Original article

Optimal fishing samplers to reveal the morphological structure of a fish assemblage in a subtropical tidal flat

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Morphological characters of species are essential for assessing the functional structure of a fish assemblage, since differences between them, for example in body shape, are related to many functional and ecological traits (*e.g.*, swimming, search for food, striking and capturing prey, evading predators, spawning). Globally, tidal flats are relevant to fish assemblages by offering feeding, refuge, and reproduction grounds. To analyze the morphofunctional structure of the fish assemblage from a tidal flat on the Brazilian coast, we conducted standardized sampling using nine different fishing gears. The geometric morphometric method was applied to describe the fish shapes and verify the morphological structure of the assemblage. Here, we present the influence/susceptibility of each gear type on the morphological diversity of the fish assemblage. The results indicated that beach seine, otter trawl, marginal encircling gillnet, and fish traps, together, were the most effective gears to represent the maximum morphological variability of fish inhabiting that tidal flat. Moreover, the assemblage showed high morphological redundancy considered as a resistance of the ecosystem for avoiding functional diversity loss, emphasizing the importance of complementary gear use when determining fish assemblages in a conservation context.

Keywords: Ichthyofauna, Geometric morphometrics, Morphological diversity, Multiple fishing gears, Morphological redundance.

Os caracteres morfológicos das espécies são essenciais para avaliar a estrutura funcional de uma assembleia de peixes, uma vez que as diferenças entre elas são indicativas de distintas características ecológicas. De forma geral, as planícies de maré são importantes para assembleias de peixes por oferecerem áreas para alimentação, refúgio e reprodução. Para analisar a estrutura morfofuncional da assembleia de peixes de uma planície de maré na costa brasileira, realizamos amostragens utilizando nove diferentes artes de pesca. Para descrever as formas dos peixes e verificar a diversidade morfológica da assembleia foi aplicado o método de morfometria geométrica. Aqui, apresentamos a influência/suscetibilidade de cada arte de pesca na composição morfológica da assembleia de peixes, uma vez que a forma do corpo está relacionada a diversos aspectos funcionais e ecológicos (como por exemplo nadar, procurar ativamente por comida, atacar e capturar presas, evadir de predadores, se reproduzir). Os resultados indicaram que o arrasto de praia, o arrasto de fundo, a rede de emalhar marginal e as armadilhas, em conjunto, foram os apetrechos mais efetivos para representar a máxima diversidade morfológica dos peixes que habitam esta planície de maré. Além disso, a assembleia apresentou elevada redundância morfológica, fato que indica resistência deste ecossistema para evitar a perda de diversidade funcional.

Palavras-chave: Ictiofauna, Diversidade morfológica, Morfometria geométrica, Múltiplos petrechos de pesca, Redundância morfológica.

Introduction

Tidal flats are important for many fish species that use these ecosystems during flood tides for feeding, refuge, growth and reproduction (Semeniuk, 2005; Lugendo *et al.*, 2006; Nagelkerken, 2009). This use may occur only during

part of their life cycles (*e.g.*, as nursery ground), on a daily basis or seasonally, during migrations (*e.g.*, pathways in diadromous migrations) for spawning or pursuing preferred prey items, or throughout their entire life span (Whitlatch, 1980; Lenanton, 1982; Nagelkerken *et al.*, 2000; Adams *et al.*, 2006; Franco *et al.*, 2006). Many artisanal fisheries

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depend upon these specific coastal habitats that provide abundant food resources for fishes and shelter against predators, favouring their recruitment and population replenishment (Lipcius *et al.*, 2008; Seitz *et al.*, 2014; Sheaves *et al.*, 2014; Sundblad *et al.*, 2014). Since these ecosystems provide services to billions of people worldwide, knowledge on the composition and structure of the fish assemblages of tidal flats is indispensable (World Bank, 2004; Millennium Ecosystem Assessment, 2005; Salas *et al.*, 2011; Mackinnon *et al.*, 2012). Additionally, fishing activity and how fishing gears select fish sizes and shapes is a key question for fisheries management (Recasens *et al.*, 1998; Alós *et al.*, 2014; Liang *et al.*, 2014).

The Araçá Bay (southeastern Brazil) is a tidal flat ecosystem (~ 500,000 m²) with highly diverse habitats occupied by more than 1,364 species, with 56 novel species catalogued, as well as 16 threatened species (Amaral *et al.*, 2015). The latter including ten benthic species (three polychaetas, five echinoderms, and two enteropneustas); one bird, the royal tern (*Thalasseus maximus* (Boddaert, 1783)), which reproduces on the Brazilian coast exclusively in São Paulo State (Yorio, Efe, 2008); one sea turtle, *Chelonia mydas* (Linnaeus, 1758); and five marine fishes, including the dusky grouper (*Epinephelus marginatus*), the mutton snapper (*Lutjanus analis*), the cubera snapper (*Lutjanus cyanopterus* (Cuvier, 1828), and two rays, the chola guitarfish valid as *Pseudobatos percellens* (Walbaum, 1792) and the spiny butterfly ray (*Gymnura altavela* (Linnaeus, 1758)) (Amaral *et al.*, 2010; Amaral *et al.*, 2015; MMA, 2014; Lamas *et al.*, 2016; Contente, Rossi-Wongtschowski, 2017).

In addition to this biodiversity, many fish species (*e.g.*, sardines, snooks, white mullets, mojarras, groupers, and croakers) are important for surrounding artisanal fishing activities. One of the most abundant fish species in Araçá, the Clupeidae *Sardinella brasiliensis* (Steindachner, 1879), is the main Brazilian fishery resource and at the same time has great ecological importance. It acts as a link in coastal food webs, transferring energy from plankton and small organisms to larger fishes and other organisms positioned at higher trophic levels (Ganias, 2014). The higher phytoplankton concentration inside the bay than in adjacent areas (Ciotti *et al.*, 2015) attracts clupeid and engraulid juveniles in high abundances, allowing larger piscivores to feed in the bay (Matsuura, 1998; Contente, Rossi-Wongtschowski, 2017). Also, high concentrations of mature sardine spawners are frequently found in the region surrounding the São Sebastião Island and the São Sebastião Channel (Fig. 1), close to Araçá bay (Matsuura, 1998). Moreover, Araçá contains areas with the last remaining mangroves along the northern coast of São Paulo State, attesting its vitality and social-ecological importance (Amaral *et al.*, 2015; Schaeffer-Novelli *et al*. 2018). Overall, this makes the bay an ideal example area of a highly productive and diverse subtropical tidal flat.

Morphological characters of species are essential for assessing the functional structure of an assemblage (Schoener, 1974), since morphological differences indicate distinct eco-logical strategies of fish species (Norton *et al.*, 1995). For that reason, morphological techniques have been applied to measure temporal and spatial fluctuations in fish diversity with the purpose of evaluating the environmental and biological factors influencing the community's functional organization. Knowledge on the functional organization of the fish community is extremely useful and can be used to predict structural alterations following disturbances (Winemiller, 1992; Motta *et al.*, 1995). Results of fish morphology studies have demonstrated the relevance of this method to detect variation in functional diversity between ecosystems (Villéger *et al.*, 2010; Lombarte *et al.*, 2012; Farré *et al.*, 2015; Cernansky, 2017).

