

SPATIAL AND SEASONAL VARIATION OF THE ICHTHYOFAUNA AND HABITAT USE IN THE INNER PORTION OF THE BRAZILIAN AMAZON ESTUARY*

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ABSTRACT

It was analyzed the diversity of the ichthyofauna in the inner portion of the Amazon Estuary, its spatial and temporal distribution and abundance considering the salinity gradient and the importance of the area as reproduction and nursery grounds. Data was obtained in Guajará and Marajó Bays, and the Guamá River. Specimens were captured in the main channel (gillnets and trawl nets) and tidal creeks (block nets) between 2004 and 2011 during the dry (July-December) and rainy seasons (January-June). A total of 41,516 specimens of 136 taxa were observed. Differential fish composition, abundance and use of the zones as nursery and breeding area were observed, driven mainly by the salinity. The main river channel of Marajó Bay returned the highest values of abundance, especially during the dry season. The tidal creeks were used more frequently as reproduction area than the main river channels. Small-sized fishes predominated in all zones. Total species richness (S), diversity and abundance (main river channel) was highest in Marajó Bay and lowest in Guamá River (richness) and Guajará Bay (Margalef's D and Shannon's H'). The most species, especially in Guajará and Marajó Bays, were occasional and accessory, characterizing the study area as a transitional zone, with the presence of freshwater, estuarine and marine species in all stages of the life history. The systematic monitoring of the area should be given the highest priority, considering the importance of this area in terms of biodiversity and as a source of income and subsistence for local populations.

Keywords: diversity; functional ecology; ichthyofauna; Marajó Bay

VARIAÇÃO ESPACIAL E SAZONAL DA ICTIOFAUNA E USO DO HABITAT NA PORÇÃO INTERNA DO ESTUÁRIO BRASILEIRO AMAZÔNICO

RESUMO

Foi analisada a diversidade da ictiofauna na parte interna do Estuário Amazônico, sua distribuição espacial e temporal e abundância considerando o gradiente de salinidade e a importância da zona para reprodução e berçário. Os dados foram obtidos nas baías de Guajará e Marajó e no rio Guamá. Os espécimes foram capturados no canal principal (redes de emalhar e redes de arrasto) e canais de maré (redes de tapagem) entre 2004 e 2011 durante a estação seca (julho-dezembro) e estação chuvosa (janeiro-junho). Um total de 41.516 espécimes e 136 táxons foi observado. Diferenças na composição dos peixes, abundância, uso da zona para berçário e criação, impulsionada, principalmente, pela salinidade, foram observadas. O canal principal da baía de Marajó resultou nos maiores valores de abundância, especialmente durante a estação seca. O canal de maré foi usado mais frequentemente como área de reprodução do que os canais principais. Peixes de pequeno porte predominaram em todas as zonas. A riqueza de espécies (S), diversidade e abundância (canal principal) foi maior na baía de Marajó e menor no rio Guamá (riqueza) e Guajará (Margalef's D e Shannon's H'). A maioria das espécies, especialmente nas baías de Guajará e Marajó, foi ocasional e acessória, caracterizando a área de estudo como zona de transição, com a presença de espécies de água doce, estuarinas e marinhas em todas as fases do ciclo de vida. O acompanhamento sistemático da área deve ser da mais alta prioridade, considerando a importância desta área em termos de biodiversidade e fonte de renda e subsistência para as populações locais.

Palavras chave: diversidade; funções ecológicas; ictiofauna; baía do Marajó

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INTRODUCTION

Estuaries are areas of great importance for reproduction and as nurseries for the juveniles of many species, given that this environment presents favorable characteristics for the initial stages of development and growth of many fish species, provided by a rich variety of feeding resources (BLABER, 2000). Considering that many species are strictly dependent on the integrity of specific habitats, such as channels or inlets, in which they pass specific stages of their life cycle, understanding the biological diversity of an estuarine system is essential (AMEZCUA-LINARES and YAÑEZ-ARANCIBIA, 1980; FREIRE and AGOSTINHO, 2000; TEIXEIRA *et al.*, 2005; MOURÃO and LUCENA FRÉDOU, 2014). The economic value and ecological function of estuaries are not only related to a set of physical, chemical, and biological variables, but also by the importance of these areas as breeding and nursery grounds (ABLE, 1978; BLABER, 2000, 2002; LAFFAILLE *et al.*, 2000; MINELLO *et al.*, 2003). The effective management of estuarine systems depends on the knowledge of the use of different habitats by the resident or visiting species and the effects of these environments on their diversity and abundance, demography, spatial-temporal variation and migratory patterns within the system (LAFFAILLE *et al.*, 2000; MINELLO *et al.*, 2003). Within the many species that visit the estuaries, fish populations are the principal natural resource, in terms of their value as a source of animal protein and the quantity of biomass available (YAÑEZ-ARANCIBIA, 1978).

The Amazon Estuarine Complex, which includes the coastal zone of the states of Pará, Amapá and Maranhão, measures approximately 2,250 km (straight line) (SOUZA FILHO, 2005). The enormous volume of water, solutes, and suspended particles, and the complexity of the ecosystems that constitute this environment (BARLETTA *et al.*, 2010) combine to make the Amazon estuary both unique, and one of the most complex estuaries in the World (PAIVA, 1997; SMOAK *et al.*, 2005). These characteristics are fundamental to the diversity of its fauna (CAMARGO and ISAAC, 2001) and flora (PROST and RABELO, 1996). The inner portion of this estuary, where the Marajó and Guajará Bays and the Guamá River are located, is formed by

innumerable swamps, rivers, bays, channels and tidal creeks, which contain an ample variety of marine and freshwater fishes and crustaceans (BARTHEM, 1985; BARTHEM and GOULDING, 1997; VIANA *et al.*, 2010; BENTES *et al.*, 2011) exploited by the local artisanal fishermen as a source of both subsistence and income (OLIVEIRA and LUCENA FRÉDOU, 2011). This area was considered as priority for conservation by the Brazilian Ministry of Environment (MMA, 2007) with medium to high conservation priorities, using the multicriteria approach (MOURÃO *et al.*, 2014).

Despite the considerable ecological and economic value of this estuarine system, the area suffers from an ongoing process of degradation resulting from diverse and widespread anthropogenic impacts (VIANA *et al.*, 2010, 2013; VIANA and LUCENA FRÉDOU, 2014). These impacts include busy shipping lanes, unregulated urban development and inadequate public sanitation, ports and industrial installations, all of which contribute to the discharge of domestic and industrial effluents into the waters of the estuary (RIBEIRO, 2004; GONÇALVES *et al.*, 2006; GREGÓRIO and MENDES, 2009; VIANA *et al.*, 2010).

In the present study, we analysed the diversity of the ichthyofauna, its spatial and temporal distribution and abundance considering a salinity and longitudinal gradient in order to identify patterns along the internal portion of the Amazon Estuary. The importance of the area as reproduction and nursery grounds was also investigated. We expect that this study will provide guidelines for the development of conservation and/or management strategies for the local fish fauna, considering the ecological and social-economic importance of the area.

MATERIAL AND METHODS

Study area

The Amazon Estuary, located in Northern Brazil, is formed by the discharge of the Amazon and the Tocantins River, resulting in the annual mixture of approximately 6,300 km³ of river water carrying 9.3×10^8 tons of sediments from the Atlantic Ocean (MEADE *et al.*, 1979). This work

was conducted at the aquatic environments surrounding the city of Belém (state of Pará), including three zones: mouth of the Guamá River (and Combu Island); Guajará (Onças Island) and Marajó (Mosqueiro Island) Bays, in the southeast of the Amazon Estuary (Figure 1). The area is located in the internal sector of the Amazon Estuary, with a mean annual temperature of 25 °C, air humidity above 80% and a rainfall of 2,889 mm y⁻¹ (BEZERRA *et al.*, 2011). The tidal

propagation goes on for several kilometers upstream, characterizing a broad zone of fluvial-marine transition under the impact of semidiurnal tides (GREGÓRIO and MENDES, 2009). This region is classified as a tidally-influenced area of river (tidal fresh: salinity <0.5-limnetic; Guamá River and Guajará Bay) (according to VENICE SYSTEM, 1958) and oligohaline environment (salinity 0.5-3.0; Marajó Bay) (according to VENICE SYSTEM, 1958 and KNOX, 2001).

