Spatial variation of parrotfish assemblages at oceanic islands in the western Caribbean: Evidence of indirect effects of fishing?

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Fish populations that bear considerable pressure levels tend to show a decline in the average size of individuals, with the small and unexploited species replacing the large and exploited ones. It is important to carry on with their characterization in areas where they are becoming a n important source of food for local human populations. An example of such species are parrotfishes, whose responses to external factors such as fishing need to be understood and predicted. In this study, we used a diver-operated stereo-video to examine individual body size, sex ratios and proportion of species of the parrotfish assemblage and analyze them on a qualitative fishing pressure gradient at four oceanic islands in the Colombian Caribbean. We reported over 10000 occurrences of eleven parrotfish species, of which we estimated the total length of over 90%, grouping them into three size categories (large, medium, and small). Our data showed a spatial variation of parrotfishes' abundances, biomass, and individual body size. Observed differences are size-category-dependent throughout the qualitative fishing pressure. In general, the medium-bodied species had smaller sizes, lower abundances , and thus lower contribution to the total parrotfish biomass at the most heavily fished island. Unexpectedly, we found evidence of possible indirect effects over the small-bodied species *Scarus iseri* and *Scarus taeniopterus* with significantly greater abundances, and larger sizes of males of *S. iseri,* at the higher fishing pressure sites. Overall, our data highlights the extent of the spatial variation in the parrotfish communities at relatively short distances, and present new insights into the responses of parrotfish species on a spectrum of body sizes along a gradient of human pressure.

1   **SPATIAL VARIATION OF PARROTFISH ASSEMBLAGES AT OCEANIC ISLANDS**
2   **IN THE WESTERN CARIBBEAN: EVIDENCE OF INDIRECT EFFECTS OF**
3   **FISHING?**

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Abstract

Fish populations that bear considerable pressure levels tend to show a decline in the average size of individuals, with the small and unexploited species replacing the large and exploited ones. It is important to carry on with their characterization in areas where they are becoming an important source of food for local human populations. An example of such species are parrotfishes, whose responses to external factors such as fishing need to be understood and predicted. In this study, we used a diver-operated stereo-video to examine individual body size, sex ratios and proportion of species of the parrotfish assemblage and analyze them on a qualitative fishing pressure gradient at four oceanic islands in the Colombian Caribbean. We reported over 10000 occurrences of eleven parrotfish species, of which we estimated the total length of over 90%, grouping them into three size categories (large, medium, and small). Our data showed a spatial variation of parrotfishes' abundances, biomass, and individual body size. Observed differences are size-category-dependent throughout the qualitative fishing pressure. In general, the medium-bodied species had smaller sizes, lower abundances, and thus lower contribution to the total parrotfish biomass at the most heavily fished island. Unexpectedly, we found evidence of possible indirect effects over the small-bodied species *Scarus iseri* and *Scarus taeniopterus* with significantly greater abundances, and larger sizes of males of *S. iseri,* at the higher fishing pressure sites. Overall, our data highlights the extent of the spatial variation in the parrotfish communities at relatively short distances, and present new insights into the responses of parrotfish species on a spectrum of body sizes along a gradient of human pressure.

Subjects: Biodiversity, Ecosystem Science, Marine Biology, Natural Resource Management.
Keywords: Labrids, Scarines, Seaflower Biosphere Reserve, Size, Stereo-video, Spatial scale

Introduction

Local stressors such as overfishing have caused significant changes in the structure and function of coral reefs (*Jackson et al., 2001; McLean et al., 2016*). Overexploited fisheries tend to shift towards lower trophic levels (*Taylor et al., 2014*), with growing captures of smaller and less commercial species, usually herbivores (*Burke et al., 2011*). The assessment of herbivores populations in coral reefs subject to fishing activities is compulsory, yet the lack of rigorous data on fishing effort remains one of the main obstacles to understanding fishing effects (*Stewart et al., 2010*). Therefore, to assess populations in localities with poorly documented coastal fishing efforts, it is necessary to resort to additional information linked to such efforts.

Different measures, such as human population density, have been proposed to indicate fishing effort (*Stewart et al., 2010*). There are two ways in which human density can affect fish populations locally (*Williams et al., 2008*). Directly, through overfishing, with a selective effect on targeted species, and indirectly, through habitat degradation, with a more widespread effect on both targeted and non-targeted species (*Pauly, 1990; Williams et al., 2008; Stewart et al., 2010*). Studies in insular territories around the world have shown a negative relationship between human population density and biomass and abundance of fish populations in coral reefs adjacent to inhabited territories (*Clua & Legendre, 2008; Williams et al., 2008; Bellwood et al., 2012*). Related information such as access to local markets and urbanization are also reliable indicators to approach the fishing pressure level of a particular locality (*Aswani & Sabetian, 2009; Brewer et al., 2012, 2013; Cinner et al., 2013*). In addition, different biological attributes in fish populations are also proposed as features to study fishing effects.

