Josafá José do Carmo Reis Júnior

Application of geometric morphometrics to understand ecological aspects of marine fish in Southwestern Tropical Atlantic

Recife

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PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOMETRIA E ESTATÍSTICA APLICADA

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This thesis was considered appropriate for obtaining the title of Ph.D. in Biometrics and Applied Statistics, defended and unanimously approved on 16/01/2023 by the examining committee

Concentration Area: Biometrics and Applied Statistics

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I dedicate this work to my mother,
Rosemêre, for having invested in my
education that made me get this far.

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“Passo pelo teste. Diminuirei e partirei para o Oeste, e continuarei sendo Galadriel.”

O espelho de Galadriel

“Voltei. Mais uma vez voltei pra teus braços.
Tenho corpo fechado.
Minha vida é o mar.”

Dorival (Academia da Berlinda – 2016)

Abstract

The phenotype of organism is the result of the interaction of a set of genetic, ecological, and environmental factors. Functional morphology investigates these phenotypic variations and geometric morphometry serves as a tool that helps in the understanding of ecological phenomena related to morphology. In this work we use geometric morphometry techniques on the marine fish body to understand ecological aspects linked to trophic ecology and habitat access at a community level. Fish were collected along the continental shelf of northeastern Brazil (4-9°S), and underwater footage was used to classify bottom habitat type into SWCR (sand with corals and rocks), Algae, and Sand. Individuals were photographed in lateral view, and shape was extracted using landmarks or contours techniques along the individuals' bodies. In total we analyzed 120 species distributed in 16 orders and 45 families of demersal fish. The relationship between body shape and trophic ecology indicated that lower trophic levels (herbivores and omnivores) are characterized by a deep body and large dorsal and anal fin bases. Top predators showed an elongated body and narrow fins. Using a multiple linear regression, we found that 46% of the variability in trophic level can be explained by morphometric variables, with increasing trophic level related to body elongation and fish size, the first time such a model has been proposed. Interestingly, intermediate trophic categories (e.g., low predators) showed morphological divergence for a given trophic level. The relationship between body shape and habitat type at first did not indicate clear patterns, when looking at the volume and morphological dispersion of the morphospace. However, when we considered the morphospace composed of the species with the highest abundances in each habitat type (All species present in the habitat, species with abundance $\geq 25\%$ and with abundance $\geq 50\%$), we concluded that there is a tendency to find fish with more elongated body shape in the Sand type habitat when compared to the Algae and SWCR habitats. Overall, the 120 species are divided among 13 main fish shape groups, and body elongation rate was the main axis of variation found. The morphological characteristics found are directly related to swimming performance, where success in prey capture (e.g., top predators) and habitat access (species adapted to live in an open environment with high water flow velocity, e.g., sand habitats) are favored in species with elongated body shape. Morphological proximity had low congruence with the phylogenetic tree, indicating that our morphological approach cannot be used to observe phylogenetic proximity. Our results can be expanded to other tropical or non-tropical systems, showing that morphometric data can provide important insights into the functional characteristics of fish, especially in trophic ecology and habitat use.

Key-words: geometric morphometrics, demersal fish, trophic ecology, habitat access, fish phenotypic expression, tropical marine habitats

Resumo

O fenótipo do organismo é resultado da interação de um conjunto de fatores genéticos, ecológicos e ambientais. A morfologia funcional investiga essas variações fenotípicas e a morfometria geométrica serve como ferramenta que ajuda na compreensão dos fenômenos ecológicos relacionados a morfologia. Nesse trabalho nos utilizamos técnicas de morfometria geométrica no corpo de peixes marinhos, para entender aspetos ecológicos ligados a ecologia trófica e acesso ao habitat em um nível de comunidade. Os peixes foram coletados ao longo da plataforma continental do nordeste do Brasil (4-9°S), e filmagens subaquáticas foram utilizadas para classificar o tipo de habitat de fundo em SWCR (areia com corais e rochas), Alga e Areia. Os indivíduos foram fotografados em vista lateral, e a forma foi extraída através das técnicas de pontos homólogos ou contornos ao longo do corpo dos indivíduos. No total analisamos 120 espécies distribuídas em 16 ordens e 45 famílias de peixes demersais. A relação entre forma corporal e ecologia trófica indicou que níveis tróficos menores (herbívoro e onívoros) são caracterizados por um corpo profundo e largas bases de nadadeiras dorsal e anal. Predadores de topo apresentaram corpo alongado e nadadeiras estreitas. Usando uma regressão linear múltipla, nos verificamos que 46% da variabilidade do nível trófico pode ser explicada por variáveis morfométricas, com aumento do nível trófico relacionado com alongamento corporal e tamanho do peixe, sendo a primeira vez que um modelo desse tipo foi proposto. Curiosamente, as categorias tróficas intermédias (ex., baixos predadores) apresentaram divergência morfológica para um dado nível trófico. A relação entre forma do corpo e tipo de habitat a princípio não indicou padrões claros, quando observamos o volume e dispersão morfológica do morfoespaço. Contudo, quando consideramos o morfoespaço formado pelas espécies com maiores abundâncias em cada tipo de habitat (Todas as espécies presente no habitat, espécies com abundância ≥ 25% e com abundância ≥ 50%), concluímos que existe uma tendência de encontrarmos peixes com forma corporal mais alongada no habitat do tipo Areia, quando comparado com os habitats Alga e SWCR. No geral, as 120 espécies estão divididas entre 13 principais grupos de forma de peixes, e a taxa de alongamento corporal foi o principal eixo de variação encontrado. As características morfológicas encontradas possuem relação direta com performance de nado, onde o sucesso em capturas das presas (ex., predadores de topo) e acesso ao habitat (espécies adaptadas a viver em um ambiente aberto que possue alta velocidade de fluxo d’agua, ex., habitat do tipo Areia) são favorecidas em espécies com formato corporal alongado. A proximidade morfológica teve baixa congruencia com a arvore filogenética, indicando que nossa abordagem morfológica não pode ser usada para observar proximidades filogenéticas. Nossos resultados podem ser expandidos a outros sistemas tropicais ou não-tropicais, mostrando que os dados morfométricos podem fornecer conhecimentos importantes sobre as características funcionais dos peixes, especialmente na ecologia trófica e uso do habitat.

Palavras-chave: morfometria geométrica, peixes demersais, ecologia trófica, acesso ao habitat, expressão fenotípica de peixes, habitats tropicais marinhos

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CHAPTER 1

GENERAL INTRODUCTION

Fish are one of the most diverse groups within the animal kingdom. Updated data from FishBase, a global database of fish information, indicate that there are currently just over 34,000 known and registered fish species (Froese and Pauly, 2022), distributed in freshwater, estuarine, and marine systems around the globe. Thousands of researchers have developed scientific studies with fishes, generating knowledge in several areas, such as reproduction (Teixeira et al., 2004; Silva et al., 2018), age and growth (Lessa & Duarte-Neto, 2004; Duarte-Neto et al., 2012; Gonzalez et al., 2022), taxonomy and phylogeny (Palacios et al., 2016; Souza et al, 2022), distribution (Rocha, 2003; Camargo et al., 2004), trophic ecology (Albuquerque et al., 2019; Santos et al., 2022), habitat use (Anderson et al., 2019; Sabetian et al., 2021), aquaculture and production (Bezerra et al., 2016; Fonseca et al., 2017) and morphology (Langerhans et al., 2003; López-Fernández et al., 2012). Among these and other areas of ichthyology, morphology, more specifically functional morphometry, stands out for its importance and for still being a promising area.

The functional morphology investigates the relationships between morphology and functionality, highlighting changes in the function and performance of organisms caused by morphological variations and how this influences the use of their environment (Zelditch et al., 2004; Kirchheim & Goulart, 2010). In fish, functional morphology has investigated: swimming performance (Webb, 1982, 1984a; Liao, 2002), trophic relationships such as predation and common resource use (Burns et al., 2009; Farré et al., 2016; Kumar et al., 2017), physical environmental factors (Langerhans, 2008; Sfakianakis et al., 2011), phylogeny and evolution (Ward & Brainerd, 2007; Claverie & Wainwright, 2014), trophic ecology (Scharf et al., 2000; Ward-Campbell et al., 2005; Collar et al., 2009; Faye et al., 2012; López-Fernández et al., 2012), habitat use and adaptation (Yamada et al., 2009; Neat & Campbell, 2013; Foster et al., 2015), and others.

Ecological aspects related to trophic ecology and habitat use are perhaps some of the most important topics in ichthyology. The fish trophic ecology is an essential characteristic in the understanding of ecosystems, especially when we consider that studies have shown the usability of trophic level to generate good results in stock assessment models, contributing to estimate mortality and production rates, degree of resource exploitation and ecosystem conservation (Sibert et al, 2006; Gaichas et al., 2010;

Jayasinghe et al., 2017; Lira et al., 2018). Consequently, understanding the mechanisms that permeate and define trophic relationships, as well as their functionalities, are also important in the sustainable management of these communities (Frisch et al., 2014; Lira et al., 2018; Pita & Freire, 2019). In turn, understanding habitat use by fish, which is also important in ecosystem comprehension, has generated good results in environmental conservation planning, defining important areas for fish communities (Farré et al., 2015; Eduardo et al., 2018).

Most of the works that have investigated morphological relationships with trophic ecology and habitat have analyzed a low diversity of species or are scarce, especially when we consider the application of recent techniques of geometric conservation of individual shape (i.e., geometric morphometrics). For the relationship between shape versus trophic ecology, we can cite the studies with the families Sparidae (Costa & Cataudella, 2007; Antonucci et al., 2009) and Cichlidae (López-Fernández et al., 2012). Studies that establishe a relationship between fish shape in different marine habitats, encompassing a large diversity of species and assessed areas, are scarce. For example, Farré et al. (2015, 2016) analyzed the morphological pattern in different habitats in the western Mediterranean Sea (92 and 125 species, respectively), and Larouche et al. (2020) used a dataset of 3322 species to compare morphological variables (using linear morphometric) between reef and non-reef fishes. There are no studies of this magnitude (community level) in the tropical western Atlantic (tropical shelf of northeastern Brazil).

The continental shelf of northeastern Brazil is characterised as narrow, with an average width of 40 km, average depth around 60 m, and the sediments that dominate are sandy and siliciclastic (inner part of the shelf) and carbonate (middle and outer part of the shelf) (Vital, 2014). The region is influenced by the South Equatorial Current and is characterized as a warm tropical zone, with oligotrophic waters poor in primary productivity (Heileman, 2009). Despite this, the northeastern brazilian shelf has a high fish diversity (Eduardo et al., 2018), this is also reflected in the diversity exploited by fisheries (Muller-Karger et al., 2017). Furthermore, we can also find within this region several Marine Protected Areas (e.g. ‘APA Costa dos Corais’, ‘APA dos Corais’, ‘APA Guadalupe’, ‘APA Santa Cruz’, ‘APA Ponta da Baleia/Abrolhos, and others) (Prates & Blanc, 2007). However, the northeastern marine ecosystem has been experiencing various anthropogenic pressures, such as those caused by fisheries (Freire & Pauly, 2010) and recently pollution due to oil spills (Soares et al., 2020). Therefore, developing research within these ecosystems and communities are important in environmental management and conservation.

Since 2015, the ABRACOS project (Acoustics along the BRAzilian COaSt) has been developing oceanological research on the continental shelf of northeastern Brazil. Having as main objective to initiate an integrated approach to monitor tropical marine ecosystems in this region and understand the connectivity between the subsystems that compose it, a 3D characterization of the abiotic and biotic compartments and their interactions in Northeast Brazil has been being carried out (Bertrand, 2015, 2017). This understanding has been done through several levels: using physical-chemical (Assunção et al., 2020), oceanographic (Silva et al., 2021, 2022), and biological (Eduardo et al., 2018, 2020; Melo et al., 2020) data.

In the present thesis, we try to understand ecological aspects using morphology of fish communities collected by ABRACOS, applying geometric morphometrics techniques. These thechniques correspond to a set of methods for acquiring, processing, and analyzing shape variables that retain the geometric information of the object or individual, which do not vary with changes in size, position, and orientation (Zelditch et al., 2004; Slice, 2005). Instead of using linear measurements on the individual, as in traditional linear morphometrics, geometric morphometrics uses points with coordinates in two or three dimensions (Zelditch et al., 2004; Aguirre and Prado, 2018). Besides the conservation of geometric properties, geometric morphometrics offers a variety of visual resources facilitating the interpretation of the results (Zelditch et al., 2004; Mitteroecker & Gunz, 2009; Klingenberg, 2013). There are two main analyzes used in geometric morphometrics depending on the shape extraction technique used: Generalized Procrustes Analysis used when we get the shape by the method of the landmarks and Elliptic Fourier Analysis used when we get the shape by the method of the outlines. Mathematical procedures of these two analyses have been summarized in Appendix A at the end of this thesis.

The main objective of the present work is to use techniques of geometric morphometrics on the body of marine fish species, to understand ecological aspects linked to trophic ecology and habitat at the community level, on the continental shelf of Northeastern Brazil. More specifically, it was aimed at:

- To establish for the first time a quantitative approach between body shape and trophic ecology for a diverse community of marine demersal fish in northeastern Brazil;
- To verify which morphological features are related to trophic level (i.e., which characteristics can serve as proxy for trophic level determination in fish);
- To determine the main shape groups of demersal fish found in the study region;
- Study morphology within taxonomic gradient for species analyzed;
- Application of morphospace to understand the relationship between body shape and different habitats (SWCR - sand with coral and rocks, Algae and Sand) on the continental shelf of northeastern Brazil.

This PhD thesis was prepared in the form of scientific articles. The chapters are within the guidelines of the following journals: Chapter 2 – Journal of Fish Biology (Online ISSN: 1095-8649, in review) and Chapter 3 – Regional Studies in Marine Science (Online ISSN: 2352-4855).

CHAPTER 2

Community-scale relationships between body shape and trophic ecology in tropical demersal marine fish of northeast Brazil

Abstract: Functional morphology investigates the relationships between morphological characters and external factors, such as environmental, physical and ecological features. Here, we evaluate the functional relationships between body shape and trophic ecology of a tropical demersal marine fish community using geometric morphometrics techniques and modelling, hypothesizing that shape variables could partially explain fish trophic level. Fish were collected over the continental shelf of Northeast Brazil (4-9°S). Analysed fish were distributed into 14 orders, 34 families and 72 species. Each individual was photographed in lateral view, and 18 landmarks were distributed along the body. A PCA applied on morphometric indices revealed that fish body elongation and fin base shape were the main axes of variation explaining the morphology. Low trophic levels (herbivore and omnivore) are characterised by deep bodies, and longer dorsal and anal fin bases, while predators present elongated bodies and narrow fin bases. Fin position (dorsal and anal fins) on the fish body is another important factor contributing to (i) body stability at high velocity (top predators) or (ii) manoeuvrability (low trophic levels). Using multiple linear regression, we verified that 46% of trophic level variability could be explained by morphometric variables, with trophic level increasing with body elongation and size. Interestingly, intermediate trophic categories (e.g., low predators) presented morphological divergence for a given trophic level. Our results, which can likely be expanded to other tropical and non-tropical systems, show that morphometric approaches can provide important insights into fish functional characteristics, especially in trophic ecology.

Keywords: functional morphology, geometric morphometrics, morphological divergence, swimming performance, trophic level

1. INTRODUCTION

From a community perspective, trophic ecology has been related to a variety of features of fish biology and behaviour, such as resource use and overlapping food niches (Aguilar-Medrano *et al*., 2019; Carrassón & Cartes, 2002; Pusey & Bradshaw, 1996), seasonality and changes in dietary habits (Dantas *et al*., 2015; Novakowski *et al*., 2008), habitat use

(Gibran, 2007; Souza *et al*., 2011), functional relationships with fishing activity (Freire & Pauly, 2010; Pauly *et al*., 1998), and individual functional morphology (López-Fernández *et al*., 2012). This last approach investigates the relationships between morphology and functionality, highlighting changes in the function and performance of organisms caused by morphological variation and how this influences the use of their environment (Kirchheim & Goulart, 2010; Zelditch *et al*., 2004).

Fish functional morphology is related, among other, to swimming performance (Liao, 2002; Webb, 1984a), trophic relationships such as predation and common resource use (Burns *et al*., 2009; Farré *et al*., 2016), habitat (Foster *et al*., 2015; Yamada *et al*., 2009), physical environmental factors (Langerhans, 2008; Sfakianakis *et al*., 2011), phylogeny, and evolution (Claverie & Wainwright, 2014; Ward & Brainerd, 2007). Specifically, works studying body shape as a function of trophic ecology have related individual body characteristics to dietary content (López-Fernández *et al*., 2012; Pessanha *et al*., 2015), phylogenetic variations of trophic morphology (Linde *et al*., 2004; Muschick *et al*., 2012), morphological relations between prey and predator (Akin & Winemiller, 2008). A strong correlation between morphology and feeding behaviour has been observed in several fish species (Brandl & Bellwood, 2013, 2014). Body shape relationships to trophic level have been developed but only for two fish families, Sparidae (Antonucci *et al*., 2009; Costa & Cataudella, 2007; Ventura *et al*., 2017) and Cichlidae (López-Fernández *et al*., 2012), a community approach is therefore still lacking.

Geometric morphometrics (GM) is a relevant tool to achieve such a goal. This collection of methods allows studying morphological variations of individuals, preserving the geometrical proprieties contained in the data (Zelditch *et al*., 2004). Indeed, the effects of size, position and rotation are removed before analysis, which is an advantage over traditional methods (i.e., linear morphometry) (Aguirre & Prado, 2018; Zelditch *et al*., 2004). Besides the conservation of geometric properties, GM offers a variety of visual resources facilitating the interpretation of the results (Klingenberg, 2013; Mitteroecker & Gunz, 2009; Zelditch *et al*., 2004).

To extend the such analysis from one family to communities, we use the continental shelf of northeast Brazil, a typical tropical region that has a high demersal fish diversity (Eduardo *et al*., 2018), as a model ecosystem. We took advantage of a fish collection including 72 species from 34 families of demersal fish to propose a community perspective. Our main goal was to apply a GM approach to quantify the relationships between fish body shape and food chain position, hypothesizing that shape variables could partially explain fish trophic level. We show that factors such as locomotion, predation and habitat access serve as a basis to elucidate a functional relationship between body shape and trophic ecology. Using multiple linear regression, we also show that the geometric shape representation combined with the maximum fish size can be used as a proxy for estimating the trophic level.

2. MATERIALS AND METHODS

2.1 Sampling

The study area encompassed the Northeast Brazilian coast, from Rio Grande do Norte to Alagoas states (4-9ºS). In this region the continental shelf is relatively narrow (~40 km wide). It is a western boundary current system under the influence of the North Brazil Undercurrent (Dossa *et al*., 2021) characterized by a rather low stratification and deep thermocline (from ∼70 m to ∼170 m) with warm (typically 26-29°C) and saline (typically 36.5-37.5) waters in the mixed-layer (Assunção *et al*., 2020). This oligotrophic region (Farias *et al*., 2022) is characterized by a relatively high biodiversity (Eduardo *et al*., 2018; Giachini-Tosetto *et al.*, 2022).

Fish were collected during the Acoustics along the Brazilian coast 2 (ABRACOS 2; Bertrand, 2017) survey in May-April 2017, aboard the R/V Antea, along the continental shelf of Northeast Brazil (4º-9ºS) (Figure 1). At each sampling station (19), fish were captured using a bottom trawl (body mesh: 40 mm, cod-end mesh: 25 mm and horizontal x vertical mouth dimensions: 28 x 10 m), at depths ranging from 10 to 60 m. Individuals were tagged and frozen for posterior analysis. For more details on the sampling process, see Eduardo *et al.* (2018).

