Drivers of abundance and biomass of Brazilian parrotfishes

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ABSTRACT: Parrotfishes may affect the structure of benthic communities and reef ecosystem functioning. Despite extensive studies worldwide, parrotfishes in the southwestern Atlantic are relatively understudied, limiting our ability to propose effective management strategies. We assessed abundance, biomass and size class distribution of parrotfish assemblages in northeastern Brazil and identified habitat preferences based on reef attributes. Outer-shelf reefs sustained larger individuals and higher biomasses for all species (except *Sparisoma radians*). In contrast, inner-shelf reefs supported higher abundances of small individuals. Even though most species occurred across all areas, their abundances, biomass and size-class distributions were variable and related to their respective feeding modes and reef attributes. Benthic cover, reef structural complexity, depth and distance from the coast affected the composition of parrotfish assemblages, but had different effects on each species. The endemic greenbeak parrotfish *Scarus trispinosus* was more abundant on calcareous substrates and higher-complexity reefs. *Sc. zelindae* and *Sp. amplum* were more common in deeper biogenic reefs further from the coast, which were characterized by high abundances of sponges, stony corals and cyanobacterial mats. *Sp. axillare* and *Sp. radians* were more abundant on reefs that had high cover of large-bladed macroalgae, while *Sp. frondosum* was ubiquitous across all studied reefs. Such heterogeneity in habitat use is suggestive of functional complementarity rather than functional redundancy among parrotfish assemblages. Conservation of Brazilian endemic parrotfishes requires protecting reefs with diverse attributes and a better understanding of habitat connectivity and the role of different habitats in parrotfish reproduction and life cycle.

KEY WORDS: Habitat preference · Reef fish · Endemics · Southwestern Atlantic

1. INTRODUCTION

Parrotfishes (Labridae: Scarinae) are among the most ubiquitous and dominant reef fish worldwide, both in abundance and biomass (Horn 1989, Bellwood et al. 2004, Francini-Filho & Moura 2008, Choat et al. 2012). Their fused beak-like jaws allow them to perform important ecological functions by grazing or excavating benthic substrates (Bonaldo et al. 2006, 2012, Francini-Filho et al. 2008, 2010, Bonaldo & Bellwood 2011, Adam et al. 2015), affecting the physical structure and composition of benthic communities (Bonaldo et al. 2014). The ecological functions performed by parrotfishes are variable and dependent on morphological attributes, body size and local abundance (Bonaldo & Bellwood 2008, Lokrantz et al. 2008). Therefore, by understanding habitat preferences and size class distributions of parrotfishes, it

may be possible to infer functional roles, complementarity and redundancy, and their potential impacts on benthic communities (Burkepile & Hay 2008, Adam et al. 2015, 2018).

Given their ubiquity and ecological importance, parrotfishes have been extensively studied worldwide (Bonaldo et al. 2014). The distribution, abundance, biomass, size classes and habitat preferences of parrotfishes in reef environments may be driven by many factors, such as evolutionary history (Choat et al. 2012, Kulbicki et al. 2018), biophysical processes (Taylor et al. 2018), habitat structure (Gratwicke & Speight 2005), availability of preferred dietary resources (Clements et al. 2016), fishing pressure (Hawkins & Roberts 2004a, Bender et al. 2014) or a combination of these factors. There is increasing concern over the maintenance of functional roles performed by nominally herbivorous fishes in reef ecosystems. Indeed, declines in herbivory can lead to phase-shifts on reefs from coral to algal-dominated states (Mumby 2006, Hughes et al. 2007, Lokrantz et al. 2009, Bellwood et al. 2012, Bozec et al. 2016). These top-down processes are complex and vary depending on the herbivore assemblages and the reef environment (Burkepile & Hay 2008), and may not apply to all reef environments (Russ et al. 2015). In fact, parrotfishes may graze not only on macroalgae and algal turfs, but also on many other benthic organisms, including sponges, coralline algae and stony corals (Bonaldo et al. 2014). Recent evidence suggests that the nutritional targets of parrotfishes are protein-rich epilithic and endolithic microbes associated with these various substrates (Clements et al. 2016). While parrotfishes graze on these resources, their feeding mode leads to major consequences in the reef ecosystem. By ingesting calcareous substrates, for example, parrotfishes produce and transport sediments, exerting a major role as bioeroders of calcium carbonate in many reef ecosystems of the Pacific, Caribbean and Indian Oceans (Bellwood 1995, Bruggemann et al. 1996, Ong & Holland 2010, Morgan & Kench 2016, Yarlett et al. 2018). Despite the increasing body of literature on parrotfish ecology, much of the effort is still geographically limited.

Most studies on parrotfish biology and ecology come from the Indo-Pacific, Great Barrier Reef and the Caribbean, where many patterns and processes have been investigated. These studies include: functional analysis (Bellwood & Choat 1990, Bruggemann et al. 1996, Hoey & Bellwood 2008, Yarlett et al. 2018); resource and habitat use (McAfee & Morgan 1996, Rotjan & Lewis 2006); foraging behavior (Adam et al. 2015, 2018); demography (Choat et al. 1996,

2003, Taylor & Choat 2014); patterns of distribution (Hoey & Bellwood 2008, Taylor et al. 2018); and fishing impacts (Hawkins & Roberts 2004b, Mumby 2006, Thyresson et al. 2011, Bellwood et al. 2012, Loh et al. 2015). In the southwestern Atlantic most of these topics have not been studied as thoroughly, with most studies focusing on diet and foraging behavior of Brazilian parrotfishes (e.g. Bonaldo et al. 2006, Ferreira & Gonçalves 2006, Francini-Filho et al. 2008, 2010, Pereira et al. 2016, Tâmega et al. 2016), and fishing (e.g. Bender et al. 2014, Roos et al. 2016). It is important to understand how different species of parrotfishes interact with the benthos to predict how changes in parrotfish assemblages could affect benthic communities and reef ecosystems. A critical step to predict changes in the structure and function of parrotfish assemblages along the southwestern Atlantic is to understand their current distribution, abundance and biomass patterns in different types of reefs.