55 Individual body size is one of the most operational features to evaluate the effects of overfishing
56 (*Rochet & Trenkel, 2003*). However, size-based analyses have typically examined assemblage-
57 level patterns of the entire reef fish communities (*Jennings et al., 2002; Dulvy et al., 2004; Graham*
58 *et al., 2005*), ignoring possible variation within groups of fishes. In the Caribbean, size-based
59 studies have shown a turnover of fisheries towards species of lower trophic levels, such as
60 parrotfishes (*Hawkins & Roberts, 2004; Hardt, 2009; Vallès & Oxenford, 2014*) and a size-based
61 study conducted on this group can add resolution to the existing literature on this topic.
62 Parrotfishes (Labridae: Scarinae) and surgeon fishes (Acanthuridae) are two of the main herbivore
63 clades in coral reefs of the Caribbean (*Mumby et al., 2006*). Former studies in the Caribbean have
64 linked patterns of spatial variation in parrotfish communities with overfishing. Those studies found
65 a negative relationship between fishing pressure and biomass of large-bodied species and with the
66 individual body weight of all parrotfish species (*Hawkins & Roberts, 2004; Vallès & Oxenford,*
67 *2014; Vallès et al., 2015*). Overfishing has also been associated with indirect effects on fish
68 communities through compensatory increases of small species when the larger ones decrease
69 (*Dulvy et al., 2004*). However, there is scarce evidence of this effect in parrotfish communities. A
70 largescale study by *Hawkins & Roberts (2003)* found that the abundance of the small-bodied
71 *Sparisoma atomarium* increased with fishing pressure. *Vallès et al. (2015)* found that at higher
72 fishing pressure, *Scarus iseri* and *Scarus vetula* were still more and less abundant, suggesting a
73 possible event of competitive release between the two species, but no significant differences
74 supported such hypothesis. Therefore, it is relevant to provide a better characterization of
75 parrotfish spatial variation to explore emergent exploitation impacts within fisheries, especially in
76 small-scale spatial gradient of fishing pressure and in areas where these effects are still unknown.
77 Furthermore, parrotfishes are an interesting group to assess fishing effects on sex ratios and body
78 sizes of protogynous species, the most common form of sequential hermaphroditism of reef fishes
79 (*Gemmell et al., 2019*), an issue than remains poorly examined (*Buxton, 1993; Colleman et al.,*
80 *1996; McGovern et al., 1998; Hawkins & Roberts, 2003; O'Farrell et al., 2016*). In Bonaire,
81 abundances of males of *S. vetula*, *Sparisoma viride*, *Sparisoma aurofrenatum* and *Scarus*
82 *taeniopterus* increased after a fishing ban (*O'Farrell et al., 2016*). Likewise, most parrotfish
83 species evaluated by *Hawkins & Roberts* (*2003*) showed a decreased in body sizes of males and
84 females with fewer males at higher fishing pressure. In marine protected areas, the authors also
85 found an increase in time of body sizes of males and females of most species. Hence, adding
86 resolution to these relationships is pertinent to monitor their populations over time.
87 In this study, we used diver-operated stereo-video to assess parrotfish populations and explore the
88 effects of fishing pressure in oceanic islands of the Colombian Caribbean. The stereo-video
89 technique allowed us to gather high-resolution body-length data for a size-based analysis under a
90 qualitative fishing pressure gradient in which we included the best available local information. We
91 anticipated that fishing exploitation would reduce the abundance and average body size of medium
92 and large-bodied species, with a minor contribution of those species to the overall parrotfish
93 biomass. Consequently, small-sized species would have a greater contribution to the overall
94 parrotfish biomass either by having greater abundances at higher fishing pressure or mainly
95 because of the lower contribution of the medium and large-bodied species proportions.

96 Materials & Methods

97 *Sampling sites and fishing pressure gradient*

98 The Seaflower Biosphere Reserve (SBR) is a complex of islands, atolls, cays, and shoals in the
99 Colombian Caribbean, including one of the largest Caribbean coral reefs complexes (*Abril Howard*
100 *et al., 2012a*) and over 77% of the coral formations of the country (*Abril-Howard et al., 2012b*).

101 We recorded parrotfish species in coral reef areas of several islands of the SBR: San Andrés (SA),
102 Bolívar Cay (BOL), Albuquerque Cay (ALB), and Providencia and Santa Catalina (PRO). The
103 main island of the archipelago is SA, located 90 km south of PRO, the other inhabited populated
104 island, while BOL and ALB are two small uninhabited cays, 25 and 37 km south of SA,
105 respectively (Fig. 1).
106 Considering the selectivity of fisheries for large fishes (*O'Farrell et al., 2016*), metrics such as
107 individual body size, sex ratio, and overall proportions of parrotfishes would reflect different
108 responses to exploitation by comparing them across a fishing gradient *(Rochet & Trenkel, 2003;*
109 *Dulvy et al., 2004)*. However, at the SBR, no standardized information precludes us to quantify
110 fishing pressure. Therefore, we considered additional drivers based on the literature of the topic
111 (*Clua & Legendre, 2008; Williams et al., 2008; Aswani & Sabetian, 2009; Bellwood et al., 2012;*
112 *Brewer et al., 2012, 2013; Cinner et al., 2013*). To include species with different levels of interest
113 for the fisheries, we evaluated eleven species of parrotfish across a wide range of body sizes along
114 the established human pressure gradient. We separated the species into three categories: small-
115 sized ones (maximum total length <30 cm) including *S. taeniopterus*, *S. iseri*, *S. aurofrenatum* and
116 *S. atomarium*; medium-sized species (maximum total length >30 - <70 cm) *Sparisoma*
117 *chrysopterum* and *Sparisoma rubripinne*, in addition to *S. vetula* and *S. viride*. The large-bodied
118 species (maximum total length >70 cm) included *Scarus coelestinus*, *Scarus coeruleus*, and *Scarus*
119 *guacamaia*.
120 The proposed ranking of localities from highest to lowest fishing pressure was: SA, BOL, ALB,
121 and PRO. This order was based on: [1] Human population density (number of inhabitants per
122 square kilometer of reef structure) in SA is 784 inhabitants/km^2, while in PRO is 18
123 inhabitants/km^2 (*Gamboa et al., 2012*; *Cámara de Comercio de San Andrés, Providencia y Santa*
124 *Catalina, 2016; DANE, 2016*). Bolívar and Albuquerque cays have no human population besides
125 a dozen Colombian soldiers; however, fishers of San Andrés frequently visit these islets due to
126 their proximity to the main island. [2] SA has easy access to fishing grounds from the coastline,
127 allowing for shore fishing. This activity is conducted by independent fishers, whose population is
128 not characterized and quantified, and targets multiple species, including parrotfishes, grunts
129 (Haemulidae), and jacks (Carangidae), with unknown catch volumes (*Castro, 2005*). [3] In 1953,
130 SA was designated as a tax-free region, which promoted an enormous increase in tourism and a
131 significant immigration of people to the island (*Meisel, 2003; Abril Howard et al., 2012a*).
132 Artisanal fishery went from local subsistence to a specialized and institutionalized activity based
133 on the local market demand (*Olmos, 2019*). In contrast, those changes have not significantly
134 impacted PRO (*Meisel, 2003; Abril Howard et al., 2012a*). [4] Catch per unit effort (CPUE) in SA
135 has shown a decline since 2009, which has been related to an increase in overfishing on the island
136 (*Santos-Martínez et al., 2017, 2019*). Additionally, reports show a greater effort and capture
137 volumes in SA over nearby fishing grounds, including BOL and ALB cays (*Castro et al., 2007;*
138 *Rojas et al., 2015*). The fishing pressure distinction between BOL and ALB was based merely on
139 their distance from SA.
140 ***Surveys***
141 We used a diver-operated stereo-video approach (*Harvey et al., 2003*; *Langlois et al., 2010*) to
142 collect field data. Before each field trip, we performed the stereo-video calibration using the CAL
143 software (*SeaGIS Pty Ltd. Bacchus Marsh, Victoria, Australia*) following *Harvey & Shortis*
144 (*1998*). During the calibration process, a cube with approximately 80 targets was filmed in 20
145 different positions with the stereo-video system. With the CAL software, the targets were located
146 in those different positions of the cube, generating a calibration archive with the exact

