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Trophic ecology and resource partitioning of Haemulidae species along the Northeastern Brazilian continental shelf

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In the Southeastern Tropical Atlantic, Haemulidae family play an important role both environmentally, acting as a link between lower and higher trophic levels, and socioeconomically, being widely caught by artisanal fleets. This study aimed to describe the trophic ecology of three grunt species (*Haemulon aurolineatum*, *H. plumierii* and *H. squamipinna*) considering spatial, temporal and ontogenetic aspects, integrating stomach content and stable isotopes analysis. Sampling occurred in 26 stations along the Northeast of Brazil (04°– 09°S), in August 2015 and April 2017, using bottom trawling net. There was greater feeding intensity at night, at latitudes below 08°S and in the inner continental shelf. Higher values of $\delta^{15}N$ were reported for *H. aurolineatum* and *H. plumierii* collected near coastline. The isotopic niche breadth indicated that *H. aurolineatum* has a narrower diet than *H. plumierii*. For the three species, the trophic level ranged between three and four. Considering stomach content and isotopic niche, diet was similar comparing species. This trophic ecology pattern reveals a likewise use of the habitat, which may be essential for identifying priority areas for conservation on an ecosystem basis, especially in rich reef zones that are subject to several increasing pressures, such as those in Northeast Brazil.

Keywords: Feeding, Grunts, Stable isotopes, Stomach contents, Trophic ecology.

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No Atlântico Tropical Sudeste, peixes da família Haemulidae desempenham um papel importante tanto ambientalmente, atuando como um elo entre os níveis tróficos mais baixos e mais altos, quanto socioeconomicamente, sendo amplamente capturados pelas frotas artesanais. Este estudo teve como objetivo descrever a ecologia trófica de três espécies de roncadores (*Haemulon aurolineatum*, *H. plumierii* e *H. squamipinna*) considerando aspectos espaciais, temporais e ontogenéticos integrando conteúdo estomacal e análise de isótopos estáveis. A amostragem ocorreu em 26 estações ao longo do Nordeste do Brasil (04°– 09°S), em agosto de 2015 e abril de 2017, utilizando rede de arrasto de fundo. Houve maior intensidade de alimentação à noite, em latitudes abaixo de 08°S e na plataforma continental interna. Valores mais altos de $\delta^{15}N$ foram reportados para *H. aurolineatum* e *H. plumierii* coletados perto da linha costeira. A amplitude do nicho isotópico indicou que o *H. aurolineatum* tem uma dieta mais estreita do que o *H. plumierii*. Para as três espécies, o nível trófico variou entre três e quatro. Considerando o conteúdo estomacal e o nicho isotópico, a dieta foi semelhante comparando as espécies. Este padrão de ecologia trófica mostra um uso semelhante do habitat, que pode ser essencial para identificar áreas prioritárias para conservação em uma base ecossistêmica, especialmente em zonas ricas de recifes que estão sob várias pressões crescentes, como as do Nordeste do Brasil.

Palavras-chave: Alimentação, Conteúdo estomacal, Ecologia trófica, Isótopos estáveis, Roncadores.

INTRODUCTION

Fishes of the Haemulidae family are extremely important for the food web balance, mainly for reef communities, and comprise the main prey of many larger fishes with great commercial value such as Lutjanidae and Carangidae (Palazón-Fernández, 2007; Frédou *et al*., 2009; Pereira *et al*., 2011; Rindone *et al*., 2015). The genus *Haemulon* is considered very abundant and rich, has great representativeness within tropical fish, encompassing 19 species from the eastern Pacific to the western Atlantic (Rocha *et al*., 2008).

In the Atlantic Ocean, *Haemulon* are restricted to the tropical regions of Brazil, from northeastern to southeastern coast (Rocha *et al*., 2008), inhabiting mostly coral reefs and rocky bottoms (Ilarri *et al*., 2008). With demersal behavior, they feed mainly of preys associated to the seabed such as the macrobenthic fauna, but is also reported on the water column, carrying on small daily migrations from the reef to sandbanks near seagrass meadows (Parrish, 1989; Rocha *et al*., 2008; Pereira, Ferreira, 2013; Pereira *et al*., 2015). There are nine species of *Haemulon* reported for the Brazilian coast (Rocha, Rosa, 1999; Tavera *et al*., 2012; Cerqueira *et al*., 2021) highlighting *Haemulon aurolineatum* Cuvier, 1830, *H. plumierii* (Lacepède, 1801), and *H. squamipinna* Rocha & Rosa, 1999, giving their high abundance and wide spatial distribution (Rocha *et al*., 2008; Pereira *et al*., 2015).

In the Northeastern Brazil, Haemulidae (grunts) are part of the bycatch of the lobster (*Panulirus argus* and *P. laevicauda*) and goatfish (*Pseudupeneus maculatus*) fisheries but, giving the decrease in abundance of these target species, nowadays, they are targeted in the region (Nóbrega, Lessa, 2007; Marques, Ferreira, 2010), being also relevant for the aquarium business (Rocha *et al*., 1998; Lessa, Nóbrega, 2000; Shinozaki-Mendes *et al*., 2013). Moreover, due to their wide distribution and great abundance, *H. aurolineatum*, *H. plumierii*, and *H. squamipinna* have a critical role to trophic dynamic of marine ecosystems in the Brazilian coastline (Rocha *et al*., 2008).

Studies on the trophic dynamic are essential for wildlife conservation (Gheler-Costa *et al*., 2018), encompassing many facets such as niche overlap and intraspecific interactions, whether in temporal or spatial realms (Esteves, Aranha, 1999), providing a better understanding of ecosystem functioning (Vieira, 2019). The traditional method to evaluate the fish diet composition is by stomach content analysis which provides an initial "snapshot" of the ecosystem trophic functions, observing each prey importance and identifying their relationship with the predator (Hahn *et al*., 2002). Stable isotopes composition provides diet information based on what is incorporated in the predator tissues to longer period (Fry, 2006). The stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been widely used on studies of feeding habit of marine fishes (Gonzalez *et al*., 2019; Richards *et al*., 2019; Soares *et al*., 2020), providing information on energy sources (Peterson, Fry, 1987; Vander-Zanden *et al*., 2011) and trophic position (Bastos *et al*., 2017). Therefore, stable isotope analysis can provide complementary information to stomach content analyses, especially considering that nutrient assimilation varies according to prey ingested type, regardless of amount found in stomachs (Melville, Connolly, 2003).

The use of integrated techniques in trophic ecology for marine fish species is still scarce in Brazil (Freitas *et al*., 2011, 2017; Pimentel *et al*., 2018; Gonzalez *et al*., 2019). Although integrated approaches (stomach content and stable isotopes) for *Haemulon* species have been employed in Bahamas (Chittaro *et al*., 2004; Zhu *et al*., 2019), Panama Isthmus (Stuthmann, Castellanos-Galindo, 2020), Caribean Sea (Morinière *et al*., 2003; Nagelkerken *et al*., 2008) and Gulf of Mexico (Peterson *et al*., 2020), no such attempt has yet been made in Brazil, mainly considering a wide spatial scale and incorporating the influence of environmental factors (Pereira *et al*., 2015).

