Acta Scientiarum

http://www.periodicos.uem.br/ojs/
ISSN on-line: 1807-863X
Doi: 10.4025/actascibiolsci.v43i1.52230

ECOLOGY

Diet composition of abundant fish species in the shallow waters of the Todos os Santos Bay, Bahia, Brazil

Rafael Lima Oliveira[1*], Leonardo Evangelista Moraes[2] and Alexandre Clistenes de Alcântara Santos[1,3]

[1]Laboratório de Ecologia de Peixes Marinhos, Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal do Espírito Santo, Rodovia BR-101 Norte, Km 60, s/n, 29932-540, São Mateus, Espírito Santo, Brazil. [2]Laboratório de Recursos Pesqueiros e Aquicultura, Centro de Formação em Ciências Ambientais, Universidade Federal do Sul da Bahia, Porto Seguro, Bahia, Brazil. [3]Laboratório de Ictiologia, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil. *Author for correspondence. E-mail: oliveirarl.uesb@gmail.com

ABSTRACT. Coastal habitats have great ecological importance with estuarine environments providing feeding sites for many fish species, especially during juvenile life stages. This study investigates the diet composition and trophic guild organization of the common and abundant ichthyofauna in shallow areas of the Todos os Santos Bay (TSB), Bahia, Brazil, and their relationships with environmental parameters. Six fish sampling campaigns were carried out in the shallow zones (infralittoral) of the Paraguaçu River estuary which encompasses the inner and outer (marine exposure) reaches of the TSB. The stomach contents of 1231 individuals belonging to common and abundant species were examined. A total of 32 food items were identified and fish were into four trophic guilds: detritivores, zoobenthivores I, zoobenthivores II, and zooplanktivores. The relationship between the guilds and environmental parameters showed that zoobenthivores II and zooplanktivores guilds had a positive relationship with salinity and pH, explaining 86% of data variability, though only the salinity variable was significant. This study provides basic information about the diet composition of common and abundant species in the TSB and their organization into trophic guilds. In addition, demonstrates that shallow waters fish across all guilds have broadly similar diets, comprising food items that are usually associated with bottom waters.

Keywords: bay; diet; tropical estuaries; fish; trophic guild.

Received on February 17, 2020.
Accepted on April 23, 2021.

Introduction

Studies on food ecology provide valuable insights into the complex interactions between species and their environment (Berg, 1979; Ferry & Cailliet, 1996; Brodeur, Smith, Mcbride, Heintz, & Farley, 2017). Evaluating the diet and dietary aspects of species is still a primary concern in general and applied ecology (Albouy et al., 2011). These studies provide basic information on ecological aspects and the life history of many species, as well as the role of species in the trophic structure and organization of aquatic ecosystems (Brown, Bizarro, Cailliet, & Ebert, 2011; Braga, Bornatowski, & Vitule, 2012).

Coastal habitats are of great ecological importance. Within these regions, the estuarine environments stand out for their use as feeding sites by many fish species, especially during juvenile life stages. Considered to be one of the most productive aquatic ecosystems, the availability of food resources in estuarine areas can therefore be a key factor in limiting the growth and survival of juveniles (Blaber, 2000; Martinho, Cabral, Azeiteiro, & Pardal, 2012; Potter, Tweedley, Elliott, & Whitfield, 2013).

Estuarine environments are home to abundant and diversified sources of primary producers, allowing for complex trophic webs with large numbers of prey and predators due to the abundance of shelter and the connection with continental and marine aquatic environments (Duarte & García, 2004; Vasconcelos-Filho, Neumann-Leitão, Eskinazi-Leça, Schwamborn, & Oliveira, 2010). In addition, these environments serve as migration routes and as sites for spawning, reproduction, recruitment, and feeding, with some species completing their entire life cycle in estuaries (Potter et al., 2013). Thus, these environments play important roles as nursery areas for juveniles of a large number of species, especially ones that depend on estuaries, many of which are economically important (Martinho et al., 2012; Sales, Baeta, Lima, & Pessanha, 2017).

In northeastern Brazil, the coast of Bahia state is rich in recesses with estuaries that serve as nursery areas for many fish species. Various bays in the region have particular economic importance with activities including fishing, tourism, real estate speculation, and logistics. These bays face significant human pressure, while their importance for marine fish populations remains poorly understood. This study therefore examines the diet composition and trophic organization of the most common and abundant ichthyofauna in the shallow areas of the Todos os Santos Bay (TSB), Bahia, focusing on the consumption of food resources in order to delineate and assess the respective importance of the area's trophic guild. The relationships between guilds and environmental parameters are also evaluated.

Material and methods

Study area

The study was conducted in the Todos os Santos Bay (TSB), located at 12°50'05" S, 38°46'20" W (Figure 1). The bay is the second-largest in Brazil, with an area of approximately 1,100 km^2 (Cirano & Lessa, 2007; Couto, Guimarães, & Oliveira, 2013; Vale & Schaeffer-Novelli, 2018). TSB is home to extensive stretches of coral reefs, estuaries, and mangroves. Most of these ecosystems are associated with the region's freshwater tributaries (Hatje & Andrade, 2009; Lessa, Cirano, & Genz, 2009). TSB has a wet climate with an average of 53% of the total annual rainfall occurring between April and July (Lessa et al., 2018).

