

# 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.

1 Fabián Pina-Amargós<sup>1</sup>, Gaspar González-Sansón<sup>2</sup>, Félix Martín-Blanco<sup>3</sup> and Abel Valdivia<sup>4\*</sup>

2 <sup>1</sup>Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, Morón, Ciego de Ávila, CP 69

3 400, Cuba,

4 <sup>2</sup>Department of Studies for Sustainable Development of the Coastal Zone, University of

5 Guadalajara, Jalisco, Mexico

6 <sup>3</sup>Tropical Research and Education Center, University of Florida, Homestead, FL 33031, USA

7 <sup>4</sup>Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599

8 USA

9 \*Correspondence author email: [abel.valdivia@unc.edu](mailto:abel.valdivia@unc.edu)

## 10 INTRODUCTION

11 Marine reserves have been largely beneficial for the recovery of fish density, biomass, and  
12 diversity (Côté *et al.* 2001; Halpern 2003; Molloy *et al.* 2009). Studies have shown an increase in  
13 abundance of targeted species, families, and even functional groups after the establishment of no-  
14 take marine reserves (Russ *et al.* 2003; Alcala *et al.* 2005; Claudet *et al.* 2008). Positive effects  
15 have been observed in average size (20-30% increase), species richness (11-23% increase), and  
16 reproductive capacity (Mosquera *et al.* 2000; Côté *et al.* 2001; Russ & Alcala 2003; Palumbi  
17 2004). The benefits of protection have been detected as early as one to five years following  
18 fishing bans (Gell & Roberts 2003; Halpern 2003; Russ *et al.* 2003; Palumbi 2004) with positive  
19 effects increasing over time (Halpern & Warner 2002; Maypa *et al.* 2002; Alcala *et al.* 2005;  
20 Claudet *et al.* 2008). Although marine reserves are presumed to restore several species from  
21 exploitation, not all species respond positively to protection due to their ecological characteristics  
22 (Claudet *et al.* 2010).

23         The response to protection is greatly variable among fish taxa depending on their  
24 commercial value, body size, mobility and other life-history and ecological traits. Overall,  
25 strongly exploited species of larger body size tend to respond significantly better and faster than  
26 unexploited and relatively smaller species (Mosquera *et al.* 2000; Russ *et al.* 2003; Claudet *et al.*  
27 2008, 2010). Furthermore, relative long-lived species with great mobility and variable  
28 recruitment may respond slower to fishing closures than short-lived species with narrow spatial  
29 requirements and steady recruitment (Gell & Roberts 2003; Russ *et al.* 2003; Palumbi 2004). In  
30 fact, beneficial effects could take decades to detect in very mobile species. For instance, pelagic  
31 fish species, which movement patterns expand beyond reserve boundaries, respond slower than  
32 less vagile coastal species (Roberts & Sargant 2002; Micheli *et al.* 2004). Nonetheless, exploited  
33 mobile species with wide home ranges still benefited from protection (Claudet *et al.* 2010). In  
34 contrast, non-commercial bycatch and unexploited species rarely respond to protection and may

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

37 Several factors can hinder the detection of positive effects in marine reserves.

38 Dissimilarities in habitat structural complexity and benthic community composition can lead to  
39 differences in fish assemblages that are independent of protection status, as the abundance of a  
40 number of fish species is correlated with substratum characteristics (McClanahan 1994; Roberts  
41 & Sargant 2002; Friedlander *et al.* 2003; Harborne *et al.* 2012). Similarly, the acquired behavior  
42 of target fish species towards divers (e.g. due to feeding practices in some areas) could lead to  
43 overestimation of fish abundances (Kulbicki 1998; Hawkins *et al.* 1999). Additionally, lack of  
44 appropriate spatial and temporal replication in some studies (Halpern & Warner 2002; Halpern  
45 2003; Alcalá *et al.* 2005), the use of different methods to compare fish abundances (Maypa *et al.*  
46 2002; Ward-Paige *et al.* 2010), temporal fluctuations in population abundance (Babcock *et al.*  
47 2010), and ineffective enforcement (Pomeroy *et al.* 2005; Mora *et al.* 2006) can thwart the  
48 detections of beneficial effects of marine reserves.

49 Most studies addressing the effects of marine reserves on fish assemblages in the  
50 Caribbean have focused on relative small protected areas (Polunin & Roberts 1993; Roberts  
51 1995; Roberts & Hawkins 1997; Roberts *et al.* 2001). This is because few relative large and  
52 continuous marine reserves exist in the region and their fish communities can be highly variable  
53 due to natural intra habitat differences (Chiappone & Sullivan-Sealey 2000; Harborne *et al.*  
54 2008). Relative larger marine reserves, however, may have more implications for the recovery of  
55 large and mobile reef fish populations than smaller reserves at scales necessary for conservation  
56 and fisheries management (Halpern 2003; Claudet *et al.* 2008; Gaines *et al.* 2010). But effective  
57 enforcement and management in relative large marine reserves is difficult to achieve, especially  
58 in developing countries where there is limited amount of resources for conservation (Mora *et al.*  
59 2006; Guidetti *et al.* 2008). Thus, understanding the dynamics of relative large marine reserves in

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

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

## 79 MATERIAL AND METHODS

### 80 Study sites and survey design

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

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

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

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

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

### 116 **Fish densities**

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

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

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.