Therefore, even with a high social, economic, and environmental importance in Southwestern Tropical Atlantic (Pereira, Ferreira, 2013; Pereira *et al*., 2015; Eduardo *et al*., 2018; Cardoso de Melo *et al*., 2020), *Haemulon* species still does not have an extensive knowledge of many biological aspects (*e.g*., diet, growth, and reproduction patterns), their fishery is open access, and the management is absent. In addition, the integrated approaches of their biology and ecology are still unknown, or restricted in terms of spatial coverage. Thus, the present study aimed to describe the trophic ecology of *H. aurolineatum*, *H. plumierii*, and *H. squamipinna*, applying an integrative approach which combines stomach contents and carbon and nitrogen stable isotopes. We also tested the effect of the spatial (habitats, shelf position, latitudes), temporal (capture time), and biological (ontogenetic differences) factors into the feeding habits of Haemulidae in the South Atlantic. We expect that the information on the habitat use and trophic relationship between species associated to other studies, such as distribution patterns and fisheries (Eduardo *et al*., 2018; Cardoso de Melo *et al*., 2020), may be useful for future management and conservation actions, as for example, to identify priority areas for conservation (*e.g*., Marine Protection Areas, MPAs). This information may also be useful as input for ecosystem modelling (*e.g*., Ecopath).

MATERIAL AND METHODS

Study area and sampling procedures. Biological samples were collected during the project Acoustic Along Brazilian Coast (ABRACOS), composed of two scientific expeditions (Bertrand, 2017, 2015) carried out in August 2015 and April 2017, both on board the research ship R/V ANTEA. The study area (Fig. 1) comprised the Northeast Brazilian continental shelf, between the states of Rio Grande do Norte (RN) and Alagoas (AL) (04°– 09°S). Fishes were sampled at 26 stations, between 15 and 65 m deep. This region is considered of high diversity (Eduardo *et al*., 2018), encompassing several Marine Protected Area (*e.g*., "Costa dos Corais", "Guadalupe", "Santa Cruz", "APA Barra de Mamanguape") (Ferreira, Maida, 2007; Pereira *et al*., 2021). The region's continental shelf average width is approximately 40 km, almost all covered by carbonate sediments with an average depth between 40 and 80 m (Vital *et al*., 2010). Fishing was carried out for five minutes in average using a bottom trawling net (mesh: 40 mm; cod mesh: 25 mm; mouth dimensions: 28 x 10 m), during night and day.

Diet was described considering the following factors: habitat type, latitude, distance from the coast, period of the day and ontogeny. Habitats were classified according to Eduardo *et al*. (2018): I – Sand; II – Algae; III – SWCR (substrate with rocks, coralline formations and sponges). Latitudes were divided into five strata according to Eduardo *et al*. (2018): A (all points above 5°S), B (05° to 06°S), C (06° to 07°S), D (07° to 08°S), and E (all points below 08°S). Given the average width of the continental shelf of 40 km, the distance from the coast was classified as inner (< 20 km) and outer (> 20 km) continental shelf. For the period of the day, samplings carried out from 9 AM to 6 PM were considered diurnal and from 6 PM to midnight as nocturnal. Adults and juveniles were classified according to the mean size at first maturity of each species (Cardoso de Melo *et al*., 2020).

On board, for the 26 stations (no replicates for each station), 30 individuals were randomly sub-sampled, labelled, and frozen. For all species, it was not possible to use the entirely collected individuals for simultaneous diet and stable isotope studies, given the poor preservation condition of some stomachs. In the laboratory, individuals were measured for standard length (SL, cm), weighted (g), and dissected for the stomach removal procedure. Removed stomachs were fixed in a formaldehyde solution (4%) and then transferred to 70% alcohol for further contents analysis. Each stomach content item was identified to the lowest possible taxonomic level, counted, and weighed.

Diet and feeding habits. Vacuity index (*Vi*) was estimated as the proportion of empty stomachs over the total sample size. Fulness index (*Fi*) was defined as a proxy of the feeding intensity indicator $[Fi = \frac{Sw}{Tw} . 100]$ (Zavala-Camin, 1996). Differences on *Fi* were tested through the non-parametric test of Kruskal-Wallis, as the data did not follow the assumptions for a parametric test. Diet was described by three quantitative indices: frequency of occurrence (%FO), numerical frequency (%N), and relative weight (%W) (Hyslop, 1980; Bowen, 1996). Subsequently, two importance indices were calculated: Index of Relative Importance $[IRI = (\%N + \%W) . \%Fo]$ (Pinkas *et al*., 1971) and Alimentary Index $[IAI = \frac{\%Fo . \%W}{\Sigma \%Fo . \%W} . 100]$ (Kawakami, Vazzoler, 1980) adapted by Oliveira *et al*. (2004). The IRI uses frequency of occurrence, weight, and quantity of each item, while IAi is based on frequency of occurrence and volume of each item, which was replaced by the weight (Oliveira *et al*., 2004).

