Morphological diversity of tropical demersal fishes across different marine habitats

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Abstract

Fish morphology, a key aspect of phenotype, is influenced by a wide range of environmental interactions involving physical, chemical, and ecological factors. Here, we investigate the morphological pattern of a community of 120 demersal bony fish species in a tropical marine environment (Brazil between 4°-9°S) and examine the relationships between morphology and the different benthic habitat types present in this region. Using geometric morphometric techniques, we established shape groups and evaluated morphology across phylogenetic and taxonomic gradients. We also used the resulting morphospace to understand how morphology correlates with the habitats in which demersal fish species occur. We found 13 major shape groups, demonstrating the high morphological diversity. Body elongation was the main source of morphological variation, followed by caudal fin shape and dorsal fin shape. The morphological clustering showed low congruence with the phylogenetic tree, indicating that our morphological approach is not effective to observe phylogenetic proximities. The more complex benthic habitats, like sand with rocks, coralline formations, and sponges, showed the highest values of diversity and maximum morphological distance. In addition, the greater morphological similarity occurred in the sandy habitat, where we observed the highest abundance of species with elongated body patterns, well adapted to live in open habitats with higher water flow. We recommend that this work be extended to other areas, as morphological understanding is fundamental to gaining insights into ecosystem dynamics, especially in coral reefs.

Introduction

The phenotype of an organism is a complex interplay of genetic, ecological, and environmental factors (Hill and Mulder 2010). Fish morphology, a key aspect of phenotype, is influenced by a diverse array of environmental interactions, encompassing physical (Georgakopoulou et al. 2007), chemical (Crispo and Chapman 2010; Pauly and Cheung 2018), and ecological (Costa and Cataudella 2006; Burns et al. 2009; López-Fernández et al. 2012) factors. For instance, the morphological patterns of fish are intricately linked to the complexity of their environment and water flow (see Langerhans 2008; Yamada et al. 2009; Brandl and Bellwood 2014; Brandl et al. 2015; Bejarano et al. 2017), with body elongation being a prominent feature observed (Price et al. 2019). Additionally, the habitat in which fish species reside plays a crucial role in shaping their morphology (Yamada et al. 2009; Farré et al. 2016). The field of functional morphology investigates these phenotypic variations by studying the relationships between morphology (i.e., phenotypic expression) and external factors, whether environmental 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 yielded promising results, shedding light on significant ecological questions within ichthyology, especially those about trophic ecology and organism functionality.

Many studies have explored the relationships between fish shape and habitat. The majority have 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 are limited to specific families or a narrow collection of marine species (e.g., Antonucci et al. 2009; Price et al. 2011, 2013; Mohadasi et al. 2014; Ventura et al. 2017; Mihalitsis and Bellwood, 2019; Martinez et al. 2021; Corn et al. 2022). On the other hand, fewer studies have explored marine fish body shape in relation to habitat characteristics, encompassing a diverse array of species within communities (Farré et al. 2015, 2016; Larouche et al. 2020; Caillon et al. 2018; Claverie and Wainwright 2014), and none focused on the tropical southwestern Atlantic.

The tropical shelf of northeastern Brazil is highly diverse, including sandbanks, algae banks, seagrass, and mainly coral reefs (Leão et al. 2016; Eduardo et al. 2018; Fontes et al. 2020). Coral reefs, in particular, provide a complex habitat that shelters a rich diversity of species (Messmer et al. 2011), serving as a refuge or feeding grounds. In this area of high fish diversity, species richness and diversity are known to increase with habitat complexity (Eduardo et al. 2018). However, the morphological aspects, especially those linked to body shape at the community level, have not yet been evaluated along a habitat gradient, especially in the marine shelf of northeastern Brazil.

