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*Research Article*

# Diet and trophic organization of the fish assemblage from the Mamanguape River Estuary, Brazil

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**ABSTRACT.** The present work aims to characterize a fish assemblage from a northeastern Brazilian estuary according to its diet and trophic organization along the estuarine-reef gradient. Sampling was performed at the Mamanguape Estuary, and fishes were collected using three types of nets at seventeen sites, grouped into four regions according to salinity range: reefs and the lower, middle, and upper estuary. The most abundant species were *Atherinella brasiliensis, Mugil curema,* and *Sphoeroides testudineus*. The highest species abundance and richness was observed for the lower estuary. Zooplankton was the most consumed category, recorded for forty-two species. Among the guilds, piscivores were the most abundant, followed by crab eaters. Herbivores, mostly represented by *Abudefduf saxatilis,* had a higher abundance in reefs, being correlated according to ANOSIM analysis to this region, while piscivores and crab eaters showed a high contribution to inner regions of the Mamanguape Estuary.

**Keywords:** guilds, feeding ecology, niche partitioning, estuarine-reef gradient, piscivores, herbivores.

## INTRODUCTION

Tropical estuaries are characterized by the presence of mangrove environments (Faunce & Serafy, 2006; Nagelkerken *et al*., 2008) that have high structural complexity, serving as substrates for algae development and diatom colonization (Hindell & Jenkins, 2004); therefore, tropical estuaries have high resource availability (Wang *et al*., 2009). Estuarine environments play an especially important role as nurseries, as they have characteristics that are advantageous for young individuals, such as high temperatures, high prey availability, and refuge from predators, which may increase growth rates and survival (Beck *et al*., 2001; Potter *et al*., 2015).

Diet and feeding ecology studies are important to understand ecosystems, as they may elucidate the trophic relationships and, indirectly, the energy flow between species (Yáñez-Arancibia & Nugent, 1977; Hajisamaea *et al*., 2003; Correa *et al*., 2011; Campos *et al*., 2015). This information may also aid ecosystem management, as it can be used to construct trophic models (Elliott *et al*., 2002; Dantas *et al*., 2013) or be applied to studies of trophic ecology that include spatial, seasonal and ontogenetic changes in the diet of species (Guedes *et al*., 2015).

In the same direction, knowing guilds is essential to understanding the community structure of complex ecosystems (Garrison & Link, 2000). Competitive interactions are much stronger within than between different guilds in a given community (Root, 1967; Pianka, 1980), and when competition is for food resources, it could affect patterns of habitat selection, niche overlap and diel activity (David *et al*., 2007).

Competition happens when two or more organisms (or populations, for example) interfere with or inhibit each other (Pianka, 1981), which occurs when organisms share a given resource (*i.e*., habitat, food), but only if the shared resources are limited (Pianka, 1974; Sánchez-Hernandez *et al*., 2011). Thus, diet analysis is useful for understanding interspecific interactions and the mechanisms that determine food partitioning between species (Dantas *et al*., 2013).

The present study investigated the diet of a fish assemblage along a mangrove-reef gradient, describing the trophic relationships between different fish species

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and guilds (or trophic groups) structured according to food resources.

## MATERIALS AND METHODS

### Study area

The study was conducted at the Mamanguape River Estuary, located in the Mamanguape River Environmental Protection Area (EPA), on the northern coast of the state of Paraíba, between coordinates 06º43’02”-05º16’54”S and 35º07’46”-34º54’00”W (Brasil, 2014) (Fig. 1).

Ecosystems such as mangroves, sandstone reefs, Atlantic Forest, restinga forest, dunes, lagoons, lakes, beaches, and reef formations are included in the EPA. The mangrove that borders the Mamanguape Estuary is very dense and the most well preserved in the state (Brasil, 2014).

There is an extensive sandstone reef belt adjacent to the estuary (Silva, 2002) that becomes partially exposed during low tides, revealing an extremely complex plateau, forming tide pools (Xavier *et al*., 2012).

### Fish collection

Twelve fish collections were carried out over two non-consecutive years. Six collections were performed during the dry season (October 2011, November 2011, January 2012, November 2012, October 2014 and February 2015) and six during the rainy season (March 2012, May 2012, July 2012, September 2012, April 2015 and August 2015).

Seventeen sites were selected, from the reef to the upper portion of the estuary, reaching salinity 0 (Fig. 1). The samples were performed during the day, always during spring tides (0.0 to 0.3 m), using three types of nets: a cast net (3 m radius, 12 mm mesh), a trawl (10 m length, 2 m height and 12 mm mesh) and a drifting gillnet (50 m length, 1 m height and 12 mm mesh). At the reef, only the cast net was used due to the presence of submerged sandstone blocks, which made it impossible to use other types of fishing gear.

The individuals collected were anesthetized with clove oil (according to Cunha & Rosa, 2006), and preserved in 10% formalin. In the laboratory, species were identified by consulting specialized literature (Figueiredo & Menezes, 1978, 1980, 2000; Menezes & Figueiredo, 1980, 1985; Carpenter, 2002a, 2002b) and consultation with specialists (from the Systematics and Ecology Department at Federal University of Paraíba). The standard and total lengths of all specimens were measured using calipers.

### Diet analysis

Diet was analyzed directly from stomach contents. Food items were quantified using the occurrence method (Hyslop, 1980) and the rapid volumetric method or biovolume (Hellawell & Abel, 1971). The use of volume percent, compared to the frequency of occurrence, was considered a better metric for quantifying the relative importance of different food items (Bowen, 1996). Therefore, the frequency of occurrence (%FO) and biovolume (%VO) was used to calculate the feeding index (FI) (Kawakami & Vazzoler, 1980), using the formula $FI = (FO_i \times VO_i)/\sum(FO \times VO)$.

Thirty-three food items were identified and grouped into the 15 food categories: Plant material (unidentified plant remains); algae; phytoplankton; sessile invertebrates; zooplankton; meiofauna; annelida/worms; mollusks; bivalves; unidentified crustaceans; shrimp; Brachyura (crabs); insects; Teleostei; sediment, following pertinent literature (Stachowitsch, 1992; Ruppert *et al*., 2005; Brusca & Brusca, 2007) and consultation with specialists (from the Systematics and Ecology Department as cited before).