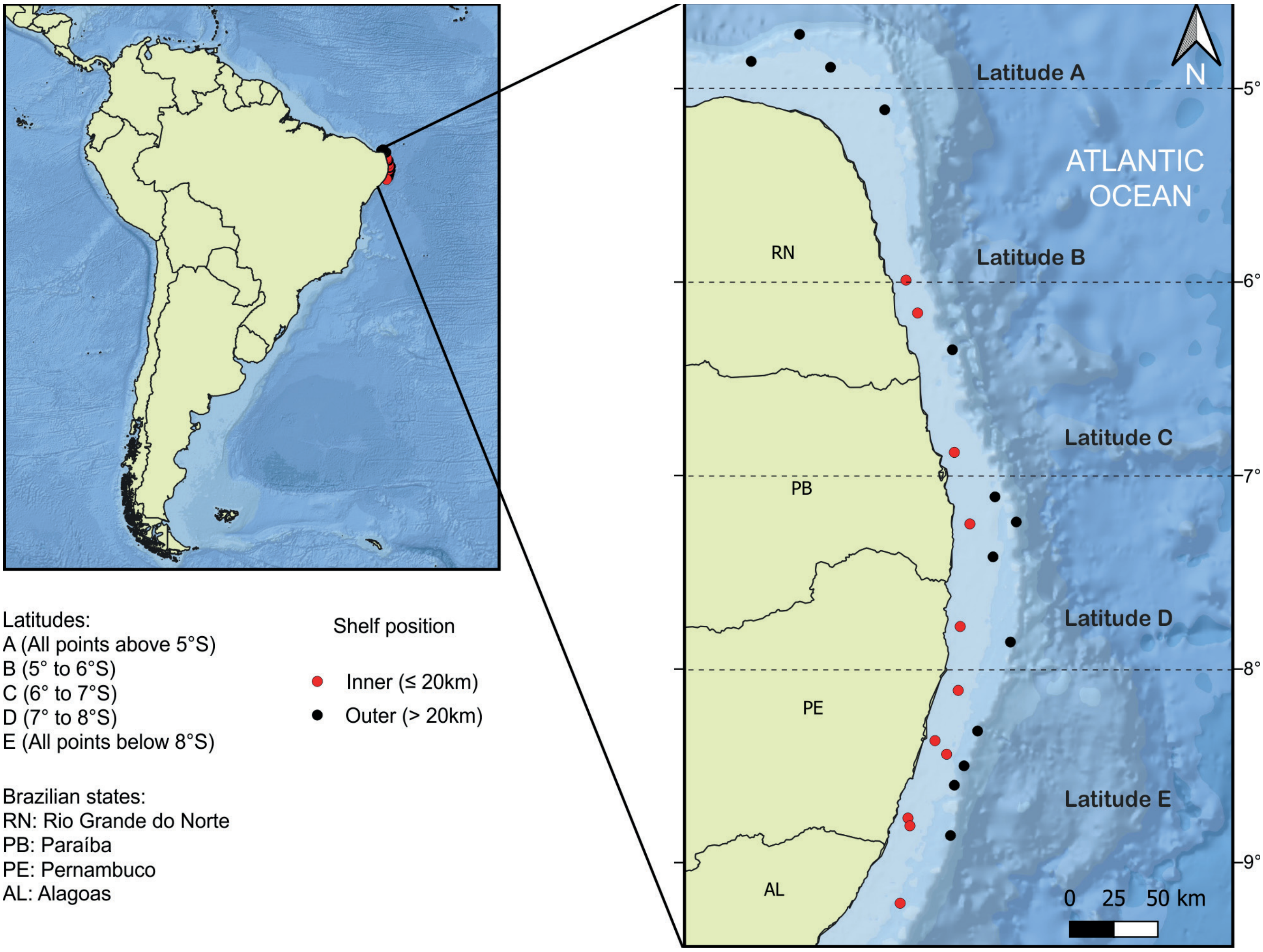

FIGURE 1 | Study area and sample points along the continental shelf of the northeast coast of Brazil. Red dots indicate samples for inner position (≤ 20 km) and black dots for outer (> 20 km).

Feeding strategy was assessed through the modified Costello diagram (Amundsen *et al*., 1996), which is a representation of the degree of diet variability of a predator by plotting prey-specific abundance (*Pi*) vs the frequency of occurrence (*%Fo*) of each prey taxon. Niche breadth (*Bi*) was estimated using standardized Levins' index (Hurlbert, 1978), which ranges from 0, when the species consumed only one type of food, to 1, when the species equally consumed all types of food items analyzed. Bi ≤ 0.3 are considered narrow; 0.6 ≥ Bi > 0.3 are moderate and Bi > 0.6 are considered a wide trophic niche breadth. For both, diet overlap and trophic niche breadth, percentual values were used. For diet overlap (*Oi*), the Pianka's index (Pianka, 1973) was used. This index ranges from 0 to 1, where 0 means the niches do not overlap and 1 means the total niche overlap.

Stable Isotopes and trophic position. For stable isotope analysis (SIA), at least ten individuals of each species and the zooplankton were obtained for each sampling point. From these, samples of the dorsal muscular tissue of fish were collected, cleaned with distilled water to remove scales and remaining bones, and dried in an oven at 60° C for 48h. Subsequently, the tissue was ground to a powder with a tamper and pestle. Isotope analysis of zooplankton samples were made in duplicate: part of them was selected to remove carbonate ($CaCO_3$), by adding hydrochloric acid (HCl) and were used for the analysis of carbon isotopes (Fry, 1988); the rest of the samples (non-acidified) were used for nitrogen. Both subsamples were placed in an oven at 60°C for 24 hours and ground to a powder. Stable isotope analysis for carbon and nitrogen were run on a mass spectrometer (Thermo Delta V +) together with an element analyzer (Thermo Flash 2000, ConFio IV interface) on the Ocean Spectrometry Platform (IUEM, France). The isotopic ratios are expressed using the delta (δ) notation in parts per thousand (Peterson, Fry, 1987) and derived from the formula $\delta X = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] x10^3$ where δX corresponds to $\delta^{13}C$ or $\delta^{15}N$ and R to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and a known standard, for carbon or nitrogen, respectively. The standards used for $\delta^{13}C$ and $\delta^{15}N$ were the PeeDee Belemnite (PDB) limestone and atmospheric nitrogen, respectively. The analytical precision of the analysis was monitored through the analysis of an internal standard (Thermo – Acétanilide) every six samples, resulting in an accuracy of 0.10‰ and 0.07 ‰ for carbon and nitrogen isotopes, respectively.

Resource assimilated by consumers was first assessed by visualizing biplots ($\delta^{13}C$ x $\delta^{15}N$) of consumer and zooplankton values. The mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated considering spatial (habitats, shelf position, latitudes), temporal (capture time) and biological (ontogenetic differences) factors. Significant differences between these factors were tested, within and between species, using the Kruskal-Wallis tests. The trophic position of each species was estimated based on Post (2002) methodology and considering a trophic discrimination factor (TDF) of 2.54‰ (Vanderklift, Ponsard, 2003).

Finally, the isotopic niche of the three species was assessed using the standard ellipses area (SEA). This method allows to quantify the space occupied by a species in a bi-dimensional plane ($\delta^{13}C$ vs. $\delta^{15}N$) and is less sensitive to differences in sample size than other isotopic metrics (Jackson *et al*., 2011). However, both the position and width of a species isotopic niche is equally dependent to the isotopic composition of their prey and the organic matter sources sustaining the food web (Ben-David, Flaherty, 2012). Therefore, the isotopic niches of Haemulidae species were used to quantify the extent to which they may use available food sources. The overlap in their SEA's area was considered to reflect the degree that they may rely on similar food resources. It was estimated through pairwise comparisons of the overlapping area between species and by using a Bayesian approach to assess the mean and 95% credible intervals (CI95) (Jackson *et al*., 2011). Zooplankton from the second size class was assumed the best primary consumer to be the baseline source due its trust of distribution and its homogeneity, composed mainly by copepods (Figueiredo *et al*., 2020). All analyses were performed by using the R program with the packages tRrophicPosition (Quezada-Romegialli *et al*., 2018) and SIBER ("Stable Isotope Bayesian Ellipses in R" (Jackson *et al*., 2011). In all analyses a significant level of 95% was considered.

RESULTS

A total of 229 individuals were analyzed for stomach content analysis (SCA), in which 143 of them were *Haemulon aurolineatum* (9.2–18.0 cm SL), 68 of *H. plumierii* (10.7–22.5 cm SL), and 20 *H. squamipinna* (12.6–14.5 cm SL). For stable isotope analysis (SIA), 257 individuals were analyzed: 112 *H. aurolineatum*, 85 *H. plumierii*, and 60 *H. squamipinna*. The description of the diet by the SCA was performed only for *H. aurolineatum* and for *H. plumierii*. *Haemulon squamipinna* did not present enough stomachs with food content to perform a reliable description of its diet. However, SIA were performed for the three species.

Diet composition and feeding habits. In general, a similar proportion of full and empty stomachs was found for *H. plumierii* (*Vi*=54.4%) and for *H. aurolineatum* (*Vi*=59.4%). However, the majority of the empty stomachs were collected at daytime for both species (*H. plumierii*=67.6%; *H. aurolineatum*=58.8%).

Feeding intensity (*Fi*) of *H. aurolineatum* is significantly higher at night (Kruskal-Wallis; chi-squared=7.1632; p=0.0074). Feeding intensity was also significantly different (Kruskal-Wallis; chi-squared=11.99; p=0.0074) among latitude strata, specifically between areas A and B (p=0.025), and A and E (p=0.017). *Fi* also significantly varied among shelf positions (Kruskal-Wallis; chi-squared=10.31; p=0.0013), with individuals collected close to the coast having higher *Fi* values than those from the shelf break areas. Juveniles also had significantly higher *Fi* than adults (Kruskal-Wallis; chi-squared=4.3077; p=0.0379). There was no significant difference of *Fi* between habitats. For *H. plumierii* the analysis by ontogeny could not be carried out, given the low number of juveniles, and no significant differences of *Fi* was recorded for any other factor considered (Fig. 2).

