Seaweed beds harbor higher abundance of juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape

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ABSTRACT: Seascape connectivity is regarded essential for healthy reef fish communities in tropical shallow systems. A number of reef fish species use separate adult and nursery habitats, and hence contribute to nutrient and energy transfer between habitats. Seagrass beds and mangroves often constitute important nursery habitats, with high structural complexity and protection from predation. Here, we investigated if reef fish assemblages in the tropical south-western Atlantic demonstrate ontogenetic habitat connectivity and identify possible nurseries on three reef systems along the Eastern Brazilian coast. Fish were surveyed in fore reef, back reef, *Halodule wrightii* seagrass beds and seaweed beds. Seagrass beds contained lower abundances and species richness of fish than expected, while *Sargassum*-dominated seaweed beds contained significantly more juveniles than all other habitats (average juvenile fish densities: 81.4 per 100 m² in *Sargassum* beds, 28.0 per 100 m² in back reef, 25.2 per 100 m² in fore reef, and 12.6 per 100 m² in seagrass beds), including several species that are found in the reef habitats as adults. Species that in other regions worldwide (e.g. the Caribbean) utilise seagrass beds as nursery habitats were here instead observed in *Sargassum* beds or back reef habitats. Coral cover was not correlated to adult fish distribution patterns; instead, type of turf was an important variable. Connectivity, and thus pathways of nutrient transfer, seems to function differently in East Brazil compared to many tropical regions. *Sargassum*-dominated beds might be more important as nurseries for a larger number of fish species than seagrass beds. Due to the low abundance of structurally complex seagrass beds we suggest that seaweed beds might influence adult reef fish abundances, being essential for several keystone species of reef fish in the tropical South Western Atlantic.

Key words: *Nursery grounds, reef fish, habitat choice, seaweed, ontogeny, connectivity*

1. Introduction

Habitat use in organisms is strongly influenced by foraging requirements, competition and predation risk (Werner and Gilliam 1984). Habitat requirements change through different life stages and for some species it is beneficial to shift habitat to maximise growth rates and survival (Dahlgren and Eggleston 2000). Numerous reef fish species are dependent on multiple habitats during their different life stages, and perform foraging and spawning migrations and ontogenetic habitat shifts in the coastal seascape (e.g. Ogden 1977, Verweij et al. 2007). Non-reef and reef habitats of coastal areas are hence linked by fish movement on different temporal and spatial scales (Nagelkerken et al. 2000a). Migrations can occur over a large range of distances, which often are region- and species-specific (e.g. Pittman et al. 2007, Olds et al. 2012). By migration, fish sustain ecosystem processes like herbivory and predation over habitat boundaries and thus contribute to the resilience within the seascape (Meyer and Schultz 1985, Nyström and Folke 2001). Connectivity by reef fishes is therefore considered an important component in shallow-water tropical systems (e.g. Sheaves 2009, Berkström et al. 2013a). However, species using multiple habitats throughout their life cycle can become more vulnerable to stressors such as habitat destruction and fragmentation in the coastal seascape (Nyström and Folke 2001).

Mangroves and seagrass beds have been highlighted as important non-reef components of the coastal seascape because they provide productive nursery and foraging grounds for various groups of reef fishes, such as grunts (Haemulidae), parrotfishes (Labridae, Scarini) and snappers (Lutjanidae) (e.g. Weinstein and Heck 1979, Nagelkerken et al. 2000a, Dorenbosch et al. 2005, Gullström et al. 2008, Berkström et al. 2013b). All mangrove and seagrass habitats might, however, not provide equal benefits since their ability as nurseries is

dependent on their geographical location, habitat area and habitat quality (Dorenbosch et al. 2006, Olds et al. 2012, Huijbers et al. 2013). Optimal conditions of a nursery may vary between different fish species and/or life stages due to different ecological processes underlying habitat choice (Dahlgren and Eggleston 2000, Cocheret de la Morinière et al. 2004). Habitat choice is thought to be driven by factors that would maximize growth rate and survival where shelter and food are often the primary reasons influencing habitat choice, which can be further shaped by local abiotic conditions as well as competitor- and predator density (Pratt et al. 1986, Boström and Mattila 1999, Dahlgren and Eggleston 2000, Laegdsgaard and Johnson 2001, Almany 2004). If shelter is the primary reason for a species to utilise a certain habitat, structural complexity might be more important than the habitat *per se* (Heck et al. 2003), and a range of similar structurally complex habitats can be suitable (Parsons et al. 2016). If instead a species resides in a certain habitat because of the presence of an important prey, the species might be more dependent on this particular habitat type. Examples are juvenile yellowtail snapper (*Ocyurus chrysurus*) that have been linked to high abundances of its main type of prey in seagrass sediments (e.g. Nagelkerken et al. 2000b), and juvenile snapper (*Chrysophrys auratus*) that take advantage of the seagrass' ability to provide flow refuges in current-exposed areas to facilitate capture of planktonic copepods (Parsons et al. 2015).

Brazil has an extensive coastline of about 8,000 km where mangroves, seagrass- and seaweed beds and coral reefs are present. Connectivity patterns of fish as mobile links between habitats are sparsely studied in Brazil, with very little information on connectivity dynamics, and how different habitats might be of importance to reef fishes (but see Moura et al. 2011, Feitosa and Ferreira 2014, Aschenbrenner et al. 2016). For most reef fish species, there are critical knowledge gaps in nursery habitat use and ontogenetic habitat shifts. In contrast, the

50 Caribbean, which shares several species of reef fishes with the South Western Atlantic (SWA)
51 (Floeter et al. 2008), is globally the most extensively studied area in terms of connectivity,
52 especially regarding ontogenetic migrations between habitats (Berkström et al. 2012, Olds et
53 al. 2016). The SWA shallow-water seascapes, however, differ substantially from the
54 Caribbean in many aspects. The reefs are characterized by low coral species diversity and low
55 coral cover (<20%) (Leão et al. 2003). Likewise, reef fish species richness is relatively low
56 compared to the Caribbean and Pacific regions, but a high number of endemic fish species are
57 present (371 species and 10.5% endemics, respectively) (Floeter et al. 2008). Furthermore,
58 large seagrass species such as *Thalassia testudinum*, which covers extensive shallow areas in
59 the Caribbean where it is recognized as an important nursery habitat (e.g. Nagelkerken et al.
60 2002), do not occur in Brazil (de Oliveira et al. 1983). Instead, the most common seagrass
61 taxa are *Halodule wrightii* and *Halophila* spp., which are small, low-canopy species (de
62 Oliveira et al. 1983, Copertino et al. 2016). Fish assemblages in seagrass beds in the SWA
63 have been scarcely studied (but see Pereira et al. 2010), and hence their role as nursery
64 grounds for reef fishes is not yet understood. So far, estuaries seem to be the most utilised
65 non-reef habitat by reef fishes (Vila-Nova et al. 2013), and a few studies performed in
66 mangroves show dependency or preference of these areas as nurseries for the dog snapper
67 *Lutjanus jocu* (Moura et al. 2011, Xavier et al., 2012), the Brazilian snapper *Lutjanus*
68 *alexandrei* (Aschenbrenner et al. 2016), and the Goliath grouper *Epinephelus itajara* (Hostim-
69 Silva et al. 2005). Another common, scarcely studied, shallow-water macrophyte habitat in
70 the SWA, is seaweed beds. Seaweed beds composed of fleshy algae in reef environments
71 have mostly been recognized as nuisance since they have the ability to overgrow corals and
72 potentially induce phase shifts (e.g. Adam et al. 2011), and have received little attention as
73 nurseries for coral reef fishes in Brazil (but see Ornellas and Coutinho 1998, Feitosa and
74 Ferreira 2014). However, in many reef systems around the world, seaweed beds are part of the

natural coastal seascape, and have recently been found to harbour juveniles of various reef fish families (Wilson et al. 2010, Chaves et al. 2013, Evans et al. 2013). In the tropical SWA, larger seaweed species like *Sargassum* spp. provide one of the most structurally complex macrophyte habitats, and might therefore be suitable as nurseries for reef fishes.

