Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Research Article

Resource partitioning among juvenile snappers in a semi-arid estuary in north-eastern Brazil

Silvia Yasmin Lustosa-Costa, Maria Rita Nascimento Duarte,
Priscila Rocha Vasconcelos Araújo and André Luiz Machado Pessanha

Universidade Estadual da Paraíba, Programa de Pós-graduação em Ecologia e Conservação, Campus I, Avenida das Baraúnas, 351, Bairro Universitário, 58429-500, Campina Grande, PB, Brazil

Cite this article: Yasmin Lustosa-Costa S, Nascimento Duarte MR, Vasconcelos Araújo PR, Pessanha ALM (2020). Resource partitioning among juvenile snappers in a semi-arid estuary in north-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* **100**, 807–816. https://doi.org/10.1017/S0025315420000375

Received: 4 November 2019
Revised: 2 April 2020
Accepted: 14 April 2020
First published online: 20 May 2020

Key words:
Habitats; hypersaline; *Lutjanus*; Perciformes; trophic ecology; Tubarão River estuary

Author for correspondence:
André Luiz Machado Pessanha,
E-mail: andrepessanhauepb@gmail.com

Abstract

Resource partitioning is important for species coexistence. Species with similar ecomorphological characters have a high potential for competition, especially when close phylogenetically. The diet and resource partitioning of four snappers (*Lutjanus alexandrei*, *L. analis*, *L. jocu* and *L. synagris*) was studied in the Tubarão River, north-eastern Brazil, between March and November 2012. Specimens were caught using a beach seine, and a total of 731 stomachs were analysed. The highest abundance of snappers was found near to vegetated habitats in the middle estuary. Crustaceans were dominant in the diet of all four species, being found in over 90% of the stomachs, followed by fish and molluscs. The species did not appear to compete for common resources, probably because there was not always spatial overlap, and differences in the proportions of consumption of items were observed. Ontogenetic comparisons of dietary compositions suggested differences among species, with changes in the diet related to changes in the mouth area as the body size increased. The changes were more evident in *L. analis* and *L. synagris* where microcrustaceans (Calanoida, Cyclopoida and Amphipoda) were dominant in the diet of the smaller size classes, and benthic crustaceans (Brachyura) and fish in the diet of larger individuals. The intra- and inter-specific differences in the dietary compositions, differences in the mouth area and feeding strategy contribute to allow the co-existence of these snappers in the study area.

Introduction

Competition between species for shared resources generally increases differential resource utilization and decreases niche overlap between species (Amorim *et al*., 2016). Sympatric species that interact are theoretically expected to evolve niche separation and resource partitioning to reduce competition (Araújo *et al*., 2016). Thus, ecological resource partitioning mechanisms, such as prey and habitat selection and time segregation, minimize competition and allow these species to coexist (Carvalho & Tejerina-Garro, 2014).

Closely related fish species often co-occur in the same habitat (Murie, 1995). The mutton snapper *Lutjanus analis* (Cuvier, 1828), Brazilian snapper *Lutjanus alexandrei* (Moura & Lindeman, 2007), dog snapper *Lutjanus jocu* (Bloch & Schneider, 1801) and lane snapper *Lutjanus synagris* (Linnaeus, 1758) are four of the most common snapper species along the north-eastern coast of Brazil (Resende *et al*., 2003; Frédou *et al*., 2009; Teixeira *et al*., 2010; Previero *et al*., 2011). These species form an important resource for artisanal fishing in the reef fish community. They have a similar morphology that contributes to the diet overlap and consequently increases the competition for prey (Kamukuru & Mgaya, 2004; Kadison *et al*., 2009). The juveniles of these species inhabit estuaries benefiting from optimal conditions for growth, including high food availability, water temperature and low predation risk (Aschenbrenner & Marques, 2016). The use of hypersaline habitats by early life stages snappers is related to the benefits associated with microhabitat quality, which may directly influence fish recruitment, growth and survival (Osório *et al*., 2011; Sales *et al*., 2018).

Diet composition data can play an important role in the research on some ecological issues, such as resource partitioning, which occurs during the early stages of fish life history (Castillo-Vargasmachuca *et al*., 2013). Determining the feeding ecology of a particular organism is essential to understand its role in the ecosystem. Snappers are often classified as carnivorous fishes in marine ecosystems (Freitas *et al*., 2011), although there are significant differences in the diets between species in this family (Mueller *et al*., 1994; Monteiro *et al*., 2009; Pimentel & Joyeux, 2010). Snappers are opportunistic feeders and present ontogenetic shifts in diet coupled with changes in jaw morphology and feeding strategies (Case *et al*., 2008). Juvenile snappers consume primarily Crustacea, including shrimps and crabs, while adults consume mainly fish (Franks & Vanderkooy, 2000; Wells *et al*., 2008; Monteiro *et al*., 2009; Tarnecki & Patterson, 2015).

One of the strategies to avoid intra- and inter-specific competition is segregation. This may include segregation by diet and feeding strategies and/or use of microhabitats. Many studies indicate a significant absence of competition in tropical regions due to resource partitioning, directly related to high feeding plasticity associated with high availability of food resources (Harrison & Whitfield, 2012; França *et al*., 2012). Despite the importance of studies on feeding

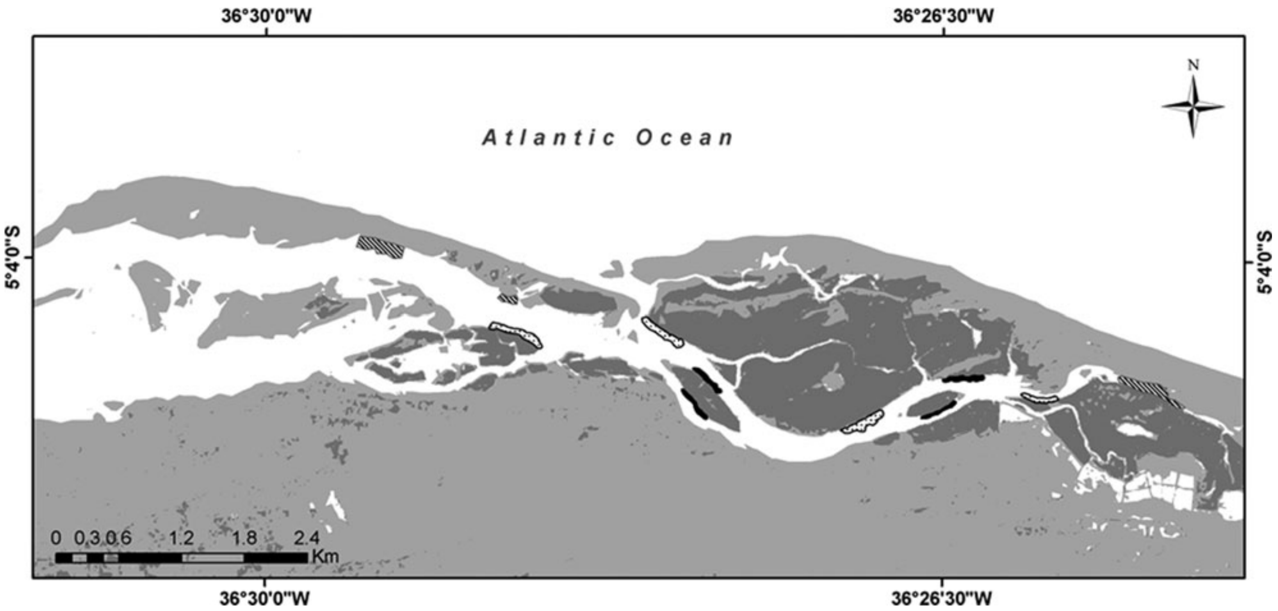

Fig. 1. Map highlighting the Tubarão River estuary, north-eastern Brazil. The sampling sites for each habitat are indicated: SNV (lines), MM (black) and MFM (black dots). Habitats: SNV = non-vegetated habitat with sand bottom, MM = mangrove fringe with mud bottom; MFM = vegetated habitat with macroalgae and mud bottom.

habits and overlap in all stages of fish life for a better understanding of ecosystems, available studies on juvenile snappers are limited in comparison with adult populations (Sheaves, 1995; Monteiro *et al*., 2009; Pimentel & Joyeux, 2010; Marshak & Heck, 2017, 2019; Marshak *et al*., 2018).