Species with more than 40 individuals collected were considered abundant when compared to other species abundances between all species captured during the study. Similar sample abundances or less were used by other studies to describe diet, trophic ecology or patterns of distribution in fish species (Nagelkerken & Van der Velde, 2004; Hammerschlag *et al*., 2010; Campos *et al*., 2015).

### Feeding niche overlap analysis

Feeding niche overlap was analyzed, using the volume percent of each prey category, to determine whether there was feeding niche overlap, using the software EcoSim (Gotelli & Entsminger, 2003). Pianka's index (Pianka, 1974) of niche overlap was used in the analysis.

The resulting index values varied between 0, indicating that the two species shared no resources (no niche overlap), and 1, indicating that the two species shared exactly the same resources (complete overlap) (Krebs, 1989). Based on this similarity matrix, a cluster analysis was performed to identify feeding guilds, or groups, using Primer 6.0 Software. Sediment was excluded from this analysis.

After identification of the different trophic guilds, an analysis of similarity (ANOSIM) was conducted to test for differences within each trophic guild between different seasons (dry and rainy) and regions (reefs and lower, middle and upper estuary). A similarity percentage (SIMPER) analysis was conducted, when

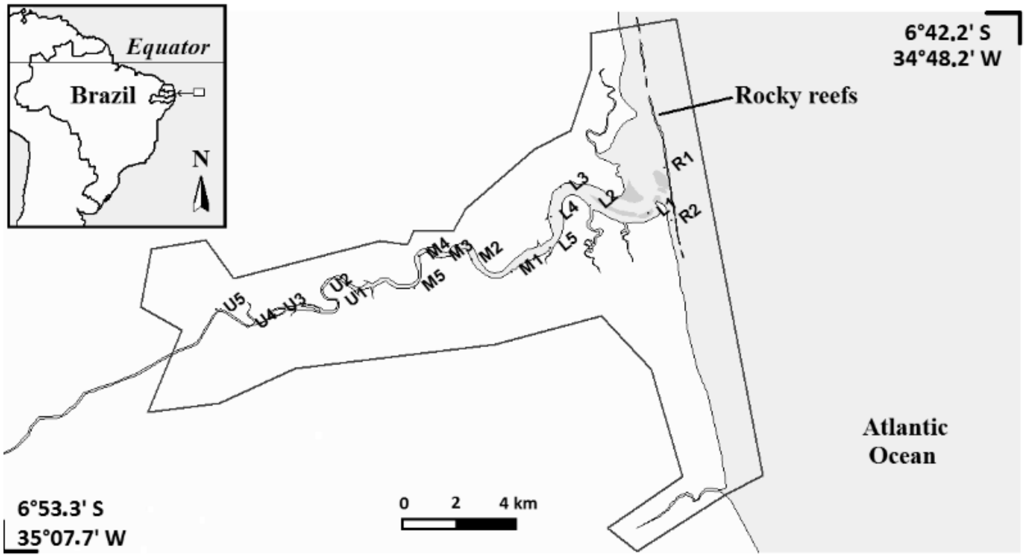

**Figure 1.** Map of the Mamanguape River Estuary, Paraíba, Brazil, showing the collection points. The line indicates the perimeter of the Mamanguape Environmental Protection Area.

the ANOSIM analysis was significative ($P < 0.05$), to determine the contribution of each guild to the observed similarity (or dissimilarity) between different seasons and regions, using Primer 6.0 Software.

## RESULTS

### Fish fauna

A total of 1590 individuals from 56 species were collected (Table 1). The most abundant species was *Atherinella brasiliensis* (Quoy & Gaimard, 1825), followed by *Sphoeroides testudineus* (Linnaeus, 1758) and *Mugil curema* Valenciennes, 1836.

The highest species abundance and richness was observed for the lower estuary (n = 41), while the upper portion showed the lowest richness (n = 21).

Although species richness was low in reefs (n = 23), if compared with estuarine regions, most of the species were only found in this region such as *Acanthurus bahianus*, *Anisotremus surinamensis*, *Anisotremus virginicus*, *Haemulon parra*, *Haemulon plumierii*, *Etropus crossotus*, *Abudefduf saxatilis*, *Stegastes fuscus*, *Sparisoma axillare* and *Epinephelus adscensionis*.

Some species occurred along all the study area, from reefs to upper portions, like *Anchovia clupeoides*, *Caranx latus*, *Centropomus undecimalis*, *Eucinostomus argenteus*, *Lutjanus jocu*, *Mugil curema* and *Oligoplites palometa*.

Most species occurring in reefs, such as *Abudefduf saxatilis*, were only present in reefs, whereas species collected in the estuary, such as *C. latus*, *C. undecimalis*, and *Opistonema oglinum*, occupied more than one estuary region and sometimes the reefs as well (Table 1).

The most frequently food categories observed were zooplankton, shrimp, Brachyura, and Teleostei. The feeding index showed that *A. brasiliensis*, *C. undecimalis*, *Gobionellus oceanicus* and *S. testudineus* consumed all food categories recorded in the present study to some degree (Table 2). Zooplankton was the most frequent food category, found in the stomach content of 43 fish species, followed by Teleostei and Brachyura.

### Diet of abundant species

Sixteen species were considered abundant in this study. Most of the abundant species consumed invertebrates in different quantities (Table 2). *Anchoa spinifer*, *A. tricolor*, *Atherinella brasiliensis*, *C. undecimalis*, *E. argenteus*, *O. oglinum* and *S. brasiliensis* diets consisted mainly of zooplankton, followed by one of these categories: Brachyura (for *A. spinifer*, *A. tricolor*, *A. brasiliensis* and *C. undecimalis*), Annelida (for *Eucinostomus argenteus*), phytoplankton (for *O. oglinum*) or Teleostei (for *Sardinella brasiliensis*).

Zooplankton and Brachyura were also the main categories consumed by *Centropomus undecimalis* and *Sciades herzbergii*. While *Bathygobius soporator* consumed Brachyura and Teleostei mostly.

