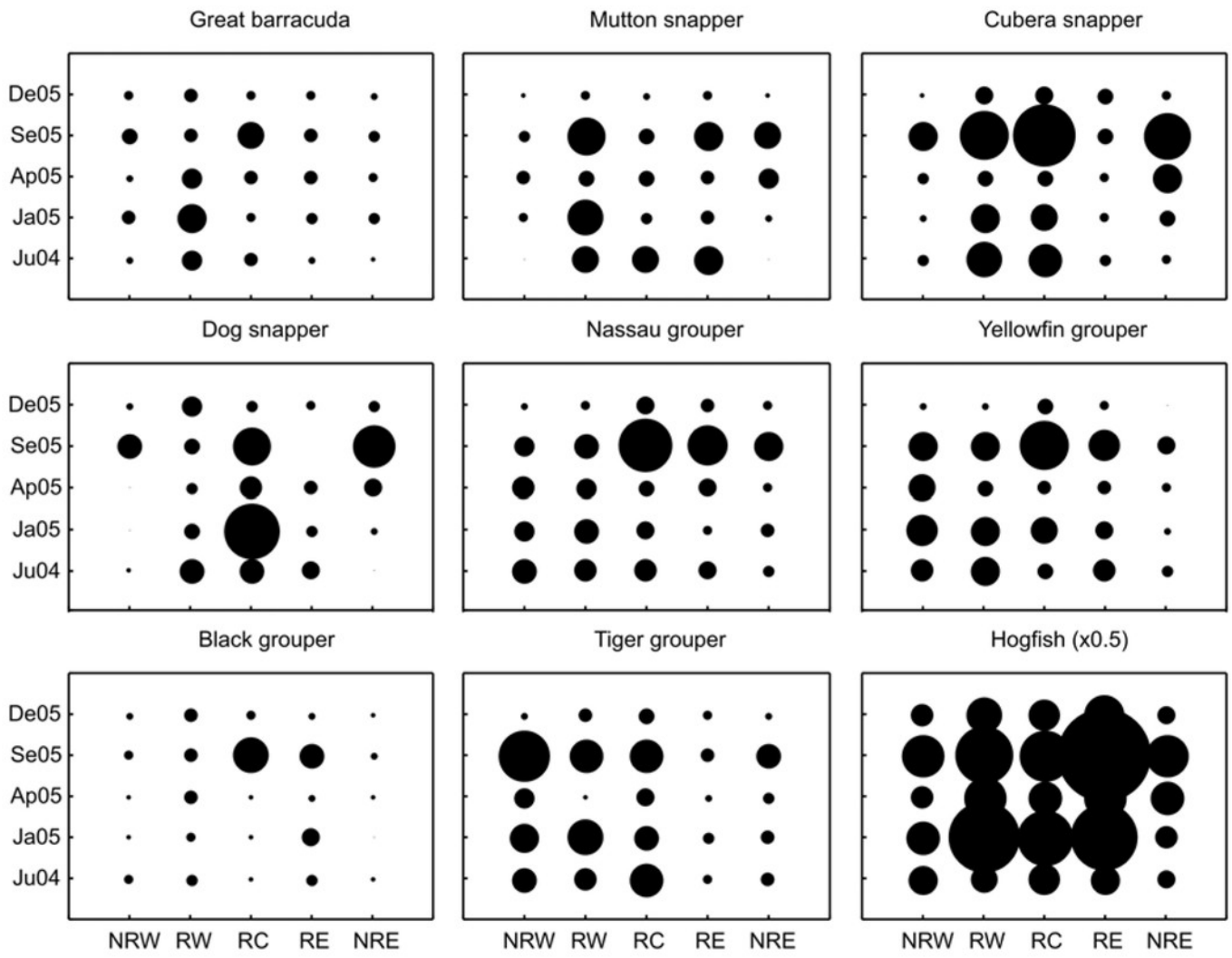

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Figure 3

Differences in fish densities between reserves and non-reserves sites for targeted trophy species.

Pooled mean densities (number of individuals 1000 m^{-2} ± 95% confidence interval) for targeted trophy species on reef slopes (A) and reef crest (B) by protection level. Non-reserve sites (white bars) and reserve sites (gray bars). Horizontal arrows denote significant differences (Table 2, Welch's test $p<0.05$).