The objectives of the current study were to provide information on the distribution pattern and ontogenetic shifts in the diets of four juvenile snappers in a tropical hypersaline environment. We intend to address the following: (1) describe the patterns of habitat use by juveniles in a tropical hypersaline environment; and (2) verify the existence of ontogenetic shifts in food resource utilization by these snappers.

Material and methods

Study area

The Tubarão estuary is 10 km long and is located on the northern coast of the state of Rio Grande do Norte state, north-eastern Brazil (5°04′37″S 36°27′24″W), within the limits of Ponta do Tubarão Sustainable Development Reserve – RDSEPT (Figure 1). The main channel of the river is between 1 and 8 m deep, and is connected to tidal creeks and other shallower channels (Queiroz & Dias, 2014). This ecosystem is located in a region of semi-arid climate (BSh according to Köppen climate classification; Alvares *et al*., 2013), the typical climate of north-eastern Brazil, characterized as very low rainfall (annual average = 537.5 mm) with a tendency to high temperatures throughout the year. This area has a severe dry season, the driest month has precipitation below 20 mm with intense evaporation due to the high solar radiation (7.1 h of sunlight/day) and greater influence of constant trade winds, mainly from the south-east, east and north-east quadrants (IDEMA, 1999). The estuary is not fed by a freshwater spring, and only receives fresh water from subjacent groundwater and the rains that occur mainly from March to May (Queiroz & Dias, 2014). The most upstream areas of the estuary showed hypersaline conditions due to the largest evaporation during all year (Sales *et al*., 2018).

The environment is bordered almost completely by mangroves, composed of Black mangrove *Avicennia germinans* L. and *Avicennia schaueriana* Stapf & Leechman, Button mangrove *Conocarpus erectus* L., White mangrove *Laguncularia racemosa* Gaerton and Red mangrove *Rhizophora mangle* L., which function as natural protection between the coastline and mainland. The soft-bottom flora of the channel is dominated by the macroalgae *Dictyota* sp., *Solieria filiformes* (Kützing), *Gracilaria cearensis* (Joly & Pinheiro), and *Gracilaria domingensis* (Kützing). Other common vegetation consists of seagrass as *Halodule wrightii* Ascherson and algae as *Hypnea musciformis* (Wulfen). These habitats provide a rich source of food while also offering refuge from predation for fish and invertebrates.

Sampling and laboratory procedures

The Tubarão estuary was sampled during the rainy (April and July 2012) and dry (September and November 2012) seasons. All sampling was restricted to daylight (06:00–17:00 h) on the low water spring tide due to logistic restrictions of sampling with seine nets. Sampling was undertaken in different subtidal microhabitats according to the following: non-vegetated habitat with sand bottom – bare sand (SNV); narrow intertidal flat adjacent to mangrove fringe and mud bottom (MM); and broad intertidal flat non-adjacent to fringe and containing expansive macroalgae (*Gracilaria domigensis*, *Hypnea musciformes*) and seagrass (*Halodule wrightii*) beds, and mud bottom (MFM) (Figure 1). Four sites were sampled for each habitat and three replicates were collected at each microhabitat by pulling a beach-seine net (10 m long and 1.5 m high, with a stretched mesh size of 5 mm) across 30 m parallel to the coast, to a maximum depth of 1.5 m (4 sites × 3 microhabitats × 3 replicates × 4 months = 144 samples). The collected fish were fixed immediately after capture for later identification in the laboratory. The total length (TL, mm) was measured for each individual.

Food resources found in stomachs were quantified using the following indices: frequency of occurrence (%F), the percentage number (%N) and the volume (%V) of different food items (Hyslop, 1980). These indices (%F, %N, %V) were combined into the Index of Relative Importance of Pinkas *et al.* (1971) with the following formula: IRI = %F × (%N + %V), which was computed for each food item. Each dietary item was identified to the lowest possible taxon. For items that could not be counted, a value of 0.1 was given for their number (%N) to offset distortions in the index (Abdurahiman *et al.*, 2010). The volumes of each item were verified in a way similar to that used by Bemvenuti (1990) and analysed by displacement methods. The total volumes of each item were obtained by summing individual volumes across all samples. The volumetric proportion of each item was then calculated based on the total volume of food eaten per consumer. Although the volumes of unidentifiable materials were also calculated, these were not considered valid dietary categories and were not included in subsequent dietary analysis (Abdurahiman *et al.*, 2010).

The body length intervals to each size class varied among species. These intervals were applied to ensure that each class included enough individuals to estimate the diet composition. The individuals were grouped into the following three size classes: small juveniles (TL_1: <70 mm), medium-sized juveniles (TL_2: 71–125 mm) and large juveniles (TL_3: >126 mm). The asymptotic length was obtained from Teixeira *et al.* (2010), Freitas *et al.* (2011) and Previero *et al.* (2011). This method was applied to standardize the size classes for all species getting a better comparison between them. Quantifying the abundance and distribution of size classes is fundamental to understand how different habitats influence the fish populations throughout estuarine systems.

The morphological measurements used were related to feed structure: mouth height (M_H) is the height of the mouth fully open; mouth width (M_w) is the width of the mouth fully open. The mouth area (M_A) (assuming an elliptical shape) was described by: $M_A = 0.25\,\pi\,(M_H M_w)$ (Karpouzi & Stergiou, 2003).

Statistical analyses

Two-way permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in fish abundance and biomass between the three habitats (SNV, MM and MFM) and seasons (dry and rainy). In all analyses, the same two-factor design (season and habitat) was used. Pair-wise test comparisons were used to determine which groups differed within factors based on 9999 permutations performed for each test (Anderson, 2001; Anderson *et al.*, 2008).

The IRI contribution of each prey taxon by species and size classes was square-root transformed and converted into a triangular matrix of similarities between all the samples (Schafer *et al.*, 2002). Hierarchical cluster analysis, using group-averaged linking, was used to examine potential diet groupings based on species and size classes. The Similarity Profile Analysis (SIMPROF) is performed when it is used to objectively identify the members of the 'real' groups present in the results returned from a classical agglomerative hierarchical clustering method. This provides a compelling alternative to more traditional methods that rely on subjective assignment of arbitrary cut-off levels (Clarke *et al.*, 2008). The Similarity Percentage (SIMPER) procedure was applied in SIMPROF groups to detect prey that contribute to within-group similarity. The Cluster analysis, SIMPROF and SIMPER procedures were performed with the PRIMER software package, version 6.0 (Clarke & Warwick, 2001).

Trophic strategy

The trophic strategy was analysed graphically with the method proposed by Amundsen *et al.* (1996), which incorporated the prey-specific abundance (volume) into Costello (1990) analysis. The Amundsen method is based on a two-dimensional representation wherein each point relates the %F of a prey to its prey-specific volume %V. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization. Predators are specialized when prey are positioned in the upper part of the graph, whereas prey positioned in the lower part were eaten occasionally (generalization).

