



# Two ubiquitous parrotfishes exhibit distinct foraging ecologies on tropical Brazilian reefs

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**ABSTRACT:** Parrotfishes (Labridae: Scarinae) are common components of reef environments known to influence the early succession dynamics of benthic communities through their foraging behavior. In the southwestern Atlantic, the sparisomatine clade predominates over the scarinine when compared to the Caribbean, with the endemic species *Sparisoma axillare* and *S. frondosum* being the most abundant and widespread parrotfishes in the Brazilian Biogeographic Province. Given that the 2 species are similar in terms of occurrence and abundance, describing their levels of niche complementarity is challenging. Investigating basic ecological distinctions between species can aid in comprehending their habitat requirements and susceptibilities. This is particularly important in the case of *S. axillare* and *S. frondosum*, both of which are listed as Vulnerable by the Brazilian Red List of Endangered Species. Here, we assessed feeding rate, substrate selectivity, niche overlap, shoaling behavior and agonistic interactions during foraging activity of both species and comparatively between ontogenetic stages. We found that despite a high niche overlap, *S. frondosum* feeds on a wider range of substrate types and interacts more with other species while foraging compared to *S. axillare*. Dissimilarities in substrate selection by the 2 species were mainly represented by algal turfs and sand but an opposite pattern was detected: *S. axillare* preferentially selected the algal turfs and *S. frondosum* selected more sand. Although fine-scale resource partitioning has not been investigated, our results provide insights into niche complementarity between the 2 species and inferences on drivers that may help explain their distribution in the Brazilian reefs.

**KEY WORDS:** *Sparisoma axillare* · *Sparisoma frondosum* · Scarinae · Southwestern Atlantic · Endemics · Reef fish

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## 1. INTRODUCTION

Parrotfishes (Labridae: Scarinae) are ubiquitous components of tropical coral reefs known for scraping and excavating benthic substrates with their fused beak-like jaws (Bonaldo et al. 2014, Gobalet 2018). The effects of parrotfishes' foraging behavior on benthic communities have been widely studied in the past decades (e.g. Bruggemann et al. 1996, Francini-Filho et al. 2008, 2010, Bonaldo & Bellwood 2009,

2011, Bonaldo et al. 2012, Rempel et al. 2020), and recent studies have revealed that protein-rich microscopic phototrophs are their main nutritional targets (Clements et al. 2017, Clements & Choat 2018, Nicholson & Clements 2020). Still, parrotfishes act as major agents of bioerosion and sediment processing in reef environments (Bellwood 1995, Bonaldo et al. 2014, Morgan & Kench 2016).

Feeding modes and ecological functions performed by parrotfishes are strongly linked to their morpho-

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logical traits (Bellwood 1994, Bonaldo et al. 2014, Hoey 2018). For example, species with robust oral and pharyngeal jaw apparatuses, particularly those from the scarinine clade, are able to excavate calcium carbonate from benthic substrates (Ong & Holland 2010, Morgan & Kench 2016, Yarlett et al. 2018). In contrast, species with less pronounced apparatuses, particularly those from the sparismatine clade, are mostly scrapers and browsers that graze on macroalgae (Bonaldo et al. 2014). Such functional diversity is not evenly distributed across biogeographical regions (Kulbicki et al. 2018). For example, the Indian-Pacific Ocean harbors most of the excavating species, many of which are coral predators (Bonaldo & Rotjan 2018). By contrast, the Atlantic Ocean harbors most of the browsing species, with only 3 species recognized as excavators (Bruggemann et al. 1996, Francini-Filho et al. 2008, Lellys et al. 2019).

The genus *Sparisoma* is exclusive to the Atlantic Ocean (Robertson et al. 2006) and predominates over the genus *Scarus* in the southwestern Atlantic compared to the Caribbean region (Hoey et al. 2018, Longo et al. 2019). The Brazilian Biogeographic Province encompasses unique reef formations in the southwestern Atlantic, with most biogenic coral reefs limited to the northeast coast and an overall dominance of macroalgae across reefs (Aued et al. 2018). Such macroalgae dominance may explain the prevalence of the sparismatine clade in this province (Hoey et al. 2018). The endemic parrotfishes *Sparisoma axillare* and *S. frondosum* are both widely distributed and abundant along the Brazilian coast, with higher abundances found in the northeast (Ferreira et al. 2004, Francini-Filho et al. 2010, Cordeiro et al. 2016, Roos et al. 2019). Because both species generally occur in the same areas, determining the magnitude of their niche complementarity is challenging. The foraging behavior of these species was previously compared in studies with different scopes, revealing slightly varied results across distinct study areas. In the Fernando de Noronha Archipelago, for example, *S. axillare* and *S. frondosum* preferred the same feeding substrate types (Bonaldo et al. 2006). In contrast, in the Abrolhos Bank, eastern Brazil, *S. axillare* had a higher preference for algal turfs compared to *S. frondosum* (Francini-Filho et al. 2010). Through a comparative analysis of their gut contents, both species presented similar amounts of algal portions (Ferreira & Gonçalves 2006). However, *S. axillare*'s algal content had a higher proportion of foliose and thick-leathery algae, while that of *S. frondosum* had a higher proportion of articulated coralline algae (ACA) (Ferreira & Gonçalves 2006).

In this regard, levels of complementarity may be unveiled when multiple traits and attributes are assessed, such as ontogenetic stages, feeding rates, feeding modes (Bonaldo et al. 2006, Adam et al. 2015, Feitosa & Ferreira 2015), nutritional targets (Clements et al. 2017, Mendes et al. 2018, Nicholson & Clements 2020), social organization (Bruggemann et al. 1994, Feitosa et al. 2021) and interactions with other species (Overholtzer & Motta 2000, Davis et al. 2017). For example, initial phase (IP) individuals of the Caribbean parrotfish *S. viride* have higher feeding rates than their terminal phase (TP) counterparts due to the time TP individuals spend on territorial defense (Bruggemann et al. 1994). Parrotfish feeding rates were also found to be higher when individuals foraged in intra- and interspecific groups (Overholtzer & Motta 2000) but lower in zones with higher densities of territorial damselfish (Feitosa & Ferreira 2015). Moreover, the Caribbean parrotfish *S. rubripinne* (a sister species to *S. axillare*) feeds more frequently on brown macroalgae (mainly *Dictyota* spp.) compared to *S. chrysopterum* (a sister species to *S. frondosum*) (Adam et al. 2018). Such knowledge may provide clues to how losses in parrotfish densities can affect the structure of benthic communities from a 'top-down control' perspective (Hughes 1994, Bellwood et al. 2004, Folke et al. 2004), or even how changes in the structure of benthic communities can affect parrotfish densities from a 'bottom-up control' perspective (Russ et al. 2015, Taylor et al. 2020).

In Brazil, parrotfishes are common targets of artisanal and recreational fishers (Francini-Filho & Moura 2008, Roos et al. 2016, 2020, Roos & Longo 2021), and alarming signs of population declines have been reported (Bender et al. 2014, Pereira et al. 2021). *S. axillare* and *S. frondosum* in particular are usually caught with hook and line, traps and gillnets by artisanal fishers, and with spearguns by recreational fishers (Cunha et al. 2012, Roos et al. 2016, Roos & Longo 2021). Despite being listed as Data Deficient by the IUCN, *S. axillare* and *S. frondosum* are listed as Vulnerable by the Brazilian Red List of Endangered Species/BRL-EndS (Decree No. 445, 2014).