Information on how species that originate from the Caribbean (and occur both in the Caribbean and the SWA) are distributed in different seascapes might provide insights into ecological processes that influence habitat importance for different species and consequently habitat choice. An interesting example is what effect the different characteristics of the seagrass species in the two biogeographical provinces have on fish habitat choice. In Brazil, information on ontogenetic migrations and connectivity patterns is urgent, since the Brazilian coastal seascape is under high anthropogenic pressure from overfishing, coastal development, mass tourism and pollution (Moura 2000, Leão et al. 2003, Floeter et al. 2006, Costa et al. 2008). Trampling and anchoring can for example damage seagrass- and seaweed beds (Walker et al. 1989, Creed and Amado Filho 1999, Azevedo et al. 2011). It is thus important to identify critical habitats to be able to incorporate priorities in management plans. The aim of this study was therefore to describe the distribution of fish from different life history stages among four common habitat types in the SWA, which may be used to infer nursery habitat and ontogenetic shifts in habitat for some species. For the definition of a nursery habitat, we refer to Beck et al. (2001). We tested the hypotheses that seagrass- and seaweed beds would function as nurseries and contain more juveniles than reef habitats. Furthermore, we hypothesised that within-habitat factors such as coral cover and canopy height would be important for habitat choice and in structuring of the adult and juvenile reef fish assemblages.

2. Material and Methods

2.1. Study site

Field data were collected in March and April 2015 on three shallow coastal reefs in south Bahia state, Brazil: Recife de Fora, Coroa Alta and Araripe reef (Fig. 1). The reefs are biogenic, comprised of beach rock and coral (Castro and Pires 2001). Depth varies from 0 to 18 m, with parts of the reef flats becoming exposed during low tide. The bottom substrate around the reefs is composed of soft sediment of siliciclastic mud (Costa et al. 2001). The very fine sediment and outflow from rivers adjacent to the reefs contribute to high turbidity, resulting in visibility that seldom exceeds 10 m even in the dry season (November-March). Seagrass beds composed of *Halodule wrightii* and *Halophila* spp. are present in the soft bottoms, *H. wrightii* in shallow sheltered bays of the reefs and *Halophila* spp. generally deeper (>7 m) around the reefs. Stretches of the fire coral *Millepora alcicornis* are found on all reefs, but the overall coral cover is low (2.3-9.4%) (Leão et al., 2010). Mangroves are present along all rivers, but occur only along river banks and around the river mouths. Recife de Fora is a marine park where fishing is not allowed, but protection is weakly enforced (Chaves et al. 2010, Bender et al. 2013). All reefs are subjected to environmental stressors in terms of fishing, tourism and river effluence (Costa 2007, Bender et al. 2013). The reef areas were roughly mapped using satellite images from Google Earth and ground truthing in the field to identify habitat types. This was done with a GPS by marking areas of certain habitats (e.g. reef flats, *Sargassum* beds) and then identifying them on the satellite map using the GPS data. Surveys took place in fore reef and back reef habitats, seaweed beds dominated by *Sargassum* spp. and seagrass beds (*H. wrightii*) (Fig. 1). *Halodule wrightii* beds were not present at Araripe reef. Fore reef habitats were defined as locations at the exposed ocean-ward side of the reefs, and back reef habitats on the landward side. Surveys in the two reef habitats

were performed in locations with little or no *Sargassum* cover. The *Sargassum* beds occurred on hard substrate on the reefs, and only dense beds (>30% vegetation coverage) were included in the study. Fore reef habitats were surveyed in 2.5-5 m depth, back reef habitats in 1-4 m depth and *Sargassum* spp. beds between 0.5 and 1.5 m depth. Depth in the *H. wrightii* beds were 1.5-3 m. All data was collected with SCUBA or snorkelling in low tide. It was only possible to conduct surveys in low tide due to the limited visibility in incoming and high tides. Surveys were conducted during day-time, meaning that diurnal migrations are not included in the study. The field survey was performed during March-April 2015 and hence any variations in recruitment patterns between years and time of the year were not covered.

2.2. Fish assemblages

Data on fish assemblages in the different habitats were collected by visual census. Ten 20 m transects were randomly placed within each habitat at each location, and a diver swam two times along the transect lines and recorded all observed fish within 1 m of each side of the transect line. Mobile species were recorded in the first run, when the transect line was unwound, and small juveniles and cryptic species during the second run, when the transect line was rewound. Fish were identified to the lowest taxonomic level possible and lengths were estimated to the closest centimetre. All observations were noted on a PVC tube (one for each diver) carried on each diver's arm. Each census was performed by one diver. Two divers (Eggertsen and Fontoura) conducted all visual censuses to minimize bias due to variability in species identification and length estimates. SCUBA gear was used in the reef habitats and snorkel gear in the vegetated habitats.

Since data on fish length at maturity were not available for all species, fish were divided into life stages (juvenile, subadults and adults) using the method proposed by Nagelkerken and van der Velde (2002). This method defines juveniles as $<1/3$ of the maximum length of the species, $1/3$ to $2/3$ as subadults, and $>2/3$ as adults. The advantage of including the subadult category is that no adults will be classified as juveniles and vice versa. Maximum lengths were obtained from *Fishbase* (Froese and Pauly 2015) except for the greenbeak parrotfish *Scarus trispinosus*, where maturity length was obtained from Freitas et al. (38.5cm, unpubl. data). *Scarus trispinosus* was divided into small juveniles (total length of ≤ 10 cm) (still showing juvenile striped coloration), large juveniles/subadults ($>10 < 38$ cm) and initial phase (IP) (≤ 38 cm). No terminal phase individuals were observed. It was not possible to differentiate between juvenile *S. trispinosus* and *S. zelindae* since they both display a striped pattern as juveniles (pers. obs. L. Eggertsen). Literature in combination with observations from this study was used to assign each species to an associated habitat category where they would be most likely to occur (e.g. Froese and Pauly 2015).

2.3. Benthic community and environmental variables

Benthic cover was estimated by placing a 0.25 m^2 quadrat at 3-5 points randomly chosen along each fish survey transect, with a minimum distance of 5 m between each quadrat. The lower number of quadrats were used along the transects in more homogenous areas (e.g. the seagrass beds). Each quadrat was photographed and in the reef habitats, benthos was classified into morphological groups (Table A1, Appendix A). Cover of different benthic groups was then visually estimated from the photographs, and a mean estimated cover was calculated for each transect. Back reef habitats were represented by 96 quadrats along 31 transects and fore reef habitats by 126 quadrats along 30 transects. Seaweed species were

assigned to morphological groups modified from Littler and Littler (1984). For example, *Caulerpa* species did not fit any group and was categorized as “siphonous turf” following Balata et al. (2011) (Table A1, Appendix A). For the *Sargassum* beds, coverage of seaweeds was estimated for each quadrat. Canopy height was measured for *H. wrightii* and *Sargassum* beds by measuring the estimated highest plant in each quadrat. Environmental variables recorded were rugosity and depth. Rugosity was estimated only in the reef habitats, on a 4-grade scale, where 1 corresponded to zero complexity (i.e. sand or gravel), 2 to low complexity with presence of some rocks and holes, 3 to medium complexity (larger boulders, rocks and an abundance of holes) and 4 to very high complexity, similar to category 3 but usually with presence of *M. alcicornis*. Depth was measured at the beginning and end of each transect with a dive computer.