In tropical and subtropical ecosystems, fish biodiversity includes widely variable forms. However, most studies on this subject have been performed based on a single gear type (Miranda *et al.*, 2008; Rocha *et al.*, 2010; Soeth *et al.*, 2015; Work *et al.*, 2017), even though different gears perform better for specific components. The use of a single gear often underestimates the species richness and the morphofunctional diversity of the system, thereby contributing to an inaccurate assessment of its health (Diekmann *et al.*, 2005; Garcia *et al.*, 2012). Therefore, it is important to combine gears to ensure that all possible compartments and assemblages are included (Baker *et al.*, 2016). Among the factors that can affect habitat-specific gear selection are depth, substratum type, vegetation type and density, and wood or other types of structures (*i.e.*, artificial reefs) (Clement *et al.*, 2014).

Recently, in Araçá Bay, Contente, Rossi-Wongtschowski (2017) used multiple sampling methods and showed that this approach improved the characterization of the fish assemblage composition. However, that study did not cluster the fishing gears according to their catch similarity. Here, our main goal was to perform a morphological analysis of these fish assemblage structures to provide knowledge for its management and conservation. We believe the morphofunctional analysis is an adequate approach to revealing the fishing gear's influence on the fish assemblage organization since the body shape is related to many functional and ecological traits (*i.e.*, swimming, search for food, striking and capturing prey, evading predators, migration, courtship dances, defending territories and spawning) (Wainwright, Richard 1995; Langerhans *et al.*, 2004; Walker, 2010; Azzurro *et al.*, 2014). To achieve this, we used the same fishing samplers as Contente, Rossi-Wongtschowski (2017) to determine which samplers are more efficient to represent the total morphological diversity, independent of fish abundance, which could be biased for several reasons.

Material and Methods

Study area. Araçá Bay (23°48'52"S 45°24'17"W) is a small, semi-secluded coastal area on the north coast of São Paulo State (southwestern Atlantic Ocean), sheltered behind the São Sebastião Island (Fig. 1). Considered as

a natural nursery (Amaral *et al.*, 2015), it shelters a high diversity of organisms and contains the last remaining mangrove of the northern coast of the São Paulo State (Schaeffer-Novelli *et al.*, 2018). There are six nuclei of black mangroves (*Avicennia schaueriana* Stapf & Leechm. ex Moldenke), white mangroves (*Laguncularia racemosa* (L.) C.F.Gaertn.), and red mangroves (*Rhizophora mangle* L.), which cover an area of 3,644 m² (6% of the bay's total area) (Schaeffer-Novelli *et al.*, 2018). Sandy beaches are interspersed between these mangrove spots, two small islets and rocky shores, with one side of the bay delimited by a rockfill. The sediment is mostly sandy-muddy (Amaral *et al.*, 2010) and the hydrodynamics are driven by tides under the action of low-amplitude waves (Dottori *et al.*, 2015). The bay is exposed to the São Sebastião Channel dynamics, a highly energetic region influenced by wind flows (Castro, Miranda, 1998). Large tidepools arise in the bay when the semi-diurnal tides are low (> 50 m²) (Brenha--Nunes *et al.*, 2016).

Although being a rich environment, the Araçá bay is under anthropogenic pressure by activities of the São Sebastião Port (SBP) and eventual oil leaks from the Almirante Barroso Terminal (Petrobrás). In addition, it is susceptible to other constant anthropic effects, such as irregular occupations, domestic sewage, and the presence of one sea outfall (Amaral *et al.,* 2010, 2015). Since its construction in 1936, the SBP has been expanded through successive landfills, two of which (in 1987 and 1994) covered part of the bay, changing the original configuration of the nearby beaches (Albuquerque, 2013). In 2009, a new port expansion project was proposed, involving the construction of a concrete slab covering 75% of the area (CPEA, 2011), which would affect all ecosystem processes (Pardal-Souza *et al.*, 2016). After a scientific evaluation involving a group of experts being made (Amaral *et al.*, 2018), this expansion has been heavily debated and the port project was discontinued by competent authorities. Accordingly, a new environmental assessment is required to proceed with the lawsuit.
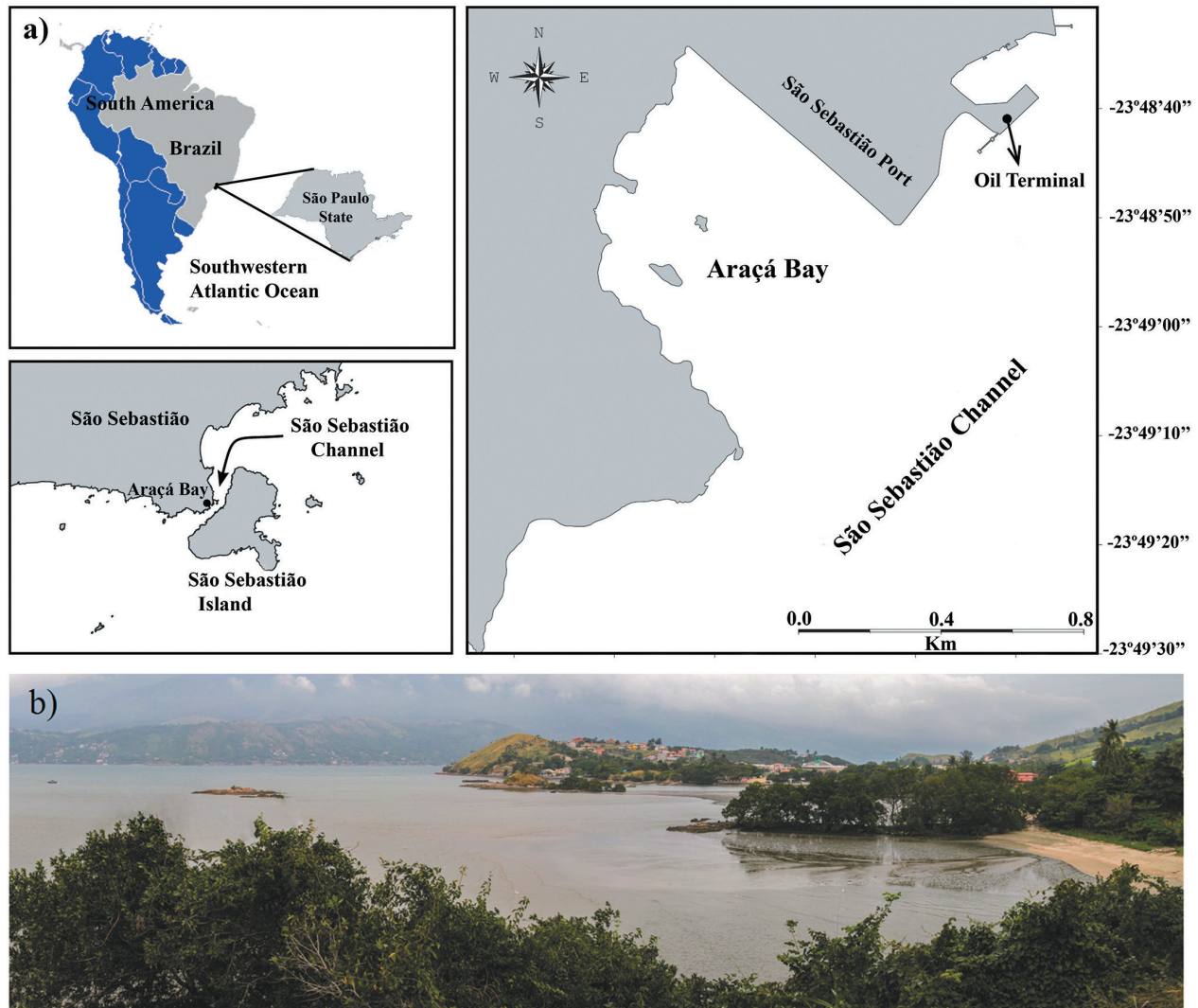
Fig. 1. a. Araçá Bay location, bordering São Sebastião Channel, north shore of São Paulo State, Brazil; **b.** Araçá Bay (Photo: Gabriel Monteiro).

