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

Natalia Rivas [1] Arturo Acero P.[1], Jose Julián Tavera[2]

[1]Instituto de Estudios en Ciencias del Mar (Cecimar), Universidad Nacional de Colombia sede Caribe, El Rodadero, Santa Marta, Colombia
[2]Departamento de Biología, Universidad del Valle, Cali, Colombia

Corresponding Author:
Natalia Rivas
Calle 25 # 2-55, El Rodadero Sur-Playa Salguero, Santa Marta, 470006, Colombia
Email address: narivase@unal.edu.co

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 ~~T~~to understand and predict parrotfish populations' responses to external factors such as fisheries,~~ it is important to carry on with their characterization in areas where they are becoming an important source of food for local human populations~~. 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 ~~it~~ them ~~in relation~~ to 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 ~~were able to~~ 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 ~~of parrotfishes~~. Observed differences are size-category-~~–~~dependent throughout the qualitative fishing pressure. In general, ~~at the most heavily fished island,~~ 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 ~~at the higher fishing pressure sites as well as~~, and larger sizes of males of *S. iseri*, at the higher fishing pressure sites. Overall, our data highlights the extent of the spatial variation ~~on~~ in the parrotfish communities at relatively short distances, and present new insights ~~on~~ 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 ~~major~~ significant changes in the structure and function of coral reefs (*Jackson et al., 2001; McLean et al., 2016*). Overexploited fisheries tend to shift towards ~~species of~~ lower trophic level species (*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 ~~are~~ is compulsory, yet~~,~~ the lack of rigorous data on fishing effort remains ~~as~~ one of the main obstacles to understanding fishing effects (*Stewart et al., 2010*). Therefore, to assess ~~them~~ populations in localities with poorly documented coastal fishing efforts, it is necessary to resort to additional ~~measures~~ information? linked to such efforts.

Different measures, such as human population density, have been proposed ~~as an indicator of~~to indicate fishing effort (*Stewart et al., 2010*). There are two ways in which human population 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 the populations of 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 (*Bellwood et al., 2012; Clua & Legendre, 2008; Williams et al., 2008*). ~~Supplementary measures~~ Related information? such as access to local markets and urbanization are also reliable indicators to approach ~~to~~ the fishing pressure level ~~of fishing pressure~~ of a ~~certain~~ particular locality (*Aswani & Sabetian, 2009; Brewer et al., 2012, 2013; Cinner et al., 2013*). In addition, different attributes in fish populations are also proposed as features to study fishing effects.

Individual body size is one of the most operational features to evaluate the effects of overfishing (*Rochet & Trenkel, 2003*). However, size-based analyses have typically examined assemblage-level patterns of the entire reef fish communities (*Jennings et al., 2002; Dulvy et al., 2004; Graham et al., 2005*), ignoring possible variation within groups of fishes. ~~At~~ In the Caribbean region, size-based studies have shown a turnover of fisheries towards species of lower trophic levels, such as parrotfishes (*Hawkins & Roberts, 2004; Hardt, 2009*; *Vallès & Oxenford, 2014*) and a size-based study conducted on this group can add resolution to the existing literature on this topic.

Parrotfishes (Labridae: Scarinae) and surgeon fishes (Acanthuridae) are two of the main herbivore families in coral reefs of the Caribbean (*Mumby et al., 2006*). Former studies in the Caribbean region have linked patterns of spatial variation in parrotfish communities with overfishing. ~~Overall, t~~Those studies found a negative relationship between fishing pressure and biomass of large-bodied species and with the individual body weight of all parrotfish species (*Hawkins & Roberts, 2004; Vallès & Oxenford, 2014; Vallès et al., 2015*). Overfishing has also been associated with indirect effects on~~over~~ fish communities~~,~~ through compensatory increases of small species when the larger ones decrease~~d~~ (*Dulvy et al., 2004*). However, there is scarce evidence of this effect in parrotfish communities. A large-scale study by *Hawkins & Roberts (2003)* found that the abundance of the small-bodied *Sparisoma atomarium* increased with fishing pressure. *Vallès et al. (2015)* found that at higher fishing pressure, *Scarus iseri* and *Scarus vetula* were still more and less abundant, suggesting a possible event of competitive release between the two species, but no significant differences supported such hypothesis. Therefore, it is relevant to provide a better characterization of~~on~~ parrotfish spatial variation to explore emergent exploitation impacts ~~of exploitation~~ within fisheries, especially in areas where these effects are still unknown.