Geometric morphometrics, with its ability to capture geometric information without loss (Zelditch et al. 2004), plays a pivotal role in understanding the morphological patterns of the diverse array of species found in tropical marine waters. Here, we investigate the morphological pattern of a demersal fish community in a tropical marine environment (Brazil between 4°-9°S), examining relationships between morphology and the various bottom habitat types present in this region. We employed Elliptic Fourier Analysis (EFA) as an innovative approach to capture detailed information about the body outline of fishes. Unlike traditional methodologies based on fixed anatomical landmarks, EFA allows the entire body shape to be represented in continuous coordinates, ensuring the inclusion of fin details and overall body profile. Furthermore, the use of landmarks could reduce the analyses of some morphological traits due to the lack of homology between species. Therefore, this approach can be particularly useful for capturing the high morphological diversity found in tropical marine fish communities. We establish shape groups and evaluate morphology across phylogenetic and taxonomic gradients. Furthermore, using the morphospace obtained, we aim to comprehend how morphology correlates with the habitats in which demersal fish species are found.

Materials and Methods

Study area and fish sampling

The study area encompasses the continental shelf of northeastern Brazil, characterised by a narrow shelf (40 km in average) with a shelf break at ~ 80 m. The region primarily consists of sandy and siliciclastic in the inner part of the shelf and carbonate formations in the middle and outer part (Vital 2014). The area is encompassed in a western boundary current system associated with the North Brazil Undercurrent, defining it as a warm tropical zone with low primary productivity (Assunção et al., 2020; Dossa et al., 2021; Farias et al., 2022). Despite this, the northeastern Brazilian shelf boasts a high fish diversity (Eduardo et al. 2018), supporting various fisheries (Muller-Karger et al. 2017). Additionally, several species in this region face varying degrees of exploitation and sustainability threats (Eduardo et al. 2018; Passarone et al. 2019). The region offers diverse habitats and interconnected ecosystems, notably coral reefs (Castro and Pires 2001; Bittencourt et al. 2008).

Fish were collected during the two ABRACOS (Acoustics Along the Brazilian Coast) surveys in August-September 2015 and April-May 2017, aboard the French R/V ANTEA (Bertrand 2015, 2017). The sampling covered the continental shelf of Northeastern Brazil (4º–9ºS) (Fig. 1). Bottom trawls (body mesh: 40 mm, cod-end mesh: 25 mm, and horizontal x vertical mouth dimensions: 28 x 10 m) were used to capture individuals at each of the 37 sampling stations, between 10 to 60 m deep, for approximately 5 minutes of trawling. Fish were tagged and frozen for later analyses.

Videos footages obtained using an underwater camera (model GOPRO HERO 3) fitted on the top of the net mouth aided in classifying 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 detailed information on the sampling process and habitat classification methodology, see Eduardo et al. (2018).

Image acquisition and processing

In the laboratory, each fish was identified up to the species level and photographed separately using a digital camera (model: CANON SX520, 16 Megapixels). This study focused on bony fishes belonging to the Actinopterygii class. The methodology, synthesized in Fig. 2, involved photographing each specimen in lateral view, with the head positioned to the left and the dorsal region upwards (Step 1 in Fig. 2). The imaging process followed standardized orientations and configurations to ensure accurate morphometric analysis aligning with the methodology from Muir et al. (2012). For each species, a single image was selected based on specific criteria: adult individuals and fish positioned in lateral view with all fins open and visible (Fig. S1 shows an example of this standardisation). These images were supplemented by data obtained from FishBase (Froese and Pauly 2021), fish catalogues or articles (Rocha 2004; Williams et al. 2010; Deda and Barbosa 2016), and online image databases (Robertson and Tassel 2019) (Table S1 in Online Resource 1).

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 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.

Data analysis

All analyses were performed in R version 3.6.1 (R Development Core Team 2019). Elliptical Fourier Analysis (EFA) was utilized to extract shape information from the fish outline, obtained as binarized images using the *Momocs* package version 1.3.2 (Bonhomme et al. 2014) (Step 2 in Fig. 2).

EFA is a parametric function that represents the *x* and *y* directions 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). They describe variations in the outline that reflect biological traits such as body depth and fin shapes, which have implications for functional ecology, including swimming performance and habitat use.