Population declines of Brazilian parrotfishes further strengthen our need to better understand the ecological aspects of the group. The present study aims to identify ecological differences between the 2 most ubiquitous Brazilian parrotfishes (*S. axillare* and *S. frondosum*) within the scope of *in situ* observations encompassing feeding rate, substrate selection, shoaling behavior and agonistic interactions, aspects that have not yet been simultaneously and comparatively evaluated between these 2 species. The study was guided

by the following questions: (1) Do feeding rates differ between the 2 species and among their ontogenetic stages? (2) Is there specific substrate selection by the species and their ontogenetic stages? (3) What is the magnitude of niche overlap between species in terms of substrate selection? (4) Do the species interact differently with other fishes during foraging activity?

## 2. MATERIALS AND METHODS

### 2.1. Study area

This study was conducted at the APARC (from the Brazilian Portuguese acronym Área de Proteção Ambiental dos Recifes de Corais), a multiple-use marine protected area located at the Rio Grande do Norte state, Northeast Brazil, approximately 6 km off the coast (5° 00'–5° 30' S, 35° 10'–35° 30' W) (Fig. 1). The APARC is divided into different zones designated for tourism, fishing activities and fishing exclusion. Reef

environments typically consist of shallow patchy reefs (~2 m deep) interspersed in a sandy matrix. Sampling was carried out at Maracajaú reef, the southernmost shallow reef complex in the APARC (Fig. 1).

### 2.2. Sampling procedures

Data were collected fortnightly between September 2011 and February 2012, encompassing the spring and summer seasons. Abundances of *Sparisoma axillare* and *S. frondosum* were assessed through underwater visual censuses carried out along 60 randomly distributed belt transects located ~10 m from each other, at ~2 m deep, each encompassing a 60 m<sup>2</sup> (30 × 2 m) area (adapted from Floeter et al. 2007). Visual censuses consisted of a specialized snorkeler counting the individuals, estimating their total length and categorizing their ontogenetic stages (i.e. juvenile, IP and TP).

The point intercept transect method (Rogers et al. 1994) was conducted within each of the same 60 belt

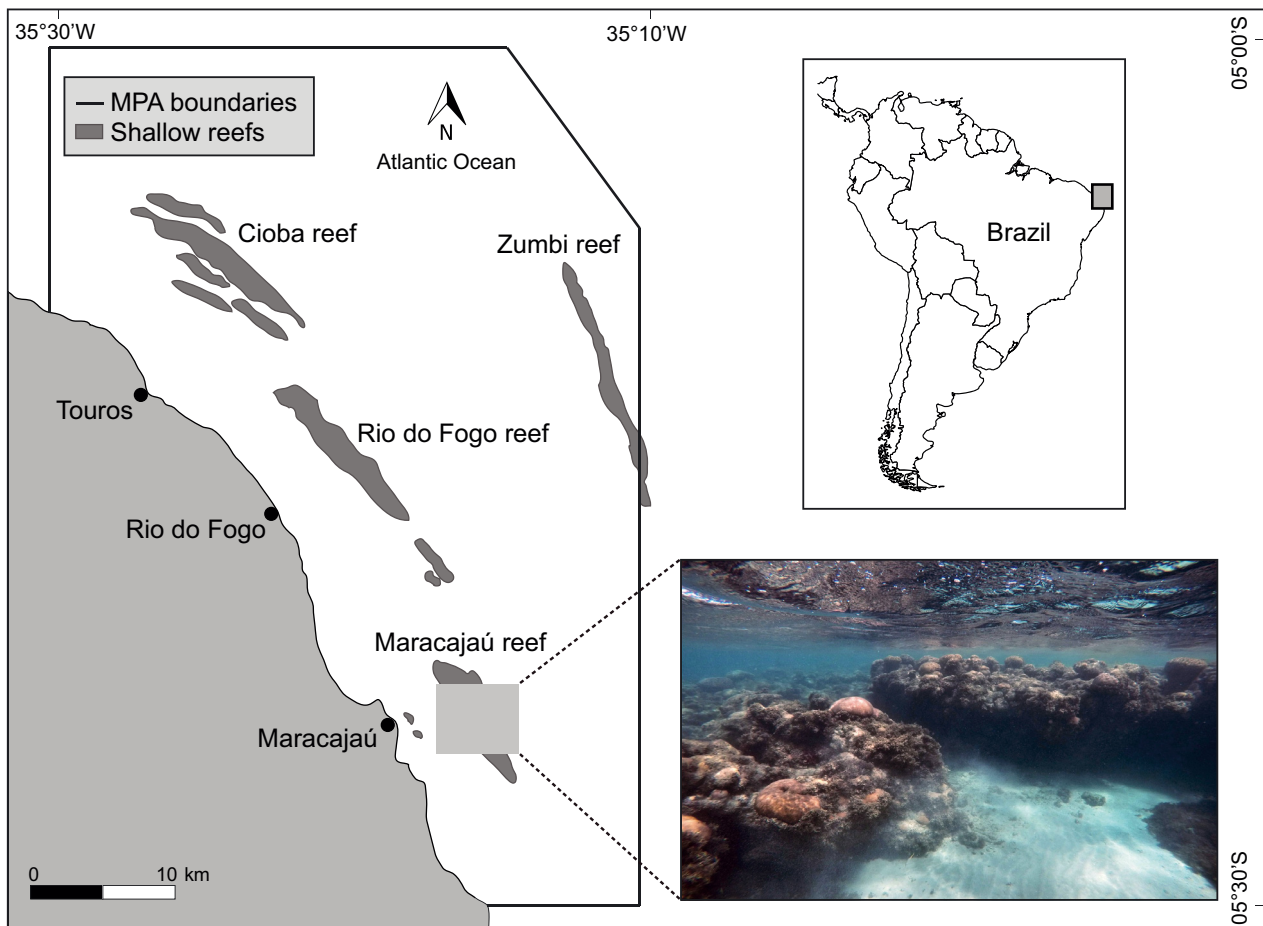


Fig. 1. Study area, Northeast Brazil, indicating the marine protected area (MPA) limits, locations of the shallow reefs, and the sampled area Maracajaú reef. Photo by Natalia C. Roos

transects to estimate benthic cover. Benthic organisms located below each 1 m interval of the transect (30 points per transect, 1800 points in total) were identified and classified into major groups (see species grouping details in Table S1 in the Supplement at [www.int-res.com/articles/suppl/m730p079\\_supp.pdf](http://www.int-res.com/articles/suppl/m730p079_supp.pdf)).

The foraging behavior of *S. axillare* and *S. frondosum* was recorded while snorkeling during the daytime between 09:00 and 15:00 h. The 'focal animal' and 'all occurrences' sampling techniques were employed during observational sessions, which consist of observing an individual animal for a pre-established period of time, during which all occurrences of a specific behavior are recorded (Altmann 1974, Lehner 1979). Substrate selection, feeding frequency and shoaling behavior of both species were recorded while observing randomly selected individuals. After a short period of acclimation of about 30 s (to minimize initial diver disturbance), the focal individual was identified to the species level, and its ontogenetic stage and shoaling behavior were determined. Then, the number of bites and substrate types selected by the fish were recorded continuously for 1 min (Francini-Filho et al. 2008). Agonistic interactions were also recorded in separate samplings, also during 1 min observations.