147 configuration of the camera system, including the inward angle and distance between the cameras,
148 among other parameters. After testing the calibration with a known-size devise, the stereo video
149 was set to be used in the field (Fig. S1A).
150 The stereo-video technique allowed us to gather reliable data on individual body size, sex ratio,
151 and overall proportions of the parrotfishes' assemblage in the SBR with high resolution and low
152 estimation error. In the absence of previous data from this technique to compare with, four
153 considerations influenced our final sampling design: (i) to sample each location as close together
154 in time as possible, (ii) to select sites with similar coral reef bottoms and with a similar number of
155 shallow (3-8 m), medium (8-15 m) and deep (15-30 m) stations surveyed at each locality (Table
156 S1), (iii) to minimize associated researcher biases by having the same researcher handling the
157 stereo-video and processing the videos, and (iv) to produce a balanced set of samples across errant
158 diver specific timed surveys.
159 ***Sample allocation and video processing***
160 We sampled 16 stations per locality for a total of 64 stations between October and November 2018
161 in SA, BOL, ALB, and PRO, and 32 stations a year later in 2019 in SA and PRO (Fig. 1; Table
162 S1). In addition, in 2019, we sampled a greater number of shallower stations (< 6 m) close to
163 seagrass meadows to gather more data on *S. rubripinne* and *S. chrysopterum*, which had a small
164 sample size in the 2018 surveys. Consequently, the sampling design was unbalanced when
165 comparing SA and PRO between the two years (Table S1).
166 We used the guides of *Humann & Deloach* (*2014*) and *Robertson et al.* (*2015*) to identify the
167 individuals to species level and to give a sex designation. Following *Hawkins & Roberts* (*2004*),
168 we considered parrotfishes in juvenile and initial color phases as females and in terminal color
169 phases as males. In the case of *S. coelestinus,* with no color phases, there was no sex designation.
170 To distinguish between the initial phases of *S. taeniopterus* and *S. iseri* we used the color of the
171 edges of the caudal fin (light for the first and dark brown upper and lower edges for the second
172 species) (*Robertson et al., 2015*). From the videos, we recorded occurrence, sex, and total length
173 data (TL), measured from the tip of the mouth to the median projection of caudal fin lobes with
174 the EventMeasure software (*SeaGIS Pty Ltd. Bacchus Marsh, Victoria, Australia*; Fig. S1B).
175 We took special attention during video processing to minimize the possibility of counting fish
176 twice. Whenever two similar fish were observed and there was a doubt on whether it was the same
177 individual, length estimated by the software was examined. If sizes were very different and the
178 accuracy index (RMS; *SeaGIS Pty Ltd. Bacchus Marsh, Victoria, Australia*) indicated by the
179 software was acceptable (<20 mm), fish were considered to be different individuals. Further,
180 additional features in the coloration and distinct marks on the individuals were considered.
181 ***Statistical analysis***
182 **Total length data.** Considering the hierarchical structure of our data with individual body size per
183 species nested within each video station and each video station nested within each locality, we
184 used Generalized Additive Mixed Effects Models (GAMMs) fit by REML (statistical packages
185 "nlme" v. 3.1-157 and "mgcv" v. 1.8-39) (*Barry & Welsh, 2002*). The Mixed Effects Models
186 approach allowed us to examine the overall interaction between species, sex, years, and localities
187 while accounting for within study variance structure due to random effects. In our case, video-
188 stations were used as random effect due to the expected correlation between the multiple
189 observations (individual body size) from the same video station.
190 For the optimal model selection, we followed the top-down protocol described by *Zuur et al.*
191 (*2009*). Therefore, we started with a full linear regression model, including every possible
192 explanatory variable within the fixed part (sex, species, localities, year) and their interactions. To

193   include video stations, we fit the model with generalized least-squares (GLS) regression models
194   and compare the linear regression model with the linear mixed effect model (LMEM) using the
195   likelihood ratio test and confirmed with the Akaike Information Criterion (AIC; Table S2)
196   (*Burnham & Anderson, 2003*). Finally, we performed model validation by inspecting the residuals
197   of the best-fitted models (statistical package "lattice" v. 3.1-157), as patterns were observed within
198   the residuals, we applied GAMMs fitted by REML. Species without sex designation were excluded
199   when the sex explanatory variable was included as fixed effect in the model. Likewise, BOL and
200   ALB were excluded from the model when comparing data for 2018 and 2019, as only SA and PRO
201   were surveyed during those years (Table S2).
202   **Abundances and biomass.** Biomass was calculated per individual with the estimated individual
203   total length and the equation $B = aL^b$ (*Marks & Klomp, 2003*) where "B" is the biomass in grams,
204   "L" is body length in cm and parameters "a" and "b" are constants available in FishBase
205   (www.fishbase.org). We performed a square root transformation of abundances and biomass data
206   so that each taxon could contribute to the similarity among samples by softening the influence of
207   the more dominant taxa. In addition, we standardized the biomass data by dividing the estimated
208   values per species by the total biomass of parrotfishes at each station per locality. To determine if
209   localities were statistically distinct from each other in their parrotfish community structure, under
210   the fishing gradient established, we ran a PERMANOVA (*Anderson, 2001*) with a Bray-Curtis
211   similarity matrix. Finally, we ran a SIMPER test (*Clarke, 1993*) to assess the average percent
212   contribution of each species to the dissimilarity (statistical packages "vegan" v. 2.5-7; "ggplot2"
213   v. 3.3.5).
214   All analyses used a p-value significance level of 5% and were carried out in R (v 4.0.2, R
215   Foundation for Statistical Computing, Vienna, Austria). In addition, the data gathered in 2018 and
216   2019 were analyzed independently as we did not sample BOL, and ALB in the second year.
217   Likewise, to evaluate changes in time, only the data from SA and PRO in 2018 were included in
218   the analysis.

219 Results

220   We recorded a total of 10438 parrotfishes (6665 in 2018 and 3763 in 2019). The most frequently
221   observed species were *S. iseri*, *S. taeniopterus*, *S. aurofrenatum*, and *S. viride*. As expected, the
222   large-sized species *S. coelestinus*, *S. coeruleus*, and *S. guacamaia* were rare and almost exclusively
223   observed in PRO, the site with the lowest level of fishing pressure. We were able to estimate the
224   total length of 9788 individuals, corresponding to over 90% of the reported occurrences.
225   Abundance, biomass, and individual body size of parrotfishes varied widely among the islands,
226   species, and sexes (Tables S3 and S4). We present the results per metrics evaluated, emphasizing
227   the general patterns observed per size category under the fishing pressure gradient proposed.