158 **Reef structural complexity and benthic communities**

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

168 **Data analysis**

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

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

## 182 **RESULTS**

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

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

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

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

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

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

253 Our results support the hypothesis that the implementation of the JDLR marine reserve has  
254 promoted higher densities of commercially valuable and relative large reef fish species. This is  
255 consistent with previous meta-analyses that found that the greatest benefits of reserves are the  
256 recovery of exploited species, especially large ones (Côté *et al.* 2001). The relative larger size of  
257 this reserve (over 900 km<sup>2</sup>) may have provided greater benefits to species, such as top predators,  
258 that have large area requirements and that are not effectively protected in small reserves (Halpern  
259 2003). There is no long-term data set addressing changes in the fish communities before and after  
260 this reserve establishment, therefore evidence of protection based on a before and after approach  
261 is impossible to demonstrate. Nonetheless, the patterns observed in the density of trophy species  
262 are unlikely the response to several confounding factors such as, within reef type heterogeneity,  
263 spatially different fishing efforts before the reserve establishment, lack of appropriate replication,  
264 alteration of fish behavior due to observers, differential recruitment, or a combination of them.  
265 By surveying multiple control sites outside the reserve, replicating our study in space and time,  
266 and critically analyzing these aforementioned cofactors we can demonstrate that protection from  
267 fishing and a gradient of enforcement, from the center to outside the reserve, is the most plausible  
268 explanation for the differences observed.

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

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

285 Understating fishing pressure before the establishment of marine reserves is important to  
286 determine the potential effects of protection after fishing has ended (Russ & Alcala 1998;  
287 Halpern 2003; Alcala *et al.* 2005; Osenberg *et al.* 2006). This approach is fundamental to avoid  
288 confounding factors such as spatial differences in fishing activities. In JDLR, for both reef  
289 habitats on all zones, except NWR, catch and fishing effort were homogeneously distributed  
290 along the archipelago before the reserve establishment, suggesting similar spatial abundance of  
291 finfishes before protection (Pina-Amargós *et al.* 2008a; Claro *et al.* 2009). With the declaration of  
292 the marine reserve in 1996, catch and fishing effort were relocated to outside the reserve (Claro  
293 *et al.* 2001; Pina-Amargós *et al.* 2008a). After ten years of protection, Pina-Armagós *et al.*  
294 (2008a) found strong negative association between landings and fish abundance of most  
295 commercially important species across the JDLR archipelago. This suggests that fishing pressure  
296 has been lower inside the reserve where fish were more abundant (Pina-Amargós *et al.* 2008a).  
297 Thus, the fish abundance distribution in JDLR (greater inside the reserve) was unlikely related to  
298 uneven fishing pressure before the establishment of the protected area.

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

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

306 Observations of fish behavior in JDLR archipelago showed that species of most  
307 commercial value tended to flee from divers, when closely approached, more often in non-reserve  
308 sites than reserve sites (Pina-Amargós *et al.* 2008b). Comparisons of flight distance (i.e. *distance*  
309 *at which an organism begins to flee an approaching threat*) inside and outside long-established  
310 reserves indicate fish behavior can be modified by the presence/absence of fishing (Gotanda *et*  
311 *al.* 2009; Feary *et al.* 2011). For example, fish respond to divers in fished areas by fleeing or  
312 swimming away, while in protected areas they are less afraid and more curious (Gotanda *et al.*  
313 2009; Feary *et al.* 2011). Thus, this modified behavior can be used as a metric of fishing intensity.  
314 The previously reported contrasting behavior of trophy species between outside and inside the  
315 JDLR (Pina-Amargós *et al.* 2008b) support our hypothesis of stronger protection in the reserve.

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

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

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

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



353 2003). In fact, a grouper spawning hot spot has been confirmed inside the reserve (in RC) (Pina-  
354 Amargós *personal observation*). Therefore, several potential spawning aggregation sites could be  
355 producing larvae and being dispersed homogeneously along the entire JDLR archipelago.

356 Out of the ten trophic species analyzed in our study, six showed significantly higher  
357 densities in both reef habitats (slope and crest) inside the marine reserve at some time during the  
358 study. Differences between reserves and non-reserves may be stronger for the reef slope than the  
359 crest habitat where fishes are naturally more abundant. These species (yellowfin grouper, Nassau  
360 grouper, cubera snapper, dog snapper, mutton snapper and hogfish) are also among the most  
361 commercially valuable and targeted in the region (Claro & Lindeman 2003; Pina-Amargós *et al.*  
362 2008a; Claro *et al.* 2009). Therefore, as expected, these species have benefited the most from  
363 protection when fishing stopped or was drastically reduced (Côté *et al.* 2001; Micheli *et al.* 2004;  
364 Russ *et al.* 2008). Tiger grouper and schoolmaster did not clearly respond to protection and  
365 positive effects were not consistent between reef habitats for black grouper and great barracuda.  
366 These last four species are less targeted by recreational fisheries in the JDLR archipelago (Pina-  
367 Amargós *et al.* 2008a; Claro *et al.* 2009). The main reasons, based on the semi-structure  
368 interviews, were that schoolmaster was regarded as low quality for consumption in the region,  
369 which support prior finding that less targeted species are generally unaffected by reserve  
370 establishment (Micheli *et al.* 2004; Claudet *et al.* 2010). Similarly, tiger grouper, black grouper  
371 and great barracuda are prone to “ciguatera” (i.e. fish poisoning) in the region and fishers may  
372 avoid them (Claro *et al.* 2001). In contrast, fishing regulations in Cuba have limited catch  
373 allowances for larger specimens of black grouper, cubera snapper and dog snapper around the  
374 island (Claro *et al.* 2009) and although they are also prone to ciguatera (Claro *et al.* 2001) they  
375 may still caught and consumed. Nonetheless, our results support that commercially valuable  
376 species has increased in abundance after the establishment of marine reserves, hence responding  
377 better to protection.