In this study, we used diver-~~-~~operated stereo-video to assess parrotfish populations and explore the effects of fishing pressure in oceanic islands of the Colombian Caribbean. The stereo-video technique allowed us to gather high-~~-~~resolution body-length data for a size-based analysis under a qualitative fishing pressure gradient in which we included the best available local information. We anticipated that fishing exploitation would ~~produce a reduction in~~reduce the abundance and average body size of medium and large-~~-~~bodied species, with a ~~smaller~~ minor contribution of those species to the overall parrotfish biomass. ~~As a consequence~~Consequently, small-sized species would have a greater contribution to the overall parrotfish biomass either by having greater abundances at higher fishing pressure or manly because of the lower contribution of the medium and large-bodied species proportions.

Materials & Methods

Sampling sites and fishing pressure gradient

The Seaflower Biosphere Reserve (SBR) is a complex of islands, atolls, cays, and shoals in the Colombian Caribbean, including one of the largest Caribbean coral reefs complexes (*Abril*

Comment [PRD1]: I am unsure if "measurements" would be the best word to describe fishing-related information that could be just mentioned in fishing or non-fishing-related reports. For example, were the access to markets or human population densities initially measured strictly for fishing pressure? Probably not. It is just a question of selecting a better word by considering that all these related factors were not conceived for characterizing fishing pressure at first, however, we have linked them as proxies of it.

Comment [PRD2]: Consider adding a justification of why developing this study in your area is essentialt in terms of knowledge gaps or the possibility of comparing the parrotfish biological responses to a small-scale spatial gradient of fishing pressure. I suggest the knowledge gap, but you can add others reasons in the paragraph below.

Howard et al., 2012a) and over 77% of the coral formations of the country (*Abril-Howard et al., 2012b*). We recorded parrotfish species in coral reef areas of San Andrés Island (SA), Bolivar Cay (BOL), Albuquerque Cay (ALB), and Providencia and Santa Catalina Islands (PRO). The main island of the archipelago is SA, located 90 km south of PRO, the other inhabited island, while BOL and ALB are two small cays, 25 and 37 km south of SA, respectively (Fig. 1).

Considering the selectivity of fisheries for large fishes (*O~~'~~'Farrell et al., 2016*), metrics such as individual body size, sex ratio, and overall proportions of the parrotfishes would reflect different responses to exploitation by comparing them across a fishing gradient *(Rochet & Trenkel, 2003; Dulvy et al., 2004)*. However, at the SBR, ~~there is~~ no standardized information ~~that allows~~preclude us to quantify fishing pressure. Therefore, we considered additional drivers based on the literature ~~on~~ of the topic (*Clua & Legendre, 2008; Williams et al., 2008; Aswani & Sabetian, 2009; Bellwood et al., 2012; Brewer et al., 2012, 2013; Cinner et al., 2013*). To include species with different levels of interest for the fisheries, we evaluated eleven species of parrotfish across a wide range of body sizes along the established human pressure gradient. We separated the species into three categories: small-sized ones (maximum total length ≤30 cm) including *Scarus taeniopterus*, *S. iseri*, *Sparisoma aurofrenatum* and *S. atomarium*; medium-sized species (maximum total length ≥30 - ≤70 cm) *Sparisoma chrysopterum* and *Sparisoma rubripinne*, in addition to *Scarus vetula* and *Sparisoma viride*. ~~And t~~The large-bodied species (maximum total length ≥ 70 cm) ~~which~~ included *Scarus coelestinus*, *Scarus coeruleus*, and *Scarus guacamaia*.