The Shannon–Wiener diversity index using a natural logarithm (Krebs, 1989), which corresponds to dietary breadth, was calculated for each species using the volumetric data of feeding. The Simplified Morisita Index Modified (Krebs, 1989) was used to assess niche overlap among species and size classes. Niche overlap was considered significant when it exceeded the value of 0.6 (Labroupoulou & Eleftheriou, 1997; Mendoza-Carranza & Vieira, 2009). For this calculation, the values of volume were also used.

Results

A total of 796 juvenile snappers were collected during the study. *Lutjanus analis* was the most abundant species accounting for 59.3% of the total catch. It was followed by *L. alexandrei* (17.6%), *L. synagris* (17.1%) and *L. jocu* (6.0%). Overall, PERMANOVA revealed significant differences between estuarine habitats in the biomass (PERMANOVA, $F_{2,144} = 2.26$, $P = 0.0152$), but not in the number of individual juvenile snappers (PERMANOVA, $F_{2,144} = 1.30$, $P = 0.2556$) (Figure 2) (Table 1). On the other hand, there were no significant temporal differences for number (PERMANOVA, $F_{2,144} = 1.14$, $P = 0.338$) and biomass (PERMANOVA, $F_{2,144} = 0.91$, $P = 0.468$) (Figure 2) (Table 1). MM estuarine habitat had the highest number of individuals (1.7 ± 0.32 individuals/haul) followed by MFM (1.6 ± 0.51) and SNV (0.1 ± 0.03). Spatial patterns in fish biomass showed similar trends to the number of individuals: the mean biomass in the MFM habitat (8.36 ± 1.68 g $haul^{-1}$) was about five times lower than in the MM estuary (26.15 ± 5.21 g $haul^{-1}$).

Juvenile *L. analis* were present in all habitats, and the highest abundance was recorded at MM and MFM habitats whilst biomass was highest in the MM habitat. *Lutjanus jocu* juveniles were collected in higher abundance and biomass in MM habitat. Higher catches of *L. synagris* occurred at MM and MFM habitats, while *L. alexandrei* was often caught in high abundance and biomass in the same habitats (Figure 2). No clear trend was shown for *L. alexandrei* and *L. jocu* (PERMANOVA, $P > 0.05$). Only *L. synagris* and *L. analis* showed significant differences (PERMANOVA, $P < 0.05$) in biomass, with highest values being recorded in MM and MFM habitats, respectively (Figure 2).

The snapper species corresponded to immature size classes ranging from 11 to 205 mm TL. In relation to fish size distribution in the estuary, the smallest and medium-sized individuals of snappers of all species were observed in high frequency especially in MM and MFM habitats. Large individuals of *L. jocu* were observed with higher frequency in SNV habitat (Figure 3).

Diet

Stomach contents were found in 112 of the 122 *L. alexandrei* (92%), 49 of the 52 *L. jocu* (94%), 106 of the 117 *L. synagris* (91%) and 401 of the 440 *L. analis* (91%). Crustaceans were dominant in the diet of snapper species, being found in over 90% of the stomachs, followed by fish and molluscs. Crustaceans were mainly represented by decapods and microcrustaceans (Calanoida, Cyclopoida and Amphipoda) (Table S1 and Table S2).

In general, the diet composition in terms of the main prey items differed between habitats. In SNV habitat, the diet of *L. analis* and *L. synagris* consisted of microcrustaceans (Amphipoda and Cyclopoida), and the diet of *L. jocu* was predominantly fish. The contributions of Brachyura and Peneidae

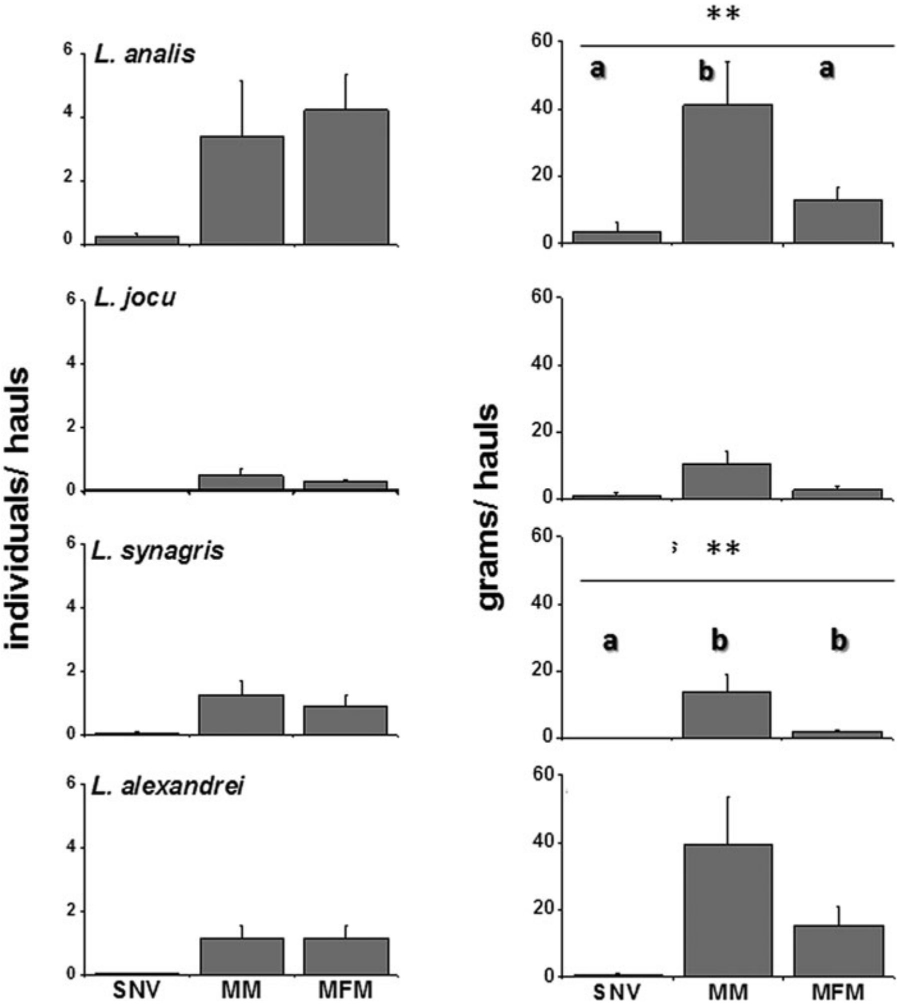

Fig. 2. Variations of abundance (number of individuals per haul – CPUE) and Biomass (grams per haul) of four snappers in the estuary of the Tubarão River, north-eastern Brazil (average ± SE). Habitats: SNV = non-vegetated habitat with sand bottom, MM = mangrove fringe with mud bottom; MFM = vegetated habitat with macroalgae and mud bottom. The double asterisk indicates a highly statistically significant difference ($P < 0.01$). Within each graph, bars sharing the same letter are not significantly different (PERMANOVA, pairwise tests, $P > 0.05$).

Table 1. Results from the multivariate permutational analysis (PERMANOVA) of differences in total abundance and biomass between habitat and season

PERMANOVA	df	SS	MS	Pseudo-F	P (perm)
Abundance					
Habitat	2	6586.9	3293.4	1.3093	0.2556
Season	1	2891.9	2891.9	1.1497	0.3391
Biomass					
Habitat	2	13,229	6614.4	2.2643	0.0152
Season	1	2673.8	2673.8	0.91529	0.4684
Pairwise test		*t*	P (perm)		
SNV – MFM		1.6103	0.0266		
SNV – MM		1.8501	0.0056		
MFM – MM		1.0596	0.3469		

SNV, non-vegetated habitat with sand bottom; MM, mangrove fringe with mud bottom; MFM, vegetated habitat with macroalgae and mud bottom.

to the diet of all snappers increased in MM habitat; contributions made by microcrustaceans increased in *L. analis* and *L. synagris* in MFM habitat, whereas that of Brachyura remained very high in the diet of *L. alexandrei* and *L. jocu* (Figure 4).