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378 Finally, effective management is essential for the success of marine reserves (Pomeroy *et*  
379 *al.* 2005; Mora *et al.* 2006). Ultimately, the positive response of fish to protection is indicative of  
380 good compliance with fishing restrictions (Smith *et al.* 2006; Guidetti *et al.* 2008). Thus, fish  
381 responses to protection can be indirectly used to evaluate the effectiveness of fully no-take areas  
382 (Smith *et al.* 2006; Guidetti *et al.* 2008). According to Pina-Amargós *et al.* (2008a), effective  
383 protection decreases from RC, with the least human impact, to RW and RE with moderate  
384 protection, and NRW and NRE with the highest human activity. Although the JDLR marine  
385 reserve is not formally enforced by any national entity (Pina-Amargós *et al.* 2008a), the area has  
386 mostly escaped the high fishing pressure recorded in the rest of the Caribbean (Hawkins &  
387 Roberts 2004). This seems related to the relative remoteness of the archipelago, the economic  
388 situation of the country, restricted accessibility, and the limited amount of resources (e.g. boats,  
389 fuel, ice) that local recreational and commercial fishermen have faced for decades (Claro *et al.*  
390 2009). Enforcement in the park is achieved indirectly by the reserve users. For example, former  
391 fishermen have become tour operators for the small resort that operates within the park (within  
392 the RC zone), where only ~1000 divers and fly-fishers (catch and release) are allowed every year.  
393 This model have indirectly promoted a reduction of illegal fishing by fostering protection (Pina-  
394 Amargós *et al.* 2008a) since the revenue from local tourism is highly more profitable than fishing  
395 (Figueredo-Martín *et al.* 2010). Yet adequate protection in JDLR marine reserve closer to the  
396 boundaries of the park might be an issue (as reflected in relative lower trophy fish densities)  
397 because most of the touristic activities, thus indirect enforcement, occur at the center of the  
398 reserve (Pina-Armargós, *personal observations*).

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

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

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#### 420 **REFERENCES**

- 421 1.  
422 Alcalá, A.C., Russ, G.R., Maypa, A.P. & Calumpong, H.P. (2005). A long-term, spatially  
423 replicated experimental test of the effect of marine reserves on local fish yields. *Can. J. Fish.*  
424 *Aquat. Sci.*, 62, 98–108.
- 425 2.  
426 Appeldoorn, R.S. & Lindeman, K.C. (2002). A Caribbean-wide survey of marine reserves: spatial  
427 coverage and attributes of effectiveness. *Gulf and Caribbean Research*, 14, 139–154.
- 428 3.

- 429 Babcock, R.C., Shears, N.T., Alcalá, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., *et al.* (2010).  
430 Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects.  
431 *Proceedings of the National Academy of Sciences*, 107, 18256–18261.
- 432 4.  
433 Chiappone, M. & Sullivan-Sealey, K.M. (2000). Marine reserve design criteria and measures of  
434 success: lessons learned from the Exuma Cays Land and Sea Park, Bahamas. *Bulletin of Marine*  
435 *Science*, 66, 691–705.
- 436 5.  
437 Claro, R. & Lindeman, K.C. (2003). Spawning aggregation sites of snapper and grouper species  
438 (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research*, 14, 91–  
439 106.
- 440 6.  
441 Claro, R., Lindeman, K.C. & Parenti, L.R. (2001). *Ecology of the marine fishes of Cuba*.  
442 Smithsonian Institution Press, Washington [D.C.].
- 443 7.  
444 Claro, R., Mitcheson, Y.S. de, Lindeman, K.C. & García-Cagide, A.R. (2009). Historical analysis  
445 of Cuban commercial fishing effort and the effects of management interventions on important  
446 reef fishes from 1960–2005. *Fisheries Research*, 99, 7–16.
- 447 8.  
448 Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-  
449 Ruzafa, Á., *et al.* (2008). Marine reserves: size and age do matter. *Ecology Letters*, 11, 481–489.
- 450 9.  
451 Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., *et al.*  
452 (2010). Marine reserves: Fish life history and ecological traits matter. *Ecological Applications*,  
453 20, 830–839.
- 454 10.  
455 Côté, I.M., Mosqueira, I. & Reynolds, J.D. (2001). Effects of marine reserve characteristics on  
456 the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, 59, 178–189.
- 457 11.  
458 Feary, D.A., Cinner, J.E., Graham, N. a. J. & Januchowski-Hartley, F.A. (2011). Effects of  
459 customary marine closures on fish behavior, spear-fishing success, and underwater visual  
460 surveys. *Conservation Biology*, 25, 341–349.
- 461 12.  
462 Figueredo-Martín, T., Pina-Amargós, F., Angulo-Valdés, J. & Gómez-Fernández, R. (2010).  
463 Buceo contemplativo en Jardines de la Reina, Cuba: caracterización y percepción sobre el estado  
464 de conservación del área. *Rev. Invest. Mar*, 31, 23–32.
- 465 13.  
466 Francini-Filho, R.B. & Moura, R.L. (2008). Evidence for spillover of reef fishes from a no-take