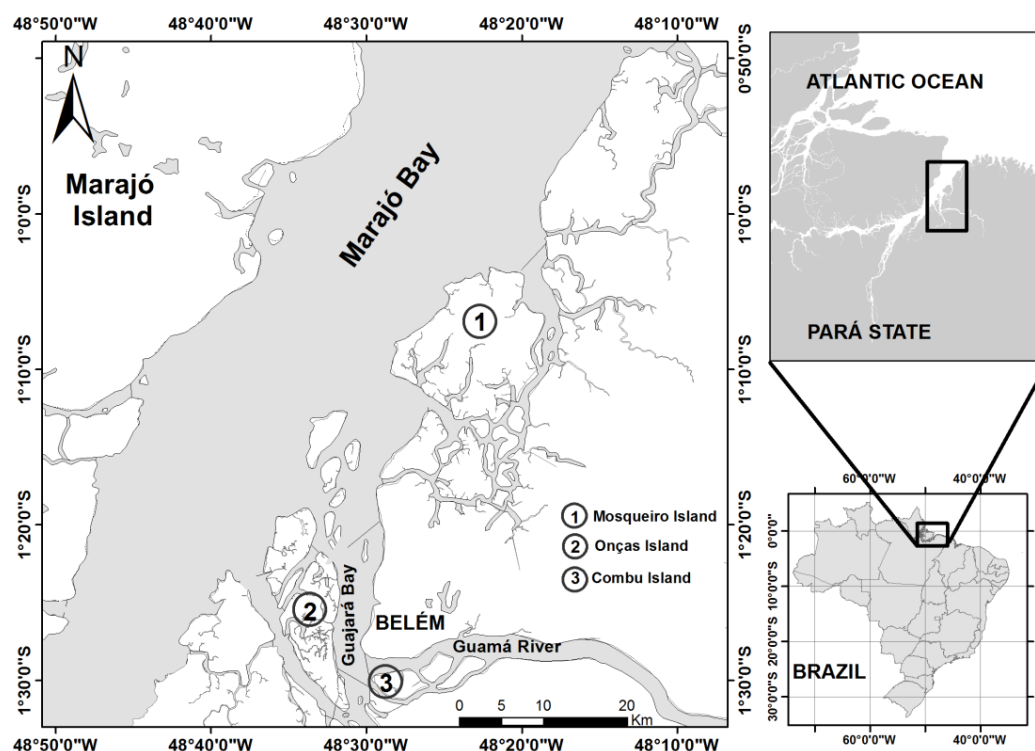


Figure 1. Location of study area and its adjacent islands.

Data collection

For all zones, two different types of habitat – the main river channel and tidal creek (inside the islands) – were considered. Data were collected in the Guamá River and Combu Island in 2004-2005 and 2008-2009; in Guajará Bay and Onças Island in 2004-2005 and 2007-2008; and in Marajó Bay and Mosqueiro Island in 2008-2011. In all three zones, samples were collected in both the dry and rainy seasons (EGLER and SCHWASSMANN, 1962), corresponding to the months of July to December and January to June, respectively.

Distinct collection procedures were used in the different habitats. In the main river channels, gillnets (knot-to-knot meshes of 25, 30, 40, 50, 60 and 70 mm) were used. Nets were set in a random configuration twice for two to three hours at a time. A second procedure applied in the main channel (except on the islands, due to the presence of submerged trunks and branches) was trawling with a net equipped with doors. This net had a mesh of 5 mm, length of 5.50 m, height of 0.60 m, and opening of 1.10 m. Three trawls of approximately 20 minutes were conducted in each study zone at a mean velocity of 1.62 knots. Multifilament block nets with a 25 mm mesh were used in the tidal

creeks. These nets were 50 m long and 5 m high. Blocking was initiated at the end of the high tide and continued throughout the entire ebb tide cycle, of approximately six hours. The tidal creeks (inside island) drain completely at low tide, and the specimens were either gilled in the net (smaller fishes) or collected manually from remaining pools. A total of 284 samples (sets) were carried out in the main river channel (167 and 117 of gill and trawl nets respectively) and 29 in tidal creek, using block net.

All specimens were stored on ice and transported to the laboratory for processing. The specimens were identified to the lowest possible taxonomic level, based on CERVIGÓN (1991), CERVIGÓN *et al.* (1992), FIGUEIREDO and MENEZES (1980), KEITH *et al.* (2000), LE BAIL *et al.* (2000), ESPÍRITO SANTO *et al.* (2005), sized (Total Length, TL), weighed (Total Weight, TW) and had their gonads and stomach removed and weighed. The salinity was measured in the field using a portable conductivimeter Orion model 115.

Data analysis

The three study zones were compared taking seasonal variation and differences in the configuration of the habitat (principal channel or tidal creek) into consideration. The relative abundance of fish is expressed here as the CPUE (catch per unit effort) for either abundance (number of individuals, n) or biomass (total weight, b). In the main channels, where specimens were captured using gillnets, $CPUE_b = (b/At) \times 100$ and $CPUE_n = (n/At) \times 100$, where A = the sum total area of the nets (m^2) and t = the time (hours) it was set. For the trawls, density was given by $D = n/A$ or $D = b/A$, where A = the area trawled (in m^2). For each sample, the area was estimated by $A = S - S_0 \times B$, where $S - S_0$ is the distance trawled (m) and B = the net opening (m). In the case of the tidal creeks, the value was obtained by dividing n or b by A_i , where A_i = the area flooded, estimated for each creek at the peak of the high tide. Differences between zones and seasons were tested using a one-way ANOVA. When necessary, the data were log ($x+1$) transformed to standardize the variance.

Community structure was evaluated using species richness, i.e., total species present (S),

diversity (Shannon's H' , Margalef's D , and Simpson's λ), and evenness (Pielou's J). Spatial and temporal differences (between seasons and among zones) in the indexes of diversity and abundance were tested using a one-way ANOVA and the Tukey's *post hoc* test (ZAR, 1996). Frequency of different species was analyzed based on the method described by DAJOZ (1973). Species with a frequency $\geq 50\%$ were considered constant, those with a frequency between 25 and 50% were considered accessory and those with a frequency of $< 25\%$ were considered occasional.

The set of species captured in each study zone was classified by size, based on the scheme of VIANA *et al.* (2010) and VIANA and LUCENA FRÉDOU (2014). Species with a total length of less than 15 cm were classified as small, those between 15 cm and 30 cm in length as medium, and fish over 30 cm in length as large. Gonads maturation was determined based on VAZZOLER (1996): stage A: immature; stage B: maturing; stage C: mature; stage D: spent. The use of different zones as reproduction and nurseries for the juveniles was classified according to the approach of VIANA *et al.* (2010, 2012), in which individuals with mature and spent gonads (stages C and D, respectively) were considered to be using the zone as a reproduction, while the presence of individuals with immature gonads (stage A) was interpreted as evidence of the use of the zone as a nursery.

Multivariate multidimensional scaling (MDS) was used to compare species composition in relation to spatial and seasonal variables. The numerical CPUE was used as input of data. All groups defined in the MDS were tested through similarity analysis (Two-way nested ANOSIM). These analyses were run in Primer 6.1.6.