Ten species within 4 genera of scarinid labrids occur in the southwestern Atlantic: *Scarus trispinosus*, *Sc. zelindae*, *Sparisoma amplum*, *Sp. axillare*, *Sp. frondosum*, *Sp. rocha*, *Sp. tuiupiranga*, *Sp. radians*, *Cryptotomus roseus* and *Nicholsina usta*. In Brazil, species of *Scarus*, represented only by *Sc. trispinosus* and *Sc. zelindae*, are classified as scrapers (Bellwood & Choat 1990, Bonaldo et al. 2014, Hoey 2018). However, even though the beak morphology of *Sc. trispinosus* is more related to those of scraping species (Hoey 2018), large individuals that may reach up to 90 cm in total length can also act as excavating bioeroders (Ferreira & Gonçalves 2006, Francini-Filho et al. 2008, Longo et al. 2014, Bellwood et al. 2019). In fact, given their beak morphology, the only true excavating bioeroding species in Brazil are large individuals of *Sp. amplum* (Francini-Filho et al. 2008, Bonaldo et al. 2014). Other species from the sparisomatine clade are classified as browsers (Bonaldo et al. 2014), although large individuals of *Sp. frondosum* and *Sp. axillare* may also act as scrapers (Ferreira & Gonçalves 2006, Clements & Choat 2018, Bellwood et al. 2019). With such variability within a genus, classification of parrotfishes into functional groups based on feeding modes may hide interspecific differences and hinder our understanding of functional complementarity and redundancy among parrotfishes (Burkepile et al. 2018, Hoey 2018). Given that critical functional roles of parrotfishes are threatened by human activities such as fishing (Bellwood et al. 2012), understanding the functional redundancy versus complementarity among species may help inform our understanding of the magnitude

of fishing effects on parrotfish species and their functions in the reefs.

Parrotfish exploitation has occurred along the Brazilian coast in the last 3 decades (mainly focused on *Sc. trispinosus*, *Sp. frondosum*, *Sp. axillare* and *Sp. amplum*; see Francini-Filho et al. 2008, Bender et al. 2014, Roos et al. 2016). Four endemic species are now threatened at some level: *Sc. trispinosus*, the largest Brazilian parrotfish, is listed as Endangered by the International Union for Conservation of Nature (IUCN, Ferreira et al. 2012) and by the Brazilian Red List of Endangered Species/BRL-EndS (Decree no. 445, Ministerio do Meio Ambiente 2014); and *Sc. zelindae*, *Sp. axillare* and *Sp. frondosum* are listed as Data Deficient by the IUCN and vulnerable by the Brazilian Red List; however, *Sp. amplum* and *Sp. radians* are considered as Least Concern by the IUCN and are not listed in the Brazilian Red List. Signs of depletion of some species (Bender et al. 2014) bolster our need to understand habitat preferences, assemblage structure and size class distributions across different reef types to inform conservation and management.

We assessed the abundance, biomass and size class distribution of 6 species of parrotfish (*Sc. trispinosus*, *Sc. zelindae*, *Sp. amplum*, *Sp. axillare, Sp. frondosum* and *Sp. radians*) in heterogeneous reef areas of northeastern Brazil and identified habitat preferences of these species. We expected that small-sized parrotfish would be more abundant on inshore reefs with higher structural complexity and numerous shelters (Gratwicke & Speight 2005), while reefs further from the coast would sustain higher biomass of larger individuals (Taylor et al. 2018), because juveniles and adults often exhibit different habitat requirements related to food and shelter availability and biophysical attributes of the reefs (Gratwicke & Speight 2005, Hoey & Bellwood 2008, Taylor et al. 2018). Most Brazilian reefs are covered by algal turfs (i.e. epilithic algal matrix) and frondose macroalgae (Aued et al. 2018), which are important feeding substrates for parrotfishes (Bonaldo et al. 2006, Francini-Filho et al. 2010, Pereira et al. 2016). Therefore, we expected most parrotfish species to be distributed across reefs with different traits, but that their abundance, biomass and size-class distribution would vary and be related to benthic resources linked to their feeding strategies. Excavating bioeroding species, for instance, would be more abundant in areas with a higher proportion of calcareous substrates (i.e. stony corals and coralline algae), while grazing sparisomatines would be more abundant in reefs with a higher proportion of macroalgae due to variability in

morphology, foraging and feeding modes among these groups (Francini-Filho et al. 2008, 2010, Bonaldo et al. 2014).

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in northeastern Brazil, in the state of Rio Grande do Norte (between 4°00′S, 37°00′W and 7°00′S, 34°00′W), where the Brazilian coastline forms a corner between a northern and an eastern bounded coast (Fig. 1). The continental shelf in this region extends 40 km from the coastline (Gomes & Vital 2010) and harbors heterogeneous marine habitats (Gomes et al. 2016, Rovira et al. 2019). The northern shelf harbors a wave- and tide-dominated coast with dunes, ebb-tidal deltas, large estuarine areas and offshore biogenic reefs and submerged beachrocks, recognized as ancient coastlines (Vital et al. 2010, Gomes et al. 2016). Strong longshore currents flow west, driven by a combination of trade winds and oceanic and tidal processes, which play an important role in controlling the morphology and sediment distribution in the northern shelf (Testa & Bosence 1999, Gomes et al. 2016). The eastern shelf harbors a wave-dominated coast with dunes, sea cliffs, beach-ridge terraces, shallow patchy reefs and offshore rocky reefs (Vital et al. 2010). This shelf experiences longshore currents that flow north, and sea surface temperatures throughout the region range from 26.5°C in the winter (June to September) to 29°C in the summer (December to March; Testa & Bosence 1999). Wind speed also varies between seasons, peaking in the winter and being weaker in the summer, due to the east–west movement of high-pressure zones in the tropical Atlantic Ocean (Testa & Bosence 1999).