The diet of the Haemulidae were mainly composed by crustaceans and polychaetas (Tab. 1). For *H. aurolineatum*, crustaceans, mainly decapods, carideans, and brachyurans, were generally the main source of food. The most frequent item was non-identified crustaceans (%FO=31), followed by polychaetas (%FO=20) and decapods (%FO=15). The same pattern was observed for numerical frequency (%N) and for relative weight (%W). Echinoderms were also one of the most consumed items, but with minor importance when compared to the aforementioned (Tab. 2).

Haumulon plumierii mainly based its diet on echinoderms, polychaetas, and crustaceans and teleost fishes (Tab. 1). The most frequent items were echinoderms (%FO=26), polychaetas and crustaceans, especially brachyurans. Teleost fishes were also one of the most frequent groups. In number, the most abundant item was non-identified crustaceans (%N=17), brachyurans (%N=13) and echinoids (%N=11). Polychaetas were the most numerically frequent food item (%N=17), followed by echinoderms and teleosts (both %N=16). Crustaceans also had high biomass, with non-identified crustaceans and brachyurans (Tab. 2).

The niche breadth of *H. plumierii* was very wide (Levin's index: 63%). On the other hand, *H. aurolineatum* tends to feed on a smaller diversity of prey (50%). There was moderate dietary overlap between *H. plumierii* and *H. aurolineatum* (*Oi* > 84%).

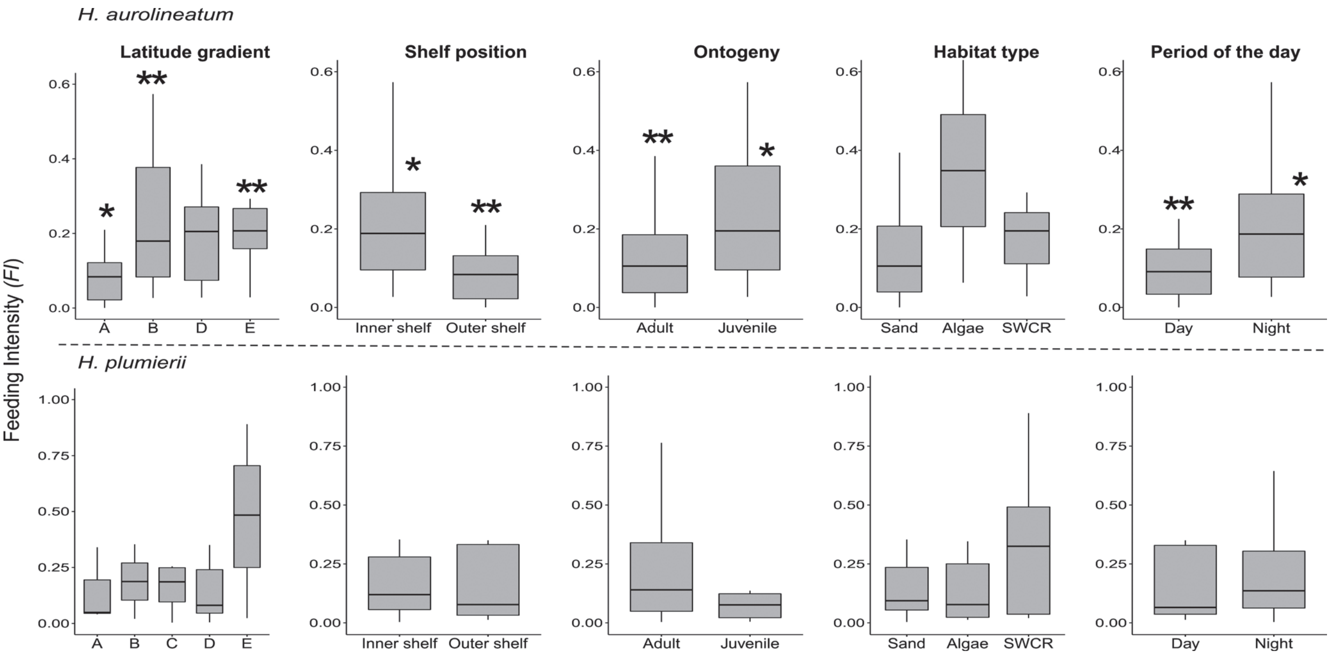

FIGURE 2 | Feeding intensity indicator (Fi) of *Haemulon aurolineatum* and *H. plumierii* in different habitats, latitude gradient, shelf position, ontogeny and period of the day. The black horizontal line and box represent the median value and the interquartile range, while the vertical lines represent the upper and lower limits. Outliers were not included in the plot. Different symbols (* and **) represent significant difference.

According to the Costello diagram (Fig. 3), no specific food item was preferred by any Haemulidae species. Instead, for all species, items were generally placed in the left side of the plot, characterizing the fishes as mostly generalist predators. For *H. aurolineatum* specifically, even though most items had low frequency of occurrence, these items, when present, were very important in weight (Fig. 3).

Stable isotopes. The isotopic ratios for *H. plumierii* were very wide for $\delta^{15}N$ (7.40 to 13.44 ‰) but not for $\delta^{13}C$ (-17.01 to -13.92 ‰). For *H. aurolineatum* ratios varied between -17.01 to -13.22 ‰ and 7.53 to 13.23 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. *Haemulon squamipinna* had the narrowest ranges: -16.88 to -14.91 ‰ for $\delta^{13}C$ and 7.76 to 11.24 ‰ for $\delta^{15}N$. For both *H. plumierii* and *H. aurolineatum*, there were no significant differences for these ratios among habitats (Tab. 3; Fig. 4). *Haemulon squamipinna* had significantly higher mean $\delta^{15}N$ and $\delta^{13}C$ ratio in sand than in SWCR. No individuals of *H. squamipinna* were reported on Algae. All species had higher mean $\delta^{15}N$ ratio in the inner platform (Tab. 3; Fig. 4).

Significantly higher values of $\delta^{15}N$ ratio were measured in *H. plumierii* in latitude A than in latitudes C, D and E (Tab. 3; Fig. 5). The values of $\delta^{15}N$ ratio in *H. aurolineatum* varied significantly between strata A and B, A and D, A and E, B and D, and B and E. For both species, the highest values were measured in the southernmost zones (Tab. 3; Fig. 5). Unlike the other two species, *H. squamipinna*, was only sampled in latitudes D and E and no significant difference between of $\delta^{15}N$. No significant differences of $\delta^{15}N$ were recorded between adults and juveniles for any species (Tab. 3; Fig. 5).

The trophic level was similar for all species, between the 3rd and 4th trophic position, classifying all species as carnivore predators. The trophic level was not significantly affected by any abiotic factor (Tab. 4).

TABLE 1 | Contribution of each item of prey to the *Haemulon aurolineatum* and *H. plumierii* diets in the Southtern Atlantic considering the frequency of occurrence (%FO), number (%N), weight (%W) and respective relative importance (IRI) and food intensity (%IAI) (UI: unidentified).