Ontogenetic variation in diet of the four snapper species was evident (Figure 5). The contributions made by Amphipoda to the diet of *L. alexandrei* and *L. jocu* declined progressively from nearly 60–80% IRI in the smallest juvenile to zero in large juveniles. The relative importance of Brachyura tended to increase with size class (medium and large juveniles), whereas, in contrast, *L. synagris* and *L. analis* consumed far greater volumes of Cyclopoida (71 and 47% IRI, respectively) and Amphipoda (42% and 54% IRI, respectively) by small juveniles, whereas large juveniles ingested Brachyura (51% and 52% IRI, respectively) (Figure 4).

When the IRI data of each size class were plotted in a dendrogram, samples from smaller size classes (small juveniles) appeared on the left side of the dendrogram and samples of larger-size (medium and large juveniles) were shown on the right side (Figure 5). SIMPROF showed that dietary compositions of

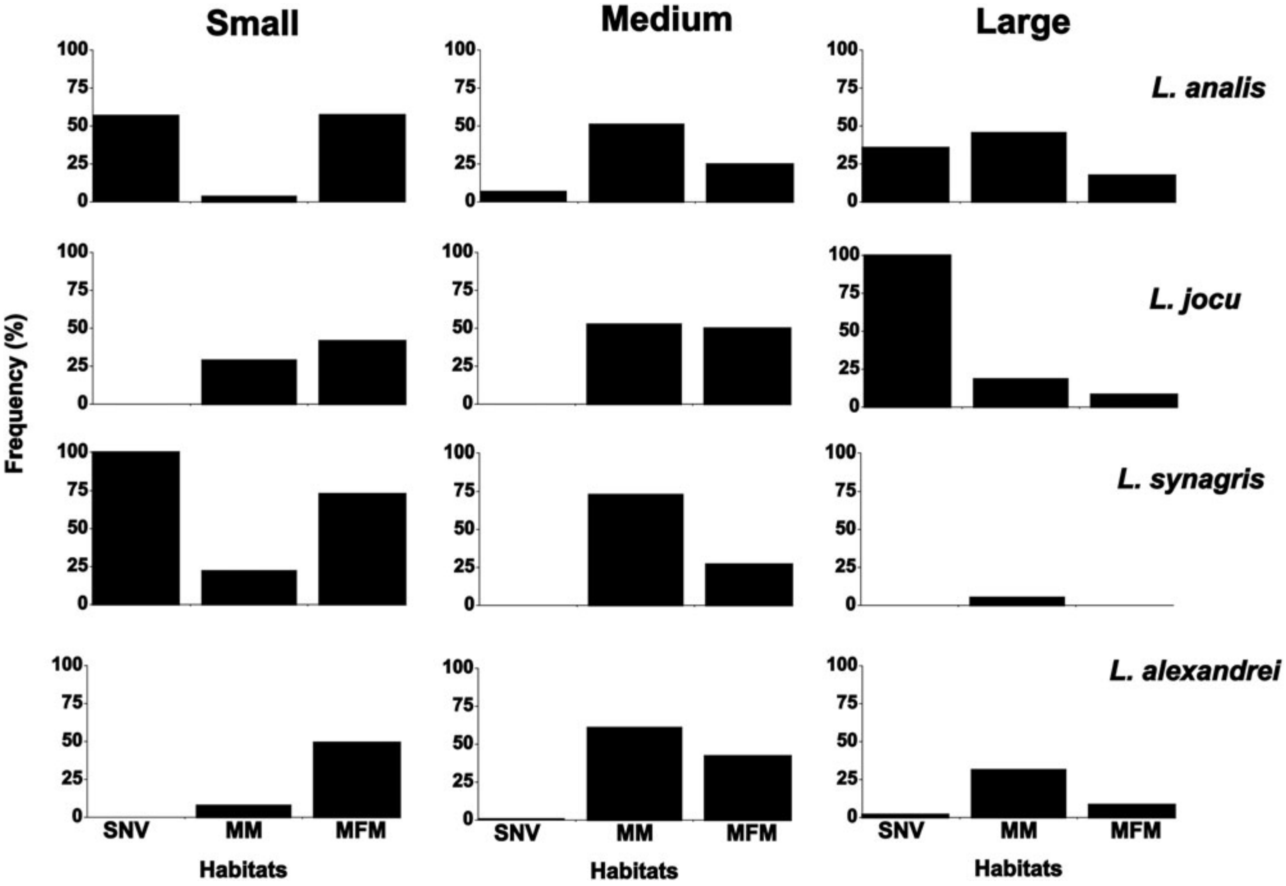

Fig. 3. Distributions of size classes (small, medium and large juveniles) in relation to habitats registered in Tubarão River estuary, north-eastern Brazil. Habitats: SNV = non-vegetated habitat with sand bottom, MM = mangrove fringe with mud bottom; MFM = vegetated habitat with macroalgae and mud bottom.

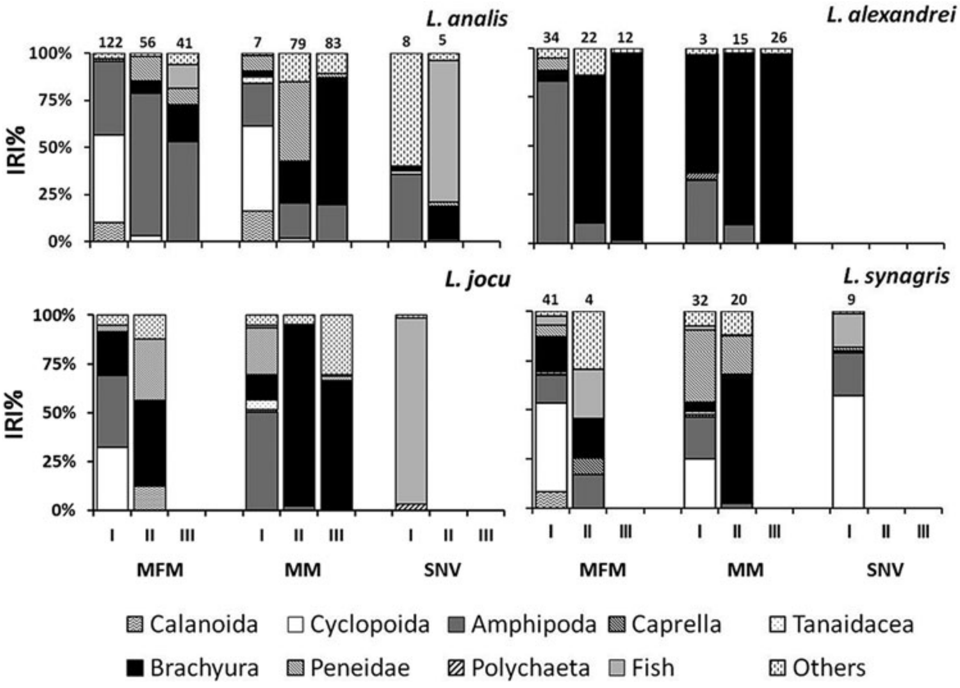

Fig. 4. Index of Relative Importance (% IRI) in relation to habitats and size classes registered in Tubarão River estuary, north-eastern Brazil. Habitats: SNV = non-vegetated habitat with sand bottom, MM = mangrove fringe with mud bottom; MFM = vegetated habitat with macroalgae and mud bottom. Numbers of stomachs analysed are indicated above the bars.