2.4. Data analysis

To compare differences in habitat use between species and different life stages, non-metric multi-dimensional scaling (nMDS) ordination with Bray-Curtis similarity index was performed with the data from all surveys, displaying similarity in fish assemblage composition among habitats separated by life stage. Because the data included many zeros, it was square-root transformed. To investigate if differences visualized in the nMDS in fish assemblage composition among habitats and among the same habitats between sites were significant, a permutational multivariate analysis of variance (PERMANOVA) was conducted on the square-root transformed data, based on the dissimilarities in the abundance distance matrices in all habitats from the three reef sites, with habitats nested within sites (Bray-Curtis similarity index, Adonis, 4999 permutations). This was done separately for the adult, subadult and juvenile assemblages. To identify which species contributed the most to variations in fish

assemblage composition among habitats and among sites, similarity of percentage (SIMPER) analysis was carried out. To identify significant differences in the total abundance of adults, subadults and juveniles (all species combined) among the four habitats, all sites were pooled and a one-way analysis of variance (ANOVA) and *post hoc* multiple comparison tests were performed. Data was tested for normality with the Shapiro Wilk test and square-root transformed when not normally distributed.

The relationship between juvenile abundance and *Sargassum* canopy height and cover in *Sargassum* beds was investigated with linear regression. Data was visually checked for normality distributions of residuals with QQ-plots and square root transformed to meet assumptions for linear regression. To understand which of the *Sargassum* variables that were the most important for juvenile fish abundance, the Akaike Information Criteria (AIC) was calculated for each model, and the models were ranked accordingly. Since fish abundances were very low in seagrass habitats, it was not possible to perform any analyses on the relationship between seagrass height/cover and fish abundances.

In order to understand how the benthos and environmental variables influenced the fish community in the reef habitats, Canonical Correspondence Analysis (CCA) ordination was performed. Mean coverage of each benthic morphological group and rugosity and depth along each transect were used as predictors. The ordination was then redone using only the significant variables. To investigate if certain variables were important for different life stages, CCA was performed for the adult, subadult and juvenile assemblages separately. Lastly, one CCA ordination was performed including all life stages but excluding species with less abundance than two individuals in total, to avoid too much influence of rare species. All

analyses were performed in the software R (version 3.2.2) and the vegan package in R was used for the multivariate analyses (version 2.4-1).

3. Results

3.1. Fish assemblages

In total, 3697 fishes from 62 species of 23 families were recorded. Species richness was highest (47 species) in reef habitats, and lowest (12 species) in seagrass beds, which contained very few fish specimens (on average 5.6 ± 3.4 ind. per 100m^2). Larger (>40 cm) macro-carnivores and parrotfishes (those targeted by fishing) were generally rare in all surveyed habitats.

The different habitats harboured distinct fish assemblages, both in terms of species and life stages, except for seagrass habitats that did not contain any characteristic fish assemblage (Fig. 2). *Sargassum* beds contained significantly higher abundance of juveniles than the three other habitats (ANOVA, $df=3$, $p<0.05$), while most of the adults were recorded in the reef habitats (Fig. 3). Fish assemblage compositions (separated into adult, subadult and juvenile fish) were significantly different among the different habitats (PERMANOVA, $df=3$, $p<0.01$) as well as among sites in some habitats (PERMANOVA, $df=2$, $p<0.05$) (Fig. 2). The adult assemblage composition differed between the two reef habitats, mainly due to differences in abundance of *S. fuscus* that was more abundant in back reef habitats (PERMANOVA, $df=2$, $F=3.515$, $p<0.05$). The subadult assemblage composition also differed among sites in the back reef habitat (PERMANOVA, $df=2$, $F=3.004$, $p<0.01$). This was mainly due to higher abundance of *H. aurolineatum* in Recife de Fora (SIMPER, Table 1).

For the juvenile fish, there were significant differences in assemblage composition among sites in the fore reef habitat (PERMANOVA, $df=2$, $F=4.758$, $p<0.05$) as well as among sites in *Sargassum* beds (PERMANOVA, $df = 2$, $F =5.042$, $p<0.05$) (Fig. 2). The species that contributed the most to the observed differences was *S. axillare*, which was also the most abundant species in these two habitats. In back reef and seagrass habitats, the grunt *Haemulon. aurolineatum* was the most common species and primarily observed as juveniles (Table B1, Appendix B).

Sargassum beds were foremost characterised by juveniles of two species of surgeonfishes, *Acanthurus bahianus* and *Acanthurus chirurgus*, and juvenile parrotfishes of the genus *Scarus* (Figs. 4 and 5, Table B1, Appendix B). The two acanthurid species constituted the largest proportion of juveniles recorded in this habitat (25%). *Sparisoma axillare*, which was the most abundant parrotfish species at juvenile life stage in the study, was found in highest abundances in *Sargassum* beds, but also occurred in all other habitats (Table B1, Appendix B). No *Scarus* spp. larger than 10 cm were recorded in the *Sargassum* beds. The adults and subadults of acanthurids and parrotfish were recorded mainly in fore reef habitats where they formed large multi-species schools, however, no *S. trispinosus* specimen larger than 45 cm was observed (Figs. 4 and 5).

Seagrass beds harboured very few fish; however, it was the only habitat where juveniles of the snapper *Lutjanus synagris* were recorded. Juveniles of the snapper *O. chrysurus* were mainly found in back reef habitats, and no adults were recorded in the study.

In total, 42% of the recorded fish species were found exclusively in the reef habitats during all life stages, while 48% were recorded within at least two different habitats, of which the most common combination was reef and seaweed beds (44%). Three species of different life stages

were exclusively found in seagrass habitats, although in very low abundances; juvenile *Lutjanus synagris*, juvenile *Diplectrum radiale* and adult *Coryphopterus* sp. (Table B1, Appendix B). Seven species (12%) were recorded within seagrass beds in addition to other habitats, but always in low abundances. Roving herbivores were the most common trophic group in fore reef habitats (38.1%), while territorial herbivores (mainly *S. fuscus*) and invertivores were the most common in back reef habitats (35.2 and 31.2%, respectively). In the *Sargassum* beds, roving herbivores and invertivores were the most common trophic groups (35.8 and 34.6% respectively), while invertivores was the only trophic group recorded in seagrass beds.

3.2. Habitat characteristics

3.2.1. Macrophyte habitats

The two seagrass beds at Coroa Alta and Recife de Fora were rather small (approximately 50 000 and 70 000 m², respectively) and comprised monospecific *H. wrightii* beds. The Coroa Alta *H. wrightii* bed had both higher seagrass coverage and taller canopy height than the Recife de Fora bed (73.3±3% and 19.25±1 cm compared to 12.6±1% and 4±0 cm, respectively). Seaweed beds were dominated by *Sargassum* spp. Other frequently occurring seaweeds were *Lobophora variegata*, *Halimeda* spp and sheet-like forms of *Dictyotacea*. Total seaweed coverage was high with an average of 87.2±2% at Araripe reef, 51.1±4% at Coroa Alta and 84.0±4% at Recife de Fora. *Sargassum* beds were generally rather homogenous in terms of canopy height but differed somewhat among the three sites (average canopy height: 42.4±1 cm, 20.1±1 cm and 38.0±3 cm for Araripe, Coroa Alta and Recife de Fora, respectively). Average depth during surveys varied between 1.5 and 3 m in the seagrass beds and between 0.5 and 1.5 m in the *Sargassum* beds.