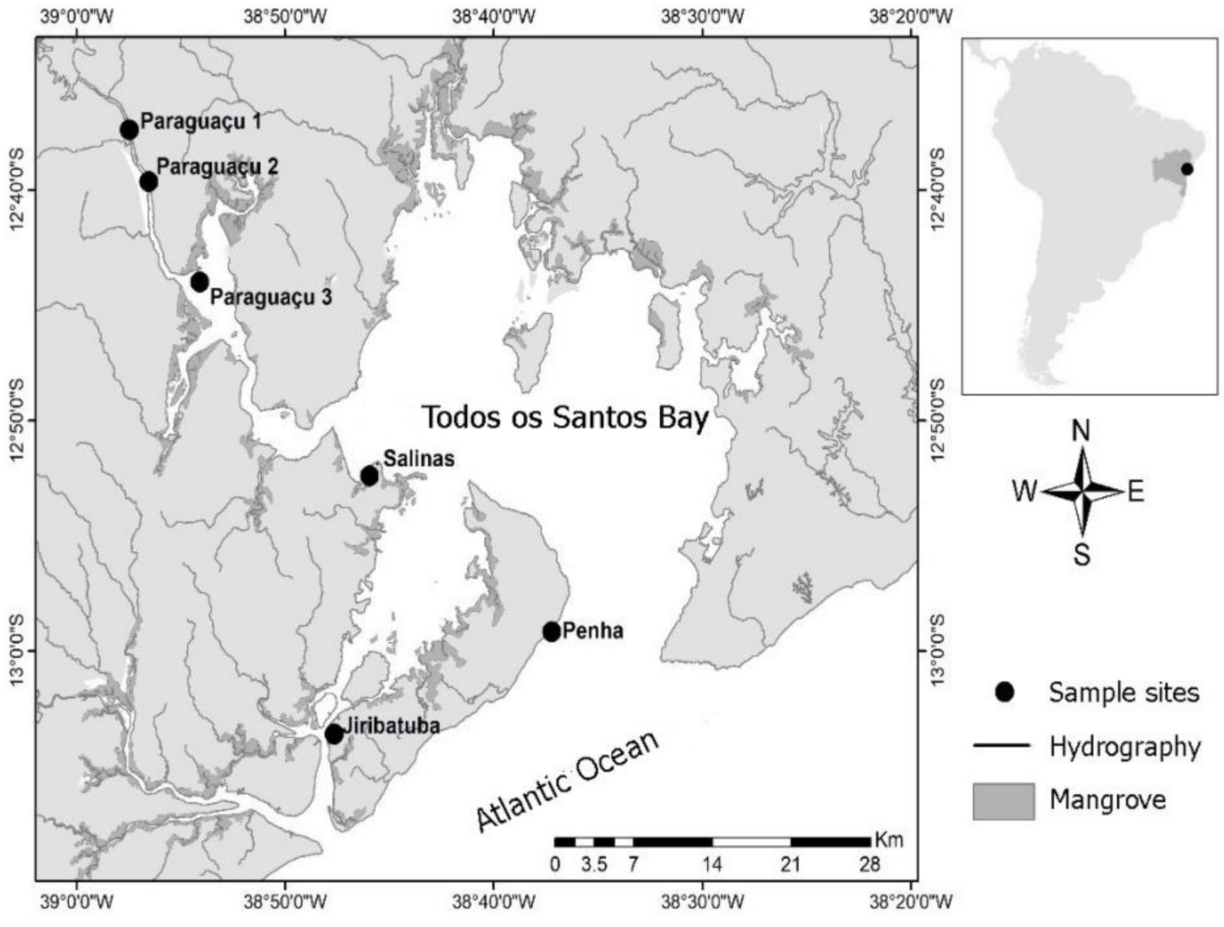

Figure 1. Map showing the sampling points in the Todos os Santos Bay, Bahia, Brazil.

The Paraguaçu River, the main freshwater tributary of the TSB, occupies a drainage area of approximately 56,300 km^2, with its main discharge in the bay. Two other large drainage basins (Jaguaripe and Subaé) flow into the TSB, with all three basins representing 74% of the total river discharge, with the remaining discharge coming from 91 smaller basins that generate a diffuse discharge effect during the rainy season. The average annual flow in the TSB is less than 50 $m^3 s^{-1}$ due to the semi-arid climate that prevails in the drainage basins, while the bay's hydrodynamics are primarily driven by the semi daily tide, with the basin drainage flow making a smaller contribution (Hatje & Andrade, 2009; Lessa et al., 2009).

Fish sampling

Six fish sampling campaigns were carried out in the shallow zones (infralittoral) of the Paraguaçu River estuary extending to the inner and outer (marine exposure) regions of the TSB (Figure 1). During the spring tides, sampling was always conducted during the daytime low tide. For each sampling point, five hauls were carried out in a straight line over a 30m path, using beach seine net-type trawls (10 × 1.5 m; 5 mm mesh).

Environmental variables were measured simultaneously as ichthyofauna sampling with a Horiba U50 Multiparameter Water Quality Checker, as follows: salinity, temperature, pH, dissolved oxygen, density, and water conductivity. Sampling campaigns were grouped into two seasonal periods. The rainy period corresponds to the sampling campaigns conducted in May and July 2017 and April 2018, while the dry period corresponds to the campaigns carried out in August, September, and November 2018. During the sampling months, monthly rainfall data were obtained from Brazil's National Meteorological Institute website (INMET) (www.inmet.gov.br).

Once captured, all individuals were kept on ice and transported to the laboratory, where they were frozen for further processing. In the laboratory, fishes were identified, measured for the total length (TL, to the nearest cm), and weighed (to the nearest g). Subsequently, their stomachs were removed and placed into containers containing 70% alcohol for later diet analysis.

Data analysis

By combining abundance and occurrence data, all species collected were initially classified as abundant, frequent, and rare, according to Garcia & Vieira (2001). This procedure was used to identify the 10 dominant species in the study area (i.e., species with high abundance and frequency), representing 70% of the total collected individuals. These species were thus chosen for further analysis in this study. Although all species play some role in the trophic context, the dominant species reflect the most common patterns and conditions in the environment (Magurran, Khachopisitsak, & Amhad, 2011). The diet analysis was carried out on each dominant species with a minimum of 30 individuals collected per period (dry and wet season). The food items found in the fish stomachs were analyzed under a stereoscopic and optical microscope (when necessary) and identified to the lowest taxonomic resolution, depending on the degree of digestion of each item. The following references were consulted to identify food items: Costa et al. (2006), Brusca & Brusca (2007), Barnes, Calow, & Golding (2008), and Fransozo & Negreiros-Fransozo (2016).

Diets were characterized using the Feeding Index (IAi), expressed as a percentage in order to calculate the relative importance of each item found in the stomach contents. This index consists of the ratio between the product of the frequency of occurrence and volume, measured using a millimeter Petri dish covered on the outside with 1x1 graph paper (Albrecht & Caramaschi, 2003) for each item divided by the sum of products for all items found (Kawakami & Vazzoler, 1980), Equation 1:

$$IAi = (FOi \times VOi) / (\sum FO \times VO) * 100 \quad (1)$$

Where: FOi is the frequency of occurrence of item i (%), and VOi is the relative volume of item i (% of total). To quantify diatoms, a combination of the volumetric method was used under the stereomicroscope, followed by the qualitative and quantitative evaluation of a sub-sample under an optical microscope. A Neubauer counting chamber was used to count these organisms (Taylor, Harding, & Archibald, 2007).

The food items were then grouped into 11 broad food categories, as follow: (1) diatoms; (2) protists (Foraminifera); (3) plant remains (unidentified plant remains and seeds); (4) Annelida (Polychaeta worms); (5) Arachnida (Araneae and Hydracarina); (6) mollusks (gastropods and bivalves); (7) microcrustaceans (Amphipoda, Copepoda, Ostracoda, and Isopoda); (8) crustacean remains (Brachyura remains); (9) insects (Hemiptera, Thysanoptera, ants, immature and adult forms of Diptera, and insect remains); (10) fish (fish remains and scales); (11) digested (unidentified) animal matter. These categories were used in the analyses, graphic representations, and data comparisons. Trophic guilds were defined based on the similarity of the species' food resources determined during the stomach content analysis. To do this, a cluster analysis was performed based on the Bray-Curtis index using the *vegdist* function, following which the minimum variance method (Wards Method) was applied using the *hclust* function, based on the volume values of the food categories.

To analyze the relationship between environmental parameters and the abundance of species from each trophic guild, a canonical correspondence analysis (CCA) was performed using the *cca* function. The variance inflation factor (VIF) was calculated using the *vif.cca* function to evaluate multicollinearity among environmental variables. Environmental variables with VIF values > 5 were excluded from the CCA analysis. The cluster and CCA analyses were carried out in the R environment (R Core Team, 2019) using the *vegan* package (Oksanen et al., 2019).

Results

Diets of abundant species

The stomach contents of 1,231 individuals from 10 common and abundant species (Table 1) were analyzed, and a total of 32 food items were recorded and identified (Table 2).

Table 1. Abundant species in the Todos os Santos Bay, Bahia, Brazil, and the total number of individuals on which stomach content analysis was carried out.