2.2. Field procedures

A total of 46 reef sites with depths varying from 2 to 30 m were sampled between July 2016 and November 2017, with fieldwork interspersed through time according to variable oceanographic conditions (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m623p117_supp.pdf). At each site, parrotfish assemblages were assessed through underwater visual censuses along a belt transect in which a diver identified, counted and estimated the total length of parrotfish species inside an area of 40 m^2 (20 × 2 m, sensu Floeter et al. 2007). Fish size was esti-
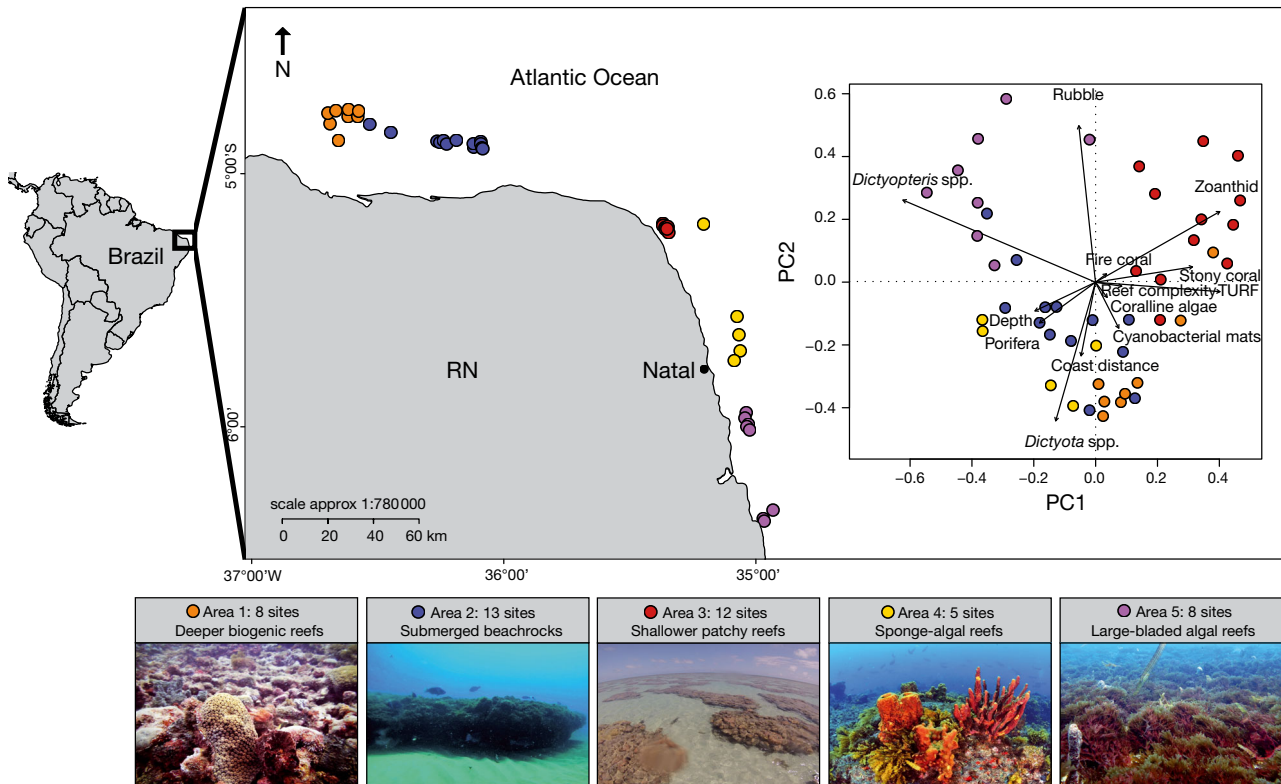
Fig. 1. Study area with sampled sites and a principal component analysis (PCA) of reef attributes. Different colors indicate the areas that were grouped according to similarities in parrotfish biomass and reef attributes (see details in Section 2). The color key is presented with a picture of each area

mated to the nearest cm, and all individuals larger than 3 cm were counted. Parrotfish biomass was estimated using length–weight relationships available in the literature (Froese & Pauly 2016). In total, 303 visual censuses were conducted within the 46 sites, most of them by the same observer (N. C. Roos, with a few censuses by G. O. Longo) to minimize the variance in the size estimates. The number of transects at each site varied from 2 to 11, depending on the depth and available reef area. A second diver traversed the same belt transect while taking photos of the benthos every 2 m, resulting in 10 photos transect^{-1}. Each photograph was analyzed with the software 'photoQuad' (Trygonis & Sini 2012), by randomly laying 30 points over a standardized area of 25 × 20 cm and identifying the organisms below each point into morpho-functional groups, and to species or genus level when possible. In total, 3030 photographs were analyzed.

2.3. Reef structural complexity, depth and distance from the coast

Reef structural complexity was estimated using a habitat assessment score, considering the amount of refuges (gaps and small caves in habitat architecture), galleries (connected holes within the habitat substrate, forming a 'Swiss-cheese-like' structure), reef height and reef area. Refuges and galleries were assessed visually and classified within a ranking based on 4 categories, where 0 = none, 1 = little, 2 = medium and 3 = many. For reef height, the categories were: 0 = <2 m, 1 = 2–3.9 m, 2 = 4–5.9 m, 3 = >6 m; and for reef area, the categories were: 0 = <80 m^2, 1 = 80–160 m^2, 2 = 160–240 m^2, 3 = >240 m^2. The final score was obtained by the sum of the values of each attribute with equal weights. We also recorded the depth of each transect during the fieldwork and measured the distance from each sampled site to the coast using GPS (Table S1).

2.4. Data analysis

The structure of parrotfish assemblages was compared among sites using a cluster analysis (average clustering method) on a Euclidean distance matrix obtained from biomass data. The same analysis was used to compare the structure of reef attributes among sites. A hierarchical clustering with boot-

strapped p-values was used to determine the significance of the clusters. The relationship among sites and reef attributes (i.e. benthic cover, reef structural complexity, depth and distance to coast) was evaluated through a principal component analysis (PCA). We conducted these analyses at the site level to provide additional support for the classification of sites within 5 areas, highlighting the differences among them. Differences in the abundance and biomass among species within and among areas per species were assessed through separated permutation-based ANOVA and Tukey's honestly significant difference (HSD) test for the significant contrasts. This analysis was conducted on the area level so the differences in parrotfish assemblages would reflect the heterogeneity of reef attributes among the areas. We chose the permutation-based ANOVA rather than more classic approaches because it does not require normality or homogeneity of variances, since all estimates and coefficients are obtained from permutation (Wheeler 2016).

Two complementary approaches were used to assess the relationship between parrotfishes and reef attributes, using data on the transect level to account for the heterogeneity of attributes regardless of sites and areas. First, the intrinsic relationships between the abundance and biomass of parrotfish assemblage and reef attributes were assessed through redundancy analyses (RDA). Variables with a variance inflation factor (VIF) >3 were removed to avoid high collinearity (Zuur et al. 2010). Then, to assess which variables explained the occurrence and biomass of each parrotfish species on the studied reefs, we used 2 models for each species. First, we used generalized linear models (GLMs) with binomial distribution to model presence/absence data per transect (response variable) as a function of reef attributes (explanatory variables, see details in Supplement 2). We then used GLMs with Gaussian distribution to analyze the positive biomass values per transect (response variable) as a function of the reef attributes (explanatory variables, see details in Supplement 2). Before running GLMs, the normality of the positive biomass values was checked both graphically with a density plot and statistically with the Shapiro test. When data did not meet the normality assumption, a log-transformation was applied to enable the use of Gaussian distribution in the models. In cases in which data did not meet the normality assumptions, even after the log-transformation, a gamma distribution was implemented (see details in Supplement 2). Model selection was performed via a forward procedure, using Akaike's

information criterion (AIC), the total deviance explained (%) and the significance (p-value) of the variables as selection criteria. The significance level for all statistical analysis was 5% (α = 0.05). The complementarity between the 2 approaches lies in the fact that RDA provides information on how the parrotfish assemblage responds to reef attributes (multi-specific perspective), while the generalized models provide a species-specific response to reef attributes.