Prey items		***Haemulon aurolineatum***					***Haemulon plumierii***				
		%FO	**%N**	**%W**	**%IRI**	**%IAI**	**%FO**	**%N**	**%W**	**%IRI**	**%IAI**
Algae											
		-	-	-	-	-	3.22	1.47	0.00	0.15	0.00
Cnidaria											
	Hydrozoa	-	-	-	-	-	3.22	1.47	0.00	0.15	0.00
Echinodermata											
	Echinoidea	10.34	9.78	5.89	4.89	3.65	25.80	11.76	16.39	22.67	24.73
	Holothuroidea	1.72	1.09	0.97	0.11	0.10	-	-	-	-	-
Polychaeta											
	Amphinomidae	0.94	0.65	10.90	13.60	13.49	1.08	0.43	11.44	12.95	15.10
	Dorvilleidae	0.94	0.65	0.05	0.06	0.06	1.08	0.43	0.05	0.06	0.07
	Eunicidae	4.70	3.26	0.87	1.09	1.08	5.38	2.14	0.92	1.04	1.21
	Nereididae	2.82	1.96	1.66	2.07	2.05	3.23	1.29	1.74	1.97	2.30
	Onuphidae	1.88	1.30	0.29	0.37	0.36	1.08	0.43	0.17	0.19	0.22
	UI Polychaeta	9.40	8.48	2.50	3.13	3.10	10.75	5.58	2.63	2.98	3.47
Crustacea											
	Anomura	1.72	1.09	0.96	0.11	0.10	6.45	4.41	4.12	1.71	1.55
	Amphipoda	5.17	3.26	2.95	0.97	0.91	6.45	8.82	1.13	2.00	0.42
	Brachyura	8.62	5.43	8.06	3.51	4.16	22.58	13.23	14.70	19.68	19.41
	Caridea	13.79	13.04	9.94	9.55	8.20	6.45	2.94	1.65	0.92	0.62
	Decapoda	15.52	11.96	12.71	11.54	11.80	9.68	5.88	3.01	2.68	1.70
	Isopoda	1.72	1.09	1.72	0.15	0.18	-	-	-	-	-
	Malacostraca	3.45	2.17	2.48	0.48	0.51	-	-	-	-	-
	Stomatopoda	6.90	4.35	5.42	2.03	2.23	3.22	1.47	1.82	0.33	0.34
	Thanaidacea	-	-	-	-	-	6.45	2.94	2.22	1.04	0.84
	UI Crustacea	31.03	21.74	24.35	43.11	45.19	16.12	17.65	9.10	13.46	8.58
Mollusca											
	Cephalopoda	-	-	-	-	-	3.22	1.47	3.22	0.47	0.60
	Gastropoda	1.72	1.09	1.72	0.15	0.18	7.89	2.94	5.96	1.79	2.25
	UI Mollusca	8.62	6.52	4.81	2.94	2.48	6.45	5.88	3.55	1.90	1.34
Chordata											
	Teleostei	1.72	1.09	1.72	0.15	0.18	16.12	7.35	16.12	11.81	15.20

TABLE 2 | Ranking of importance of each category of prey item identified in the stomach content of *Haemulon aurolineatum* and *H. plumierii* according to each importance index (UI, unidentified).

Rank	*Haemulon aurolineatum*		*Haemulon plumierii*	
	IRI	IAI	IRI	IAI
1	UI Crustacea	UI Crustacea	Echinoidea	Echinoidea
2	Polychaeta	Polychaeta	Brachyura	Polychaeta
3	Decapoda	Decapoda	Polychaeta	Brachyura
4	Caridea	Caridea	UI Crustacea	Teleostei
5	Echinoidea	Brachyura	Teleostei	UI Crustacea

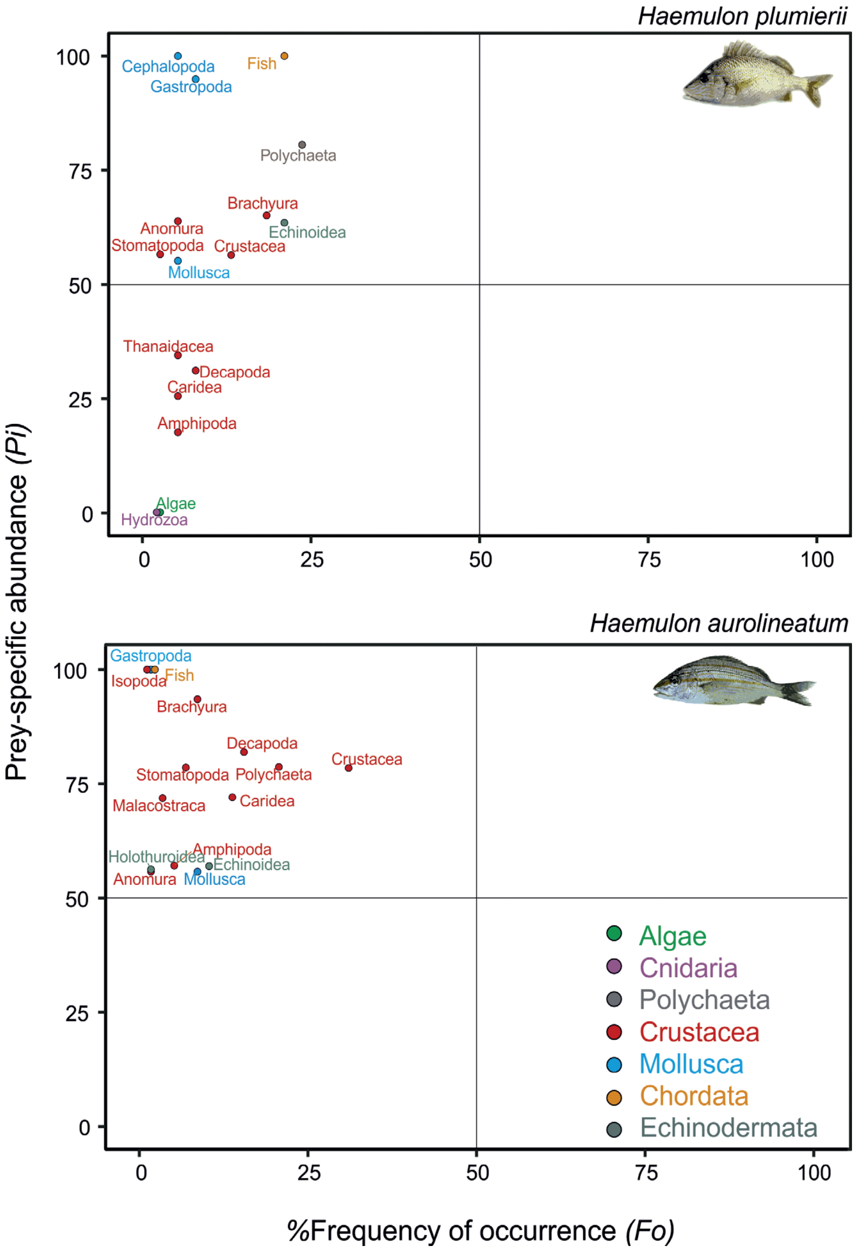

FIGURE 3 | Modified Costello diagram (Pi, prey specific abundance; Fo, frequency of occurence), a scatterplot containing all prey items, showing the feeding strategy of *Haemulon aurolineatum* and *H. plumierii* captured along the northeast coast of Brazil.

TABLE 3 | Statistic differences in $\delta^{15}N$ and $\delta^{13}C$ values by habitat type, shelf position, latitude strata and ontogeny for *Haemulon aurolineatum*, *H. plumierii*, and *H. squamipinna* caught in Northeast Brazilian continental shelf. All caught specimens of *H. squamipinna* were considered adults, not allowing ontogenetic analysis. Significant values are identified by *.