### 2.3. Statistical analysis

Differences in species abundance and feeding rate, for both species and ontogenetic stages, were tested through pairwise permutational tests using the 'pairwisePermutationTest' function of the 'rcompanion' package (Mangiafico 2020). We chose this pairwise permutation-based test rather than other approaches because it does not require normality or homogeneity of variances, given that estimates and coefficients are obtained from permutation. Non-metric multidimensional scaling (nMDS) ordinations were plotted to visualize differences in substrates selected by both species and ontogenetic stages using the 'metaMDS' function of the 'vegan' package (Oksanen et al. 2022). Those differences were then assessed through a permutational analysis of variance (PERMANOVA) using the function 'adonis2' of the 'vegan' package (Oksanen et al. 2022). The PERMDISP test was used to compare the homogeneity of dispersions using the functions 'vegdist' and 'betadisper' of the 'vegan' package. SIMPER analysis was used to identify the percent contribution of each substrate type to the dissimilarity between the number of bites taken by each species and ontogenetic stages using the function 'simper' of the 'vegan' package. PERMANOVA and

SIMPER analyses were based on Bray-Curtis compositional dissimilarities, while PERMDISP was based on Euclidian distances. Substrates representing less than 2% of the total bites were not included.

Substrate selectivity patterns of each species and ontogenetic stages were evaluated with Ivlev's electivity index ( $E$ ), as follows:

$$E = (r_i - p_i) / (r_i + p_i) \quad (1)$$

where  $r_i$  is the percentage of bites towards each substrate type  $i$  and  $p_i$  is the total percentage of the substrate type  $i$  in the environment (Ivlev 1961).  $E$  varies from  $-1$  to  $+1$ , with positive values indicating positive selection, negative values indicating avoidance and near-zero values indicating a random selection (Ivlev 1961, Jacobs 1974). To test its significance, a 95% confidence interval was calculated for each  $E$  value and, therefore, near-zero intervals were categorized as non-significant. Substrates representing less than 2% of the bites were not included.

Niche overlap between species for each ontogenetic stage was determined by Schoener's index of niche overlap (Schoener 1970) as follows:

$$T = [\Sigma(P_{xi} - P_{yi})] \quad (2)$$

where  $T$  is the index of niche overlap between species  $x$  and  $y$ ;  $P_{xi}$  is the proportion of the food type  $i$  selected by species  $x$ ; and  $P_{yi}$  is the proportion of the food type  $i$  selected by species  $y$ .  $T$  varies from 0, indicating low or no niche overlap, to 1, when both species select the same food types in the same proportions. This index was calculated with the 'niche.overlap' function of the 'spaa' package (Zhang 2016). The overlap is considered high when values are greater than 0.60 (Zaret & Rand 1971, Wallace 1981).

PERMANOVA, PERMDISP, SIMPER and  $T$  were calculated considering IP and TP of *S. frondosum* individuals combined as 'adults'. Differences in shoal size, number of fishes chasing focal individuals and number of fishes chased by focal individuals, for both species and ontogenetic stages, were tested through pairwise permutational tests using the 'pairwisePermutationTest' function of the 'rcompanion' package (Mangiafico 2020). All the abovementioned analyses were performed in R software version 4.2.1 (R Core Team 2022).

## 3. RESULTS

### 3.1. Abundance, benthic cover and feeding rate

Juveniles of *Sparisoma frondosum* were the most abundant ( $-0.11$  ind.  $m^{-2}$ ), followed by juveniles and

IP individuals of *S. axillare* (0.05 ind. m<sup>-2</sup> each), IP individuals of *S. frondosum* (~0.03 ind. m<sup>-2</sup>) and TP individuals of *S. frondosum* (~0.01 ind. m<sup>-2</sup>; Fig. 2A; p-values are given in Table S2). TP individuals of *S. axillare* were not recorded, which was somewhat ex-

pected, as they occur almost exclusively in relatively deeper reefs of the region (~20 m deep), although they are still rarely seen (Roos et al. 2019).

The benthic community was mostly represented by zoanthids (mainly *Palythoa caribaeorum*), red macro-