Sampling. Four sampling nocturnal campaigns (Permits nos. 5218, 5553, 5866 and 6104, authorized by Brazil's Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio), each lasting 12 days, were carried out between March 2013 and January 2014 along the Araçá Bay. At night (after 6:30 pm) the tidal flat is almost totally flooded, increasing the habitat availability for fish sampling. During high tide in Araçá Bay, four habitats are recognized: intertidal habitat (mean ± standard deviation 0.6 ± 0.3 m), marginal shallow sublittoral habitat (0.8 ± 0.4 m), inner shallow sublittoral habitat (1.2 ± 0.5 m), and outer sublittoral habitat (8.4 ± 4.1 m) with soft and rocky bottoms. To consider the main habitats of the bay, samplings were performed using nine gears of regional common use, as follows: Otter trawls were carried out from a small boat equipped with two nets (9.5 m opening x 6.7 m sac; 10 mm mesh between nodes), one on each side of the boat. Seven fishing launches were performed for five minutes each in the sublittoral zone bordering the São Sebastião Channel, following random direction but not overlapping; Beach seine netting (15 m length x 4 m sac; 5 mm mesh between nodes) was conducted by two fishermen maintaining the net mouth opening toward the beach front. This procedure was repeated in the five sandy beaches of Araçá; Encircling gillnet 1 (eg1) (590 m length x 3 m height; 30 mm mesh between nodes) was employed using a canoe where the fisherman spreads the net in a circle, with the starting point marked by an indicator buoy. The procedure was accomplished twice, one in each half of the bay (right and left inner sides); Encircling gillnet 2 (eg2) (590 m length x 3 m height; 30 mm mesh between nodes) was spread in a "J" format on the sides of the bay, near the rocky shores (marginal); Large gillnet was a single nylon net arranged in an L-shape maintained during 12 hours (Larger portion = 154 m length x 3.3 m height, small portion = 87.75 m length x 3.15 m height; 50 mm mesh between nodes, in both). A fisherman performed fish removal every 6 hours; Small gillnet with two nets (154 m length x 2.6 m height; 32 mm mesh between nodes) was arranged in parallel in front of the mangrove, between the two islets present at the bay core. A fisherman performed fish removal every 6 hours; Cast net (4 m of radius and 30 mm between nodes) was launched randomly three times in each one of the bay's six zones; Fish traps (80 cm length x 53 cm height x 37 cm width; 1.5 cm of mesh) were placed consecutively along the right rocky shore, for 48 hours. Fish removal was realized every 6 hours; Hook and line were used along the sampling period, sardines and shrimps being used as lures, on the border of the SSC.

Details regarding samplings, gear design, and operation are described by Contente, Rossi-Wongtschowski (2017). However, we considered the encircling gillnet as two different gears because the same net was employed in distinct habitats (the inner shallow sublittoral and the marginal shallow sublittoral). Samplings occurred on consecutive nights, during high tides on a quarterly basis. Beach seine, otter trawl, cast net, encircling gillnets 1 and 2, large and small gillnets were used in soft-bottoms, intertidal, and sublittoral habitats. Fish trap, and hook and line were used over the rocky bottoms in the outer sublittoral.

Fishes were euthanized through thermal shock. The classification followed the description by Fricke *et al.* (2019). All fresh specimens were measured to the nearest 1.0-mm total length (TL). Structures such as fins, beards, cutaneous appendages, and extended fin rays were fixed with formalin and trapped in a white background base using entomological pins. Standardized images (around 4,000) of the left side of the body were obtained for all species. Samples, which included 10 fishes (when possible), fit into 10-mm intervals, were obtained. Vouchers were deposited and catalogued at the Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP) (the voucher number of specimens is presented at **S1** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni and is also available at Lamas *et al.*, 2016).

Geometric morphometric data and analysis. Geometric morphometric method was used to quantify and describe the shapes of species and to represent morphological variability within a morphospace. Fish morphometric data were obtained considering 27 landmarks and semilandmarks (Tab. 1, Fig. 2) following Recasens *et al.* (2006), Farré *et al.* (2013), and Tuset *et al.* (2014). Landmarks are homologous coordinate points positioned in anatomical structures of interest, which are utilized to define the geometric shape of specimens (Bookstein *et al.*, 1985). When important biological information (*e.g.*, the presence of barbel in fish) cannot be defined using landmarks, an additional type of coordinate points can be used to define the shape of boundary curves or of not fixed structures, and are named semilandmarks (Bookstein, 1991; Bookstein *et al.*, 1997). Semilandmarks were necessary and important to differentiate species concerning their fin adaptations or sensory organs presence, given the ecological value associated to these features. For each species, a consensus image was built from the composed samples (10 fish images) using tpsDig, v.2.16 (Rohlf, 2001) and following Recasens *et al.* (2006) and Lombarte *et al.* (2012). The landmarks and semilandmarks were digitalized, rotated, scaled (to unit centroid size), and translated. Then, a generalized least-square superimposition (GLS) procedure (generalized Procrustes) was applied using tpsRel 1.24 (Rohlf, 2001). A thin-plate spline representation was used to fit the interpolated function to an average map (consensus configuration) of the profile shape, resulting in uniform components of the shape variation (relative warps, RW). Finally, a relative warp analysis allowed changes in shapes to be visualized (following Rohlf, Marcus, 1993). According to Recasens *et al.* (2006) and Lombarte *et al.* (2012), the first eight RWs explain more than 95% of the total morphological variability and describe each species. The morphospaces based on qualitative data (presence/absence) were generated using only three warps, since they represented around 70% of the variability, allowing the structural complexity of the fish assemblage of each gear and all gears together to be discerned. The Euclidean distances between all pairs of aligned and scaled specimens in the tangential plane, and the Procrustes distances between all pairs of specimens

in the Kendall shape space, were compared using TpsSmall 1.33 (Rohlf, 2015). The correlations indicated minimal variation between all fishing gears ($r > 0.9999$), confirming that for the nine gears both tangential spaces were nearly identical. Kernel density plots indicate the shapes of major occurrence.

Measuring morphological diversity. Three morphological indices were estimated for each fishing gear and all gears together based on the presence/absence data matrix. The Morphological Richness Index, $MR = \sum jCC$ (Farré *et al.*, 2013), Morpho-geometric Diversity Index, $EM1 = \sum jCC/(N-1)$ (Recasens *et al.*, 2006; Lombarte *et al.*, 2012), and Morphological Disparity, $MD = \sum jRWj^2/(N-1)$ (Zelditch *et al.*, 2003; Antonucci *et al.*, 2009) were calculated and classified by hierarchical agglomerative cluster analysis using the Euclidean distance (where, CC is the cluster coefficient, j is the species, N is the total number of species, and RWj represents the species relative warps). Directly related to richness, the MR index quantifies the diversity of distinct morphologies within an assemblage (Farré *et al.*, 2013,

2016). Complementary, MD index measures and defines the morphospace size and configuration, while EMI determine the degree of species clustering within the morphospace (Lombarte *et al.*, 2012; Farré *et al.*, 2013, 2016).
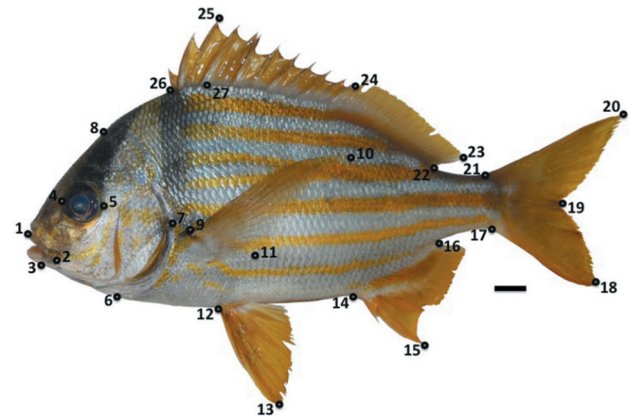
Fig. 2. Landmarks and semilandmarks used in the geometric morphometric analysis (scale bar= 1 cm).