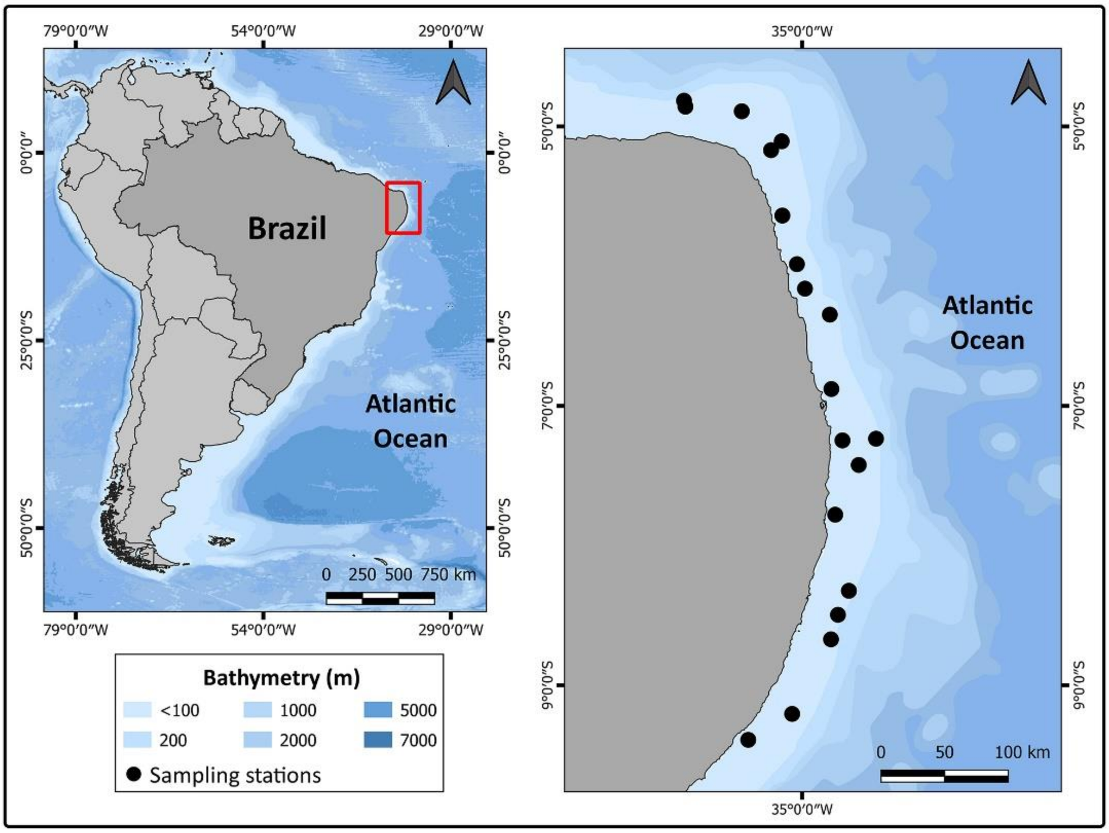

Figure 1. Study area off Northeast Brazil Shelf.

2.2 Images acquisition and obtaining the landmarks

Each individual was identified to species level in the laboratory and photographed after unfreezing using a digital camera (CANON SX520, 16 Megapixels). Up to three adult individuals from each species were photographed in lateral view, with the head positioned to the left and the dorsal region upwards, following the methodology from Muir *et al.* (2012). To reduce errors in morphometric analyses, the camera lens was positioned parallel to the side surface of the fish using a tripod with a water level attached as a stabilizer, with the same illumination pattern and equipment adjustment. We also used some images obtained from FishBase (Froese & Pauly, 2022) for species with a sample size of less than three (Supplementary Information 1 - Table S1), following the same criteria: adult individuals and visible structures (i.e., fins, caudal peduncle, eye, among others) easy to identify in the images.

Based on structures found in all specimens we defined 18 landmarks (12 true landmarks, 2 semi-landmarks, and 3 projected semi-landmarks) distributed along the body of the individuals (Figure 2). Semi-landmarks were used to overcome the lack of homology among species due to the large fish diversity of the present work. The projected semi-landmarks were allocated from known landmarks with the help of three lines drawn along the body of each individual (see details in Figure 2). The first line was traced from the end of the upper lip to the middle of the caudal peduncle. The second line corresponded to a perpendicular intersection of the first line, passing through the centre of the eye and upper (landmark 2) and lower body (landmark 13) extremities. Finally, the third line was drawn perpendicularly to the first line passing through the lower base of the lateral fin to the lower body extremity (landmark 12). For the allocation of landmarks 3, 4, and 5, we used as a criterion the region/perimeter covered by fins, regardless of the quantity or type of dorsal fin (i.e. with spines or soft rays). Thus, landmarks were allocated at the beginning of the dorsal fin perimeter (landmark 3) and at the end (landmark 5, when the entire region covered by the dorsal fin effectively ends), permitting the inclusion of species with one or two dorsal fins, or that have spiny fins, soft rays, among others (Figure 2). The TPS family programs (tpsUtil64 and tpsDig232) (Rohlf, 2015) were used to obtain the landmark and semi-landmark coordinates (x, y). The 18 landmarks were obtained by a single operator to minimize errors. To estimate this error, the digitalization was repeated by the same operator three months later on images of a 15% random subsample (30 individuals from different species). The repeatability coefficient was calculated using the inter (individual variation) and intragroup (repeated measurements) components of variance calculated from the mean square values of the Analysis of Variance (ANOVA, Supplementary Information 1 - Table S2) (Fruciano, 2016).

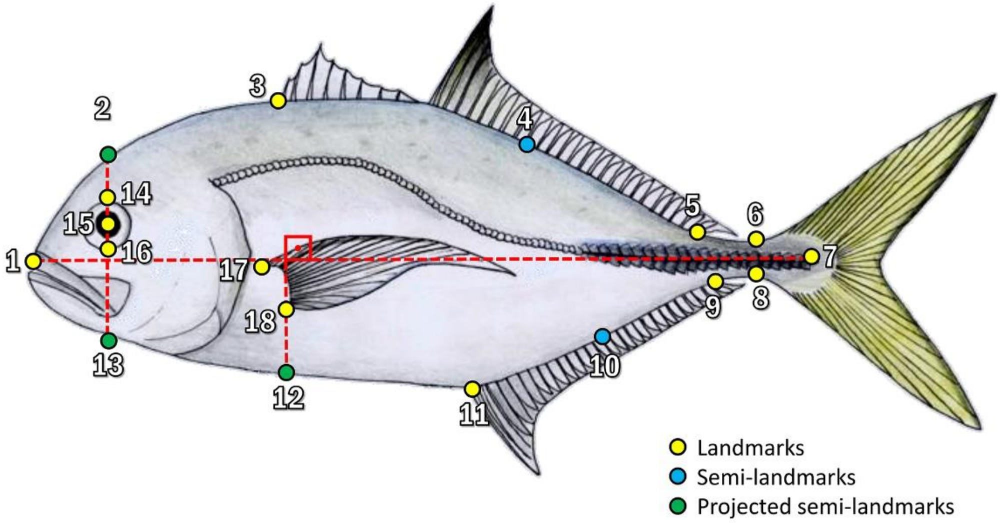

Figure 2. Landmarks, semi-landmarks, and projected semi-landmarks used in this study. Image adapted from Froese and Pauly (2021). (1) Tip of the upper lip of mouth; (2) Uppermost point of the body touched by the perpendicular line passing through the center

of the eye; (3) Anterior beginning of dorsal perimeter covered by fins; (4) Middle point of dorsal surface covered by fins; (5) Posterior end of dorsal perimeter covered by fins; (6) Upper point of greatest concavity of the caudal peduncle; (7) Lateral midpoint of the caudal peduncle before the caudal fin begins; (8) Lower point of greatest concavity of the caudal peduncle; (9) Posterior point of anal fin; (10) Midpoint of anal fin; (11) Anterior point of anal fin; (12) Lower extremity of the body touched by the perpendicular line passing through the lower base of the lateral fin; (13) Lowermost point of the body touched by the perpendicular line passing through the centre of the eye; (14) Upper end of eye diameter; (15) Middle point of eye diameter; (16) Lower end of eye diameter; (17) Upper base of lateral fin; (18) Lower base of the lateral fin. Red lines: Line 1: 1-7, Line 2: 2-13 and perpendicular to line 1, Line 3: 18-12 and perpendicular to line 1.

2.3 Trophic level

The trophic level (TL) expresses the position of a species within the food chain. It is estimated from the diet composition by assessing the dietary content of individuals (Costa & Cautadella, 2007; Pauly & Palomares, 2000; Stergiou & Karpouzi, 2002). The TL of each species is calculated by adding 1 to the sum of the trophic level of the prey items based on their contribution to the fish diet, where TL_j is the trophic level of prey item *j*, DC_{ij} is the proportion of item *j* in the diet of species *i* and *G* is the number of prey items consumed, as a result we have the following equation: $TL = 1 + \sum_{j=1}^{G} DC_{ij} \times TL_j$ (Pauly & Palomares, 2000). The TL typically ranges from 2.0 to ~5.0 for fish. It is conventionally partitioned into five trophic categories: herbivore, with TL between 2.0-2.2 (consuming preferentially ≥80% of vegetable matter); omnivore, with TL between 2.2-2.8 (consuming 20% to 80% of herbivory animals); and predator with TL >2.8 (consuming preferentially 80% of animals of the omnivore TL). The last category can be subdivided into low predator (TL between 2.8-3.8), mid predator (TL between 3.8-4.2) and top predator (TL >4.2) (Antonucci *et al.*, 2009; Pauly & Palomares, 2000). TLs were obtained for each species from FishBase (Froese & Pauly, 2022), and these values were estimated from a number of food items using a randomized resampling routine. When no TL was available for a species, its expected TL was estimated from the mean of the values observed for species of the same genus collected in this study (see Supplementary Information 1 - Table S1). Subsequently, we classified each species within one of the five established trophic categories (herbivore, omnivore, low predator, mid predator, or top predator). We also obtained the maximum total length (L_{max}, cm) for each species from FishBase (Froese & Pauly, 2022), from the ABRACOS surveys (Bertrand, 2015, 2017), or other scientific papers (Supplementary Information 1 - Table S1).

2.4 Data analysis

All analyses were performed in R version 3.6.1 (R Development Core Team, 2019). To extract the shape information of the individuals, we applied the Generalized Procrustes Analysis (GPA) to the matrix of landmark and semi-landmarks coordinates (x, y) of all specimens, using the ‘gpagen′ function from the 'geomorph' package version 3.1.3 (Adams *et al.*, 2019). The GPA is a procedure that translates all individuals to the same origin using a unit centroid scale through a least-squares criterion, making all the coordinates of the corresponding points align as closely as possible (Rohlf & Slice, 1990, Zelditch *et al.*, 2004). The matrix of Procrustes shape variables resulting from this analysis, which represents the shape of each specimen, is invariant to size, position and rotation effects (Zelditch *et al.*, 2004).

A Principal Component Analysis (PCA) was applied on the matrix of Procrustes variables to identify and characterise the main variations in fish shapes. The number of principal components (PCs) retained was determined from a segmented regression between the components and the variation explained by each, using the ‘segmented’ function from the 'segmented' package version 0.5-3.0 (Muggeo, 2008). The regression breakpoint was then used as a reference to determine the number of retained components and reduce the subjectivity of the scree plot criterion (Jackson, 1993). The body elongation was calculated for each species individually using the ‘coo_elongation’ function from the ‘Momocs’ package version 1.4.0 (Bonhomme *et al.*, 2014). This index calculates the elongation based on the following formula: $\sqrt{(\mu_{20} - \mu_{02})^2 + 4\mu_{11}^2}/(\mu_{20} + \mu_{02})$, where μ_{20}, μ_{02}, and μ_{11} are the central moments of the ellipse circumscribed to the analysed shape (i.e., the fish body) (Roisin, 2005). As a result, this index informs the fish elongation, ranging from 0 to 1: closer to 1 - more elongated shape; or closer to 0 - deeper shape. This index was calculated to verify if any significant PCs explained the body elongation of the analysed species.

The matrix of average PC scores by species was then used as input data to a Canonical Variate Analysis (CVA) to verify the degree of separation between trophic categories, that is, how similar or different the trophic categories are, using the 'CVA' function from the 'Morpho' package version 2.7 (Schlager *et al.*, 2019). Subsequently, a MANOVA (overall and pairwise between trophic categories) was applied under the scores of the CVA to check the difference in shape between trophic categories (Zelditch *et al.*, 2004).

A Multiple Linear Regression (MLR) was finally used to quantitatively assess the extent to which the TL can be estimated from shape variables (mean scores of the principal components retained for each species) and fish size. The order in which the explanatory variables were included in the model was defined based on the highest fit (R^2) found in simple linear regressions between TL and the shape variables and L_{max}. The relationship between trophic level and L_{max} for fish is already known from several studies showing that the trophic level is positively related to fish size, where larger fish consume larger prey (i.e., of higher trophic levels) (Akin & Winemiller, 2008; Froese *et al.*, 2004; Keppeler *et al.*, 2020; Romanuk *et al.*, 2011; Stergiou & Karpouzi, 2002). Body size is indeed a key variable influencing trophic interactions and the structure of the aquatic food chain, known as a good predictor of fish trophic levels (Akin & Winemiller, 2008). Beyond the facts presented above, L_{max} is a specie parameter available in several sources: scientific articles, FishBase, and the sampling data of the study. Thus, a model for TL that uses only shape variables (obtained with geometric morphometric techniques) and the maximum size of the species was proposed in this study. The final model was chosen according to the lowest value for the Akaike Information Criterion (AIC) (Bozdogan, 1987). All analyses were performed with a significance level of 5%.

2.5 Ethics statement

The authors confirm that all methods were approved and carried out in accordance with relevant guidelines and regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 47270–5).

3. RESULTS

We analysed 204 adult fish individuals distributed over 14 orders, 34 families and 72 species (see Supporting Information Table S1). The digitalization of the landmarks was responsible for only 0.5% of the data variation (the repeatability coefficient was equal to

99.5%), confirming the reliability of the landmark allocation (see Supplementary Information 1 - Table S2).

Only the first three principal components of the PCA, explaining 78.6% of the fish shape variation, were retained for posterior analyses (Figure 3a, b). PC1 (46.8% of the total variance) was related to the body elongation (Pearson correlation coefficient between PC1 and body elongation: 0.89) of individuals and the shape of the bases of the dorsal and anal fins. Fish with deeper bodies and longer dorsal and anal fin bases in the anterior-posterior dimension presented extreme negative values, while species with the highest body elongation rate and narrower fins presented positive values (Figure 3c). PC2 (20.4% of the total variance) was related to the anterior region height of the body (i.e., head region) and the position of the dorsal fin. Individuals with the narrowest height (i.e., a fusiform body) and widest dorsal fin, positioned more anteriorly on the body (positive values in PC2) were opposed to the tallest individuals with the dorsal fin positioned in the posterior region of the body (more aligned with the anal fin) (Figure 3c). Finally, PC3 (11.4% of the total variance) was related, more weakly, to the alignment of the dorsal and anal fins. Fish with fins aligned (negative values in PC2) were opposed to those presenting less aligned dorsal and anal fins (Figure 3c). Species representative of the extremes of each PC were: *Acanthurus coeruleus* (-PC1), *Fistularia tabacaria* and *F. petimba* (+PC1), Ostraciidae and Monacanthidae families (+PC2), *Scomberomorus brasiliensis* (-PC2), *Echeneis naucrates* (-PC3), and *Bagre marinus* (+PC3) (Figure 3c).

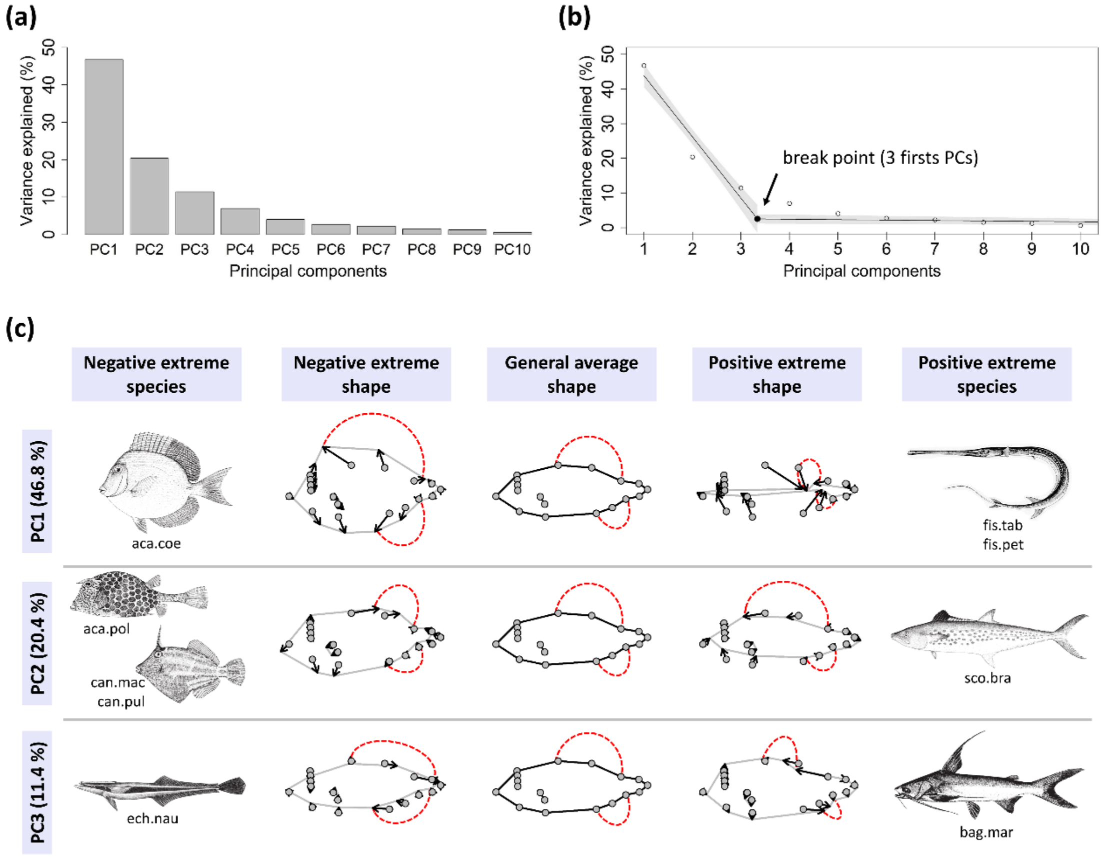

Figure 3. The variance explained by the first ten principal components (PC) (a), and scree plot of the segmented regression indicating the first three significant PCs: PC1 (46.8%), PC2 (20.4%) and PC3 (11.4%) (b). Fish body shape variation as a function of the degree of deformation concerning the general average shape, at the extreme values (negative and positive) in the three first principal components (PCs) (c). The codes and respective species names are described in Supplementary Information 1 (Table S1). Red dotted lines represent the base variation in dorsal and anal fins. Black arrows on extreme shapes indicate deformation direction compared to the average shape. Source of fish drawings: Carpenter (2002a,b).

The morphospace occupied by the species on the biplot of average scores of the three PCs facilitated the interpretation of the data at the species level (Figure 4) and by trophic category (Figure 5a,b). Lower trophic categories (herbivore and omnivore) were restricted to negative values of PC1, and the intermediary category (e.g., low predator) had greater amplitude for all PCs. In contrast, top predators occupied only positive values of PC1 (Figure 5a,b). According to the trophic category, the deformation of fish shape from the general average clearly reveals that body elongation increases with the trophic category; lower trophic categories present a deeper body shape (Figure 5c). The

MANOVA revealed a significant difference between fish shapes by trophic category (Wilk's Lambda=0.014; df=4, 16; F=36.9; p<0.001). The pairwise MANOVA indicated differences between all trophic categories, except between herbivores and omnivorous (Table 1).