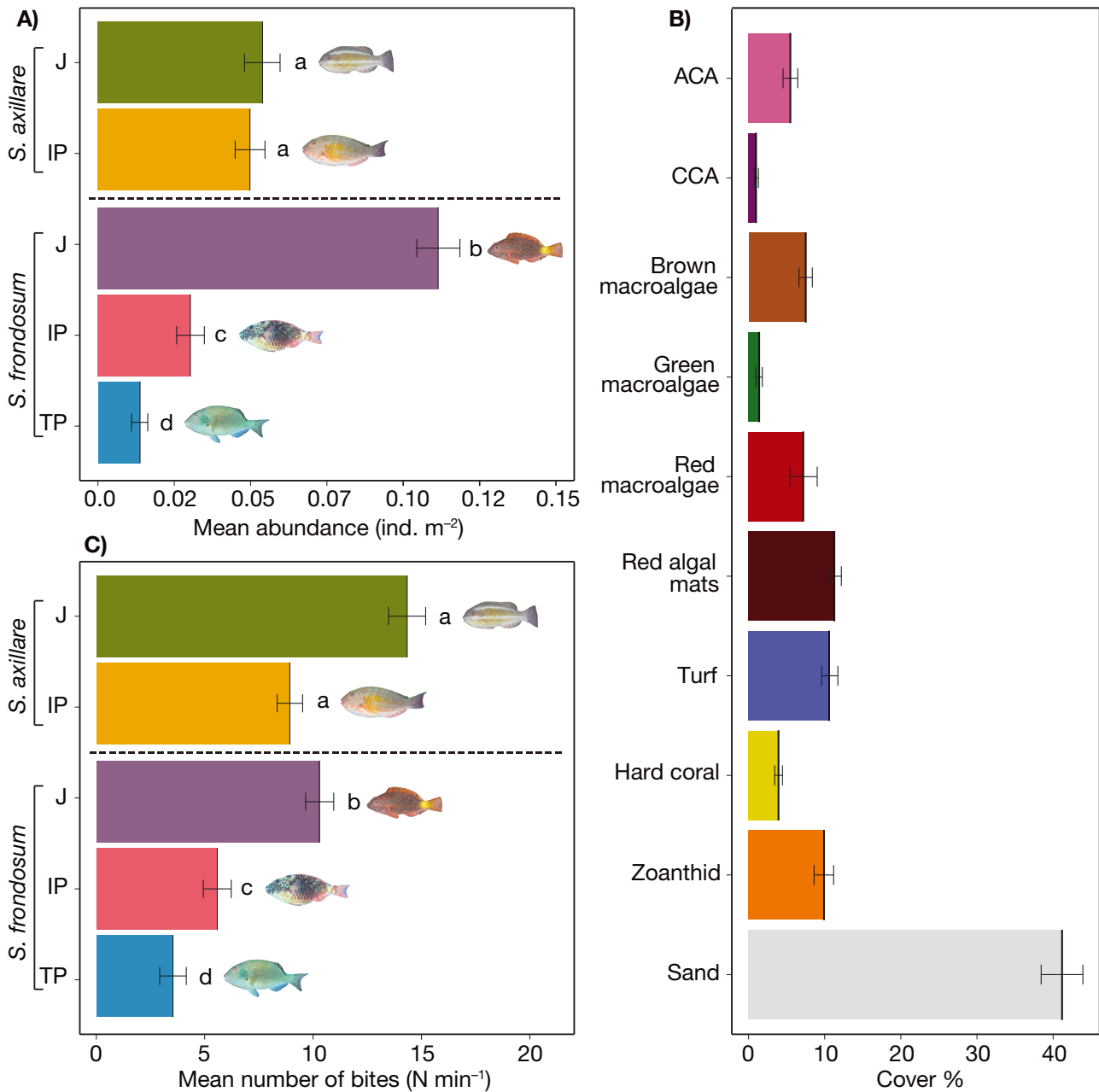


Fig. 2. (A) Mean abundances (ind. m<sup>-2</sup> ±SE) of juvenile (J) and initial phase (IP) individuals of *Sparisoma axillare* (green and yellow bars, respectively) and of J, IP and terminal phase (TP) individuals of *S. frondosum* (purple, pink and blue bars, respectively); (B) percent cover (±SE) of benthic groups; and (C) feeding rate (no. of bites min<sup>-1</sup> ±SE) of J and IP individuals of *S. axillare* (green and yellow bars, respectively) and of J, IP and TP individuals of *S. frondosum* (purple, pink and blue bars, respectively). Horizontal bars: mean values of abundance, percentage cover and feeding rate; ontogenetic stages of the 2 species (A and C) and benthic categories (B) are assigned to different bar colors; different letters in (A) and (C) indicate significant differences at a 5% significance level; p-values are shown in Table S2 for differences in mean abundances (A), and in Table S3 for differences in feeding rates (C). Benthic categories are detailed in Table S1. ACA: articulated coralline algae; CCA: crustose coralline algae

algae (mainly *Cryptonemia* spp. and *Laurencia* spp.), red algal mats (mainly *Gelidium* spp. and *Gelidiella* spp.), brown algae (mainly *Dictyota* spp., *Dictyopteris* spp. and *Sargassum* spp.), algal turfs (i.e. epilithic algal matrix, mostly filamentous algae mixed with sediment and/or detritus) and ACA (mainly *Jania* spp. and *Amphiroa* spp.; Fig. 2B). Sponges and ascidians were not recorded along transects due to their low abundance in the area (Roos et al. 2019).

A total of 3457 bites were recorded from 409 focal fishes, of which 163 individuals were *S. axillare* (62 juveniles, 101 IP) and 246 were *S. frondosum* (95 juveniles, 86 IP and 65 TP). Differences in the feeding rate between the 2 species and among ontogenetic stages were observed (Fig. 2C, p-values given in Table S3). Juveniles of *S. axillare* had the highest feeding rate, followed by juveniles of *S. frondosum*. IP and TP individuals of *S. frondosum* had the lowest feeding rates (Fig. 2C, p-values given in Table S3).

### 3.2. Substrate selection and niche overlap

Among the 3457 recorded bites, 1662 were taken on turf (46.9%), 718 on sand (20.76%), 488 on foliose brown algae (14.11%), 382 on red algal mats (11.05%), 99 on ACA (2.86%), 46 on red macroalgae (1.33%), 38 on sponges (1.09%), 14 on zoanthids (0.4%), 8 on crustose coralline algae (0.23%) and 2 on hard corals (0.05%; Fig. 3).

Despite the high overlap between species and among ontogenetic stages, juveniles and adults of *S. frondosum* presented a wider dispersion of points in the nMDS analysis compared to *S. axillare* (Fig. 4). The composition of bitten substrates differed between juveniles of both species (PERMANOVA: pseudo- $F = 7.4$ ,  $p = 0.001$ ) and between adults of both species (PERMANOVA: pseudo- $F = 8.6$ ,  $p = 0.001$ ). However, for both juveniles and adults, the dispersion was significantly different between species (PERMDISP:  $F = 8.2$ ,  $p = 0.004$ , PERMDISP:  $F = 20$ ,  $p < 0.001$ , respectively), with the composition of bites taken by *S. axillare* being more homogeneous across different substrates.

Dissimilarities between the substrate types bitten by juveniles of both species were mainly driven by turf (47.9%) and sand (17.1%), with both substrates accounting for 65% of the dissimilarity (Table 1). Specifically, regarding juveniles, *S. axillare* took almost twice as many bites on turf compared to *S. frondosum*. In contrast, *S. frondosum* took 3 times more bites on sand compared to *S. axillare* (Table 1, Fig. 3). The same pattern was observed for adults, with turf and sand ac-

counting for 60.1% of the dissimilarity between the composition of substrate types bitten by both species (Table 1). *S. axillare* also took more bites on turf, while *S. frondosum* took more bites on sand (Fig. 3).

Similar patterns of substrate selectivity were found between species and among ontogenetic stages, including their overall preference for turf and foliose brown algae (i.e. *Dictyota* spp., *Dictyopteris* spp. and *Sargassum* spp.) and their avoidance of red macroalgae (*Cryptonemia* spp., *Laurencia* spp.) and sand (Fig. 5). However, *S. axillare* showed a higher preference for turf (especially juveniles) and a higher avoidance of sand, while *S. frondosum* showed a lower avoidance of sand (especially IP individuals) and a lower preference for turf (Fig. 5). The overall avoidance of sand is likely explained by its high availability in the study area (Fig. 2B), once  $E$  is calculated based on both biting rate and food availability, and the biting rate on sand is not proportionally as high as its availability. In addition, 2 *S. axillare* juveniles were observed biting sponges, which are not abundant in the study area, 5 *S. frondosum* individuals were observed biting the zoanthid *Palythoa caribaeorum* and 2 juveniles (one of each species) were observed biting the hard coral *Siderastrea stellata* (see details by species in Table S4).

Overall, both species and their ontogenetic stages presented a high niche overlap (Table 2). The lowest overlap was observed between *S. axillare* juveniles and *S. frondosum* adults, which may be explained by their preferred foraging substrates: while *S. axillare* juveniles took more bites on turf and fewer bites on sand compared to all other ontogenetic stages or species, *S. frondosum* adults took more bites on sand and fewer bites on turf compared to all other ontogenetic stages or species (see Fig. 3).

### 3.3. Interactions during foraging activity

The shoaling behavior of all 409 focal individuals was recorded. The mean number of fish associated with focal individuals did not differ between juveniles of the 2 species (Fig. 6, see p-values in Table S5). However, *S. frondosum* adults (both IP and TP individuals) had significantly more fish associated with them during foraging activity (Fig. 6). For *S. axillare*, only 18% of juveniles and 2% of IP individuals were associated with other fish during foraging activity, and most observations consisted of intraspecific pairs (Fig. 6). In contrast, *S. frondosum* juveniles associated mostly with an interspecific pair (36%) or with interspecific groups (41%). *S. frondosum* IP individuals associated mostly with IP individuals of their own species, either