RESULTS

The mean salinity of the main river channel in the dry season increased along a limnic-marine gradient, i.e., between the Guamá River and Marajó Bay. Variation in mean salinity was recorded only in Marajó Bay ($\bar{x} = 2$; max = 2.9; min = 0.7). In Guajará Bay low salinity ($\bar{x} = 0.018$; max = 0.15; min = 0) was recorded in the rainy season (Table 1). Salinity was zero in the tidal creeks of all three zones throughout the years.

Table 1. Minimum (Min.), maximum (Max.) and mean values and standard deviation (\bar{x} and SD) of salinity in Guamá River, Guajará and Marajó Bays, in the main channel and tidal creek, dry and rainy seasons.

| Site - Season | Guamá River | | | | Guajará Bay | | | | Marajó Bay | | | |
|----------------------|-------------|-----|-----------|-------|-------------|------|-----------|-------|------------|-----|-----------|-------|
| | Min | Max | \bar{x} | SD | Min | Max | \bar{x} | SD | Min | Max | \bar{x} | SD |
| Main channel - Dry | 0 | 0.2 | 0.087 | 0.074 | 0.1 | 0.75 | 0.3 | 0.223 | 0.7 | 2.9 | 2 | 0.953 |
| Tidal creek - Dry | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Main Channel - Rainy | 0 | 0 | 0 | 0 | 0 | 0.15 | 0.018 | 0.049 | 0 | 0 | 0 | 0 |
| Tidal creek - Rainy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Composition and Abundance

A total of 41,516 fish specimens were collected, representing 136 taxa, 38 families and 12 orders (Table 2). In general, the families Sciaenidae (10.9% of the species recorded), Loricariidae (10.9%), Engraulidae (8.7%), and Cichlidae (6.5%) were the most diverse. In relation to the zones it was observed 55 species in Guamá River, 94 in Guajará Bay and 95 in Marajó Bay. The proportion of exclusive species also increased along the limnic-marine gradient, from 2% in the Guamá to 21% in the Guajará Bay and 27% in the Marajó Bay. Overall, most species was considered as occasional (77%) and only 9% was considered constant (*Anchoa spinifer*,

Lycengraulis batesii, *Pellona flavipinnis*, *Plagioscion squamosissimus*, *Plagioscion surinamensis*, *Aspredo aspredo*, *Ageneiosus ucayalensis*, *Lithodoras dorsalis*, *Pimelodella* gr. *Altipinnis*, *Brachyplatystoma rousseauxii*, *Brachyplatystoma vaillantii* and *Hypophthalmus marginatus*) (Table 2). Considering each zone, occasional and accessory species corresponded to 31.5% in Guamá River, 60.3% Guajará Bay and 61.0% in Marajó Bay. In the main channel, 85 species were occasional and 12 were constant while in the tidal creek, 44 species were occasional and 11 were constant. For both habitat types, a minimum percentage of species were constant.

Table 2. Composition and constancy of the ichthyofauna captured in the three sampling zones. Habitat type: Main River Channel - Ch and Tidal creek - Tc; Seasonality: Dry - D and Rainy - R. N - number of specimens. W - mean weight. (*) species present in all the zones and habitat types.

| Family | Species | Habitat type | Seasonality | N | W (kg) | Constancy |
|-------------------|--------------------------------------|--------------|-------------|-----|--------|------------|
| | | Ch / Tc | D / R | | | |
| Acestrorhynchidae | <i>Acestrorhynchus</i> sp. | Tc | R | 1 | 0.076 | Occasional |
| Achiridae | <i>Achirus achirus</i> | Ch / Tc | D | 8 | 0.7607 | Occasional |
| | * <i>Apionichthys dumerili</i> | Ch / Tc | D / R | 783 | 0.9441 | Accessory |
| | <i>Syacium papillosum</i> | Tc | D | 1 | 0.016 | Occasional |
| Anablepidae | <i>Anableps anableps</i> | Tc | D / R | 33 | 2.543 | Accessory |
| Anostomidae | <i>Leporinus fasciatus</i> | Ch | R | 4 | 0.91 | Occasional |
| | <i>Leporinus friderici</i> | Ch / Tc | D / R | 5 | 0.725 | Occasional |
| Apterontidae | <i>Apterontus albifrons</i> | Tc | D / R | 12 | 1.508 | Occasional |
| | <i>Orthosternarchus tamandua</i> | Ch | D / R | 2 | 0.1332 | Occasional |
| | <i>Sternarchella schotti</i> | Ch | R | 7 | 0.0826 | Occasional |
| | <i>Sternarchella sima</i> | Ch | D / R | 8 | 0.0997 | Occasional |
| | * <i>Sternarchella terminalis</i> | Ch / Tc | D / R | 494 | 1.7886 | Accessory |
| | * <i>Sternarchogiton</i> sp. | Ch / Tc | D / R | 345 | 1.1921 | Occasional |
| | * <i>Sternarchorhamphus muelleri</i> | Ch / Tc | D / R | 41 | 1.5302 | Occasional |
| | <i>Sternarchorhynchus cf. roseni</i> | Ch | R | 1 | 0.0095 | Occasional |
| | <i>Cathorops</i> sp. | Ch | D / R | 67 | 12.601 | Occasional |
| | <i>Cathorops spixii</i> | Ch | D / R | 429 | 11.891 | Occasional |

Table 2. (cont.) Composition and constancy of the ichthyofauna captured in the three sampling zones. Habitat type: Main River Channel - Ch and Tidal creek - Tc; Seasonality: Dry - D and Rainy - R. N - number of specimens. W - mean weight. (*) species present in all the zones and habitat types.