**Table 1.** Total abundance (n = 1590), species abundance, distribution based on relative abundance for each species, total length (±SD) and Guilds based on diet analysis of fish species collected in the Mamanguape River Estuary, Paraíba, Brazil. n: individuals number, R: reefs, L: lower estuary, M: middle estuary, U: upper estuary. Guilds: I. Herbivorous, II. Invertivore (mainly shrimps), III. Zooplanktivore, IV. Invertivore (mainly crabs), V. Piscivore.

| Family | Species | Code | TL (mm SD) | n | Relative abundance/region | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | R | L | M | U | Guild |
| Acanthuridae | *Acanthurus bahianus* Castelnau, 1855 | Acabah | 112.7 ± 19.7 | 1 | 1 | | | | I |
| Achiridae | *Achirus declivis* Chabanaud, 1940 | Achdec | 102.5 ± 28.1 | 9 | | 0.11 | 0.89 | | V |
| Achiridae | *Achirus lineatus* (Linnaeus, 1758) | Achlin | 120.8 ± 67.5 | 5 | | 0.20 | 0.80 | | IV |
| Ariidae | *Aspistor quadriscutis* (Valenciennes, 1840) | Aspqua | 101 ± - | 1 | | 1 | | | II |
| Ariidae | *Cathorops spixii* (Agassiz, 1829) | Catspi | 100 ± 1 | 3 | | 0.67 | 0.33 | | III |
| Ariidae | *Sciades herzbergii* (Bloch, 1794) | Sciher | 100 ± 15 | 72 | | 0.03 | 0.96 | 0.01 | IV |
| Atherinopsidae | *Atherinella brasiliensis* (Quoy & Gaimard, 1825) | Athbra | 100.9 ± 15 | 203 | | 0.58 | 0.01 | 0.40 | III |
| Batrachoididae | *Thalassophryne nattereri* Steindachner, 1831 | Thanat | 80 ± - | 1 | | 1 | | | IV |
| Belonidae | *Strongylura timucu* (Walbaum, 1792) | Strtim | 341.3 ± 22.7 | 7 | | 0.29 | 0.14 | 0.57 | II |
| Carangidae | *Caranx latus* Agassiz, 1831 | Carlat | 94.6 ± 23.9 | 58 | 0.12 | 0.55 | 0.12 | 0.21 | V |
| Carangidae | *Oligoplites palometa* (Cuvier, 1832) | Olipal | 93.9 ± 17.7 | 13 | 0.08 | 0.46 | 0.38 | 0.08 | V |
| Centropomidae | *Centropomus pectinatus* Poey, 1860 | Cenpec | 120.6 ± 19.6 | 17 | | 0.41 | 0.59 | | V |
| Centropomidae | *Centropomus undecimalis* (Bloch, 1792) | Cenund | 138.1 ± 19.6 | 71 | 0.01 | 0.76 | 0.04 | 0.18 | III |
| Clupeidae | *Harengula clupeola* (Cuvier, 1829) | Harclu | 110.3 ± 9.2 | 4 | 0.75 | 0.25 | | | V |
| Clupeidae | *Opisthonema oglinum* (Lesueur, 1818) | Opiogl | 123.6 ± 21.6 | 58 | 0.05 | 0.907 | | 0.05 | III |
| Clupeidae | *Sardinella brasiliensis* (Steindachner, 1879) | Sarbra | 98.5 ± 7.2 | 64 | | 0.98 | 0.02 | | III |
| Cynoglossidae | *Symphurus tessellatus* (Quoy & Gaimard, 1824) | Symtes | 100 ± 12.2 | 14 | | 0.07 | 0.93 | | III |
| Dactylopteridae | *Dactylopterus volitans* (Linnaeus, 1758) | Dacvol | 102 ± - | 1 | | 1 | | | IV |
| Eleotridae | *Eleotris pisonis* (Gmelin, 1789) | Elepis | 96 ± - | 1 | | | | 1 | - |
| Elopidae | *Elops saurus* Linnaeus, 1766 | Elosau | 169.7 ± 39.4 | 9 | | 0.89 | | 0.11 | III |
| Engraulidae | *Anchoa spinifer* (Valeciennes, 1848) | Ancspi | 107.2 ± 9.2 | 47 | | 0.02 | 0.98 | | III |
| Engraulidae | *Anchoa tricolor* (Spix & Agassiz, 1829) | Anctri | 112.6 ± 22.2 | 53 | | 0.75 | 0.19 | 0.06 | III |
| Engraulidae | *Anchovia clupeoides* (Swainson, 1839) | Anvclu | 135.5 ± 20.5 | 44 | 0.07 | 0.70 | 0.20 | 0.02 | V |
| Ephippidae | *Chaetodipterus faber* (Broussonet, 1782) | Chafab | 102 ± - | 1 | | 1 | | | I |
| Gerreidae | *Diapterus rhombeus* (Cuvier, 1829) | Diarho | 83 ± 15.3 | 24 | | 0.25 | 0.58 | 0.17 | - |
| Gerreidae | *Eucinostomus argenteus* (Baird & Girard, 1855) | Eucarg | 86.4 ± 8.6 | 77 | 0.04 | 0.22 | 0.04 | 0.70 | III |
| Gerreidae | *Eucinostomus gula* (Quoy & Gaimard, 1824) | Eucgul | 88.8 ± 12.2 | 8 | 0.13 | 0.75 | | 0.13 | III |
| Gobiidae | *Bathygobius soporator* (Valenciennes, 1837) | Batsop | 94.3 ± 11.5 | 66 | | 0.59 | 0.41 | | IV |
| Gobiidae | *Gobionellus oceanicus* (Pallas, 1770) | Goboce | 172.9 ± 47.1 | 46 | | 0.11 | 0.67 | 0.22 | IV |
| Haemulidae | *Anisotremus surinamensis* (Bloch, 1791) | Anisur | 77.3 ± 12.6 | 2 | 1 | | | | IV |
| Haemulidae | *Anisotremus virginicus* (Linnaeus, 1758) | Anivir | 140.5 ± 29.7 | 4 | 1 | | | | III |
| Haemulidae | *Haemulon parra* (Desmarest, 1823) | Haepar | 124.1 ± 28.3 | 14 | 1 | | | | IV |
| Haemulidae | *Haemulon plumierii* (Lacepède, 1801) | Haeplu | 94 ± 9.9 | 2 | 1 | | | | IV |
| Hemiramphidae | *Hyporhamphus roberti* (Valenciennes, 1847) | Hyprob | 145.9 ± 22.5 | 9 | | 0.22 | | 0.78 | - |
| Hemiramphidae | *Hyporhamphus unifasciatus* (Ranzani, 1841) | Hypuni | 159.5 ± 87 | 2 | | 0.5 | | 0.50 | IV |
| Lutjanidae | *Lutjanus alexandrei* Moura & Lindeman, 2007 | Lutale | 151.4 ± 35.8 | 5 | 0.20 | 0.60 | 0.20 | | IV |
| Lutjanidae | *Lutjanus jocu* (Bloch & Schneider, 1801) | Lutjoc | 121.9 ± 33.1 | 25 | 0.08 | 0.64 | 0.20 | 0.08 | IV |
| Lutjanidae | *Lutjanus synagris* (Linnaeus, 1758) | Lutsyn | 79 ± 4.9 | 4 | 0.25 | 0.75 | | | II |
| Mugilidae | *Mugil curema* Valenciennes, 1836 | Mugcur | 97.9 ± 17.3 | 104 | 0.06 | 0.52 | 0.34 | 0.09 | IV |
| Paralichthyidae | *Citharichthys spilopterus* Günther, 1862 | Citspi | 101 ± 23.5 | 82 | 0.02 | 0.24 | 0.73 | | V |
| Paralichthyidae | *Etropus crossotus* Jordan & Gilbert, 1882 | Etrcro | 102.5 ± 2.1 | 2 | 1 | | | | IV |
| Polynemidae | *Polydactylus virginicus* (Linnaeus, 1758) | Polvir | 128.1 ± 14.3 | 6 | | 0.67 | 0.33 | | III |
| Pomacentridae | *Abudefduf saxatilis* (Linnaeus, 1758) | Abusax | 112.2 ± 32.9 | 45 | 1 | | | | I |
| Pomacentridae | *Stegastes fuscus* (Cuvier, 1830) | Stefus | 120 ± 40.6 | 2 | 1 | | | | I |
| Scaridae | *Sparisoma axillare* (Steindachner, 1878) | Spaaxi | 113.5 ± 44.5 | 2 | 1 | | | | - |
| Sciaenidae | *Bairdiella ronchus* (Cuvier, 1830) | Bairon | 127.8 ± 23 | 5 | | | 1 | | II |
| Sciaenidae | *Cynoscion acoupa* (Lacepède, 1801) | Cynaco | 108 ± 7.5 | 3 | | 0.33 | 0.67 | | V |
| Sciaenidae | *Pogonias cromis* (Linnaeus, 1766) | Pogcro | 81 ± 6 | 4 | | 1 | | | V |
| Sciaenidae | *Stellifer brasiliensis* (Schultz, 1945) | Stebra | 83.5 ± 6.4 | 5 | | | 1 | | V |