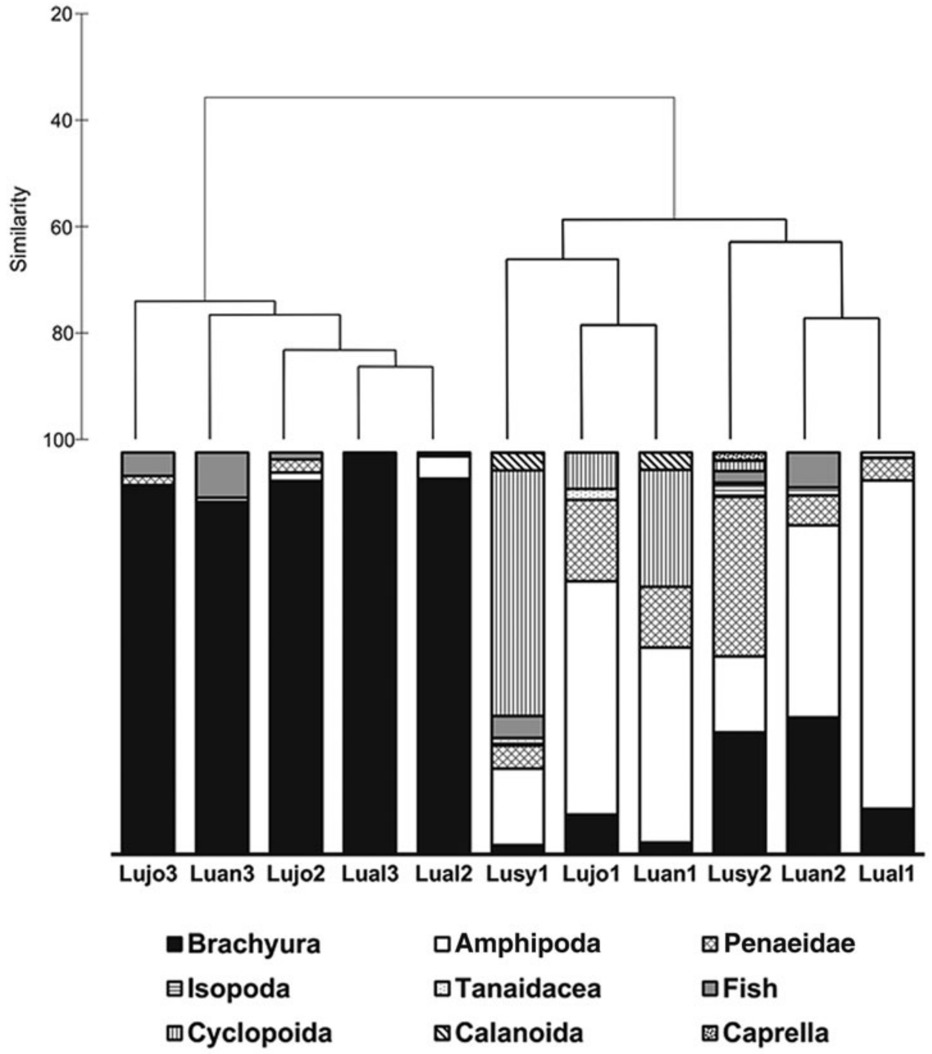

Fig. 5. Classification of % IRI data for size classes of four snapper species in the Tubarão River estuary, north-eastern Brazil. Small (1); medium (2) and large juveniles (3). Luan = *Lutjanus analis*, Lujo = *Lutjanus jocu*, Lusy = *Lutjanus synagris* and Lual = *Lutjanus alexandrei*.

different size classes in each pairwise comparison were significantly different ($\pi = 5.4$, $P < 0.05$). SIMPER analysis showed that the main prey of group A were Amphipoda, Penaeidae and Cyclopoida (average similarity = 62.74) and of group B were Brachyura and fish (average similarity = 77.83).

Feeding strategy and mouth area

The feeding strategy observed in the size classes of the four species of snappers is summarized in the Amundsen plots. From the prey importance axis, the smallest size class for *L. synagris*, *L. jocu* and *L. analis* showed a diet mostly based on rare prey taxa that were eaten occasionally and in relatively small- to medium-volume, such as Amphipoda, Cyclopoida and Brachyura (Figure 6). In the other size classes there were differences between species: for *L. synagris* and *L. analis* the generalist feeding strategy was continued with predation on Amphipoda and Brachyura, while *L. jocu* and *L. alexandrei* demonstrated a more specialized feeding strategy on Brachyura (Figure 6).

Niche breadth for the four co-occurring snappers presented higher values for *L. synagris* and *L. analis* ($H' = 0.19$ and $H' = 0.21$, respectively), and lower values for *L. jocu* and *L. alexandrei* ($H' = 0.18$ and $H' = 0.14$, respectively). Similarly, the Shannon-Wiener index values also showed changes of niche breadth according to size classes of snappers, with it being inversely proportional to body length in all species. Inter-specific niche overlap occurred at smallest sizes of four snapper species, and intra-specific niche overlap between the largest sizes (Table 2).

When the mouth area of different size classes was analysed among species, it was observed that *L. synagris* and *L. analis* presented lower ranges (Lusy$_1$ = 6.58 mm^2, Lusy$_2$ = 54.65; Luan$_1$ = 3.48 mm^2, Luan$_2$ = 28.62 mm^2, Luan$_3$ = 120.60 mm^2), compared with *L. jocu* and *L. alexandrei* (Lujo$_1$ = 20.05 mm^2, Lujo$_2$ = 80.75 mm^2, Lujo$_3$ = 177.32 mm^2; Lual$_1$ = 37.36 mm^2, Lual$_2$ = 65.94 mm^2, Lual$_3$ = 173.78 mm^2).

Discussion

The greater abundance and degree of inter-specific food partitioning of snapper fishes suggested that this hypersaline environment provides an important nursery area and feeding ground habitats. Habitats that support high juvenile densities, and may contribute juveniles to adult populations, have historically been referred to as nurseries (Beck *et al.*, 2001). There are a few tropical estuaries on the borders of semi-arid regions in north-eastern Brazil, which provide good shelter for juvenile snappers and other juvenile reef fish, as proposed by Sales *et al.* (2016). The results presented here could be due to (1) habitat use by species and (2) differences in trophic strategy and mouth area, resulting in resource