Tab. 1. Functional traits derived from 27 landmarks and semilandmarks, points number and ecological meaning correspondences (ecological meaning correspondences according to Recasens *et al.* 2006; Farré *et al.* 2013, 2016).

Functional Trait	Points Number	Ecological Meaning Correspondence
Mouth position and size in relation to the head and body size	1 and 2	Food aquisition, and relative size of preys
Presence and size of sensorial barbells	3	Life strategies and feeding behavior
Size and position of the eyes in relation to the head and body size	4 and 5	Life strategies and prey detection
Relative head size (height and width) respect to the body size	6 to 8	Life strategies and prey detection
Size, shape and position of pectoral fins	9 to 11	Swimming, stability in the water column, life strategies, feeding behaviour and avoiding of predators
Size, shape and position of pelvic fins	12 and 13	Stability in the water column and over the bottom, life strategies
Size, shape and position of the anal fin	14 to 16	Stability in the water column and over the bottom, life strategies
Shape and size of the peduncle and of the caudal fin	17 to 21	Propulsion during swimming, food aquisition, avoiding of predator
Second dorsal fin position and ending	22 and 23	Stability in the water column, life strategies
Presence of one or two dorsal fins	24	Taxonomic value
First dorsal-fin position and starting	25 and 26	Stability in the water column, propulsion, preys attractive, life strategies
Maximum height of the body shape	27	Swimming and life strategies

Statistical analysis. To explore the influence of the gears on the morphological structure of the fish assemblage, a redundancy analysis (RDA) (Legendre, Legendre, 1998) was performed on all nine fishing gears. This technique uses one matrix showing the presence/absence of each species for each fishing gear (predictor variables) to quantify the variation in a matrix of response variables (the first two relative warps of all species). The explained variance was derived from the sum of squares on a regression (Richards *et al.*, 1996).

Results

Composition and morphological structure of the fish assemblage. Overall, 106 Actinopterygii species (**S2** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni),

belonging to 47 families were identified at species level. The most common species were: *Harengula clupeola*, *Sardinella brasiliensis* (Clupeidae), *Eucinostomus argenteus*, *Diapterus rhombeus* (Gerreidae), *Atherinella brasiliensis* (Atherinopsidae), *Mugil curema* (Mugilidae), and *Haemulopsis corvinaeformis* (Haemulidae).

Morphological analyses revealed a wide variety of shapes, such as, anguilliform (*e.g., Gymnothorax ocellatus*), fusiform (*e.g., Epinephelus marginatus*), elongated (*e.g., Hemiramphus brasiliensis*), oblong (*e.g., Prionotus punctatus*), oval (*e.g., Lagocephalus laevigatus*), asymmetrical flatfish (*e.g., Citharichthys macrops*), and seahorse (*e.g., Hippocampus reidi*). In the general morphospace, the first axis (RW 1, 37.5% of the total variance) was related to the position of the first dorsal fin and body shape; elongated for positive values, and higher bodies, laterally compressed for

negative values (Fig. 3). The second axis (RW 2, 25.4%) defined elongated fish shapes with the first dorsal fin distant to the head (positive values), and benthic fishes with dorsal-ventral flattened shapes or elongated dorsal and anal fins (negative values) (Fig. 3). The third axis (RW 3, 7.8%) expressed the pelvic fin position and gave positive values when anterior and near the scapular girdle or negative values when the pelvic fin was posterior or modified (Fig. 3). Within the convex hull, two major groups were identified: one formed by demersal species, such as grunts (Haemulidae), mojarras (Gerreidae), and croakers (Sciaenidae), and another formed by active swimmers, such as clupeids, en-

graulids, and neotropical silversides (Atherinopsidae) (Fig. 4, indicated as grey ellipses). The remaining species tended to disperse in the morphospace depending on their morphological specialization and on the relative warp used to represent the external variability (Fig. 4a with the first and second warp; 4b with the first and third warp). The species located in the peripheral morphospace provided the highest morphological dispersion and variability of the fish assemblage, *i.e.*, eel-like fishes (Anguilliformes), flatfishes (Pleuronectiformes), porcupinefishes (Diodontidae), halfbeaks (Hemiramphidae), seahorses (Syngnathiforms), and some carangids.
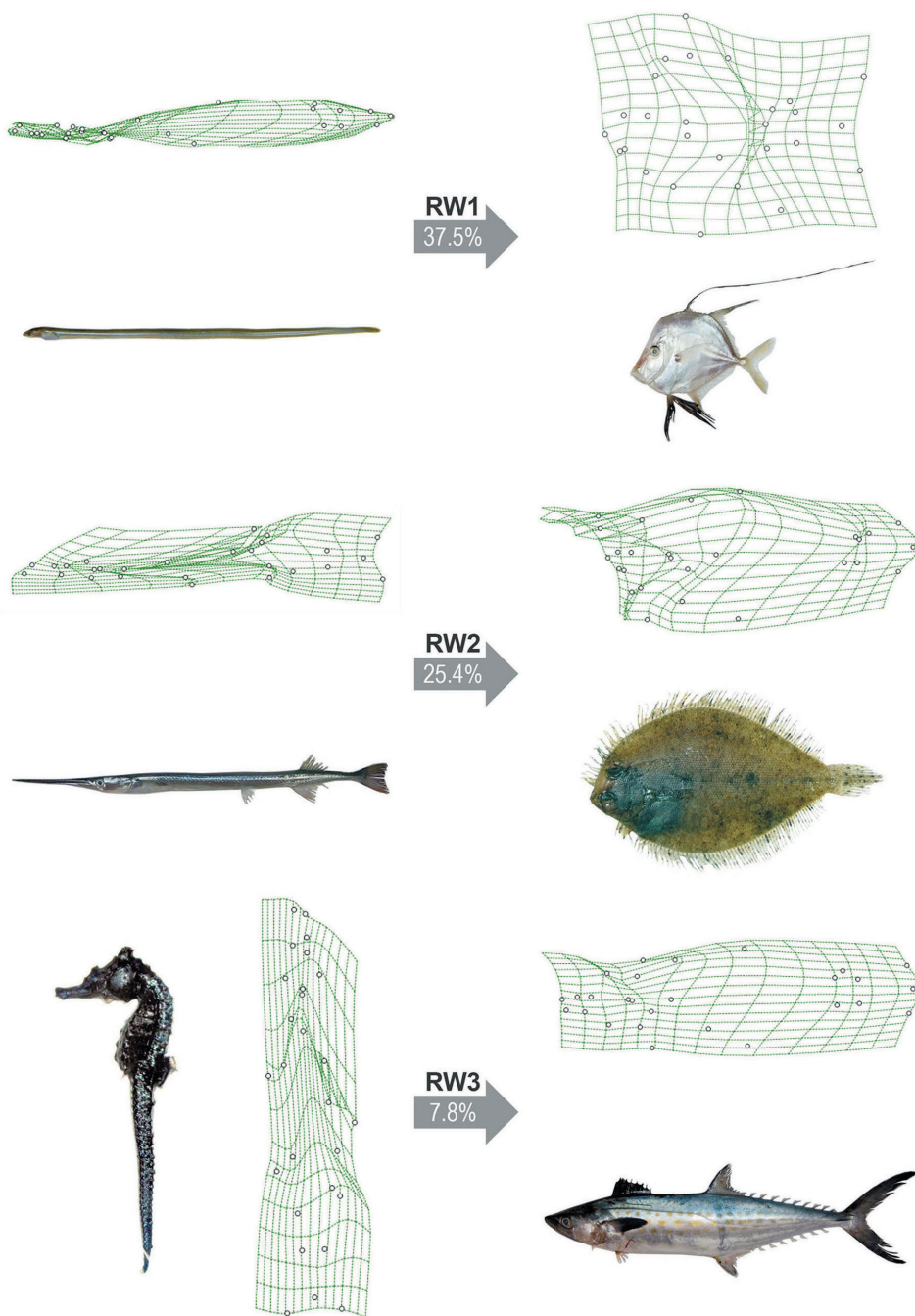
Fig. 3. Morphological diversification and variance explained for the relative warps (RW) 1 to 3 using the thin-plate spline.