228   *Variation of the individual total length*

229   The best-fitted models for the individual total length had sex, year, species and locality as fixed
230   effects, including the interaction between them and video stations as random effects (Table S2).
231   From the 2018 data set, the total length of the medium-sized species showed a negative relationship
232   with fishing pressure, with the smallest individuals found on the most heavily fished island (SA,
233   Table S3; Fig. 2A). *S. viride* had larger sizes in PRO (β=4.77, SE=8.77, *p*= 1.91e-06; Fig. 2A) and
234   significantly smaller ones in SA (β=-5.39, SE=9.42, *p*= 7.25e-08; Fig. 2A). Females of the species
235   reached larger sizes in PRO (β=5.81, SE=12.84, *p*= 0.000275; Fig. 2C), and smaller in SA (β=-
236   4.47, SE=8.95, *p*= 8.14e-06; Fig. 2C) while males had greater sizes in BOL (β=8.45, SE=3.86, *p*=
237   0.00011; Fig. 2B) and smaller in SA (β=-5.98, SE=11.02, *p*= 3.11e-09; Fig. 2B). On the other
238   hand, *S. vetula* had larger sizes in PRO (β=3.64, SE=13.01, *p*= 6.7 e-09; Fig. 2A) and BOL

239   (β=3.26, SE=12.34, *p*= 0.0011; Fig. 2A), with females reaching larger sizes in the former (β=5.81,
240   SE=12.84, *p*= 0.000275; Fig. 2C). In contrast, only the males of the small sized species *S. iseri*
241   had larger individual body sizes at the most heavily exploited island of SA (β=3.1, SE=7.6, *p*=
242   0.0019; Fig. 2C). *S. aurofrenatum* showed no clear pattern related to fishing pressure, although
243   their individual body sizes presented significant differences among the localities (β=3.8, SE=7.34,
244   *p*= 0.00014).
245   We found no differences between the two years evaluated (DF=6, F=1.45, p=0.19). Nevertheless,
246   in 2019 the differences between localities and species remained the same, with the medium size
247   species showing smaller sizes in SA, including *S. vetula* (β=-6.01, SE=8.91, *p*= 2.13s-09; Fig. 3;
248   Table S4) and *S. viride* (β=-10.3, SE=7.53, *p*=<2e-16), and the small-sized *S. iseri* having larger
249   sizes in SA (β=3.73, SE=6.68, *p*= 0.0002). In addition, in 2019 we were able to gather a greater
250   sample size of the other two medium-bodied species, and both species showed smaller sizes in SA:
251   *S. rubripinne* (β=-5.78, SE=12.01, *p*=8.27e-09) and *S. chrysopterum* (β=-3.49, SE=10.57, *p*=
252   0.00049).
253   *Variation of abundances and biomass*
254   The PERMANOVA applied to parrotfishes abundance in 2018 showed significant differences
255   (*DF*=3, *MS*= 1013.2, *F*=1.99, *p*=0.01) between SA and the remaining three localities (DF=30;
256   SA:ALB *t*=1.59, *p*=0.023; SA:BOL *t*=1.52 *p*=0.026; SA:PRO *t*=1.71, *p*=0.026). The results
257   dropped by the SIMPER test showed that the greater abundances of *S. taeniopterus* females in SA
258   contributed the most to the differences between this island and the other three localities (Fig. 4;
259   Table S5). We also found significant differences in 2019 between SA and PRO in the proportions
260   of the parrotfish composition (*DF*=1, *MS*= 3849.5, *F*=4.44, *p*=0.002). Likewise, *S. taeniopterus*
261   females showed to be more abundant in SA and were largely the major contributors to the
262   differences found by the SIMPER analysis (Table S6).
263   Biomass data showed significant differences (*DF*=3, *MS*= 1903.1, *F*=2.81, *p*=0.01) between SA
264   and the other three localities (DF=30; SA:ALB *t*=2.28, *p*=0.003; SA:BOL *t*=1.92 *p*=0.012;
265   SA:PRO *t*=2.39, *p*=0.002). Also, the 2019 biomass data showed SA and PRO to be significantly
266   different (*DF*=1, *MS*= 4045.2, *F*=4.57, *p*=0.004). In both studied years, the species that contributed
267   most to the overall differences were the small-sized species *S. taeniopterus,* and the medium-sized
268   species *S. vetula* and *S. viride* (Table S7 and S8). The former had a higher load in the overall
269   parrotfish biomass in SA, while the other two contributed in greater proportion in the other three
270   localities. In addition, at the least exploited site of PRO we found a higher contribution of the
271   medium-bodied species *S. rubripinne* and *S. chrysopterum* and the large-bodied species *S.
272   coelestinus*, *S. coeruleus*, and *S. guacamaia* (Figs 5; Table S6 and S7). As with individual body
273   sizes, no significant differences were found at SA and PRO between the two years evaluated in
274   terms of abundances (*DF*=1, *MS*= 929.32, *F*=1.57, *p*=0.158) and biomass (*DF*=1, *MS*= 851.61,
275   *F*=0.9, *p*=0.474).

Discussion

277   Effects of artisanal fishing pressure on parrotfish species populations, sex change, and sex ratios
278   have been previously described (*Hawkins & Roberts, 2003, 2004; Hardt, 2009; Vallès &
279   Oxenford, 2014; Vallès et al., 2015; O'Farrell et al., 2016*). In this study, we have further
280   investigated these relationships under a qualitative fishing pressure gradient, including a
281   comprehensive sample size of eleven species and a high-resolution technique for the underwater
282   assessment of body sizes (diver-operated stereo-video). Overall, our data suggest that fishing
283   pressure is indeed related to the spatial variation in abundance, biomass, and individual body size