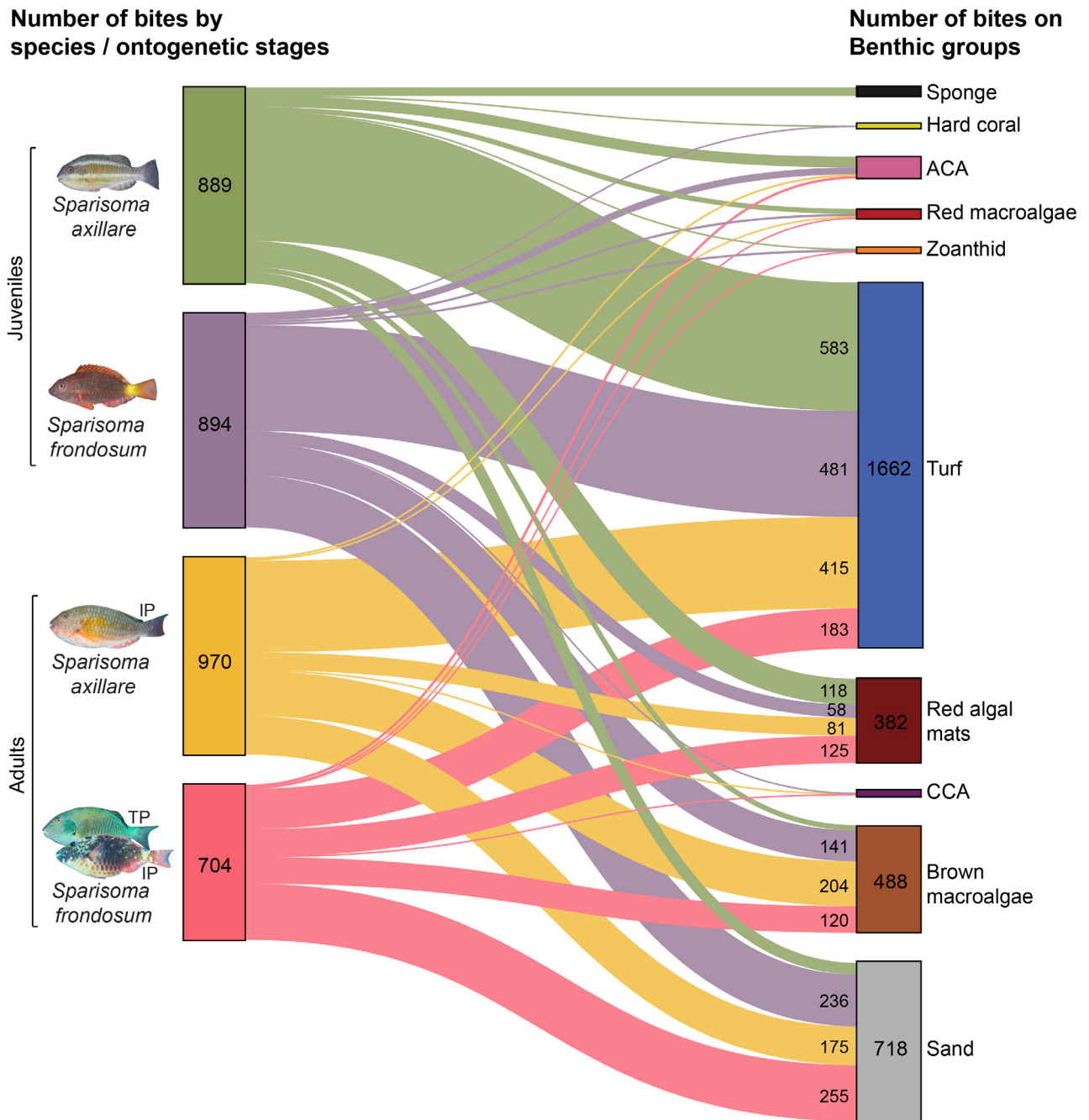


Fig. 3. Number of bites taken by juveniles and adults of *Sparisoma axillare* and *S. frondosum* on different substrate types. Number of bites by species are shown for the most representative benthic groups. Juveniles (J) and initial phase (IP) individuals of *S. axillare* are represented by green and yellow colors, respectively, and J and adult (IP and terminal phase [TP]) individuals of *S. frondosum* are represented by purple and pink colors, respectively. ACA: articulated coralline algae; CCA: crustose coralline algae

in pairs (34%) or in groups (24%). Lastly, *S. frondosum* TP individuals associated mostly with interspecific groups (73%; Fig. 6).

Within shoals, most of the *S. axillare* juveniles were associated with other juveniles of their own species (Fig. 6). Conversely, *S. frondosum* juveniles were as-

sociated with a more diverse group, including the surgeonfish *Acanthurus chirurgus*, the most prominent representative. IP and TP *S. frondosum* individuals showed a similar pattern, associating mostly with *A. chirurgus* but also with other surgeonfish such as *A. coeruleus* and *A. bahianus*, as well as with other

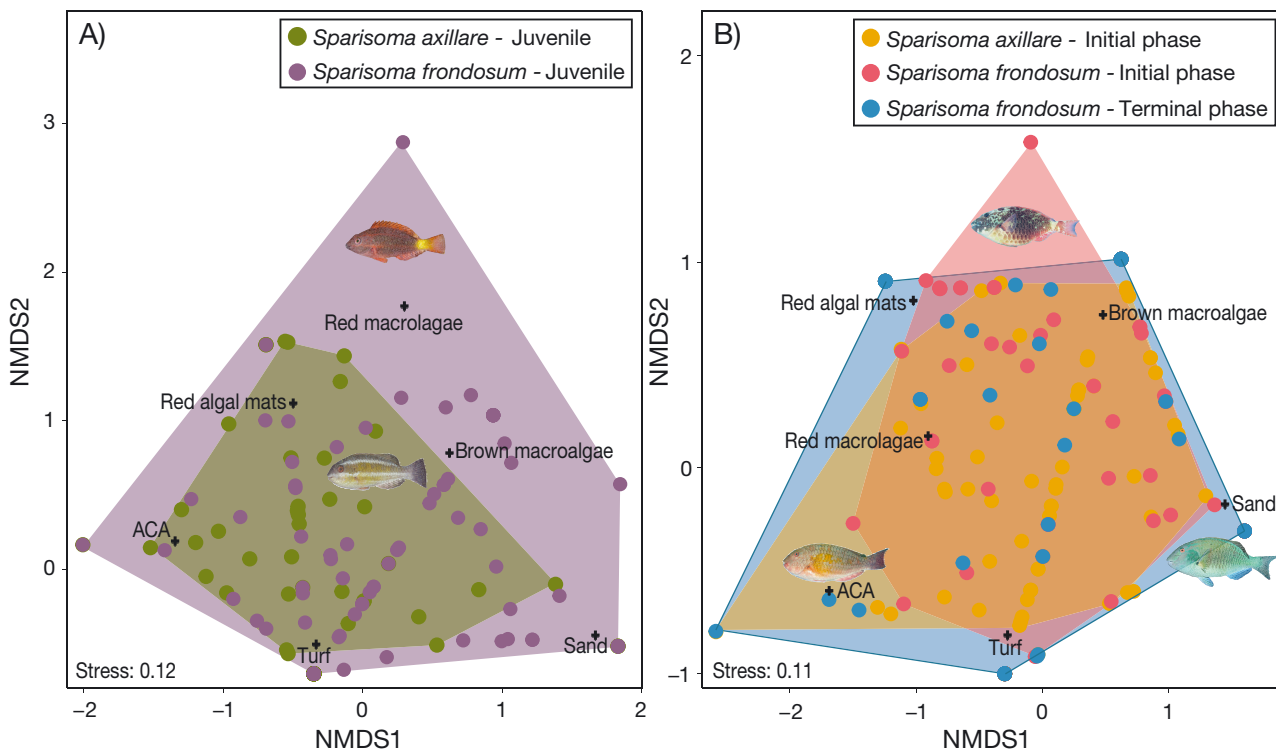


Fig. 4. Non-metric multidimensional scaling (nMDS) of the number of bites taken on different substrate types by (A) juveniles and (B) adults of *Sparisoma axillare* and *S. frondosum*. Juveniles and initial phase individuals of *S. axillare* are represented by green and yellow colors, respectively, and juveniles, initial phase and terminal phase individuals of *S. frondosum* are represented by purple, pink and blue colors, respectively. nMDS ordinations are based on a Bray-Curtis dissimilarity matrix. ACA: articulated coralline algae; CCA: crustose coralline algae

Table 1. Summary of SIMPER results for the composition of substrate types bitten by juveniles and adults of *Sparisoma axillare* and *S. frondosum*, including mean number of bites on each substrate, their contribution to within-group dissimilarity and the cumulative contributions. ACA: articulated coralline algae

Substrate type	Mean no. of bites		Contribution (%)	Cumulative contribution (%)
	<i>S. axillare</i>	<i>S. frondosum</i>		
<b>Juveniles</b>				
Turf	9.55	5.17	47.9	47.9
Sand	0.85	2.53	17.1	65
Red algal mats	1.93	0.62	14.5	79.5
Brown macroalgae	0.37	1.51	10.6	90.1
ACA	0.80	0.33	7.1	97.2
Red macroalgae	0.37	0.10	2.8	100
<b>Adults</b>				
Turf	4.23	1.40	38.3	38.3
Sand	1.78	1.9	21.8	60.1
Brown macroalgae	2.08	0.92	21.7	81.8
Red algal mats	0.82	0.96	15.1	96.9
ACA	0.08	0.08	1.8	98.7
Red macroalgae	0.07	0.04	1.3	100

parrotfishes (especially *Scarus trispinosus*) and IP and TP individuals of their own species (Fig. 6).