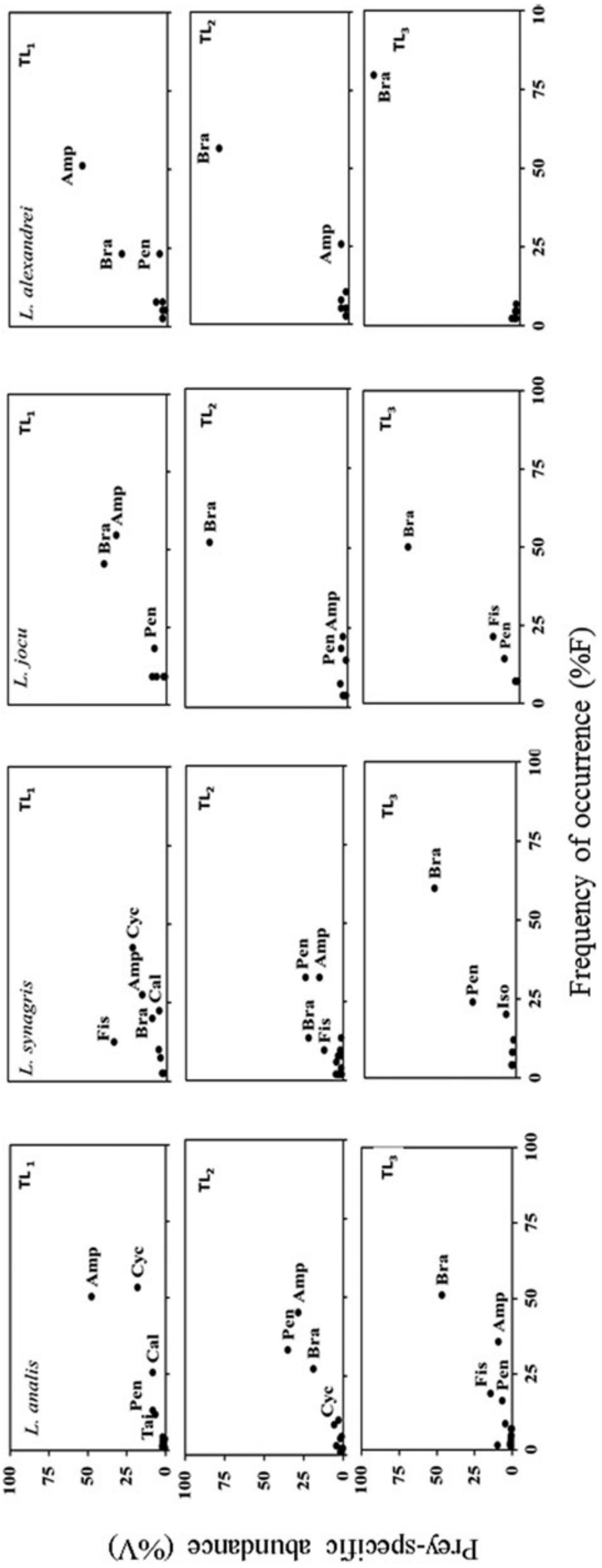

Fig. 6. Feeding strategy for the size classes of four snappers in the Tubarão River estuary, north-eastern Brazil. Food items: Amp, Amphipoda; Bra, Brachyura; Cal, Calanoida; Cyc, Cyclopoida; Fis, Fish; Iso, Isopoda; Pen, Penaeidae; Tai, Tanaidacea. Small (TL_1), medium (TL_2) and large juveniles (TL_3).

partitioning. For example, Adite & Winemiller (1997) and Boyle & Horn (2006) showed that the sharing of food resources by congeners is facilitated through differences in habitat use, in response to environmental heterogeneity in ecosystems.

The results point to clear differences in utilization of different habitat types by juvenile snappers in the Tubarão estuary. The higher abundance of snappers registered in the MFM and MM habitats of the Tubarão estuary was demonstrated, revealing the structural complexity provided by proximity to habitats (such as seagrass and mangrove roots) as an important factor. Similar results were found by Sales *et al.* (2016) who argued that the greater abundance and fish richness in this estuary might depend on the substratum type and more complex and heterogeneous habitats, such as mangrove fringe and macroalgae beds. Aschenbrenner *et al.* (2016) also found that habitat selection by snapper species in Brazilian estuaries is related to higher densities of juveniles in mangrove areas. Habitat selection among snapper species has been very evident, mainly due to formation of schools of conspecifics in order to improve safety while foraging (Igulu *et al.*, 2011). These results support the hypothesis that the hypersaline ecosystems are potential or alternative nursery grounds for these juvenile fish to minimize mortality and maximize growth.

The results show the importance of different habitats as nurseries for snapper species. Despite the differences between habitats in abundance of snappers, juveniles of *L. analis* and *L. synagris* showed some degree of similarity in habitat utilization, with highest biomass in the MM habitat, due to the presence of medium- and large-sized individuals close to the mangrove fringes. It is important to note that small individuals of these species were caught predominantly in SNV habitats. Differences in the distribution of size classes among different habitats in our study can be used to infer about the discontinuity hypothesis – resources are patchily distributed so their availability varies among spatial scales. Greater use of mangrove fringes by *L. analis* and *L. synagris* is as reported in other studies (Ley *et al.*, 1999; Doncel & Paramo, 2010), and suggests that distribution of snappers was influenced by food resources which may be overabundant and also dependent on abiotic factors. Nagelkerken *et al.* (2000) have described a clear spatial separation in seagrass and mangrove utilization among closely related fish species and among different size groups within species, suggesting avoidance of competition. Burke (1995) suggested that biotic and abiotic gradients interact to create and guide fishes to species-specific nursery habitats. In a number of studies, a greater abundance of snapper species has been found in habitats with higher complexity (mangrove roots and seagrass) (Mueller *et al.*, 1994; Monteiro *et al.*, 2009; Freitas *et al.*, 2011); these confer strong advantages for young stages, such as a reduction of predation risk and access to different prey species (Szedlmayer & Lee, 2004), with potential consequences for growth rate (Aschenbrenner & Marques, 2018).

In the present study we found that the four juvenile snapper species were exclusively carnivorous, feeding mainly on microcrustaceans and benthic crustaceans. The importance of these items in the diet of snappers is highlighted here and corroborated by earlier studies in tropical estuaries and mangroves (Dorenbosch *et al.*, 2004; Kamukuru & Mgaya, 2004), evidencing the ability of these species to exploit them. In our study, the segregations in diet among species were related to the habitat types and relative abundances of their potential prey, and this strategy contributes to species coexisting by facilitating resource partitioning. For example, *L. synagris* and *L. analis* forage in the water column and seagrass, feeding on Cyclopoida and Amphipoda in a generalist way according to prey availability, whereas *L. alexandrei* and *L. jocu* forage near the substrate feeding on Brachyura, behaving more like a specialist. This difference was due to choice of the way to feed in response to patterns of food density: a higher

Table 2. Niche overlap index per size class (TL) for the four fish species (Luan = *Lutjanus analis*, Lujo = *Lutjanus jocu*, Lusy = *Lutjanus synagris* and Lual = *Lutjanus alexandrei*) in the Tubarão River estuary, north-eastern Brazil

	Luan$_1$	Luan$_2$	Luan$_3$	Lual$_1$	Lual$_2$	Lual$_3$	Lujo$_1$	Lujo$_2$	Lujo$_3$	Lusy$_1$	Lusy$_2$	Lusy$_3$
Luan$_1$	–											
Luan$_2$	**0.66**	–										
Luan$_3$	0.21	0.36	–									
Lual$_1$	**0.81**	**0.63**	0.58	–								
Lual$_2$	0.07	0.12	0.12	0.50	–							
Lual$_3$	0.02	**0.89**	**0.74**	0.46	**0.99**	–						
Lujo$_1$	**0.67**	**0.62**	**0.80**	**0.91**	**0.72**	0.46	–					
Lujo$_2$	0.07	0.17	**0.91**	**0.99**	**0.99**	**0.99**	**0.71**	–				
Lujo$_3$	0.04	**0.94**	**0.94**	**0.96**	**0.96**	**0.96**	**0.68**	**0.97**	–			
Lusy$_1$	0.53	0.50	0.15	0.31	0.04	0.05	0.29	0.03	0.18	–		
Lusy$_2$	0.50	**0.82**	0.55	**0.65**	0.55	0.50	**0.73**	0.55	**0.64**	0.49	–	
Lusy$_3$	0.15	**0.62**	**0.81**	0.44	**0.76**	**0.74**	**0.66**	**0.78**	**0.80**	0.17	**0.81**	–

Values in bold indicate biologically significant overlap (>0.6) according to Labroupoulou & Eleftheriou (1997). Small (TL$_1$) Medium (TL$_2$) and Large juveniles (TL$_3$).

abundance of macroinvertebrates was recorded by Queiroz & Dias (2014) and Medeiros *et al.* (2016) in Tubarão estuary in association with algae beds, sandy and muddy bottoms, while the abundance of Brachyura and Penaeidae increased as they approached mangroves. Similar diet shifts related to habitat changes have been reported for *Lutjanus campechanus* in the north-east Gulf of Mexico (Szedlmayer & Lee, 2004).