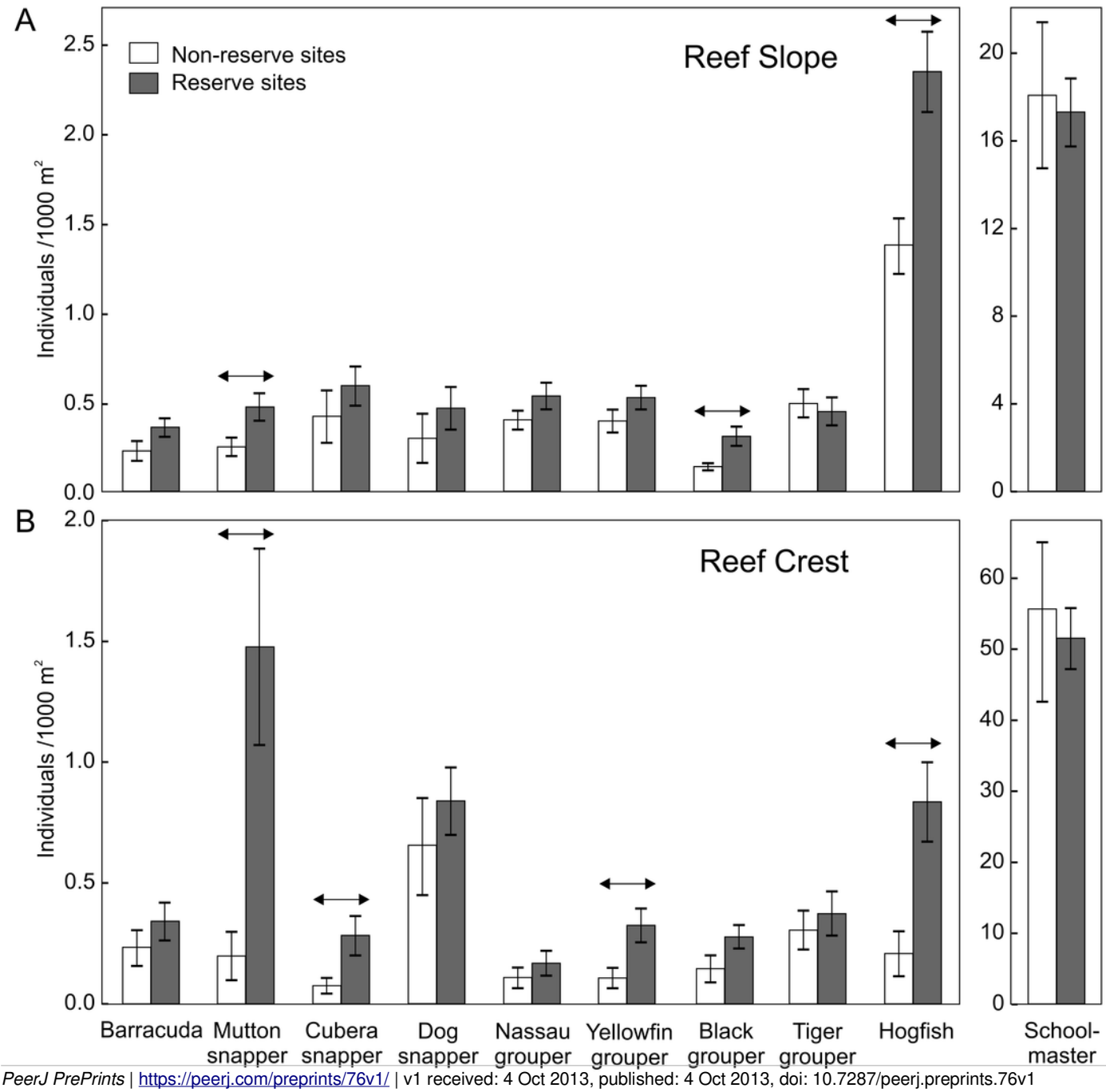

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Figure 4

Relative comparisons of mean densities of targeted trophy species (above trophy size) per zones and survey time on reef crest habitats.