Family	Species	Code	Rainy Season	Dry Season	Total
Engraulidae	*Anchoa januaria*	Ancjan	30	30	60
Gobiidae	*Ctenogobius boleosoma*	Ctebol	36	60	96
Gobiidae	*Gobionellus oceanicus*	Goboce	30	30	60
Atherinopsidae	*Atherinella brasiliensis*	Athbra	38	178	216
Carangidae	*Oligoplites saurus*	Olisau	59	30	89
Gerreidae	*Diapterus rhombeus*	Diarho	30	75	105
Gerreidae	*Eucinostomus argenteus*	Eucarg	71	49	120
Achiridae	*Achirus lineatus*	Achlin	54	30	84
Tetraodontidae	*Sphoeroides greeleyi*	Sphgre	79	236	315
Tetraodontidae	*Sphoeroides testudineus*	Sphtes	30	56	86
		Total = 1231			

Table 2. Diet composition of the most abundant species in the Todos os Santos Bay, Bahia, Brazil, and their respective Feeding Index (IAi%) values. DOM= digested organic matter; DAM = digested animal matter.

Itens/Species	Achlin n=84	Ancjan n=60	Athbra n=216	Ctebol n=96	Diarho n=105	Eucarg n=120	Goboce n=60	Olisau n=89	Sphgre n=315	Sphtes n=86
Foraminífera	-	-	0.11	2.45	0.03	-	-	-	-	-
Diatoms	-	-	-	0.02	-	-	100	-	-	-
Filamentous algae	-	-	-	3.24	-	-	-	-	-	-
Plant remains	-	-	0.28	0.39	0.20	0.90	-	0.06	2.18	0.06
Seeds									<0.01	0.05
Polychaeta	20.03	-	-	8.34	21.63	0.06	-	-	-	-
Aranae			<0.01	-	-	-	-	-	-	-
Acarí	-	-	-	0.09	-	<0.01	-	-	-	-
Bivalve	-	0.03	0.02	-	0.24	0.03	-	-	4.36	9.41
Gastropoda	0.01	0.07	0.35	1.96	0.07	3.56	-	-	6.13	4.71
Megalopa	-	13.01	-	-	-	-	-	-	-	-
Crustaceans remains	-	-	0.57	-	-	0.59	-	0.06	57.47	69.60
Barnacles	-	-	-	-	-	-	-	-	-	0.74
Isopoda	-	-	0.01	-	-	-	-	0.03	<0.01	-
Copepoda	-	-	3.69	19.24	2.36	53.07	-	28.27	<0.01	-
Amphipoda	-	-	-	-	0.52	-	-	0.22	-	-
Ostracoda	-	18.63	0.01	1.98	0.40	1.39	-	-	<0.01	-
Decapoda	-	-	-	0.04	-	-	-	-	0.04	-
Shrimp	-	-	0.03	-	-	-	-	0.90	-	-
Insect remains	-	-	2.90	-	-	0.02	-	-	-	-
Diptera	-	-	0.02	-	-	-	-	-	-	-
Pupa *dasyhelea*	-	-	-	-	-	0.07	-	-	-	-
Hymenoptera	-	-	0.09	-	-	-	-	-	-	-
Formicidae	-	-	0.40	-	-	-	-	-	-	<0.01
Hemiptera	-	-	0.06	-	-	-	-	-	-	0.02
Thysanoptera	-	-	<0.01	-	-	-	-	-	-	-
Fish	-	-	0.20	-	-	-	-	2.57	0.02	0.04
Scale	-	-	-	-	-	<0.01	-	9.07	-	-
DOM*	10.84	67.88	91.38	39.24	48.65	36.81	-	55.25	27.50	13.08
DAM*	67.06	-	-	11.48	25.45	0.17	-	2.99	<0.01	-
Sediment	2.05	0.34	0.06	3.51	0.40	3.23	-	0.54	2.25	2.23
							Total =		1231	

In general, a high amount of digested organic matter was found in the diet of most species. Most items comprised organisms associated with the hyperbenthic zone (e.g., Polychaeta, Mollusca, and diatoms) and, to a lesser extent, zooplankton (e.g., Copepoda and Amphipoda). Additionally, allochthonous food items (e.g., insects) were particularly abundant in the diet of *A. brasiliensis*.

The dendrogram generated from the cluster analysis identified four trophic guilds: detritivore, zoobenthivores I, zoobenthivores II, and zooplanktivores (Figure 2).

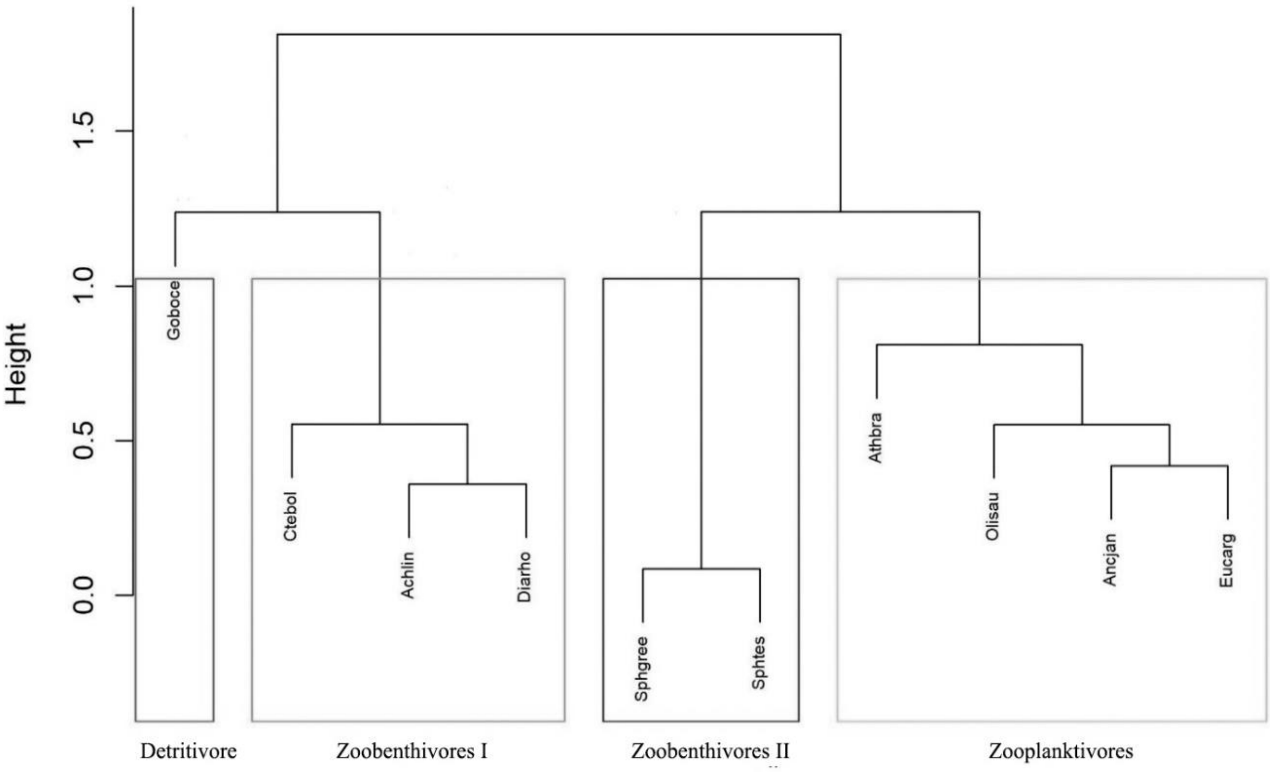

Figure 2. Cluster analysis showing the trophic guilds formed by fish species, using the volume values of the food categories. See Table 1 for abbreviations.