| Family | Species | Habitat type | Seasonality | N | W (kg) | Constancy |
|-----------------|--------------------------------------|--------------|-------------|------|--------|------------|
| | | Ch / Tc | D/R | | | |
| Apterontidae | <i>Sciades couma</i> | Ch / Tc | D / R | 36 | 5.54 | Accessory |
| | * <i>Sciades herzbergii</i> | Ch / Tc | D / R | 20 | 1.353 | Occasional |
| Aspredinidae | <i>Aspredinichthys filamentosus</i> | Ch / Tc | D / R | 125 | 1.7946 | Accessory |
| | <i>Aspredinichthys tibicen</i> | Ch | D / R | 27 | 0.2363 | Occasional |
| | * <i>Aspredo aspredo</i> | Ch / Tc | D / R | 3099 | 14.904 | Constant |
| Auchenipteridae | * <i>Ageneiosus ucayalensis</i> | Ch / Tc | D / R | 507 | 36.859 | Constant |
| | <i>Ageneiosus inermis</i> | Tc | D | 1 | 0.535 | Occasional |
| | <i>Auchenipterus nuchalis</i> | Tc | D | 1 | 0.052 | Occasional |
| | * <i>Pseudoauchenipterus nodosus</i> | Ch / Tc | D / R | 61 | 3.3006 | Accessory |
| | * <i>Trachelyopterus galeatus</i> | Ch / Tc | D / R | 69 | 4.1159 | Accessory |
| Belontiidae | <i>Strongylura timucu</i> | Ch | D / R | 2 | 0.0178 | Occasional |
| Carangidae | <i>Oligoplites palometa</i> | Ch | D | 36 | 3.1 | Occasional |
| | <i>Trachinotus carolinus</i> | Ch | D | 2 | 0.218 | Occasional |
| Cetopidae | <i>Cetopsis coecutiens</i> | Ch | D | 2 | 0.1479 | Occasional |
| Characidae | <i>Acestrocephalus</i> sp. | Ch / Tc | D / R | 11 | 0.1053 | Occasional |
| | <i>Astyanax fasciatus</i> | Tc | D / R | 41 | 0.827 | Accessory |
| | <i>Astyanax</i> sp. | Ch / Tc | D / R | 8 | 0.114 | Occasional |
| | <i>Pristobrycon calmoni</i> | Ch / Tc | D | 4 | 0.072 | Occasional |
| | <i>Serrasalmus</i> sp. | Ch / Tc | D | 6 | 0.206 | Occasional |
| | <i>Triportheus elongatus</i> | Ch / Tc | D / R | 21 | 1.6256 | Occasional |
| | <i>Cichla</i> sp. | Ch / Tc | D / R | 8 | 2.642 | Occasional |
| Cichlidae | <i>Crenicichla cincta</i> | Ch / Tc | D / R | 5 | 0.91 | Occasional |
| | <i>Crenicichla johanna</i> | Tc | D / R | 6 | 0.835 | Occasional |
| | <i>Crenicichla lugubris</i> | Tc | D | 3 | 0.744 | Occasional |
| | <i>Crenicichla semifasciata</i> | Tc | R | 3 | 0.446 | Occasional |
| | <i>Crenicichla</i> sp. | Tc | D / R | 4 | 0.317 | Occasional |
| | <i>Geophagus proximus</i> | Ch / Tc | D / R | 27 | 2.083 | Occasional |
| | <i>Geophagus</i> sp. | Ch | D | 1 | 0.172 | Occasional |
| | <i>Geophagus surinamensis</i> | Ch / Tc | D / R | 12 | 0.868 | Occasional |
| Clupeidae | <i>Rhinosardinia amazonica</i> | Ch | D | 3 | 0.0011 | Occasional |
| Ctenoluciidae | <i>Boulengerella cuvieri</i> | Ch | D / R | 2 | 0.496 | Occasional |
| Curimatidae | * <i>Curimata inornata</i> | Ch / Tc | D / R | 110 | 3.85 | Accessory |
| Cynodontidae | <i>Raphiodon vulpinus</i> | Ch | D | 1 | 0.192 | Occasional |
| Doradidae | * <i>Lithodoras dorsalis</i> | Ch / Tc | D / R | 935 | 288.44 | Constant |
| | <i>Lithodoras</i> sp. | Ch / Tc | D / R | 2 | 0.152 | Occasional |
| Engraulidae | * <i>Anchoa spinifer</i> | Ch / Tc | D / R | 866 | 12.605 | Constant |
| | * <i>Anchovia surinamensis</i> | Ch / Tc | D / R | 757 | 3.1444 | Accessory |
| | <i>Anchoviella cayennensis</i> | Ch | D / R | 39 | 0.0868 | Occasional |
| | <i>Anchoviella guianensis</i> | Ch | D / R | 79 | 0.05 | Occasional |
| | <i>Cetengraulis edentulus</i> | Ch | D / R | 42 | 1.7 | Occasional |
| | Engraulidae sp. 1 | Ch | D | 1 | 0.004 | Occasional |
| | Engraulidae sp. 2 | Ch | D | 1 | 0.018 | Occasional |

Table 2. (cont.) Composition and constancy of the ichthyofauna captured in the three sampling zones. Habitat type: Main River Channel - Ch and Tidal creek - Tc; Seasonality: Dry - D and Rainy - R. N - number of specimens. W - mean weight. (*) species present in all the zones and habitat types.

| Family | Species | Habitat type | Seasonality | N | W (kg) | Constancy |
|------------------|--|--------------|-------------|------|--------|------------|
| | | Ch / Tc | D/R | | | |
| Engraulidae | Engraulidae sp. 3 | Ch | D | 1 | 0.004 | Occasional |
| | * <i>Lycengraulis batesii</i> | Ch / Tc | D / R | 249 | 9.8253 | Constant |
| | <i>Lycengraulis grossidens</i> | Ch | D | 8 | 0.136 | Occasional |
| | <i>Pterengraulis atherinoides</i> | Ch / Tc | D / R | 14 | 0.6452 | Occasional |
| Erythrinidae | <i>Hoplias malabaricus</i> | Tc | D / R | 20 | 1.886 | Occasional |
| Gasteropelecidae | <i>Gasteropelecus levis</i> | Ch | D | 1 | 0.002 | Occasional |
| Gobiidae | <i>Gobioides broussonnetii</i> | Ch | D / R | 24 | 0.1315 | Occasional |
| Haemulidae | <i>Genyatremus luteus</i> | Ch | D | 2 | 0.126 | Occasional |
| Heptapteridae | * <i>Pimelodella</i> gr. <i>altipinnis</i> | Ch / Tc | D / R | 1792 | 11.817 | Constant |
| | <i>Pimelodella</i> sp. | Ch | D | 1 | 0.078 | Occasional |
| | <i>Rhamdia quelen</i> | Tc | D / R | 12 | 0.955 | Occasional |
| Hypopomidae | <i>Steatogenys elegans</i> | Ch | D / R | 181 | 0.7185 | Occasional |
| Loricariidae | <i>Acanthicus hystrix</i> | Ch | R | 1 | 3.62 | Occasional |
| | <i>Ancistrus</i> sp. | Ch | R | 1 | 0.026 | Occasional |
| | <i>Ancistrus</i> sp. 1 | Tc | R | 1 | 0.034 | Occasional |
| | <i>Ancistrus</i> sp. 2 | Tc | D / R | 2 | 0.168 | Occasional |
| | <i>Ancistrus</i> sp. 3 | Tc | R | 3 | 0.236 | Occasional |
| | <i>Farlowella</i> cf. <i>hasemani</i> | Ch | D | 1 | 0.072 | Occasional |
| | <i>Hypostomus plecostomus</i> | Ch | D / R | 13 | 1.3382 | Occasional |
| | <i>Hypostomus punctatus</i> | Ch | D | 1 | 0.108 | Occasional |
| | <i>Hypostomus</i> sp. | Tc | R | 1 | 0.142 | Occasional |
| | <i>Limatulichthys griseus</i> | Tc | D | 1 | 0.02 | Occasional |
| | * <i>Loricaria cataphracta</i> | Ch / Tc | D / R | 43 | 1.1482 | Accessory |
| | * <i>Peckoltia</i> sp. | Ch / Tc | D / R | 44 | 2.0164 | Occasional |
| | <i>Peckoltia</i> sp. 1 | Ch / Tc | D / R | 3 | 0.58 | Accessory |
| | <i>Pseudacanthicus histrix</i> | Ch | D | 1 | 1.65 | Occasional |
| | <i>Pseudacanthicus spinosus</i> | Ch | R | 1 | 0.04 | Occasional |
| Mugilidae | <i>Mugil curema</i> | Ch | D | 35 | 5.666 | Occasional |
| | <i>Mugil incilis</i> | Ch | D | 13 | 1.846 | Occasional |
| | <i>Mugil</i> sp. | Ch / Tc | D | 2 | 0.0645 | Occasional |
| Muraenidae | Not identified | Ch | D | 1 | 0.0002 | Occasional |
| Paralichthyidae | <i>Citharichthys spilopterus</i> | Ch | D | 2 | 0.032 | Occasional |
| Pimelodidae | <i>Brachyplatystoma filamentosum</i> | Ch | D / R | 75 | 44.28 | Accessory |
| | <i>Brachyplatystoma platynemum</i> | Ch | D / R | 7 | 10.136 | Occasional |
| | <i>Brachyplatystoma rousseauxii</i> | Ch | D / R | 420 | 122.2 | Constant |
| | * <i>Brachyplatystoma vaillantii</i> | Ch / Tc | D / R | 260 | 15.108 | Constant |
| | * <i>Hypophthalmus marginatus</i> | Ch / Tc | D / R | 229 | 32.985 | Constant |
| | * <i>Pimelodus blochii</i> | Ch / Tc | D / R | 32 | 2.565 | Occasional |
| | <i>Platystomatichthys sturio</i> | Ch / Tc | R | 4 | 0.38 | Occasional |
| | <i>Propimelodus eigenmanni</i> | Tc | R | 1 | 0.106 | Occasional |
| Potamotrygonidae | <i>Plesiotrygon iwamae</i> | Ch | D / R | 5 | 0.4912 | Occasional |
| | <i>Plesiotrygon</i> sp. | Ch | D / R | 5 | 16.28 | Occasional |