284 of the parrotfish species, but most importantly, that there might be indirect effects of fishing
285 pressure on small-sized species.
286 Following our initial predictions, we expected to find smaller sizes and lower proportions of large
287 and medium-bodied species at a greater fishing pressure. This was indeed the case for most of the
288 species and is consistent with previous studies, where a negative relationship between fishing
289 pressure, body sizes, sex ratios, and abundances were found (*Hawkins & Roberts, 2003, 2004;*
290 *Vallès & Oxenford, 2014; Vallès et al., 2015*). Likewise, Mixed Effects Models considering sex
291 showed that females of the medium-bodied species *S. vetula* and *S. viride* had larger sizes at lower
292 fishing pressure. This finding could be due to selective fishing for large females at the high fishing
293 pressure sites, but it could also indicate that, at least in less exploited locations, sex change occurs
294 at larger sizes than at more heavily fished grounds (*Hawkins & Roberts, 2004; O'Farrell et al.,*
295 *2016*). What was most striking, however, were the differences found in the small-sized species *S.*
296 *iseri* and *S. taeniopterus.* We found that parrotfish proportions at the most heavily fished locality
297 showed significant differences with the other three least exploited fishing grounds evaluated and
298 that higher abundances and biomass of *S. iseri* and *S. taeniopterus* contributed the most to those
299 differences. Furthermost, this is the first documented study, to our knowledge, to record larger
300 individual sizes of a small-sized parrotfish species at a heavily fished locality, as is the case of the
301 males of *S. iseri* in SA.
302 Differences found in biomass are certainly driven by the mentioned changes observed in the
303 abundances and individual body sizes. The higher proportion of small-sized species in the total
304 assemblage of parrotfishes predicted at the beginning of this work is not only a product of a lower
305 contribution of individual body size and proportions of medium and large-bodied species but also
306 an outcome of the higher abundances and individual body sizes of small species. We consider that
307 the higher contribution of *S. iseri* and *S. taeniopterus* in the most heavily fished locality suggests
308 an indirect effect of fishing on these two small-sized parrotfish species. *Dulvy et al (2004)*
309 suggested that indirect effects of fishing pressure may be due to reduced predation or interspecific
310 competition. In theory, once predators are removed from the ecosystem, their preys should increase
311 as there is no control over them, yet, there is no clear evidence of this relation (*Clua & Legendre*
312 *2008*). Some studies have found no changes in preys after the demise of predators (*Jennings &*
313 *Polunin, 1997; Taylor et al., 2018; Roff et al., 2019*). Other authors have linked greater biomass
314 of predators such as *Epinephelus striatus* with smaller sizes of *S. iseri* and *S. aurofrenatum*
315 (*Mumby et al., 2006*). In our study, although the greater size and abundance of *S. iseri* and *S.*
316 *taeniopterus* due to lower predation in SA cannot be completely ruled out and requires further
317 examination, to our knowledge, there are no potential predators that may be significantly more
318 abundant in BOL, ALB, and PRO in contrast to SA. Also, as described by *Mumby et al.* (*2006*),
319 we should have found greater sizes of the other small-sized species (i.e., *S. aurofrenatum*, which
320 is smaller than *S. taeniopterus*) at the locality with supposedly fewer predators due to higher fishing
321 pressure (SA); still, this was not the case.
322 Instead, we believed that competitive release might be playing a role in the results found with *S.*
323 *iseri* and *S. taeniopterus.* Through stable isotope analysis and intestinal content, *Dromard et al.*
324 (2015) recognized an overlap in the trophic niche between *S. vetula*, *S. viride*, *S. iseri* and *S.*
325 *taeniopterus.* Therefore, it could be argued that when the medium-bodied species (i.e., *S. vetula*,
326 *S. viride*) are removed from the system, the small-bodied ones (i.e., *S. iseri*, *S. taeniopterus*) may
327 be favored, as some resources for which they actively compete become more available.
328 Consequently, in an intensely exploited locality such as SA, small species can reach larger sizes
329 and higher abundances than in less exploited localities, where larger species limit the resources

330   they compete for. In addition, *Hawkins & Roberts (2004)* found greater abundances of the smallest
331   species of parrotfish (*S. atomarium*) in Jamaica, the most heavily exploited island in their study.
332   The intense pressure exerted on parrotfishes in Jamaica has been documented *(Hardt, 2009),* and
333   we wonder if SA, the most heavily exploited island considered in our study, is showing a step in a
334   chain of changes that follows as parrotfishes are gradually depleted according to sizes of interest
335   for fisheries. Hence, it is essential to monitor parrotfish populations in the Reserve as small size
336   species, like *S. aurofrenatum*, may become of interest to fisheries. Such monitoring may also give
337   insights into phase shift processes in coral reefs as *S. aurofrenatum* is a critical consumer of the
338   seaweed *Dyctiota* in the Caribbean reefs (*Dell et al., 2020*), a highly opportunistic algae and a
339   great competitor of corals (*Fong et al., 2003*).
340   The differences found in parrotfish assemblages can likely influence many biological traits of the
341   species, such as reproduction, but also at the ecosystem level. On the one hand, given the positive
342   relationship between body length and egg production, the reduction of mean body sizes of
343   parrotfish populations due to overfishing is probably negatively affecting their reproductive
344   productivity (*Hawkins & Roberts, 2004*). On the other hand, the differences found in this study
345   could have a flow-on influence on ecosystem functions (*Bonaldo et al., 2008; Robinson et al.,*
346   *2019; Shantz et al., 2020*). Larger individuals of parrotfishes have greater roles in processes like
347   bioerosion, corallivory, and grazing of certain macroalgae (*Bonaldo et al., 2008*). *Shants et al.*
348   *(2020)* found that the removal of large parrotfish on Caribbean coral reefs increases the abundance
349   of macroalgae and decreases the growth of massive and reef-building corals. This result suggests
350   that it should be necessary to protect fishes larger than 20 cm to maintain their functional diversity.
351   Hence, the functional roles of large parrotfish species are not necessarily replaced by higher
352   abundances or larger sizes of the small-sized species. Bioerosion and coral predation are two
353   ecological functions highly susceptible to overfishing as their rates increases with the body size of
354   parrotfishes (*Bellwood et al., 2012*). *Scarus vetula* and *S. viride* are important bioeroders
355   (*Bruggemann et al., 1996*), and they had smaller sizes in SA; this could cause lower bioerosion
356   rates at the locality. Concerning the consumption of algae, recent studies show that species not
357   consistently considered as part of the herbivore community in the Caribbean, such as *Acanthurus*
358   *coeruleus, Acanthurus tractus,* and *Kyphosus* spp., are critical consumers of macroalgae (*Duran*
359   *et al., 2019; Dell et al., 2020*), which are the type of algae that are dominating degrading coral
360   reefs (*Perry et al., 2018*). Consequently, future studies should include these groups of herbivores
361   to determine the effect of herbivores removal on the ecosystem function.
362   Our findings did not show significant differences between the two years evaluated. However,
363   sampling efforts differ between years as a greater number of shallower stations nearby seagrass
364   meadows were examined in both localities (SA and PRO) in 2019. Therefore, it is relevant to
365   continue monitoring the parrotfish populations, hopefully at the same stations to accurately
366   evaluate possible differences in time. Nonetheless, our sampling effort was balanced between the
367   localities in 2019 and allowed us to gather a greater sampling size of *S. rubripinne* and *S.*
368   *chrysopterum*. Those two medium-sized species had smaller sizes in the most heavily fished
369   locality. At present, neither of these two species has a threat category assigned in Colombia
370   (*Chasqui et al., 2017*), and it is premature to speak of threat due to fishing pressure when their
371   comparable data is only given in two localities. However, it is important to consider that *S.*
372   *chrysopterum* had a negative relationship with fishing pressure (*Valles & Oxenford, 2014*) and,
373   according to a report from the continental shores of Colombia, it is one of the most captured species
374   of parrotfishes (*INVEMAR-MADS, 2017*). Therefore, we recommend increasing the sampling