The gobiid *G. oceanicus* was the unique representative of the detritivore guild since its diet was the only one composed exclusively of diatoms associated with sediments. The zoobenthivores I guild, represented by *C. boleosoma*, *A. lineatus,* and *D. rhombeus*, was characterized by the consumption of Polychaeta and digested animal matter. The congeneric species *S. greeleyi* and *S. testudineus* were classified as zoobenthivores II due to the high consumption of crustaceans and mollusks. The four species of the last guild (*A. brasiliensis*, *O. saurus*, *A. januaria,* and *E. argenteus*), were mainly characterized by the consumption of microcrustaceans and were therefore classified as zooplanktivores.

The cluster analysis of the trophic guild organization during the wet and dry periods indicated that some species switched guilds during the wet season (Figure 3). Specifically, a greater number of species were classified as zooplanktivores during the rainy season, while one jointed the zoobenthivores guild. The species *A. brasiliensis* and *D. rhombeus* were assigned to the zooplanktivores I guild during the rainy season (characterized by the consumption of microcrustaceans), while the latter species was grouped into the zoobenthivores guild during the dry season due to the high proportion of Polychaeta in its diet.

It is worth mentioning that, in addition to microcrustaceans, insects represented a large portion of the rainy-season diet of *A. brasiliensis*. The species *A. januaria*, classified as a zooplanktivores during the dry season, was allocated to the zoobenthivores II guild in the rainy season due to its consumption of crustaceans, joining the congeneric *S. greeleyi* and *S. testudineus*. In addition, *C. boleosoma* changed from the zoobenthivores to the zooplanktivores guild in the wet season, leaving *A. lineatus* as the only species in the zoobenthivores I guild during the wet season.

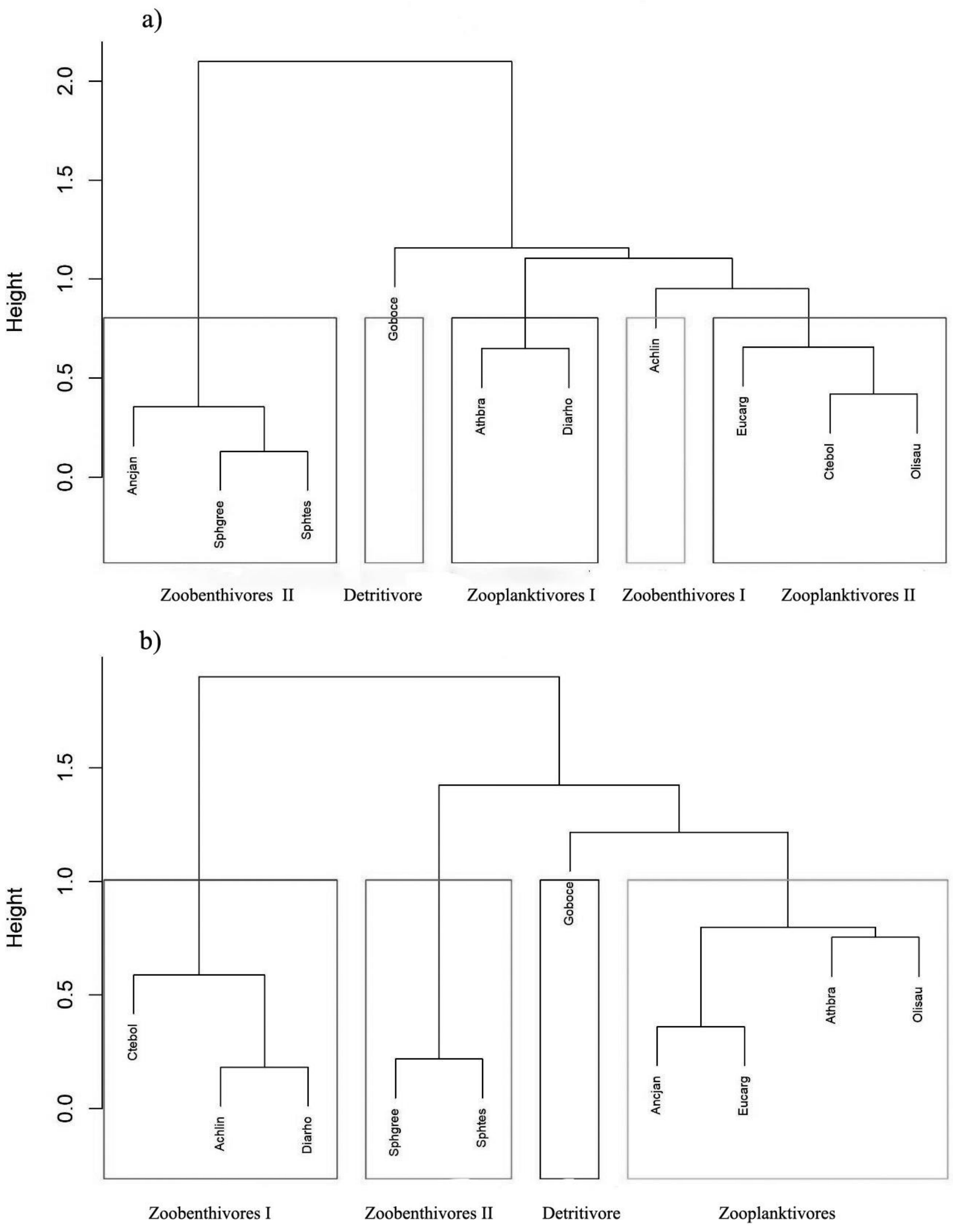

Figure 3. Cluster analysis showing the trophic guilds formed by fish species, using the volume values of the food categories for the (a) rainy season and (b) dry season. See Table 1 for abbreviations.

The canonical correspondence analysis showed the relationship between the abundance of the species in each trophic guilds and environmental parameters. The analysis indicated that the zoobenthivores II and zooplanktivores guilds had a positive relationship with the salinity and pH vectors on the first axis, which accounted for 86% of the variation in the data, and were inversely related with dissolved oxygen (Figure 4), though only the correlation with salinity was significant ($p < 0.05$) The temperature and precipitation were the main variables on the second axis, accounting for 11% of the variability.