- 467 marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fisheries*  
468 *Research*, 93, 346–356.
- 469 14.  
470 Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R. & Rodgers, K.S. (2003). Effects of  
471 habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the  
472 Hawaiian archipelago. *Coral Reefs*, 22, 291–305.
- 473 15.  
474 Gaines, S.D., White, C., Carr, M.H. & Palumbi, S.R. (2010). Designing marine reserve networks  
475 for both conservation and fisheries management. *PNAS*, 107, 18286–18293.
- 476 16.  
477 Gell, F.R. & Roberts, C.M. (2003). Benefits beyond boundaries: the fishery effects of marine  
478 reserves. *Trends in Ecology & Evolution*, 18, 448–455.
- 479 17.  
480 Gotanda, K., Turgeon, K. & Kramer, D. (2009). Body size and reserve protection affect flight  
481 initiation distance in parrotfishes. *Behavioral Ecology and Sociobiology*, 63, 1563–1572.
- 482 18.  
483 Graham, N. (2007). Ecological versatility and the decline of coral feeding fishes following  
484 climate driven coral mortality. *Marine Biology*, 153, 119–127.
- 485 19.  
486 Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M., Pais, A., *et al.* (2008). Italian  
487 marine reserve effectiveness: Does enforcement matter? *Biological Conservation*, 141, 699–709.
- 488 20.  
489 Halpern, B.S. (2003). The impact of marine reserves: do reserves work and does reserve size  
490 matter? *Ecological Applications*, 13, 117–137.
- 491 21.  
492 Halpern, B.S., Lester, S.E. & Kellner, J.B. (2009). Spillover from marine reserves and the  
493 replenishment of fished stocks. *Environmental Conservation*, 36, 268–276.
- 494 22.  
495 Halpern, B.S. & Warner, R.R. (2002). Marine reserves have rapid and lasting effects. *Ecology*  
496 *Letters*, 5, 361–366.
- 497 23.  
498 Harborne, A., Mumby, P. & Ferrari, R. (2012). The effectiveness of different meso-scale rugosity  
499 metrics for predicting intra-habitat variation in coral-reef fish assemblages. *Environmental*  
500 *Biology of Fishes*, 94, 431–442.
- 501 24.  
502 Harborne, A.R., Mumby, P.J., Kappel, C.V., Dahlgren, C.P., Micheli, F., Holmes, K.E., *et al.*  
503 (2008). Reserve effects and natural variation in coral reef communities. *Journal of Applied*  
504 *Ecology*, 45, 1010–1018.

- 505 25.  
506 Hawkins, J.P. & Roberts, C.M. (2004). Effects of artisanal fishing on Caribbean coral reefs.  
507 *Conservation Biology*, 18, 215–226.
- 508 26.  
509 Hawkins, J.P., Roberts, C.M., Van 'T Hof, T., De Meyer, K., Tratalos, J. & Aldam, C. (1999).  
510 Effects of recreational Scuba diving on Caribbean corals and fish communities. *Conservation*  
511 *Biology*, 13, 888–897.
- 512 27.  
513 Hixon, M.A. & Beets, J.P. (1993). Predation, prey refuges, and the structure of coral-reef fish  
514 assemblages. *Ecological Monographs*, 63, 77–101.
- 515 28.  
516 Johansen, J.L., Bellwood, D.R. & Fulton, C.J. (2008). Coral reef fishes exploit flow refuges in  
517 high-flow habitats. *Mar Ecol Prog Ser*, 360, 219–226.
- 518 29.  
519 Jones, G.P., McCormick, M.I., Srinivasan, M. & Eagle, J.V. (2004). Coral decline threatens fish  
520 biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United*  
521 *States of America*, 101, 8251–8253.
- 522 30.  
523 Kulbicki, M. (1998). How the acquired behaviour of commercial reef fishes may influence the  
524 results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology*,  
525 222, 11–30.
- 526 31.  
527 Lindeman, K.C., Lee, T.N., Wilson, W.D., Claro, R. & Ault, J.S. (1999). Transport of larvae  
528 originating in southwest Cuba and the Dry Tortugas: evidence for partial retention in grunts and  
529 snappers. In: *52 Proceedings of the Fifty Second Annual Gulf and Caribbean Fisheries Institute*.  
530 Key West, Florida, USA, pp. 732–747.
- 531 32.  
532 Lindeman, K.C., Pugliese, R., Waugh, G.T. & Ault, J.S. (2000). Developmental patterns within a  
533 multispecies reef fishery: management applications for essential fish habitats and protected areas.  
534 *Bulletin of Marine Science*, 66, 929–956.
- 535 33.  
536 Maypa, A.P., Russ, G.R., Alcala, A.C. & Calumpong, H.P. (2002). Long-term trends in yield and  
537 catch rates of the coral reef fishery at Apo Island, central Philippines. *Mar. Freshwater Res.*, 53,  
538 207–213.
- 539 34.  
540 McClanahan, T.R. (1994). Kenyan coral reef lagoon fish: effects of fishing, substrate complexity,  
541 and sea urchins. *Coral Reefs*, 13, 231–241–241.
- 542 35.

- 543 McClanahan, T.R., Graham, N.A.J., Maina, J., Chabanet, P., Bruggemann, J.H. & Polunin, N.  
544 (2007). Influence of instantaneous variation on estimates of coral reef fish populations and  
545 communities. *Mar Ecol Prog Ser*, 340, 221–234.
- 546 36.
- 547 Micheli, F., Halpern, B.S., Botsford, L.W. & Warner, R.R. (2004). Trajectories and correlates of  
548 community change in no-take marine reserves. *Ecological Applications*, 14, 1709–1723.
- 549 37.
- 550 Molloy, P.P., McLean, I.B. & Côté, I.M. (2009). Effects of marine reserve age on fish  
551 populations: a global meta-analysis. *Journal of Applied Ecology*, 46, 743–751.
- 552 38.
- 553 Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., *et al.* (2006). Coral  
554 reefs and the global network of marine protected areas. *Science*, 312, 1750–1751.
- 555 39.
- 556 Mosquera, I., Côté, I.M., Jennings, S. & Reynolds, J.D. (2000). Conservation benefits of marine  
557 reserves for fish populations. *Animal Conservation*, 3, 321–332.
- 558 40.
- 559 Newman, M.J.H., Paredes, G.A., Sala, E. & Jackson, J.B.C. (2006). Structure of Caribbean coral  
560 reef communities across a large gradient of fish biomass. *Ecology Letters*, 9, 1216–1227.
- 561 41.
- 562 Osenberg, C.W., Bolker, B.M., White, J.S.S., Mary, C.M.S. & Shima, J.S. (2006). Statistical  
563 issues and study design in ecological restorations: lessons learned from marine reserves.  
564 *Foundations of restoration ecology*, 280.
- 565 42.
- 566 Palumbi, S.R. (2004). Marine reserves and ocean neighborhoods: The spatial scale of marine  
567 populations and their management. *Annual review of environment and resources*, 29, 31–68.
- 568 43.
- 569 Paris, C.B., Cowen, R.K., Claro, R. & Lindeman, K.C. (2005). Larval transport pathways from  
570 Cuban snapper (*Lutjanidae*) spawning aggregations based on biophysical modeling. *Marine*  
571 *Ecology Progress Series*, 296, 93–106.
- 572 44.
- 573 Pina-Amargós, F., González-Sansón, G. & Cabrera-Paez, Y. (2008a). Effects of fishing activity  
574 reduction in Jardines de la Reina Marine Reserve, Cuba. In: *Proceedings of the 60th Annual*  
575 *Meeting of the Gulf and Caribbean Fisheries Institute*. pp. 334–348.
- 576 45.
- 577 Pina-Amargós, F., González-Sansón, G., Jimenez del Castillo, A., Zayas, A., Martin-Blanco, F. &  
578 Acosta de la Red, W. (2008b). Movement of adult fish in the Jardines de la Reina marine reserve,  
579 Cuba. In: *Proceedings of the Symposium on Caribbean Connectivity*. pp. 127–144.
- 580 46.