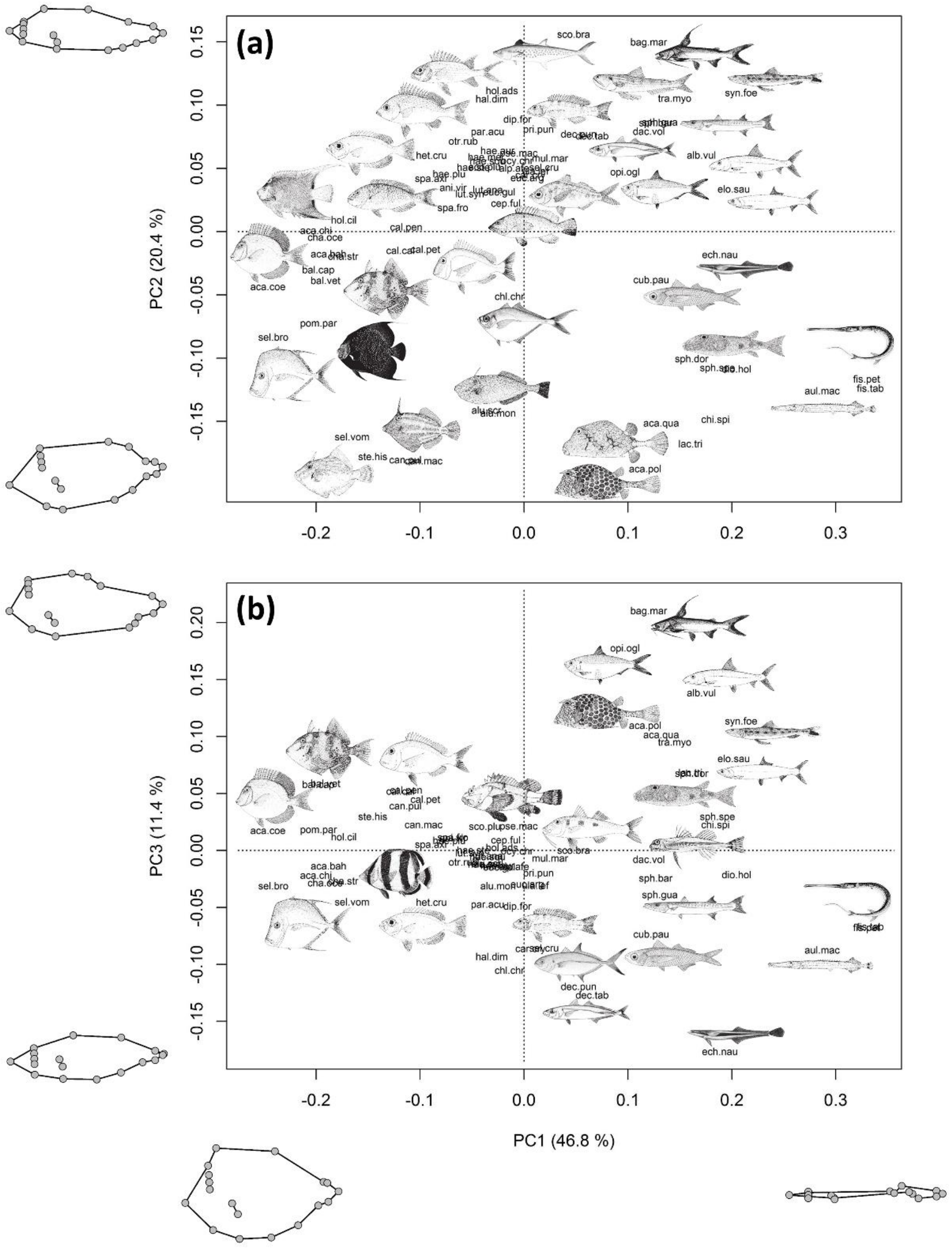

Figure 4. Average PCs for the 72 fish species analysed in this study, plotted for PC1 vs PC2 (a) and PC1 vs PC3 (b). The codes and respective species names can be seen in Supplementary Information 1 (Table S1). Source of fish drawings: Carpenter (2002a,b).

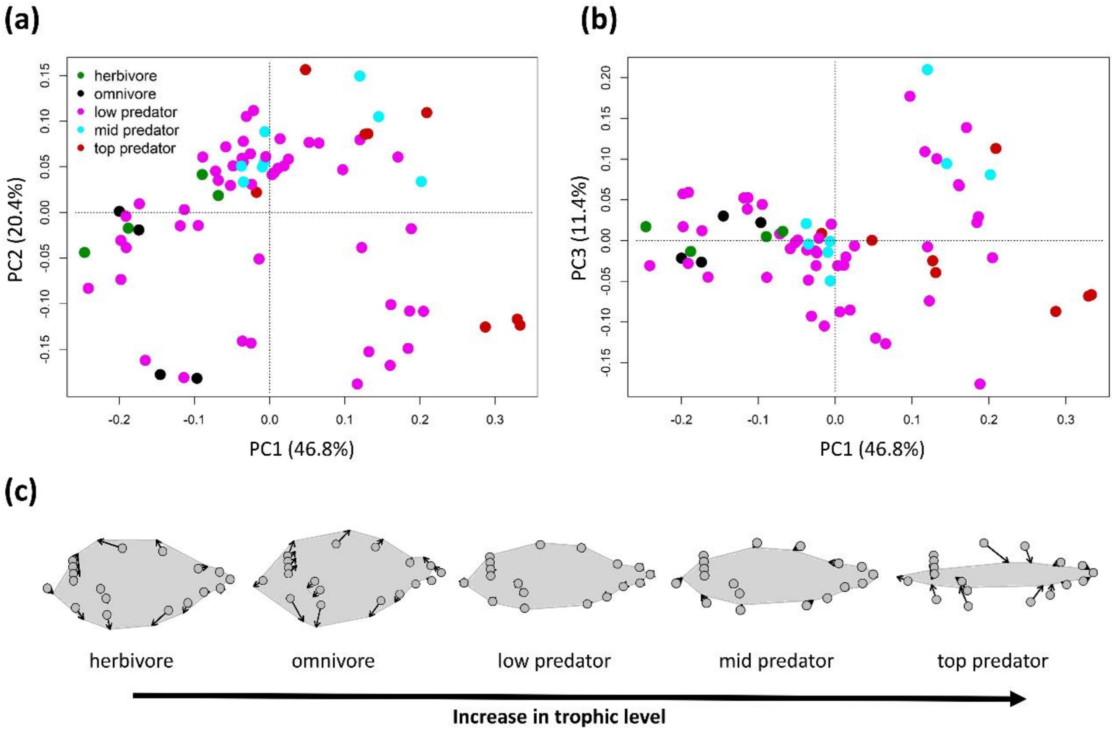

Figure 5. PCs scores for the 72 fish species analysed, discriminated by trophic category, plotted for PC1 vs PC2 (a) and PC1 vs PC3 (b). Evolution of the average fish shape according to the trophic level (c) - black arrows in each trophic category indicate the direction of deformation compared to the overall average shape.

Table 1. MANOVA results between trophic categories of the analysed fish. Values represents F statistics and p-value (in parenthesis) for pairwise MANOVA between trophic categories.

Trophic category	**Herbivore**	**Omnivore**	**Low predator**	**Mid predator**
Omnivore	**2.3 (p=0.189*)**			
Low predator	28.9 (p<0.001)	17.5 (p<0.001)		
Mid predator	10.7 (p<0.001)	23.1 (p<0.001)	29.9 (p<0.001)	
Top predator	138.2 (p<0.001)	26.9 (p<0.001)	71.9 (p<0.001)	22.7 (p<0.001)

* p>0.05, no statistically different.

The results of simple and multiple linear regressions are presented in Table 2. Individually, PC1 was the variable that most explained fish TL variability (R^2 = 0.34). The positive angular coefficient of this regression indicates that the more elongated the body, and the narrower the base of dorsal and anal fins, the higher the trophic position. Other variables, such as maximum total length (L_{max}) and PC2, influenced to a lesser extent, emphasising the L_{max}, which individually explained 25% of data variation and presented a positive relationship with TL. The PC3 did not show any relationship with TL, so it was not included in the final model. The model with the lowest AIC value was the full model (without PC3), which explained approximately 46% of the fish TL (Table 2). This indicates that morphometric characteristics can be considered variable indicators of the fish trophic level.

Table 2. Coefficients of the evaluated models (simple and multiple) of the relationships between trophic level (a numerical representation of the trophic category), the shape variables (PC1, PC2, and PC3) and maximum total length (L_{max}) of the analysed tropical marine fish. AIC = Akaike Information Criterion. R^2 = Multiple determination coefficients.

Model	**Intercept**	**PC1**	**L_{max}**	**PC2**	**PC3**	**F test**	**AIC**	**R^2**
				Simple models				
NULL	3.5103	—	—	—	—		121.15	
1	3.5047	2.3299	—	—	—	35.4	93.72	0.340
2	3.1438	—	0.0065	—	—	23.8	102.11	0.253
3	3.5132	—	—	1.3545	—	4.6	119.47	0.050
4	3.5103	—	—	—	0.0264	**0.0007***	123.15	1.0×10^{-5}
				Multiple models				
5	3.2951	1.7613	0.0037	—	—	23.0	88.43	0.399
6 (final model)	3.2971	1.7860	0.0038	1.4640	—	19.1	**83.11**	**0.460**

* p>0.05, not statistically significant. '—' represents that the variable was not included in the model.

4. DISCUSSION

Body elongation rate was the most significant source of morphological variation among fish species. This result confirms previous studies (Astudillo-Clavijo *et al.*, 2015; Caillon *et al.*, 2018; Claverie & Wainwright, 2014; López-Fernández *et al.*, 2012) and generalises this perspective to a community-scale encompassing a broad range of species (14 orders, 34 families and 72 species). Evolutionarily, a more elongated body in fish is related to the segmentation and number of vertebrae of the vertebral column and to the increased length of the head (Ward & Mehta, 2010), a characteristic previously depicted in

Actinopterygii in general (Ward & Brainerd, 2007), Gobiidae family (genus *Luciogobius*) (Yamada *et al*., 2009), and Elopomorpha species (Mehta *et al*., 2010).

Webb (1984a) proposed three main fish body morphotypes that influence swimming performance: the first characterized by a deep body (manoeuvring specialist), and the last two for fish with a more elongated body shape; one for species with a narrow caudal peduncle (cruising specialist) and another with a deep caudal peduncle (acceleration specialist) (Webb, 1984a). Swimming is also intrinsically related to the more pointed head shape, allowing for better hydrodynamics of the fish (Liao, 2002). The body shape in conjunction with the base shape of the fins, another key characteristic depicted in our results, acts directly on fish locomotion (Webb, 1984a,b). The fins evaluated in the present study were the dorsal and anal fins, which, together with the caudal fin, are called 'median fins' (Lauder & Drucker, 2004). The dorsal fin acts mainly in the execution of manoeuvres and helps the caudal fin in propulsion, while the anal fin helps the dorsal fin to maintain the fish body stability in the water (Lauder & Drucker, 2004), all these characteristics act together during locomotion.

Body maintenance within the water column is a primary factor in the foraging behaviour of many fish species. For instance, the deep body shape (which reduces vertical turning during manoeuvres, Webb, 1984a) and longer dorsal and anal fin bases of Acanthuridae and Chaetodontidae families permit the execution of precise movements in resource exploration (Brandl & Bellwood, 2013, 2014), mainly in structured environments such as coral reefs where these species usually inhabit (Dias *et al*., 2008). Our results (i.e. PC1) opposed fish with a deep body and longer fin bases to those presenting more elongated body shapes. The first group corresponds to low TL species, typically herbivores, omnivorous, and some low predators (Figure 5a,b). This morphology allows precise movements enabling access to structured environments according to their ecological niche. In turn, the TL increases with the body-shape elongation. Similar results were found in Sparidae (Antonucci *et al*., 2009; Costa & Cataudella, 2007) and Cichlidae (López-Fernández *et al*., 2012). An elongated fish shape increases the success of prey capture for active predators, especially during the search for dispersed prey (Costa & Cataudella, 2007; Webb, 1984b; Winemiller, 1991), by permitting quick acceleration and high speed during the hunt (Blake, 2004). Besides, several other factors act on the success of prey capture, including mouth morphology, teeth, jaw strength, and capture tactics (Wainwright & Bellwood, 2002). *Sphyraena* *barracuda* (TL=4.50 and positive PC1 axis) is a large predator that has a strong bite and uses the rapid acceleration of its body to capture its prey (Grubich *et al*., 2008). Similar behaviour has been observed in hunting and capture tactics in trumpetfish (order Syngnathiformes, TL=4.43-4.50) (Auster, 2008; Tegge *et al*., 2020).

Our analysis discriminated high TL species, with narrower fin bases (positive PC1 axis), from lower TL ones with longer fin bases. In addition, the position of the dorsal and anal fins plays an important role in balancing the fish's body by acting together (Breda *et al*., 2005; Lauder & Drucker, 2004). The asymmetry of the dorsal fin with anal fins (negative PC2 axis) serves as a stabilising rudder during propulsion and high speeds, preventing the fish from rotating around its longitudinal axis (Breda *et al*., 2005). Species that presented this characteristic, such as the spanish mackerel (*Scomberomorus brasiliensis*) or the great barracuda (*Sphyraena barracuda*) are top predatory and highly migratory species that can travel long distances (Batista & Fabré, 2001; O'Toole *et al*., 2011). This can also be observed in large tuna migrators (Itoh *et al*., 2003).

On the other hand, symmetrical fins allow a synchronised movement of dorsal and anal fins, together with the caudal fin, providing stability. Such motion is often used in body braking, allowing precise manoeuvres (Breda *et al*., 2005). Reef species such as Ostraciidae (box-fish) and Monacanthidae (Eduardo *et al*., 2020) present such characteristics (Figures 3c and 4). They inhabit a structured environment, where locomotion is not characterised by high speeds but by manoeuvres. Box-fish are indeed known to use strategic movements of their fins and body to enhance swimming ability in complex environments (Van Wassenbergh *et al*., 2015).

As much as 46% of trophic level variability could be explained by morphometric variables. These results are the first ones using multiple regression, considering a set of morphometric and size variables, to understand trophic level in a quantitative approach. We also found a significant positive relationship between body size and fish TL; the greater L_{max}, the greater their trophic position (Table 2). This pattern was classically observed (Akin & Winemiller, 2008; Froese *et al*., 2004; Keppeler *et al*., 2020; Romanuk *et al*., 2011; Stergiou & Karpouzi, 2002), with L_{max} being a good predictor of fish trophic levels. Many studies also have associated the maximum fish size with the extension of the habitats they live in (Nash *et al*., 2015; Welsh & Bellwood, 2014), for example, in reef fish, larger fish live in wider habitats (Nash *et al*., 2015). The trophic position of an individual or its morphological aspects is the result of many factors' interaction and finding the final equation of complex natural processes involves the analysis and knowledge of the individual relationships between those factors.

Other factors are also related to the fish body shape. A classic example is the water flow where fish inhabit. The need to break the physical barrier imposed by the water speed (high flow) selects an elongated body shape (Foster *et al*., 2015; Langerhans, 2008; Liao, 2002). On the opposite, species with a deep body (better manoeuvres) flourish in a structured environment such as coral reefs and rocky bottoms, presenting natural barriers that decrease water dynamics and velocity (Bejarano *et al*., 2017; Johansen, 2014).

Low predators were characterised by a high morphological amplitude, occupying several positions within the morphospace (Figure 5a,b). Such wide large morphological space for a given trophic level may be related to a set of niches and external factors, which also influence different degrees of the fish shape besides morphology and trophic ecology (Portner *et al*., 2010). Indeed, a variety of other factors are known to influence fish body shape, such as predator-prey relationships (Burns *et al*., 2009; Price *et al.*, 2015), physicochemical conditions (Farré *et al*., 2016; Georgakopoulou *et al.*, 2007; Sfakianakis *et al*., 2011) or genetic (Marcil *et al.*, 2006). Phenotypic variation in body shape can act on how individuals will use the resources around them and may also limit their feeding range due to specialisation (Collar *et al*., 2009; López-Fernández *et al*., 2012). Conversely, morphological specialisation (i.e., a highly specialised shape in one function) does not always follow a parallel path with feeding specialisation, as verified in reef fish (Brandl *et al*., 2015). Therefore, it is evident that the low predators from the same trophic position (TL: 2.8-3.8) may present a wide range of morphological features; that is, even though they are feeding on prey from the same TL they present very diversified body shapes. Despite the high diversity of the species analysed in the present study, the trophic categories do not have equally balanced diversity as a matter of sampling (e.g., herbivores with only four species belonging to two genera). This makes it difficult to account for phylogenetic effects within trophic categories. Therefore, we recommend that future studies take this into consideration by encompassing a greater diversity of species within different trophic levels.

5. CONCLUSIONS

Here we present the first quantitative relationship between fish morphology and trophic ecology at a community level. Our results which may likely be expanded to other tropical and non-tropical systems show that fish with elongated body shapes had a high TL, while those with deep body shapes had a low TL. The shape of the base of the dorsal and anal fins also contributed to explaining the TL. Top predators were characterised by narrow fin bases while herbivores and omnivorous presented longer fins related. Between these extremes, the intermediate trophic category (low predator) shows morphological divergence as a function of TL.

From a broader perspective, the geometric morphometric and regression analyses allowed us to infer more precisely the contribution of the morphological aspects of the fish body in their trophic ecology. Body elongation and fin characteristics were the main explanatory variables for fish TL. Combined with maximum fish size (L_{max}), they explained 46% of the TL variability and can be considered an excellent *proxy* to represent the trophic pattern of fish species. Fish morphology is, therefore, a key factor in the ecological study of communities, especially in trophic ecology.

SUPPLEMENTARY INFORMATION 1

Table S1. List of 72 tropical marine fish species analysed in this study, caught on the shelf of northeastern Brazil. L_{max} (maximum total length in cm). *Approximate Trophic level based on the average value of the species of the same genus found in the present study or on the trophic level of closest relatives. L_{max} values according to: [a] Benevides *et al*. (2016); [b] Fonseca *et al*. (2021). Other L_{max} values were obtained from FishBase (Froese & Pauly, 2022). BE is the average body elongation index per specie, and Total length is the total length variation (min-max, in cm) of the sampled individuals. Source images: ABRACOS surveys (Ab) and/or FishBase (FB).