The parametric functions proposed by Kuhl and Giardina (1982) are defined in *x(t)* and *y(t)*, respectively, (Equations (1) e (2)) as:

$$x\left(t\right)=A_0+\sum{}_{n=1}^{N}a_n\cos nt+\sum{}_{n=1}^{N}b_n\sin nt, \qquad (1)$$

and $y\left(t\right)=C_0+\sum{}_{n=1}^{N}c_n\cos nt+\sum{}_{n=1}^{N}d_n\sin nt, \qquad (2)$

where a_n, b_n, c_n, and d_n are the *n*th-harmonic coefficients, A_0 and C_0 are constants, and *N* is the maximum number of harmonics. Harmonics are the sine and cosine functions in the above equations, which, when combined, reconstruct the shape’s outline. The 1st harmonic captures the most basic shape, similar to an ellipse that roughly fits the fish’s body. As more harmonics are included, the shape representation becomes more accurate. However, the dimensionality of the data increases since each harmonic adds four coefficients. There is a point beyond which adding more harmonics no longer captures significant variations in the contour. In our case, using 12 harmonics allowed us to retain approximately 99% of the overall contour representation (Step 3 in Fig. 2). The removals of size, rotation, and position effects were done through the normalization process using the first three coefficients of the first harmonic ($a_1 = 1$ and $b_1 = c_1 = 0$) (Crampton 1995) (Steps 4 and 5 in Fig. 2). For more details of EFA's mathematical procedures, see Lestrel (2008).

One limitation of Fourier analyses is that they describe shape only at the frequency level, not at the spatial scale level, making it difficult to interpret local shape variations. Therefore, combining Principal Component Analysis (PCA) with EFA simplifies the interpretation of shape variation captured by the Fourier descriptors. It is through the interpretation of the principal components (PCs) that we understand the variation in shape across the set of contour species analysed. However, it is not necessary to retain all components, only those deemed significant. Thus, PCA was applied on the Fourier coefficients matrix to identify and characterize the main variations in fish shapes (Step 6 in Fig. 2). 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 (Step 6 in Fig. 2). 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 analysed fish species using the *fishtree_phylogeny* function of the package *fishtree* version 0.3.4 (Chang et al. 2019). 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 et al. 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. Therefore, this coefficient will be a proxy of the degree of similarity between morphological clustering and phylogenetic clustering.

The estimate 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 (Step 6 in Fig. 2). 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 range 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 analysed shape variables (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 maximum distance. 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. The maximum morphological distance is the greatest Euclidean distance between any two species within the morphospace. This value represents the highest level of body shape dissimilarity observed among the species analysed and allows us to identify the two most morphologically distinct species in the dataset. This metric complements the morphospace volume by emphasizing the range of morphological variation rather than overall diversity. For both metrics, 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 maximum distance was calculated by using the largest Euclidean distance between species in the morphospace. Fig. S2 (Online Resource 1) presents a didactic sketch showing an example of how morphospace was studied in the present work.

Volume and maximum distance 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 maximum distance) 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 above the first quartile (≥ 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 above the second quartile (≥ 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. The species abundance was obtained based on the entire ABRACOS project data set, and it was basically calculated as the number of individuals of the species in that habitat divided by the number of individuals of the species across all habitats.

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. A significant level of 5% was used in all analyses (Zar 2010).

Results

We analysed 120 species distributed in 16 orders and 45 families (Table S1 in Online Resource 1). The first three principal components were considered significant and retained for subsequent analysis, explaining approximately 74% of the fish shape variation (Fig. S3 in Online Resource 1). PC1 (53.2% of the total variance) was mainly related to body elongation (Fig. 3a). This correlation exhibited a linear relationship with the elongation aspect index (Fig. 3b), with fish with negative extreme values on this axis showing deep body shape, while species with elongated body pattern occupied positive extreme values. Additionally, the fin shapes of fish with deeper bodies are broader than those of elongated-bodied fish, which tend to have fins with narrower bases. PC2 (11.8%) was associated with caudal fin shape (Fig. 3a), as evidenced in the boxplot depicting the ‘caudal fin type’ (Fig. 3c). Species with rounded fins were at the negative extreme of this component, while fish with forked fins were at positive values of the PC2. Finally, PC3 (8.9%) explained, to a lesser extent, the shape and position of the dorsal fin, where individuals with more pointed dorsal fins positioned more posteriorly on the body were concentrated in negative PC3 values. On the other hand, individuals with pointed dorsal fins and positioned anteriorly on the body were 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).