Continuation

| Family | Species | Code | TL (mm SD) | n | Relative abundance/region | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | R | L | M | U | Guild |
| Serranidae | *Epinephelus adscensionis* (Osbeck, 1765) | Epiads | 203 ± - | 1 | 1 | | | | IV |
| Serranidae | *Rypticus randalli* Courtenay, 1967 | Rypran | 88.9 ± - | 1 | | | 1 | | V |
| Sphyraenidae | *Sphyraena barracuda* (Edwards, 1771) | Sphbar | 104.8 ± 30.6 | 4 | | 1 | | | V |
| Tetraodontidae | *Colomesus psittacus* (Bloch & Schneider, 1801) | Colpsi | 91.9 ± 16.1 | 12 | | 0.08 | 0.92 | | IV |
| Tetraodontidae | *Lagocephalus laevigatus* (Linnaeus, 1766) | Laglae | 102 ± - | 1 | | | | 1 | IV |
| Tetraodontidae | *Sphoeroides greeleyi* Gilbert, 1900 | Sphbar | 172.3 ± 66.4 | 14 | | 1 | | | V |
| Tetraodontidae | *Sphoeroides testudineus* (Linnaeus, 1758) | Sphgre | 82.9 ± 13.8 | 150 | | 0.32 | 0.59 | 0.09 | V |

*Gobionellus oceanicus* and *Mugil curema* exhibited a high volume of sediment in this study. Excluding sediment of the analysis, Brachyura appeared as the most important food item in both species diet.

Teleostei was the main component in the diet of *Anchovia clupeoides*, *Caranx latus*, *Citharichthys spilopterus* and *Sphoeroides testudineus*, followed by Brachyura (for *Anchovia clupeoides* and *Sphoeroides testudineus*), shrimp (for *Caranx latus*) and zooplankton (for *Citharichthys spilopterus*).

*Abudefduf saxatilis* was the only abundant specie in the present study in which its diet was basically composed by one food category: algae.

### Feeding niche overlap

The feeding niche overlap for the fish assemblage of the Mamanguape River Estuary was higher than expected ($P < 0.05$), indicating that the community was structured according to the available food resources. The cluster analysis grouped the species belonging to the genera *Eucinostomus* spp., *Anchoa* spp., *Sphoeroides* spp. and *Haemulon* spp. into the same feeding guilds (Fig. 2).

In other cases, however, species from the same genus were placed in different groups. This was the case for species from the genera *Achirus* spp., *Centropomus* spp. and *Lutjanus* spp.

*Diapterus rhombeus*, *Eleotris pisonis*, and *Hyporhamphus roberti* were not grouped with any guilds.

### Trophic groups

The cluster analysis, based on the trophic niche similarity matrix and diet, identified five different trophic groups (Fig. 2):

Group I Herbivores: *A. saxatilis*, *Acanthurus bahianus*, *Chaetodipterus faber* and *Stegastes fuscus*.

Group II Invertivores: mostly shrimps, *Aspistor quadriscutis*, *Bairdiella ronchus*, *Lutjanus synagris* and *Strongylura timucu*.