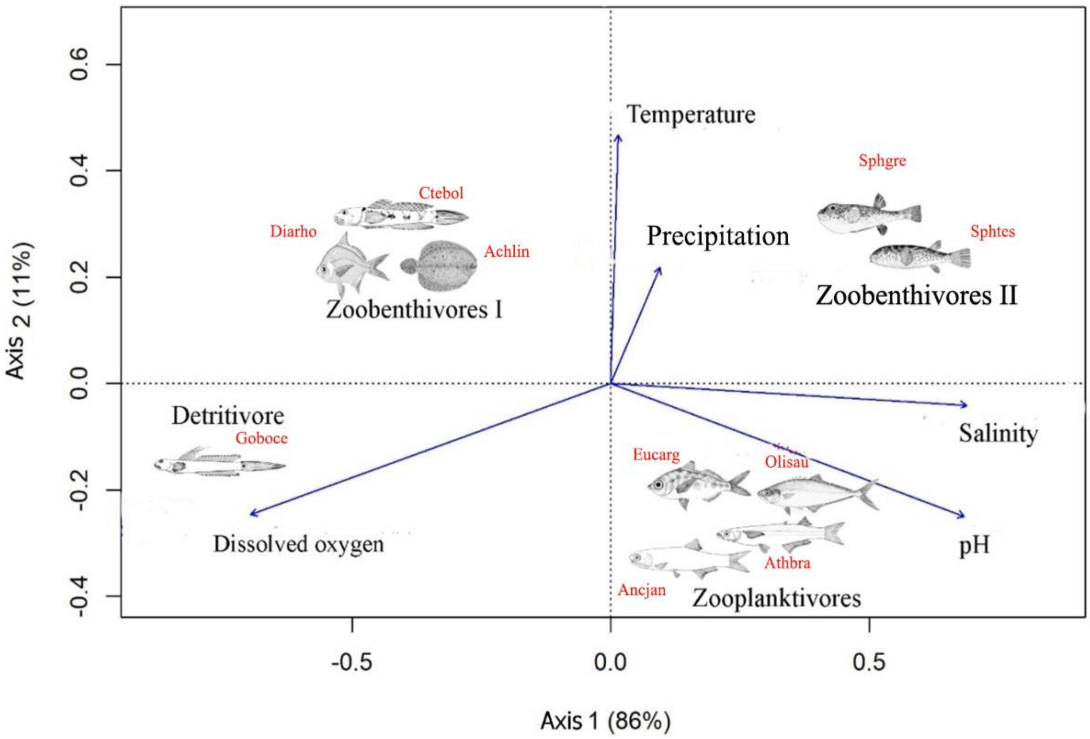

Figure 4. Ordination diagram of the first two axes of canonical correspondence analysis (CCA) based on the trophic guilds and environmental variable data from the Todos os Santos Bay, Bahia, Brazil. See Table 1 for abbreviations.

Discussion

Four trophic guilds were identified among the ichthyofauna of the Todos os Santos bay. Of these, three guilds were comprised of species feeding on organisms commonly associated with substrate/sediment (benthic compartment). Classifying fish species into trophic guilds is an important step in the understanding and definition of groups with functionally similar species (Garrison & Link, 2000). Tropical estuarine environments are known for their wide variety of available food, mainly due to the diversity of habitats found in these areas and the interactions between saltwater, freshwater, and adjacent terrestrial habitats (Blaber, 2000). The shallower estuarine zones play an important role as nursery areas for fish due to the abundant food supply and protection against predators (França, Costa, & Cabral, 2009; Moraes, Paes, Garcia, Moller, & Vieira, 2012; Santos, Santos, Moraes, Condini, & Garcia, 2020). In the estuaries, nutrients and light are not limiting factors for primary production throughout the water column, even in the benthic compartment, where phytobenthos, seagrass, and macroalgae are important carbon sources for the trophic web. This abundance of primary production is responsible for the high abundance of fish juveniles and sub-adults in these areas (Santos et al., 2020). Additionally, most fish species found in estuarine environments have morphological and physiological adaptations that allow them to feed on the estuarine floor, indicating that substrate plays an important role in the functioning of trophic webs (Day, Yanz-Arancibia, Kemp, & Crump, 2012).

Detritivore species greatly contribute to the estuarine trophic web, especially in terms of energy and nutrient flows from the phytobenthos to other consumers (Day et al., 2012; Oliveira, Bastos, Caludino, Assumpção, & Garcia, 2014; Claudino, Pessanha, Araújo, & Garcia, 2015). Several species of this guild are present in TSB, such as mullets (Reis-Filho, Nunes, & Ferreira, 2010). However, most of these were not among the dominant species examined in this study. Thus, *G. oceanicus* was the sole representative of the detritivore guild in shallow estuarine areas. With a diet composed exclusively of diatoms associated with sediments, *G. oceanicus* can be classified as a specialist species, similarly to other studies (e.g., Vasconcelos-Filho et al., 2003; Pessanha et al., 2015).

Species from the zoobenthivores guild often feed on benthic macrofauna living on the sediment (epifauna) or which bury themselves (infauna), as well as feeding on organisms living above the sediment (hyperbenthos) (Elliott et al., 2007). In this regard, the development of organisms associated with the benthic compartment in the TSB is a consequence of the large flow of nutrients from the freshwater drainages to the bay, increasing the availability of organic material, which in turn allows the proliferation of benthic macrofauna (e.g., Polychaeta, Crustacea, and Mollusca) (Barros et al., 2008; Santos & Rodriguez, 2011). The species *A. lineatus*, *D. rhombeus,* and *C. boleosoma* were grouped into the zoobenthivores I guild, due to their consumption of Polychaeta. Flounders and gobies are ecologically diverse groups with conspicuous benthic behavior. These species have morphological characteristics (e.g., body shape and coloring, modified fins) that enable them to successfully explore the benthos, which is reflected in the diet (Carpenter, 2002; Helfman, Collette, Facey, & Bowen, 2009). Most flounders and gobies are typically classified as bottom-dwelling carnivores of small benthic invertebrates, although planktivorous and piscivorous habits have also been recorded (Almeida, Genevois, & Vasconcelos-Filho, 1997; Vasconcelos-Filho, 2010). Mojarras are demersal species with a protrusible (tube-like) mouth that allows them to feed by foraging the bottom and picking up their prey using suction pressure (Carpenter, 2002; Helfman et al., 2009). Although they have morphological differences, these feeding result in flounders, gobies, and mojarras having a similar diet.

The congeneric species *S. greeleyi* and *S. testudineus* were grouped into the same trophic guild (zoobenthivores II) since they fed mainly on crustaceans and mollusks. These species are characterized by their terminal mouth with four fused teeth in jaws (i.e., beak-like specialized dentition) allowing them to crush hard-shelled organisms (Krumme, Keuthen, Saint-Paul, & Villwock, 2007; Lima, Clark, Sales, & Pessanha, 2018), such as crustaceans and mollusks. Previous studies from northeastern Brazil also classified them into the zoobenthivores guild and showed that their diet composition primarily consisted of crustaceans and mollusks (Vasconcelos-Filho, Silva, & Acioli, 1998; Vasconcelos-Filho et al., 2010; Santos & Rodriguez, 2011; Pessanha et al., 2015). Congeneric species with similar ecological attributes that share the same space tend to show feeding overlap, and consequently, some level of intraspecific competition. However, in a productive environment such as the estuaries, the food supply tends to reduce the competitive pressures, promoting the co-occurrence of these species as found in Garcia et al. (2018), as well as the present study. In addition, Targett (1978) assessed the partition of food resources between *S. splengleri* and *S. testudineus* and found that these species were able to share resources, indicating that both species fed on benthic resources, even with similar spatial overlap and morphology.