All analyses were performed in R version 3.2.3 (R Core Team 2015; www.r-project.org) and the packages 'pvclust' (Suzuki & Shimodaira 2015), 'vegan' (Oksanen et al. 2017), 'lme4' (Bates et al. 2015), 'lmPerm' (Wheeler & Torchiano 2016) and 'ggplot2' (Wickham 2009). The small-scale map (Fig. 1) was plotted with the 'maptools' package (Bivand & Lewin-Koh 2013), and the graphs in Fig. 2 were plotted with the 'yarrr' package (Phillips 2017).

3. RESULTS

Sites were grouped into 5 areas (Fig. 1) according to the following criteria: (1) proximity among sites; (2) geological composition; and (3) overall similarities revealed by PCA (Fig. 1), the cluster analysis on parrotfish biomass (Fig. S1 in Supplement 3) and reef attributes (benthic cover, reef structural complexity, depth and distance from the coast; Fig. S2). Our sampling effort comprised a high heterogeneity of habitats regarding physical characteristics and benthic cover (Fig. 1). The areas were mainly covered by *Dictyota* spp. and algal turfs (i.e. epilithic algal matrix), but showed differences in the coverage of stony corals, coralline algae, sponges and large-bladed macroalgae (i.e. *Dictyopteris* spp.; Fig. S3). Area 1 consisted of biogenic reefs (Gomes et al. 2016) located deeper and further from the coast in comparison to the other areas (~28 m deep; ~35 km from coast), covered by the highest proportion of stony coral (mainly *Montastraea cavernosa* and *Siderastrea stellata*) and cyanobacterial mats, and the second highest proportion of sponges in comparison to the other areas. Area 2 consisted of submerged beachrocks recognized as ancient coastlines composed of sandstone structures (Vital et al. 2010, Gomes et al. 2016), forming a large and complex reef system (~11 m deep) located ~22 km from the coast and covered by the highest proportion of coralline algae in comparison to the other areas. Area 3 comprised shallower patchy reefs (~2 m deep) near shore (~6 km), covered by a high propor-

tion of stony corals (mainly *Siderastrea stellata*, *Favia gravida*, *Porites astreoides* and *Agaricia agaricites*), zoanthids (mainly *Palythoa caribaeorum*) and coralline algae. Area 4 is located ~17 km from the coast and consisted of large rocky reefs (~18 m deep) covered by the highest proportion of sponges (mainly *Aplysina lactuca* and *A. fulva*). Area 5 comprised small and short patches of macroalgae-dominated rocky reefs (~16 m deep) mainly covered by large-bladed macroalgae (*i.e. Dictyopteris jolyana*, *D. justii* and *D. plagiogramma*) and located ~10 km from the coast (Fig. S3).

3.1. Parrotfish abundance and biomass

Six species of parrotfishes were recorded in this study: *Scarus trispinosus*, *Sc. zelindae*, *Sparisoma amplum*, *Sp. axillare*, *Sp. frondosum* and *Sp. radians*. Except for *Sp. radians*, which also occurs in the Caribbean, all other species are endemic to the Brazilian Province (Pinheiro et al. 2018). A total of 1778 individuals were recorded during fieldwork (average of ~6 ind. 40 m^{-2}), of which 381 (~1 ind. 40 m^{-2}) were *Scarus* species and 1397 (~5 ind. 40 m^{-2}) were *Sparisoma* species. The lowest abundances of parrotfishes were recorded in submerged beachrocks further from the coast (Area 2) with ~3 ind. 40 m^{-2}, while the highest abundance was seen in the shallow patchy reef areas close to the coast (Area 3) with ~8 ind. 40 m^{-2}. The biomass, however, followed an opposite pattern, with Area 2 presenting the highest biomass (~5.6 kg 40 m^{-2}) while Area 3 had the lowest (~0.8 kg 40 m^{-2}). The most abundant species was *Sp. axillare* (~2 ind. 40 m^{-2}), while the species with the highest biomass was *Sc. trispinosus* (~1.2 kg 40 m^{-2}). The most abundant species in absolute numbers was *Sp. axillare*, but the most ubiquitous species was *Sp. frondosum*. The rarest species was *Sp. radians* (~0.13 ind. 40 m^{-2}), consequently presenting negligible biomass values.

There were marked differences in species abundance and biomass within and among areas (Fig. 2, Table 1, Fig. S4, Table S8 in Supplement 4). The most abundant parrotfishes in deeper biogenic reefs further from the coast (Area 1) were *Sc. zelindae*, *Sp. amplum* and *Sp. frondosum* (Fig. 2A), and the abundance and biomass of *Sc. zelindae* and *Sp. amplum* were the highest compared to the other areas (Table 1, Supplement 4). The most abundant parrotfish in submerged beachrocks (Area 2) was *Sc. trispinosus*, which was significantly more abundant and had the highest biomass compared to other spe-

cies within the area (Fig. 2B), and had the higher biomass compared to other areas because of the occurrence of larger-sized individuals (>50 cm; Table 1). In shallower patchy reefs closer to the coast (Area 3) the abundance of *Sc. trispinosus* was similar to Area 2, but presented a lower biomass because most individuals were juveniles or smaller than 30 cm. This pattern was reflected in the species biomass, which was 8 times lower in Area 3 than in Area 2 (Fig. 2C). The most abundant species in Area 3 were *Sp. axillare* and *Sp. frondosum*, which were significantly more abundant compared to other species within the area. The high abundance of small individuals of both species (<15 cm) was reflected in low biomass values (Fig. 2C). The sponge-algal reefs (Area 4) were characterized by a low abundance and biomass of parrotfishes, with *Sp. frondosum* being the most abundant species in this area (Fig. 2D). Lastly, the most common species in the large-bladed algal reefs (Area 5) was *Sp. axillare* (Fig. 2E). The abundance of this species in Area 5 was similar to Area 3; however, the abundance of larger individuals (>25 cm) in Area 5 resulted in the highest biomass of *Sp. axillare* compared to other species within this area (Fig. 2E) and compared to the other areas (Table 1). The rarest species of this study, *Sp. radians*, was significantly more abundant in Area 5 compared to other areas (Fig. 2E, Table 1).

The higher parrotfish biomasses in reefs further from the coast was driven by large individuals of *Sc. trispinosus*, *Sc. zelindae* and *Sp. amplum* in deeper biogenic reefs and submerged beachrocks (Fig. 2). Juveniles of all parrotfish species in this study (except *Sp. amplum*), but most importantly *Sp. axillare*, *Sp. frondosum* and *Sc. trispinosus*, were more common in the nearshore shallow reefs of Area 3. Juveniles of *Sc. trispinosus* and *Sc. zelindae* were recorded exclusively in Area 3, while larger individuals of these species were observed in reefs further from the coast. Juvenile-phase (JP) *Sp. axillare* were abundant in the shallow patchy reefs (Area 3), but initial phase (IP) adults were more common in the large-bladed algal reefs (Area 5), and terminal phase (TP) adults were rare but mostly recorded in the sponge-algal reefs (Area 4; Fig. 2).