Table 2. (cont.) Composition and constancy of the ichthyofauna captured in the three sampling zones. Habitat type: Main River Channel - Ch and Tidal creek - Tc; Seasonality: Dry - D and Rainy - R. N - number of specimens. W - mean weight. (*) species present in all the zones and habitat types.

| Family | Species | Habitat type | Seasonality | N | W (kg) | Constancy |
|------------------|-------------------------------------|--------------|-------------|-------|--------|------------|
| | | Ch / Tc | D / R | | | |
| Potamotrygonidae | <i>Potamotrygon motoro</i> | Ch | D / R | 7 | 23.062 | Occasional |
| | <i>Potamotrygon</i> sp. | Ch | D | 1 | 0.382 | Occasional |
| | <i>Potamotrygon</i> sp. 1 | Ch | R | 1 | 0.078 | Occasional |
| | <i>Potamotrygon</i> sp. 2 | Tc | R | 1 | 0.082 | Occasional |
| | <i>Potamotrygon orbignyi</i> | Ch | R | 1 | 0.832 | Occasional |
| | <i>Potamotrygonidae</i> | Ch | R | 1 | 6.01 | Occasional |
| Pristigasteridae | <i>Pellona castelanaeana</i> | Ch | D | 5 | 1.99 | Occasional |
| | * <i>Pellona flavipinnis</i> | Ch / Tc | D / R | 133 | 61.316 | Constant |
| Rhamphichthyidae | <i>Rhamphichthys marmoratus</i> | Ch / Tc | D / R | 15 | 3.094 | Occasional |
| | * <i>Rhamphichthys rostratus</i> | Ch / Tc | D / R | 71 | 14.087 | Accessory |
| Sciaenidae | <i>Cynoscion acoupa</i> | Ch | D | 128 | 6.4486 | Occasional |
| | <i>Cynoscion leiarchus</i> | Ch | D | 20 | 0.1323 | Occasional |
| | <i>Cynoscion</i> sp. | Ch | D | 1 | 0.0006 | Occasional |
| | <i>Macrodon ancylodon</i> | Ch | D / R | 405 | 11.144 | Occasional |
| | <i>Menticirrhus americanus</i> | Ch | D | 81 | 0.014 | Occasional |
| | <i>Micropogonias furnieri</i> | Ch | D / R | 197 | 1.0987 | Occasional |
| | <i>Nebris microps</i> | Ch | D | 1 | 0.868 | Occasional |
| | <i>Ophioscion</i> sp. | Ch | D | 1 | 0.0007 | Occasional |
| | * <i>Pachypops fourcroi</i> | Ch / Tc | D / R | 78 | 4.0424 | Accessory |
| | * <i>Plagioscion auratus</i> | Ch / Tc | D / R | 74 | 1.9816 | Accessory |
| | * <i>Plagioscion squamosissimus</i> | Ch / Tc | D / R | 5004 | 163.95 | Constant |
| | * <i>Plagioscion surinamensis</i> | Ch / Tc | D / R | 1153 | 33.994 | Constant |
| | <i>Stellifer microps</i> | Ch | D / R | 14727 | 3.8286 | Accessory |
| | <i>Stellifer naso</i> | Ch | D / R | 4045 | 4.1937 | Accessory |
| | <i>Stellifer rastrifer</i> | Ch | D / R | 1558 | 0.6026 | Occasional |
| Scombridae | <i>Scomberomorus brasiliensis</i> | Ch | D | 1 | 1.3 | Occasional |
| Sternopygidae | <i>Rhabdolichops caviceps</i> | Ch / Tc | D / R | 18 | 0.2589 | Occasional |
| | * <i>Rhabdolichops eastwardi</i> . | Ch / Tc | D / R | 668 | 1.6837 | Occasional |
| | * <i>Sternopygus macrurus</i> | Ch / Tc | D / R | 32 | 5.107 | Occasional |
| Tetraodontidae | <i>Colomesus asellus</i> | Ch / Tc | D / R | 49 | 0.3935 | Accessory |
| Trichiuridae | <i>Trichiurus lepturus</i> | Ch | D | 3 | 1.066 | Occasional |
| Trichomycteridae | <i>Trichomycterus</i> sp. | Ch | R | 2 | 0.0033 | Occasional |

The CPUE for the main river channels (obtained by gillnet) was significantly different ($F = 12.5488$; $p < 0.05$) among the study zones only for biomass, with the highest value being recorded in Marajó Bay. For the trawls, significant differences were recorded among zones for both abundance and biomass ($F(\text{CPUE}_n) = 19.9654$; $F(\text{CPUE}_b) = 3.2092$, $p < 0.05$), with the highest values being also recorded in Marajó Bay.

Seasonal differences were observed only in the case of abundance (based on the CPUE_n for gillnet), with higher values being recorded during the dry season ($F = 5.3881$; $p < 0.05$). In the case of the trawl catches, however, biomass was significantly higher in the rainy season in Marajó Bay, while abundance was higher in this same zone in the dry season ($F(\text{CPUE}_n) = 4.9762$; $F(\text{CPUE}_b) = 4.0825$; $p < 0.05$) (Figure 2).

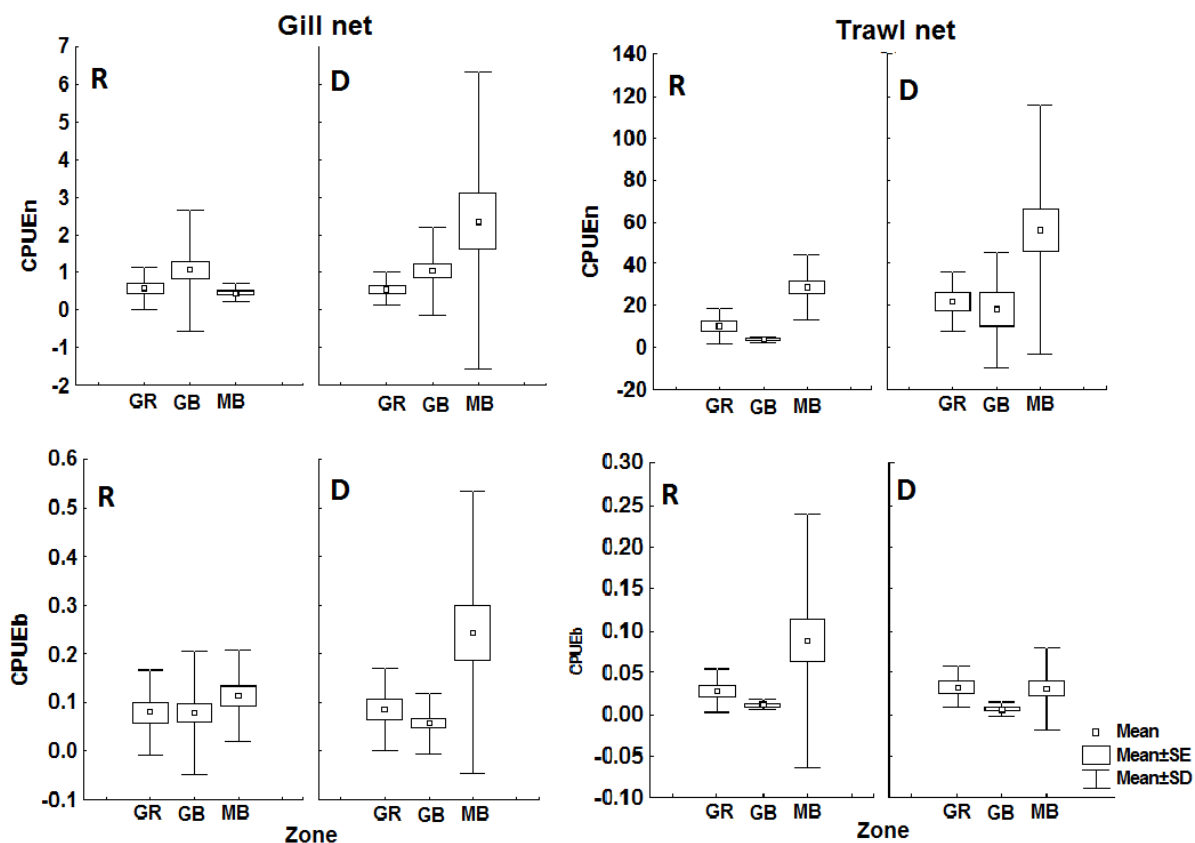


Figure 2. CPUE values in the main channel for both numerical abundance (number of individuals) and biomass (weight), considering: zone - GR (Guamá River), GB (Guajará Bay), MB (Marajó Bay); gear - Gill net and Trawl net; and seasonality - Dry season (D) and Rainy season (R).