298

299 3.2.2. Reef habitats

300 Back reef and fore reef habitats were rather different in terms of benthic coverage (Table 2A,
301 Appendix A). In general, fore reef habitats had higher coverage of calcareous (*Amphiroa* and
302 *Jania* spp.) and siphonous turf algae (i.e. *Caulerpa* spp.) than back reef habitats (Table 2A,
303 Appendix A). Back reef habitats were mainly covered with a mixture of short (<1 cm),
304 heavily sediment-laden unidentified epilithic algae and zoanthids (mainly *Palythoa*
305 *caribaeorum*). Very little calcareous turf algae occurred in back reef habitats (e.g. *Amphiroa*
306 and *Jania* spp). The fore reef at Recife de Fora was relatively similar to back reef habitats in
307 general, mainly due to lower coverage of intermingling calcareous turf at the Recife de Fora
308 fore reef sampling location and a higher cover of the sediment-laden mixture of short epilithic
309 algae. Coral cover was similar in the two reef habitats; however, massive corals were more
310 common in back reef areas (Table 2A, Appendix A). Rugosity differed little between the two
311 reef habitats, but was slightly higher in the fore reef habitats. Average depths during surveys
312 were 2 m in back reef habitats and 3.35 m in fore reef habitats (Table 2A, Appendix A).

313

314 3.3. Effects of within-habitat variables on fish assemblages

315

316 There was a significant positive relationship between mean canopy height of *Sargassum* spp.
317 and juvenile fish abundance ($p < 0.01$, $df = 28$, $r^2 = 0.57$). The model only including canopy
318 height explained juvenile fish abundance slightly better than the model using both canopy
319 height and seaweed coverage according to the AIC values (AIC 92.12 and AIC 96.80,
320 respectively). No relationships between canopy height and/or cover were found for the
321 subadult or adult fish assemblages.

322

In the reef habitats, the fish assemblage composition, including all life stages, was significantly correlated to the benthic categories “Depth” and “Sediment-laden short EAM” and “octocoral” with the four first axes explaining 86.2% of the variation (CCA, $p < 0.05$). The categories “jointed calcareous algae”, “encrusting calcareous algae” and “siphonous turfing” were close to significant ($p = 0.088$, 0.054 and 0.089 respectively). The first axis separated “calcareous turf algae”, “encrusting calcareous algae” and “siphonous turfing” from “sediment-laden short EAM” and “octocoral”, distinguishing back reef from fore reef habitats (Fig. 6). The adult fish assemblage was in addition to these variables also correlated to “sheet like algae”, while the subadult assemblage was equal to the whole assemblage but without any correlation to “siphonous turfing”. Abundance of adult and subadult *A. chirurgus*, *A. bahianus* and *S. axillare* were all positively correlated to fore reef conditions while abundance of adults and subadults of the grunt *H. aurolineatum* was correlated to back reef habitats. No benthic variables were significantly correlated with juvenile fish assemblage structure.

3. Discussion

The different surveyed habitats contained distinct fish assemblages, both in terms of species- and life stage composition. Our findings in seaweed habitats are consistent with our hypothesis that macrophyte habitats function as nursery habitats for reef fishes. A number of fish species were found to use seaweed beds during juvenile life stages, but not as adults. However, the findings regarding seagrass beds were not consistent with our hypothesis. Contrary to distribution patterns of juveniles in many regions worldwide, with high abundances of juveniles in seagrass beds (e.g. Jackson et al. 2001, Heck et al. 2003, Nagelkerken et al. 2000, Dorenbosch et al. 2007, Gullström et al. 2012), the seagrass beds in

the current study did not contain large numbers of juveniles of any species. An average density of 12.1 juveniles per 100 m² found here can be compared to juvenile abundances of nursery associated species at 50 individuals per 100 m² in the least productive *T. testudinum* seagrass site in a study in Aruba in the Caribbean (Dorenbosch et al. 2007), including several species that were also recorded in this study. In this study, these species were recorded in other habitats. Seaweed beds dominated by *Sargassum* spp. was the habitat where most juvenile reef fishes were encountered. Furthermore, within-habitat variables such as canopy height was important for total juvenile abundance. Contrary to other studies in tropical reef systems (reviewed by Coker et al. 2014), coral cover did not show any significant relationship with abundances of juvenile fish, nor with sub-adult or adult fish abundances. The adult fish community was instead largely influenced by the composition of the epilithic algal matrix (EAM), a conglomeration of small algal turfs, sediment, detritus, and associated invertebrates (Wilson and Bellwood 1997).

4.1 Macrophyte habitats

Our finding showing that few fish species were associated with seagrass beds is in contrast to the Caribbean and the Indo-Pacific where several species are highly dependent on seagrass habitats during certain life stages or during their whole life cycle (e.g. Nagelkerken et al. 2000a, Gullström et al. 2011). High abundances of juvenile fish have been recorded in Caribbean *H. wrightii* beds, but mainly including pinfish (*Lagodon rhomboides*) and other species that do not occur in the SWA (Stoner 1983). The absence of seagrass-associated species and a characteristic fish assemblage in the surveyed seagrass beds in the present study might be explained by the limited availability of this habitat and its poor structural complexity, offering less shelter and food for small fishes compared to the seaweed beds

along the Brazilian coast. In the Caribbean, *T. testudinum* beds are one of the most extensive biotopes in shallow-water habitats besides mangroves and coral reefs, and the high production of juvenile fish from seagrass beds is likely an effect of the large size of this habitat (Nagelkerken et al. 2000a). In contrast, most shallow seagrass beds in Eastern Brazil do not cover very large areas (Copertino et al 2016). Different plant structures of seagrasses have been found to attract different species of fish (Hyndes et al. 2003, Gullström et al. 2002, 2008), and may explain why some species that in the Caribbean are strongly associated with the more complex *T. testudinum* seagrass beds (e.g. *O. chrysurus*, the doctorfish *A. chirurgus*, and *Sparisoma viride*, which is the sister species of the Brazilian parrotfish *Sparisoma amplum*) (Nagelkerken et al. 2000a) were absent in the less complex *H. wrightii* beds in the present study. *Halodule wrightii* beds might, however, sustain other important functions, such as the provision of nocturnal feeding grounds (Pereira et al. 2010), or be important for other groups of organisms such as invertebrates, or for provision of other ecological services. It is also possible that *H. wrightii* beds when associated with seaweeds, as reported for some habitats in the Abrolhos Archipelago in East Brazil (Copertino et al. 2016), can provide a better nursery function compared to the monospecific *H. wrightii* beds in the present study. Recorded species in the present study included highly mobile fish such as *Caranx ruber*, shoaling *H. aurolineatum* and juvenile *S. axillare*. Only two seagrass beds were surveyed in the present study and collecting data from additional seagrass beds would be necessary to further increase our understanding of their ecological function for fish.