- 581 Pina-Amargós, F., Hernandez, L., Clero, L. & González-Sansón, G. (2008c). Características de  
582 los hábitats coralinos en Jardines de la Reina, Cuba. *Rev. Invest. Mar*, 29, 225–237.
- 583 47.
- 584 Pina-Amargós, F., Sansón, G., del Castillo, A., Fernández, A., Blanco, F. & de la Red, W. (2010).  
585 An experiment of fish spillover from a marine reserve in Cuba. *Environmental Biology of Fishes*,  
586 87, 363–372.
- 587 48.
- 588 Polunin, N.V.C. & Roberts, C.M. (1993). Greater biomass and value of target coral-reef fishes in  
589 two small Caribbean marine reserves. *Mar Ecol Prog Ser*, 100, 167–176.
- 590 49.
- 591 Pomeroy, R.S., Watson, L.M., Parks, J.E. & Cid, G.A. (2005). How is your MPA doing? A  
592 methodology for evaluating the management effectiveness of marine protected areas. *Ocean &*  
593 *Coastal Management*, 48, 485–502.
- 594 50.
- 595 Quinn, G.P. & Keough, M.J. (2002). *Experimental Design and Data Analysis for Biologists*.  
596 Cambridge University Press.
- 597 51.
- 598 Richards, B.L., Williams, I.D., Nadon, M.O. & Zgliczynski, B.J. (2011). A towed-diver survey  
599 method for mesoscale fishery-independent assessment of large-bodied reef fishes. *Bulletin of*  
600 *Marine Science*, 87, 55–74.
- 601 52.
- 602 Roberts, C.M. (1995). Rapid build-up of fish biomass in a Caribbean marine reserve.  
603 *Conservation Biology*, 9, 815–826.
- 604 53.
- 605 Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2001). Effects of marine  
606 reserves on adjacent fisheries. *Science*, 294, 1920–1923.
- 607 54.
- 608 Roberts, C.M. & Hawkins, J.P. (1997). How small can a marine reserve be and still be effective?  
609 *Coral Reefs*, 16, 150–150.
- 610 55.
- 611 Roberts, C.M. & Sargent, H. (2002). Fishery benefits of fully protected marine reserves: why  
612 habitat and behavior are important. *Natural Resource Modeling*, 15, 487–507.
- 613 56.
- 614 Russ, G., Alcala, A. & Maypa, A. (2003). Spillover from marine reserves: the case of *Naso*  
615 *vlamingii* at Apo Island, the Philippines. *Marine Ecology Progress Series*, 264, 15–20.
- 616 57.
- 617 Russ, G.R. & Alcala, A.C. (1998). Natural fishing experiments in marine reserves 1983 – 1993:  
618 roles of life history and fishing intensity in family responses. *Coral Reefs*, 17, 399–416.



- 619 58.  
620 Russ, G.R. & Alcala, A.C. (2003). Marine reserves: rates and patterns of recovery and decline of  
621 predatory fish, 1983-2000. *Ecological Applications*, 13, 1553–1565.
- 622 59.  
623 Russ, G.R., Cheal, A.J., Dolman, A.M., Emslie, M.J., Evans, R.D., Miller, I., *et al.* (2008). Rapid  
624 increase in fish numbers follows creation of world's largest marine reserve network. *Current*  
625 *Biology*, 18, R514–R515.
- 626 60.  
627 Sale, P.F. (1991). Habitat structure and recruitment in coral reef fishes. In: *Habitat structure: the*  
628 *physical arrangement of objects in space*. S.S. Bell, E.D. McCoy and H.R. Mushinsky (eds.).  
629 Chapman & Hall, London, U.K, pp. 197–210.
- 630 61.  
631 Smith, M.D., Zhang, J. & Coleman, F.C. (2006). Effectiveness of marine reserves for large-scale  
632 fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 153–164.
- 633 62.  
634 StatSoft, I. (2007). STATISTICA (data analysis software system) version 8.0. Available at:  
635 www.statsoft.com. Last accessed: 12 December 2007.
- 636 63.  
637 Underwood, A.J. (1996). *Experiments in Ecology: their logical design and interpretation using*  
638 *analysis of variance*. Cambridge University Press.
- 639 64.  
640 Ward-Paige, C., Mills Flemming, J. & Lotze, H.K. (2010). Overestimating fish counts by non-  
641 instantaneous visual censuses: consequences for population and community descriptions. *PLoS*  
642 *ONE*, 5, e11722.
- 643 65.  
644 Westera, M., Lavery, P. & Hyndes, G. (2003). Differences in recreationally targeted fishes  
645 between protected and fished areas of a coral reef marine park. *Journal of Experimental Marine*  
646 *Biology and Ecology*, 294, 145–168.
- 647 66.  
648 Willis, T. j., Millar, R. b., Babcock, R. c. & Tolimieri, N. (2003). Burdens of evidence and the  
649 benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation*, 30,  
650 97–103.