A total of 381 focal individuals were further observed to record their agonistic interactions with other fishes. Among these, 153 individuals were *S. axillare* (56 juveniles and 97 IP) and 228 individuals were *S. frondosum* (88 juveniles, 79 IP and 61 TP). Chases against focal individuals were mostly performed by the damselfish *Stegastes fuscus* and by other parrotfishes, and occasionally by other species (Fig. 7A). No differences in the number of chases against focal individuals were found between *S. axillare* and *S. frondosum* and their ontogenetic stages (Fig. 7B, Table S6). Furthermore, all ontogenetic stages of *S. frondosum* and *S. axillare* showed similar chasing rates against other fishes (Fig. 7B, Table S6).



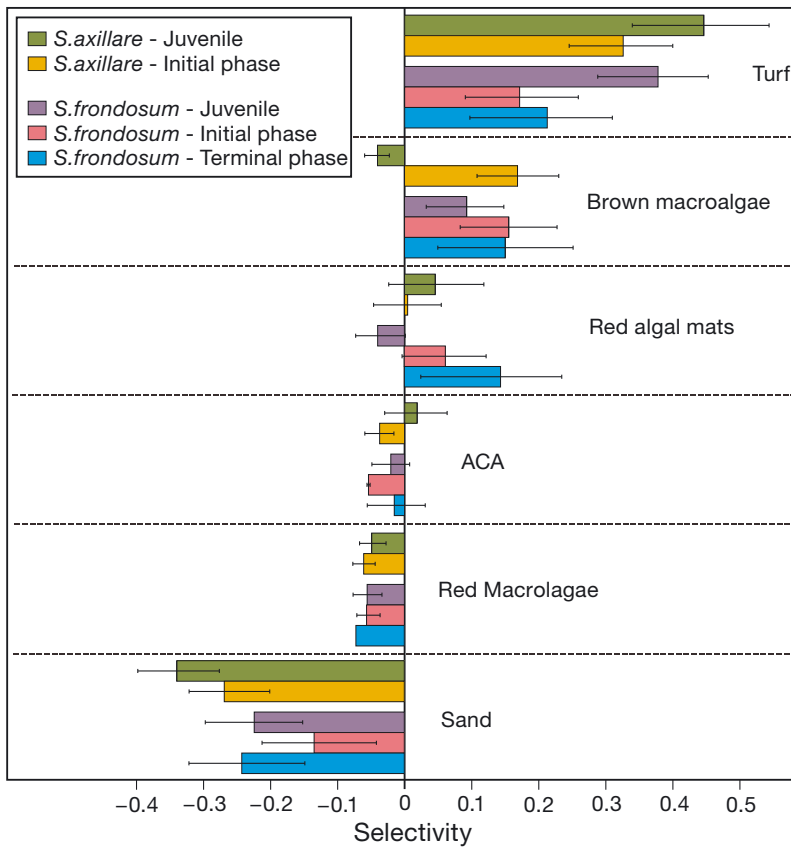


Fig. 5. Substrate selection (Ivlev's electivity index  $\pm 95\%CI$ ) for the 6 substrate types that encompass more than 93% of the bites taken by *Sparisoma axillare* and *S. frondosum*. Juveniles and initial phase individuals of *S. axillare* are represented by green and yellow colors, respectively, and juveniles, initial phase and terminal phase individuals of *S. frondosum* are represented by purple, pink and blue colors, respectively. ACA: articulated coralline algae

Table 2. Schoener's index of niche overlap between juveniles and adults of *Sparisoma axillare* and *S. frondosum*

Species / ontogenetic stage	<i>S. axillare</i> adults	<i>S. frondosum</i> adults	<i>S. axillare</i> juveniles
<i>S. frondosum</i> adults	0.744		
<i>S. axillare</i> juveniles	0.655	0.517	
<i>S. fronsodum</i> juveniles	0.883	0.750	0.685

#### 4. DISCUSSION

We recorded feeding selectivity and ecological interactions that revealed differences in the foraging behavior of the 2 most ubiquitous Brazilian parrotfish species. Our *in situ* observations indicated that compared to *Sparisoma axillare*, *S. frondosum* fed on a wider range of substrate types. Moreover, *S. frondosum* aggregated significantly more with other fishes while

foraging, with the surgeonfish *Acanthurus chirurgus* representing the highest proportion of fish in their shoals. For agonistic interactions, the damselfish *Stegastes fuscus* was by far the main species chasing focal individuals.

Feeding rates of parrotfishes are often expected to decrease with increasing body size. Therefore, juveniles tend to show higher feeding rates compared to IP and TP individuals (Bruggemann et al. 1994, Lokrantz et al. 2008, Ong & Holland 2010, Hoey 2018). Likewise, juveniles of *S. axillare* and *S. frondosum* showed higher feeding rates compared to their adult counterparts, but the magnitude of variation differed between species. *S. axillare* juveniles had the highest feeding rate, whereas the feeding rate of *S. frondosum* juveniles was lower, to the point of not differing from that of *S. axillare* IP individuals. The lower feeding rate of *S. frondosum* was also observed in adults. In fact, the lowest feeding rate was recorded for *S. frondosum* TP individuals. Differences in feeding rates between species and among ontogenetic stages may be explained by several factors, including the increased time spent in territory defense (Bruggemann et al. 1994), as in the case of *S. frondosum* TP individuals, and the cost–benefit ratio of different feeding strategies. For instance, it is expected that species that feed more intensively on low-quality food and have high energetic demands need to compensate by increasing their feeding rates (Longo et al. 2019). We hypothesized that the higher feeding plasticity observed for *S. frondosum* can be a strategy to increase its protein intake efficiency, leading to a lower feeding rate compared to *S. axillare*.