3.2. Habitat preferences

Reef attributes combined explained 24% of the abundance (RDA, F = 7.09, p = 0.001, Fig. S5 in Supplement 5) and 22% of the biomass (RDA, F = 6.58, p = 0.001, Fig. 3) of parrotfish assemblages across the
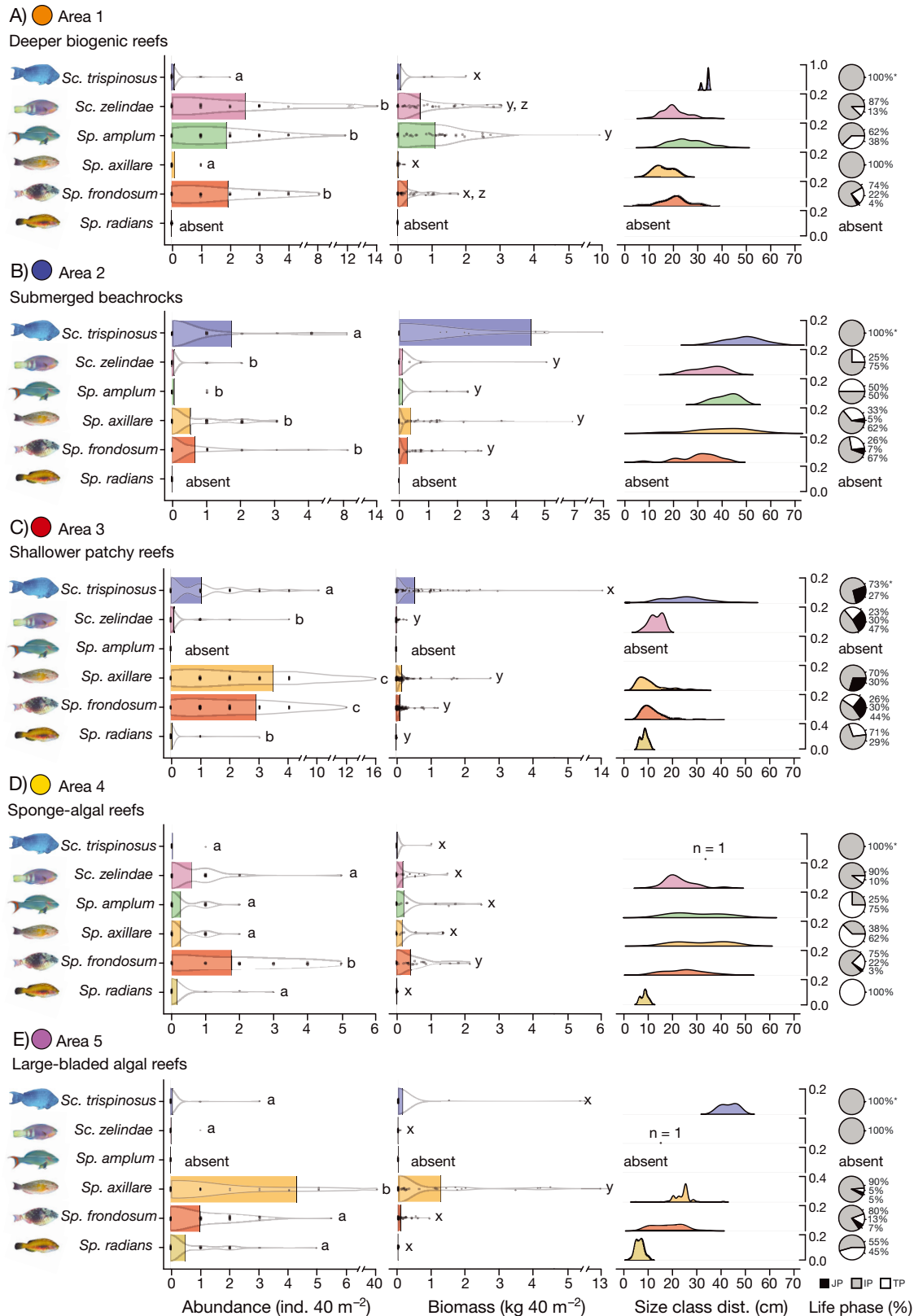
Fig. 2. Abundance (ind. 40 m^{-2}), biomass (kg 40 m^{-2}) and size class distribution (densities) of *Scarus trispinosus*, *Sc. zelindae*, *Sparisoma amplum*, *Sp. axillare*, *Sp. frondosum* and *Sp. radians* in (A) Area 1, (B) Area 2, (C) Area 3, (D) Area 4 and (E) Area 5. Horizontal bars indicate the mean values; different colors indicate different species; light grey points indicate data dispersion; line contours represent the density of data points (i.e. thicker areas indicate a higher density of points); JP: juvenile phase; IP: initial phase; TP: terminal phase. *Only JP and 'adult' phases were recorded for *Sc. trispinosus*; different letters within each area indicate significant differences at a 5 % significance level

Table 1. Differences in parrotfish abundance (Abund.; ind. 40 m^{-2}) and biomass (Biom.; kg 40 m^{-2}) among areas. Different superscript letters within each column indicate significant differences at the 5% significance level. Areas are described in Fig. 1. *Sc.*: *Scarus*; *Sp.*: *Sparisoma*; na: not available

Area	*Sc. trispinosus* Abund.	Biom.	*Sc. zelindae* Abund.	Biom.	*Sp. amplum* Abund.	Biom.	*Sp. axillare* Abund.	Biom.	*Sp. frondosum* Abund.	Biom.	*Sp. radians* Abund.	Biom.
1	0.09[a]	0.08[x]	2.52[a]	0.65[x]	1.88[a]	1.08[x]	0.11[a]	0.01[x]	1.93[a,b]	0.28[x,y,z]	na	na
2	0.70[b]	4.17[y]	0.06[b]	0.11[y]	0.06[b]	0.13[y]	0.53[a]	0.41[x]	0.65[c,d]	0.30[x]	na	na
3	1.02[a,b]	0.52[x]	0.11[b]	>0.01[y]	na	na	3.46[b]	0.16[x]	2.88[a,d]	0.10[z]	0.05[a]	>0.01[x,y]
4	0.02[a]	0.02[x]	0.58[b]	0.19[y]	0.26[b]	0.22[y]	0.26[a]	0.17[x]	1.76[a,d]	0.40[x,w]	0.17[a]	>0.01[y,z]
5	0.07[a]	0.13[x]	0.01[b]	>0.01[y]	na	na	4.45[b]	1.20[y]	0.90[b,d]	0.08[y,z]	0.50[b]	>0.01[z]