Our results suggest that the morphological pattern of the demersal fish bodies analyzed could be divided into 13 main shape groups (Fig. 4a). These 13 morphological patterns were identified on a cutoff of approximately 10% of the Euclidean distance in the clustering dendogram. We have chosen a cutoff value that visually separated appropriate groups and ensured that the species in each group are morphologically very close, i.e. the similarity between species of the same group represents 10% of the greatest dissimilarity found among the analysed species. The grouped species showcased fish with more common body shapes (i.e., groups 9, 7, 12, and 10, with higher species numbers ranging from 12 to 23 species) and, on the opposite side, groups of rarer body shapes with lower species number (groups 1, 4, 5, and 13 with 2 to 5 species) (Fig. 4a). The comparison of the phylogenetic tree with the morphological clustering, involving 103 analysed species (Fig. 4b) revealed that phylogenetic proximity does not consistently correspond to morphological proximity (evidenced by low Baker's Gamma correlation = 0.20). This suggests that morphologically similar individuals (right dendrogram) may be phylogenetically distant species (e.g., first and last branch of the morphological clustering, and others). However, the greater the morphological distance, the higher the taxonomic level (Fig. 5).

Out of the 37 analysed sampling stations, 20 were classified as SWCR, four as Algae, 12 as Sand, and one station was unclassified (Fig. 6a, b). Morphospace volume ($\times 10^6$) values ranged from 2 to 28,668 and maximum morphological distance ($\times 10^2$) from 8 to 97. Both of these metrics, being shape space metrics, lack specific measurement units. Volume and maximum distance did not show a defined latitudinal spatial pattern in the study area (Figs. 6a, b). The relationships between morphospace volume vs. species number and maximum morphological distance 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 maximum distance) increase with the number of species present in the morphospace (Fig. 6c).

Morphospace volume and maximum distance 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. 6d and 7). In the SWCR habitat, the volume and maximum distance remained high regardless of the species abundance observed (Fig. 7a). However, in Algae and Sand, both metrics decreased as species total abundance (%) in that habitat type increased (Figs. 7b, c).

The morphological pattern found in the habitat types changed according to the species total abundance (Fig. 8). Initially, 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 Table 1). However, when considering the habitat morphospaces formed only by species with total abundance ≥ 25%, the MANOVA (Wilks' Lambda = 0.899, $p < 0.01$) revealed a 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 Table 1). 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 Table 1). Conversely, variables PC2 and PC3 did not exhibit differences between bottom types and species abundance in the habitats (Table 1). 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.

Table 1

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

All species present in habitat			
Shape variable	**Comparison**	**Test statistic (z-value)**	**p-value**
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

Discussion

In this study, we assessed the morphological patterns of a diverse community of 120 marine tropical bony fish species. Few studies have delved into morphological diversity at the fish community level using geometric morphometric methods, placing our results within a small yet significant set of investigations that have explored fish community morphology across various marine habitats (e.g., Farré et al. 2015, 2016; Aguilar-Medrano and Calderon-Aguilera 2016; Aguilar-Medrano and Arias-González 2018). Our classification of the 120 species into 13 distinct body morphotypes underscores the high shape diversity observed in the tropical southeastern Atlantic, aligning with similar studies in Mexico (Aguilar-Medrano and Calderon-Aguilera 2016; Aguilar-Medrano and Arias-González 2018), the tropical Indo-Pacific (Claverie and Wainwright 2014), and the Mediterranean Sea (Farré et al. 2015, 2016).