Parrotfishes are microphage foragers targeting epilithic, endolithic and epiphytic microscopic phototrophs (e.g. cyanobacteria) as protein-rich nutritional food resources (Clements et al. 2017, Nicholson & Clements 2020). Most of the sparisomatine parrotfishes have less robust buccal and pharyngeal apparatuses compared to those of the scarinine clade (Bellwood 1994, Clements et al. 2017, Lellys et al. 2019), including in their diets of seagrasses and macroalgal

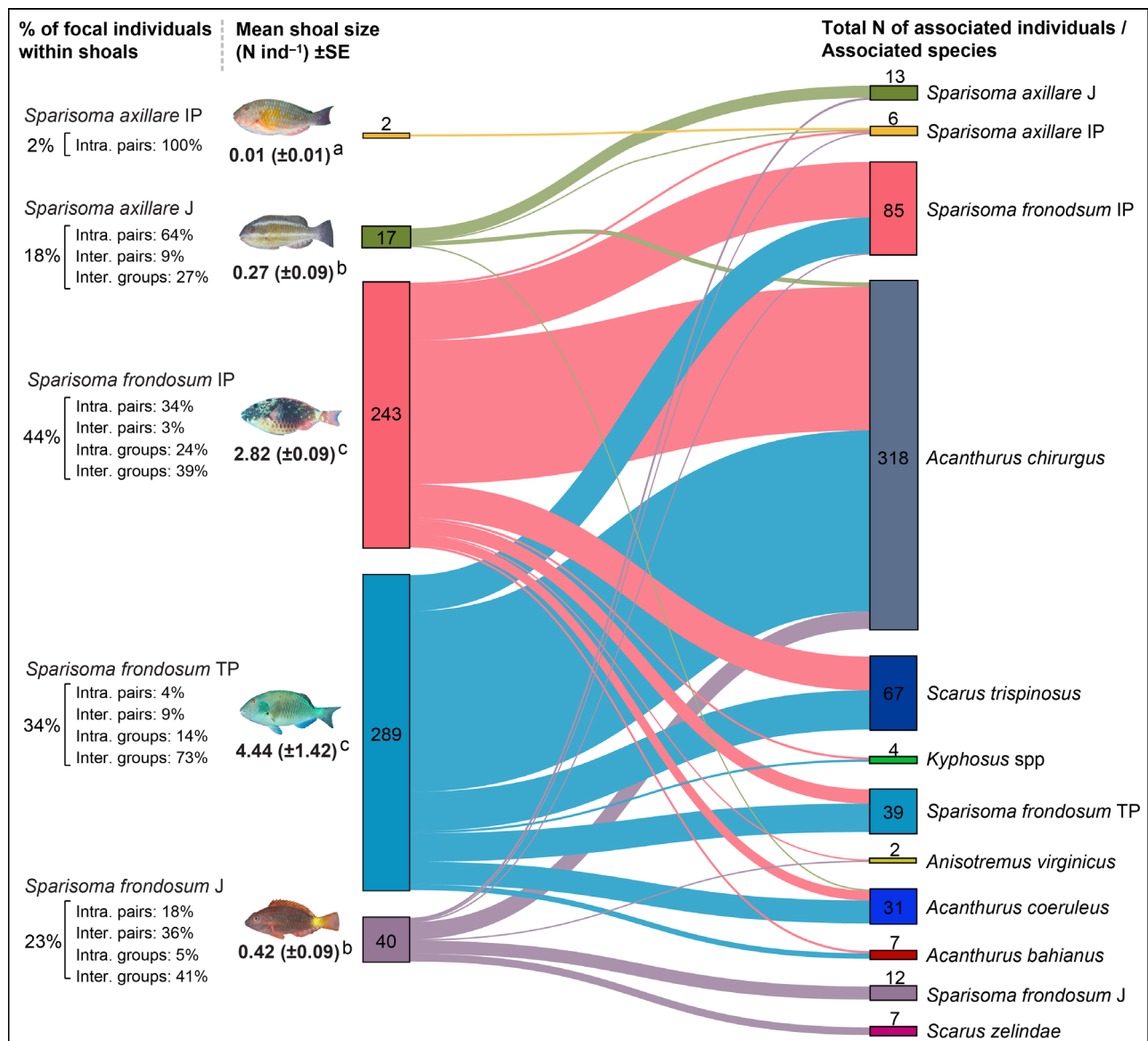


Fig. 6. Shoaling behavior of juveniles and adults of *Sparisoma axillare* and *S. frondosum*, including percentage of focal individuals in shoals and percentage of association types, including intraspecific pairs (Intra. pairs), interspecific pairs (Inter. pairs), intraspecific groups (Intra. groups), and interspecific groups (Inter. groups); mean shoal size per focal individual; and the number of associated individuals of each species. On the left side (focal individuals), juveniles (J) and initial phase (IP) individuals of *S. axillare* are represented by green and yellow colors, respectively, and J, IP and terminal phase (TP) individuals of *S. frondosum* are represented by purple, pink and blue colors, respectively; different letters beside the mean shoal size indicate significant difference at a 5% significance level; p-values are shown in Table S5

matrices (Bonaldo et al. 2006, Adam et al. 2015), substrates that also have high quantities of epiphytic microscopic phototrophs (Lefèvre & Bellwood 2010). However, resource partitioning among species within the same group may be difficult to infer by visual feeding behavior assessment alone, especially when they are targeting microscopic food resources. In this regard, new approaches have been used to better

understand reef fish resource partitioning, including DNA metabarcoding (e.g. Casey et al. 2019, Brandl et al. 2020a,b) and fine-scale analysis of grazed substrates (e.g. Nicholson & Clements 2020, 2023). Still, observing substrate selection is an easy and useful *in situ* methodology that makes possible large geographical comparisons and first inferences about how parrotfishes use available space and rough food re-