Order	**Family**	**Species**	**Code**	**Trophic level**	**Trophic category**	**L_{max}**	**BE**	**Total length (min-max, cm)**	**Images source (number)**
Acanthuriformes	Acanthuridae	*Acanthurus bahianus* Castelnau, 1855	aca.bah	2.12*	herbivore	30.0[a]	0.527	18.37 - 20.33	Ab (3)
		Acanthurus chirurgus (Bloch, 1787)	aca.chi	2.74	omnivorous	39.0	0.523	27.03 - 27.41	Ab (3)
		Acanthurus coeruleus Bloch & Schneider, 1801	aca.coe	2.15	herbivore	39.0	0.393	25.90 - 31.80	Ab (3)
	Chaetodontidae	*Chaetodon ocellatus* Bloch, 1787	cha.oce	3.50	low predator	20.0	0.335	10.98 - 14.47	Ab (3)
		Chaetodon striatus Linnaeus, 1758	cha.str	2.77	omnivorous	16.0	0.340	8.40 - 11.97	Ab (3)
	Pomacanthidae	*Holacanthus ciliaris* (Linnaeus, 1758)	hol.ads	3.12	low predator	45.0	0.399	22.44 - 24.70	Ab (3)
		Pomacanthus paru (Bloch, 1787)	pom.par	3.10	low predator	41.1	0.285	26.72 - 38.65	Ab (3)
Albuliformes	Albulidae	*Albula vulpes* (Linnaeus, 1758)	alb.vul	3.66	low predator	104.0	0.793	22.73 - 37.72	Ab (2), FB (1)
Aulopiformes	Synodontidae	*Synodus foetens* (Linnaeus, 1766)	syn.foe	4.43	top predator	53.8	0.872	19.43 - 19.61	Ab (1), FB (2)
		Trachinocephalus myops (Forster, 1801)	tra.myo	4.17	mid predator	25.0	0.797	16.40 - 19.54	Ab (1), FB (2)
Carangiformes	Carangidae	*Caranx crysos* (Mitchill, 1815)	car.cry	3.63	low predator	70.0	0.688	36.67 - 46.70	Ab (3)
		Chloroscombrus chrysurus (Linnaeus, 1766)	chl.chr	3.53	low predator	65.0	0.594	19.72 - 21.49	Ab (3)
		Decapterus punctatus (Cuvier, 1829)	dec.pun	3.26	low predator	30.0	0.785	18.81 - 19.40	Ab (3)
		Decapterus tabl Berry, 1968	dec.tab	3.22	low predator	50.0	0.810	22.56 - 23.74	Ab (3)

		Selar crumenophthalmus (Bloch, 1793)	sel.cru	3.57	low predator	70.0	0.740	23.67 - 25.53	Ab (3)
		Selene brownii (Cuvier, 1816)	sel.bro	3.67*	low predator	29.0	0.328	14.11 - 19.50	Ab (2), FB (1)
		Selene vomer (Linnaeus, 1758)	sel.vom	3.67	low predator	48.3	0.365	18.20 - 19.96	Ab (3)
	Echeneidae	*Echeneis naucrates* Linnaeus, 1758	ech.nau	3.40	low predator	110.0	0.905	52.36 - 53.45	Ab (3)
Clupeiformes	Clupeidae	*Opisthonema oglinum* (Lesueur, 1818)	opi.ogl	3.60	low predator	38.0	0.690	10.54 - 11.76	Ab (3)
Dactylopteriformes	Dactylopteridae	*Dactylopterus volitans* (Linnaeus, 1758)	dac.vol	3.68	low predator	50.0	0.821	28.41 - 31.21	Ab (2), FB (1)
Elopiformes	Elopidae	*Elops saurus* Linnaeus, 1766	elo.sau	4.11	mid predator	100.0	0.810	30.19 - 58.62	Ab (2), FB (1)
Holocentriformes	Holocentridae	*Holocentrus adscensionis* (Osbeck, 1765)	hol.cil	3.40	low predator	61.0	0.689	24.59 - 31.10	Ab (3)
Mulliformes	Mullidae	*Mulloidichthys martinicus* (Cuvier, 1829)	mul.mar	3.50	low predator	44.8	0.730	22.02 - 25.32	Ab (3)
		Pseudupeneus maculatus (Bloch, 1793)	pse.mac	3.37	low predator	30.0	0.732	20.93 - 24.29	Ab (3)
Perciformes	Gerreidae	*Eucinostomus argenteus* Baird & Girard, 1855	euc.arg	3.32	low predator	21.0	0.689	18.35 - 20.88	Ab (3)
		Eucinostomus gula (Quoy & Gaimard, 1824)	euc.gul	3.13	low predator	25.0	0.636	12.26 - 15.64	Ab (3)
		Ulaema lefroyi (Goode, 1874)	ula.lef	3.22*	low predator	23.0	0.692	13.85 - 19.90	Ab (3)
	Haemulidae	*Anisotremus virginicus* (Linnaeus, 1758)	ani.vir	3.44	low predator	40.6	0.526	17.41 - 20.58	Ab (2), FB (1)
		Haemulon aurolineatum Cuvier, 1830	hae.aur	3.19	low predator	25.0	0.676	17.65 - 20.24	Ab (3)
		Haemulon melanurum (Linnaeus, 1758)	hae.mel	3.50	low predator	33.0	0.657	28.95 - 30.41	Ab (3)
		Haemulon plumierii (Lacepède, 1801)	hae.plu	3.78	low predator	53.0	0.617	23.63 - 27.24	Ab (3)
		Haemulon squamipinna Rocha & Rosa, 1999	hae.squ	3.49*	low predator	19.5	0.652	16.40 - 17.72	Ab (3)
		Haemulon steindachneri (Jordan & Gilbert, 1882)	hae.ste	3.50	low predator	30.0	0.628	16.37 - 16.67	Ab (3)
		Orthopristis rubra (Cuvier, 1830)	otr.rub	3.60	low predator	40.0	0.647	16.92 - 18.41	Ab (3)
	Labridae	*Halichoeres dimidiatus* (Agassiz, 1831)	hal.dim	3.60*	low predator	27.0	0.734	17.82	FB (1)
	Lutjanidae	*Lutjanus analis* (Cuvier, 1828)	lut.ana	3.92	mid predator	94.0	0.627	20.19 - 27.25	Ab (3)
		Lutjanus synagris (Linnaeus, 1758)	lut.syn	3.66	low predator	60.0	0.618	18.54 - 21.92	Ab (3)

		Ocyurus chrysurus (Bloch, 1791)	ocy.chr	3.88	mid predator	86.3	0.663	33.58 - 38.53	Ab (3)
	Priacanthidae	*Heteropriacanthus cruentatus* (Lacepède, 1801)	het.cru	3.70	low predator	50.7	0.658	24.83 - 27.07	Ab (3)
	Scaridae	*Sparisoma axillare* (Steindachner, 1878)	spa.axi	2.00*	herbivore	43.6	0.584	16.53 - 27.85	Ab (3)
		Sparisoma frondosum (Agassiz, 1831)	spa.fro	2.00*	herbivore	45.0^{b}	0.631	35.00	FB (1)
	Sciaenidae	*Pareques acuminatus* (Bloch & Schneider, 1801)	par.acu	3.50	low predator	23.0	0.628	11.46 - 13.88	Ab (3)
	Scorpaenidae	*Scorpaena plumieri* Bloch, 1789	sco.plu	4.04	mid predator	45.0	0.632	20.54 - 21.32	Ab (2), FB (1)
	Serranidae	*Alphestes afer* (Bloch, 1793)	alp.afe	4.01	mid predator	33.0	0.631	24.00 - 28.30	Ab (3)
		Cephalopholis fulva (Linnaeus, 1758)	cep.ful	4.25	mid predator	44.0	0.646	25.64 - 27.58	Ab (3)
		Diplectrum formosum (Linnaeus, 1766)	dip.for	4.15	mid predator	30.0	0.729	17.65 - 18.67	Ab (3)
	Sparidae	*Calamus calamus* (Valenciennes, 1830)	cal.cal	3.44*	low predator	56.0	0.543	21.07 - 25.89	Ab (3)
		Calamus penna (Valenciennes, 1830)	cal.pen	3.35	low predator	46.0	0.545	21.41 - 23.68	Ab (3)
		Calamus pennatula Guichenot, 1868	cal.pet	3.54	low predator	37.0	0.560	21.83 - 23.76	Ab (3)
	Sphyraenidae	*Sphyraena barracuda* (Edwards, 1771)	sph.bar	4.50	top predator	200.0	0.847	37.00 - 37.64	Ab (3)
		Sphyraena guachancho Cuvier, 1829	sph.gua	4.38	top predator	200.0	0.854	44.91 - 51.92	Ab (3)
	Triglidae	*Prionotus punctatus* (Bloch, 1793)	pri.pun	3.77	low predator	45.0	0.772	15.48 - 19.12	Ab (2), FB (1)
Scombriformes	Nomeidae	*Cubiceps pauciradiatus* Günther, 1872	cub.pau	3.65	low predator	20.0	0.759	8.78 - 9.39	Ab (3)
	Scombridae	*Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, 1978	sco.bra	4.37	top predator	125.0	0.784	43.58 - 44.49	Ab (3)
Siluriformes	Ariidae	*Bagre marinus* (Mitchill, 1815)	bag.mar	3.88	mid predator	69.0	0.764	38.91 - 41.77	Ab (3)
Syngnathiformes	Aulostomidae	*Aulostomus maculatus* Valenciennes, 1841	aul.mac	4.44	top predator	100.0	0.920	27.58 - 28.71	Ab (3)
	Fistulariidae	*Fistularia petimba* Lacepède, 1803	fis.pet	4.43	top predator	200.0	0.967	51.77 - 57.18	Ab (3)
		Fistularia tabacaria Linnaeus, 1758	fis.tab	4.50	top predator	200.0	0.956	67.55 - 77.04	Ab (3)
Tetraodontiformes	Balistidae	*Balistes capriscus* Gmelin, 1789	bal.cap	3.45	low predator	60.0	0.459	31.01 - 31.79	Ab (2), FB (1)
		Balistes vetula Linnaeus, 1758	bal.vet	3.34	low predator	60.0	0.471	20.08 - 37.21	Ab (3)

Diodontidae	*Chilomycterus spinosus* (Linnaeus, 1758)	chi.spi	3.60*	low predator	28.0	0.662	22.07 - 22.28	Ab (2)
	Diodon holocanthus Linnaeus, 1758	dio.hol	3.31	low predator	50.0	0.729	19.00 - 25.40	Ab (2), FB (1)
Monacanthidae	*Aluterus monoceros* (Linnaeus, 1758)	alu.mon	3.49	low predator	76.2	0.654	28.58 - 49.90	FB (3)
	Aluterus scriptus (Osbeck, 1765)	alu.scr	3.02	low predator	110.0	0.632	36.00 - 46.00	FB (2)
	Cantherhines macrocerus (Hollard, 1853)	can.mac	2.74	omnivorous	46.0	0.526	12.63 - 14.88	Ab (3)
	Cantherhines pullus (Ranzani, 1842)	can.pul	2.90	low predator	20.0	0.472	12.88 - 15.43	Ab (3)
	Stephanolepis hispida (Linnaeus, 1766)	ste.his	2.76	omnivorous	36.9	0.432	16.88 - 19.00	Ab (3)
Ostracidae	*Acanthostracion polygonius* Poey, 1876	aca.pol	3.35	low predator	50.0	0.614	21.95 - 22.81	Ab (3)
	Acanthostracion quadricornis (Linnaeus, 1758)	aca.qua	3.77	low predator	55.0	0.660	20.76 -27.51	Ab (3)
	Lactophrys trigonus (Linnaeus, 1758)	lac.tri	3.56*	low predator	55.0	0.681	34.81 - 39.38	Ab (3)
Tetraodontidae	*Sphoeroides dorsalis* Longley, 1934	sph.dor	3.40*	low predator	20.0	0.745	14.90	FB (1)
	Sphoeroides spengleri (Bloch, 1785)	sph.spe	3.50	low predator	30.0	0.756	10.85	Ab (1)

Table S2. Analysis of variance and estimation of the Repeatability coefficient in a subsample of 15% of the analyzed individuals. SS: sum of squares, MS: mean squares.

Effect	**SS**	**MS**	**Variance component**	**Repeatability**
Intergroups (among individuals)	1.3523	0.0466	0.0232	0.995
Intragroups (between measurements)	0.0032	0.0001	0.0001	

CHAPTER 3

Fish morphological diversity versus habitat type in tropical demersal marine environment

Abstract: The marine demersal environment is composed of a set of habitats that are home to a great diversity of fish species. In a given community, fish morphology could be shaped by the habitat types they occupy. Here we studied the morphological pattern of a demersal fish community in a tropical marine environment (Brazil 4°-9°S). Fish were collected by bottom trawl during the two surveys (August-September 2015 and April-May 2017). Simultaneously underwater footage were taken to classify the habitats into SWCR (Sand with rocks, coralline formations, and sponges), Algae and Sand. Fish morphology was accessed using Elliptic Fourier Analysis, on body shape. We analyzed 120 species distributed in 16 orders and 45 families. Body elongation was the main source of morphological variation, followed by caudal fin and dorsal fin shape. We found 13 main shape groups, evidencing the great morphological diversity. The morphological clustering showed low congruence with the phylogenetic tree, indicating that our morphological approach cannot be used to observe phylogenetic proximities. Using morphospace as a three-dimensional structure reavels that the SWCR habitat showed the greatest values of diversity and morphological amplitude. In addition, the greater morphological similarity occurred in Sand habitat where we observed the greater abundance of species with elongated body patterns, that are well adapted to live in open habitats with higher water flow. We recommend that this work can be expanded to other areas, because morphological comprehension is fundamental to understanding the ecosystem dynamics, especially in coral reefs.

Keywords: Phenotypic diversity, Elliptic Fourier Analysis, Morphospace, Fish shape groups, Habitat complexity

1. INTRODUCTION

The phenotype of an organism is the result of the interaction of a set of genetic, ecological, and environmental factors (Hill and Mulder, 2010). Fish morphology is influenced, to a greater or lesser extent, by a variety environmental interactions, including those associated with physical (Georgakopoulou et al., 2007), chemical (Crispo and Chapman, 2010; Pauly and Cheung, 2018), ecological (Costa and Cataudella, 2006; Burns et al., 2009; López-Fernández et al., 2012) factors, and also through the habitat that these species live in (Yamada et al., 2009; Farré et al., 2016). Functional morphology investigates these phenotypic variations by studying the relationships between morphology (i.e., phenotypic expression) and external factors (environmental and/or biological) (Mota et al., 1995; Kirchheim and Goulart, 2010). Understanding morphological patterns in the context of species (Russo et al., 2007), community (Ventura et al., 2017) or ecosystem (Silva-Júnior et al., 2017), has generated promising results that helped elucidating important ecological questions in the field of ichthyology, especially those linked to trophic ecology and organism functionality (Villéger et al., 2017). In this context, fish morphology is influenced by several environmental interactions, to a greater or lesser extent, such as those associated with physical factors (Georgakopoulou et al., 2007), chemical (Crispo and Chapman, 2010; Pauly and Cheung, 2018), ecological (Costa and Cataudella, 2006; Burns et al., 2009; López-Fernández et al., 2012), and also through the habitat that these species live in (Yamada et al., 2009; Farré et al., 2016).

Most works studying fish shape as a function of habitat are focused on freshwater species (e.g., Svanback and Eklov, 2002; Langerhans et al., 2003; Willis et al., 2005; Franssen, 2011; Foster et al., 2015; Senay et al., 2015; Shuai et al., 2018; Silva et al., 2021) or, when studied in a marine zone, cover few analyzed species or are they focused on specific families (e.g., Antonucci et al., 2009; Price et al., 2011, 2013; Mohadasi et al., 2014; Ventura et al., 2017). In general, the complexity of the environment and water flow have influenced the fish morphological pattern (see Langerhans, 2008; Yamada et al., 2009; Brandl and Bellwood, 2014; Brandl et al., 2015; Bejarano et al., 2017), where the rate of body elongation has been the main feature observed (Price et al., 2019). Studies establishing a relationship between fish body shape in different marine habitats, encompassing a large diversity of species (i.e., at the community level) and areas assessed, are scarce, with emphasis on the works of Farré et al. (2015, 2016), which analyzed the morphological pattern in different habitats in the western Mediterranean Sea (92 and 125 species, respectively), and Larouche et al. (2020), which in general used a dataset of 3322 species, comparing morphological variables (using linear morphometry) between reef and non-reef fish. Other important studies on fish morphological diversity are Caillon et al. (2018) (85 species from the North Sea), Claverie and Wainwright (2014) (2939 species from the Indo-Pacific reef), and Price et al. (2019) (morphological pattern of 6144 species of Teleosts). There are no morphological studies of such magnitude in the tropical western Atlantic.

The tropical shelf of northeastern Brazil is highly diverse in its environments. It is possible to observe the heterogeneity of the environments through a complex set of habitats found in this region, such as sandbanks, algae banks, seagrass, and mainly coral reefs (Leão et al., 2016; Eduardo et al., 2018; Fontes et al., 2020). The latter stands out due to the variety of coral species present in the region (Leão et al., 2016) and, mainly, because they help compose an environment that enables a high diversity of species that inhabit there (Messmer et al., 2011), either for refuge, feeding or other factors.

The fish diversity found in the East Brazil Shelf LME (Large Marine Ecosystem where the northeastern platform of Brazil is included) is over 890 species. Of these, 293 are associated with coral reefs (FishBase information, Froese and Pauly, 2021). Eduardo et al. (2018) found 120 demersal fish species between latitudes 4°-9°S, where fish assemblages were mainly associated with depth and bottom habitat types assessed, whose species richness and diversity indices were influenced by habitat heterogeneity. Therefore, it is already known that ecological patterns in fish assemblages (such as richness, diversity, and distribution) are influenced by the habitat. However, morphological aspects, especially those linked to body shape at the community level, have not been evaluated in a habitat gradient, still less in the marine shelf of northeastern Brazil.

Geometric morphometrics plays, in this respect, a substantial role to understand the morphological patterns of a diverse set of species, such as those found in tropical marine waters. The main advantage is that the geometric information in the data is not lost when compared to classical morphometric techniques (i.e., linear morphometry) (Zelditch et al., 2004). Therefore, our main objective was to study the morphological pattern of a demersal fish community in a tropical marine environment (Brazil between 4°-9°S), verifying relationships between morphology and bottom habitat types present in this region. Thus, geometric morphometric techniques were used to establish shape groups and evaluate morphology across a phylogenetic path and a taxonomic gradient. Furthemore, using the obtained morphospace, we sought to understand how morphology is related to the habitats where demersal fish species are found.

2. MATERIALS AND METHODS

2.1 Study area and fish sampling

The study area of the present work corresponds to a tropical demersal marine environment. The continental shelf of northeastern Brazil is narrow, with an average width of 40 km and an average depth of around 60 m, dominated by sandy and siliciclastic (inner part of the shelf) and carbonate (middle and outer part of the shelf) in its sediment composition (Vital, 2014). The region is influenced by the South Equatorial Current and is defined as a warm tropical zone, with low primary productivity waters (Heileman 2009). Despite this, the northeastern Brazilian shelf has a high fish diversity (Eduardo et al., 2018), reflected in the diversity exploited by fisheries (Muller-Karger et al., 2017), where also several species are threatened in different degrees of exploitation and sustainability (Eduardo et al., 2018; Passarone et al., 2019). In this region, there is a diversity of habitats and highly connected marine ecosystems, especially coral reefs (Castro and Pires, 2001; Bittencourt et al., 2008). Furthermore, we can also find several Marine Protected Areas (e.g., ‘APA Costa dos Corais’, ‘APA dos Corais’, ‘APA Guadalupe’, ‘APA Santa Cruz’, ‘APA Ponta da Baleia/Abrolhos, and others) (Prates and Blanc, 2007).

Fish were collected in the ABRACOS (Acoustics Along the Brazilian Coast) surveys during the two sampling events, which occurred in August-September 2015 and April-May 2017, onboard the French R/V ANTEA (Bertrand, 2015, 2017), along the continental shelf of Northeastern Brazil (4º-9ºS) (Fig. 1). At each sampling station (37 in total), individuals were captured using bottom trawls (body mesh: 40 mm, cod-end mesh: 25 mm, and horizontal x vertical mouth dimensions: 28 x 10 m), between depths of 10 to 60 m, and for approximately 5 minutes of trawling at each station. They were tagged and stored on ice for posterior analysis.

We used videos footages obtained by an underwater camera (model GOPRO HERO 3) attached to the top of the net mouth. These footages were used to classify the bottom habitats into three types: (i) SWCR (Sand with rocks, coralline formations, and sponges) - primarily sand bottom with 10% or greater distribution of biogenic rocks, corals, calcareous algae and sponges, (ii) Algae - substrates with 10% or greater distribution of any combination of numerous species of leafy red, green or brown algae, and (iii) Sand - coarse sediment typically found in areas exposed to currents or wave energy. For more details on the sampling process and habitat classification methodology of the ABRACOS surveys, see Eduardo et al. (2018).