	H. aurolineatum	*H. plumierii*	*H. squamipinna*
Habitat type	$\delta^{15}N$ chi-squared=0.4423; p=0.8016 $\delta^{13}C$ chi-squared=5.8939; p=0.0525	$\delta^{15}N$ chi-squared=6.3978; p=0.0938 $\delta^{13}C$ chi-squared=5.8939; p=0.0773	$\delta^{15}N$ chi-squared=13.079; p=0.0057* $\delta^{13}C$ chi-squared=22.923; p=0.0006*
Shelf position	$\delta^{15}N$ chi-squared=29.035; p=0.0001* $\delta^{13}C$ chi-squared=18.775; p=0.0001*	$\delta^{15}N$ chi-squared=4.1876; p=0.0407* $\delta^{13}C$ chi-squared=7.9109; p=0.0049*	$\delta^{15}N$ chi-squared=21.229; p=0.0001* $\delta^{13}C$ chi-squared=0.0419; p=0.8376
Latitude strata	$\delta^{15}N$ chi-squared=36.754; p=0.0001* $\delta^{13}C$ chi-squared=20.840; p=0.0003*	$\delta^{15}N$ chi-squared=14.904; p=0.0049* $\delta^{13}C$ chi-squared=9.4218; p=0.0514	$\delta^{15}N$ chi-squared=1.8005; p=0.1797 $\delta^{13}C$ chi-squared=0.0244; p=0.8757
Ontogeny	$\delta^{15}N$ chi-squared=1.5287; p=0.2100 $\delta^{13}C$ chi-squared=1.9023; p=0.1600	$\delta^{15}N$ chi-squared=0.0156; p=0.9005 $\delta^{13}C$ chi-squared=0.9541; p=0.3287	-

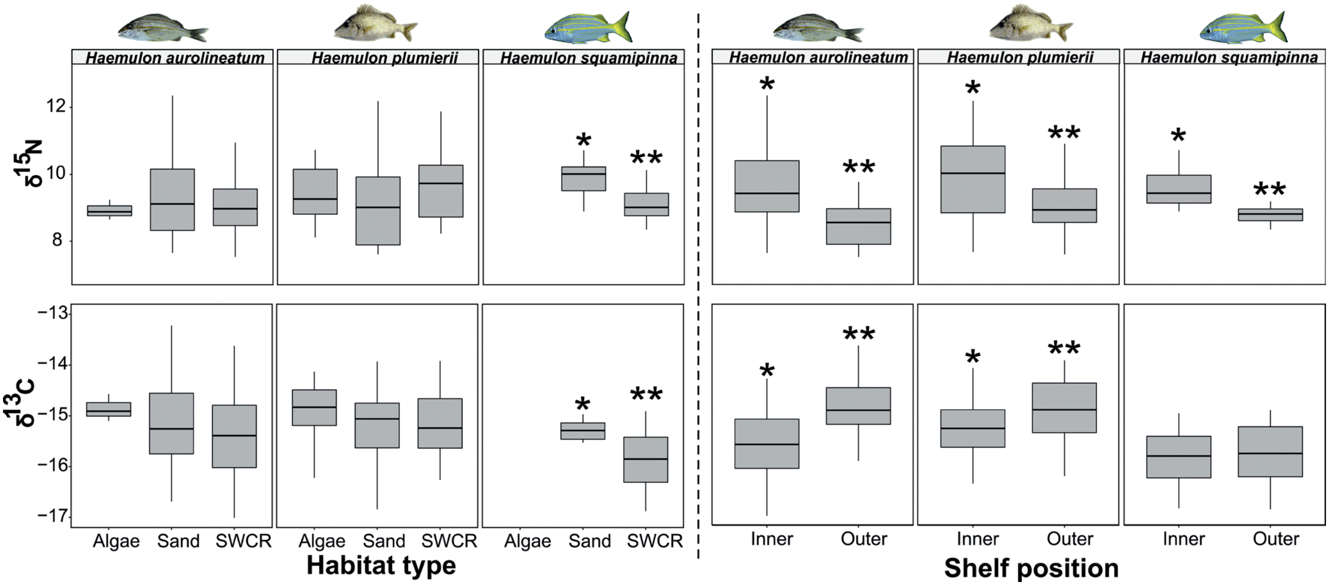

FIGURE 4 | Isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of *Haemulon plumierii*, *H. aurolineatum*, and *H. squamipinna* in different habitats and shelf position captured along the northeast coast of Brazil. The black horizontal line and box represent the median value and the interquartile range, while the vertical lines represent the upper and lower limits. Outliers were not included in the plot. Different symbols (* and **) represent significant difference.

All species had generally significant differences in mean $\delta^{13}C$ ratio (Kruskal-Wallis; chi-squared=35.822; p=0.0001, Kruskal-Wallis) but not in $\delta^{15}N$ (Kruskal-Wallis; chi-squared=3.6714; p=0.160). These differences were partly reflected in the isotopic niche of Haemulidae since *H. aurolineatum* (2.57 ‰; CI95 2.1–3.0 ‰) and *H. plumierii* (2.33 ‰; CI95 1.8–2.8 ‰) had similar SEAs (Fig. 6A). These later comprehended more than two folds of the area occupied by *H. squamipina* (1.02 ‰; CI95 0.7–1.3 ‰). Although only 9.6% of the total area occupied by them (3.51 ‰) was shared by the three species, the percentage of overlap between their isotopic niches varied according to each pairing of species (Fig. 6B). Particularly, *H. aurolineatum* occupied considerable part of the SEAs of both *H. plumierii* (71.2%; CI95 45.9–94.8%) and *H. squamipina* (68.9%; CI95 37.2–99.8%). The opposite was only true for *H. plumierii*, which shared 64.3% (CI95 41.6–87.6%) of *H. aurolineatum* isotopic niche. *Haumulon squamipina* and *H. plumierii* shared smaller percentages of their areas with each other (Fig. 6B). In turn, overlaps in their total SEAs were higher between *H. aurolineatum* – *H. plumierii* (51.6%; CI95 28.4–75.3%) than *H. aurolineatum* – *H. squamipina* (24.7%; CI95 9.7–40.0%), and *H. plumierii* – *H. squamipina* (12.1%; CI95 0–24.8%).