The proposed ranking of localities from highest to lowest fishing pressure was: SA, BOL, ALB, and PRO. This order was based on: [1] Human population density (number of inhabitants per square kilometer of reef structure) in SA is 784 inhabitants/km^2, while in PRO is 18 inhabitants/km^2 (*Gamboa et al., 2012*; *Cámara de Comercio de San Andrés, Providencia y Santa Catalina, 2016; DANE, 2016*). Bolívar and Albuquerque cays have no human population besides a dozen Colombian soldiers; however, fishers from San Andrés frequently visited these islets ~~are frequently visited by fishers from San Andrés~~ due to their proximity to the main island. [2] SA has easy access to fishing grounds from the coastline, ~~which~~ allowing~~s~~ for shore fishing. This activity is ~~carried out~~conducted by independent fishers, whose population is not characterized and quantified, and targets multiple species, including parrotfishes, grunts (Haemulidae), and jacks (Carangidae), with unknown catch volumes (*Castro, 2005*). [3] In 1953, SA was designated as a tax-free region, which promoted ~~not only~~ an enormous increase in tourism ~~but also~~and a ~~great~~ significant immigration of people ~~in~~to the island (*Meisel, 2003; Abril Howard et al., 2012a*). Artisanal fishery went from local subsistence to a specialized and institutionalized activity based on ~~the demand of~~ the local market demand (*Olmos, 2019*). In contrast, those changes have not significantly impacted PRO ~~has not been significantly impacted by those changes~~ (*Meisel, 2003; Abril Howard et al., 2012a*). [4] Catch per unit effort (CPUE) in SA has shown a decline since 2009, which has been related to an increase in overfishing on the island (*Santos-Martínez et al., 2017, 2019*). Additionally, reports show a greater effort and capture volumes in SA over nearby fishing grounds, including BOL and ALB cays (*Castro et al., 2007; Rojas et al., 2015*). The ~~F~~fishing pressure distinction between BOL and ALB was based merely on their distance from SA.

Comment [PRD3]: Consider to change the MS to an active voice writing. Here an example.

Comment [PRD4]: Another example of active voice.

Surveys

We used a diver-operated stereo-video approach (*Harvey et al., 2003*; *Langlois et al., 2010*) to collect field data. Before each field trip, we performed the stereo-video calibration using the CAL software (*SeaGIS Pty Ltd. Bacchus Marsh, Victoria, Australia*) ~~and~~ following *Harvey & Shortis* (*1998*). The stereo-video technique allowed us to gather reliable data on individual body size, sex ratio, and overall proportions of the parrotfish~~e~~s assemblage in the SBR with high resolution and low estimation error. In the absence of previous data from this technique to compare with, four considerations influenced our final sampling design: (i) to sample each location as close together in time as possible, (ii) to select sites with similar coral reef bottoms and with a similar number of shallow (3-8m), medium (8-15m) and deep (15-30m) stations surveyed at each locality (Table S1), (iii) to minimize associated researcher ~~associated~~ biases by having the same researcher handling the stereo-video and processing the videos, and (iv) to produce a balanced set of samples across errant diver specific timed surveys.

Sample allocation and video processing

We sampled 16 stations per locality for a total of 64 stations between October and November 2018 in SA, BOL, ALB, and PRO, and 32 stations a year later in 2019 in SA and PRO (Fig. 1; Table S1). In addition, in 2019, we sampled a greater number of shallower stations (< 6 m)~~,~~ close to seagrass meadows~~,~~ to gather more data ~~of~~ on *S. rubripinne* and *S. chrysopterum*, which had a small sample size in the surveys of 2018. In this sense, the sampling design was unbalanced when comparing SA and PRO between the two years (Table S1).

We used the guides of *Humann & Deloach* (*2014*) and *Robertson et al.* (*2015*) to identify the individuals to species level and to give a sex designation. Following *Hawkins & Roberts* (*2004*), we considered parrotfishes in juvenile and initial color phases as females and in terminal color phases as males. In the case of *S. coelestinus,* with no color phases, there was no sex designation. To distinguish between the initial phases of *S. taeniopterus* and *S. iseri* we used the color of the edges of the caudal fin (light for the first and ~~a~~ dark brown upper and lower edges for the second species) (*Robertson et al., 2015*). From the videos, we recorded occurrence, sex, and total length data (TL), measured from the tip of the mouth to the median projection of caudal fin lobes with the EventMeasure software (*SeaGIS Pty Ltd. Bacchus Marsh, Victoria, Australia*).