Group III Zooplanktivores: *A. tricolor*, *A. spinifer*, *Anisotremus virginicus*, *A. brasiliensis*, *Cathorops spixii*, *C. undecimalis*, *Elops saurus*, *E. argenteus*, *Eucinostomus gula*, *O. oglinum*, *Polydactylus virginicus*, *S. brasiliensis* and *Symphurus tesselatus*.

Group IV Invertivores: mostly Brachyura in addition to shrimp (*e.g.*, *A. lineatus* and *H. parra*), insects (*e.g.*, *Colomesus psittacus*), or zooplankton (*e.g. S. herzbergii*).

Group V Piscivore species: most of the diet was fishes and species that consumed fishes to different degrees as *C. latus*, *C. pectinatus*, *Cynoscion acoupa* and *Sphyraena barracuda*.

The ANOSIM revealed differences in guild distribution between the dry and rainy seasons ($r = 0.049$; $P < 0.05$) and between regions ($r = 0.22$; $P < 0.05$). The non-metric multidimensional scaling (nMDS) plot for the distribution of the trophic groups throughout the study area is presented in Figure 3.

According to the SIMPER analysis, the groups that contributed most to the structure of the fish assemblage during the rainy season were group V (piscivore), which consumed fishes and a smaller quantity of phytoplankton, and group IV (brachyuran consumers). In the dry season, group III, formed by zooplanktivorous species, constituted more than 40% of the fish assemblage. Groups III and IV contributed to the structure of the community along the study area in different stages. Group I (herbivores) was part of the fish assemblage observed in reefs, whereas group V (piscivores) contributed mainly to the lower and middle estuary (Table 3).

## DISCUSSION

### Fish diet

Most species analyzed here consumed zooplankton to some degree, which may be related to its availability. These findings are in accordance with Diniz (2011), who observed a high abundance of zooplankton in fish

**Table 2.** Feeding index (FI %) for fish species collected in the Mamanguape River Estuary, Paraíba, Brazil. In bold: abundant species.