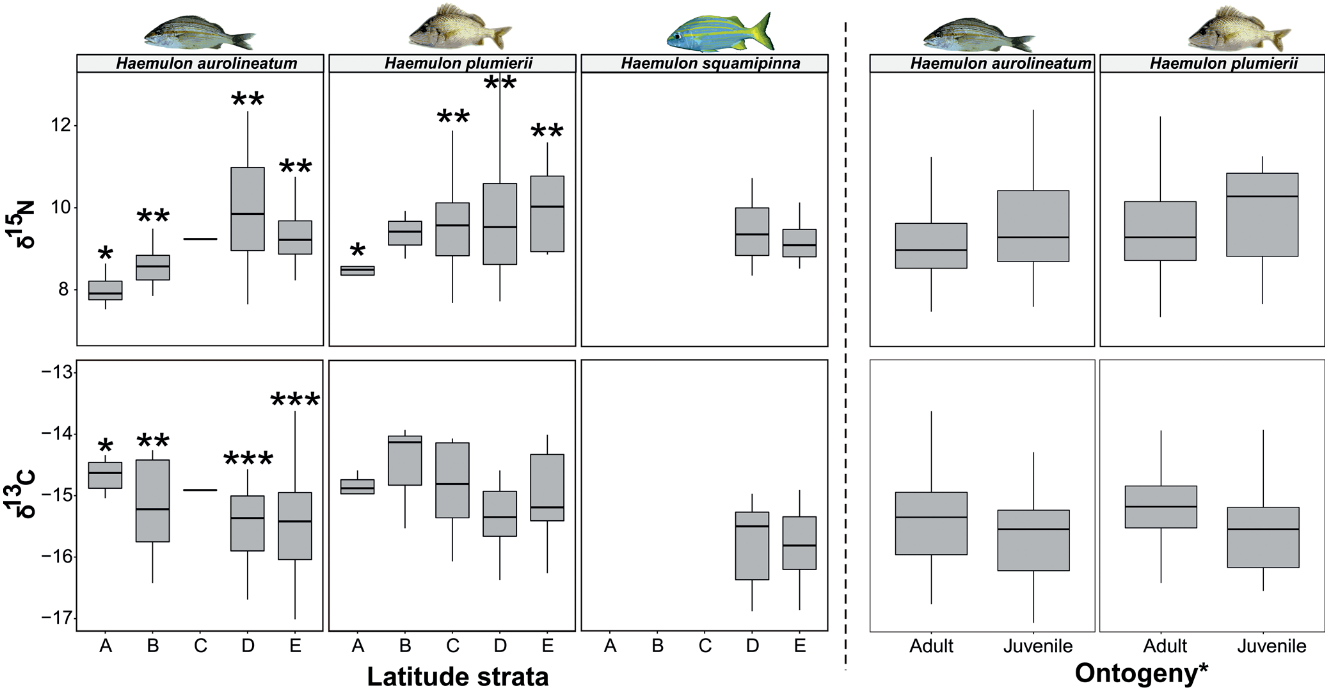

FIGURE 5 | Isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of *Haemulon plumierii*, *H. aurolineatum* and *H. squamipinna* in different latitude gradient and ontogeny captured along the northeast coast of Brazil. The black horizontal line and box represent the median value and the interquartile range, while the vertical lines represent the upper and lower limits. Outliers were not included in the plot. *All caught specimens of *H. squamipinna* were considered adults, not allowing ontogenetic analysis. Different symbols (*, ** and **) represent significant difference. Ontogeny* - All caught specimens of *H. squamipinna* were considered adults, not allowing ontogenetic analysis.

TABLE 4 | Trophic position of *Haemulon* species estimated based on the stable isotopes analysis (TP_{SIA}), its upper and lower limits, based on α=95%, and its standard deviation.

Species	Mean trophic position	Lower limit	Upper limit	Standard deviation
H. aurolineatum	3.74	3.56	3.92	0.090
H. plumierii	3.81	3.63	4.00	0.094
H. squamipinna	3.71	3.56	3.89	0.085

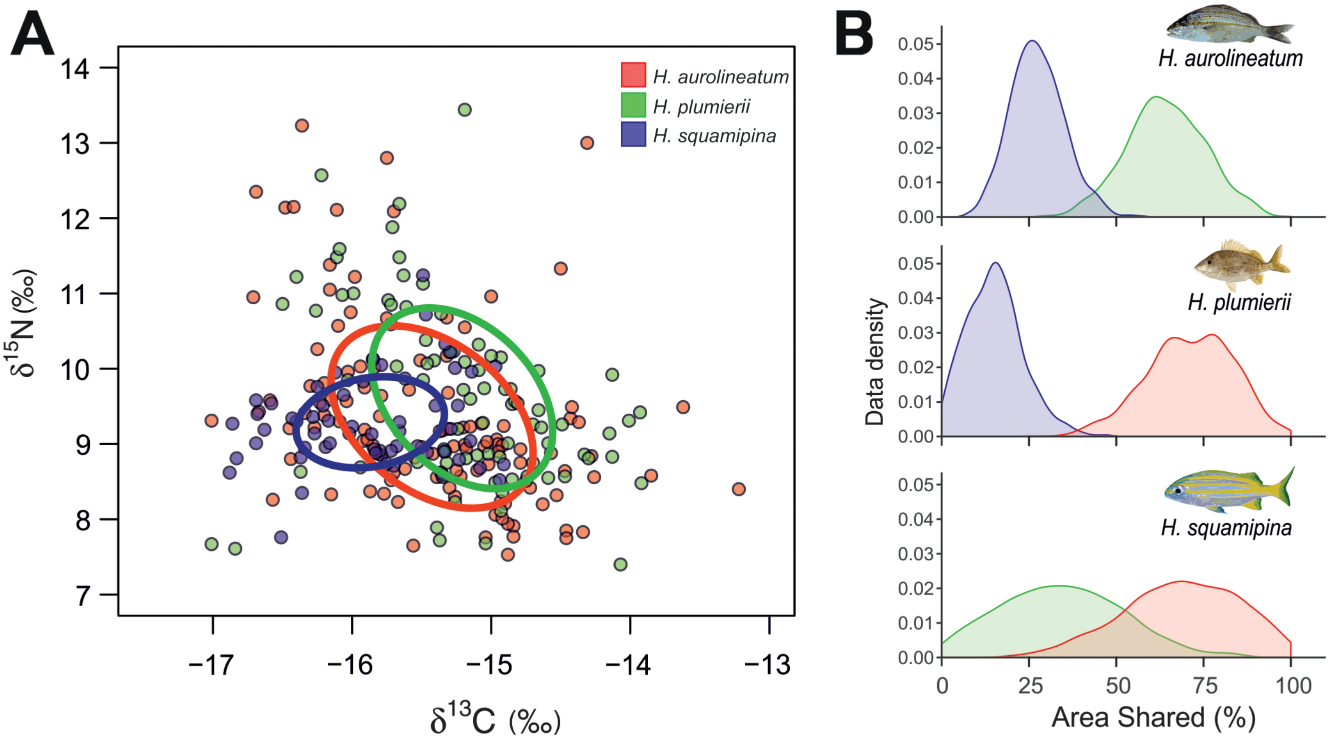

FIGURE 6 | **A.** Scaled isotopic niches and **B.** Isotopic overlap of *Haemulon aurolineatum*, *H. plumierii* and *H. squamipina* captured along the northeast coast of Brazil.

DISCUSSION

Haemulidae play a crucial role in the tropical Brazilian marine food web as they act as a linkage between lower trophic levels and the top predators. We analyzed the feeding habits and trophic ecology of three important Haemulidae species on the coast of the Northeast Brazil. It is important to mention that this is the first study about *Haemulon* genus on a large spatial scale (tropical Brazilian continental shelf), encompassing the feeding habits of three species applying a combination of approaches (stomach content and isotopic analysis).

Haemulon aurolineatum and *H. plumierii* were classified as nocturnal feeders, since most individuals with no food content were caught at daytime. It is recorded that Haemulidae are observed schooling during the day when the risk of predation is greater (Burke, 1995; Coxey, 2008). This behavior is related to the predator scape behavior (Danilowicz, Sale, 1999). However, Pereira, Ferreira (2013) also found a high frequency of foraging during the daytime for species of the family Haemulidae. In addition, they observed that juveniles preferred feeding in the water column, while adults foraged mainly in sand and bare rock (Pereira, Ferreira, 2013). The formation of schools for Haemulidae fishes may be related to the protective function and anti-predation mechanism (Ward *et al.*, 2002; Braga *et al.*, 2009), but also, with increased efficiency in foraging (Pereira, Ferreira, 2013).