Sargassum-dominated seaweed beds, on the other hand, were common on all reef sites, indicating high availability of this habitat. Seaweed beds thus seem to be more critical as nursery grounds for a larger number of reef fish species in the studied area than seagrass beds, a pattern that probably could be applied to extended areas of the tropical and subtropical

398 Brazilian coast. Seaweed beds composed of brown algae like *Sargassum* spp. provide high
 399 structural complexity and a large surface for associated invertebrates and epiphytic
 400 filamentous algae (Venekey et al. 2008). These traits might make seaweed beds a high-value
 401 nursery habitat for herbivorous fishes that feed on filamentous algae, such as juvenile
 402 parrotfishes (Feitosa and Ferreira 2014) and juvenile acanthurids (Dias et al. 2001). Also
 403 invertivorous fishes have been recorded in high abundances in seaweed beds, probably
 404 because of the large number of invertebrates associated with the seaweeds (Evans et al. 2013,
 405 Tano et al. 2016, 2017). Less competition due to lower abundances of the territorial
 406 damselfish *S. fuscus* in *Sargassum* habitats compared to back reef habitats could also be a
 407 factor positively influencing fish recruit abundance in the seaweed habitats. Considerably less
 408 predators were also recorded in the *Sargassum* habitat compared to the reef habitats (Table
 409 B1, Appendix B). In the present study, *Sargassum* beds were the preferred habitat for
 410 juveniles of the parrotfishes *Scarus* spp. and *S. axillare*, and for juveniles of *A. chirurgus* and
 411 *A. bahianus*. It seems that a habitat shift occurs at a body length of approximately 10 cm for
 412 *Scarus* spp., since no individuals larger than 10 cm were recorded in the studied *Sargassum*
 413 beds. *Acanthurus coeruleus*, which also occurs in the Caribbean, where it is not particularly
 414 associated with seagrass beds, did not show as strong nursery association with *Sargassum*
 415 beds as the other two acanthurids. Instead, it occurred in the reef habitats with similar
 416 distribution patterns to *A. coeruleus* in the Caribbean (Nagelkerken et al. 2000a).
 417
 418 The absence of juvenile *O. chrysurus* in the macrophyte habitats may be related to the poor
 419 shelter in the seagrass habitat and lack of its preferred prey in the seaweed habitats. Juveniles
 420 of *O. chrysurus* usually seek shelter during the day and feed at night, and its occurrence in *T.*
 421 *testudinum* beds in the Caribbean has been correlated with high abundances of its prey items
 422 in the sediment of seagrass habitats (e.g. Tanaidacea, Mysidacea) (Nagelkerken et al. 2000b,

Cocheret de la Morinière et al. 2003). To clarify habitat choice and requirements of nursery habitats by this species in Brazil, studies on diets of juveniles are needed. This would be valuable information because *O. chrysurus* is also important in the local fishery (Costa et al. 2003).

Interestingly, *H. wrightii* beds were the only habitat where juveniles of *Lutjanus synagris* were found, although in very low densities. *Lutjanus synagris* also occurs in estuaries as juveniles, especially in open areas, where it mainly feeds on epibenthic crustaceans (Pimentel and Joyeaux 2010). Similar conditions for its prey items (i.e. sparsely vegetated sediment) might link *L. synagris* to *H. wrightii* beds.

Positive correlations between canopy height in seaweed beds and juvenile fish abundance have been recorded in Western Australia (Evans et al. 2013) and in South Western Brazil (Ornellas and Coutinho 1998). Likewise, there was a positive correlation between *Sargassum* canopy height and total juvenile fish density in the present study. A tall canopy height may increase protection from larger predatory fish and support better shelter (Ornellas and Coutinho 1998). Other local-scale conditions such as predator density and seaweed cover can also influence juvenile fish abundance, while the importance of these variables may be highly species-specific (Wilson et al. 2017). Likewise, predators using different foraging strategies might be more or less successful in differently structured canopies (Horinouchi et al. 2009). Canopy height might have shown a strong influence on fish abundance in the present study because few species dominated the juvenile fish assemblage, while a more diverse fish assemblage might have included species using different strategies.

Each surveyed seaweed bed in the present study was very homogenous, and a canopy height effect could therefore only be detected combining the three reef sites. Since all three sites are located relatively close to each other and with similar predatory fish composition, it is unlikely that there would be large differences in predator pressure. The observed juvenile density patterns might be explained by less favourable conditions in short canopy-height sites, indicating importance of preserving high-canopy seaweed beds.

3.2. Reef habitats

The reef habitats harboured a higher proportion of adult fish compared to the macrophyte habitats. This was mainly due to the large number of juveniles in the seaweed habitats, of which some were recorded as adults in the reef habitats, inferring ontogenetic habitat shifts. The lack of influence of coral cover on fish abundance and composition, which is in contrast to reef environments in other tropical regions (reviewed by Coker et al. 2014), might be due to the lack of acroporid species in the SWA (Leão et al. 2003). Few species of fish are dependent on living coral in the Caribbean (2%) compared to the Indo Pacific (9%) (Coker et al. 2014), and since both coral- and fish species richness is lower in the SWA compared to the Caribbean (Kulbicki et al. 2013), it may explain why the number of coral-dependent species is even lower in the SWA. Species correlated to coral cover include the blennid *Emblemariopsis signifera* (associated with *Mussismilia braziliensis*) (Chaves et al. 2010) and the yellowtail damselfish *Microspathodon chrysurus* (associated with *M. alcicornis*) (Oliveira et al. 2013). *Millepora alcicornis*, which is the most common branching coral species in the SWA, sometimes harbour juvenile reef fishes of several species, likely due to its structural complexity (Oliveira et al. 2013). However, we found almost no juveniles in *M. alcicornis* colonies except for a few *M. chrysurus* specimens. This could be due to unfavourable local

conditions not identified in this study, or presence of adjacent habitats that could also be suitable as nurseries (e.g. high-canopy *Sargassum* beds).

The composition of the epilithic algal matrix (EAM), however, had a significant effect on the adult coral reef fish assemblage composition on the fore- and back reef. This is in accordance with previous findings where the distribution of nominally herbivorous fishes has been linked to the EAM distribution on tropical reefs (e.g. Ferreira and Gonçalves 2006, Chaves et al. 2010). In the present study, fore- and back reef habitats differed in their composition of EAM. In general, fore reef habitats had higher coverage of calcareous- and siphonous turf algae than back reef habitats, while back reef habitats were dominated by heavily sediment-laden short epilithic algae and zoanthids. The observed relationship between fish distribution patterns and composition of EAM is most likely related to food resources for some species. For instance, subadult and adult *A. bahianus*, *A. chirurgus* and *S. axillare* (all found in highest abundances on the fore reef) graze on the articulate calcareous algae matrix (Ferreira and Gonçalves 2006, Feitosa and Ferreira 2014, Mendes et al. 2015) that was the dominant EAM on fore reefs. The primary resource target might, however, not be the turf algae itself, but instead protein-rich endolithic cyanobacteria (Clements et al. 2016) and detritus trapped in the calcareous turf (Crossman et al. 2001, Choat et al. 2002, Wilson et al. 2003, Ferreira and Gonçalves 2006). The high abundance of calcareous EAM on the fore reef habitats probably make this habitat an important foraging area for acanthurids and parrotfishes (Ferreira and Gonçalves 2006, Mendes et al. 2015). Similarly, *Scarus trispinosus* was mainly recorded in fore reef habitats. This species also grazes on encrusting calcareous algae (Francini Filho et al. 2010), which was common in fore reef habitats. Sediment, on the other hand, can impede grazing of herbivorous fish (Bellwood and Fulton 2008), which might explain the lower abundance of acanthurids and parrotfish in the sediment-laden back reef habitats.