| FI % | Plant Mat. | Algae | Phytoplankton | S. Inv. | Zooplankton | Meiofauna | Annelida | Mollusk | Bivalvia | Crustacean | Shrimp | Brachyura | Insects | Teleostei | Sediment |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abusax | **0** | **99.99** | **0** | **0** | **<0.01** | **0** | **0** | **0** | **0** | **<0.01** | **0** | **0** | **0** | **<0.01** | **0** |
| Acabah | 0 | 99.98 | 0 | 0 | <0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Achdec | 5.10 | 0 | 9.36 | 0 | 0.19 | 1.68 | 0 | 0 | 0 | 0 | 10.70 | 0 | 9.52 | 63.45 | 0 |
| Achlin | 0 | 0 | 0 | 0 | 13.03 | 0 | 2.1 | 0 | 0 | 0 | 53.24 | 24.98 | 0 | 6.22 | 0.42 |
| Ancspi | **0.17** | **<0.01** | **<0.01** | **0** | **81.58** | **0.03** | **0.86** | **<0.01** | **<0.01** | **0** | **0.54** | **15.8** | **<0.01** | **0.32** | **0.52** |
| Anctri | **0.29** | **0** | **4.01** | **<0.01** | **59.08** | **0.39** | **2.53** | **0.31** | **0.9** | **<0.01** | **1.12** | **15.97** | **1** | **13.93** | **0.76** |
| Anisur | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 91.74 | 0 | 8.26 | 0 |
| Anivir | 0 | 0 | 0 | 0 | 48.90 | 0.94 | 9.40 | 0 | 0 | 0 | 15.67 | 25.08 | 0 | 0 | 0 |
| Anvclu | **0.2** | **0.8** | **0.8** | **0.1** | **0.4** | **<0.01** | **0** | **<0.01** | **0.6** | **0** | **1.24** | **5.85** | **<0.01** | **90.49** | **0.23** |
| Aspqua | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 | 0 | 0 | 0 | 0 |
| Athbra | **0.34** | **<0.01** | **1.79** | **<0.01** | **72.58** | **0.14** | **5.25** | **0.03** | **0.1** | **0.02** | **0.89** | **15.55** | **0.003** | **2.97** | **0.03** |
| Bairon | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10.48 | 0 | 68.06 | 15.09 | 0 | 6.37 | 0 |
| Batsop | **0.69** | **<0.01** | **5.00** | **0** | **12.11** | **<0.01** | **0.55** | **<0.01** | **<0.01** | **<0.01** | **1.22** | **48.89** | **1.23** | **30.10** | **0** |
| Carlat | **<0.01** | **0** | **<0.01** | **0** | **1.37** | **0.15** | **<0.01** | **<0.01** | **<0.01** | **<0.01** | **11.21** | **1.51** | **0.37** | **85.21** | **0** |
| Catspi | 0 | 0 | 0 | 0.58 | 56.31 | 0 | 0.19 | 1.17 | 0 | 0 | 0 | 2.91 | 0 | 0 | 38.83 |
| Cenpec | 0 | 0 | 0 | 0.00 | 3.13 | 0 | 0.28 | 0 | 0 | 0.17 | 28.16 | 0 | 0 | 68.26 | 0 |
| Cenund | **0.35** | **<0.01** | **2.00** | **0.58** | **48.30** | **0.12** | **0.87** | **<0.01** | **0.25** | **<0.01** | **14.65** | **29.88** | **0.23** | **2.75** | **0** |
| Chafab | 0 | 60.00 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 |
| Citspi | **1.71** | **<0.01** | **13.05** | **<0.01** | **28.16** | **0.02** | **1.35** | **0** | **<0.01** | **<0.01** | **6.28** | **3.08** | **1** | **45.38** | **0.19** |
| Colpsi | 0 | 0 | 0 | 0.96 | <0.01 | 0 | 0 | 1.59 | 0 | 0 | 10.76 | 40.15 | 34.70 | 11.81 | 0 |
| Cynaco | 0 | 0 | 1.07 | 0 | 1.79 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10.79 | 86.33 |
| Dacvol | 0 | 0 | 0 | 0 | 2.70 | 0 | 0 | 0 | 0 | 0 | 0 | 97.30 | 0 | 0 | 0 |
| Diarho | <0.01 | 0 | 0 | 0 | 17.91 | 0.05 | 0.8 | 0 | <0.01 | 0.03 | 0.93 | 0 | 15 | 11.61 | 53.42 |
| Elepis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 | 0 | 0 | 0 | 0 | 0 |
| Elosau | 0.33 | 0 | 0.18 | 2.00 | 38.77 | <0.01 | 0.73 | <0.01 | 9.54 | 0 | 4.09 | 21.25 | 0 | 23.05 | 0 |
| Epiads | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 60.00 | 40.00 | 0 | 0 | 0 |
| Etrcro | 0 | 0 | 0 | 0 | 16.83 | 0 | 0 | 0 | 0 | 0 | 0 | 83.17 | 0 | 0 | 0 |
| Eucarg | **2.69** | **0** | **7.07** | **0.13** | **75.98** | **0.22** | **8.37** | **0.03** | **0.3** | **0.05** | **0.76** | **0.8** | **2** | **1.92** | **0.1** |
| Eucgul | 0.63 | 0 | 0.60 | 2.92 | 95.34 | 0.36 | 0.15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Goboce | **0.5** | **3.2** | **1.11** | **6.79** | **1.27** | **0.07** | **0.03** | **0.02** | **5** | **0.02** | **0.05** | **48.12** | **<0.01** | **0.04** | **33.61** |
| Haepar | 0 | 0 | 0 | 0 | 1.08 | <0.01 | 0 | 0 | 0 | 0 | 53.60 | 40.37 | 0 | 4.92 | 0 |
| Haeplu | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20.00 | 80.00 | 0 | 0 | 0 |
| Harclu | 0 | 0 | 54.05 | 0 | 0.54 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 34.59 | 10.81 |
| Hyprob | 53.36 | 0 | 0.23 | 6.96 | 0.93 | 0 | 0 | 0 | 9.74 | 0 | 1.39 | 15.78 | 11.60 | 0 | 0 |
| Hypuni | 0 | 0 | 0 | 0 | 6.15 | 0 | 15.38 | 0 | 0 | 0 | 0 | 70.77 | 7.69 | 0 | 0 |
| Laglae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.18 | 0 | 0 | 0 | 96.82 | 0 |
| Lutale | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 92.58 | 0 | 7.42 | 0 |
| Lutjoc | <0.01 | <0.01 | 0 | 0 | 0.15 | <0.01 | 0 | 0 | <0.01 | 0.03 | 16.65 | 80.22 | 0 | 2.83 | 0.04 |
| Lutsyn | 0 | 0 | 0 | 0 | <0.01 | 0 | 0 | 0 | 0 | 0 | 75.50 | 0 | 0 | 24.45 | 0 |
| Mugcur | **0.1** | **<0.01** | **<0.01** | **0** | **2.35** | **<0.01** | **<0.01** | **<0.01** | **<0.01** | **<0.01** | **0.04** | **3.66** | **0.001** | **1.83** | **91.77** |
| Olipal | 0 | 0 | <0.01 | 0 | 11.56 | <0.01 | 1.52 | <0.01 | 0 | 0 | 1.12 | 0.26 | 0.69 | 84.82 | 0 |
| Opiogl | **0.19** | **0** | **15.39** | **<0.01** | **75.01** | **<0.01** | **0.49** | **<0.01** | **0** | **0** | **0.49** | **3.36** | **0.002** | **4.3** | **0.51** |
| Pogcro | 0.20 | 0 | 0 | 0 | 47.06 | 0.20 | 0 | 0 | 0 | 5.49 | 0 | 0 | 0 | 47.06 | 0 |
| Polvir | 0 | 0 | 0.19 | 0 | 41.94 | 0 | 1.94 | 0 | 0.19 | 0 | 17.63 | 0 | 0 | 38.10 | 0 |
| Rypran | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 | 0 |
| Sarbra | **1.25** | **0** | **0.43** | **0** | **67.8** | **0.8** | **2.06** | **0** | **0** | **0** | **1.98** | **9.68** | **1** | **10.57** | **4.27** |
| Sciher | **4.4** | **<0.01** | **1.95** | **0** | **38.1** | **0.01** | **6.02** | **<0.01** | **<0.01** | **0.02** | **0.71** | **34.51** | **1** | **9.03** | **4.36** |
| Spaaxi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 |
| Sphbar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 | 0 |
| Sphgre | 0.66 | 8.29 | 0 | 0 | 38.25 | 0.16 | 0.21 | 0 | 7.53 | 0 | 0.78 | 1.03 | 9.66 | 33.44 | 0 |
| Sphtes | **1.27** | **<0.01** | **4.77** | **0.9** | **5.38** | **0.04** | **0.15** | **12.96** | **1.22** | **0.06** | **1.69** | **26.48** | **<0.01** | **33.72** | **0.23** |
| Stebra | 0.22 | 0 | 68.33 | 0 | 5.61 | 0 | 0 | 0 | 0 | 0 | 0 | 25.06 | 0 | 0 | 0.75 |
| Stefus | 0 | 100.00 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Strtim | 0 | 0 | 0 | 0 | 0.13 | 0 | 1.20 | 0 | 0 | 0 | 73.72 | 0.51 | 0 | 24.44 | 0 |
| Symtes | <0.01 | 0 | 0 | 0 | 87.44 | <0.01 | 0.24 | 0 | <0.01 | 0 | 0.12 | 12.08 | 0 | 0 | 0 |
| Thanat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100.00 | 0 | 0 | 0 |

diets at Barra de Mamanguape. Campos *et al*. (2015) studied 17 fish species from Barra do Mamanguape and observed high consumption of zooplankton. Zooplankton may play a fundamental role in the equilibrium of the studied ecosystem, especially considering the high percentage of young individuals of several different species presented in the current study that consumed this category.

It is important to notice that most species did not consume exclusively one resource, but abundant fish species consumed more than one resource in different proportions, mostly zooplankton. These results corroborate Guedes *et al*. (2015), who conducted a study at Sepetiba Bay, Rio de Janeiro, and suggested several factors that promote niche partitioning in that tropical fish community.