In the tidal creeks, only biomass varied significantly ($F = 3.6115$; $p < 0.05$), with the highest value being recorded in Guajará Bay, and the

lowest in Marajó Bay. No significant seasonal variation in abundance was recorded ($F(\text{CPUE}_n) = 0.3667$, $F(\text{CPUE}_b) = 1.3682$; $p > 0.05$) (Figure 3).

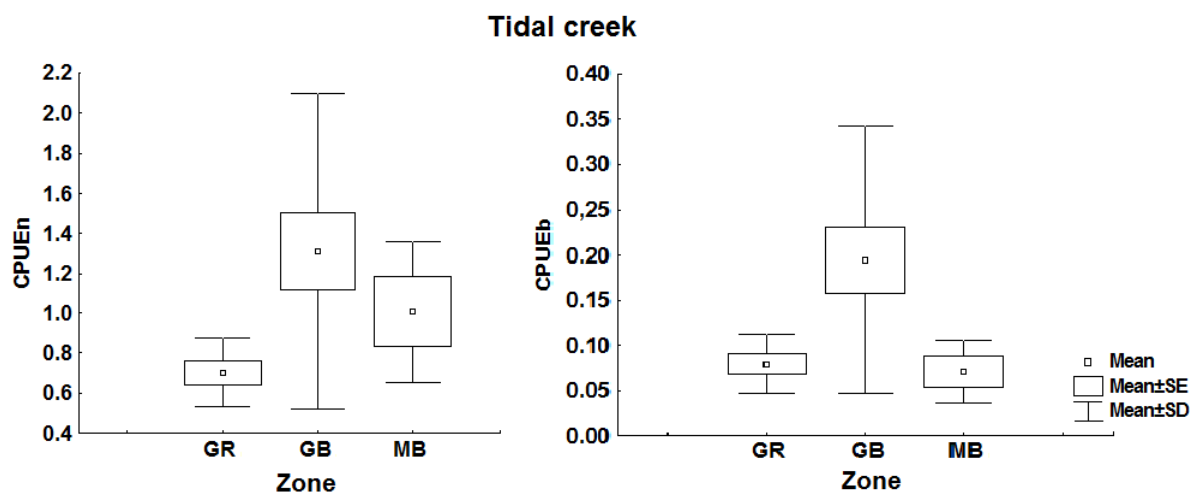


Figure 3. CPUE values in the tidal creek (inside island) for both numerical and abundance (number of individuals and biomass), considering the zone - GR (Guamá River), GB (Guajará Bay) and MB (Marajó Bay).

Measures of diversity

Significant differences were found among zones for all indexes ((S)F = 32.0207; (D)F = 7.5787; (J')F = 16.9644; (H')F = 4.8168; (λ)F = 3.6204; $p < 0.05$). The *post hoc* test identified higher species richness (S) in Marajó Bay. Margalef's (D) and Shannon's (H') diversity indices were lowest in

Guajará Bay. The results observed for Pielou's (J') and Simpson's (λ) indices were similar among zones (Table 3), although relatively low values were recorded in Marajó Bay. No significant seasonal variation was observed for any indexes ((S)F = 0.2242; (D)F = 1.0894; (J')F = 2.8494; (H')F = 1.1936; (λ)F = 1.9388; $p > 0.05$).

Table 3. Mean \pm standard deviation of diversity index by zone and season: species richness (S); diversity Margalef's index (D); Pielou's evenness index (J'); diversity Shannon's index (H') and Simpson index (λ). Different letters in column indicate significant differences ($\alpha = 0.05$).

| | | S | D | J' | H' | λ |
|-------------|-------|----------------------|---------------------|---------------------|----------------------|----------------------|
| Guamá River | Total | 11.10 \pm 5.26 (b) | 2.38 \pm 0.89 (a) | 0.78 \pm 0.15 (a) | 1.73 \pm 0.56 (a) | 0.77 \pm 0.16 (a) |
| | Dry | 10.75 \pm 5.46 | 2.23 \pm 0.94 | 0.72 \pm 0.18 | 1.57 \pm 0.57 | 0.71 \pm 0.17 |
| | Rainy | 11.52 \pm 5.16 | 2.55 \pm 0.80 | 0.83 \pm 0.08 | 1.91 \pm 0.49 | 0.83 \pm 0.10 |
| Guajará Bay | Total | 7.77 \pm 6.03 (c) | 1.89 \pm 1.05 (b) | 0.77 \pm 0.20 (a) | 1.39 \pm 0.58 (b) | 0.71 \pm 0.21 (ab) |
| | Dry | 7.88 \pm 5.68 | 1.83 \pm 0.93 | 0.78 \pm 0.14 | 1.42 \pm 0.49 | 0.73 \pm 0.16 |
| | Rainy | 7.66 \pm 6.40 | 1.95 \pm 1.16 | 0.76 \pm 0.24 | 1.35 \pm 0.66 | 0.69 \pm 0.25 |
| Marajó Bay | Total | 14.33 \pm 5.23 (a) | 2.39 \pm 0.86 (a) | 0.60 \pm 0.18 (b) | 1.56 \pm 0.52 (ab) | 0.65 \pm 0.19 (b) |
| | Dry | 14.46 \pm 6.30 | 2.27 \pm 0.95 | 0.55 \pm 0.20 | 1.44 \pm 0.57 | 0.61 \pm 0.21 |
| | Rainy | 14.18 \pm 3.61 | 2.53 \pm 0.72 | 0.65 \pm 0.14 | 1.71 \pm 0.41 | 0.71 \pm 0.14 |

Habitat use

Small-sized fish (TL < 5 cm) predominated in Marajó Bay, with 76% of the total number of individuals (Figure 4). However, the largest specimens were also captured in this zone. Similar patterns were observed between seasons.

The analysis of habitat use revealed that the fish species use the study area mainly as a nursery (Figure 5A). The same conclusion was observed

when the main river channels and tidal creeks (inside island) were analyzed separately (Figures 5B and 5C). In the main channel, more than 90% of the individuals used this habitat as nursery, for both seasons, while in the tidal creek, the breeding activity is higher especially in Marajó Bay, also for both rainy and dry seasons. No seasonal variation was found in the relative use of channels and creeks as reproduction or nurseries (Figure 5).