The cluster analysis demonstrated that diet composition of snappers is different between size classes, suggesting resource partitioning. The diet shifts gradually between size classes of *L. synagris*, *L. alexandrei* and *L. analis* from predominantly microcrustaceans to Brachyura, fish and molluscs. This result was corroborated by studies on diet of two of these species in oceanic islands and reefs (Doncel & Paramo, 2010). On the other hand, *L. jocu* ate Brachyura and Penaeidae at all size classes, which has been noted in other studies in tropical estuaries (Monteiro *et al.*, 2009; Pimentel & Joyeux, 2010). The juvenile reef fish presented ontogenetic dietary changes once they were in the nursery habitats (Cocheret de la Moriniére *et al.*, 2003; Wells *et al.*, 2008). The switch of a diet based on microcrustaceans to a Brachyura- or Penaeidae-based diet probably occurred because these items are more energetically profitable for larger individuals, maximizing energy input (Yeager *et al.*, 2014). Ross (1986) suggested that changes in dietary preferences due to ontogeny may reduce competition for resources between different life history stages.

Other aspects of the ontogenetic shifts in diet were related in changes in mouth area. Snapper range size increased with size classes accompanied by a switch from microcrustacean prey in small juveniles to Brachyura in larger juveniles, which supports the hypothesis that optimal prey size is related to the opening of the predator's mouth. In addition, these changes indicated that predator performance becomes more efficient, with hard prey, such as crabs and molluscs, being incorporated into the diet as the fish grow. For instance, Case *et al.* (2008) found that ontogenetic change in the mouth morphology allowed large juvenile red snapper (*Lutjanus campechanus*) to explore harder types of prey. Previous studies also suggest that the progressive increase of larger prey in the diet could be related to increase in mouth size and ability to handle and crush prey in Lutjanidae (Szedlmayer & Lee, 2004; Yeager *et al.*, 2014) and other carnivorous fish such as Sparidae (Sarre *et al.*, 2000) and Serranidae (Labroupoulou & Eleftheriou, 1997).

Significant overlaps between size classes were observed due to the prevalence of particular items in the diets of snappers. However, segregation along two resource axes (habitat and trophic) may have played an important role in niche segregation of snappers, to avoid potential inter-specific food competition among size classes. Furthermore, snappers adopted different strategies among and within species to reduce competition; thus *L. synagris* and *L. analis* tended to have broader diets while *L. jocu* and *L. alexandrei* were more specialists. Our study supports the hypothesis that resource partitioning between congeneric fish species is related to spatial patterns of habitat use and ontogenetic diet shifts, and also highlights the importance of hypersaline ecosystems as nursery grounds for snappers.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315420000375.

Acknowledgements. The authors thank the members of the Laboratório de Ecologia de Peixes, Universidade Estadual da Paraíba (UEPB) for their invaluable assistance with fieldwork.

Financial support. This work was partially supported by the CNPq – Brazilian National Agency for Scientific and Technological Development (Proc. 477663/2011-7); and UEPB/PROPESQ (Proc. 115/2011).

References

Abdurahiman KP, Nayak TH, Mohamed KS and Zacharia PU (2010) Trophic organisation and predator-prey interactions among commercially exploited demersal finfishes in the coastal waters of the south eastern Arabian Sea. *Estuarine, Coastal and Shelf Science* **87**, 601–610.

Adite A and Winemiller KO (1997) Trophic ecology and ecomorphology of fish assemblages in coastal lakes of Benin, West Africa. *Ecoscience* **4**, 6–23.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM and Sparovek G (2013) Köppen's climate classification map of Brazil. *Meteorologische Zeitschrift* **22**, 711–728.

Amorim E, Ramos S, Elliott M and Bordalo AA (2016) Immigration and early life stages recruitment of the European flounder (*Platichthys flesus*) to an estuary nursery: the influence of environmental factors. *Journal of Sea Research* **107**, 56–66.

Amundsen PA, Gabler HM and Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data – modification of Costello (1990) method. *Journal of Fish Biology* **48**, 607–614.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**, 32–46.

Anderson MJ, Gorley RN and Clarke KR (2008) *PERMANOVA for PRIMER: Guide to Software and Statistical Methods*. Plymouth: PRIMER-E.

Araújo ALF, Dantas RP and Pessanha ALM (2016) Feeding ecology of three juvenile mojarras (Gerreidade) in a tropical estuary of northeastern Brazil. *Neotropical Ichthyology* **14**, 1–10.

Aschenbrenner A and Marques S (2018) First record of foraging association between juveniles of endemic Brazilian snapper (*Lutjanus alexandrei*) and green moray at mangrove prop roots in the southwestern Atlantic. *Marine Biodiversity* **48**, 1275–1276.

Aschenbrenner A, Hackradt CW and Ferreira B (2016) Spatial variation in density and size structure indicate habitat selection throughout life stages of two Southwestern Atlantic snappers. *Marine Environmental Research* **113**, 49–55.

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF and Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51**, 633–641.

Bemvenuti MA (1990) Hábitos alimentares de peixe-rei (Atherinidae) na região estuarina da Lagoa dos Patos. *Atlântica* **12**, 79–102. (In Portuguese)

Boyle KS and Horn MH (2006) Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. *Marine Ecology Progress Series* **319**, 65–84.

Burke JS (1995) Role of feeding and prey distribution of summer and southern flounder in selection of estuarine nursery habitats. *Journal of Fish Biology* **47**, 355–366.

Carvalho RA and Tejerina-Garro FL (2014) Environmental and spatial processes: what controls the functional structure of fish assemblage in tropical rivers and headwater streams? *Ecology of Freshwater Fish* **24**, 317–328.

Case JE, Westneat MW and Marshall CD (2008) Feeding biomechanics of juvenile red snapper (*Lutjanus campechanus*) from the northwestern Gulf of Mexico. *Journal of Experimental Biology* **211**, 3826–3835.

Castillo-Vargasmachuca S, Ponce-Palafox JT, Arredondo-Figueroa JL, Chávez-Ortiz E, Rodríguez-Chávez G and Seidavi A (2013) Effects of temperature and salinity on growth and survival of the Pacific red snapper *Lutjanus peru* (Pisces: Lutjanidae) juvenile. *Latin American Journal of Aquatic Research* **41**, 1013–1018.

Clarke KR and Warwick RM (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd Edn. Plymouth: PRIMER-E.

Clarke KR, Somerfield P and Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* **366**, 56–69.

Cocheret de la Moriniére E, Pollux BJA, Nagelkerken I and Van der Velde G (2003) Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations. *Estuarine, Coastal and Shelf Science* **57**, 1079–1089.

Costello MJ (1990) Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* **36**, 261–263.

Doncel O and Paramo J (2010) Hábitos alimenticios del pargo rayado, *Lutjanus synagris* (Perciformes: Lutjanidae), en la zona norte del Caribe colombiano. *Latin American Journal of Aquatic Research* **38**, 413–426. (In Spanish)

Dorenbosch M, Vanriel MC, Gelkerken I and Van der Velde G (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuarine, Coastal and Shelf Science* **60**, 37–48.

França S, Vasconcelos RP, Cabral HN, Costa MJ, Fonseca VF, Reis-Santos P and Tanner SE (2012) Predicting fish community properties within estuaries: influence of habitat type and other environmental features. *Estuarine, Coastal and Shelf Science* **107**, 1–10.

Franks JS and VanderKooy KE (2000) Feeding habits of juvenile lane snapper *Lutjanus synagris* from Mississippi coastal waters, with comments on the diet of gray snapper *Lutjanus griseus*. *Gulf and Caribbean Research* **12**, 11–17.

Frédou T, Ferreira BP and Letourneur Y (2009) Assessing the stocks of the primary snappers caught in Northeastern Brazilian reef systems. 1 – Traditional modeling approaches. *Fishery Research* **99**, 90-96.