areas, both presenting similar relationships with reef attributes. Turf and *Dictyota* spp. were excluded from this analysis due to high VIF values (Fig. S6). Both RDAs presented similar results. *Sc. trispinosus* was mainly associated with highly complex reefs with higher cover of calcareous substrates, such as coralline algae and stony corals. *Sp. frondosum* and *Sp. axillare* presented a similar relationship as *Sc. tripinosus*, but *Sp. frondosum* was more central in the analysis, reflecting its ubiquity across the study areas, while *Sp. axillare* was more strongly associated with large-bladed macroalgae and rubble habitats. *Sc. zelindae* and *Sp. amplum* shared similar habitat preferences and were associated with deeper reefs further from the coast characterized by high cover of cyanobacterial mats and sponges. *Sp. radi-*

ans also shared similar habitat preferences with *Sp. axillare*, but it was mainly associated with large-bladed macroalgae habitats.

The major drivers of occurrence and biomass of parrotfishes varied among species (Table 2, see detailed models in Supplement 2). The occurrence of *Sc. trispinosus* was mainly explained by higher cover of crustose coralline algae (CCA) and turf, and shallow habitats. Likewise, the biomass of *Sc. trispinosus* was higher in outer-shelf reefs with higher cover of CCA, turf, *Dictyota* spp. and rubble. This pattern was driven by a higher abundance of small individuals in shallow reefs, while larger individuals occurred further from the coast. The occurrence of *Sc. zelindae* was positively related to depth and distance from the coast (Area 1), but negatively related to *Dictyopteris* spp. and articulated coralline algae (ACA) that were not abundant in the reefs where *Sc. zelindae* was present. The only variable that explained the biomass of *Sc. zelindae* was distance from the coast, with larger biomass recorded in outer-shelf reefs. The occurrence of *Sp. amplum* was explained by similar factors, but its biomass was also positively related to high cover of cyanobacterial mats. The occurrence of *Sp. axillare* was explained by higher cover of *Dictyopteris* spp. and stony coral, but had a negative relationship with depth. The biomass of this species was also explained by higher cover of *Dictyopteris* spp. and distance from the coast. These results indicate a similar pattern of high abundance of small individuals in shallow depths and larger individuals further from the coast, observed for *Sc. trispinosus*, *Sc. zelindae* and *Sp. amplum*. The occurrence of *Sp. frondosum* was ex-
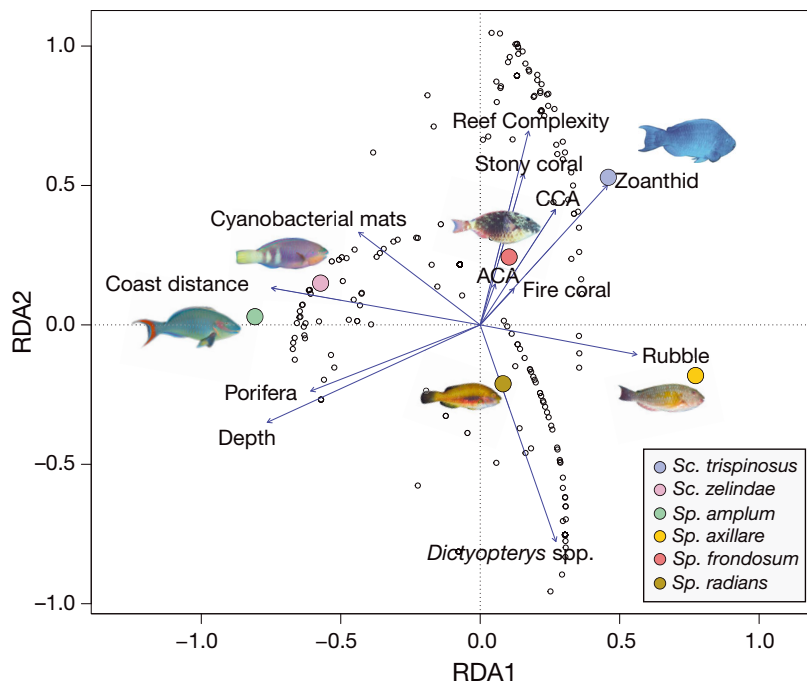

Fig. 3. Redundancy analysis (RDA) on the biomass of parrotfishes and reef attributes ($F = 6.08$, p = 0.001). CCA: crustose coralline algae, ACA: articulated coralline algae. The white dots represent the score of each transect (N = 303)

Table 2. Summary of the best fitted binomial and generalized linear models relating the occurrence and biomass of the 6 parrotfishes to the explanatory variables, respectively (see detailed models in Supplement 2). CCA: crustose coralline algae; ACA: articulated coralline algae; coast dist.: distance to coast; *Dictyop.*: *Dictyopteris*; cyano.: cyanobacterial

Variable	Estimate	SE	z	p	Variable	Estimate	SE	t	p
	Occurrence model					Biomass model			
Scarus trispinosus									
Intercept	−1.685	0.808	−2.085	0.037	Intercept	−8.626	1.716	−5.027	<0.001
CCA	2.992	1.464	2.043	0.041	CCA	5.542	1.871	2.962	0.004
Turf	4.205	0.994	4.229	<0.001	*Dictyota* spp.	2.854	1.045	2.732	0.008
Depth	−6.754	1.896	−3.562	<0.001	Rubble	2.750	1.116	2.464	0.016
					Turf	3.395	1.486	2.285	0.025
					Coast dist.	17.095	2.572	6.647	<0.001
Scarus zelindae									
Intercept	−5.114	0.761	−6.718	<0.001	Intercept	−4.469	0.688	−6.534	<0.001
ACA	−14.719	7.118	−2.068	0.038	Coast dist.	8.894	1.655	5.374	<0.001
Dictyop. spp.	−4.713	1.417	−3.324	<0.001					
Depth	5.053	2.912	1.735	0.082					
Coast dist.	8.269	2.950	2.803	0.005					
Sparisoma amplum									
Intercept	−20.178	2.987	−6.755	<0.001	Intercept	−26.102	8.951	−2.916	0.005
Dyctiota spp.	3.668	1.591	2.306	0.021	Cyano. mats	12.661	1.943	6.516	<0.001
Depth	21.191	5.242	4.042	<0.001	Depth	26.353	10.15	2.608	0.012
Coast dist.	24.489	4.719	5.189	<0.001	Coast dist.	30.780	14.693	2.095	0.042
Sparisoma axillare									
Intercept	1.322	0.504	2.619	0.008	Intercept	−3.889	0.598	−6.502	<0.001
Dictyop. spp.	3.302	0.676	4.879	<0.001	*Dyctiota* spp.	1.794	0.714	2.511	0.012
Stony coral	3.484	1.196	2.912	0.003	*Dictyop.* spp.	3.712	0.612	6.064	<0.001
Depth	−9.956	1.652	−6.024	<0.001	Coast dist.	6.605	2.129	3.121	0.002
Sparisoma frondosum									
Intercept	−1.555	0.478	−3.252	0.001	Intercept	−1.531	0.232	−6.581	<0.001
ACA	−0.078	0.047	−1.664	0.096	Stony coral	−0.025	0.013	−1.880	0.061
Fire coral	−0.199	0.120	−1.648	0.099	Zoanthid	−0.029	0.011	−2.679	0.008
Porifera	0.049	0.023	2.102	0.035	Coast dist.	0.040	0.010	3.874	<0.001
Rubble	0.018	0.008	2.204	0.027					
Turf	0.020	0.009	2.252	0.024					
Stony coral	0.048	0.024	2.021	0.043					
Zoanthid	0.032	0.017	1.930	0.053					
Complexity	0.102	0.054	1.888	0.058					
Sparisoma radians									
Intercept	−4.573	1.109	−4.124	<0.001					
Dictyop. spp.	5.845	1.599	3.662	<0.001					
Stony coral	7.192	3.001	2.396	0.016					
Turf	−3.955	2.307	−1.174	0.086					