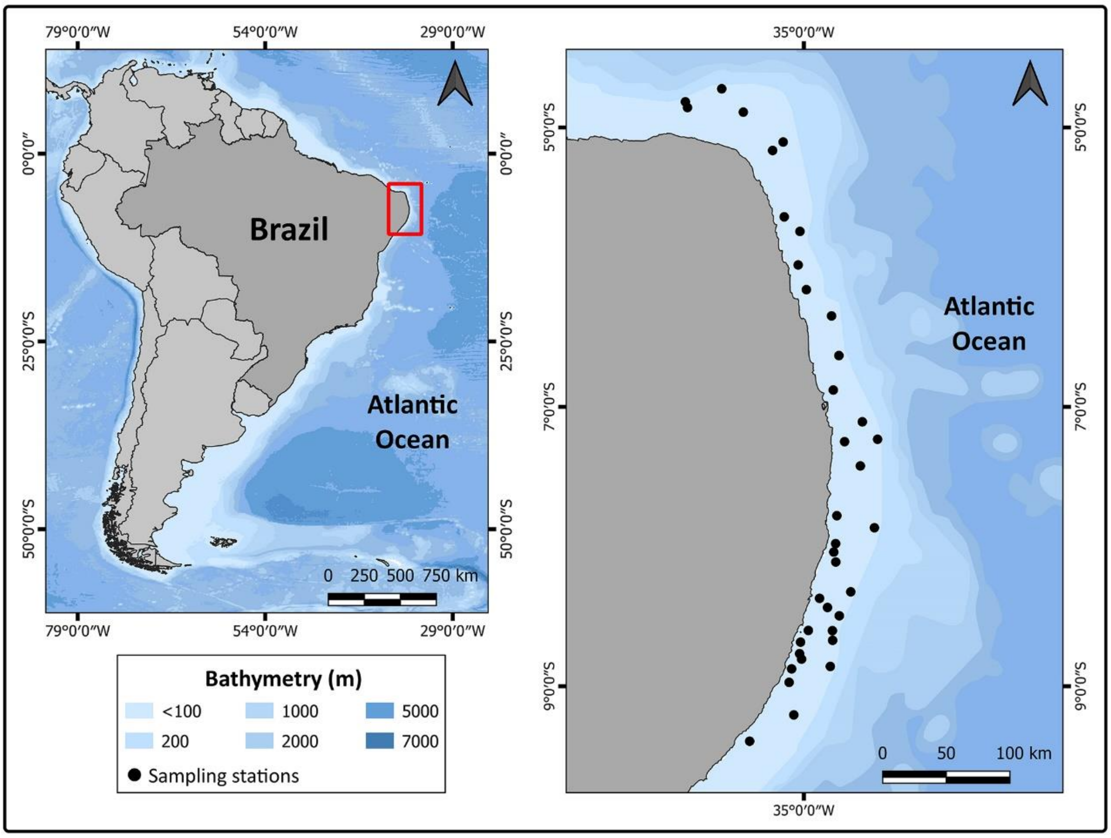

Fig. 1 Tropical marine area (continental shelf of northeastern Brazil) studied in this work, with sampling stations.

2.2 Image acquisition and processing

In the laboratory, each individual was identified up to the species level and photographed separately using a digital camera (model: CANON SX520, 16 Megapixels). In this study, we analyzed only the bony fishes belonging to the Actinopterygii class. Each specimen was photographed in lateral view, with the head positioned to the left and the dorsal region upwards. The methodology described in Muir et al. (2012) was followed, where the camera lens was positioned at 90° about the fish surface, and fish orientation, lighting, and equipment configuration had been standardized to avoid errors and inaccuracies in morphometric analysis. We also used some images obtained from FishBase (Froese and Pauly, 2021), fish catalogs or articles (Rocha, 2004; Williams et al., 2010; Deda and Barbosa, 2016), and online image database (Robertson and Tassel, 2019) (Appendix S1 in Supplementary Information 2).

From each species, only one image was chosen following two main criteria: adult individuals and fish positioned in lateral view with all fins open and visible. Each species was also classified into four types of caudal fin: rounded, truncated, emarginated, and forked. Finally, all species images were binarized into black silhouettes with a white background using an image editing software. The pelvic fin was not included because many images could not be identified and/or many species do not exhibit this fin type.

2.3 Data analysis

All analyses were performed in R version 3.6.1 (R Development Core Team, 2019), and a flowchart of the data analysis process can be consulted in Fig. 2. We applied the Elliptical Fourier Analysis (EFA), using the ‘Momocs’ package version 1.3.2 (Bonhomme et al., 2014), on the fish outline extracted in coordinates (x, y) from the binarized images with black silhouette to get the shape information of the individuals.

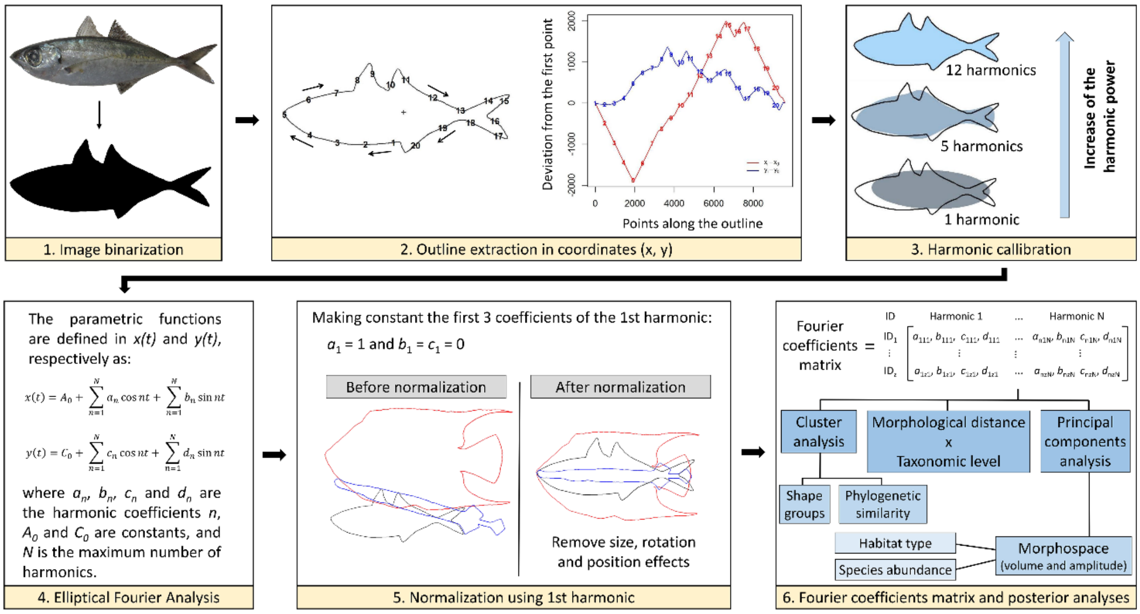

Fig. 2 Flowchart of the data analysis process used in this work.

EFA represents a parametric function in the sense that the *x* and *y* directions are configured separately as cumulative functions of a third variable *t* along the outline. The Fourier descriptors resulting from these functions are invariant in size, rotation, and position (Kuhl and Giardina, 1982; Lestrel, 2008). The parametric functions proposed by Kuhl and Giardina (1982) are defined in *x(t)* and *y(t)*, respectively, (Equations (1) e (2)) as:

$$x(t) = A_0 + \sum_{n=1}^{N} a_n \cos nt + \sum_{n=1}^{N} b_n \sin nt, \tag{1}$$

and

$$y(t) = C_0 + \sum_{n=1}^{N} c_n \cos nt + \sum_{n=1}^{N} d_n \sin nt, \tag{2}$$

where a_n, b_n, c_n and d_n are the harmonic coefficients n, A_0 and C_0 are constants, and N is the maximum number of harmonics. We used 12 harmonics in total, which retained 99% of the shape information of the data. The removals of size, rotation, and position effects were done through the normalization based on the first hamonic, as a result the first three coefficients of the first harmonic are transformed into a_1=1 and b_1=c_1=0 (Crampton, 1995). The generated Fourier coefficient matrix is used in the subsequent analyses. For more details of the mathematical procedures of EFA, see Lestrel (2008).

Principal component analysis (PCA) was applied on the Fourier coefficients matrix to identify and characterize the main variations in fish shapes. The number of principal components (PCs) retained was determined from a segmented regression between the components and the variation explained by each, using the 'segmented' package version 0.5-3.0 (Muggeo, 2008). The regression breakpoint was then used as a reference to determine the number of significant components and reduce the subjectivity of the scree plot criterion.

The elongation aspect index (Roisin, 2005) was calculated for each species separately (the higher the value the more elongated the fish body) and verified the relationship with the significant principal components using a simple linear regression. Similarly, the relationship between caudal fin-type (rounded, truncated, emarginated, or forked) and the significant components was verified using a boxplot, and differences were tested using the non-parametric Kruskal-Wallis and Dunn tests (Zar, 2010).

Cluster analysis was applied on the Fourier coefficient matrix to determine the main demersal fish shape groups present in the study area. Ward’s hierarchical clustering method and the Euclidean distance as an index of dissimilarity were used (Johnson and Wichern, 2014). The morphological similarities in fish body shape were used to determine the main morphological groups of the species. The groups had their average shapes determined and ranked in descending order according to the species number present in each group as common and rare shapes.

We obtained the phylogenetic tree of the analyzed fish species using the `fishtree_phylogeny` function of the package 'fishtree' version 0.3.4 (Chang et al., 2019). In order to compare the morphological path with the phylogenetic path, we converted the phylogenetic tree into a dendrogram-type object using the package 'phylogram' version 2.1.0 (Wilkinson and Davy, 2018). Then, the two dendrograms (phylogenetic vs. morphological) were compared using the `tanglegram` function ('dendextend' package version 1.16.0, Galili, 2015) and calculated Baker's Gamma correlation coefficient

(Baker, 1974), which measures the similarity between two dendrograms, ranging from -1 to 1, with values closer to 0 indicating that the two dendrograms are not similar.

The estimative of morphological distance (based on Euclidean distance) used the Fourier coefficient matrix to test the hypothesis that taxonomically proximate individuals have a similar morphological pattern. It proceeded with the non-parametric Mann-Whitney test for independent samples (Zar, 2010) within three taxonomic levels (genus, family, and order).

In the context of this study, morphospace, also called shape space, is the mathematical space that describes and relates the morphological configuration of the analyzed fish (Mitteroecker and Gunz, 2009). Thus, morphospace was used to verify the diversity and morphological amplitude of the species. The morphological configuration of each species is represented as a single point, and the space dimensionality is determined by the number of shape variables analyzed (i.e., the significant principal components) (Mitteroecker and Gunz, 2009).

We evaluated morphospace as a three-dimensional (3d) structure created through the first three principal components. Two geometric metrics were extracted from this structure: volume and amplitude. The volume of the 3d structure, or volume of the morphospace, is the morphological diversity found within the species group that composes the shape space. The larger the volume, the greater the phenotypic diversity found in the morphospace. Morphological amplitude can be interpreted as the greatest distance between two vertices of the 3d structure (i.e., the greatest distance between two species that composes the same shape space). Thus, the amplitude was used to find the most morphologically different species within the morphospace (i.e., the greatest amplitude value found within the morphospace indicates the two most different species). For both analyses, the input data was the significant principal component matrix. Volume was calculated using the 'geometry' package version 0.4.5 (Habel et al., 2019), and amplitude by using the largest Euclidean distance between species in the morphospace. The Fig. S1 (Supplementary Information 2) presents a didactic sketch showing an example of how morphospace was studied in the present work.

Volume and amplitude were compared to the species number observed at each sampling station using power models ($y = ax^b$) to observe the behavior of the morphospace metrics. Morphospace (volume and amplitude) within bottom habitat types was evaluated in this study in three different situations of observed species abundance: (i) All species - where the criterion evaluated was presence or absence, and all species present in the habitat type were considered in the analysis, regardless of total abundance; (ii) species with total abundance ≥ 25% - all species that occurred at an abundance of 25% or greater in that habitat type, relative to the total of that species captured in the study area; and (iii) species with total abundance ≥ 50% - all species that occurred at an abundance of 50% or greater in that habitat type, relative to the total of that species captured in the study area.

A canonical variable analysis (CVA) was applied on the significant principal component matrix to check the degree of morphospace separation within each bottom habitat type. Multivariate analysis of variance (MANOVA) was applied on the CVA scores to verify if there is a morphological difference between the morphospaces of the three bottom habitat types. Finally, the Dunn test for multiple pairwise comparisons (Dunn, 1964) was applied to evaluate the influence of habitat type on the shape variables (i.e., significant PCs). The three previous analyses (CVA, MANOVA, and Dunn test) were performed considering the three situations of species abundance observed (all species, ≥ 25% and ≥ 50%). The objective of applying the Dunn test was to answer the following hypothesis: the fish morphological pattern (i.e., shape variables) in a given habitat can be explained in part by the abundance of the species that are found in that habitat, assuming that the more abundant a species is in a given environment, the more morphologically adapted the species is to live in that habitat. A significance level of 5% was used in all analyses (Zar 2010).

3. RESULTS

We analyzed 120 species distributed in 16 orders and 45 families (Appendix S1 in Supplementary Information 2). The first three principal components were considered significant and retained for further analysis, explaining approximately 74% of the fish shape variation (Fig. S2 in Supplementary Information 2). PC1 (53.2% of the total variance) was related to the fish body elongation (Fig. 3a). The relationship between PC1 and elongation aspect index was directly proportional (Fig. 3b). That is, fish with negative extreme values of this axis showed deep body shape, while species with elongated body pattern occupied positive extreme values. PC2 (11.8%) explained the caudal fin shape (Fig. 3a), as evidenced in the boxplot with the variable ‘caudal fin type’ (Fig. 3c). Species with rounded fins are positioned at the negative extreme of this component, while fish with forked fins can be found at more positive values of the PC2. Finally, PC3 (8.9%) explained, to a lesser extent, the shape and position of the dorsal fin, where individuals that have more pointed dorsal fins and positioned more posteriorly on the body were concentrated in negative PC3 values. On the other hand, individuals that have pointed dorsal fins and positioned anteriorly on the body are at the positive end (Fig. 3a). Species representative of the extremes of each PC were: *Pomacanthus paru* (-PC1), *Fistularia petimba* (+PC1), *Achirus lineatus* (-PC2), *Selene vomer* (+PC2), *Bothus lunatus* (-PC3), and *Holocanthus ciliaris* (+PC3) (Fig. 3a).

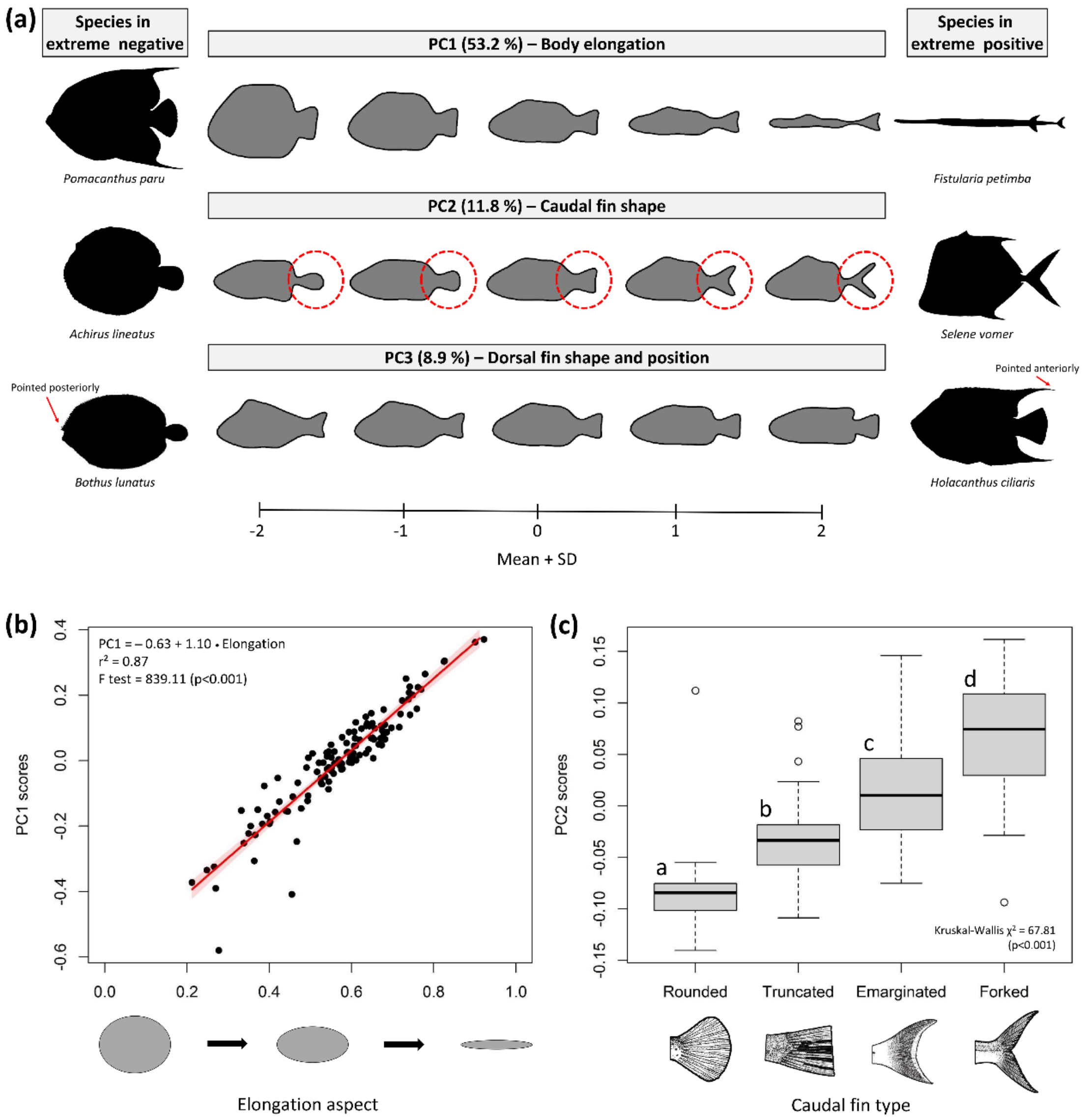

Fig. 3 Variation of fish body shape in the three axes of the principal components (PCs), and species that occupied the extreme values (negative and positive) (a). Relationship between PC1 scores and elongation aspect (b). Relationship between PC2 scores and caudal fin type. Kruskal-Wallis test indicated a significant difference in PC2 scores among caudal fin types and different letters indicate statistically significant difference (Dunn test, $p<0.01$) (c).

Our results suggest the morphological pattern of the demersal fish bodies analyzed could be divided into 13 main shape groups (Fig. 4a). These 13 morphological patterns represent the groups that are formed at a cutoff of approximately 10% of the Euclidean distance in the clustering dendogram. The species were grouped according to morphological similarity, where it is possible to observe fish with more common body shapes (i.e., groups with higher species number, with 23 to 12 species; the groups 9, 7, 12, and 10) and, in a opposite side, groups of rarer body shapes with lower species number (2 to 5 species, the groups 1, 4, 5, and 13) (Fig. 4a). We compared the phylogenetic tree with the morphological clustering for 103 analyzed species (Fig. 4b). Overall, we observed that phylogenetic proximity does not necessarily determine morphological proximity (evidenced by low Baker's Gamma correlation = 0.20), with morphologically similar individuals (right dendrogram) represented by phylogenetically distant species (e.g., first and last branch of the morphological clustering, and others). However, the morphological distance is greater the higher the taxonomic level (Fig. 5).

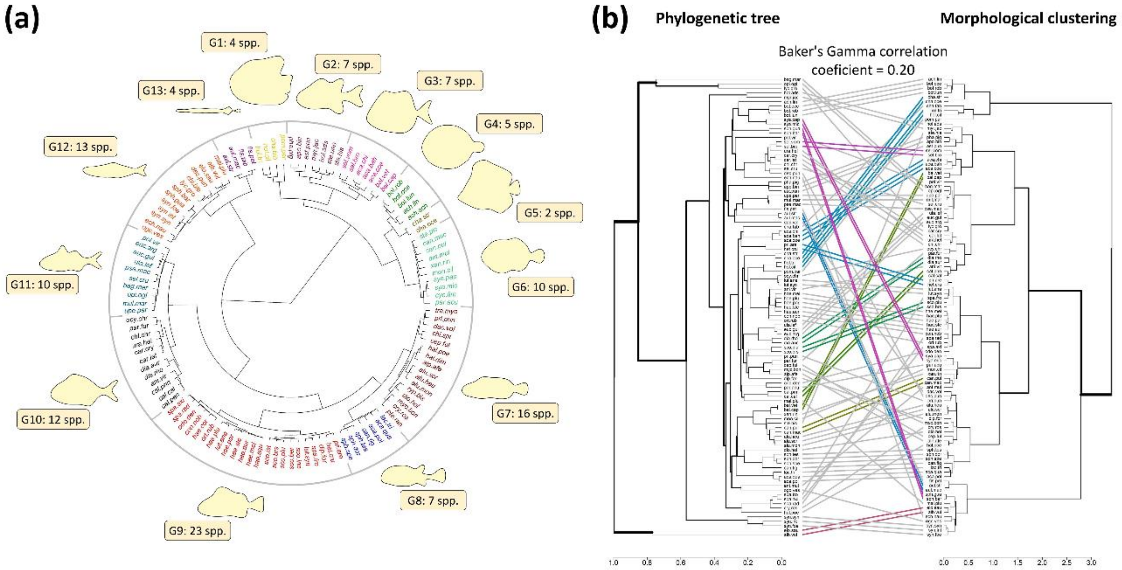

Fig. 4 Main shape groups of marine demersal fishes evaluated in this study, indicating the reconstructed average shape and species number in each group (a). Phylogenetic reconstruction for 103 species analyzed in this study compared with morphological clustering based on body shape. Baker's Gamma correlation coefficient (0.20) indicated a low congruence between phylogeny and body morphology (b).