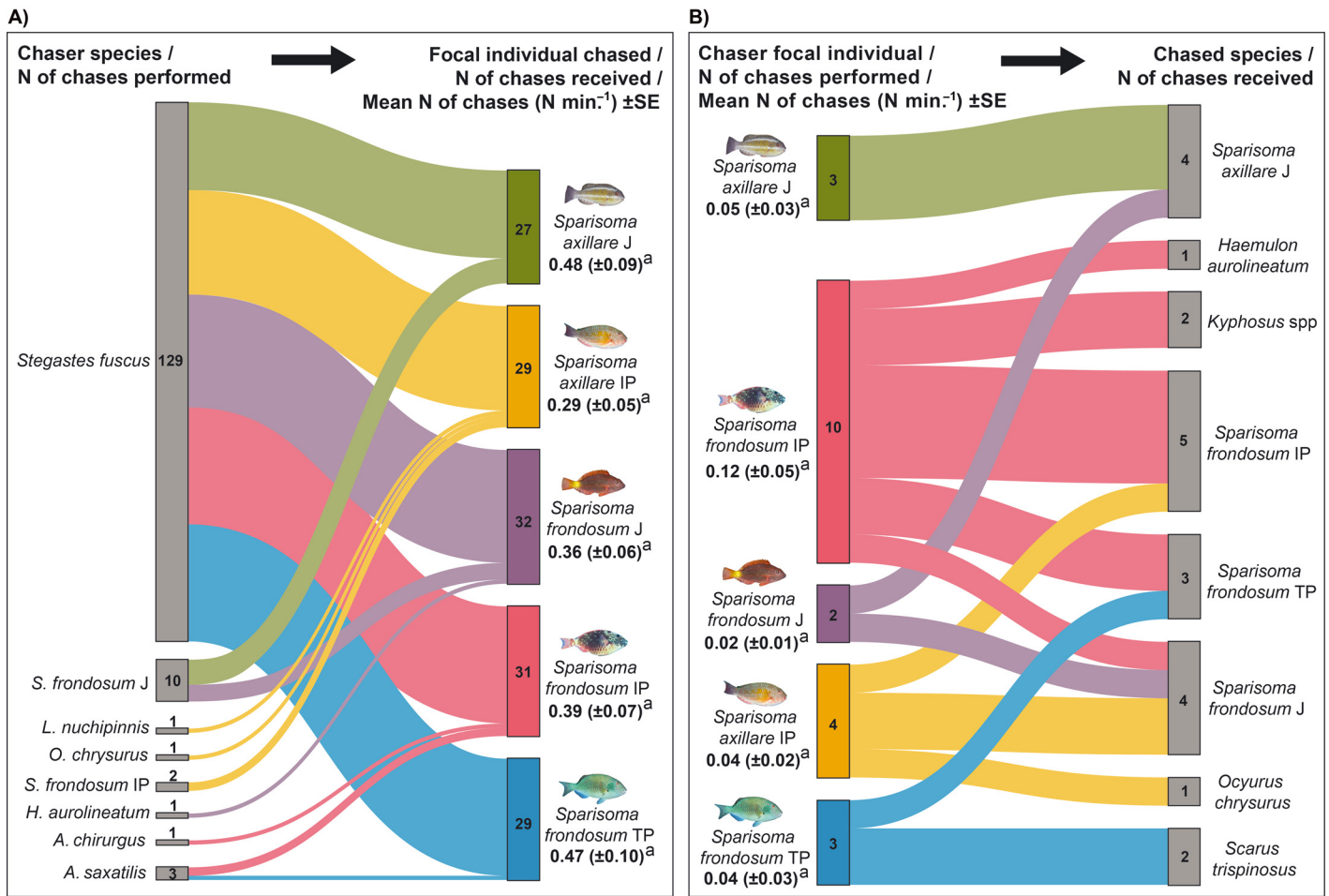


Fig. 7. Agonistic interactions of juveniles and adults of *Sparisoma axillare* and *S. frondosum* with other species, including the mean number of chases (A) against focal individuals and (B) performed by focal individuals. Juveniles (J) and initial phase (IP) individuals of *S. axillare* are represented by green and yellow colors, respectively, and J, IP and terminal phase (TP) individuals of *S. frondosum* are represented by purple, pink and blue colors, respectively. Same letters beside the mean number of chases indicate no significant differences. p-values are shown in Table S6

sources (Bonaldo et al. 2006, Francini-Filho et al. 2010, Adam et al. 2015, 2018, Hoey 2018).

Habitat preferences of these species based on tropical reef attributes have already been described (Roos et al. 2019) and are reflected in some of the results found here. *S. axillare* has been shown to be more abundant in shallower habitats where brown macroalgae cover is higher, while *S. frondosum* is ubiquitous across several types of habitats, including deeper reefs (Roos et al. 2019). Brown macroalgae comprise a considerable portion of *S. axillare*'s gut content (Ferreira & Gonçalves 2006), although the species displays a nitrogen-rich dietary composition compared with *A. chirurgus*, also a nominally herbivorous fish (Mendes et al. 2018). This indicates that *S. axillare*'s preferred nutritional targets may come from protein-rich epiphytes together with lipids present in brown

macroalgae, which are also highly energetic and assimilable by parrotfish (Clements et al. 2017).

In contrast, we hypothesize that the ubiquity of *S. frondosum* may be attributed to its feeding plasticity, as preferred dietary resources are major drivers of species movement and distribution (Floeter et al. 2007). Opportunistically, *S. frondosum* has been observed feeding on unusual organisms such as freshly dead spotted sea hares *Aplysia dactylomela* (Moreira & Rosa 2014) and on bryozoans at deeper reefs (~35 m deep; N. C. Roos pers. obs.). If these organisms possess any epiphytic association with micro primary producers and/or their nutritional composition can be assimilated by *S. frondosum*, further investigation is needed. Furthermore, the stronger preference of *S. frondosum* for sand reported here is likewise also related to layers of primary producers (e.g. cyano-

bacteria) that colonize this substrate. This behavior has been reported elsewhere for parrotfish (Clements et al. 2017 and for other nominally herbivorous fish (Tebbett et al. 2022). Such feeding plasticity may enhance the ability of *S. frondosum* to inhabit different habitats, from shallow to deep reefs. *S. frondosum* was the only parrotfish observed in the Great Amazon Reef System at depths between 100 and 140 m (Francini-Filho et al. 2018). This generalist behavior could also be a major driver that makes it possible for this species to disperse beyond the Brazilian Province, including the Southeast Caribbean (Rocha 2003) and the Cabo Verde Island in Africa (Freitas et al. 2014).

The extent to which fishes explore different reef areas may also be influenced by their shoaling behavior (Overholtzer & Motta 2000, Nyström & Folke 2001). Although the formation of mixed-species shoals depends on fishes' social behavior, the frequency at which these associations occur is determined by the magnitude of niche and home range overlap among species and individuals. Compared to *S. axillare*, we found that *S. frondosum* associates significantly more with other individuals and species while foraging, a behavior that may also be linked to its feeding strategy. For example, benthic disturbance caused by large feeding schools of the surgeonfish *A. chirurgus*, an herbivore–detritivore (Ferreira & Gonçalves 2006, Mendes et al. 2018) recently classified as a sediment-sucking species (Tebbett et al. 2022), may expose *S. frondosum*'s preferred food resources, making it beneficial for *S. frondosum* to follow foraging *A. chirurgus* individuals. Although this hypothesis requires further investigation, it is known that schools of *A. chirurgus* modify sediment, detritus and turf dynamics in reef environments (Tebbett et al. 2022) and that substrate disturbance is one of the main factors attracting opportunistic follower fishes (Krajewski 2009, Inagaki et al. 2020). In contrast, the low sighting of *S. axillare* IP in shoals may be linked to the time of the day this species prefers to aggregate with other individuals. At the Fernando de Noronha Archipelago, for example, *S. axillare* groups were more common in the afternoon (Bonaldo et al. 2006). Following behaviors can facilitate the accessibility of parrotfishes to areas that are highly defended by farming damselfishes (Francini-Filho et al. 2010, Tebbett et al. 2022). In our study, the damselfish *S. fuscus* was by far the most aggressive species that chased the focal individuals, equally affecting both species and their ontogenetic stages. Damselfishes can affect nominally herbivorous fishes by limiting their access to food resources and by decreasing their feeding rate (Robertson et al. 1979, Feitosa & Ferreira 2015). However, the negative effect

caused by damselfishes may be overcome through the shoaling and/or schooling behavior of nominally herbivorous fishes (Tebbett et al. 2022).

Drawing upon observations of substrate selectivity and ecological interactions, our study showed that the 2 most abundant and ubiquitous Brazilian parrotfishes differed in foraging behaviors despite their high niche overlap. Although fine-scale resource partitioning deserves investigation, for example through methods such as DNA metabarcoding (e.g. Casey et al. 2019) or the fine-scale analysis of grazed substrates (e.g. Nicholson & Clements 2023), the observed species-specific differences in habitat use highlight the niche complementarity between *S. axillare* and *S. frondosum* on a broad scale and provide insights into the drivers of their distribution in the Brazilian reefs. *S. axillare* seems to be more restricted to shallower reefs with high proportions of foliose and leathery brown macroalgae, which may make this species more vulnerable to overfishing. In contrast, *S. frondosum* is common in different habitat types, including deeper reefs (Francini-Filho et al. 2018, Roos et al. 2019). Differences in foraging behavior between the 2 species are somehow linked to the observed differences in habitat use and spatial distribution. In particular, *S. frondosum* has a relatively broad foraging ecology, which may enable it to recover better from habitat-specific anthropic disturbances, whereas *S. axillare* displays a comparatively more specialized foraging ecology. Nonetheless, both species are fishing targets and are officially listed as Vulnerable by the Brazilian Red List of Endangered Species. Understanding the differences in their ecological demands for space and food resources at a large geographical scale in the Brazilian Province is, therefore, of central importance to advance our fundamental knowledge of their ecology and to improve ecosystem-based management strategies.

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