497

498 3.3. *Ontogenetic migrations and implications for management*

499

500 This study indicates that *Sargassum* beds should be recognized as nursery areas, since the
501 strongest links across the surveyed habitats were found between *Sargassum*-dominated beds
502 and fore reef habitats through ontogenetic migrations by nominally herbivorous fish. The
503 observed pattern also included *S. trispinosus*. *Scarus trispinosus* is a keystone species on
504 SWA reefs, but it is critically endangered due to overfishing (IUCN; Padovani-Ferreira et al.
505 2016). *Sargassum* beds seem to support adult populations by providing important nurseries
506 for this species, and serve as links between the very shallow-water reef environment and
507 deeper waters. The ontogenetic migrations indicated by the different size distributions of fish
508 do not seem to necessarily occur over very large distances (<1 km), since *Sargassum* beds
509 were present within all of the reef systems (mainly on the shallow parts of the reefs). It is,
510 however, possible that *S. trispinosus* and *S. axillare* move away to deeper waters when they
511 grow larger, escaping from fishing and thus extending connectivity further as has been
512 recorded for targeted fish species elsewhere (Lindfield et al. 2014). The results indicate that
513 preserving high canopy *Sargassum* beds might be favourable for populations of several fish
514 species. Trampling and anchoring on *Sargassum* beds can damage the plants and should
515 therefore be avoided (Azevedo et al. 2011). During the last decades, mass tourism, intense
516 overfishing and urbanization, associated with little enforcement, have certainly degraded the
517 reefs. Efforts are needed to establish the integrity of these reefs while preserving all habitats
518 that are important for species that host vital functional roles that sustain ecosystem
519 functioning.

520

521 **Conclusions**

The fundamental differences in seascape arrangement and habitat composition in East Brazil compared to the Caribbean and other parts of the world may have shaped the distinct patterns of fish habitat use and ontogenetic migration pathways between macrophyte- and reef habitats found in the present study. *Sargassum* beds were the most important juvenile habitats for several reef fish species, including the keystone species *S. trispinosus*. Seagrass beds were not utilized as nurseries, except perhaps by *L. synagris*. The spatially small and structurally low-complex monospecific *H. wrightii* beds might not provide sufficient shelter to function as a nursery ground comparable to *T. testudinum* beds in the Caribbean. Reef fishes in the SWA may therefore use alternative habitats compared to the same species in the Caribbean. This adaptation to conditions along the Brazilian coast was probably crucial when species originating in the Caribbean established themselves in the SWA. Consequently, connectivity patterns and nutrient pathways between habitats will also be different in the tropical SWA compared to the Caribbean and other parts of the world.

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815 816 Figures and Tables 817

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820 Figure 1. Map showing the study area and sites; 1 = Araripe reef, 2 = Coroa Alta reef and 3 = Recife de Fora reef.

Figure 2. Non-metric multidimensional scaling plot based on Bray-Curtis similarities showing juvenile, subadult and adult fish assemblage composition in the different habitats on the three sites based on fish abundance data. Data is square-root transformed with Wisconsin double standardization.

Figure 3. Abundance (median and quartile) per transect (40 m^2) of adults, subadults and juveniles in the four surveyed habitats; BR = Back reef, FR = Fore reef, SA = Sargassum beds and SG = Seagrass beds. Whiskers correspond to the 25th and 75th percentile and black dots are outlier values. Extreme values are caused by schooling species, mainly *Haemulon aurolineatum* and *acanthurids*. Different letters above boxes indicate that the average fish abundance of the age class was significantly different between habitats (ANOVA, Tukey HSD).

Figure 4. Abundance (mean $\pm$ SD) of different life stages of *Acanthurus bahianus* and *Acanthurus chirurgus* in back reef, fore reef and Sargassum habitats. The large variation in abundance at fore reef habitats for subadult and adult fish are due to the schooling behaviour of these species. Probability density of size distributions in the different habitats are shown to the right. Seagrass habitats are not included due to no records of these species in this habitat.

Figure 5. Abundance (mean $\pm$ SD) of different life stages of *Scarus zelindae* and *Scarus trispinosus* in back reef, fore reef and Sargassum habitats. Probability density of size distributions in the different habitats are shown to the right. Seagrass habitats are not included due to no records of these species in this habitat.

Figure 6. Ordination plot of selected fish species and the significant predictor variables in the reef habitats. Fish species are represented by 7 letter codes; acanbah = *Acanthurus bahianus*, acanchi= *Acanthurus chirurgus*, acancoe = *Acanthurus coeruleus*, anismor= *Anisotremus moricandi*, haemaur = *Haemulon aurolineatum*, scartri = *Scarus trispinosus*, sparaxi = *Sparisoma axillare* and stegfus = *Stegastes fuscus*. Environmental variables are represented by arrows with length of arrow proportional to strength of variable. The upper panels represent fore reef conditions, while the lower left panel reflects back reef habitats. Coral symbols courtesy of the Integrated Application Network.

Table 1. SIMPER analysis table showing the four fish species that on average contributed most to dissimilarity in species composition between habitats (all sites combined). Values correspond to percentage of dissimilarity. The habitat in which the species was most abundant is indicated in brackets where BR = Back reef, FR = Fore reef, SA = Sargassum beds and SG = Seagrass beds.

Adults	Fore reef		Sargassum		Seagrass	
Back reef	<i>Stegastes fuscus</i> (BR)	32.12	<i>Stegastes fuscus</i> (BR)	60.89	<i>Stegastes fuscus</i> (BR)	57.44
	<i>Sparisoma axillare</i> (FR)	11.22	<i>Anisotremus moricandi</i> (BR)	9.42	<i>Anisotremus moricandi</i> (BR)	8.68
	<i>Acanthurus bahianus</i> (FR)	9.13			<i>Pomacanthus paru</i> (BR)	7.08
	<i>Anisotremus moricandi</i> (BR)	9.05				
Fore reef			<i>Stegastes fuscus</i> (BR)	49.79	<i>Stegastes fuscus</i> (BR)	47.61
			<i>Sparisoma axillare</i> (FR)	9.28	<i>Pomacanthus paru</i> (FR)	9.95
			<i>Pomacanthus paru</i> (FR)	7.74	<i>Sparisoma axillare</i> (FR)	8.89
			<i>Acanthurus bahianus</i> (FR)	6.63	<i>Eucinostomus</i> sp. (SG)	6.46
Sargassum					<i>Coryphopterus</i> sp. (SG)	20.83
					<i>Eucinostomus</i> sp. (SG)	18.27
					<i>Pomacanthus paru</i> (FR)	18.27
					<i>Malacoctenus</i> sp. (SA)	13.18
Subadults	Fore reef		Sargassum		Seagrass	
Back reef	<i>Abudefduf saxatilis</i> (BR)	15.26	<i>Halichoeres poeyi</i> (SA)	31.87	<i>Stegastes fuscus</i> (BR)	19.84
	<i>Sparisoma axillare</i> (FR)	12.54	<i>Stegastes fuscus</i> (BR)	12.96	<i>Abudefduf saxatilis</i> (BR)	14.3
	<i>Stegastes fuscus</i> (BR)	12.48	<i>Haemulon aurolineatum</i> (BR)	10.79	<i>Eucinostomus</i> sp. (SG)	12.28
	<i>Haemulon aurolineatum</i> (BR)	11.36	<i>Abudefduf saxatilis</i> (BR)	9.52	<i>Haemulon aurolineatum</i> (SG)	12.28
Fore reef			<i>Halichoeres poeyi</i> (SA)	31.79	<i>Sparisoma axillare</i> (FR)	14.1
			<i>Sparisoma axillare</i> (FR)	10.02	<i>Eucinostomus</i> sp. (SG)	12.63
			<i>Abudefduf saxatilis</i> (FR)	8.64	<i>Abudefduf saxatilis</i> (FR)	12.44
			<i>Stegastes variabilis</i> (SA)	8.52	<i>Acanthurus coeruleus</i> (FR)	8.57
Sargassum					<i>Halichoeres poeyi</i> (SA)	51.55
					<i>Stegastes variabilis</i> (SA)	12.07
					<i>Eucinostomus</i> sp. (SG)	11.11
Juveniles	Fore reef		Sargassum			
Back reef	<i>Sparisoma axillare</i> (SA)	20.82	<i>Sparisoma axillare</i> (SA)	14.67		
	<i>Abudefduf saxatilis</i> (FR)	12.52	<i>Acanthurus bahianus</i> (BR)	13.03		
	<i>Haemulon aurolineatum</i> (BR)	8.54	<i>Halichoeres poeyi</i> (SA)	12.08		
	<i>Ocyurus chrysurus</i> (BR)	8.04	<i>Abudefduf saxatilis</i> (SA)	6.46		

Supplementary Material – Appendix A.