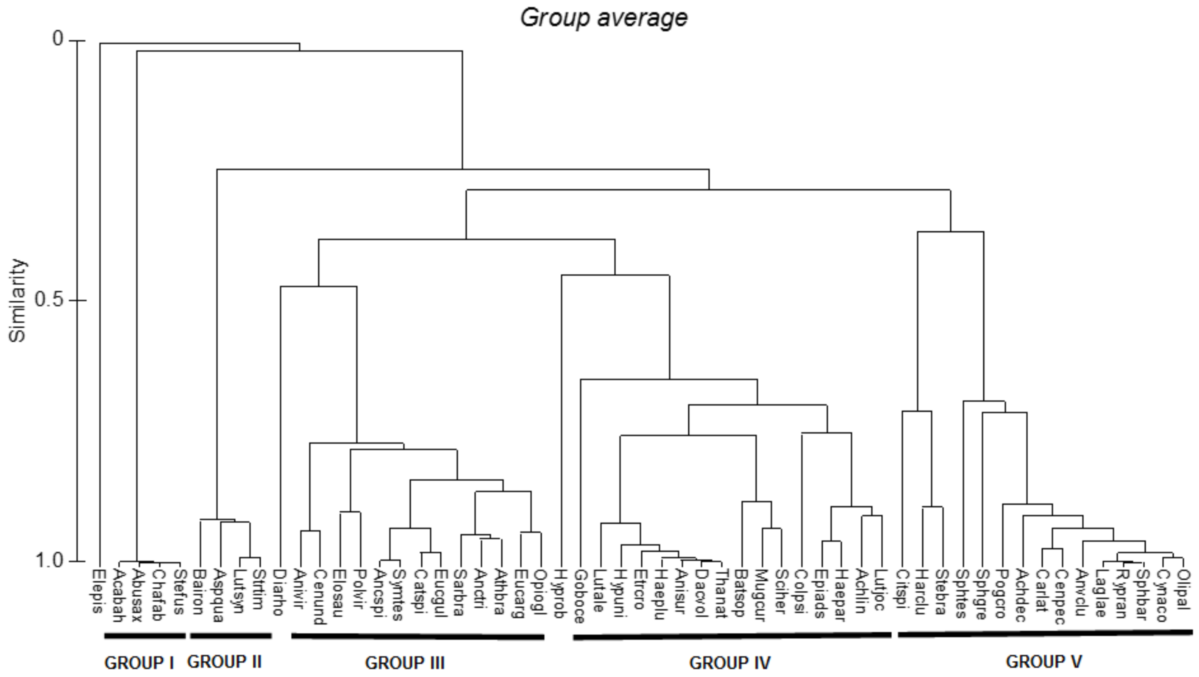

**Figure 2.** Cluster analysis, based on Pianka's similarity matrix, for fish species from the Mamanguape River Estuary, Paraíba, Brazil.

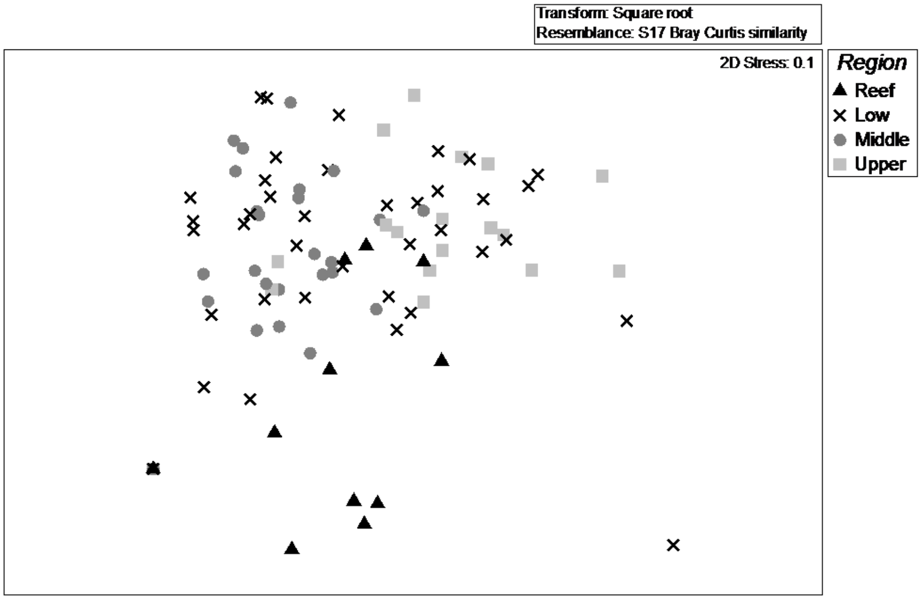

**Figure 3.** Non-metric multidimensional scaling (nMDS) plot for the trophic groups identified at the Mamanguape Environmental Protection Area. The regions shown are the upper estuary, middle estuary, lower estuary and the reefs.

Some species as *Atherinella brasiliensis*, *Caranx latus*, and *Centropomus undecimalis* had more than one food category playing a fundamental role in their diets. Such variation in diet items may supplement fish demand, compensating for the scarcity of other food resources. As shown in Table 4, the abundant species with the main consumed items and examples of other studies which support our findings.

In such environments as estuaries, with variations in physical and chemical characteristics, increasing the range of food resources consumed is a good strategy for individuals. These differences were mostly observed in

**Table 3.** Percentage contributions of the different trophic groups per region identified at the Mamanguape River Estuary, Brazil.

| Region | Trophic groups (guilds) | Main category | % Contribution |
|---|---|---|---|
| Reefs | | | |
| Average similarity: 54.28% | IV | Brachyura | 61.63 |
| | I | Macroalgae | 26.44 |
| | III | Zooplankton | 4.72 |
| Lower Estuary | | | |
| Average similarity: 45.09% | V | Teleostei | 44.55 |
| | III | Zooplankton | 37.38 |
| | IV | Brachyura | 17.73 |
| Middle Estuary | | | |
| Average similarity: 58.22% | V | Teleostei | 55.81 |
| | IV | Brachyura | 30.54 |
| | III | Zooplankton | 13.63 |
| Upper Estuary | | | |
| Average similarity: 58.22% | III | Zooplankton | 77.41 |
| | V | Teleostei | 14.42 |