Circle diameters are proportional to the mean density of each species at each combination of survey site and time. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center. Survey date labels show month (first two letters) and year (last two digits).

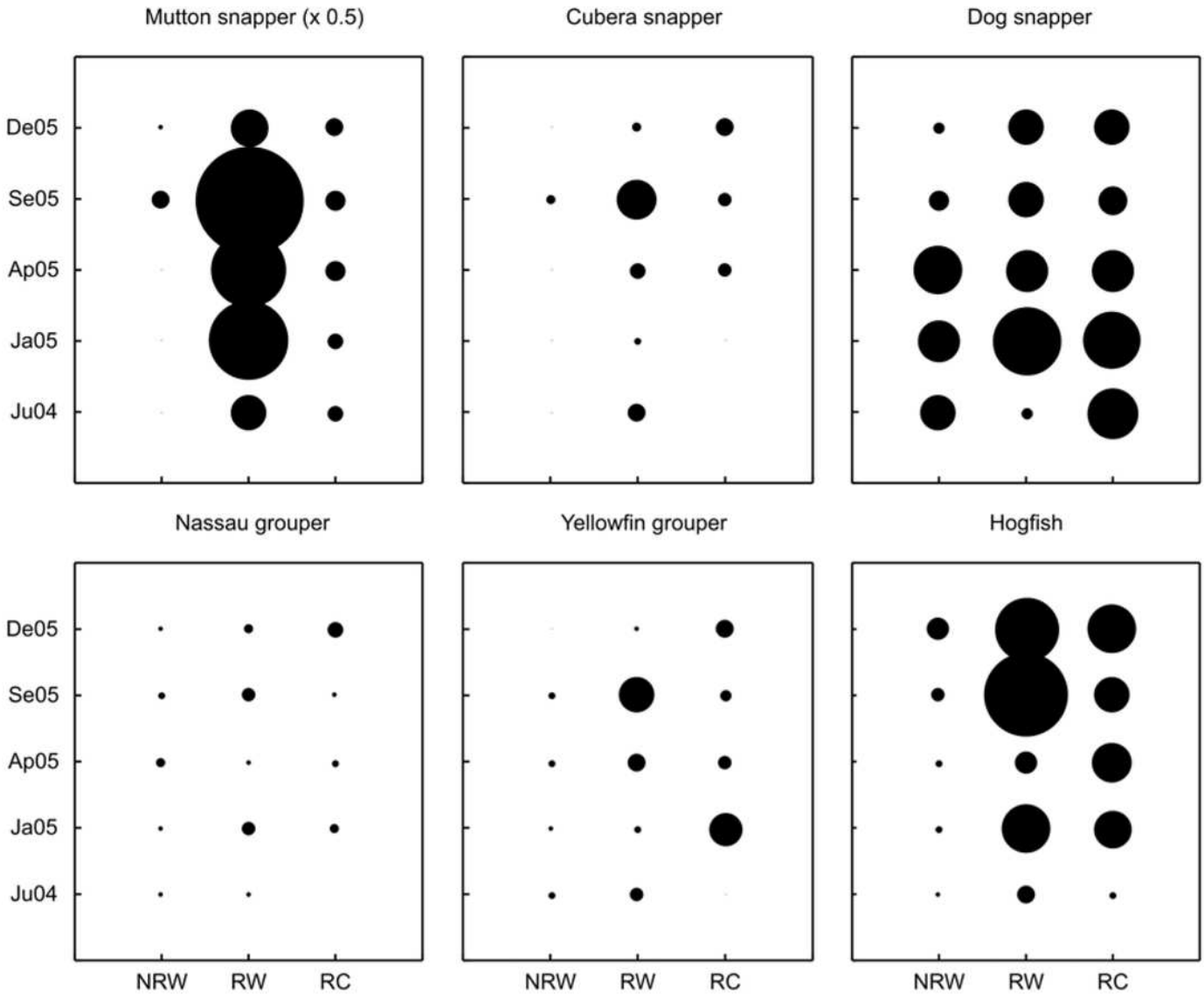

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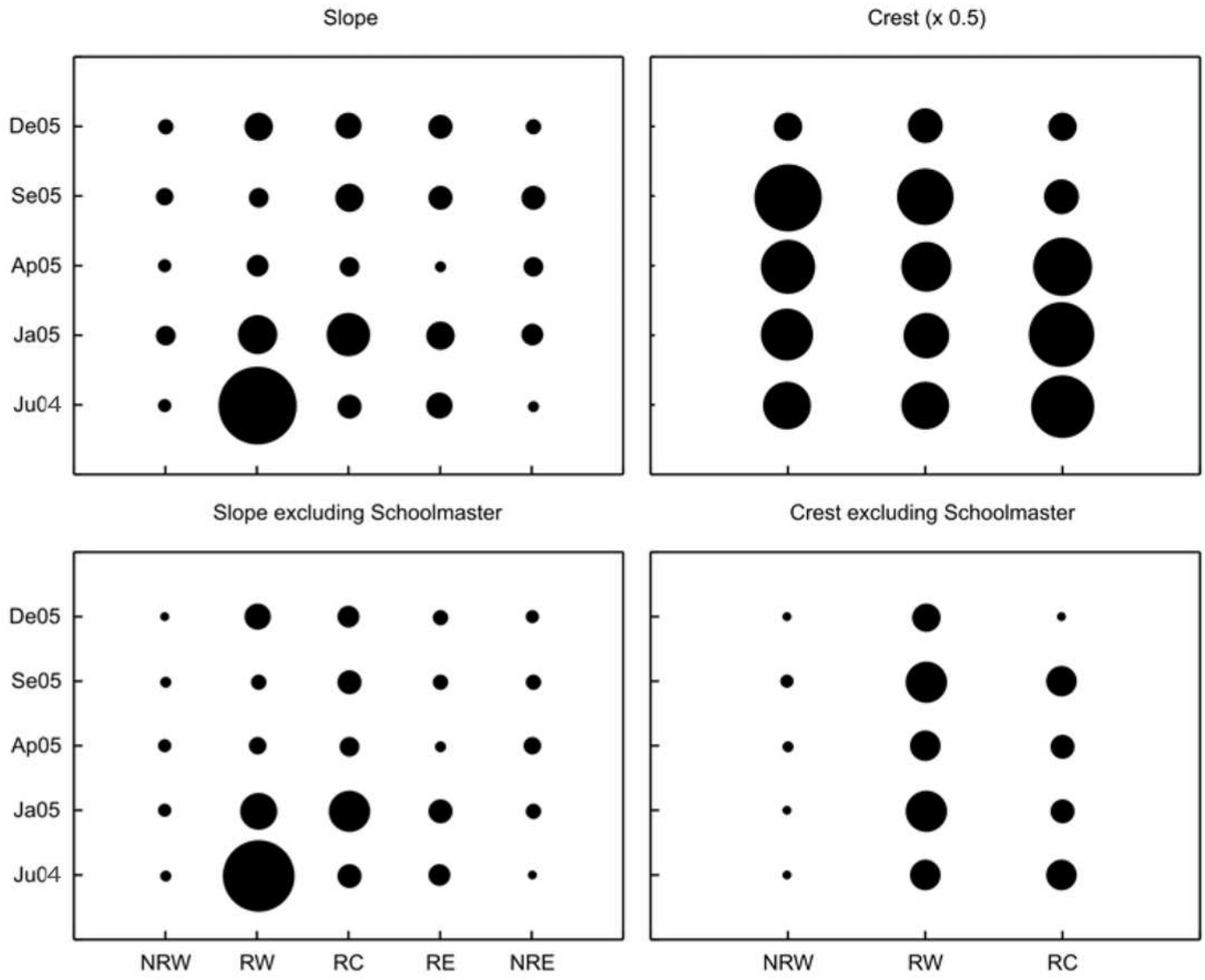
Figure 5

Comparison of pooled averages of the most frequent (f>50%) trophy species for the combination of reef habitat, zone, and time.

Top panel included the first ten species in Table 1. Bottom panel included nine species and excluded the schoolmaster. Circle sizes are proportional to the mean density of each group. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center; RE, Reserve East; NRE, Non-Reserve East. Survey date labels shows month (first two letters) and year (last two digits).



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