The zooplanktivores guild was likewise composed of species with attributes typically associated with the environment. The fusiform shape, pale body with darker upper half, forked tail, and terminal mouth are characteristics that indicate that these species are ideally adapted to feeding on zooplankton in the pelagic component (Ross, Martinez-Palacios, Valdez, Beveridge, & Sanchez, 2006; Mouillot, Dumay, & Tomasini, 2007). Like mojarras, the neotropical silverside *A. brasiliensis* also has a superior protractile mouth that helps capture its plankton prey by suction pressure (Carpenter, 2002; Helfman et al., 2009). In the TSB, the zooplankton community is comprised of tropical estuarine species, with holoplankton organisms predominating (e. g., Copepoda and Brachyura) (Lessa et al., 2018). In the zooplanktivores guild, the diet of *A. brasiliensis* shows high diversity, especially due to allochthonous contributions, with a predominance of insects represented by the order Hymenoptera, mostly ants. A wide array of prey types in this species diet result from a generalized and opportunistic feeding strategy, that includes the consumption of terrestrial insects, mainly among the juvenile stages (Contente, Stefanoni, & Spach, 2011; Alves et al., 2016). The Brazilian silverside is an estuarine resident species that is dominant in shallow areas, and predominantly found in lower salinity waters, in river mouths along the coast (Santos, Castullicci, Nepomuceno, Santos, & Sena, 1999; Garcia, Vieira, Winemiller, & Grimm, 2004). This ability to explore environments with less salinity, including rivers, allows *A. brasiliensis* to benefit from items of terrestrial origin that fall or are carried into the water. Additionally, the Brazilian silverside's superior and protrusible mouth helps it feed on the surface items (Helfman et al., 2009). Previous studies have also indicated the same guild classification for this species (e.g., Contente et al., 2011; Campos, Silva, Sales, Oliveira, & Pessanha, 2015; Medeiros, Xavier, Silva, Aires-Souza, & Rosa, 2018).

The relationship between trophic guilds and environmental parameters indicated a positive correlation with salinity, which drove most of the variability for the zooplanktivores and zoobenthivores II guilds. The species in these guilds were more abundant in sampling sites with higher salinity. The opposite trend was seen for zoobenthivores I and detritivores guilds with greater abundance in areas associated with the Paraguaçu River estuary, where the lowest salinity was recorded. The dynamic interactions among climatic variations in the continental zone and the adjacent marine areas associated with the estuarine environment may result in variations in the physical and chemical characteristics of the water, such as temperature, salinity, pH, and dissolved oxygen, which can vary on different spatial and temporal scales, especially in shallow areas (Allen, Yoklavich, Cailliet, & Horn, 2006; Raimonet & Cloern, 2016). The salinity gradient in the estuaries increases gradually along their length and may influence the establishment of specific fauna (Blaber, 1997; Elliott & Mclusky, 2002). Preferences for specific salinity ranges may reflect the physiological ability of species to withstand osmotic stress. That is why salinity is generally used to distinguish different areas and habitats throughout the estuarine environment (Whitfield, 2015). In the TSB, a semi-diurnal tidal regime predominates, and the hydrodynamics shows a predominance of marine water, leading to high average salinity (above 30) (Cirano & Lessa, 2007).

Conclusion

Our study provides basic information on the diet composition of common and abundant species in the TSB and their organization into trophic guilds. In addition, it highlights the fact that the species comprising these guilds in the shallow waters feed mainly on similar food items, with benthic organisms predominating. We also show the importance of investigating seasonal and ontogenetic diet shifts in these areas and their relationship with environmental parameters, which can vary drastically, especially in shallow areas.

Acknowledgements

We thank the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (*CAPES), for the scholarship granted to the first author (Finance Code 001) and *Programa de Pós-graduação em Ecologia e Evolução, Universidade Estadual de Feira de Santana* for all structural support. The *Fundação de Amparo à Pesquisa do Estado da Bahia* (FAPESB) for the project support (4413/2014). We are also grateful to Ilver Eduardo Gutierrez Alabat for their assistance in statistical analysis.

References

Albouy, C., Guilhaumon, F. Villeger, S., Mouchet, M., Mercier, L., Culioti, J. M., ...Mouillot, D. (2011). Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. *Marine Ecology Progress Series, 436*(1), 17-28. DOI: http://dx.doi.org/10.3354/meps09240

Albrecht, M. P., & Caramaschi, E. P. (2003). Feeding Ecology of *Leporinus riderici* (Teleostei, Anostomidae) in the upper Tocantins River, central Brazil, before and after installation of a hydroelectric plant. *Studies in Neotropical Fauna and the Environment, 38*(1), 33-40. DOI: http://dx.doi.org/10.1076/snfe.38.1.33.14033

Allen, L. G., Yoklavich, M. M., Cailliet, G. M., & Horn, M. H. (2006). Bays and Estuaries. In L. G. Allen, D. J, Pondella, & M. H. Horn (Eds.), *The ecology of marine fishes: California and adjacent waters* (p. 119-148). Berkeley, CA: University of California Press.

Almeida, Z. S., Genevois, V. F., & Vasconcelos-Filho, A. L. (1997). Alimentação de *Achirus lineatus* (Teleostei, Pleuronectiformes: Achiridae) em Itapissuma-PE. *Boletim do Laboratório de Hidrobiologia, 10*(1), 79-95.

Alves, V. E., Patrício, J., Dolbeth, M., Pessanha, A., Palma, A. R., Dantas, E. W., & Vendel, A. L. (2016). Do different degrees of human activity affect the diet of Brazilian silverside *Atherinella brasiliensis*? *Journal of Fish Biology, 89*(2), 1239-1257. DOI: http://dx.doi.org/10.1111/jfb.13023

Barnes, R. S. K., Calow, P. J. W., & Golding, D. W. (2008). *Os invertebrados. Uma síntese*. São Paulo, SP: Atheneu.

Barros, F., Hatje, V., Figueiredo, M. B., Magalhães, W. F., Dórea, H. S., & Emídio, E. S. (2008). The structure of the benthic macrofaunal assemblages and sediments characteristics of the Paraguaçu estuarine system, NE, Brazil. *Estuarine Coastal and Shelf Science, 78*(4), 753-762. DOI: http://dx.doi.org/10.1016/j.ecss.2008.02.016

Berg, J. (1979). Discussion of methods of investiganting the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Marine Biology, 50*(3), 263-273. DOI: http://dx.doi.org/10.1007/BF00394208

Blaber, S. J. M. (1997). Fish and Fisheries in Tropical Estuaries. New York: Springer Netherlands.

Braga, R. R., Bornatowski, H., & Vitule, J. R. S. (2012). Feeding ecology of fishes: an overview of worldwide publications. *Reviews in Fish Biology and Fisheries, 22*(4), 915-929. DOI: http://dx.doi.org/10.1007/s11160-012-9273-7

Brodeur, R. D., Smith, B. E., Mcbride, R. S., Heintz, R., & Farley, E. (2017). New perspectives on the feeding ecology and trophic dynamics of fishes. *Environmental Biology of Fishes, 100*(4), 293-297.

Brown, S. C., Bizzarro, J. J., Cailliet, G. M., & Ebert, D. A. (2011). Breaking with tradition: redefining measures for diet description with a case of the Aleutian Skate *Bathyraja aleutica*. *Environmental Biology of Fishes, 95*(1), 3-20. DOI: http://dx.doi.org/10.1007/s10641-011-9959-z

Brusca, R. C., & Brusca, G. J. (2007). *Invertebrados*. Rio de Janeiro, RJ: Guanabara-Koogan.