## 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<sup>-2</sup> ± 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.

1 Table 1

Common name	Trophy (cm)	Reef slope			Reef crest		
		<i>f</i> (%)	Mean ± SE	Size (cm)	<i>f</i> (%)	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

## 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  $T_{\text{welch}}$  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.

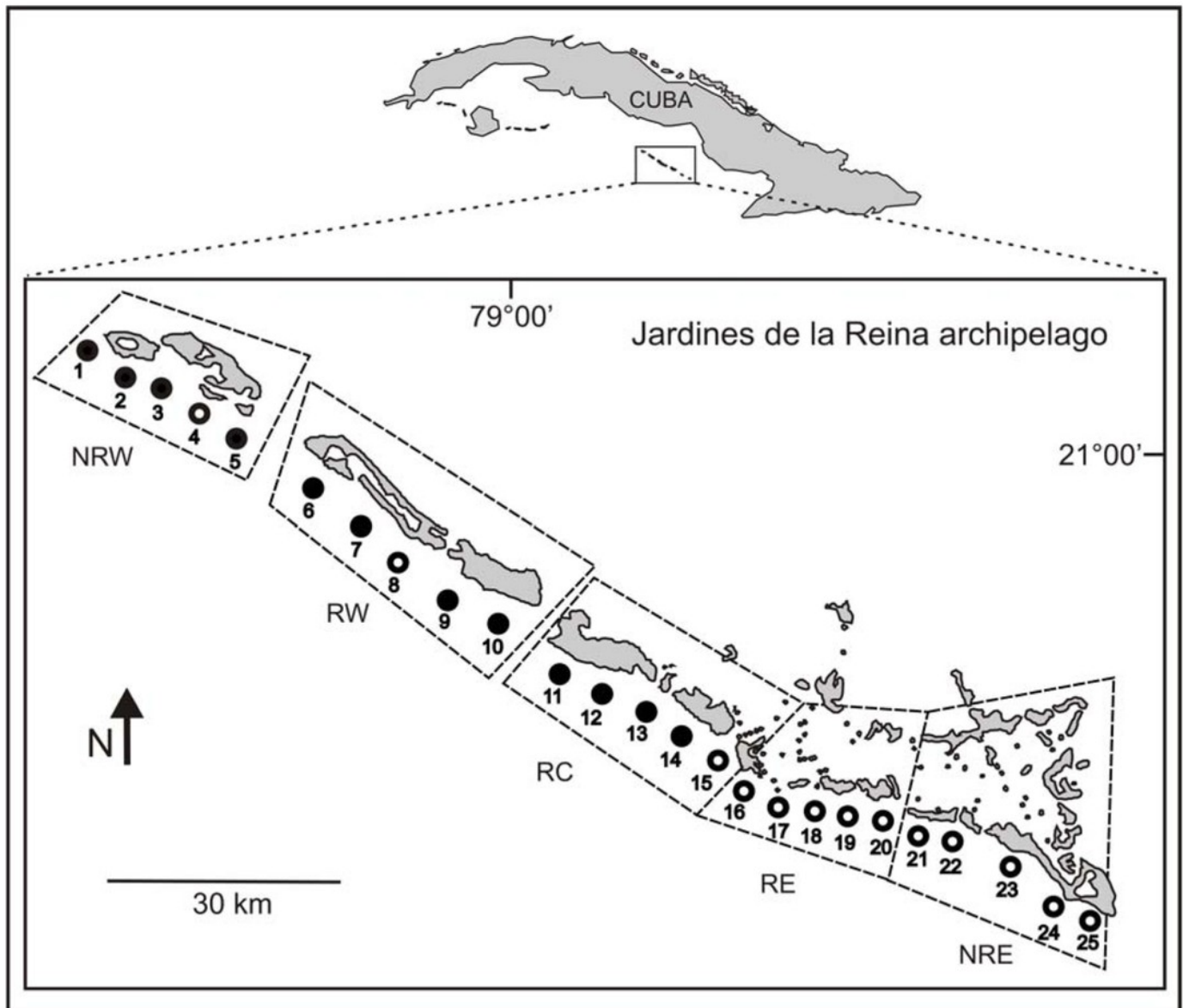
1 Table 2

A. ANOVA	Reef slope x Time		Reef crest x Time	
	Species/groups	F <sub>(16, 215)</sub>	p	F <sub>(8, 105)</sub>
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 <i>t</i> test	Reef Slope		Reef Crest	
	Species/groups	T <sub>welch</sub>	p	T <sub>welch</sub>
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*