Table A1. Benthic cover classification into morphological groups of the observed benthos (modified from Littler and Littler 1984).

Group	Morphological category	Taxa
Algae	Encrusting calcareous	<i>Lithothamnion</i> spp
	Jointed calcareous	<i>Halimeda</i> spp, <i>Amphiroa</i> spp, <i>Corallina</i> spp, <i>Jania</i> spp
	Sediment-laden short EAM	Short (<1cm) matrix of unidentified species
	Sheet-like	<i>Dictyota</i> spp, <i>Canistocarpus</i> spp., <i>Dictyopteris</i> spp.
	Siphonous turf	<i>Caulerpa racemosa</i> , <i>Caulerpa verticillata</i>
	Thick-leathery	<i>Lobophora variegata</i> , <i>Sargassum</i> spp, <i>Udotea</i> spp
Echinoderms	Echinoderms	<i>Tropiometra</i> , sea urchins
Sponges	Encrusting sponges	<i>Porifera</i>
	Erect sponges	<i>Aplysina</i> spp
Coral	Encrusting coral	<i>Porites</i> , <i>Siderastrea</i> spp, <i>Montastrea</i> , <i>Agaricia</i>
	Massive coral	<i>Favia gravida</i> , <i>Mussismilia braziliensis</i>
		<i>Mussismilia harttii</i> , <i>Mussismilia hispida</i>
	Milleporids	<i>Millepora alcicornis</i> , <i>Millepora braziliensis</i>
	Octocoral	<i>Muriceopsis</i> spp , <i>Phyllogorgia</i> spp , <i>Plexaurella</i> spp
	Zoanthids	<i>Palythoa caribaeorum</i>

Table A2. Ranges and average values of depth in all habitats and rugosity and benthic cover in the reef habitats.

Environmental variables		Back reef			Fore reef			Sargassum			Seagrass		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
	Depth (m)	1	2	4	2.5	3.35	5	0.5	0.86	1.5	0.5	1.46	3
	Rugosity	2	2.63	3	2	2.93	4						
Benthic categories (coverage %)													
Algae	Calcareous articulated	0	0.33	1.67	0	3.15	29						
	Calcareous turf	0	2.01	13.5	0	23.34	54.71						
	Encrusting calcareous	0	0.6	0.52	0	11.47	37.5						
	Sediment-laden short EAM	12.5	49.39	84	0	12.46	63.6						
	Siphonous turf	0	2.29	23	0	18.46	65						
	Sheet-like	0	1.35	13.75	0	0.97	17						
Coral	Thick-leathery	0	1.29	5.3	0	0.89	9.6						
	Encrusting	0	6.3	16	0	4.59	36.25						
	Massive	0	7.1	31	0	1.52	8.25						
	Millepora spp.	0	8.18	35.67	0	8.35	36.67						
	Octocoral	0	4.73	16.67	0	1.37	10.6						
	Zoanthids	0	14.66	61.17	0	1.7	21.2						
Echinoderms	Echinoderms	0	0.52	3.33	0	0.75	7.25						
Sponges	Encrusting	0	0.37	1.33	0	3.26	35						
	Erect	0	0.67	4.86	0	3.35	100						
Other	Coral rubble	0	0.21	6.25	0	3.24	47.5						
	Sand	0	0	0	0	1.13	20						

Supplementary Material – Appendix B.

Table A2. Abundance per transect (40 m²) of all fish recorded in the four surveyed habitats showed by life stage.

Species	Lifestage	Back reef	Fore reef	Sargassum	Seagrass
<i>Abudefduf saxatilis</i>	J	0.94 ± 0.29	1.77 ± 0.61	1.10 ± 0.40	0
	SA	1.87 ± 0.51	1.67 ± 0.59	0.07 ± 0.05	0
	A	0	0	0	0
<i>Acanthurus bahianus</i>	J	0.16 ± 0.08	0.30 ± 0.12	4.17 ± 0.85	0
	SA	0.03 ± 0.03	2.53 ± 1.09	0.30 ± 0.18	0
	A	0.19 ± 0.20	2.00 ± 1.18	0	0
<i>Acanthurus chirurgus</i>	J	0.10 ± 0.07	0.03 ± 0.03	1.17 ± 0.29	0
	SA	0.16 ± 0.16	1.00 ± 0.59	0	0
	A	0.10 ± 0.10	0.07 ± 0.07	0	0
<i>Acanthurus coeruleus</i>	J	0.26 ± 0.10	1.03 ± 0.19	0.27 ± 0.12	0
	SA	0.68 ± 0.49	1.80 ± 0.81	0.33 ± 0.33	0
	A	0	0.67 ± 0.33	0	0
<i>Anisotremus moricandi</i>	J	0	0	0.10 ± 0.10	0
	SA	0.03 ± 0.03	0	0	0
	A	1.23 ± 0.53	0.07 ± 0.05	0	0
<i>Anisotremus surinamensis</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0	0.1 ± 0.06	0	0
<i>Anisotremus virginicus</i>	J	0.16 ± 0.12	1.27 ± 0.64	0	0
	SA	0.13 ± 0.05	0.20 ± 0.10	0	0
	A	0	0.10 ± 0.06	0	0
<i>Bodianus rufus</i>	J	0.10 ± 0.07	0.03 ± 0.03	0	0
	SA	0.23 ± 0.09	0.20 ± 0.09	0	0
	A	0.10 ± 0.07	0.03 ± 0.03	0	0
<i>Cantherhines pullus</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.03 ± 0.03	0	0	0
<i>Carangoides bartholomaei</i>	J	0	0.10 ± 0.10	0.23 ± 0.20	0.25 ± 0.25
	SA	0	0	0	0
	A	0	0	0	0

<i>Caranx crysos</i>	J	0.32 ± 0.23	0	0	0
	SA	0	0	0	0
	A	0	0	0	0
<i>Caranx latus</i>	J	1.00 ± 0.98	0.20 ± 0.12	0	0
	SA	0	0	0	0
	A	0	0	0	0
<i>Cephalopholis fulva</i>	J	0	0	0	0
	SA	0.13 ± 0.06	0.20 ± 0.09	0	0
	A	0	0	0	0
<i>Chaetodon striatus</i>	J	0	0	0.27 ± 0.08	0
	SA	0.19 ± 0.10	0.03 ± 0.03	0.37 ± 0.13	0
	A	0	0	0	0
<i>Chromis multilineata</i>	J	0	0	0	0
	SA	0	0.03 ± 0.03	0	0
	A	0	0	0	0
<i>Coryphopterus sp</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0	0	0	0.05 ± 0.05
<i>Diodon hystrix</i>	J	0	0	0	0
	SA	0.03 ± 0.03	0	0	0
	A	0	0.07 ± 0.07	0	0
<i>Diplectrum radiale</i>	J	0	0	0	0.05 ± 0.05
	SA	0	0	0	0
	A	0	0	0	0
<i>Elacatinus figaro</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.06 ± 0.06	0.07 ± 0.05	0	0
<i>Epinephelus adscensionis</i>	J	0.03 ± 0.03	0	0	0
	SA	0	0	0	0
	A	0	0	0	0
<i>Gramma brasiliensis</i>	J	0	0	0	0
	AS	0	0	0	0
	A	0	0.1 ± 0.07	0	0
<i>Haemulon aurolineatum</i>	J	2.87 ± 1.91	0.03 ± 0.03	0	4.25 ± 3.19
	SA	5.03 ± 2.66	0	0	0
	A	0.45 ± 0.28	0	0	0