Statistical analysis

Total length data. Considering the hierarchical structure of our data with individual body size per specie nested within each video station and each video station~~s~~ nested within each locality, we used Generalized Additive Mixed Effects Models (GAMMs) fit by REML (statistical packages ~~“~~""nlme~~”~~"-" v. 3.1-157 and ~~“~~""mgcv~~”~~"-" v. 1.8-39) (*Barry & Welsh, 2002*). The Mixed Effects Models approach allowed us to examine the overall interaction between species, sex, years, and localities while accounting for within study variance structure due to random effects. ~~For the model selection we followed the top-down process described by *Zuur et al.* (*2009*)~~We followed the top-down process described by Zuur et al. (2009) for the model selection. Therefore, we started with the full model, including every possible explanatory variable within the fixed part (sex, species, localities, year) and their interactions. Then, ~~T~~the full model was run with different random effects structures and compared them using the Akaike Information Criterion (AIC; Table S2) (*Burnham & Anderson, 2003*). Finally, we performed model validation by inspecting the residuals of the best-~~-~~fitted models (statistical package ~~“~~""lattice~~”~~"-" v. 3.1-157). Species without sex designation were excluded when the sex explanatory variable was included as a fixed effect in the model~~ as fixed effect~~. Likewise, BOL and ALB were excluded from the model when comparing data ~~of~~ for 2018 and 2019, as only SA and PRO were surveyed during those years (Table S2).

Abundances and biomass. Biomass was calculated per individual with the estimated individual total length and the equation $B = aL^b$ (*Marks & Klomp, 2003*) where ~~“~~""B~~”~~"-" is the biomass in grams, ~~“~~""L~~”~~"-" is body length in cm and parameters ~~“~~""a~~”~~"-" and ~~“~~""b~~”~~"-" are constants available in FishBase (www.fishbase.org). We performed a square root transformation of abundances and biomass data so that each taxon could contribute to the similarity among samples by softening the influence of the more dominant taxa. In addition, we standardized the biomass data by dividing

Comment [PRD5]: Consider providing information here or in the supplementary material on how you accounted for solving issues related to individuals being counted twice – a question addressed by James Robinson

Comment [PRD6]: Consider specifying the sources of random variation in the text. Showing the effect size estimates of each fixed factor is still pending in table S2, as well as the random factor variance and the models' marginal and conditional r2's to describe the influence of random factors on explaining model variation.

Comment [PRD7]: It is unclear if you used only GAMMs to relate predictors to your response variables. In table S2, you reported models and compared AIC values only for generalized least-squares (GLS) regression models without random factors and linear mixed-effect models (LMEM) with random factors, both not even mentioned them in the statistical analysis. Also, you did not include GAMMs in the model comparisons, despite the fact that you claim to compare the full model with different random effects structures using the AIC and selected GAMMs. Why were GAMMs not included in the model comparisons? Your other reviewer made a specific note regarding using other statistical tests that were not explained in the manuscript. In the methods or supplementary material, it is necessary to clarify why you used the GLS and LMEM and why the GAMM does not appear in the model comparison table for each response variable. Probably that is a simple step that solves the issue.

the estimated values per species by the total biomass of parrotfishes at each station per locality. To determine if localities were statistically distinct from each other in ~~terms of~~ their parrotfish community structure, under the fishing gradient established, we run a PERMANOVA (*Anderson*, *2001*) with a Bray-Curtis similarity matrix. Finally, we run SIMPER (*Clarke*, *1993*) to assess the average percent contribution of each species to the dissimilarity (statistical packages ~~“~~""vegan~~”~~"-" v. 2.5-7; ~~“~~""ggplot2~~”~~"-" v. 3.3.5).
All analyses ~~described~~ used a p-value significance level of 5% and were carried out in R (v 4.0.2, R Foundation for Statistical Computing, Vienna, Austria). In addition, the data gathered in 2018 and 2019 were analyzed independently as we did not sample BOL, and ALB ~~were not sampled~~ in the second year. Likewise, to evaluate changes in time, only the data from SA and PRO in 2018 were included in the analysis.

Results

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

Variation of the individual total length

The best-fitted models for the individual total length had sex, year, species and locality as fixed effects, including the interaction between them and video stations as random effects, which accounted for spatial and temporal autocorrelation associated with the repeated sampling per locality (*Zuur et al.*, *2009*).