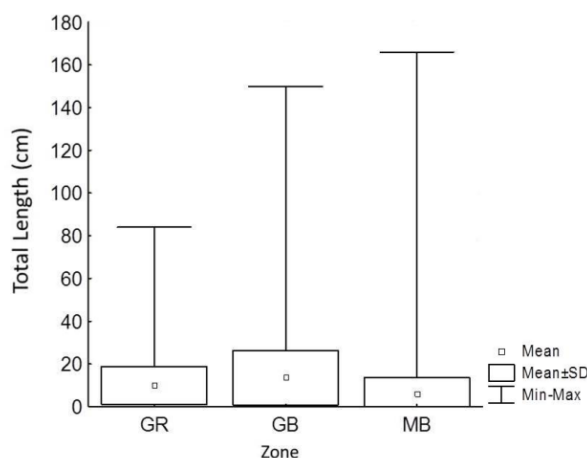


Figure 4. Total length of fish by zone: Guamá River (GR); Guajará Bay (GB) and Marajó Bay (MB).

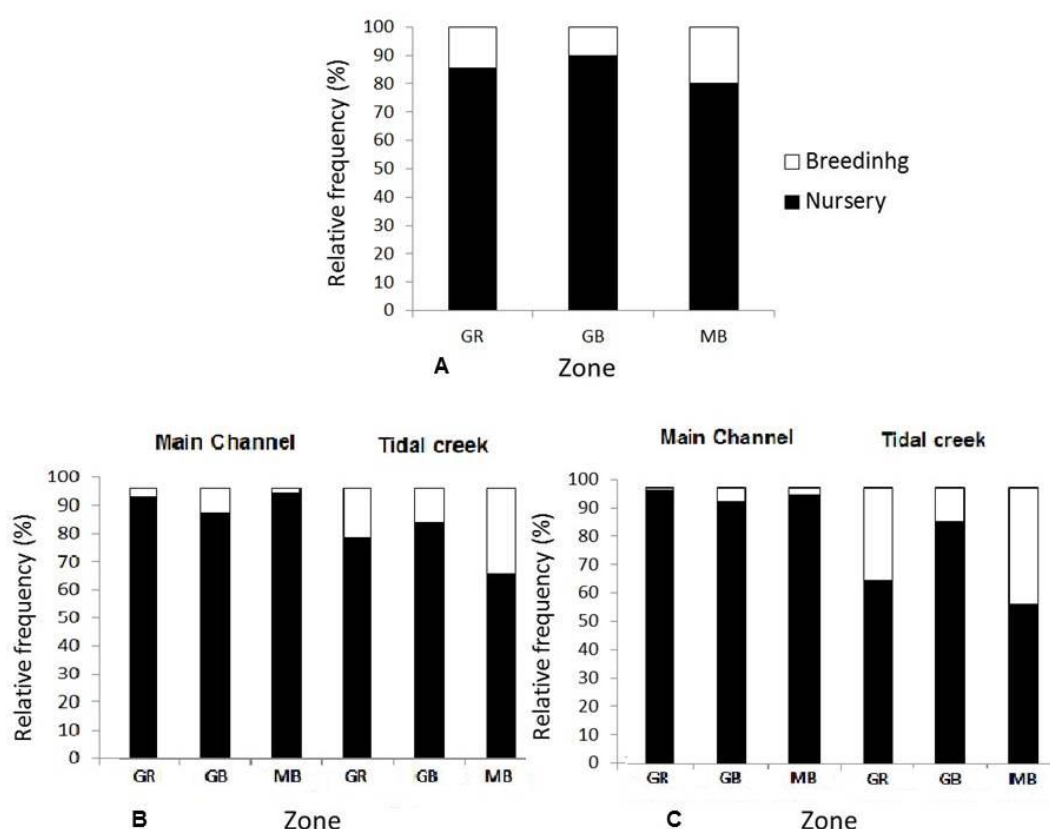


Figure 5. Percentage of relative frequency using the area as nursery and reproduction by zone (Guamá River - GR; Guajará Bay - GB and Marajó Bay - MB) (A); Habitat Type (Main Channel; Tidal creek) and season (rainy season; B; dry season; C).

Multivariate analysis

Fish assemblages caught between the dry and rainy seasons for both habitat types (and all gears) did not vary (ANOSIM, R values were either very low or statistically insignificant, Table 4).

When compared by zone, the species composition of the catch from Marajó Bay (MB)

was significantly different from the two other zones except for the gill net when the biomass was considered (Table 4; Figure 6). Gill net catches species composition within GB and MB showed a large variation whereas GR remained homogeneous. Catches of the main channel (trawl nets) in the three areas were significantly different considering both numerical and biomass CPUE.

Table 4. Synthesis of ANOSIM results. GB: Guajará Bay, GR: Guamá River, MB: Marajó Bay ns: non-significant.

| Sampler | CPUE | Seasonality | Area comparison | |
|-----------------------------|---------|--------------------|--------------------|----------------|
| | | Global R statistic | Global R statistic | Pairwise tests |
| Block net (Tidal creek) | Number | ns | 0.355 | (GB, GR) ≠ MB |
| | Biomass | ns | 0.349 | (GB, GR) ≠ MB |
| Gillnet (Main Channel) | Number | 0.018 | 0.067 | (GB, GR) ≠ MB |
| | Biomass | ns | 0.148 | (MB, GR) ≠ GB |
| Trawl net (Main Channel) | Number | ns | 0.366 | GB ≠ GR ≠ MB |
| | Biomass | ns | 0.259 | GB ≠ GR ≠ MB |

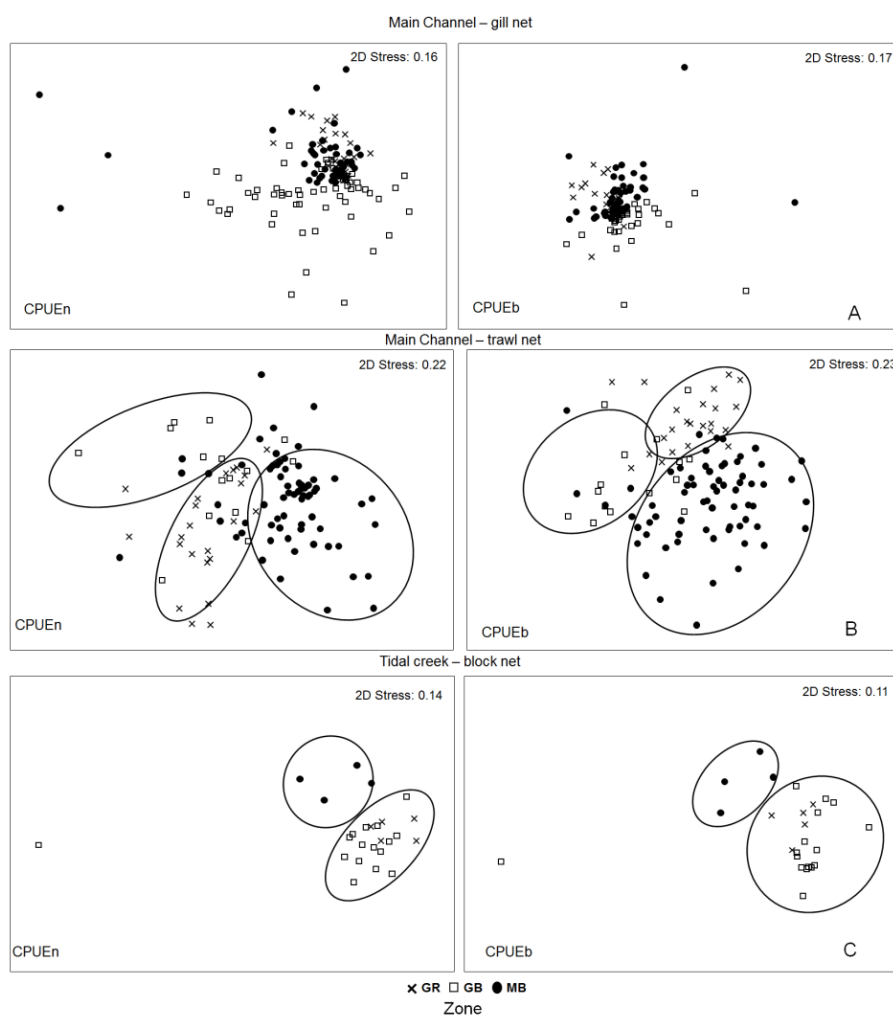


Figure 6. Multivariate multidimensional scaling analysis considering zone - GR (Guamá River), GB (Guajará Bay), MB (Marajó Bay), Habitat type (main channel and tidal creek) and gear (gill net, trawl net and block net), CPUE_n: Catch (number of individuals) per unit of effort, CPUE_b: Catch (biomass) per unit of effort: A) main channel gill net; B) main channel trawl net; and C) tidal creek block net.