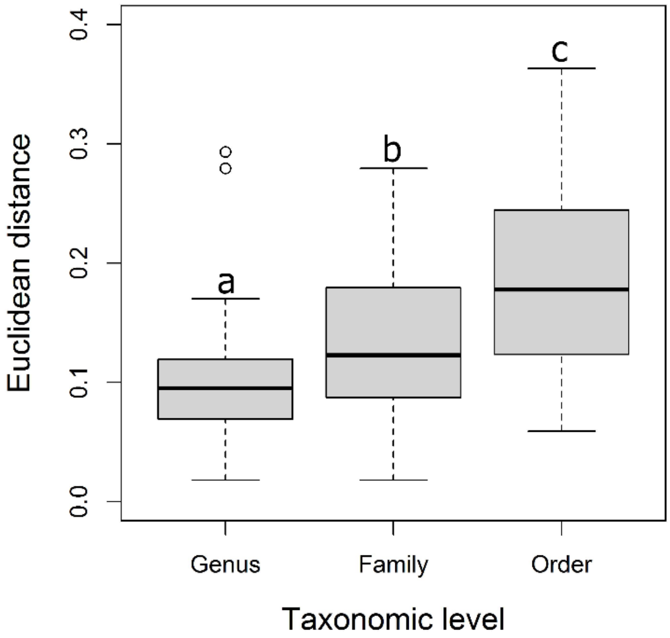

Fig. 5 Boxplot of the relationship between Euclidean distance (i.e., morphological distance) and taxonomic level. Different letters indicate a significant difference between the Euclidean distance medians among taxonomic levels (Mann-Whitney test, $p<0.05$).

Of all 37 sampling stations analyzed, 20 were classified as SWCR, four as Algae, 12 as Sand, and one station was unclassified (Fig. 6a). Morphospace volume ($\times 10^6$) values ranged from 2 to 28,668 and morphospace amplitude ($\times 10^2$) from 8 to 97, both of which have no measure unit because these are metrics calculated within a shape space. Volume and amplitude did not show a defined latitudinal spatial pattern in the study area (Figs. 6b, c). The relationships between morphospace volume vs. species number and morphospace amplitude vs. species number were $y=2E\text{-}06x^{2.8688}$ ($r^2=0.79$, $F=132.2$, $p<0.001$) and $y=0.0775x^{0.7304}$ ($r^2=0.70$, $F=81.9$, $p<0.001$), respectively, evidencing that both metrics (volume and amplitude) increase the more species present in the morphospace (Fig. 6d).

Morphospace volume and amplitude values were higher in the SWCR habitat (i.e., greater morphological diversity and greater morphological difference between two species found in this environment), when compared to Algae and Sand habitats (Figs. 6e and 7). In the SWCR habitat the volume and amplitude remained high regardless of the species abundance observed (Figs. 7a). However, in Algae and Sand, both metrics decreased the higher the species total abundance (%) in that habitat type (Figs. 7b, c).

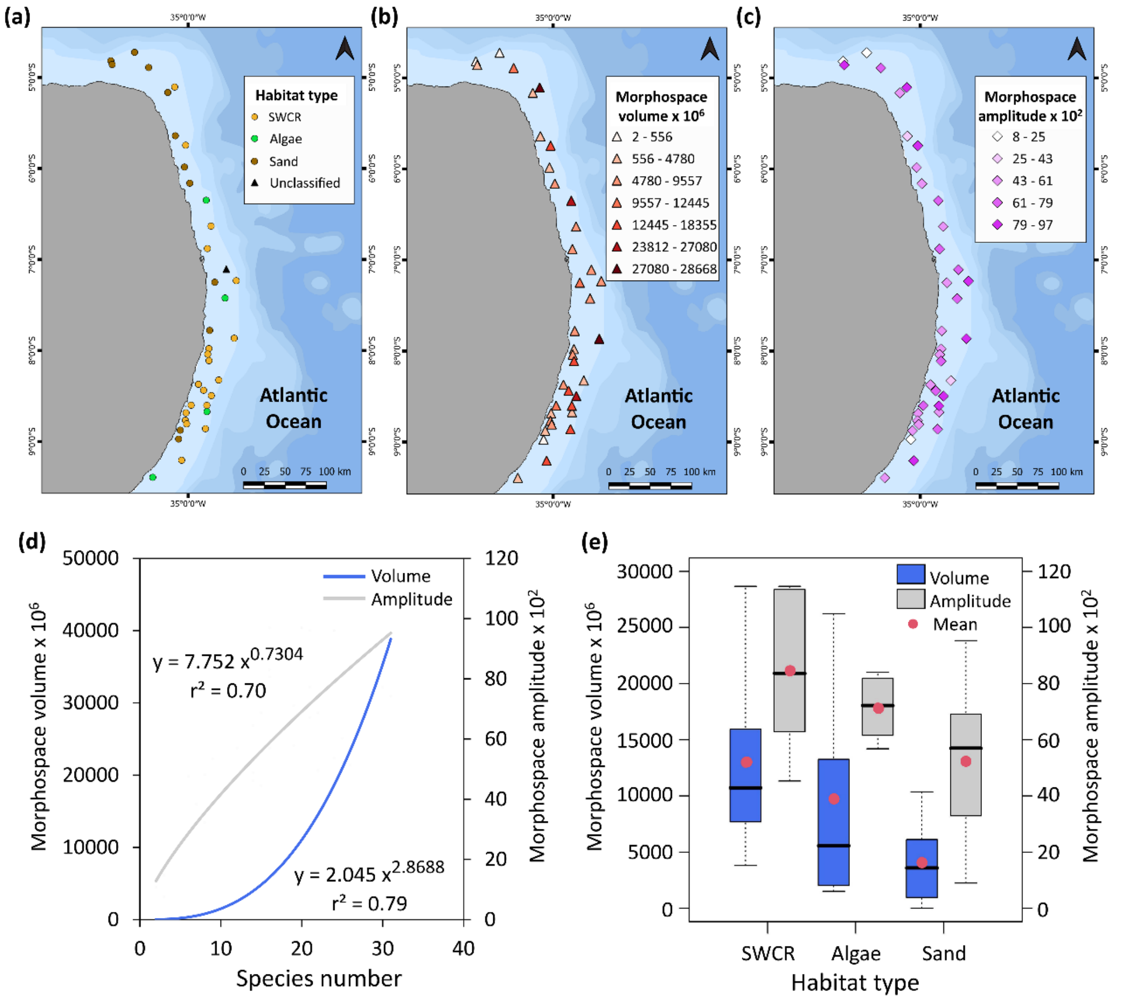

Fig. 6 Sampling station classification by bottom habitat type (a). Variation of morphospace volume (c) and morphospace amplitude (c) at each sampling station. Relationship of volume and amplitude with species number composing of the morphospace (d). Variation of volume and amplitude of morphospace in each habitat type (e).

The morphological pattern found in the habitat types changed according to the species total abundance (Fig. 8). At first, considering all species present in the habitat (independent of abundance %), no significant differences were found by MANOVA (Wilks' Lambda=0.978, p=0.360), as well as by the pairwise comparison results of the Dunn test for the three shape variables (PC1, PC2, and PC3) (All species, Fig. 8 and Appendix S2 in Supplementary Information 2). When considering the habitat morphospaces formed only by species with total abundance ≥ 25%, the MANOVA (Wilks' Lambda=0.899, p<0.01) indicated significant difference in morphological pattern. In addition, Dunn test results indicated differences for PC1 (body elongation) between Sand vs. Algae (p=0.002) and Sand vs. SWCR (p=0.015) (≥ 25%, Fig. 8 and

Appendix S2 in Supplementary Information 2). Finally, considering the situation with total species abundance ≥ 50%, the MANOVA (Wilks' Lambda=0.915, $p<0.01$) indicated morphological differences between the habitats, and PC1 continued to show significant differences in the Sand vs. Algae ($p=0.007$) and Sand vs. SWCR ($p=0.017$) comparisons (≥ 50%, Fig. 8 and Appendix S2 in Supplementary Information 2). Variables PC2 and PC3 were not different between bottom types and species abundance in the habitats (Appendix S2 in Supplementary Information 2). Therefore, we can conclude that there is a tendency to find fish with a more elongated body shape in the Sand type habitat, especially when we take into consideration the most abundant species in this environment.

4. DISCUSSION

Studies of morphological diversity at the fish community level are scarce. Here we assessed for the first time the morphological pattern of a community with 120 species of marine bony fish in the Atlantic Southwestern (4°-9°S). Our results are included within a small set of studies that used geometric morphometric methods to understand the morphological pattern of fish communities in different marine habitats (e.g., Farré et al., 2015, 2016; Aguilar-Medrano and Calderon-Aguilera, 2016; Aguilar-Medrano and Arias-González, 2018). The 13 body morphotypes found indicated that the 120 species from tropical shelf of northeastern Brazil have a high shape diversity, corroborating with work of this magnitude for demersal fish in Mexico (Aguilar-Medrano and Calderon-Aguilera, 2016; Aguilar-Medrano and Arias-González, 2018), tropical Indo-Pacific (Claverie and Wainwright, 2014), and the Mediterranean Sea (Farré et al., 2015, 2016).

However, the presence of more common body shapes associated with many different species may indicate that morphological convergence occurs, i.e., many species exhibit the same body pattern. This convergence can be interpreted as an evolutionary adaptation that grants these species access to different ecological niches (morphologically generalist species), whether related to access to different habitats, trophic ecology, or behavioral origin (Webb, 1984). On the other hand, we can also observe morphological divergence where few species have a particular body shape, indicating a specialization in the body morphology that may also reflect in a niche specialization (e.g., Collar et al., 2009; López-Fernández et al., 2012).

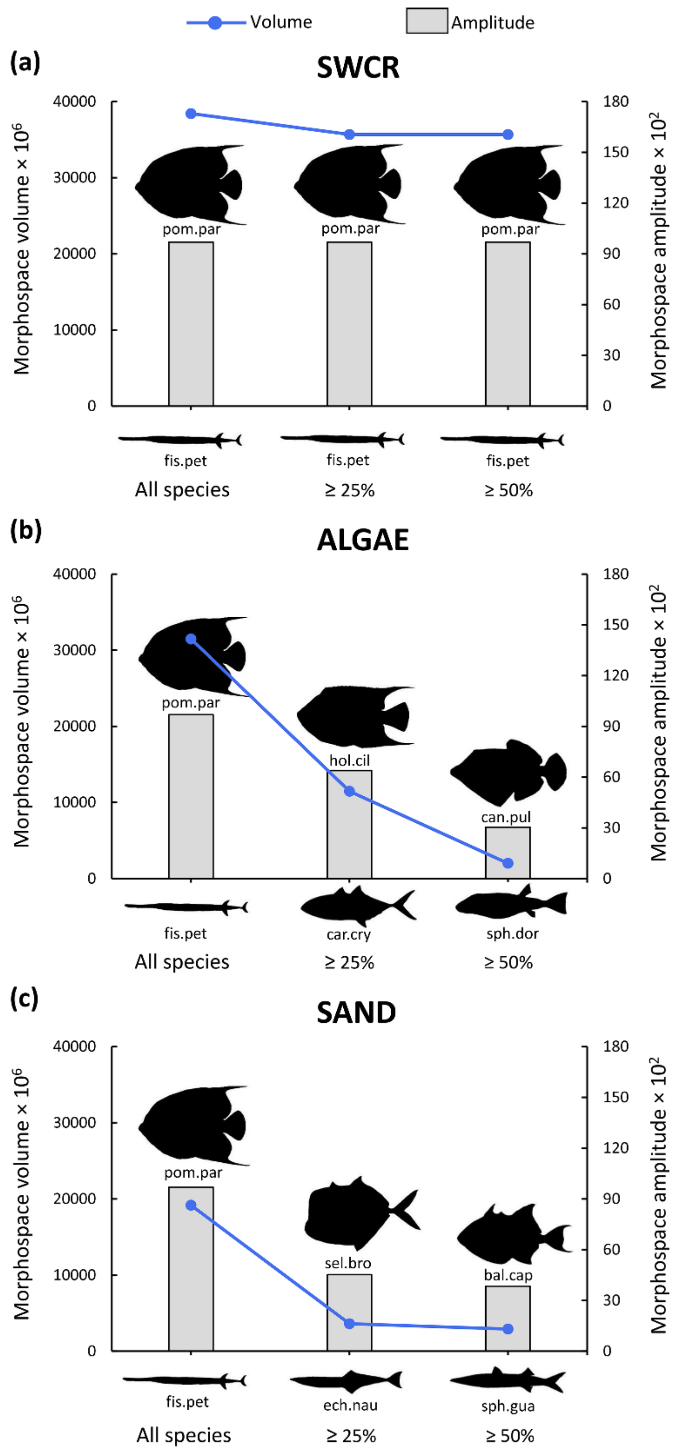

Fig. 7 Variation of morphospace volume and amplitude for the SWCR (a), Algae (b), and Sand (c) habitat types, in three different situations of species abundance: (i) All species - all species present in the habitat type were considered in the analysis, independent of total abundance; (ii) ≥ 25% - all species that occurred at an abundance of 25% or greater in that habitat type, compared to the total of that species captured in the study area; and (iii) ≥ 50% - all species that occurred at an abundance of 50% or greater in that habitat type, compared to the total of that species captured in the study area. Black fish silhouettes represent the species with the highest morphological amplitude.

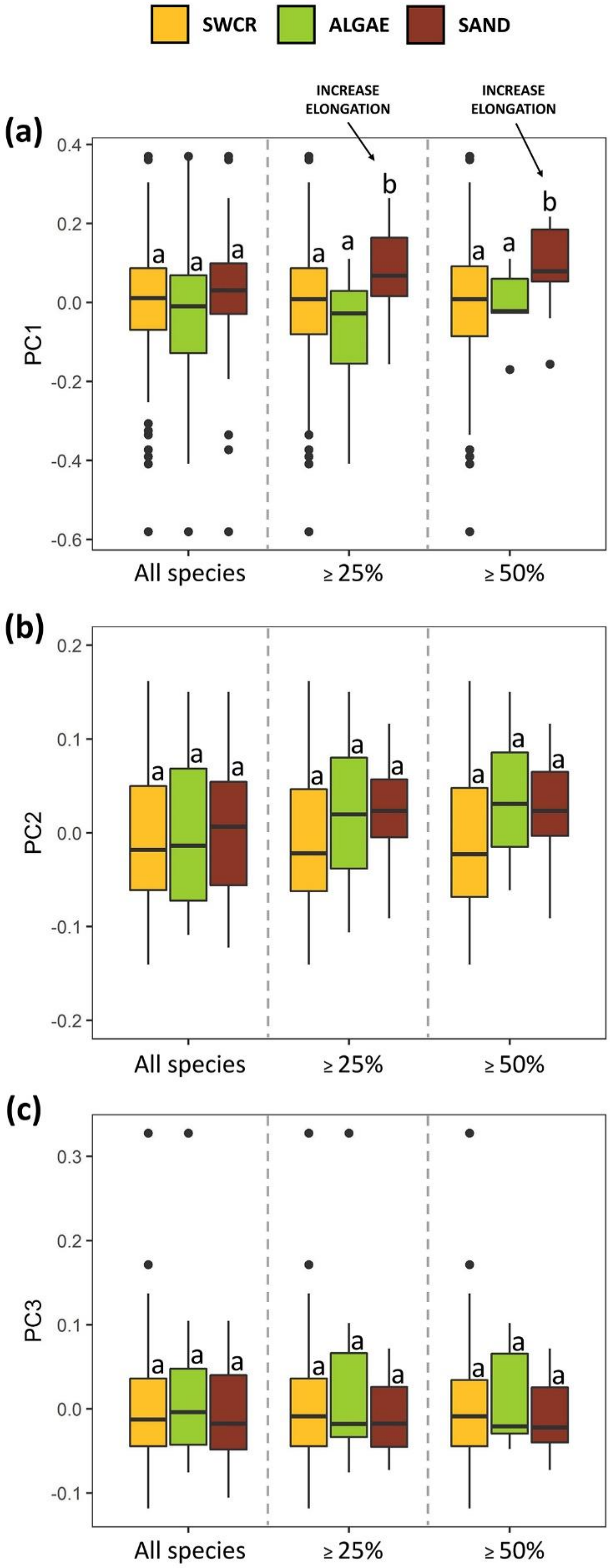

Fig. 8 Variation of PC1 (a), PC2 (b), and PC3 (c) on different habitat types, in three different situations of species abundance (All species, ≥ 25%, and ≥ 50%). Different letters indicate statistically significant difference (Dunn test, $p<0.05$).

We can observe in our results some groups that have specific body shapes: the flat-fish group (with five species of Pleuronectiformes, G4 in Fig. 4a), characterized by fish that have a specific swimming pattern in contact with the bottom, where compression and body morphology are directly linked to this behavior (Fox et al., 2018); the trumpet-fish group (with four species of Syngnathiformes, G13 in Fig. 4a), that have a very elongated body shape, which may be intrinsically related to feeding and hunting tactics, such as the camouflage behavior in the vertical position during prey searching (Auster, 2008), in addition to the elongated head and jaw morphology (Tegge et al., 2020); and finally, we can also observe the butterfly-fish group (with two species of Chaetodontidae, G5 in Fig. 4a), which are fish that have a body shape directly linked to foraging behavior, where the head and jaw morphology (Ferry-Graham et al., 2001) are very much associated with searching for sessile preys (Brandl and Bellwood, 2013, 2014), here the deep shape favors a reduction of vertical rotation around its own body, providing more precise maneuvers (Webb, 1984).

The morphological clustering showed low congruence with the phylogenetic tree, indicating that our morphological approach cannot be used to observe phylogenetic proximities for the species studied. Indeed, the use of morphological data in phylogenetic mapping is not recommended (Wiens, 2004), where one of the main discussions is about morphological data behaving as homoplastic characters. In this study, we interpret body shape as a homoplastic character, where many species have a similar body shape, but did not necessarily evolve from an immediate common ancestor (Wiley and Lieberman, 2011). This becomes evident when we observe groups that are morphologically similar but phylogenetically distant: (i) elongate body shape fish - represented by trumpet-fish (Syngnathiformes order), barracuda (Sphyraenidae family) and lizard-fish (Aulopiformes order); and (ii) deep body shape fish - represented by flat-fish (Pleuronectiformes order), and angel-fish and butterfly-fish (Acanthuriformes order). However, some studies use a large matrix of morphological variables to map and fill phylogenetic gaps in some fish groups, in these cases a series of quantitative and qualitative variables are evaluated together (e.g., Dillman et al., 2016; Girard et al., 2020). As expected, morphological distance increased the higher the taxonomic level between species; similar results were found for a fish community from the North Sea (Caillon et al., 2018).

Body elongation has been the most highlighted trait in morphological studies of fish communities (e.g., Claverie and Wainwright, 2014; Caillon et al., 2018; Price et al., 2019), explaining more than half of the morphological variation in the 120 species analyzed here. One of the most discussed functional traits with body elongation rate is swimming performance. Fish with a more elongated body shape have been attributed to individuals having greater acceleration during swimming and/or cruising-type swimming (e.g., tunas) (Webb, 1984). On the other hand, fish with deeper bodies are more specialized in maneuvering (e.g., butterfly-fish) (Webb, 1984). Another striking feature in our results was the caudal fin shape, which has been attributed to the fish's propulsion in the water column (Lauder and Drucker, 2004). The complexity of fin shapes (caudal fin and other fin types) act in conjunction with a variety of other factors to generate hydrodynamic movements during swimming (Blake, 2004; Lauder and Drucker, 2004), but the morphological pattern can also reveal how the fish are adapted to live in certain habitats (see Imre et al., 2002; Langerhans, 2008; Yamada et al., 2009).