From the 2018 data set, the total length of the medium-sized species showed a negative relationship with fishing pressure, with the –smallest individuals found ~~i~~on the most heavily fished island (SA, Table S3; Fig. 2A). *S. vetula* had larger sizes in BOL (β=3.26, SE=12.34, p= 0.0011; Fig. 2A) and PRO (β=3.64, SE=13.01, p= 6.7 e-09; Fig. 2A), with females reaching larger sizes in the latter (β=5.81, SE=12.84, p= 0.000275; Fig. 2C). On the other hand, *S. viride* had larger sizes in PRO (β=4.77, SE=8.77, p= 1.91e-06; Fig. 2A) and significantly smaller ones at SA (β=-5.39, SE=9.42, p= 7.25e-08; Fig. 2A). Females of the species reached larger sizes in PRO (β=5.81, SE=12.84, p= 0.000275; Fig. 2C), and smaller in SA (β=-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= 0.00011; Fig. 2B) and smaller in SA (β=-5.98, SE=11.02, p= 3.11e-09; Fig. 2B). In contrast, only the males of the small sized species *S. iseri* had larger individual body sizes at the most heavily exploited island of SA (β=3.1, SE=7.6, p= 0.0019; Fig. 2C). *S. aurofrenatum* showed no clear pattern related to fishing pressure, although their individual body sizes presented significant differences among the localities.

We found no differences between the two years evaluated (DF=6, F=1.45, p=0.19). Nevertheless, in 2019, the differences between localities and species remained the same, with the medium size species showing smaller sizes in SA, including *S. vetula* (β=-6.01, SE=8.91, p= 2.13s-09; Fig. 3; Table S4) and *S. viride* (β=-10.3, SE=7.53, p=<2e-16), and the small-size *S. iseri* having larger sizes in SA (β=3.73, SE=6.68, p= 0.0002). In addition, in 2019, we were able to gather a greater sample size of the other two medium-bodied species, and both species showed smaller sizes in

Comment [PRD8]: Probably referring to table S2 is needed here.

Comment [PRD9]: This statement seems more appropriate for methods or discussion, not results.

Comment [PRD10]: Consider moving PRO first than BOL as it coincides with the trend shown in Fig 2A.

Comment [PRD11]: Consider moving results for S. viride first, followed by those for S. vetula to agree wth the legend order for Fig. 2A. It makes easier to follow the results.

Comment [PRD12]: Please provide the statistical support for this finding.

SA *S. rubripinne* (β=-5.78, SE=12.01, *p*=8.27e-09) and *S. chrysopterum* (β=-3.49, SE=10.57, *p*= 0.00049).

Variation of abundances and biomass

The PERMANOVA applied to parrotfishes abundance in 2018 showed significant differences (*DF*=3, *MS*= 1013.2, *F*=1.99, *p*=0.01) between SA and the remaining three localities (DF=30; 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 dropped by the SIMPER showed that the greater abundances of *S. taeniopterus* females~~,~~ in SA~~,~~ contribute the most to the differences ~~found~~ between this island and the other three localities (Fig. 4; Table S5). We also found significant differences in 2019 between SA and PRO in the proportions of the parrotfish~~es~~ composition (*DF*=1, *MS*= 3849.5, *F*=4.44, *p*=0.002). Likewise, *S. taeniopterus* females showed to be more abundant in SA and were largely the major contributors to the differences found by SIMPER analysis (Table S6).

Comment [PRD13]: This is just a suggestion!. When we conduct permanovas, it is important to know if the significant differences are due to sources of variability or data heterogeneity within different groups. You can get an idea of it by conducting a PERMADIST (in Primer) or Smart Permutational Multivariate Analysis of Dispersion in R. In your case; it would tell you if differences in abundance and biomass are really due to the island factors (aka qualitative fishing gradient) or there is an influence by the data variability within the factors.