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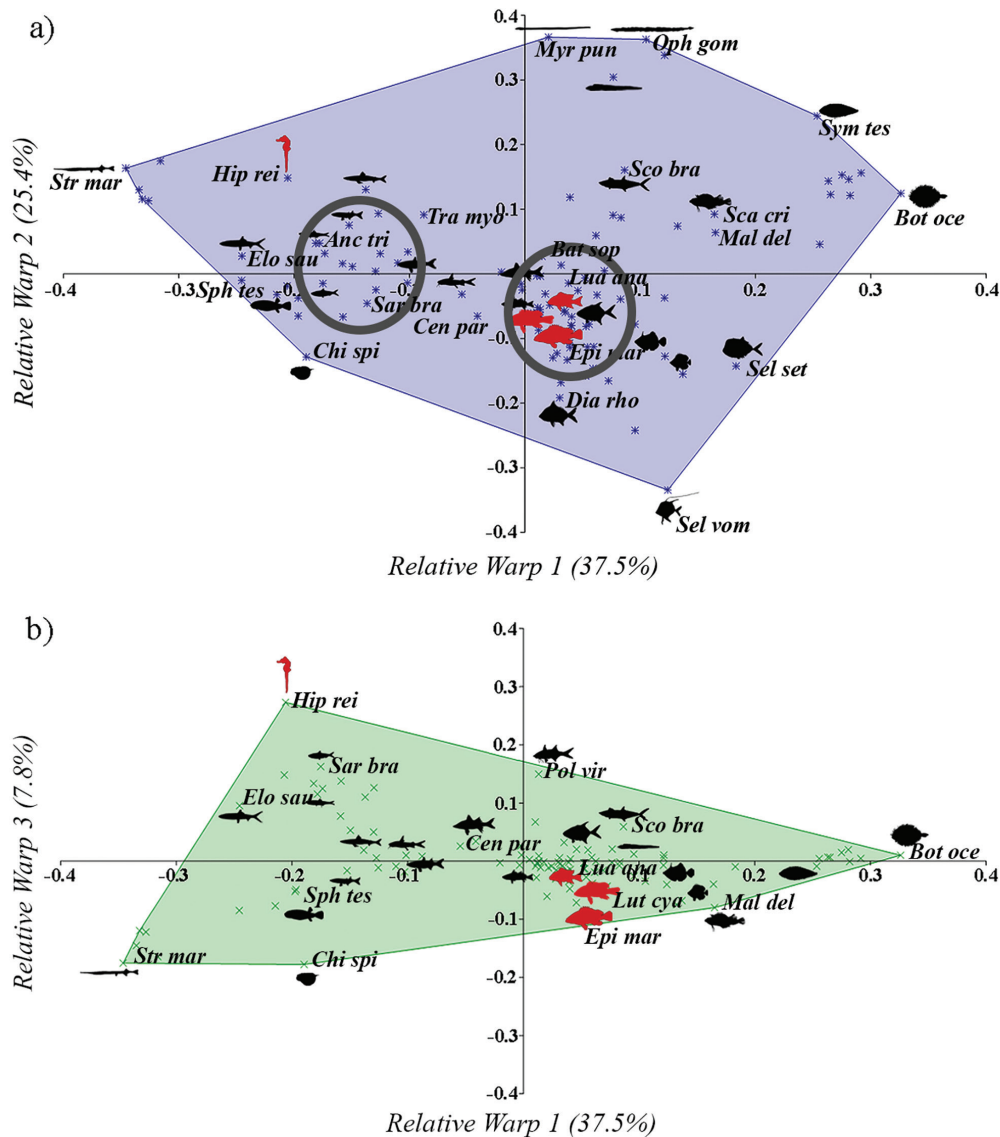
Fig. 4. Morphospace represented by shape variation of all species in the nine fishing gears grouped, using the relative warps: **a.** 1 and 2; **b.** 1 and 3. Acronyms: *Anc tri, Anchoa tricolor*; *Bat sop, Bathygobius soporator*; *Bot oce, Bothus ocellatus*; *Cen par, Centropomus parallelus*; *Chi spi, Chilomycterus spinosus*; *Dia rho, Diapterus rhombeus*; *Elo sau, Elops saurus*; *Epi mar, Epinephelus marginatus*; *Hip rei, Hippocampus reidi*; *Lut ana, Lutjanus analis*; *Lut cya, Lutjanus cyanopterus*; *Mal del, Malacoctenus delalandii*; *Myr pun, Myrophis punctatus*; *Oph gom, Ophichthus gomesii*; *Pol vir, Polydactylus virginicus*; *Sca cri, Scartella cristata*; *Sco bra, Scomberomorus brasiliensis*; *Sel set, Selene setapinnis*; *Sel vom, Selene vomer*; *Sph tes, Sphoeroides testudineus*; *Str mar, Strongylura marina*; *Sym tes, Symphurus tesselatus*; *Tra myo, Trachinocephalus myops*. Threatened species (*Hip rei*, *Lut ana*, *Lut cya*, *Epi mar*) are highlighted in red.

Morphological variability according to each gear. Otter trawl and beach seine (both active gears) captured a high number of species (53 and 52, respectively) and the highest diversity of body shapes. The otter trawl morphospace (Fig. 5) was compounded mainly by flatfishes (*Bothus ocellatus*, *Citharichthys spilopterus*, *Syacium papillosum*), moderately compressed fusiform bodies (*Diplodus argenteus*, *Haemulon steindachneri*, *Micropogonias furnieri*) or high laterally compressed (*Hemicaranx amblyrhynchus*, *Oligoplites saurus*, *Stephanolepis hispidus*), and by oval bodies (*L. laevigatus*, *Sphoeroides greeleyi*, *Sphoeroides testudineus*).