375 effort by focusing on gathering data of both species on a temporal and spatial level to better
376 understand the differences in our study.
377 Finally, among the study limitations, different factors were not considered that may influence fish
378 herbivore species' body size and abundances. Such items may include habitat quality, food
379 availability, and other environmental variables. In some studies, factors such as productivity,
380 temperature, rugosity, latitude, geomorphological attributes of reef formations and slope have
381 shown weak relationships with parrotfish community changes (*Cinner et al., 2013; Taylor et al.,*
382 *2014, 2018*). In contrast, coral cover and position of coral reefs seem to be related to changes in
383 biomass and abundance of parrotfishes (*Hoey & Bellwood, 2008; Nash et al., 2012*). Exposed reefs
384 have greater biomass of parrotfishes and erosion levels (*Russ, 1984; Gust, 2001; Hoey &*
385 *Bellwood, 2008; Taylor et al., 2014, 2018; Roff et al., 2019*). Our findings show that *S. vetula* and
386 *S. viride* reach larger sizes in the less fished locality (PRO) and in BOL, with males of *S. viride*
387 reaching larger sizes in the former. Larger sizes and levels of bioerosion of both species are
388 associated with exposed reefs (*Koltes, 1993: Bruggemann et al., 1996; Clements et al., 2017*), and
389 BOL seem to have more exposed environments than the other localities (*Gamboa et al., 2012*)
390 which could explain why such differences were found in this site. Consequently, differences in
391 body size are explained by different factors such as reefs' exposure, resource availability, and
392 demographic characteristics of fish stocks influenced by external stressors such as fishing
393 exploitation. Future efforts should include environmental factors such as reef exposure and coral
394 cover to account for our study´s intraspecific variation in body size.

Conclusions
396 Abundances, individual body sizes and biomass of parrotfish species showed significant
397 differences and varied widely depending on the fishing pressure gradient and the size category of
398 the species. On the one hand, medium and large-bodied species of parrotfishes had a negative
399 relation between fishing pressure and contribution to the overall biomass, occurrences, and
400 individual body sizes. On the other hand, we found a significant contribution of the small-size
401 species evaluated to the overall biomass at higher fishing pressure sites. The such greater
402 contribution was driven by the reduction of sizes and abundances of medium and large-bodied
403 species, directly affected by fisheries but was also a product of greater abundances and, most
404 interestingly, larger sizes of the small-sized species. We suggest this result points to indirect effects
405 of overfishing and that such effects could related to a possible case of competitive release. It is
406 relevant to establish how such variations are linked with possible effects on the species
407 reproductive productivity and ecosystem processes.
408 Overall this study provides insights into intraspecific variation in body size, and our substantial
409 volume of data adds to the existing literature on the extent of variation in parrotfish assemblages
410 over relatively short distances. While we consider our general results are better explained under a
411 fishing pressure perspective, this by no means denies the influence of other factors such as inter-
412 island environmental differences. Therefore, although the direct and indirect effects of fishing
413 pressure suggested by our work deserve attention, they should be taken as preliminary until further
414 examination on a temporal and spatial scale is conducted.

Acknowledgements

416 We would like to extend our sincere gratitude to the Comisión Colombiana del Océano (CCO) for
417 organizing and leading the expeditions to Isla Cayo Albuquerque in 2018 and to Providencia and
418 Santa Catalina in 2019 which allowed us to gather part of the data used in this research. We also
419 thank A. Puentes and J. Carvajal for their research assistance. The assistance and support of Martha
420 Patricia Rincón-Díaz (National Patagonian Center - CONICET) and James Robinson (Lancaster

421 University) is greatly appreciated. Contribution No. 544 of CECIMAR, Instituto para el Estudio
422 de las Ciencias del Mar of the Universidad Nacional de Colombia Caribbean campus.

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Figure 1

Location of the four sampling sites along the Seaflower Biosphere Reserve.

Sample allocations of 2018 and 2019 surveys are specified with red and black dots. Stations evaluated at each locality are georeferenced (QGIS v.3.14). Insert map shows location of the reserve within the Colombian Caribbean (white arrow). Localities: Providencia and Santa Catalina (PRO); Albuquerque (ALB); Bolivar (BOL) and San Andrés (SA).
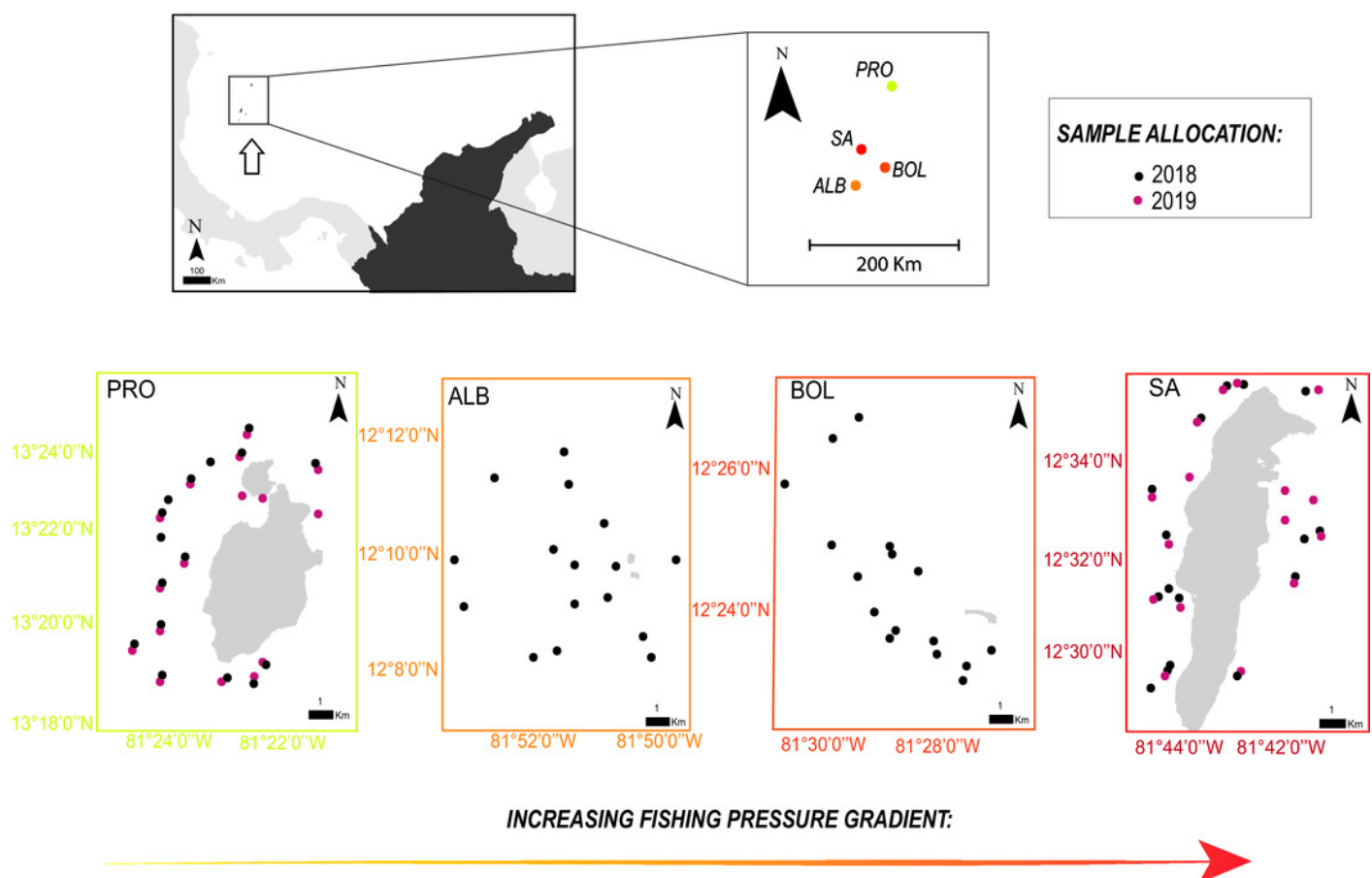
Figure 2