Biomass data showed significant differences (*DF*=3, *MS*= 1903.1, *F*=2.81, *p*=0.01) between SA and the other three localities (DF=30; SA:ALB *t*=2.28, *p*=0.003; SA:BOL *t*=1.92 *p*=0.012; SA:PRO *t*=2.39, *p*=0.002). Also, the 2019 biomass data showed SA and PRO to be significantly different (*DF*=1, *MS*= 4045.2, *F*=4.57, *p*=0.004). In both studied years, the species that contributed most to the overall differences were the small-sized species *S. taeniopterus*, and the medium-sized species *S. vetula*, and *S. viride* (Table S7 and S8). The former had a higher load in the overall parrotfish biomass in SA, while the other two contributed in greater proportion in the other three localities. In addition, at the least exploited site of PRO we found a higher contribution of the medium-bodied species *S. rubripinne* and *S. chrysopterum* and the large-bodied species *S. coelestinus*, *S. coeruleus*, and *S. guacamaia* (Figs 5; Table S6 and S7). As with individual body sizes, no significant differences were found at SA and PRO between the two years evaluated in terms of abundances (*DF*=1, *MS*= 929.32, *F*=1.57, *p*=0.158) and biomass (*DF*=1, *MS*= 851.61, *F*=0.9, *p*=0.474).

Discussion

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

Following our initial predictions, we expected to find smaller sizes~~,~~ and lower proportions of large and medium-~~-~~bodied species at a greater fishing pressure. This was indeed the case for most of the species and is consistent with previous studies, where a negative relationship between fishing pressure, body sizes, sex ratios, and abundances ~~was~~ were found (*Hawkins & Roberts, 2003, 2004; Vallès & Oxenford, 2014; Vallès et al., 2015*). Likewise, Mixed Effects Models considering sex showed that females of the medium-bodied species *S. vetula* and *S. viride* had larger sizes at lower fishing pressure. This finding could ~~simply~~ be due to selective fishing for large females at the high fishing pressure sites, but it could also indicate that, at least exploited locations, sex change occurs at larger sizes than at more heavily fished grounds (*Hawkins & Roberts, 2004; O~~´~~'Farrell et al., 2016*). What was most striking, however, were the differences found in the small-~~—~~sized species *S. iseri* and *S. taeniopterus*. We found that parrotfish proportions at the most heavily fished locality showed significant differences with the other three least exploited fishing grounds evaluated~~,~~ and that higher abundances and biomass of *S. iseri* and *S. taeniopterus* contributed the most to those differences. Furthermost, this is the first documented study, to our knowledge, to record larger individual sizes of a small-sized parrotfish species at a heavily fished locality, as ~~it ~~is the case of the males of *S. iseri* in SA.

Differences found in ~~terms of ~~biomass are certainly driven by the mentioned changes observed in the abundances and individual body sizes. The higher proportion of small-sized species in the total assemblage of parrotfishes predicted at the beginning of this work is not only a product of a lower contribution of individual body size and proportions of medium and large-bodied species~~,~~ but also an outcome of the higher abundances and individual body sizes of small species. We ~~believe ~~consider that the higher contribution of *S. iseri* and *S. taeniopterus* in the most heavily fished locality suggests an indirect effect of fishing on these two small-sized parrotfish species. *Dulvy et al (2004)* suggested that indirect effects of fishing pressure may be due to reduced predation or interspecific competition. In theory, once predators are removed from the ecosystem, their preys should increase as there is no control over them, yet, there is no clear evidence of this relation (*Clua & Legendre 2008*). Some studies have found no changes in preys after the demise of predators (*Jennings & Polunin, 1997; Roff et al., 2019; Taylor et al., 2018*).~~,~~ ~~others ~~Others have linked ~~a ~~greater biomass of predators such as *Epinephelus striatus* with smaller sizes of *S. iseri* and *S. aurofrenatum* (*Mumby et al., 2006*). In our study, although the greater size and abundance of *S. iseri* and *S. taeniopterus* due to lower predation in SA cannot be completely ruled out and requires further examination, to our knowledge, there are no potential predators that may be significantly more abundant in BOL, ALB and PRO in contrast to SA. Also, as described by *Mumby et al.* (*2006*), we should have found greater sizes of the other small-sized species (i.e., the *S. aurofrenatum*, which is smaller than the *S. taeniopterus*) at the locality with supposedly ~~less ~~fewer predators due to higher fishing pressure (SA);~~,~~ still, this was not the case.