# Figure 1

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

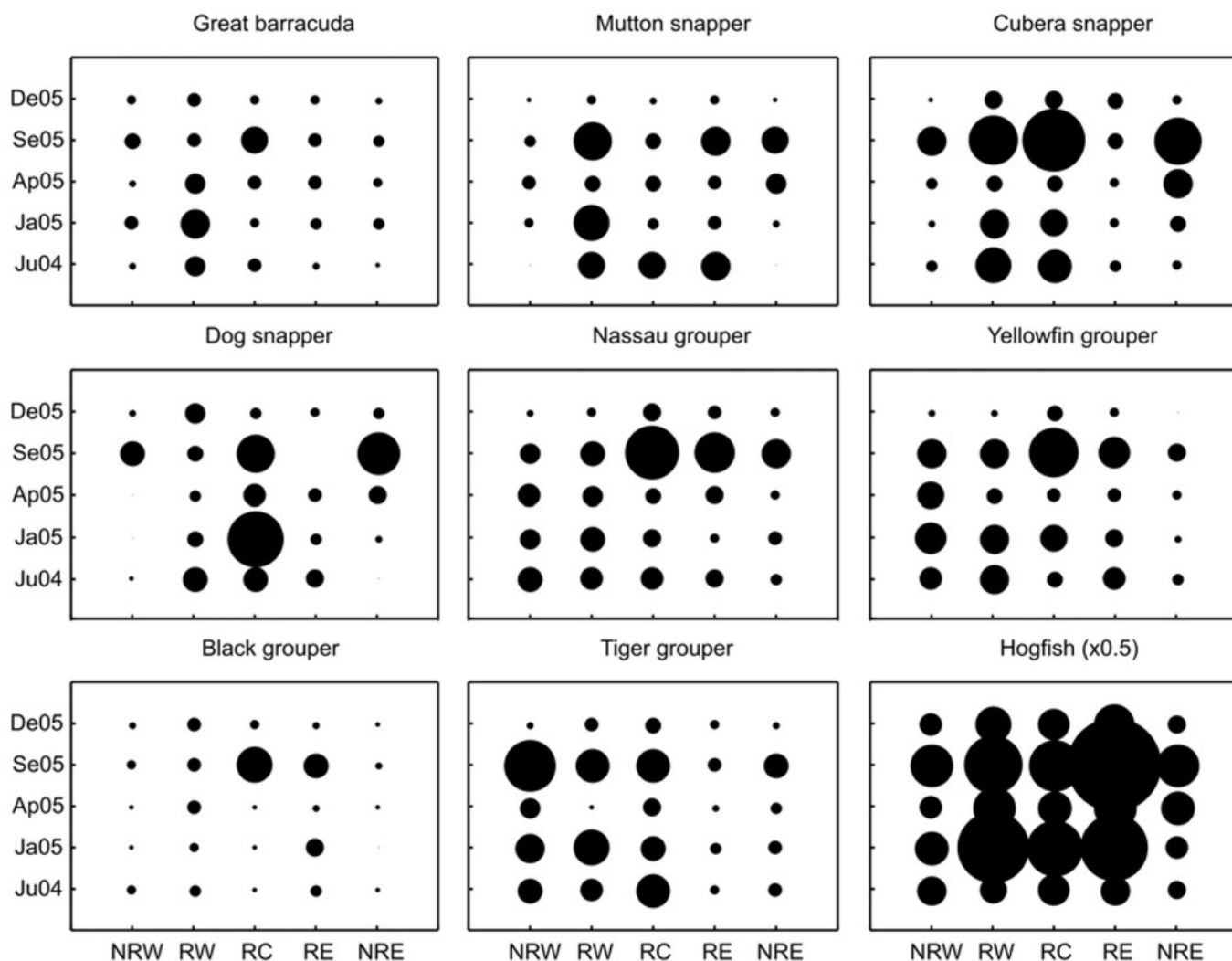
Solid black circles are sites where reef slope and reef crest were surveyed. White circles represent sites where only reef slope was sampled. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center; RE, Reserve East; NRE, Non-Reserve East.



# Figure 2

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

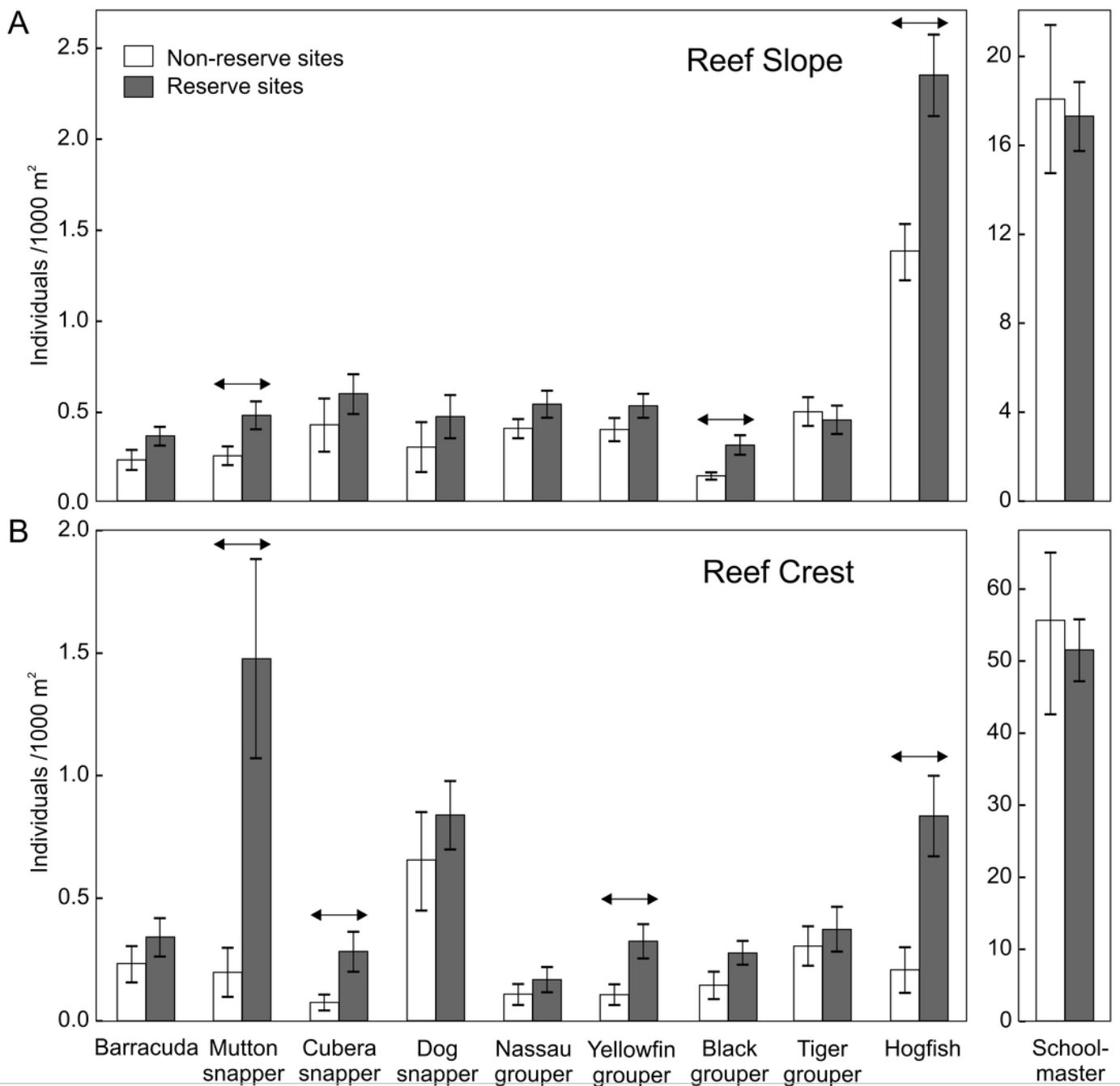
Circle diameters are proportional to the mean density of each species at each combination of surveyed site and time. NRW, Non-Reserve West; RW, Reserve West; RC, Reserve Center; RE, Reserve East; NRE, Non-Reserve East. Survey date labels show month (first two letters) and year (last two digits).