Feeding intensity, described by the *Fi* index, can be affected by availability and type of prey, size and season (Mondal, Mitra, 2016; Perelman *et al.*, 2017). At latitudes below

08° S, specifically, in areas where the abundance of Haemulidae species is well-known to be very high (Eduardo *et al*., 2018; Cardoso de Melo *et al*., 2020) were found higher values of *Fi*. The very abundant populations of Haemulidae in this area are supported by extensive coral reefs, supported by the existence of two Marine Protected Areas ("Costa dos Corais" and "Guadalupe") (Pereira *et al*., 2021), which help to maintain the environmental stability providing better conditions for the biodiversity. In addition, small resurgence processes have been reported close to these locations, which increase the supply of nutrients from the deepest layer to the surface, generating primary production, attracting prey and thus increasing food availability for the fish assemblages (MMA, 2006). Feeding intensity also differed among shelf position, with fish caught near the coast presenting higher *Fi* values than fish from the deeper areas, and higher *Fi* values reported for juveniles rather than adults. Just as for ontogeny, with higher values for juveniles than adults. As observed in our study, in the Caribbean (Verweij *et al*., 2006), and other Brazilian areas (Pereira, Ferreira, 2013), life phase and schooling patterns have direct effects on the foraging behaviour of coral-reef fishes from the genus *Haemulon*. Adults and juveniles of *Haemulon* genus have different foraging behaviour, where juveniles had higher Fi than adults, which have less active diurnal feeding rate than juveniles (Verweij *et al*., 2006).

All species preyed on a wide variety of items, mainly epibenthic organisms, such as polychaetas, crustaceans, and echinoderms. Fishes were also especially important on the diet of *H. plumierii*. This fact, together with the moderate/high spectrum of prey and the results of the feeding strategy analyses, suggested that *H. plumierii* may be considered as generalist predators. *Haemulon* species seem to have a wide trophic plasticity, feeding on preys directly associated to reef environments. For example, crustaceans and, in a smaller proportion, mollusks, echinoderms, polychaetas, and teleosts are prey items often found in the diet of these species on the reefs of Santa Marta, Colombia (Estrada, 1986), Panamá Channel (Heck, Weinstein, 1989), Rio Grande do Norte, Brazil (Silva *et al*., 2018) and Bahamas (Layman, Silliman, 2002), indicating that they have a similar feeding pattern regardless of its distribution (Pereira *et al*., 2015).

For both species, *H. aurolineatum* and *H. plumierii*, a large percentage of digested organic matter was recorded. Similarly, other studies reported a large amount of unidentified organic matter and invertebrates was observed in most stomachs of *Haemulon* (Hammerschlag *et al*., 2010). Due to the high degree of digestion (Aguiar, Filomeno, 1995; Pereira *et al*., 2015; Hornbeck, 2017; Medeiros *et al*., 2017), most stomachs found during the day are in final digestion process, often with only small exoskeletons parts, while at night, where foraging is observed, items are still in the initial digestion process (Hammerschlag *et al*., 2010).

Isotopic analysis indicated higher values of $\delta^{15}N$ in *H. aurolineatum* and *H. plumierii* for specimens collected in the inner platform, which may be related to the continental contribution of human sources as fertilizers and sewage that could assimilate in preys (Weber, 1992; Noriega *et al*., 2005; Guimarães, Mello, 2006). Nitrogen from wastewater generally has higher values of $\delta^{15}N$ than inorganic nitrogen from the marine environment, due to its human or animal origin and also isotopic discrimination during remineralization processes (volatilization of ^{14}N-ammonium during ammonification), with higher $\delta^{15}N$ values in coastal areas (Lepoint *et al*., 2004). Haemulidae, may change their isotopic composition along ontogeny, the adults are more generalists and can feed on larger preys compared to juveniles that have more specialized diets (Pereira, Ferreira, 2013). However, it was not observed for any species in this study.

Overall, the species were classified as tertiary carnivorous consumer, with trophic position ranging between 3 and 4. On the eastern Pacific and Caribbean coast of Panama in Central America, trophic level obtained for three Haemulidae species, two of *Haemulon* genus, showed results similar to those obtained in this study, remaining in same range, characterizing them as secondary predators, with a predominant zoobenthivorous habit (Stuthmann, Castellanos-Galindo, 2020). The common species in both studies (*H. plumierii*) had values close to those found here, although baseline choices were different.

Haemulidae tend to be generalists, with no specific preference, preying on what is more abundant or available in the environment (Flores-Ortega *et al*., 2014). Although with similar values of the niche breadth, *H. plumierii* seemed to be more generalist than *H. aurolineatum*, which might be explained by the fact that the former species is naturally of larger size. Larger individuals usually had larger digestive and oral apparatus, being able to capture a greater variety of prey size (Restrepo-Gómez, Mancera-Rodríguez, 2014; Pereira *et al*., 2015). Also, larger individuals are generally more efficient at chasing and capturing preys (Gerking, 1994; Cardoso *et al*., 2019).

Haemulon aurolineatum and *H. plumierii* had high diet overlapping, meaning they share more than three quarters of their prey items. Although *H. aurolineatum* and *H. squamipinna* often have similar high habitat affinity, population size and body shape (Pereira *et al*., 2015, 2021), according to Cardoso *et al*. (2019), in our study area with the same data base, *H. squamipinna* was not found at latitudes lower than 07°S. Meanwhile, *H. aurolineatum* and *H. plumierii* were jointly observed throughout the entire area. In addition, *H. aurolineatum* and *H. plumierii* displayed high affinity with the habitats of Sand With Coral and Rocks (SWCR), Sandy and Algae, while *H. squamipinna* was associated with sand and SWCR bottoms (Eduardo *et al*., 2018; Cardoso *et al*., 2019). Therefore, the higher similarity in the habitat uses among *H. aurolineatum* and *H. plumierii*, may have led to a greater prey sharing, resulting in a high diet overlapping. This was already reported in different regions, such as in Paraíba, Northeast Brazil (Medeiros *et al*., 2017) and Curaçao Island (Morinière *et al*., 2003), indicating that these species have been always partitioning resources in the different ecosystems they inhabit. However, given the diversity of preys there is no indication of competition.

The integrate techniques (stomach content and stable isotopes analysis) have been successfully implemented to understand spatial and ontogenetic factors for many fish species such as omnivores, benthivores, herbivores and for big predators (Nagelkerken *et al*., 2008; Rosende-Pereiro *et al*., 2019; Zhu *et al*., 2019) and showed complementary responses in the present study. The Haemulidae trophic ecology patterns found in this portion of the South Atlantic, carnivorous predator with trophic position varying between 3 and 4, resemble different locations around the globe.

Haemulidae fishes are considered of high socioeconomical importance, especially for the artisanal fleet, but management and conservative strategies are still lacking in the Brazilian coast, since these species exploitation is, currently, of open access. Moreover, although the effort to conserve reef ecosystems and species have increased overtime, they are still insufficient to mitigate or reverse the increasing anthropogenic impacts in this area, despite the relatively high number of Marine Protected Areas (MPA), which are not necessarily managed and/or enforced given the absence of information. Increasing knowledge about the fish biology and their respective relationships with their habitats and other species is essential for identifying priority areas for conservation in an ecosystem basis, especially in rich reef zones that are under several increasing pressures, as those in Northeast Brazil, also considered as an EBSA (Ecologically or Biologically Significant; CBD, 2014).

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ETHICAL STATEMENT

The cruises did not require the Ethical Committee for Animal Use in Experiments. The collection licenses of Sistema de Autorização e Informação em Biodiversidade (SISBIO) were ABRACOS 1–47375 and ABRACOS 2–47270).

COMPETING INTERESTS

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