Campos, D. M. A., Silva, A. F., Sales, N. S., Oliveira, R. E. M. C., & Pessanha, A. L. M. (2015). Trophic relationships among fish assemblages on a mudflat within a Brazilian Marine protected area. *Brazilian Journal of Oceanography, 63*(2), 429-442. DOI: http://dx.doi.org/10.1590/S1679-87592015091306302

Carpenter, K. E. (2002). *The living marine resources of the Western Central Atlantic. Volume 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals* (FAO species identification guide for fishery purposes and american society of ichthyologists and herpetologists special publication n. 5, p. 1375-2127). Rome, IT: FAO.

Cirano, M., & Lessa, G. C. (2007). Oceanographic characteristics of Baía de Todos Santos, Brasil. *Revista Brasileira de Geofísica, 25*(4), 363-387. DOI: http://dx.doi.org/10.1590/S0102-261X2007000400002

Claudino, M. C., Pessanha, A. L. M., Araújo, F. G., & Garcia, A. M. (2015). Trophic connectivity and basal food sources sustaining tropical aquatic consumers along a mangrove to ocean gradient. *Estuarine Coastal and Shelf Science, 167*(Part A), 45-55. DOI: http://dx.doi.org/10.1016/j.ecss.2015.07.005

Contente, R. F., Stefanoni, M. F., & Spach, H. L. (2011). Feeding ecology of the Brazilian Silverside *Atherinella brasiliensis* (Atherinopsidae) in a sub-tropical estuarine ecosystem. *Journal of the Marine Biological Association of the United Kingdom, 91*(6), 1197-1205. DOI: http://dx.doi.org/10.1017/S0025315410001116

Costa, C., Ide, S., & Simonka, C. E. (2006). *Insetos imaturos: metamorphose e identificação*. São Paulo, SP: Holos.

Couto, E. C. G., Guimarães, F. J., & Oliveira, C. A. M. (2013). O camarão Sete-barbas na Bahia: aspectos da sua pesca e biologia. *Boletim do Instituto de Pesca, 39*(3), 263-282. DOI: http://dx.doi.org/10.20950/1678-2305.2013v39n3p263

Day, J. W., Yanz-Arancibia, A., Kemp, W. M., & Crump, B. C. (2012). Introduction to estuarine ecology. In J. W. Day, A. Yanz-Arancibia, W. M. Kemp, & B. C. Crump (Eds.), *Estuarine ecology* (p. 1-20). New York, NY: John Wiley & Sons.

Duarte, L. O., & Garcia, C. B. (2004). Trophic role of small pelagic fishes in a tropical upwelling ecosystem. *Ecological Modelling, 172*(4), 323-338. DOI: http://dx.doi.org/10.1016/j.ecolmodel.2003.09.014

Elliott, M., & Mclusky, D. S. (2002). The need for definitions in understanding Estuaries. *Estuarine Coastal and Shelf Science*. 55(6), 815-827. DOI: http://dx.doi.org/10.1006/ecss.2002.1031

Elliott, M. Whitfild, A. K., Potter, I. C., Blaber, S. J. M., Cyrus, D. P., Nordlie, F. G., & Harrisson, T. V. (2007). The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries, 8*(3), 241-268. DOI: http://dx.doi.org/10.1111/j.1467-2679.2007.00253.x

Ferry, L. A., & Cailliet, G. M. (1996). Sample size and data analysis: are we characterizing and comparing diet properly? In D. Mackinlay, & Shearer (Eds.), *Feeding ecology and nutrition in fish,* (p. 71-80). São Francisco, American Fisheries Society.

França, S., Costa, M. J., & Cabral, H. N. (2009). Assessing habitat specific fish assemblages in estuaries along the Portuguese coast. *Estuarine Coastal and Shelf Science, 83*(1), 1-12. DOI: http://dx.doi.org/10.1016/j.ecss.2009.03.013

Fransozo, A., & Negreiros-Fransozo, M. L. (2016*). Zoologia dos invertebrados*. Rio de Janeiro, RJ: Roca.

Garcia, A. F. S., Garcia, A. M., Vollrath, S. R., Schneck, F., Silva, C. F. M., Marchetti, Í. J., & Vieira, J. P. (2018). Spatial diet overlaps and food resource in two congeneric mullet species revealed by stable isotopes and stomach content analyses. *Community Ecology, 19*(2), 116-124. DOI: http://dx.doi.org/10.1556/168.2018.19.2.3

Garcia, A. M., &Vieira, J. P. (2001). O aumento da diversidade de peixes no estuário da Lagoa dos Patos durante o episódio El Niño 1997-1998. *Atlântica, 23*(1),133-152.

Garcia, A. M., Vieira, J. P., Winemiller, K. O., & Grimm, A. (2004). Comparison of 1982–1983 and 1997–1998 el niño effects on the shallow-water fish assemblage of the Patos Lagoon Estuary (Brazil). *Estuaries, 27*(1), 905-914. DOI: http://dx.doi.org/10.1007/BF02803417

Garrison, L. D., & Link, J. S. (2000). Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. *Marine Ecology Progress Series, 202*(1), 231-240. DOI: http://dx.doi.org/ 10.3354/meps202231

Hatje, V., & Andrade, J. B. (2009). *Baía de Todos os Santos: aspectos oceanográficos.* Salvador, BA: EDUFBA.

Helfman, G. S., Collette, B. B., Facey, D. E., & Bowen, B. W. (2009*). The diversity of fishes*. Mandel, MA: Blackwell Science.

Kawakami, E., & Vazzoler, G. (1980). Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico, 29*(2), 205-207. DOI: http://dx.doi.org/10.1590/S0373-55241980000200043

Krumme, U., Keuthen, H., Saint-Paul, U., & Villwock, W. (2007). Contribution to the feeding ecology of the banded puffer fish *Colomesus psittacus* (Tetraodontidae) in north Brazilian mangrove creeks. *Brazilian Journal of Biology, 67*(3), 383-392. DOI: http://dx.doi.org/10.1590/S1519-69842007000300002

Lessa, G. C., Cirano, M., & Genz, F. (2009). *A oceanografia física da Baía de Todos os Santos*. In J. Andrade, & V. Hatje (Eds.), *Baía de Todos os Santos: aspectos oceanográficos* (p. 69-119). Salvador, BA: EDUFBA.

Lessa, G. C., Souza, M. F. L., Mafalda, P. O., Gomes, D. F., Souza, C. S., Teixeira, C. E. P., ... Zucchi, M. R. (2018). Variabilidade intra-anual da oceanografia da Baía de Todos os Santos: evidências de três anos de monitoramento. In V. Hatje., L. M. V. Dantas., & J. B. Andrade (Eds.), *Baía de Todos os Santos: avanços nos estudos de longo prazo* (p. 157-192). Salvador, BA: EDUFBA.