<i>Haemulon parra</i>	J	0.06 ± 0.05	0	0.50 ± 0.31	0
	SA	0	0.03 ± 0.03	0	0
	A	0	0	0	0
<i>Haemulon plumieri</i>	J	0.13 ± 0.13	0.77 ± 0.48	0.80 ± 0.28	0
	SA	0.03 ± 0.03	0.13 ± 0.06	0	0
	A	0	0	0	0
<i>Haemulon squamipinna</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.03 ± 0.03	0	0	0
<i>Halichoeres brasiliensis</i>	J	0.06 ± 0.05	0.17 ± 0.07	0	0
	SA	0	0	0.03 ± 0.03	0
	A	0	0	0	0
<i>Halichoeres penrosei</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0	0.03 ± 0.03	0	0
<i>Halichoeres poeyi</i>	J	0	0	3.63 ± 0.97	0
	SA	0.39 ± 0.14	0.37 ± 0.16	5.37 ± 0.46	0
	A	0	0.10 ± 0.06	0.13 ± 0.06	0
<i>Holacanthus ciliaris</i>	J	0	0	0	0
	SA	0.03 ± 0.03	0.07 ± 0.05	0	0
	A	0.03 ± 0.03	0	0	0
<i>Holocentrus adscensionis</i>	J	0.10 ± 0.07	0	0	0
	SA	0.16 ± 0.11	0	0	0
	A	0.06 ± 0.05	0.17 ± 0.08	0	0
<i>Labrisomus nuchipinnis</i>	J	0	0	0.03 ± 0.03	0
	SA	0	0.07 ± 0.05	0.03 ± 0.03	0
	A	0.06 ± 0.03	0	0	0
<i>Lutjanus alexandrei</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.03 ± 0.03	0	0	0
<i>Lutjanus jocu</i>	J	0	0.07 ± 0.05	0	0
	SA	0.03 ± 0.03	0	0	0
	A	0	0	0	0
<i>Lutjanus synagris</i>	J	0	0	0	0.3 ± 0.13
	SA	0	0	0	0
	A	0	0	0	0
<i>Malacoctenus delalandii</i>	J	0	0	0	0

	SA	0	0	0	0
	A	0.03 ± 0.03	0	0.07 ± 0.07	0
<i>Malaccoctenus triangulatus</i>	J	0	0	0	0
	SA	0.06 ± 0.07	0.10 ± 0.07	0.03 ± 0.03	0
	A	0.06 ± 0.05	0	0.03 ± 0.03	0
<i>Microspathodon chrysurus</i>	J	0.06 ± 0.05	0.07 ± 0.05	0.07 ± 0.07	0
	SA	0.03 ± 0.03	0.10 ± 0.06	0	0
	A	0.45 ± 0.17	0.13 ± 0.08	0	0
<i>Mycteroperca bonaci</i>	J	0	0.03 ± 0.03	0	0
	SA	0	0	0	0
	A	0	0	0	0
<i>Ocyurus chrysurus</i>	J	0.94 ± 0.20	0.10 ± 0.07	0	0.05 ± 0.05
	SA	0	0	0	0
	A	0	0	0	0
<i>Odontoscion dentex</i>	J	0	0	0	0
	SA	0.03 ± 0.03	0	0	0
	A	0	0	0	0
<i>Ophioblennius trinitatis</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.74 ± 0.20	0.93 ± 0.22	0.03 ± 0.03	0
<i>Pareques acuminatus</i>	J	0.06 ± 0.05	0	0.07 ± 0.05	0
	SA	0	0	0	0
	A	0.06 ± 0.07	0	0	0
<i>Pempheris schomburgkii</i>	J	0.65 ± 0.66	0	0	0
	SA	0	0	0	0
	A	0	0	0	0
<i>Pomacanthus arcuatus</i>	J	0	0	0	0
	SA	0	0.07 ± 0.07	0	0
	A	0.03 ± 0.03	0.03 ± 0.03	0	0
<i>Pomacanthus paru</i>	J	0	0	0.07 ± 0.05	0
	SA	0	0.07 ± 0.07	0	0
	A	0.29 ± 0.13	1.17 ± 0.44	0	0.1 ± 0.1
<i>Pseudupeneus maculatus</i>	J	0	0	0.07 ± 0.05	0
	SA	0	0	0.27 ± 0.17	0
	A	0.10 ± 0.05	0.10 ± 0.06	0.57 ± 0.28	0.1 ± 0.1
<i>Scarus sp</i>	J	0.56 ± 0.2	0.2 ± 0.1	1.93 ± 0.53	0

<i>Scarus trispinosus</i>	SA	0.1 ± 0.07	0.1 ± 0.10	0	0
	A	0	0	0	0
<i>Scarus zelindae</i>	SA	0	0.07 ± 0.07	0	0
	A	0	0	0	0
<i>Serranus flaviventris</i>	J	0	0	0	0
	SA	0	0	0	0
	A	0.1 ± 0.05	0	0	0
<i>Sparisoma amplum</i>	J	0	0	0.13 ± 0.06	0
	SA	0	0.07 ± 0.07	0	0
	A	0	0	0	0
<i>Sparisoma axillare</i>	J	1.55 ± 0.37	3.60 ± 0.61	4.60 ± 0.85	0.1 ± 0.1
	SA	1.45 ± 0.77	2.63 ± 1.12	0.27 ± 0.14	0
	A	0.26 ± 0.11	2.07 ± 0.75	0	0
<i>Sparisoma frondosum</i>	J	0.10 ± 0.07	0	0.07 ± 0.05	0
	SA	0.32 ± 0.15	0	0	0
	A	0	0	0	0
<i>Sparisoma radians</i>	J	0	0	0.10 ± 0.07	0
	SA	0	0	0.03 ± 0.03	0
	A	0	0	0	0
<i>Sphoeroides spengleri</i>	J	0	0	0.07 ± 0.05	0
	SA	0	0	0	0.05 ± 0.05
	A	0	0	0	0
<i>Stegastes fuscus</i>	J	0.90 ± 0.21	0.23 ± 0.09	0.17 ± 0.08	0
	SA	1.84 ± 0.31	0.57 ± 0.16	0.43 ± 0.24	0
	A	9.03 ± 0.99	7.30 ± 0.59	0.03 ± 0.03	0
<i>Stegastes pictus</i>	J	0	0	0	0
	SA	0.10 ± 0.07	0	0	0
	A	0.03 ± 0.03	0	0	0
<i>Stegastes variabilis</i>	J	0.03 ± 0.03	0.03 ± 0.03	1.07 ± 0.22	0
	SA	0.03 ± 0.03	0.03 ± 0.03	1.57 ± 0.37	0
	A	0	0.07 ± 0.05	0.07 ± 0.05	0

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