The presence of specific body shapes across a wide array of species from distinct phylogenetic lineages suggests the occurrence of that morphological convergence. The low correlation between the morphological and phylogenetic clustering (Baker's Gamma = 0.20) suggests that morphologically similar body shapes are shared among phylogenetically distant species. While this pattern is consistent with possible morphological convergence, we recognise that this analysis does not formally test for convergence. Future studies using comparative phylogenetic methods will be necessary to explore this hypothesis in more detail.

Although geometric morphometric analyses do not directly measure function, certain shape traits, such as body elongation and caudal fin morphology, have been consistently linked to swimming performance, manoeuvrability, and habitat use. This can be interpreted as an evolutionary functional adaptation granting these species to access different ecological niches (morphologically generalist species). These adaptations may be linked to different habitats, trophic ecology, or behavioural origin (Webb 1984). Conversely, certain morphotypes were shared by a limited number of species, indicating specialization and potentially reflecting niche specialization (e.g., Collar et al. 2009; López-Fernández et al. 2012). Three of the analysed groups can exemplify this. First, the flat-fish group (five species of Pleuronectiformes, G4 in Fig. 4a). This group is represented by fishes with specific swimming patterns in contact with the bottom, where compression and body morphology are directly linked to this behaviour (Fox et al. 2018). Second, the trumpet-fish group (with four species of Syngnathiformes, G13 in Fig. 4a). It has a very elongated body shape, which may be intrinsically related to feeding and hunting tactics, such as the camouflage behaviour in the vertical position during prey searching (Auster 2008), in addition to the elongated head and jaw morphology (Tegge et al. 2020). Third, the butterfly-fish group (with two species of Chaetodontidae, G5 in Fig. 4a) is characterized by deep body, where the head and jaw morphology (Ferry-Graham et al. 2001) are very much associated with searching for sessile prey (Brandl and Bellwood, 2013, 2014), favouring a reduction of vertical rotation around its own body, providing more precise manoeuvres (Webb 1984).

The use of morphological data for phylogenetic mapping is generally discouraged (Wiens 2004). 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 is evident when observing groups that are morphologically similar but phylogenetically distant: (i) elongated 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).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 emerged as a predominant trait, explaining more than half of the morphological variation in the 120 species we analysed. This trait is a central focus in many morphological studies of fish communities (e.g., Claverie and Wainwright 2014; Caillon et al. 2018; Price et al. 2019). Swimming performance is one of the most discussed functional traits associated with body elongation rate. Fish with elongated body shape are believed to exhibit greater acceleration during swimming and/or cruising-type swimming (e.g., tunas) (Webb 1984). Conversely, fish with deeper bodies are more specialized in manoeuvring (e.g., butterfly-fish) (Webb 1984). Also, the PC1 interpretation considers that the positioning and shape of the fins can influence the overall perception of body shape. 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). Therefore, the complexity of fin shapes (caudal fin and other fin types) acts 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).

The use of the morphospaces calculated from the three main Principal Components allowed us to relate the fish morphological pattern to different habitat types. The most complex habitat (SWCR) encompassed the highest diversity and morphological distance. Coral reef environments are widely recognized for their high fish diversity, and the complexity of these habitats supports a diverse array of ecological niches (e.g., Harmelin-Vivien 2002; Aguilar-Perera and Appeldoorn 2008; Messmer et al. 2011; Eduardo et al. 2018). Complex habitats favour high morphological diversity 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 favour a set of conditions providing high diversity of ecological niches including refuge (Johansen et al. 2008), social interactions (Gil and Hein 2017) or reproduction (Claydon 2004). Coral reef complexity 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 maximum distance 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 maximum morphological distance. Fish morphology is thus more specialized in this environment when compared to more complex ones. Open environments, such as sandbanks, have 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, and one of the most important morphological adaptations is body elongation (e.g., Langerhans 2008; Foster et al. 2015; Bejarano et al. 2017). In turbulent marine environments, which have a higher wave exposure, a morphological filter acts on the fish body shape, favouring 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 draw two important conclusions: (i)we identified high morphological connectivity among the three habitats, observing the same diversity and morphological distance for all species present in each habitat (see All species in Fig. 7), making it clear that these habitats are highly connected; (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 maximum morphological distance, besides the body pattern becoming more elongated (see Fig. 8), reinforcing that an exposed habitat favours 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.