Instead, we believed that a competitive release might play a role in the results found with *S. iseri* and *S. taeniopterus*. Through stable isotope analysis and intestinal content, *Dromard et al*. (2015) recognized an overlap in the trophic niche between *S. vetula*, *S. viride*, *S. iseri* and *S. taeniopterus*. Therefore, it could be argued that when the medium-bodied species (i.e., *S. vetula*, *S. viride*) are removed from the system, the small-bodied ones (i.e., *S. iseri*, *S. taeniopterus*) may be favored, as some resources for which they actively compete become more available.

Consequently, in a~~ strong~~n intensely? exploited locality such as SA, small species can reach larger sizes and higher abundances than in less exploited localities, where larger species limit the resources they compete for~~ and depend on~~. In addition, *Hawkins & Roberts (2004)* found greater abundances of the smallest species of parrotfish (*S. atomarium*) in Jamaica, the most heavily exploited island ~~considered ~~in their study. The ~~strong ~~intense pressure exerted on parrotfishes in Jamaica has been documented *(Hardt, 2009)*, and we wonder if SA, the most heavily exploited island considered in our study, is showing a step in a chain of changes that follows as parrotfishes are gradually depleted according to sizes of interest for fisheries. In this sense, it is essential ~~to carry on with the ~~monitor~~ing of~~ parrotfish populations in the Reserve as small size species, such as *S. aurofrenatum*, may become of interest ~~for ~~to fisheries. *Sparisoma aurofrenatum* is a critical consumer of the seaweed *Dyctiota* in the Caribbean reefs (*Dell et al., 2020*), ~~which is ~~a highly opportunistic algae and a great competitor of corals (*Fong et al., 2003*).

The differences found in parrotfish assemblages will probably ~~have effects on~~influence? many biological traits of the species, such as reproduction, but also at the ecosystem level. O~~I~~n one hand, given the positive relationship between body length and egg production,~~;~~ the reduction of mean body sizes of parrotfish populations due to overfishing is probably negatively affecting

Comment [PRD14]: This phrase was disconnected from the importance of monitoring S. aurofrenatum; perhaps you can consider that monitoring can also help understand phase shifts in coral systems as the fish species is a critical consumer of Dyctiota?.

their reproductive productivity (*Hawkins & Roberts*, *200**4***). On the other hand, the differences found in this study could have a flow-on influence on ecosystem functions (*Bonaldo et al., 2008; Robinson et al., 2019; Shantz et al., 2020*). Larger individuals of parrotfishes have greater roles ~~on~~ in processes like bioerosion, corallivory and grazing of certain macroalgae (*Bonaldo et al., 2008*). ~~In fact,~~ *Shants et al. (2020)* found that the removal of large parrotfish on Caribbean coral reefs increases the abundance of macroalgae and decreases the growth of massive and reef-building corals. This result suggests that it should be necessary to protect fishes larger than 20 cm to maintain their functional diversity ~~it should be necessary to protect fishes larger than 20 cm~~. Hence, the functional roles of large parrotfish species are not necessarily replaced by higher abundances or larger sizes of the small-sized species. Bioerosion and coral predation are two ecological functions highly susceptible to overfishing as their rates increases with the body size of parrotfishes (*Bellwood et al., 2012*). *Scarus vetula* and *S. viride* are important bioeroders (*Bruggemann et al., 1996*), and they had smaller sizes in SA; this could cause lower ~~rates of bioerosion~~bioerosion rates at the locality. Concerning the consumption of algae, recent studies show that species not consistently considered as part of the herbivore community in the Caribbean, such as *Acanthurus coeruleus*, *Acanthurus tractus*, and *Kyphosus* spp., are ~~important~~ critical consumers of macroalgae (*Duran et al., 2019; Dell et al., 2020*), which are the type of algae that are dominating degrading coral reefs (*Perry et al., 2018*). Consequently, future studies should include th~~is~~ese groups of herbivores to ~~accurately~~ determine the effect of herbivores removal on the ecosystem function.