plained by many variables, reflecting its ubiquity among the areas. The most significant variables for occurrence of *Sp. frondosum* were higher cover of sponges, rubble and turf, while biomass was positively related to high CCA and *Dictyopteris* spp. cover, and larger distances from the coast. Interestingly, the biomass of *Sp. frondosum* was negatively related to stony coral cover. The most significant variable that explained the occurrence of *Sp. radians* was *Dictyopteris* spp., and the biomass analysis could not be carried out given the negligible biomass values and low frequency in the data.

4. DISCUSSION

The Brazilian coast comprises most of the reef environments in the southwestern Atlantic, with the tropical portion harboring the highest heterogeneity of reef habitats (Leão et al. 2016, Aued et al. 2018). Given the regional scale of our sampling effort, this study comprised a great heterogeneity of reef habitats because it included biogenic reefs, which are also common on the Brazilian eastern coast (e.g. Abrolhos); rocky reefs, common in many areas from the southern to northern coast; shallow patchy reefs,

common in northeastern Brazil; and unique offshore submerged beachrocks (Vieira & Ros 2006, Leão et al. 2016). Parrotfish biomass was considerably higher in reefs further from the coast. Even though most species occurred across all study areas, their abundances, biomasses and size-class distributions were variable according to reef attributes and benthic substrates linked to their feeding modes. This pattern indicates low functional redundancy due to the heterogeneity in habitat use.

The higher parrotfish biomass in reefs further from the coast in comparison to coastal reefs observed in this study likely results from ontogenetic variability in habitat use. The shallow coastal reefs of Area 3 are likely a nursery habitat for parrotfish (Beck et al. 2001), mostly for *Scarus trispinosus, Sc. zelindae* and *Sparisoma axillare*, whose adults (TP and individuals >40 cm in the case of *Sc. trispinosus*) were mostly observed in deeper reefs further from the coast. The trend of small parrotfish occurring in inshore reefs and large individuals in offshore reefs has been reported for the Great Barrier Reef (Gust 2002, Hoey & Bellwood 2008). Juveniles tend to occur in more sheltered inshore reefs where epilithic algae are more available to be used as a food resource. In contrast, offshore reefs with higher wave energy and less epilithic algae harbor more larger adults that are able to explore endolithic algae as a food resource (Clements et al. 2016, Taylor et al. 2018). Such variation in habitat use by small and large individuals (juveniles and adults) prompts the need to understand the ecological connectivity among habitats and how this interacts with vital rates of mortality and maturation. Such information may have important implications for management and conservation in the face of increasing fishing pressure on parrotfish.

The consequences of parrotfish harvesting worldwide have been extensively discussed (Hawkins & Roberts 2004a, Mumby 2006, Hughes et al. 2007, Lokrantz et al. 2009, Bellwood et al. 2012, Edwards et al. 2014, Bozec et al. 2016), with declines in populations already documented in the Pacific (Aswani & Sabetian 2010, Hamilton et al. 2016) the Caribbean (Hawkins & Roberts 2004b, Mumby et al. 2006) and Brazil (Bender et al. 2014). The state of Rio Grande do Norte, where the present study was conducted, sustains intense artisanal fishing activities (Damasio et al. 2015, Roos et al. 2016, Fonseca et al. 2017). Among our study areas, parrotfishes are not the main fishing targets in Areas 1 and 2, which may be contributing to the maintenance of the high parrotfish biomass we recorded in these areas, and are hardly reported in catches from Areas 4 and 5 (Damasio et

al. 2015). Conversely, fishing effort focused on parrotfishes occurs in Area 3, where about 15 t of *Sc. trispinosus*, *Sp. axillare* and *Sp. frondosum* are captured every year (see details in Roos et al. 2016). The average size of individuals captured by gillnets in this area is 28.6 cm for *Sc. trispinosus* and 26 cm for *Sp. axillare* and *Sp. frondosum.* In the case of *Sc. trispinosus,* there is also an effort to capture larger individuals using spear guns, but the average size of these captures is 39.3 cm, which is still small for a species that may reach up to 90 cm. Local fishermen reported that the occurrence of larger parrotfishes in this area, particularly larger *Sc. trispinosus* (>65 cm), has always been rare, even before the increasing fishing pressure in the last decade (N. C. Roos et al. unpubl. data). Additionally, other species that are not fishing targets, such as the French angelfish *Pomacanthus paru*, the queen angelfish *Holacanthus ciliaris* and the tomtate grunt *Haemulon aurolineatum*, are mostly observed as recruits or juveniles in Area 3, reinforcing the hypothesis that these nearshore habitats are nurseries for juvenile fishes. Therefore, the higher abundances of small parrotfish in Area 3 are more likely to reflect habitat preferences than potential effects of the fishing pressure itself.