Trends in mean body size of parrotfish species under the fishing pressure gradient.

(A) Variogram with standard error (SE) bars on independent means of body size of the full sample size of the species populations in 2018, (B)Variogram with standard error (SE) bars on independent means of body size of males, (C) Variogram with standard error (SE) bars on independent means of body size of females. Species trends are specified with line shapes and their size category are specified with colors.
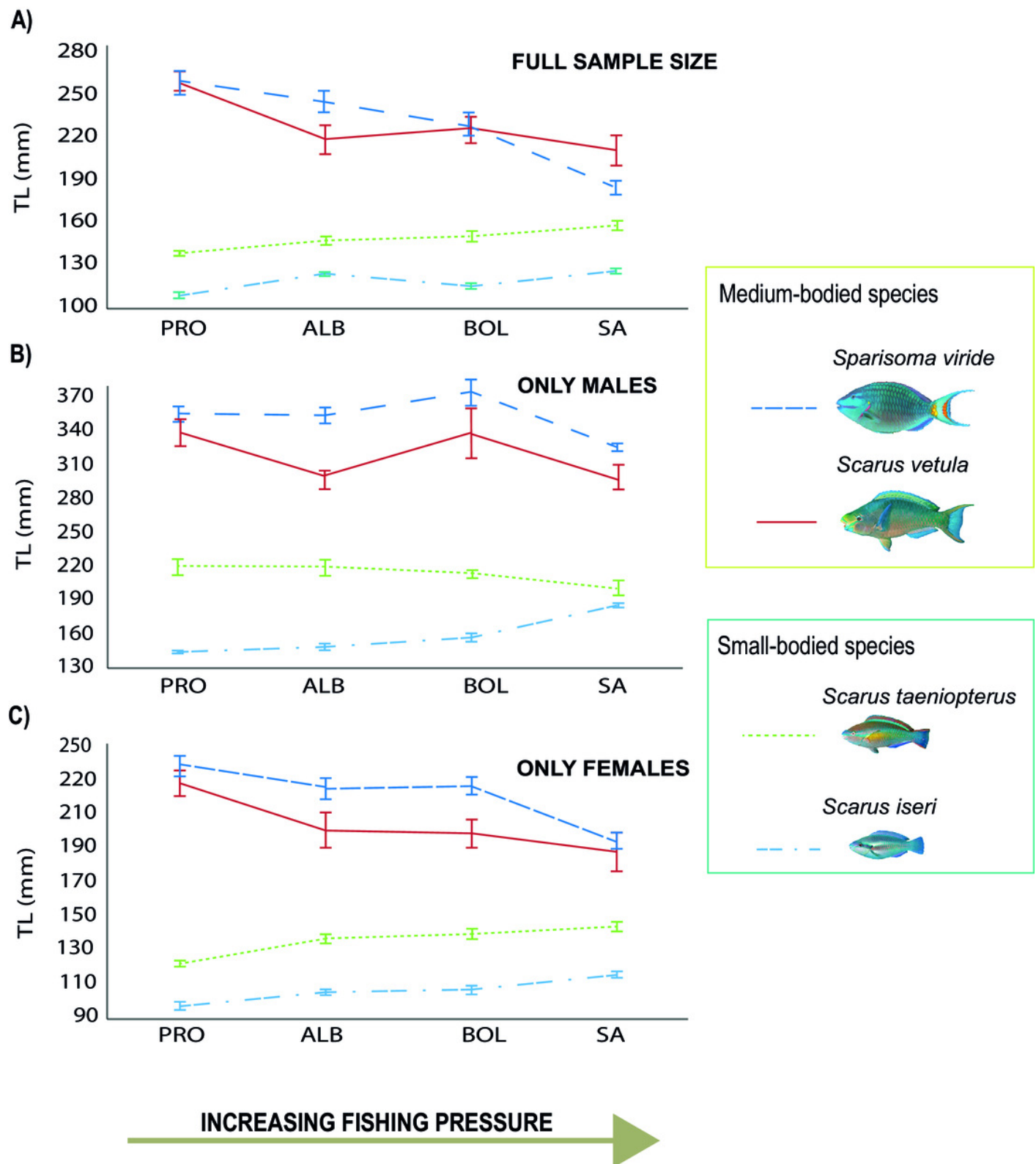
Figure 3

Boxplot of total length (TL) of parrotfish species collected in 2019 in San Andrés (SA) and Providencia (PRO).