Using morphospace as a 3d structure allowed us to understand the fish morphological pattern in the different habitat types analyzed. The heterogeneous habitat SWCR showed the highest diversity and morphological amplitude for the species. Indeed, structured coral reef environments are already widely studied with respect to high fish diversity (e.g., Harmelin-Vivien, 2002; Aguilar-Perera and Appeldoorn, 2008; Eduardo et al., 2018), and the complexity of these habitats is one of the factors favoring high ecological diversity (Messmer et al., 2011). Complex habitats, therefore, favor high morphological diversity (as we found in our study for SWCR) and, consequently, functional and ecological niche diversity (Willis et al., 2005). However, Halpern and Floeter (2008) point out that increased functions in fish communities are more associated with species diversity in different functional groups (i.e., different species acting in different functions within the environment) than species richness in the community. SWCR habitats favor a set of conditions that provide a high diversity of ecological niches with respect to the refuge (Johansen et al. 2008), social interactions (Gil and Hein, 2017), and reproductive aspects (Claydon, 2004), among others. The complexity of coral reefs also reduces predation and competition among fish species (Almany, 2004). All of this enables the coexistence of diverse species due to decreased overlapping of ecological niches (increasing niche partitioning, Hugueny, 1990), which also explains the coexistence of morphologically different fish adapted to live in SWCR habitat (see volume and amplitude greater for SWCR in Figs. 6e and 7). Furthermore, coral reefs promote the evolution of morphological diversity in some fish groups, such as Haemulidae (Price et al., 2013) and Labridae (Price et al., 2011).

Conversely, sand habitats showed the lowest diversity and morphological amplitude, which leads us to understand that fish morphology in this environment is more specialized when compared to the morphology in SWCR (more diverse and disperse). Open environments, such as sandbanks, have a much higher water flow than environments protected by structures, such as rocks, sponges, and corals (Johansen, 2014). Species living in these habitats need to break through the physical barrier present there (higher water velocity), and one of the most discussed morphological adaptations is body elongation (e.g., Langerhans, 2008; Foster et al., 2015; Bejarano et al., 2017). For instance, freshwater fish exhibit more elongated shapes in higher water currents (see e.g., Langerhans et al., 2003; Langerhans, 2008; Franssen, 2011; Foster et al., 2015). In turbulent marine environments, which have a higher wave exposure, a morphological filter acts on the fish body shape, favoring species with fusiform bodies, which have a design that minimizes the water drag, making these individuals better able to access the resources around them, compared to the deep body shape that has disadvantages in this type of habitat (Bejarano et al., 2017).

The species abundance in the habitat helped us to understand two important conclusions: (i) initially, we could identify high morphological connectivity among the three habitats, observing the same diversity and morphological amplitude for all species present in each habitat (see All species in Fig. 7), making it clear that these habitats are highly connected in the study area; (ii) by contrast, when we observed the morphospace composed of the most abundant species, we concluded that in the Sand bottom the general morphology is more specialized, with lower volume and morphological amplitude, besides the body pattern becoming more elongated (see Fig. 8), reinforcing that an exposed habitat favors species that have a morphological design adapted to those conditions.

The Algae type habitat showed intermediate morphospace values. Nevertheless, as we had only four sampling stations characterized as this type of bottom, we suggest that future work should further investigate these habitats, since they are important for ecosystem functioning, especially among lower trophic levels such as herbivores (Kopp et al., 2010). Other traits, which were not evaluated here, are also related to fish morphology, such as ecological factors (e.g., Costa and Cataudella, 2006; Price et al., 2015) and environmental physicochemical factors (e.g., Georgakopoulou et al., 2007; Crispo and Chapman, 2010). Thus, the phenotype that fish present is the result of a set of factors that act in greater or lesser intensity on the morphological pattern of these individuals.

5. CONCLUSIONS

Here, we present for the first time a morphological characterization of the demersal fish community from the northeast Brazilian shelf. The good use of geometric morphometry, accessing shape using Fourier functions, allowed us to conclude that demersal fish have a high morphological diversity. The SWCR habitat most likely has the highest functionality, as it has the highest morphological diversity and dispersion. In the Sand habitat, there is a morphological specialization focused on body elongation, related to access to the habitat due to a design more adapted to this environment. We recommend that this work can be expanded to other areas, because morphological comprehension is fundamental to understanding the ecosystem dynamics, especially in coral reefs, which have been highly impacted by anthropic pressures (Andrello et al., 2022).

SUPPLEMENTARY INFORMATION 2

Appendix S1. Taxonomy and morphological characterization of 120 fish species on the continental shelf of Northeastern Brazil (4º-9ºS). Total abundance (%) of species in three bottom habitat types: sand, algae and SWCR (Sand with rocks, coralline formations, and sponges). Caudal fin type and body elongation aspect. Scores of significant principal components explaining the morphological variation of species (PC1, PC2, and PC3), and images source: (1) ABRACOS surveys, (2) Froese and Pauly (2021), (3) Deda and Barbosa (2016), (4) Robertson and Tassel (2019), (5) Williams et al. (2010), (6) Rocha (2004).

Order	Family	Species	Code	% Sand	% Algae	% SWCR	Caudal type	Elongation aspect	PC1	PC2	PC3	Images source
Acanthuriformes	**Acanthuridae**	*Acanthurus bahianus* Castelnau, 1855	aca.bah	11.46	28.66	59.87	Truncated	0.4408	-0.1540	0.0770	0.0394	1
		Acanthurus chirurgus (Bloch 1787)	aca.chi	6.16	6.40	87.44	Truncated	0.3834	-0.1939	0.0432	0.0426	1
		Acanthurus coeruleus Bloch & Schneider, 1801	aca.coe	0.00	0.00	100.00	Emarginated	0.3380	-0.2526	0.1459	0.0383	1
	Chaetodontidae	*Chaetodon ocellatus* Bloch, 1787	cha.oce	7.64	5.73	86.62	Truncated	0.2484	-0.3349	-0.0848	-0.0436	1
		Chaetodon striatus Linnaeus, 1758	cha.str	1.61	0.23	98.17	Truncated	0.2119	-0.3727	-0.1086	-0.0724	1
	Ephippidae	*Chaetodipterus faber* (Broussonet, 1782)	cha.fab	0.00	0.00	100.00	Emarginated	0.2699	-0.3903	0.0495	0.1715	2
	Pomacanthidae	*Holacanthus ciliaris* (Linnaeus, 1758)	hol.cil	0.00	46.15	53.85	Truncated	0.4549	-0.4088	-0.1061	0.3277	1
		Holacanthus tricolor (Bloch, 1795)	hol.tri	0.00	0.00	100.00	Truncated	0.4671	-0.2475	-0.0993	0.1371	2
		Pomacanthus paru (Bloch, 1787)	pom.par	3.92	2.94	93.14	Rounded	0.2771	-0.5803	0.1120	0.0784	1
Albuliformes	**Albulidae**	*Albula vulpes* (Linnaeus, 1758)	alb.vul	50.00	0.00	50.00	Forked	0.7234	0.1833	0.0347	-0.0071	1
Aulopiformes	**Synodontidae**	*Synodus foetens* (Linnaeus, 1766)	syn.foe	0.00	0.00	100.00	Emarginated	0.7328	0.2502	-0.0004	-0.0231	1
		Synodus intermedius (Spix & Agassiz, 1829)	syn.int	0.00	0.00	100.00	Emarginated	0.7417	0.2257	-0.0233	-0.0281	4
		Synodus synodus (Linnaeus, 1758)	syn.syn	0.00	0.00	100.00	Emarginated	0.7617	0.2240	-0.0277	-0.0070	4

		Trachinocephalus myops (Forster, 1801)	tra.myo	12.90	0.00	87.10	Emarginated	0.6782	0.1555	0.0375	-0.0319	1
Carangiformes	**Carangidae**	*Caranx crysos* (Mitchill, 1815)	car.cry	50.00	50.00	0.00	Forked	0.5939	0.0872	0.0752	-0.0310	1
		Caranx latus Agassiz, 1831	car.lat	0.00	0.00	100.00	Forked	0.5881	0.0537	0.0886	-0.0336	3
		Chloroscombrus chrysurus (Linnaeus, 1766)	chl.chr	1.56	0.00	98.44	Forked	0.5053	0.0216	0.0948	-0.0574	1
		Decapterus punctatus (Cuvier, 1829)	dec.pun	100.00	0.00	0.00	Forked	0.6483	0.1444	-0.0017	-0.0428	1
		Selar crumenophthalmus (Bloch, 1793)	sel.cru	11.54	0.00	88.46	Forked	0.6065	0.0881	0.0427	-0.0746	1
		Selene brownii (Cuvier, 1816)	sel.bro	47.62	0.00	52.38	Forked	0.3319	-0.1529	0.1088	-0.0513	1
		Selene vomer (Linnaeus, 1758)	sel.vom	0.00	0.00	100.00	Forked	0.3660	-0.2275	0.1617	-0.0031	1
		Uraspis helvola (Forster, 1801)	ura.hel	0.00	0.00	100.00	Forked	0.4951	0.0087	0.0780	-0.0066	2
	Echeneidae	*Echeneis naucrates* Linnaeus, 1758	ech.nau	25.00	0.00	75.00	Emarginated	0.7793	0.2641	-0.0533	0.0108	1
Clupeiformes	**Clupeidae**	*Opisthonema oglinum* (Lesueur, 1818)	opi.ogl	0.14	0.00	99.86	Forked	0.6246	0.0977	0.1116	-0.0497	1
	Engraulidae	*Lycengraulis grossidens* (Spix & Agassiz, 1829)	lyc.gro	0.00	0.00	100.00	Forked	0.6105	0.1163	0.0482	-0.0162	4
	Pristigasteridae	*Chirocentrodon bleekerianus* (Poey, 1867)	chi.ble	0.00	0.00	100.00	Forked	0.6347	0.1336	0.0181	-0.0150	2
Dactylopteriformes	**Dactylopteridae**	*Dactylopterus volitans* (Linnaeus, 1758)	dac.vol	20.59	2.94	76.47	Emarginated	0.6510	0.1137	-0.0227	0.0310	1
Elopiformes	**Elopidae**	*Elops saurus* Linnaeus, 1766	elo.sau	100.00	0.00	0.00	Forked	0.7399	0.2076	0.0521	0.0273	1
Holocentriformes	**Holocentridae**	*Holocentrus adscensionis* (Osbeck, 1765)	hol.ads	2.64	80.76	16.60	Forked	0.5760	-0.0272	0.1502	0.1020	1
		Myripristis jacobus Cuvier, 1829	myr.jac	0.00	0.00	100.00	Forked	0.5261	-0.0684	0.0977	0.0418	5
Kurtiformes	**Apogonidae**	*Apogon binotatus* (Poey, 1867)	apo.bin	0.00	0.00	100.00	Emarginated	0.4906	-0.0217	0.0205	0.0294	2
		Astrapogon puncticulatus (Poey, 1867)	ast.pun	0.00	0.00	100.00	Emarginated	0.5255	-0.0535	0.0460	-0.0103	2
		Phaeoptyx pigmentaria (Poey, 1860)	pha.pig	0.00	0.00	100.00	Emarginated	0.5912	0.0256	0.0525	0.0249	2
Lophiiformes	**Antennariidae**	*Antennarius multiocellatus* (Valenciennes, 1837)	ant.mul	0.00	0.00	100.00	Rounded	0.4934	-0.1232	-0.0827	0.0316	2
	Ogcocephaliidae	*Ogcocephalus vespertilio* (Linnaeus, 1758)	ogc.ves	50.00	0.00	50.00	Truncated	0.7387	0.1871	-0.0612	0.0249	2

Mulliformes	**Mullidae**	*Mulloidichthys martinicus* (Cuvier, 1829)	mul.mar	0.00	0.00	100.00	Forked	0.6436	0.1053	0.0941	-0.0331	1
		Pseudupeneus maculatus (Bloch, 1793)	pse.mac	56.45	3.13	40.41	Forked	0.5774	0.0711	0.0617	-0.0726	1
		Upeneus parvus Poey, 1852	upe.par	0.00	0.00	100.00	Forked	0.6358	0.1061	0.0740	-0.0160	2
Perciformes	**Gerreidae**	*Diapterus auratus* Ranzani, 1842	dia.aur	0.00	0.00	0.00	Forked	0.4207	-0.0534	0.1444	-0.0715	2
		Diapterus rhombeus (Cuvier, 1829)	dia.rho	0.00	0.00	100.00	Forked	0.3881	-0.0778	0.1545	-0.0890	2
		Eucinostomus argenteus Baird & Girard, 1855	euc.arg	85.17	0.10	14.73	Forked	0.5398	0.0240	0.1163	-0.0388	1
		Eucinostomus gula (Quoy & Gaimard, 1824)	euc.gul	1.03	0.00	98.97	Forked	0.5445	0.0273	0.0717	-0.0541	1
		Ulaema lefroyi (Goode, 1874)	ula.lef	0.07	0.00	99.93	Forked	0.5503	0.0482	0.0847	-0.0295	1
	Haemulidae	*Anisotremus virginicus* (Linnaeus, 1758)	ani.vir	0.00	37.50	62.50	Forked	0.4692	-0.0681	0.0831	-0.0756	2
		Conodon nobilis (Linnaeus, 1758)	con.nob	0.00	0.00	100.00	Truncated	0.5315	-0.0066	-0.0132	-0.0387	2
		Haemulon aurolineatum Cuvier, 1830	hae.aur	32.60	0.00	67.40	Forked	0.5583	0.0276	0.0316	-0.0676	1
		Haemulon melanurum (Linnaeus, 1758)	hae.mel	0.00	0.00	100.00	Forked	0.5689	0.0033	0.0136	-0.0446	1
		Haemulon parra (Desmarest, 1823)	hae.par	0.00	0.00	100.00	Forked	0.5587	-0.0082	0.0048	-0.0282	1
		Haemulon plumierii (Lacepède, 1801)	hae.plu	34.15	6.74	59.11	Forked	0.5164	-0.0343	0.0297	-0.0165	1
		Haemulon squamipinna Rocha & Rosa, 1999	hae.squ	0.16	0.00	99.84	Forked	0.5211	-0.0071	0.0211	-0.0452	1
		Haemulon steindachneri (Jordan & Gilbert, 1882)	hae.ste	33.80	0.00	66.20	Forked	0.5512	0.0096	-0.0136	-0.0471	1
		Haemulopsis corvinaeformis (Steindachner, 1868)	hae.cor	0.00	0.00	100.00	Forked	0.5891	0.0238	-0.0284	-0.0410	1
		Orthopristis ruber (Cuvier, 1830)	ort.rub	94.90	0.00	5.10	Forked	0.6043	0.0226	-0.0081	-0.0266	1
	Labridae	*Halichoeres poeyi* (Steindachner, 1867)	hal.poe	0.00	0.00	100.00	Truncated	0.6783	0.0822	-0.0524	-0.0285	2
		Halichoeres dimidiatus (Agassiz, 1831)	hal.dim	0.00	33.33	66.67	Truncated	0.6712	0.0677	-0.0648	-0.0420	6
	Lutjanidae	*Lutjanus analis* (Cuvier, 1828)	lut.ana	0.00	0.00	100.00	Emarginated	0.5517	-0.0323	0.0128	0.0316	1
		Lutjanus synagris (Linnaeus, 1758)	lut.syn	36.18	27.80	36.01	Emarginated	0.5768	-0.0094	0.0198	0.0351	1

	Ocyurus chrysurus (Bloch, 1791)	ocy.chr	72.73	6.82	20.45	Forked	0.6085	0.0680	0.1092	-0.0032	1
Malacanthidae	*Malacanthus plumieri* (Bloch, 1786)	mal.plu	0.00	0.00	100.00	Emarginated	0.7589	0.1581	-0.0178	0.0099	2
Microdesmidae	*Ptereleotris randalli* Gasparini, Rocha & Floeter, 2001	pte.ran	0.00	0.00	100.00	Rounded	0.7424	0.1398	-0.0848	0.0345	2
Polynemidae	*Polydactylus virginicus* (Linnaeus, 1758)	pol.vir	0.00	0.00	100.00	Forked	0.6066	0.0443	0.1139	-0.0344	3
Pomacentridae	*Stegastes pictus* (Castelnau, 1855)	ste.pic	0.00	0.00	100.00	Forked	0.4146	-0.1577	-0.0935	0.0100	2
	Stegastes uenfi Novelli, Nunan & Lima, 2000	ste.uen	0.00	0.00	100.00	Forked	0.5442	-0.0877	0.1116	0.0904	2
Priacanthidae	*Heteropriacanthus cruentatus* (Lacepède, 1801)	het.cru	0.00	0.00	100.00	Truncated	0.5448	-0.0647	-0.0210	0.0581	1
	Priacanthus arenatus Cuvier, 1829	pri.are	0.00	0.00	100.00	Truncated	0.5942	-0.0049	-0.0284	0.0280	2
Scaridae	*Cryptotomus roseus* Cope, 1871	cry.ros	0.00	0.00	100.00	Truncated	0.7161	0.1022	-0.0719	0.0711	2
	Sparisoma axillare (Steindachner, 1878)	spa.axi	1.52	65.15	33.33	Truncated	0.5516	-0.0224	-0.0137	-0.0477	1
	Sparisoma frondosum (Agassiz, 1831)	spa.fro	8.82	0.00	91.18	Emarginated	0.6005	-0.0065	-0.0184	0.0196	2
	Sparisoma radians (Valenciennes, 1840)	spa.rad	0.00	0.00	100.00	Truncated	0.6032	0.0125	-0.0324	-0.0550	4
Sciaenidae	*Odontoscion dentex* (Cuvier, 1830)	odo.den	0.00	0.00	100.00	Truncated	0.5402	0.0127	-0.0570	-0.0179	1
	Pareques acuminatus (Bloch & Schneider, 1801)	par.acu	75.00	5.00	20.00	Truncated	0.5564	-0.0399	-0.0911	-0.0563	2
Scorpaenidae	*Scorpaena bergii* Evermann & Marsh, 1900	sco.ber	0.00	0.00	100.00	Rounded	0.5360	-0.0491	-0.0728	-0.0008	4
	Scorpaena brasiliensis Cuvier, 1829	sco.brs	0.00	0.00	100.00	Truncated	0.6112	0.0009	-0.0326	0.0332	4
	Scorpaena inermis Cuvier, 1829	sco.ine	0.00	0.00	100.00	Truncated	0.5718	-0.0044	-0.0451	0.0196	4
	Scorpaena isthmensis (Meek & Hildebrand, 1928)	sco.ist	0.00	0.00	100.00	Truncated	0.5975	0.0083	-0.0334	0.0323	4
	Scorpaena plumieri Bloch, 1789	sco.plu	0.00	0.00	100.00	Truncated	0.5715	-0.0147	-0.0297	0.0384	1
Serranidae	*Alphestes afer* (Bloch, 1793)	alp.afe	0.60	0.40	99.01	Rounded	0.6197	0.0168	-0.1010	-0.0441	2
	Cephalopholis fulva (Linnaeus, 1758)	cep.ful	0.00	3.33	96.67	Rounded	0.6529	0.0071	-0.0606	0.0136	1
	Diplectrum formosum (Linnaeus, 1766)	dip.for	69.57	0.00	30.43	Emarginated	0.6550	0.0646	0.0125	0.0600	1