Lima, C. S. S, Clark, F. J. K., Sales, N., & Pessanha, A. (2018). Strategies of resource partitioning between two sympatric puffer fishes in a tropical hypersaline estuary, Brazil. *Environmental Biology of Fishes, 101*(7), 1105-1119. DOI: http://dx.doi.org/10.1007/s10641-018-0729-z

Magurran, A. E., Khachopisitsak, S., & Amhad, A. B. (2011). Biological diversity of fish communities: pattern and process. *Journal of Fish Biology, 6*(79), 1393-1412. DOI: http://dx.doi.org/10.1111/j.1095-8649.2011.03091.x

Martinho, F. Cabral, H. N., Azeiteiro, U. M., & Pardal, M. (2012). Estuarine nursery for marine fishes: connecting recruitment variability with sustainable fisheries management. *Management of Environmental Quality an International Journal, 23*(4), 414-433. DOI: http://dx.doi.org/10.1108/14777831211232236

Medeiros, A. P. M., Xavier, J. H. A., Silva, M. B., Aires-Souza, L., & Rosa I. M. L. (2018). Distribution patterns of the fish assemblage in the Mamanguape River estuary, Northeastern Brazil. *Marine Biology Reseach, 14*(5), 524-536. DOI: http://dx.doi.org/10.1080/17451000.2018.1459724.

Moraes, L. E., Paes, E., Garcia, A. M., Möller, O., & Vieira, J. (2012). Delayed response of fish abundance to environmental changes: a novel multivariate time-lag approach. *Marine Ecology Progress Series, 456*(1), 159-168. DOI: http://dx.doi.org/10.3354/meps09731

Mouillot, D., Dumay, O., & Tomasini, J. A. (2007). Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine Coastal and Shelf Science, 71*(3-4), 443-456. DOI: http://dx.doi.org/10.1016/j.ecss.2006.08.022

Oliveira, M. C. L. M., Bastos, R.F., Claudino, M. C., Assumpção, C. M., & Garcia, A. M. (2014). Transport of marine-derived nutrients to subtropical freshwater food webs by juvenile mullets: a case study in southern Brazil. *Aquatic Biology, 20*(1), 91-100. DOI: http://dx.doi.org/10.3354/ab00544

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D, ... Wagner, H. (2019). *Package 'vegan': community ecology package* (R package version 2, 4-6). Retrieved from https://CRAN.R-project.org/package=vegan

Pessanha, A. L. M., Araújo, F. G., Oliveira, R. E. M. C. C., Silva, A. F., & Sales, N. S. (2015). Ecomorphology and resource use by dominant species of tropical estuarine juvenile fishes. *Neotropical Ichthyology, 13*(2), 401-412. DOI: http://dx.doi.org/10.1590/1982-0224-20140080

Potter, I. C., Tweedley, J. R., Elliott, M., & Whitfield, A. K. (2013). The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish Fisheries, 16*(2), 230-239. DOI: http://dx.doi.org/10.1111/faf.12050

Reis-Filho, J. A., Nunes, J. A. C. C., & Ferreira, A. (2010). Estuarine Ichthyofauna of the Paraguaçu River, Todos os Santos Bay, Bahia, Brazil. *Biota Neotropica, 10*(4), 301-312. DOI: http://dx.doi.org/10.1590/S1676-06032010000400034

R Core Team (2019). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna, AU: R.Core Team. https://www.R-project.org/

Raimonet, M., Cloern, J. E. (2016). Estuary-Ocean connectivity: fast physics, slow biology. *Global Change Biology* 23(6), 2345-2357. DOI: http://dx.doi.org/10.1111/gcb.13546

Ross, L. G., Martínez-Palacios, C. A., Valdez, M.C. A., Beveridge, M. C. M., & Sanchez, M. C. C. (2006). Determination of feeding mode in fishes: the importance of using structural and functional feeding studies in conjunction with gut analysis in a selective zooplanktivore *Chirostoma estor estor* Jordan 1880. *Journal of Fish Biology, 68*(6), 1782-1794. DOI: http://dx.doi.org/10.1111/j.1095-8649.2006.01061.x

Sales, N. S., Baeta, A. S. B. V., Lima, L. G., & Pessanha, A. L. M. (2017). Do the shallow-water habitats of a hypersaline tropical estuary act as nursery grounds for fishes? *Marine Ecology, 39*(1), 1-12. DOI: http://dx.doi.org/10.1111/maec.12473

Santos, A. C. A., Castullucci, F. R. C., Nepomuceno, C. F., Santos, E. P., & Sena, M. P. (1999). Distribuição e recrutamento do peixe-rei *Atherinella brasiliensis* (Ostheychthyes, Atherinidae) na margem continental oeste da Baía de Todos os Santos, Bahia, Brasil. *Acta Biologica Leopoldensia, 21*(1),107-118.

Santos, A. C. A., & Rodriguez, F. N. C. (2011). Ocorrência e alimentação do baiacu *Sphoeroides testudineus* (Actinopterygii – Tetraodontiformes) na margem oeste da Baía de Todos os Santos, Bahia, Brasil. *Sitientibus, 11*(1), 31-36. DOI: http://dx.doi.org/10.13102/scb81

Santos, E. P., Santos, A. C. A., Moraes, L. E., Condini, M. V., & Garcia, A. M. (2020). Spatio-temporal changes in assimilation of basal food sources by fish assemblages of a large tropical bay in the SW Atlantic Ocean. *Estuaries and Coasts, 43*(4), 894-908. DOI: http://dx.doi.org/10.1007/s12237-020-00716-1

Targett, T. E. (1978). Food resource partitioning by the pufferfishes *Sphoeroides splengleri* and *S. testudineus* from Biscayne Bay, Florida. *Marine Biology, 49*(1), 83-91. DOI: http://dx.doi.org/10.1007/BF00390732

Taylor, J. C., Harding, W. R., & Archibald, C. G. M. (2007). *A method manual for the collection, preparation and analysis of diatom samples*. Gezina, South Africa: Water Research Commission.

Vale, C. C., & Schaeffer-Noveli, Y. (2018). A zona costeira do Brasil e os manguezais. In Brasil, Ministério do Meio Ambiente, Instituto Chico Mendes de Conservação da Biodiversidade, *Atlas dos Manguezais do Brasil* (p. 37-56). Brasília DF: Instituto Chico Mendes de Conservação da Biodiversidade.

Vasconcelos-Filho, A. L., Neumann-Leitão, S., Eskinazi-Leça, E., Schwamborn, R., & Oliveira, A. M. E. (2010). Hábitos alimentares de peixes consumidores secundários do Canal de Santa Cruz, Pernambuco, Brasil. *Tropical Oceanography, 38*(2), 122-129. DOI: http://dx.doi.org/10.5914/tropocean.v38i2.5166

Vasconcelos-Filho, A. L., Neumann-Leitão, S., Eskinazi-Leça, E., Schwamborn, R., Oliveira, A. M. E., & Paranaguá M. N. (2003). Trophic interactions between fish and other compartiment communities in a tropical estuary in Brazil as indicator of environmental quality. *Transactions on Ecology and the Environment, 63*(1), 173-183. DOI: http://dx.doi.org/10.2495/ECO030161

Vasconcelos-Filho, A. L., Silva, K. C., & Acioli, F. D. (1998). Hábitos alimentares de *Sphoeroides testudineus* (Linnaeus, 1758) (Teleostei: Tetraodontidae), no Canal de Santa Cruz, Itamaracá-PE. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, 26*(1), 145-157. DOI: http://dx.doi.org/10.5914/tropocean.v26i1.2759

Withfield, A. K. (2015). Why are there so few freshwater fish species in most estuaries? *Journal of Fish Biology. 86*(4), 1227-1250. DOI: http://dx.doi.org/10.1111/jfb.12641