# Figure 3

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

Pooled mean densities (number of individuals  $1000\text{ m}^{-2} \pm 95\%$  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  $p < 0.05$ ).

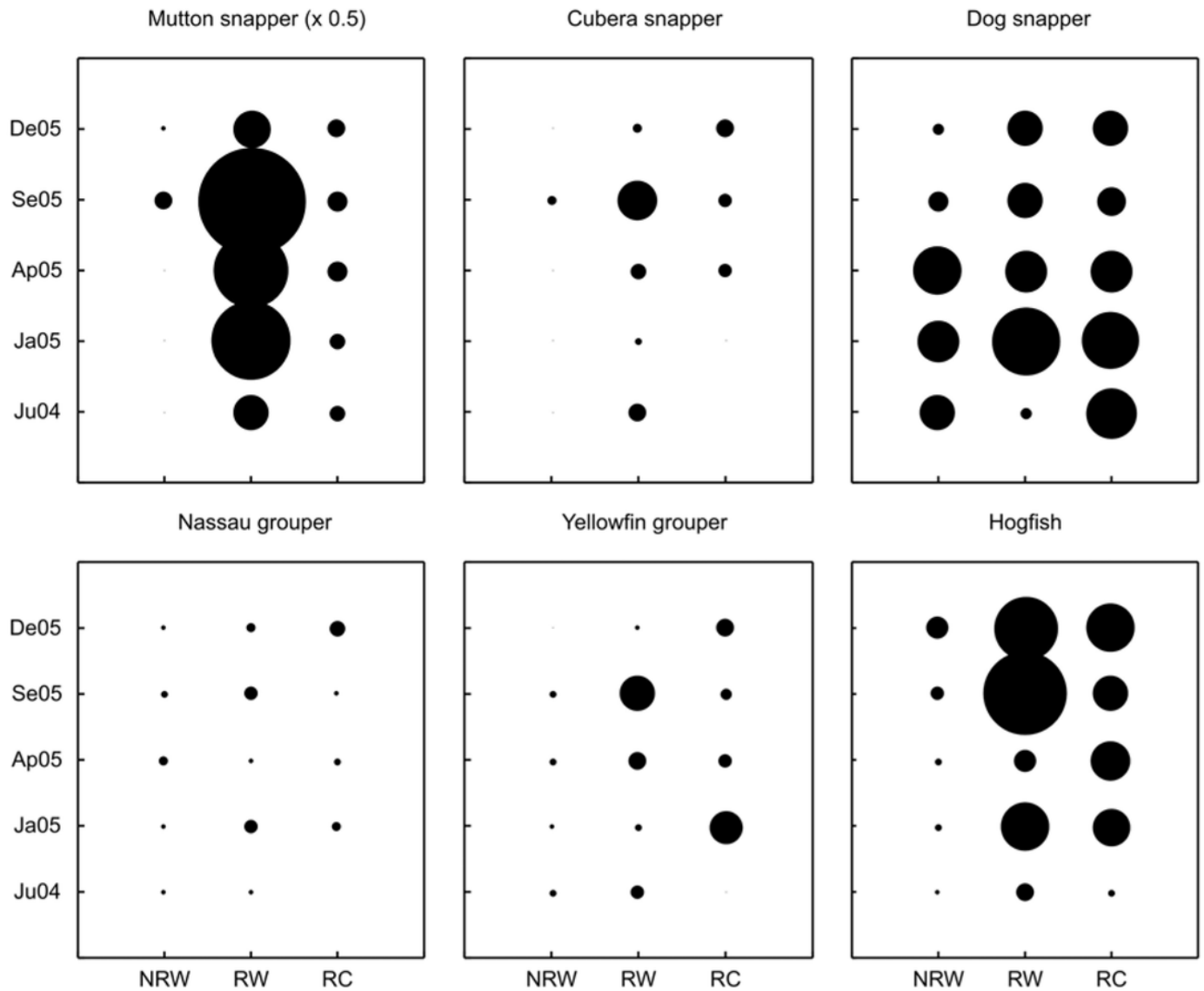




# Figure 4

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).



# Figure 5

Comparison of pooled averages of the most frequent ( $f > 50\%$ ) trophic 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).