In conclusion, this study presents the first comprehensive morphological characterization of the demersal fish community from the northeast Brazilian shelf. Utilizing Ellipitic Fourier functions to analyse fish shape, we uncovered a high morphological diversity among demersal fish. Our findings indicate that complex habitats likely have the highest functionality, boasting the highest morphological diversity and dispersion. Conversely, Sand habitats showcase a more specialized general morphology, with lower volume and maximum morphological distance, and a tendency towards an elongated body shape. This reinforces the notion that exposed habitats favour species with morphological designs adapted to those conditions. Future studies should expand on these findings, especially within coral reef habitats, which are highly impacted by anthropic pressures.

Declarations

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

All authors contributed critically to the drafts and gave final approval for publication. Reis-Junior, Bertrand and Duarte-Neto conceptualized the idea. Reis-Junior obtained the photos, proceeded with the formal analysis and wrote the original draft under the supervision of Duarte-Neto. Vasconcelos-Filho contributed to the shape analysis and participated in the result discussion. All authors have revised and contributed to the final version.

Data availability

The data underlying this paper will be shared on reasonable request to the corresponding author.

References

1. Aguilar-Medrano R, Arias-González JE (2018) Functional reef fish groups of the Mexican Caribbean: implications of habitat complexity. Revista Mexicana de Biodiversidad 89:1138-1153.

https://doi.org/10.22201/ib.20078706e.2018.4.2398

2. Aguilar-Medrano R, Calderon-Aguilera LE (2016) Redundancy and diversity of functional reef fish groups of the Mexican Eastern Pacific. Marine Ecology 37:119-133. https://doi.org/10.1111/maec.12253
3. Aguilar-Perera A, Appeldoorn RS (2008) Spatial distribution of marine fishes along a cross-shelf gradient containing a continuum of mangrove-seagrass-coral reefs off southwestern Puerto Rico. Estuarine, Coastal and Shelf Science 76:378-394. https://doi.org/10.1016/j.ecss.2007.07.016
4. Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106:275-284. https://doi.org/10.1111/j.0030-1299.2004.13193.x
5. Antonucci F, Costa C, Aguzzi J, Cataudella S. (2009) Ecomorphology of morpho-functional relationships in the family of sparidae: A quantitative statistic approach. Journal of Morphology 270:843–855. https://doi.org/10.1002/jmor.10725
6. Assunção RV, Silva AC, Roy A, Bourlès B, Silva CHS, Ternon JF, Araujo M, Bertrand A. (2020) 3D characterisation of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles. Progress in Oceanography 187: 102399. https://doi.org/10.1016/j.pocean.2020.102399
7. Auster PJ (2008) Predation tactics of trumpetfish in midwater. Neotropical Ichthyology 6:289-292. http://dx.doi.org/10.1590/S1679-62252008000200018
8. Baker FB (1974) Stability of two hierarchical grouping techniques case 1: sensitivity to data errors. Journal of the American Statistical Association 69:440-445.
9. Bejarano S, Jouffray JB, Chollett I, Allen R, Roff G, Marshell A, Steneck R, Ferse SCA, Mumby PJ (2017) The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. Functional Ecology 31:1312–1324. https://doi.org/10.1111/1365-2435.12828
10. Bertrand A (2015) ABRACOS cruise, RV Antea. https://doi.org/10.17600/15005600
11. Bertrand A (2017) ABRACOS 2 cruise, RV Antea. https://doi.org/10.17600/17004100
12. Bittencourt ACSP, Leão ZMAN, Kikuchi RKP, Dominguez JML (2008) Deficit of sand in a sediment transport model favors coral reef development in Brazil. Anais da Academia Brasileira de Ciências 80:205-214. https://doi.org/10.1590/S0001-37652008000100015
13. Blake RW (2004) Fish functional design and swimming performance. Journal of Fish Biology 65:1193-1222. https://doi.org/10.1111/j.0022-1112.2004.00568.x
14. Bonhomme V, Sandrine P, Gaucherel C, Claude J (2014) Momocs: outline analysis using R. Journal of Statistical Software 56. https://doi.org/10.18637/jss.v056.i13
15. Brandl SJ, Bellwood DR (2013) Morphology, sociality, and ecology: Can morphology predict pairing behaviour in coral reef fishes? Coral Reefs 32:835-846. https://doi.org/10.1007/s00338-013-1042-0
16. Brandl SJ, Bellwood DR (2014) Individual-based analyses reveal limited functional overlap in a coral reef fish community. Journal of Animal Ecology 83:661-670. https://doi.org/10.1111/1365-2656.12171