**Table 4.** Main items consumed by abundant fish species at the Mamanguape River Estuary, Brazil. *Studies based on Engraulidae family; **Studies based on Clupeidae family.

| Species | Main items | Other studies |
|---|---|---|
| *Abudefduf saxatilis* | Macroalgae | Randall (1967) (Described as omnivorous) |
| *Anchovia clupeoides* | Teleostei | Stergiou & Karpouzi (2001); Bacha *et al*. (2010); Zhang *et al*. (2013)* |
| *Anchoa tricolor* | Zooplankton | Stergiou & Karpouzi (2001); Bacha *et al*. (2010); Zhang *et al*. (2013)* |
| *Ancha spinifer* | Zooplankton | Stergiou & Karpouzi (2001); Bacha *et al*. (2010); Zhang *et al*. (2013)* |
| *Atherinella brasiliensis* | Zooplankton, Brachyura | Campos *et al.* (2015) |
| *Bathygobius soporator* | Brachyura, Teleostei | Lawson & Thomas, (2010) |
| *Caranx latus* | Teleostei, Crustaceans | Niang *et al.* (2010); Santic *et al.* (2013) |
| *Centropomus undecimalis* | Teleostei, Zooplankton | Luczkovich *et al.* (1995); Araujo *et al.* (2011) |
| *Citharichthys spilopterus* | Teleostei | Castillo-Rivera *et al.* (2000); Guedes & Araujo (2008) |
| *Eucinostomus argenteus* | Zooplankton, Worms | Branco *et al.* (1997); Bouchereau & Chantrel (2009) |
| *Mugil curema* | Zooplankton | Blay (1995); Rueda (2002) |
| *Opistonema oglinum* | Zooplankton | Vegas-Candeja *et al.* (1997); Chaves & Vendel (2008)** |
| *Sardinella brasiliensis* | Zooplankton | Vegas-Candeja *et al.* (1997); Chaves & Vendel (2008)** |
| *Sciades herzbergii* | Teleostei, Brachyura | Giarrizzo & Saint-Paul (2008); Ribeiro *et al*. (2012) |
| *Sphoeroides testudineus* | Brachyura, Mollusks | Targett (1978); Chi-Espínola & Vega-Cendejas (2013) |

abundant species and may indicate opportunistic feeding strategies (Selleslagh & Amara, 2015), according to changes in fauna composition along the saline gradient (Vivier *et al*., 2010; Selleslagh & Amara, 2015; Whitfield, 2015), ontogenetic changes during fish growth resulting in changes in lifestyle and consequently dietary changes (Luczkoviche *et al*., 1995), or between dry and rainy season, as noticed in *Anchovia clupeoides*, *Bathygobius soporator*, *C. latus*, *E. argenteus* and *Sciades herzbergii* (Campos *et al*., 2015).

## Trophic organization

Species of the same genus, such as *Anchoa* spp., *Eucinostomus* spp., *Haemulon* spp. and *Sphoeroides* spp. were grouped into the same guild due to the similarity of the resources they consumed, which may be related to the taxonomic proximity between the species (Fitzhugh & Fleeger, 1985).

The placement of species belonging to the same genus into different guilds (*e.g*., *Achirus* spp., *Centropomus* spp. and *Lutjanus* spp.) may be due to the prevalence of ecological factors over historical ones (*i.e*., taxonomic proximity), to avoid competition (Pianka, 1974). Darwin acknowledged a paradox inherent to the phenotypic similarity between species sharing an ancestor: on the one hand, if close species are ecologically similar, then they should share environmental requirements and could be expected to occur in the same environment. On the other hand, very close species should strongly compete, limiting their coexistence (Canvender-Bares *et al*., 2009). Thus, subtle differences in diet or other biological aspects (*e.g*., different foraging times; distinct microhabitats) and the range of prey availability could reduce direct competition, preserving their identity as different species (Clavijo, 1974; Sánchez-Hernández *et al*., 2011).

Five trophic guilds were identified: I. Herbivores, II. Shrimp feeders, III. Zooplanktivores, IV. Brachyura feeders, and V. Piscivores. These guilds are similar to those proposed by Elliott *et al*. (2007).

Factors such as changes in the life cycle of prey (Lucena *et al*., 2000) or ontogenetic changes that result in changes in the use of available resources, thereby decreasing intraspecific competition (Schoener, 1974), may be responsible for the seasonal variations observed. Ecological interactions, such as competition, play a fundamental role in the spatio-temporal structure of estuarine fish assemblages (Weinstein *et al*., 1980; Fox & Bellwood, 2013). Competitive interactions may be reduced by ecological differences in a trophic niche, such as in the resources shared and the foraging location and time (Pianka, 1974).

The SIMPER analysis indicated a high contribution of the herbivores, such as *Abudefduf saxatilis*, to the reef region. This finding may be explained by the high abundance of algae in the area, as the chain of sandstone reefs functions as a substrate for macroalgae (Xavier *et al*., 2012). Herbivorous species may also play a key role in the control of macroalgae proliferation (Mumby *et al*., 2006; Silva *et al*., 2014) and are considered important and abundant species in reef ecosystems (Randall, 1965; Francini-Filho *et al*., 2010).

The high primary production of mangroves is supported by leaf litter from local angiosperms (Bouillon *et al*., 2008), and the action of microphytobenthos, marine phanerogams (Odum, 1970) and phytoplankton (Nagelkerken & Van der Velde, 2004). Primary production can also be increased by the presence of coastal sandstone reefs, which are structurally complex due to the presence of orifices and rock fragments of different sizes (García-Charton *et al*., 2004; Gorbatkin & Isbey, 2007), allowing them to serve as substrates for macroalgae and support a great diversity of fishes (Ferreira *et al*., 1998).

A higher contribution of carnivore guilds and a lower contribution of herbivorous species are observed in estuaries according to Unsworth *et al*. (2009). This result may be related to the high abundance of young individuals of several taxa, which serve as food for carnivorous fishes and therefore attract carnivorous species from adjacent areas (*e.g*., reefs close to the estuary).

Species belonging to the same genus and placed into different guilds (*e.g*., *Achirus* spp., *Centropomus* spp. and *Lutjanus* spp.) may render important research in the future, focusing on the evolutionary and ecological processes in the area.

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