DISCUSSION

In estuaries, spatial variability in the composition of fish assemblages has been attributed to a number of variables (VILAR *et al.*, 2013). In tropical estuarine systems, salinity appears to be the principal abiotic factor determining the structure of fish communities and limiting the occurrence of species (BLABER, 2000; BARLETTA *et al.*, 2003; NORDLIE, 2003). In the inner portion of the Brazilian Amazon Estuary, salinity variation was low, ranging from 0 to 2.9, with a slight increase observed from the mouth of the Guamá River to the outer portion of Marajó Bay.

The composition of the estuarine fish assemblages can be directly linked to the longitudinal salinity gradient within these systems. Different species compositions among estuarine zones have already been reported for large tropical estuaries (BARLETTA *et al.*, 2003, 2005; PAIVA *et al.*, 2008; PASSOS *et al.*, 2013). HUDSON (1990) changed the shape of the original Remane diagram by showing the freshwater biota at a lower species diversity level than the marine biota. According to this author, within an estuarine salinity gradient, a minimum of diversity is reported in the oligohaline environment, increasing towards the mesohaline area.

Although the specific richness sampled (54, 94 and 95 species respectively for Guamá River, Guajará and Marajó Bays) was relatively high for estuarine standards (MOURA *et al.*, 2012; VIANA and LUCENA FRÉDOU, 2014), differences emerged amongst zones when the mean values of diversity indexes was analyzed. The lowest mean diversity (D and H') was observed in Guajará Bay, an oligohaline zone. Marajó Bay, considered as an oligo to mesohaline area, with a salinity observed in this study up to 2.9 within its internal section and to more than 10 in the outer part of the Bay (see BARTHEM, 1985), showed the highest mean richness and diversity. However, most species, especially in Guajará and Marajó Bays, were occasional and restricted in space and time, characterizing the study area as a transitional zone. Constant species mainly belonged to the Sciaenidae and Pimelodidae families. These families are considerably diverse and widespread along the northern coast of Brazil (BARTHEM, 1985; CAMARGO and ISAAC, 2001).

The transitional pattern of the study area is also evident when considering the environmental guilds. In Marajó Bay, estuarine species dominated, although freshwater species were also important. Freshwater migrants and stragglers dominated in Guajará Bay and Guamá River (MOURÃO and LUCENA FRÉDOU, 2014), an essentially limnetic estuary. Classical studies along marine-estuarine and freshwater ecosystems in warm-temperate estuaries of North America and Europe show that marine and estuarine-dependent fish guilds have a greater influence on species richness and abundance patterns than freshwater species (JUNG and HOUE, 2003; MARTINO and ABLE, 2003; AKIN *et al.*, 2005). However, a different pattern was found in estuaries located in the Neotropical zoogeographic region. Rivers, streams, and ponds are home for the largest freshwater fish fauna in the world (BLABER, 2000; BARLETTA *et al.*, 2005; MOURA *et al.*, 2012) as it is observed in the Amazon estuary. Even if the inner portion of the Amazon Estuary is transitional, clear patterns emerged from our study and significant differences were observed amongst fish community between the areas considered. In large estuaries in the Neotropical region, it is also reported differences within the fish community separated by large-influenced estuarine and

freshwater species (BARLETTA *et al.*, 2005; MOURA *et al.*, 2012).

The main river channel of Marajó Bay returned the highest values for both relative abundance in number and in biomass, especially during the dry season. This is a relatively productive zone, with nutrient concentrations varying from 5.0 to 7.0 mg L⁻¹ (SCHWASSMANN *et al.*, 1989). During the dry season, salinity increases from 0 to 10 (BARTHEM, 1985), resulting in the rapid flocculation of the larger sediment particles, which are deposited on the bottom, and the modification of the color of the water to greenish tones caused by the presence of a phytoplanktonic bloom. This phenomenon characterizes the area as a zone of high primary productivity, especially in the lower and upper reaches of Mosqueiro Island (MILLIMAN *et al.*, 1975; BARTHEM, 1985; SCHWASSMANN *et al.*, 1989). In the case of the tidal creeks (inside island), Guajará Bay was characterized by relatively high biomass and abundance. This may have been related to the presence of the numerous islands within this zone, in particular, the Onças Archipelago, in the west of the bay, which is made up of a large number of tidal creeks, which cross the islands and connect the main channel with the forests in their interior, forming tidal swamps (MORÁN, 1990; CARVALHO *et al.*, 1998). These swamps provide important temporary habitats rich in feeding resources (fruit, seeds, insects, etc.) and refuges from predators for the juveniles (LOWE-McCONNELL, 1999).

Small-sized fishes (TL <5 cm) predominated in all zones, which is an expected pattern for tropical estuaries, given the role of these systems as reproduction, feeding, and nurseries for many species, which may find habitats suitable for a number of different stages of their life cycles (YAÑEZ-ARANCIBIA, 1986; BLABER, 2000; ELLIOTT *et al.*, 2007; MARTINHO *et al.*, 2007). The largest specimens were collected in Marajó Bay, which is an important fishery zone for artisanal operations widespread throughout the state of Pará. These fisheries target mainly the large catfishes of the family Pimelodidae (*B. rousseauxii* and *B. filamentosum*) as well as croakers, *P. squamosissimus* and *P. surinamensis*, which may also reach relatively large sizes (OLIVEIRA and LUCENA FRÉDOU, 2011).

The tidal creeks were used relatively more frequently as reproduction area by some species than the main river channels, as observed by VIANA *et al.* (2010). The proportion of specimens with mature or spent gonads was also much greater in tidal creek of the Guamá River and Marajó Bay than in the Guajará Bay, during both the dry and rainy seasons. The low proportion of breeding individuals in Guajará Bay may be related to the ongoing degradation of the environment on its urbanized margins. Contaminants may remain longer in the tidal creeks in comparison with the main channels, given their more “closed” environments, which retain the substances for longer before they become diluted (VIANA *et al.*, 2010).

Spatial patterns in assemblage structures are driven by ecological processes that occur on multiple scales (large, regional and local scale) (VILAR *et al.*, 2013). On a local scale (this study), spatial patterns in the ichthyofauna structure have often been related to changes in a number of factors, including the salinity and the distance from the point of connection to the sea (BARLETTA *et al.*, 2003; CHAGAS *et al.*, 2006; VILAR *et al.*, 2011). Understanding the variations in fish fauna at different spatial and temporal scales can provide valuable insights for management and conservation (BARLETTA *et al.*, 2010). The results from this study suggest that, even though a relative homogeneity in salinity was reported, different fish composition and use of the zones as nursery and breeding area are also observed.

The transitory occurrence of freshwater (*S. elegans* and *P. auratus*), estuarine (*A. aspredo* and *S. naso*), and marine species (*A. spinifer* and *M. furnieri*), in larval, juvenile, and adult forms emphasizes the ecological importance of the inner portion of the Amazon estuary as breeding and feeding area and as a fishing ground. Hence, the mitigation of the anthropogenic impacts and the systematic monitoring of the inner portion of the Amazon Estuary should be considered the highest priority. Such measures will be important to guarantee the productivity of these environments for future generations, given the importance of the area in terms of biodiversity and as a source of income and subsistence for local populations.

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