The beach seine morphospace (Fig. 5) was compounded by eel-like fishes (*Myrophis punctatus*, *Ophichthus gomesii*), fishes with a pointed snout (*H. brasiliensis*, *Hyporhamphus roberti*, *Strongylura marina*), very specialized shapes (such as the seahorse *H. reidi*), cylindrical elongated bodies (*Synodus foetens*, *Trachinocephalus myops*), fusiforms adapted to living hidden or burrowed (*Bathygobius soporator*, *Ctenogobius boleosoma*, *Malacoctenus delalandii*), and some clupeid forms (*H. clupeola*, *Opisthonema oglinum*, *S. brasiliensis*). The inner encircling gillnet (Fig. 5) also caught demersal species, similar to the otter trawl, but these were mainly

mojarras (*E. argenteus*, *Eucinostomus gula*, *Eucinostomus melanopterus*), weakfishes and croakers (*Cynoscion jamaicensis*, *Cynoscion leiarchus*, *Menticirrhus americanus*), snooks (*Centropomus parallelus*, *Centropomus undecimalis*), and mugillids (*Mugil curema*, *Mugil liza*). The marginal encircling gillnet (eg2) (Fig. 6) capture was much similar to that of the inner encircling gillnet (eg1); however, fish shapes with higher mobility were also captured (*Caranx latus*, *Pomatomus saltatrix*, *Selene setapinnis*, *Selene vomer*, *Trachinotus carolinus*). The cast net (Fig. 6) operated on intertidal, marginal shallow sublittoral and inner shallow sublittoral habitats, and represented the most variable morphologies compared with the other fishing gears. Specifically, it was found to be an important way of capturing clupeids species. Among passive gears, the fish trap (Fig. 6) and hook and line (Fig. 7) caught shapes adapted to life at rocky reef habitats (*Chaetodon striatus*, *E. marginatus*, *Labrisomus nuchipinnis*, *Mycteroperca acutirostris*, *Nicholsina usta*, *Scartella cristata*). Additionally, the small gillnet (Fig. 7) allowed demersal species associated with muddy bottoms to be obtained, such as the catfish (*Genidens genidens*) and the threadfin (*Polydactylus virginicus*). The large gillnet (Fig. 7) caught fishes adapted to diverse habitats, and represented the only gear that fished the pelagic species *Anchoviella lepidentostole*, and *Tylosurus acus*. Beach seine, fish trap, hook and line, and marginal encircling gillnet registered the occurrence of three threatened species: the longs-nout seahorse (*H. reidi*), the dusky grouper (*E. marginatus*), and the cubera snapper (*L. cyanopterus*). Adult and juvenile forms of the mutton snapper (*L. analis*), another threatened species, were recorded by most of the gears, except by the cast net and fish traps.

Effect of fishing gear on the fish assemblage. The morphological indices indicated that the beach seine and otter trawl aggregated the highest morphological disparity (*MD* = 0.057 and 0.053, respectively) and morphological richness (*MR* = 7.03 and 6.35, respectively), whereas the inner encircling gillnet (*MD* = 0.042 and *MR* = 3.36) and small gillnet (*MD* = 0.045 and *MR* = 3.63) attained higher values of morphogeometric diversity (*EMI* = 0.160 and 0.158, respectively), indicating less redundancy of external morphology (Tab. 2).

The RDA demonstrated that the morphological structure of the Araçá fish assemblage is expressed by a combination of fish shapes caught by complementary gears (Monte Carlo test, Pseudo-*F* = 0.260, P < 0.001) (Fig. 8, Tab. 3). RDA1 attained 14.2% of the total inertia, and was mainly correlated to RW2 (*r* = 0.405, while *r* = -0.338 for RW1). The marginal encircling gillnet, fish trap, and beach seine were better correlated to RW1 (*r* = -0.193, *r* = -0.142 and *r* = 0.103, respectively). In contrast, the second RDA2 axis only explained 6.5%, and was correlated to both relative warps (*r* = 0.273 for RW1, and *r* = 0.229 for RW2). However, the otter trawl best defined the RDA2 axis (*r* = 0.123).
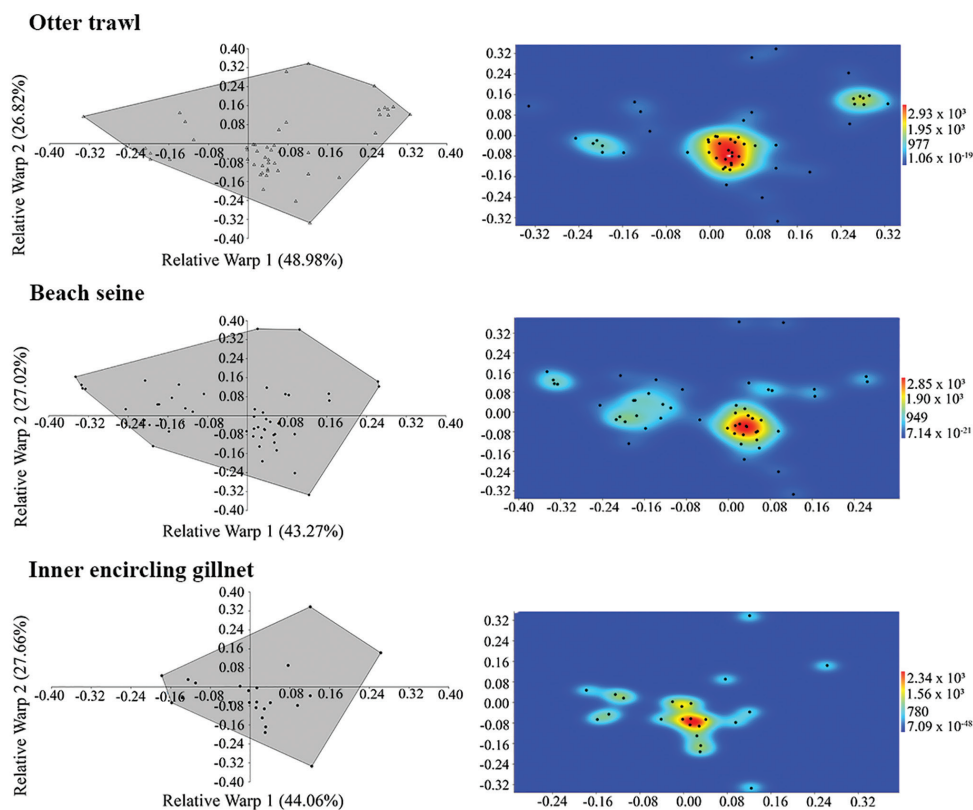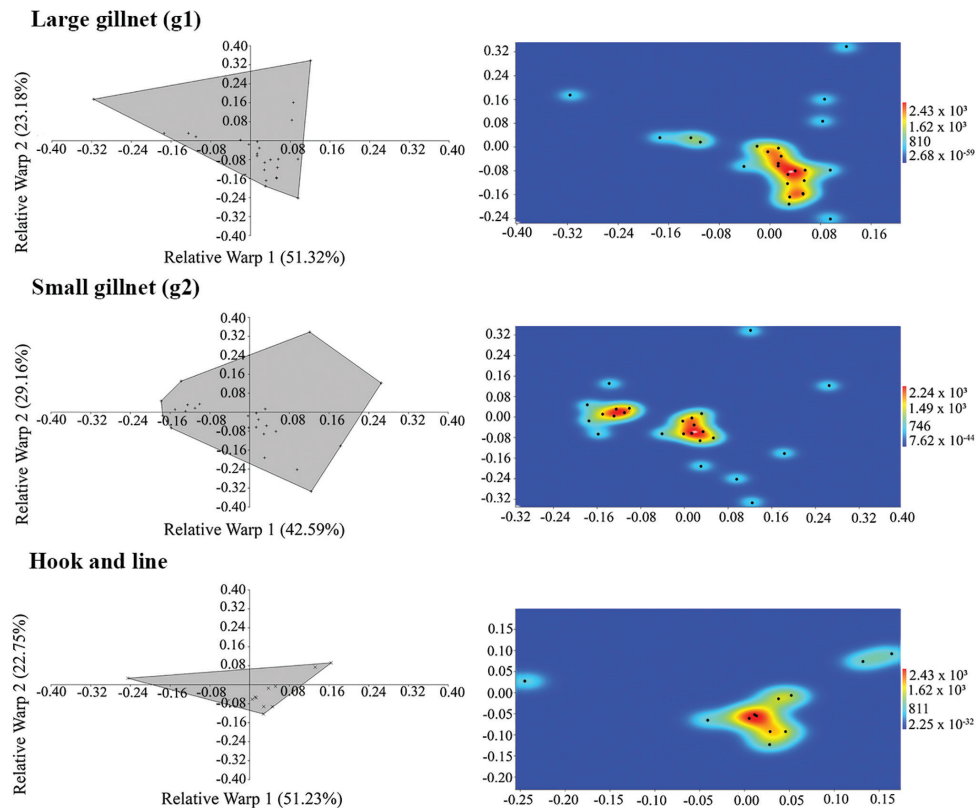