(A) Boxplot of total length calculated of the full sample size of medium and samall-bodied species populations, (B) Boxplot of total length calculated for males of medium and samallbodied species populations (C) Boxplot of total length calculated for females of medium and samall-bodied species populations. Medium-bodied species include: *Sparisoma virde, Scarus vetula, S. rubripinne* and *S. chrysopterum*. Small-bodied species include: *S. taeniopterus, S. aurofrenatum, S.iseri* and *S. atomarium.*
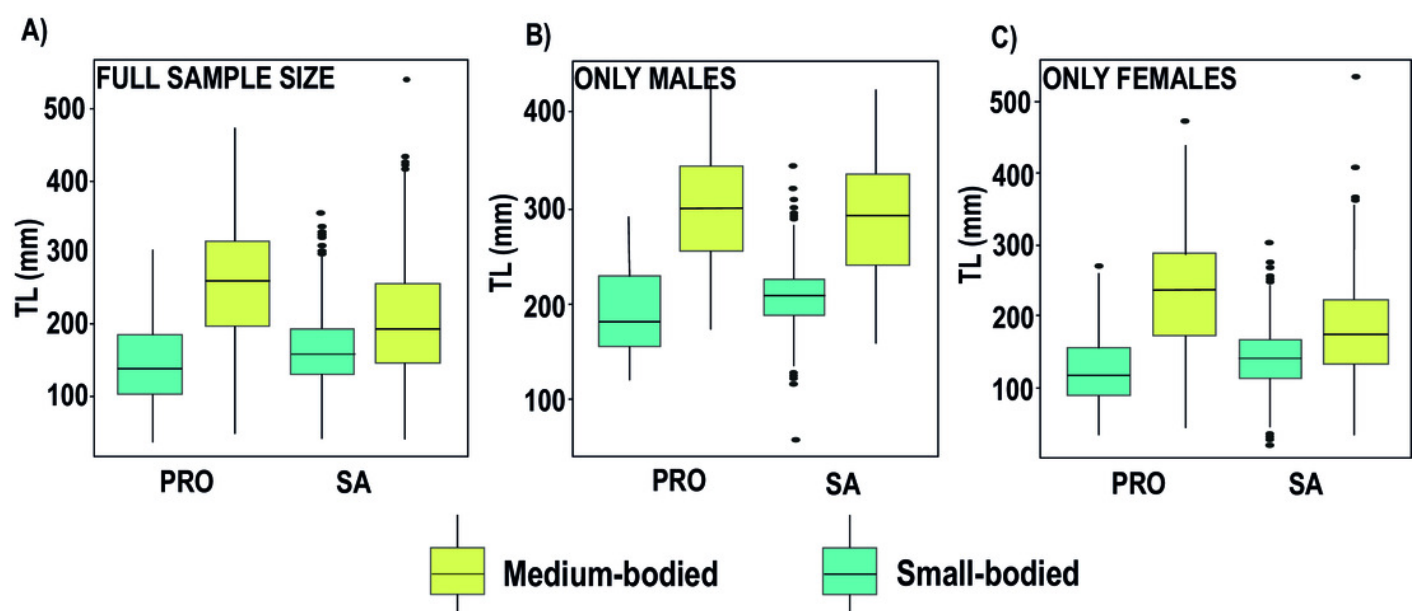
Figure 4

Parrotfishes occurrences.

Bars represent the mean abundance found per video station of each species at the four oceanic islands. The species are grouped into the size categories established and differentiated between males (_M) and females (_F).
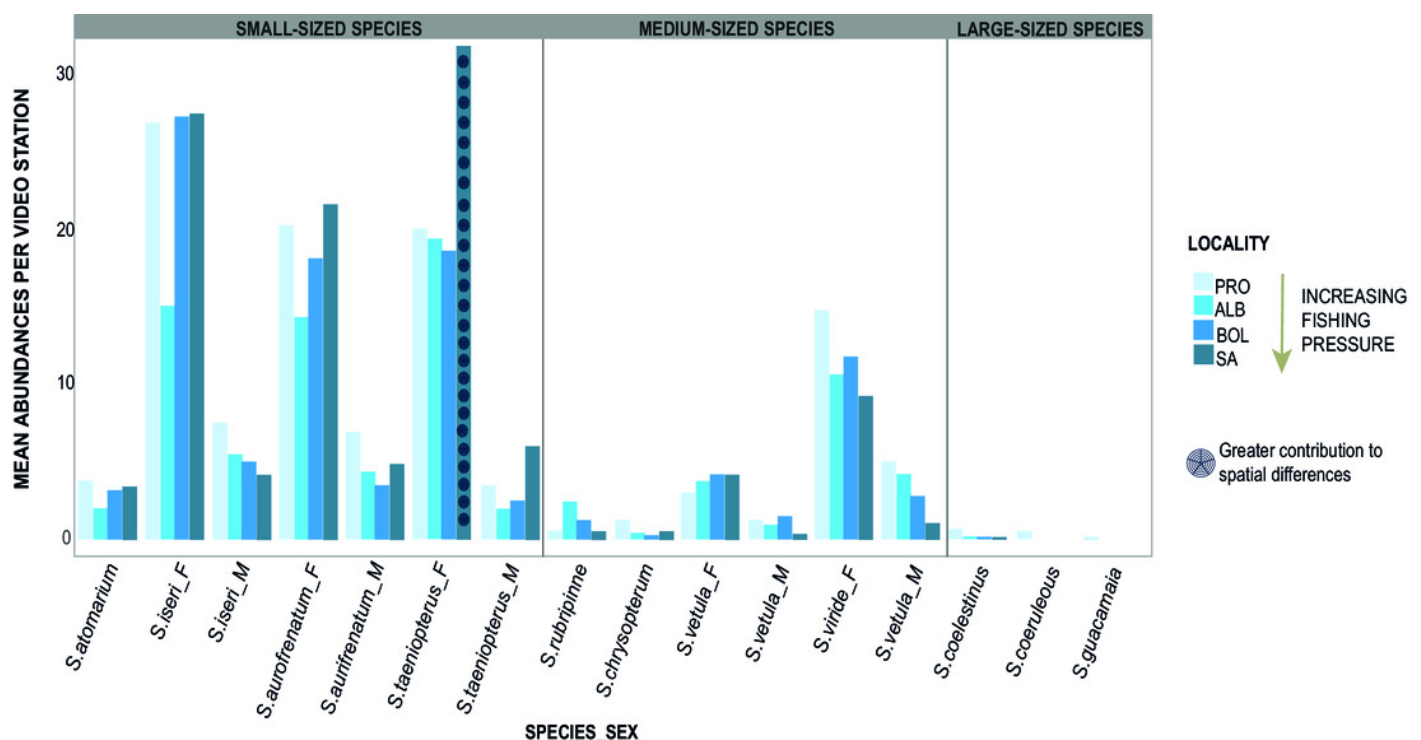
Figure 5

Species contribution to the overall parrotfish biomass.

(A) Percentage of contribution of the mean biomass per species over a gradient of fishing pressure: San Andres (SA), Bolivar (BOL), Albuquerque (ALB), and Providencia and Santa Catalina (PRO), (B) Percentage of contribution of the mean biomass per species in SA and PRO. Only species with over 30 individuals per locality are included: Medium-bodied species: *Sparisoma viride* (SVIR), *S. rubripinne* (SRUB) and *S. vetula* (SVET). Small-bodied species: *S. taeniopterus* (STAEN), *S. iseri* (SISE), *S. aurofrenatum* (SAUR), and *S. atomarium* (SATO). Inserted tables show the mean biomass (g) per specie at each locality.