Freitas MO, Abilhoa V and Silva GHC (2011) Feeding ecology of *Lutjanus analis* (Teleostei: Lutjanidae) from Abrolhos Bank, Eastern Brazil. *Neotropical Ichthyology* **9**, 411–418.

Harrison TD and Whitfield AK (2012) Fish trophic structure in estuaries, with particular emphasis on estuarine typology and zoogeography. *Journal of Fish Biology* **81**, 2005–2029.

Hyslop EJ (1980) Stomach contents analysis – a review of methods and their application. *Journal of Fish Biology* **17**, 411–429.

Idema (1999) Instituto de Desenvolvimento Econômico e Meio Ambiente do Rio Grande do Norte. Macau. *Informativo Municipal* **5**, 1–14. (in Portuguese)

Igulu MM, Nagelkerken I, Fraaije R, Ligtenberg H, Mgaya YD and Van Hintum R (2011) The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). *Journal of Experimental Marine Biology and Ecology* **401**, 118–125.

Kadison E, Nemeth RS and Blondeau JE (2009) Assessment of an unprotected red hind (*Epinephelus guttatus*) spawning aggregation on the Saba Bank in the Netherland Antilles. *Bulletin of Marine Science* **85**, 101–118.

Kamukuru AT and Mgaya YD (2004) The food and feeding habits of blackspot snapper, *Lutjanus fulviflamma* (Pisces: Lutjanidae) in shallow waters of Mafia Island, Tanzania. *African Journal of Ecology* **42**, 49–58.

Karpouzi, VS and Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology* **62**, 1353–1365.

Krebs CJ (1989) *Ecological Methodology*. New York, NY: Harper and Row.

Labroupoulou M and Eleftheriou A (1997) The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *Journal of Fish Biology* **50**, 324–340.

Ley JA, McIvor CC and Montague CL (1999) Fishes in mangrove prop-root habitats of Northeastern Florida Bay: distinct assemblages across an estuarine gradient. *Estuarine, Coastal and Shelf Science* **48**, 701–723.

Marshak AR and Heck Jr KL (2017) Interactions between range-expanding tropical fishes and the northern Gulf of Mexico red snapper *Lutjanus campechanus*. *Journal of Fish Biology* **91**, 1139–1165.

Marshak AR and Heck Jr KL (2019). Competitive interactions among juvenile and adult life stages of northern Gulf of Mexico red snapper *Lutjanus campechanus* and a tropical range-expanding congener. *Marine Ecology Progress Series* **622**, 139–155.

Marshak AR, Heck Jr KL and Jud ZR (2018) Ecological interactions between Gulf of Mexico snappers (Teleostei: Lutjanidae) and invasive red lionfish (*Pterois volitans*). *PLoS ONE* **13**, e0206749.

Medeiros CRF, Costa AKS, Lima CSS, Oliveira JM, Júnior MMC, Silva MRA, Gouveia RSD, De Melo JIM, Dias TLP and Molozzi J (2016) Environmental drivers of the benthic macroinvertebrates community in a hypersaline estuary (Northeastern Brazil). *Acta Limnologica Brasiliensia* **18**, e4. ISSN 0102-6712

Mendoza-Carranza M and Vieira JP (2009) Ontogenetic niche feeding partitioning in juvenile of white sea catfish *Genidens barbus* in estuarine environments, southern Brazil. *Journal of the Marine Biological Association of the United Kingdom* **89**, 839–848.

Monteiro DP, Giarrizzo T and Isaac V (2009) Feeding ecology of juvenile dog snapper *Lutjanus jocu* (Bloch and Schneider, 1801) (Lutjanidae) in intertidal mangrove creeks in Curuçá estuary (Northern Brazil). *Brazilian Archives of Biology and Technology* **52**, 1421–1430.

Mueller KW, Dennis GD, Eggleston DB and Wicklund RI (1994) Size-specific social interactions and foraging styles in a shallow water population of mutton snapper, *Lutjanus analis* (Pisces: Lutjanidae), in the central Bahamas. *Environmental Biology of Fishes* **40**, 175–188.

Murie DJ (1995) Comparative feeding ecology of two sympatric rockfish congeners, *Sebastes caurinus* (copper rockfish) and *S. maliger* (quillback rockfish). *Marine Biology* **124**, 341–353.

Nagelkerken I, Van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T and Den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* **51**, 31–44.

Osório FM, Godinho WO and Lotufo TMC (2011) Ictiofauna associada às raízes de mangue do estuário do Rio Pacoti – CE, Brasil. *Biota Neotropica* **11**, 415–420.

Pimentel CR and Joyeux JC (2010) Diet and food partitioning between juveniles of mutton *Lutjanus analis*, dog *Lutjanus jocu* and lane *Lutjanus synagris* snappers (Perciformes: Lutjanidae) in a mangrove-fringed estuarine environment. *Journal of Fish Biology* **76**, 2299–2317.

Pinkas L, Oliphant MS and Iverson ILK (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. California Sacramento, CA: State of California, Department of Fish and Game.

Previero M, Minte-Vera CV, Freitas MO, Moura RL and Tos CD (2011) Age and growth of the dog snapper *Lutjanus jocu* (Bloch & Schneider, 1801) in Abrolhos Bank, Northeastern Brazil. *Neotropical Ichthyology* **9**, 393-401.

Queiroz RNM and Dias TLP (2014) Molluscs associated with macroalgae of the genus *Graciliaria* (Rhodophyta): importance of algal fronds as microhabitat in a hypersaline mangrove in Northeast Brazil. *Brazilian Journal of Biology* (Impresso) **74**, 52–63.

Resende SM, Ferreira BP and Frédou T (2003) A pesca de lutjanídeos no Nordeste do Brasil: histórico das pescarias, características das espécies e relevância para o manejo. *Boletim Técnico Científico – CEPENE* **11**, 56–63. (In Portuguese)

Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* **1986**, 352–388.

Sales NS, Dias TLP, Baeta A and Pessanha ALM (2016) Dependence of juvenile reef fishes on semi-arid hypersaline estuary microhabitats as nurseries. *Journal of Fish Biology* **89**, 661–679.

Sales NS, Dias TLP, Baeta A, Lima LG and Pessanha ALM (2018) Do the shallow-water habitats of a hypersaline tropical estuary act as nursery grounds for fishes? *Marine Ecology* **39**, e12473. doi: 10.1111/maec.12473.

Sarre GA, Platell ME and Potter IC (2000) Do the dietary compositions of *Acanthopagrus butcher*i in four estuaries and a coastal lake vary with body size and season and within and amongst these water bodies? *Journal of Fish Biology* **56**, 103–122.

Schafer LN, Platell ME, Potter IC and Valesini FJ (2002) Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology* **278**, 67–92.

Sheaves M (1995) Large lutjanid and serranid fishes in tropical estuaries: are they adults or juveniles? *Marine Ecology Progress Series* **129**, 31–40.

Szedlmayer TS and Lee JD (2004) Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fishery Bulletin* **102**, 366–375.

Tarnecki JH and Patterson WF (2015) Changes in red snapper diet and trophic ecology following the deepwater horizon oil spill. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **7**, 135–147.

Teixeira SF, Duarte YF and Ferreira BP (2010) Reproduction of the fish *Lutjanus analis* (mutton snapper) (Perciformes: Lutjanidae) from Northeastern Brazil. *Revista de Biologia Tropical* **58**, 791–800.

Wells RJD, Cowan Jr JH and Fry B (2008) Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Marine Ecology Progress Series* **361**, 213–225.

Yeager LA, Layman CA and Hammerschlag-Peyer CM (2014) Diet variation of a generalist fish predator, grey snapper *Lutjanus griseus*, across an estuarine gradient: trade-offs of quantity for quality? *Journal of Fish Biology* **85**, 264–277.