Fig. 5. Morphospaces obtained using the first and second relative warps for otter trawl, beach seine and inner encircling gillnet. Warm colours in the Kernel density plots indicate the shapes of major occurrence.

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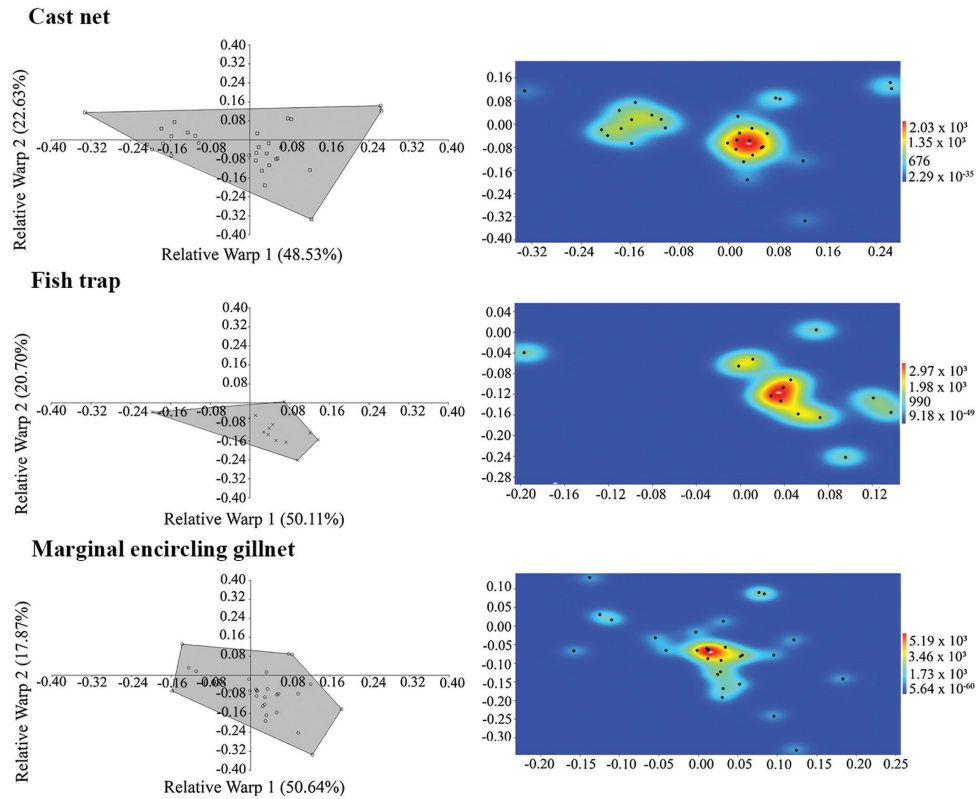
Fig. 6. Morphospaces obtained using the first and second relative warps for cast net, fish trap and marginal encircling gillnet. Warm colours in the Kernel density plots indicate the shapes of major occurrence.

Fig. 7. Morphospaces obtained using the first and second relative warps for large gillnet, small gillnet and hook and line. Warm colours in the Kernel density plots indicate the shapes of major occurrence.

Tab. 2. Morphological diversity indices estimated using incidence-based data for all grouped fishing gears and for each fishing gear apart: MD, morphological disparity; MR, morphological richness; and, EMI, morpho-geometric diversity. Bold values indicate fishing gears that aggregate highest morphological variability.
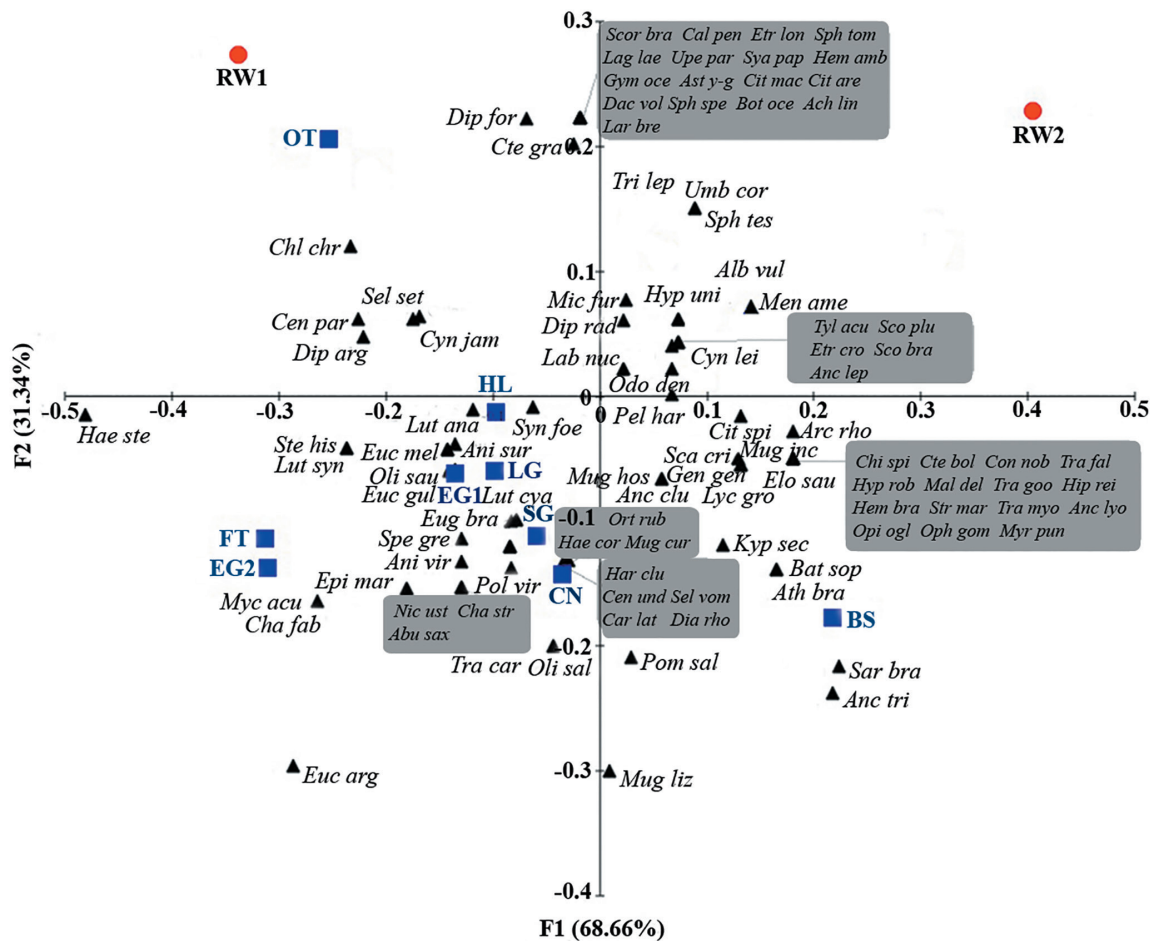
Fishing gears	Morphological		
	MD	MR	EMI
Active gears			
Beach seine	**0.057**	**7.03**	0.141
Cast net	0.044	4.16	0.149
Inner encircling gillnet	0.042	3.36	**0.160**
Marginal encircling gillnet	0.031	3.36	0.124
Otter trawl	**0.053**	**6.35**	0.122
Passive gears			
Fish trap	0.037	1.64	0.149
Hook and line	0.025	1.38	0.138
Large gillnet	0.038	3.42	0.149
Small gillnet	0.045	3.63	**0.158**
All	0.052	11.68	0.112