Our findings did not show significant differences between the two years evaluated. However, sampling efforts differ between ~~both~~ years as a greater number of shallower stations nearby seagrass meadows were examined in both localities (SA and PRO) in 2019. ~~It~~ Therefore, it is relevant to continue ~~the~~ monitoring ~~of~~ the parrotfish populations, hopefully at the same stations to accurately evaluate possible differences in time. Nonetheless, our sampling effort was balanced between the localities in 2019 and allowed us to gather a greater sampling size of *S. rubripinne* and *S. chrysopterum*. The two medium-sized species had smaller sizes in the most heavily fished locality. At present, neither of these two species has a threat category assigned in Colombia (*Chasqui et al., 2017*), and it is premature to speak of threat due to fishing pressure when their comparable data is only given in two localities. However, it is important to consider that *S. chrysopterum* had a negative relationship with fishing pressure (*Valles & Oxenford, 2014*) and, according to a report from the continental shores of Colombia, it is one of the most captured species of parrotfishes (*INVEMAR-MADS, 2017*). Therefore, we recommend increasing the sampling effort by focusing on gathering data of both species on a temporal and spatial level to better understand the differences ~~found by~~ in our study.

Finally, among the study limitations, different factors were not considered that may influence fish herbivore species' body size and abundances. Such items may include habitat quality, ~~and~~ food availability, and ~~including~~ other environmental variables. In general, factors such as productivity, temperature, rugosity, latitude, geomorphological attributes of reef formations and slope have shown poor to no~~ne relation with changes in parrotfish community~~ relation with parrotfish community changes (*Cinner et al., 2013; Taylor et al., 2014, 2018*). In contrast, coral cover and position of coral reefs ~~does~~ seem to be related ~~with~~ to changes in biomass and abundance~~s~~ of parrotfishes (*Hoey & Bellwood 2008; Nash et al., 2012)*. Exposed reefs have ~~a~~ greater biomass of parrotfishes and erosion levels (*Russ 1984; Gust, 2001; Hoey & Bellwood 2008; Taylor et al 2014, 2018; Roff et al., 2019)*. Our findings show that *S. vetula* and *S. viride* reach larger sizes ~~not only~~ in the less fished locality (PRO) ~~but also in~~and BOL, with males of *S. viride* reaching larger sizes in the former. Larger sizes and levels of bioerosion of both species are associated with exposed reefs (*Koltes 1993: Bruggemann et al., 1996; Clements et al., 2017*), and BOL seem to have more exposed environments than the other localities (*Gamboa et al., 2012*) which could explain why such differences were found in this site. ~~In consequence~~Consequently, differences in body size are explained by different factors such as reefs exposure, resource~~s~~ availability, and demographic characteristics of fish stocks ~~which are ~~influenced by external stressors such as fishing exploitation. Future efforts should include environmental factors such as reef exposure and coral cover to account for ~~the ~~our study´s ~~great ~~significant intraspecific variation in body size~~ found in our study~~.

Conclusions

Abundances, individual body sizes and biomass of parrotfish species showed significant differences and varied widely depending on the fishing pressure gradient and the size category of the species. On the one hand, medium and large-~~-~~bodied species of parrotfishes had a negative relation between fishing pressure and contribution to the overall biomass, occurrences, and individual body sizes. On the other, we found a ~~greater ~~significant contribution of the small-size species evaluated to the overall biomass at higher fishing pressure sites. The ~~S~~such greater contribution was ~~not only ~~driven by the reduction of sizes and abundances of medium and large-bodied species, directly affected by fisheries~~,~~ but was also a product of greater abundances and, most interestingly, larger sizes of the small-sized species. We suggest this result points to indirect effects of overfishing and that such effects could ~~be related~~ relate to~~with~~ a possible case of competitive release. It is relevant to establish how such variations are linked with possible effects on the species´ reproductive productivity ~~of the species ~~and ecosystem~~s~~ processes.

Overall this study provides insights into intraspecific variation in body size, and our substantial volume of data adds to the existing literature on the extent of variation in parrotfish assemblages over relatively short distances. While we consider~~ed~~ our general results are better explained under a fishing pressure perspective, this by no means denies the influence of other factors such as inter-island environmental differences. Therefore, although the direct and indirect effects of fishing pressure suggested by our work deserve attention, they should be taken as preliminary until further examination on a temporal and spatial scale is conducted.

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