		Mycteroperca bonaci (Poey, 1860)	myc.bon	0.00	0.00	100.00	Truncated	0.6857	0.0864	-0.0308	0.0233	3
		Paranthias furcifer (Valenciennes, 1828)	par.fur	0.00	0.00	100.00	Forked	0.6482	0.0682	0.1093	0.0193	2
		Rypticus bistrispinus (Mitchill, 1818)	ryp.bis	0.00	0.00	100.00	Rounded	0.6815	0.0653	-0.1013	0.0001	4
	Sparidae	*Calamus calamus* (Valenciennes, 1830)	cal.cal	23.94	1.41	74.65	Forked	0.5406	-0.0260	0.0509	-0.0494	1
		Calamus penna (Valenciennes, 1830)	cal.pnn	0.00	100.00	0.00	Forked	0.5448	-0.0211	0.0891	-0.0250	1
		Calamus pennatula Guichenot, 1868	cal.pen	0.00	3.13	96.88	Forked	0.5666	-0.0082	0.0456	-0.0039	1
	Sphyraenidae	*Sphyraena barracuda* (Edwards, 1771)	sph.bar	100.00	0.00	0.00	Emarginated	0.7489	0.2001	0.0083	0.0717	1
		Sphyraena guachancho Cuvier, 1829	sph.gua	93.75	0.00	6.25	Forked	0.7696	0.2171	-0.0002	0.0492	1
	Triglidae	*Prionotus punctatus* (Bloch, 1793)	pri.pun	5.26	5.26	89.47	Truncated	0.6568	0.0986	-0.0230	-0.0448	1
Pleuronectiformes	**Achiridae**	*Achirus achirus* (Linnaeus, 1758)	ach.ach	0.00	0.00	100.00	Rounded	0.3638	-0.3068	-0.0912	-0.1030	1
		Achirus lineatus (Linnaeus, 1758)	ach.lin	0.00	0.00	100.00	Rounded	0.2660	-0.3245	-0.1403	-0.1143	1
	Bothidae	*Bothus lunatus* (Linnaeus, 1758)	bot.lun	0.00	0.00	100.00	Rounded	0.4006	-0.1930	-0.1361	-0.1183	2
		Bothus ocellatus (Agassiz, 1831)	bot.oce	1.81	0.00	98.19	Rounded	0.4021	-0.1871	-0.1224	-0.1056	1
		Bothus robinsi Topp & Hoff, 1972	bot.rob	0.00	0.00	100.00	Rounded	0.3496	-0.2231	-0.1249	-0.0993	2
	Paralichthyidae	*Cyclopsetta fimbriata* (Goode & Bean, 1885)	cyc.fim	0.00	0.00	100.00	Rounded	0.4944	-0.1076	-0.1130	-0.0732	1
		Syacium papillosum (Linnaeus, 1758)	sya.pap	12.50	18.75	68.75	Rounded	0.5282	-0.0724	-0.0844	-0.0709	1
		Syacium micrurum Ranzani, 1842	sya.mic	0.42	0.00	99.58	Rounded	0.5782	-0.0254	-0.0753	-0.0682	1
Siluriformes	**Ariidae**	*Bagre marinus* (Mitchill, 1815)	bag.mar	96.67	0.00	3.33	Forked	0.6378	0.1132	0.0831	-0.0577	1
Syngnathiformes	**Aulostomidae**	*Aulostomus maculatus* Valenciennes, 1841	aul.mac	0.00	2.94	97.06	Rounded	0.8266	0.3042	-0.0770	0.0390	1
		Aulostomus strigosus Wheeler, 1955	aul.str	0.00	0.00	100.00	Rounded	0.8249	0.3024	-0.0782	0.0450	2
	Fistulariidae	*Fistularia petimba* Lacepède, 1803	fis.pet	0.79	10.32	88.89	Emarginated	0.9221	0.3702	-0.0752	0.0419	1
		Fistularia tabacaria Linnaeus, 1758	fis.tab	0.91	0.46	98.63	Emarginated	0.9010	0.3615	-0.0695	0.0391	1

Tetraodontiformes	**Balistidae**	*Balistes capriscus* Gmelin, 1789	bal.cap	75.00	25.00	0.00	Emarginated	0.4451	-0.1558	0.0503	-0.0274	2
		Balistes vetula Linnaeus, 1758	bal.vet	0.00	33.33	66.67	Emarginated	0.3546	-0.2003	0.0983	-0.0357	2
		Xanthichthys ringens (Linnaeus, 1758)	xan.rin	0.00	0.00	100.00	Emarginated	0.4247	-0.1256	-0.0416	-0.0566	5
	Diodontidae	*Chilomycterus spinosus* (Linnaeus, 1758)	chi.spi	20.00	20.00	60.00	Rounded	0.6738	0.0474	-0.0551	0.0747	1
		Diodon holocanthus Linnaeus, 1758	dio.hol	5.56	24.38	70.06	Rounded	0.6413	0.0344	-0.1015	0.0909	1
	Monacanthidae	*Aluterus heudelotii* Hollard, 1855	alu.heu	0.00	0.00	100.00	Truncated	0.6103	0.0454	-0.0555	-0.0282	2
		Aluterus monoceros (Linnaeus, 1758)	alu.mon	80.00	0.00	20.00	Truncated	0.6201	0.0632	-0.0580	-0.0174	2
		Aluterus scriptus (Osbeck, 1795)	alu.scr	20.00	0.00	80.00	Truncated	0.6748	0.0925	-0.0428	-0.0174	2
		Cantherhines macrocerus (Hollard, 1853)	can.mac	4.17	41.67	54.17	Rounded	0.4575	-0.1105	-0.0822	-0.0177	1
		Cantherhines pullus (Ranzani, 1842)	can.pul	5.56	55.56	38.89	Rounded	0.3955	-0.1696	-0.0610	-0.0164	1
		Monacanthus ciliatus (Mitchill, 1818)	mon.cil	0.00	0.00	100.00	Truncated	0.3720	-0.1502	-0.0571	-0.0676	2
		Stephanolepis hispidus (Linnaeus, 1766)	ste.his	5.45	0.25	94.30	Truncated	0.4776	-0.1463	0.0823	0.1046	1
	Ostraciidae	*Acanthostracion polygonius* Poey, 1876	aca.pol	3.39	3.31	93.30	Truncated	0.6667	0.0493	-0.0479	0.0651	1
		Acanthostracion quadricornis (Linnaeus, 1758)	aca.qua	25.27	8.19	66.55	Truncated	0.6974	0.1002	0.0236	0.0529	1
		Lactophrys trigonus (Linnaeus, 1758)	lac.tri	20.63	31.75	47.62	Truncated	0.6515	0.0694	0.0048	0.1014	1
	Tetraodontidae	*Canthigaster figueiredoi* Moura & Castro, 2002	can.fig	0.00	0.00	100.00	Truncated	0.6351	0.0220	0.0224	0.1261	2
		Sphoeroides dorsalis Longley, 1934	sph.dor	0.00	100.00	0.00	Truncated	0.6812	0.1099	-0.0155	0.0928	1
		Sphoeroides spengleri (Bloch, 1785)	sph.spe	0.06	0.00	99.94	Truncated	0.7192	0.1424	-0.0389	0.0999	1
		Sphoeroides testudineus (Linnaeus, 1758)	sph.tes	0.00	0.00	100.00	Truncated	0.6722	0.1065	-0.0223	0.1072	1

Appendix S2. Results of the Dunn test for multiple pairwise comparisons of shape variables (PC1, PC2, and PC3) between different habitat types and species abundance in habitat (All species, ≥ 25%, and ≥ 50%).

All species present in habitat

Shape variable	Comparison	Test statistic (z-value)	p-value
PC1	Sand x Algae	1.67	0.954
PC1	Sand x SWCR	1.14	0.254
PC1	Algae x SWCR	0.87	0.386
PC2	Sand x Algae	0.47	0.637
PC2	Sand x SWCR	0.79	0.430
PC2	Algae x SWCR	0.16	0.869
PC3	Sand x Algae	1.10	0.810
PC3	Sand x SWCR	0.37	0.810
PC3	Algae x SWCR	0.91	0.810

Species with abundance ≥ 25%

Shape variable	Comparison	Test statistic (z-value)	p-value
PC1	Sand x Algae	3.01	**0.002**
PC1	Sand x SWCR	2.42	**0.015**
PC1	Algae x SWCR	1.60	0.111
PC2	Sand x Algae	0.28	0.778
PC2	Sand x SWCR	1.97	0.584
PC2	Algae x SWCR	1.31	0.191
PC3	Sand x Algae	0.89	0.370
PC3	Sand x SWCR	0.53	0.596
PC3	Algae x SWCR	0.63	0.525

Species with abundance ≥ 50%

Shape variable	Comparison	Test statistic (z-value)	p-value
PC1	Sand x Algae	2.69	**0.007**
PC1	Sand x SWCR	2.75	**0.017**
PC1	Algae x SWCR	0.27	0.784
PC2	Sand x Algae	0.25	0.797
PC2	Sand x SWCR	1.72	0.085
PC2	Algae x SWCR	1.40	0.163
PC3	Sand x Algae	0.59	0.554
PC3	Sand x SWCR	0.36	0.716
PC3	Algae x SWCR	0.41	0.659

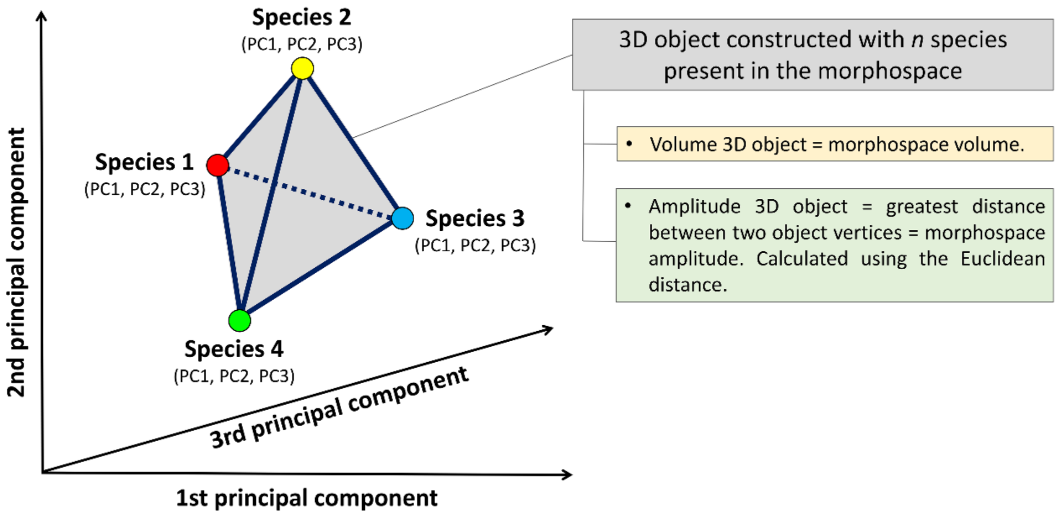

Fig. S1 Didactic sketch of the morphospace concept used in this study. *n* = species number present in the morphospace.

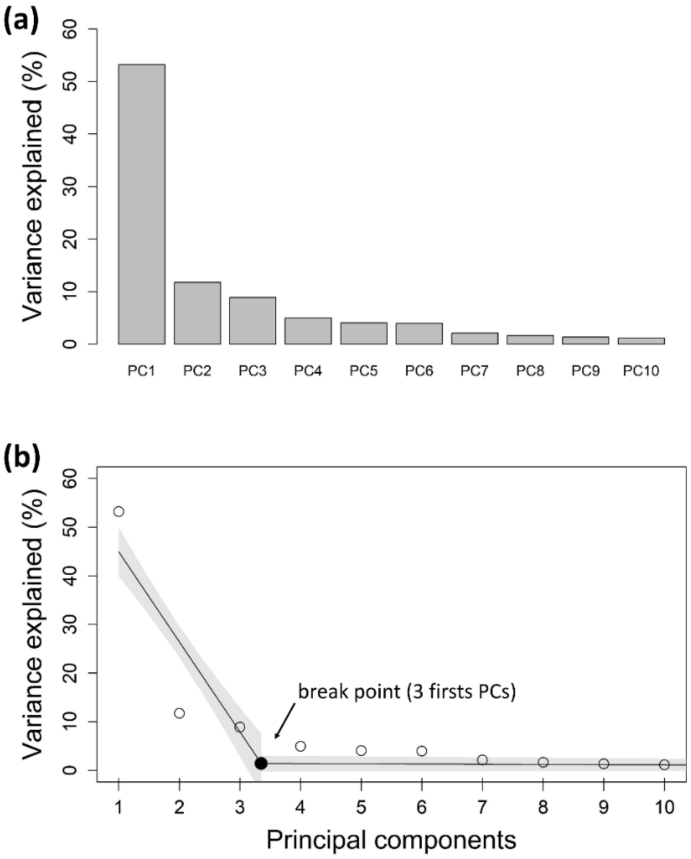

Fig. S2 Variance explained by the first 10 principal components (PC) (a), and scree plot of the segmented regression indicating the first 3 significant PCs: PC1 (53.2%), PC2 (11.8%), and PC3 (8.9%) (b).

FINAL CONCLUSIONS

The geometric morphometric techniques used in our study proved to be very efficient for understanding ecological aspects of fish at the community level. The use of landmarks is more limited due to the lack of homology in a very diverse set of fish, as in our case. Contour analysis using Elliptic Fourier Analysis is more suitable for observing morphological variability at a community level of fish, as the lack of homology is ignored in this situation. However, both techniques have proven to be very efficient in understanding ecological phenomena linked to fish morphology.

Regarding trophic ecology, our results indicated that fish with more elongated body shapes occupied higher trophic levels (TL), while those with a deep shape had lower TL. The shape of the base of the dorsal and anal fins also contributed to explaining the TL. Top predators were characterised by narrow fin bases while herbivores and omnivorous presented longer fins related. Between these extremes, the intermediate trophic category (low predator) shows morphological divergence as a function of TL. From a broader perspective, the geometric morphometric and regression analyses allowed us to infer more precisely the contribution of the morphological aspects of the fish body in their trophic ecology. Body elongation and fin characteristics were the main explanatory variables for fish TL. Combined with maximum fish size (L_{max}), they explained 46% of the TL variability and can be considered an excellent *proxy* to represent the trophic pattern of fish species.

Morphological differences linked to habitat access indicated that the SWCR habitat showed the greatest values of diversity and morphological amplitude. In addition, we can observe that for the Sand habitat there is a greater morphological similarity, with a greater abundance of species with elongated body patterns in these environments, most likely associated with better morphological adaptations to live in open habitats with higher water flow. We found 13 main shape groups, evidencing the great morphological diversity. The morphological clustering showed low congruence with the phylogenetic tree, indicating that our morphological approach cannot be used to observe phylogenetic proximities. Fish morphology is, therefore, a key factor in the ecological study of communities, especially in trophic ecology and habitat access. We recommend that this work can be expanded to other areas, because morphological comprehension is fundamental to understanding the ecosystem dynamics.

APPENDIX A

A1. GENERALIZED PROCRUSTES ANALYSIS

One way to get geometric information about objects is through landmarks. Landmarks are points with coordinates in two or three dimensions, which identify the same anatomical points in all sample individuals. Obtaining these points is usually done through digitized images or scans, and there are some criteria for selecting landmarks, such as: (i) homology (the same points should appear in all individuals in the same locations), (ii) coverage (the points should cover most of the shape of the individual), (iii) repeatability (the points should be found in all individuals with a high level of confidence), (iv) consistency in relative position (there should be the same points in the same position of the individuals in all the images analyzed), and, (v) coplanarity (the points should be in the same plane, considering that an image is all in one plane and the effect of depth is discarded) (Zelditch et al., 2004; Aguirre & Prado, 2018).

After obtaining the landmarks the mathematical and statistical procedure that is used was proposed by Gower (1975), called Generalized Procrustes Analysis (GPA). The GPA is a procedure that translates all individuals to the same origin using a unit centroid scale, through a least-squares criterion, making all the coordinates of the corresponding points align as closely as possible (Rohlf & Slice, 1990, Zelditch et al., 2004). The matrix of Procrustes shape variables resulting from this analysis, which represents the shape of each specimen, is invariant to size, position and rotation effects (Zelditch et al., 2004).

A1.1 GPA's mathematical procedures

Consider a random sample of available landmark configuration matrix $X_1,..., X_n$, and we want to estimate the mean shape of the sample. A practical approach is to use Generalized Procrustes Analysis for this purpose. The GPA method involves removing size, position and rotation effects from the relative configurations of the objects relative to each other in order to minimize a total sum of squares. The procedures below are described in Dryen & Mardia (2016), for more mathematical details see the previously cited reference:

Removing position effect: we center the landmarks settings to remove the position:

$$X_i^P = CX_i , i = 1, \dots , n$$

where X_i^P is the resulting matrix without position effect, and C is the centring matrix, defined as:

$$C = I_k - \frac{1}{k} 1_k 1_k^T$$

where k is number of landmarks, I_k is the $k \times k$ identity matrix (diagonal matrix with ones on the diagonal), and 1_k is the $k \times 1$ vector of ones.

Removing rotation effect: For the ith landmark configuration:

$$\bar{X}_{(i)} = \frac{1}{n-1} \sum_{j \neq i} X_j^P,$$

the new X_i^P is taken to be the ordinary Procrustes registration, involving only rotation, of the old X_i^P onto $\bar{X}_{(i)}$. The n landmarks configurations are rotate in turn. This process is repeated until the sum of Procrustes squares can no longer be reduced.

Removing size effect: Let ϕ be the n x n correlation matrix of the vec(X_i^P) with eigenvector $\phi = (\phi_1, ..., \phi_n)^T$ corresponding to the largest eingevalue. The scale parameter (β_i) is:

$$\beta_i = \left(\frac{\sum_{k=1}^{n} ||X_i^P||^2}{||X_i^P||^2} \right)^{1/2} \phi_i,$$

which is repeated for all landmarks configurations.

A2. ELLIPTICAL FOURIER ANALYSIS

Another method used to obtain geometric information about objects is through outline extraction. An outline can be a segment between two points, in which case it is an open outline, or a segment that returns to its point of origin, which is a closed outline. A closed outline generates a shape captured from the coordinates of a sequence of points along the analyzed structure (Rohlf, 1990). Among the outline methods used to analyzed closed countor, Elliptic Fourier Analysis (EFA) is one of the most used thechnique and has proven to be a powerful method for studying outline shape, mainly due to factors such as not requiring the same number of points on the outline for all samples (the GPA method), not needing a biologically or mathematically determined homologous point, and being able to be applied to very complex outlines (Lestrel, 2008).

A2.1 EFA's mathematical procedures

EFA represents a parametric function in the sense that the *x* and *y* directions are configured separately as cumulative functions of a third variable *t* along the outline. The Fourier descriptors resulting from these functions are invariant in size, rotation, and position (Kuhl & Giardina, 1982; Lestrel, 2008). The parametric functions proposed by Kuhl & Giardina (1982) are defined in $x(t)$ and $y(t)$, respectively as:

$$x(t) = A_0 + \sum_{n=1}^{N} a_n \cos nt + \sum_{n=1}^{N} b_n \sin nt$$

and

$$y(t) = C_0 + \sum_{n=1}^{N} c_n \cos nt + \sum_{n=1}^{N} d_n \sin nt$$

where a_n, b_n, c_n and d_n are the harmonic coefficients *n*, and *N* is the maximum number of harmonics. The Fourier coefficients for projection *x* are:

$$a_n = \frac{1}{n^2\pi} \sum_{p=1}^{q} \frac{\Delta x_p}{\Delta t_p} [\cos(nt_p) - \cos(nt_{p-1})]$$

and

$$b_n = \frac{1}{n^2\pi} \sum_{p=1}^{q} \frac{\Delta x_p}{\Delta t_p} [\sin(nt_p) - \sin(nt_{p-1})]$$

where *q* is the total of points along the polygon. Here t_p is the distance between point *p* and point $p + 1$ along the polygon, and x_p and y_p are the projections for the segments *p* to $p + 1$, respectively. The Fourier coefficients for projection *y* are:

$$c_n = \frac{1}{n^2\pi} \sum_{p=1}^{q} \frac{\Delta y_p}{\Delta t_p} [\cos(nt_p) - \cos(nt_{p-1})]$$

and

$$d_n = \frac{1}{n^2\pi} \sum_{p=1}^{q} \frac{\Delta y_p}{\Delta t_p} [\sin(nt_p) - \sin(nt_{p-1})]$$

For more details of the mathematical procedures of EFA, see Lestrel (2008). EFA has proven to be a powerful method to study shape, since it does not require the same number of points in the outline of all samples, nor a biologically or mathematically determined landmark, and can be applied to very complex outlines. The removals of size, rotation, and position effects were done through the normalization based on the first harmonic, as a result the first three coefficients of the first harmonic are transformed into a_1=1 and b_1=c_1=0 (Crampton, 1995). The generated Fourier coefficient matrix is used in the subsequent analyses.

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