Tab. 3. Scores of explanatory variables in the redundancy analysis. In bold are the fishing gears representing a major fish shape variations.

Fishing gears	F1	F2
Beach seine	**0.103**	-0.038
Cast net	-0.019	-0.054
Fish trap	**-0.142**	-0.089
Hook line	-0.033	-0.003
Inner encircling gillnet	-0.006	-0.012
Large gillnet	0.001	0.011
Marginal encircling gillnet	**-0.193**	-0.066
Otter trawl	-0.080	**0.123**
Small gillnet	0.046	-0.039

Discussion

Our findings indicate high morphological diversity in the fish fauna of the Araçá tidal flat, reflecting the heterogeneity of the habitats presents in the ecosystem, which include mangrove spots, small islets, sandy beaches, rocky shores, and tidepools. Additionally, we demonstrate that

Fig. 8. Redundancy analysis (RDA): individual species-gear relationships explained by morphological shape variability, using incidence data. In blue, fishing gear acronyms: beach seine (BS), cast net (CN), fish trap (FT), hook and line (HL), inner encircling gillnet (EG1), large gillnet (LG), marginal encircling gillnet (EG2), otter trawl (OT), small gillnet (SG).

some of the samplers (beach seine, otter trawl, marginal encircling gillnet, and traps) best represent the wide morphological diversity of the fishes, which use the resources offered by this tidal flat. Each one of these fishing gears contributed in partially emphasizing the morpho-functional structure of the assemblage, showing species that perform distinct roles in the ecological processes sustaining the ecosystem (Ricklefs, 2010; Arantes, 2014; Leitão *et al.,* 2016). However, the active fishing gears (*i.e.*, beach seine, otter trawl, and encircling gillnets) were less selective and more precise at revealing the fish spatial distribution and habitat use (Broadhurst *et al.*, 2006). In turn, capture by traps was directly or indirectly most dependent on fish behavior and morphology (Hayes *et al.*, 2010; Alós *et al.*, 2012, 2014). Beach seine was crucial to represent the richness, comprising the largest extent of morphological and taxonomical variability. Commonly used to capture mid-water and bottom-dwelling fishes (Butcher *et al.*, 2005; Dembkowski *et al.*, 2012), the beach seine captured the majority of small-to-medium species as well as elongated and active ones, such as the halfbeaks (*Hyporhamphus roberti, H. unifasciatus* and *Hemiramphus brasiliensis*), which possess long premaxillae's permitting them to feeding on the water column and lift up the substrate to find preys (Hobson, 1975; Earl *et al.,* 2011). Likewise, the beach seine retained many small shapes, probably because it was operated at the intertidal zone and close to the mangrove spots, an area of advantageous conditions for feeding and refuge.

Species with extreme morphological characters, peripherals inside the morphospace, provided more morphological variability. According Lombarte *et al.* (2012) and Farré *et al.* (2016) peripheral species usually occupy very specialized functional groups with few specimens; therefore, they are more sensible to anthropogenic disturbances. In contrast to the beach seine, the otter trawl mainly captured flatfishes (flounders) and oval shapes (pufferfishes) (both peripheral species), besides some demersal fusiforms (croakers) with great importance for local fishermen. However, otter trawl per se would slightly underestimate the fish morphological variability since it sampled not many small pelagic species at the surface. In a complementary way, the marginal encircling gillnets and traps caught the fusiform shapes centrally located at the morphospace but associated with the rocky bottoms, adding information about redundancy of the assemblages.

Worldwide, coastal shallow sandy areas (including tidal flats) are recognized as important nursery and growth grounds for fish (Gillanders *et al.*, 2003; Adams *et al.*, 2006; Favero, Dias, 2015; Le Luheme *et al.*, 2017). The peculiar presence of the small mangrove spots in Araçá Bay, the habitats heterogeneity and the advantageous hydrodynamics, provide shelter and food for juveniles of many species, including important commercial fishes, besides being a natural refuge for some globally considered threatened species, such as the snappers *L. analis* and *L.*

cyanopterus, and the dusky grouper *E. marginatus* (Lamas *et al.*, 2016; Contente, Rossi-Wongtschowski, 2017). Gibson (1994), Vasconcelos *et al.* (2013), and Le Pape, Bonhommeau (2015) consider this kind of ecosystem as a nursery ground, and according to Sheaves *et al.* (2014) and Nagelkerken *et al.* (2015), this characteristic renders a substantial importance for its maintenance.

It is well known that fish vulnerability is strongly dependent on their shape, body size, behavior and habitat (Ehlinger, 1990; Fulton, Bellwood, 2005; Fulton *et al.*, 2005; Domenici *et al.*, 2008; Alós *et al.*, 2014) and the catch effectiveness is according to the gear type selectivity (Bayley, Herendeen, 2000; Newman *et al.*, 2012; Walker *et al.*, 2017). Our results indicate that biodiversity studies with a reduced number of samplers can underestimate the morphofunctional richness, and therefore, cause an inaccurate assessment of the ecosystem fish assemblages. According to Selig *et al.* (2014), the high richness recorded in Araçá shows its greater resilience to environmental stress than other similar communities with lower richness. Nevertheless, caution is needed since little is known about the population conditions of Brazilian ichthyofauna, with most of the species classified as "Insufficient data" by the law containing the list of threatened species (MMA, 2014).

Independent of the diversity, Araçá fish assemblage showed high morphological redundancy. Since morphological redundancy can be considered as a biological resistance of the ecosystem for avoiding biodiversity loss (Micheli *et al.*, 2014), even if a specific loss occurs, other species with similar characteristics would replace its functional role.

In the future, if occurs the port expansion, the morphological analysis would be a useful tool to monitor the fish assemblage and possibly, to detect its structural changes based on multiple gear samples, as demonstrated for other fish assemblages (Wainwright, Richard, 1995; Layman *et al.*, 2005; Lombarte *et al.*, 2012; Oliver *et al.*, 2015). Even though morphological analysis is efficient to diagnose both the species composition as well as the assemblage structure, later, its employment linked to a functional diversity analysis can delineate how resilient the habitats composing that ecosystem are.

Acknowledgments

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