Habitat preferences may also result from a combination of morphological and ecological differences among species and life stages. These differences may affect foraging strategies and determine how parrotfish use reefs with different attributes. Although most species occurred in all of the study areas, their abundances and size-class distributions were variable according to reef attributes. The greenbeak parrotfish *Sc. trispinosus* was more common in reefs with higher cover of coralline algae, one of its main feeding substrata (Francini-Filho et al. 2010). Similarly, *Sc. zelindae* was mainly recorded in reefs with the highest cover of sponges, an important foraging substrate for this species (Pereira et al. 2016). Indeed, we frequently observed individuals of *Sc. zelindae* lightly scraping a thin layer of cyanobacteria growing on the sponge surface (N. C. Roos & G. O. Longo pers. obs.), indicating they were likely targeting epilithic microorganisms rather than the sponge itself (Clements et al. 2016). *Sp. axillare* were abundant in areas with high macroalgal cover, particularly brown algae. Although it is unlikely that brown algae are the nutritional targets of *Sp. axillare* due to its digestive physiology (Clements et al. 2016), brown algae are a common foraging substratum for this species and comprise a considerable portion of its gut content (Bonaldo et al. 2006, Ferreira & Gonçalves 2006, Francini-Filho et al. 2010). *Sp.*

amplum was more abundant in reefs further from the coast with the highest cover of stony corals, which may be linked to its excavating feeding mode and its affinity to reefs with oceanic conditions (Ferreira et al. 2006, Francini-Filho et al. 2008, Bonaldo et al. 2014). *Sp. frondosum* was conspicuous across all study areas and is the only endemic Brazilian parrotfish found beyond the border of the Brazilian Province (Southeast Caribbean, Rocha 2003; African islands, Freitas et al. 2014). Such a geographic range indicates that *Sp. frondosum* may adapt to different habitats (locally and regionally) and succeed in establishing new populations. *Sp. frondosum* may have a different reproductive strategy in comparison to the other parrotfishes in this study, favoring such wide distribution, but further work is needed to test this hypothesis. While TP individuals of other species were less abundant or only observed in a particular area (see Fig. 2), TP individuals of *Sp. frondosum* were abundant across all areas, including the shallow inshore reefs where even small individuals (18 cm) already displayed the TP coloration. *Sp. radians* were observed in reefs with high cover of large-bladed macroalgae, which somehow mimics their preferred substrate of submerged vegetation and seagrass habitats (Lobel & Ogden 1981, McAfee & Morgan 1996). Despite the particularities, there were differences in habitat preferences of excavating species (considering both *Sc. trispinosus* and *Sp. amplum*) and other grazing sparisomatines.

In this study, the genus *Sparisoma*, which only occurs in the Atlantic (Bernardi et al. 2000), was 5 times more abundant than the genus *Scarus*. Unlike in the Caribbean, the genus *Sparisoma* predominates over the genus *Scarus* in the southwestern Atlantic (Longo et al. 2019), which may be related not only to dispersion potential, but also to habitat requirements. Nevertheless, sister species of all Brazilian endemic parrotfishes are found in the Caribbean and diverged recently (Robertson et al. 2006, Choat et al. 2012), so Caribbean and southwestern Atlantic parrotfishes share many morphological features, feeding behavior and habitat preferences. For example, *Sc. guacamaia*, similar to its Brazilian sister species *Sc. trispinosus*, grazes predominantly on coralline algae and turf (Burkepile & Hay 2011, Adam et al. 2015). Moreover, *Sp. rubrupinne* and *Sp. chrysopterum* (sister species of *Sp. axillare* and *Sp. frondosum*, respectively) also commonly graze on brown macroalgae (Bonaldo et al. 2014, Adam et al. 2015). Feeding behavior and habitat preferences of *Sp. viride*, the largest sparisomatine of the Caribbean, is also similar to its sister species *Sp. amplum* (Bellwood & Choat

1990, Francini-Filho et al. 2008, Bonaldo et al. 2014, Adam et al. 2015), indicating that these sister species may play similar ecological roles in these different geographic regions (Longo et al. 2019).

Although parrotfishes are frequently placed in the same group of functional traits in global analyses (e.g. herbivorous–detritivorous, Mouillot et al. 2014), the functional role of each species may vary depending on its feeding mode, grazing ability, and nutritional strategy. When combined, these factors likely affect how they impact energy and nutrient flow in reef communities (Bellwood et al. 2019). Body size is also an important determinant of parrotfish ecological function (Bruggemann et al. 1994, Bonaldo & Bellwood 2008); the larger the body size, the greater is the force of the jaws while biting on the substratum (Bruggemann et al. 1994, Bonaldo & Bellwood 2008, Lokrantz et al. 2008). Individuals of *Sc. tripinosus*, for instance, have a smaller excavating potential than similar sized individuals of *Sp. amplum* (Francini-Filho et al. 2008) due to the different beak morphologies between these species. However, large individuals of *Sc. trispinosus* may act as excavators depending on the fish size and thickness of the coralline algae or coral colony growing on the substrate. The maximum size reported for *Sc. trispinosus* (90 cm) is more than twice the maximum size of *Sp. amplum* (40 cm), and *Sc. trispinosus* is more common in coastal Brazilian reefs than *Sp. amplum.* Therefore, the bioeroding and, to some extent, excavating role of large *Sc. trispinosus* may have a greater impact on Brazilian reefs when compared to *Sp. amplum* (Francini-Filho et al. 2010, Bonaldo et al. 2014). Even though these 2 species may act as bioeroders and excavators, their preferences for different reef habitats shown here and preferred foraging substrates (Francini-Filho et al. 2010) indicate that their functional roles are unlikely to be redundant. The same applies to the other sparisomatines in this study, which are often considered to have similar functions. The level of overlap in parrotfish diets and preferred habitats may indicate whether redundancy or complementarity exists within the same functional group (Burkepile & Hay 2011). Based on the different habitat preferences among species and size classes shown in the present study, we suggest that there may be more complementarity than redundancy occurring among the Brazilian endemic parrotfish, resulting from an interaction between reef attributes and species' feeding modes.

We have shown that small-sized Brazilian parrotfish use reefs closer to the coast, as either a nursery or a developing area, while larger adults are more com-

mon in reefs further from the coast. Additionally, the heterogeneous habitat use by the different Brazilian parrotfish species related to their respective feeding modes indicates low levels of redundancy and high vulnerability to species loss. Even though we did not sample deeper reefs (>30 m) which are mostly further from the coast, all Brazilian endemic parrotfishes were recorded in reefs between 50 and 60 m deep (Feitoza et al. 2005), suggesting these may also be critical habitats for parrotfishes. Shallow inshore and deeper offshore reefs may be distinct with respect to maturation schedules and rates of mortality for most Brazilian parrotfishes. These differences, if they occur, would be informative for management planning, especially for the Endangered *Sc. trispinosus*. The ongoing fishing pressure in the inshore reefs of Area 3, for instance, may be causing significant declines in adult numbers in deeper outer shelf reefs that are yet to be quantified. An effective management plan for parrotfishes depends on this information and on a better understanding of the role of different habitats for parrotfish reproduction and life cycles.

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