17. Brandl SJ, Robbins WD, Bellwood DR(2015) Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. Proceedings of the Royal Society B 282:20151147. http://dx.doi.org/10.1098/rspb.2015.1147
18. Burns JG, Di Nardo P, Rodd FH (2009) The role of predation in variation in body shape in guppies *Poecilia reticulata*: a comparison of field and common garden phenotypes. Journal of Fish Biology 75:1144–1157. https://doi.org/10.1111/j.1095-8649.2009.02314.x
19. Caillon F, Bonhomme V, Mõllmann C, Frelat R (2018) A morphometric drive into fish diversity. Ecosphere 9:e02220. https://doi.org/10.1002/ecs2.2220
20. Castro CB, Pires DO (2001) Brazilian Coral Reefs: what we already know and what is still missing. Bulletin of Marine Science 69:357–371.
21. Chang J, Rabosky DL, Smith SA, Alfaro ME (2019) An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. Methods in Ecology and Evolution 10:1118-1124. https://doi.org/10.1111/2041-210X.13182
22. Claverie T, Wainwright PC (2014) A morphospace for reef fishes: Elongation is the dominant axis of body shape evolution. Plos One 9:e112732. https://doi.org/10.1371/journal.pone.0112732
23. Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. In: RN Gibson, RJA Atkinson, JDM Gordon (eds) Oceanography and Marine Biology: An Annual Review vol 42, 1st edn. CRC Press, pp 265-302 https://doi.org/10.1201/9780203507810
24. Collar DC, O'Meara BC, Wainwright PC, Near TJ (2009) Piscivory limits diversification of feeding morphology in centrarchid fishes. Evolution 63:1557-1573. https://doi.org/10.1111/j.1558-5646.2009.00626.x
25. Corn, K.A., Friedman, S.T., Burress, E.D., Martinez, C.M., Larouche, O., Price, S.A. Wainwright, P.C. (2022) The rise of biting during the Cenozoic fueled reef fish body shape diversification. Proceedings of the National Academy of Sciences, 119, e2119828119. https://doi.org/10.1073/pnas.2119828119
26. Costa C, Cataudella S (2007) Relationship between shape and trophic ecology of selected species of sparids of the Caprolace coastal lagoon (Central Tyrrhenian sea). Environmental Biology of Fishes 78:165–175. https://doi.org/10.1007/s10641-006-9081-9
27. Crampton JS (1995) Elliptic fourier shape analysis of fossil bivalves: some practical considerations. Lethaia 28:179-186.
28. Crispo E, Chapman LJ (2010) Geographic variation in phenotypic plasticity in response to dissolved oxygen in an African cichlid fish. Journal of Evolutionary Biology 23:2091-2103. https://doi.org/10.1111/j.1420-9101.2010.02069.x
29. Deda MS, Barbosa JM (2016) Catálogo de pescados de Sergipe e norte da Bahia. Sergipe, Universidade Federal de Sergipe (Projeto de Monitoramento Participativo do Desembarque Pesqueiro).

30. Dossa AN, Silva AC, Chaigneau A, Eldin G, Araujo M, Bertrand A (2021) Near-surface western boundary circulation off Northeast Brazil. Progress in Oceanography 190: 102475. https://doi.org/10.1016/j.pocean.2020.102475.
31. Dunn OJ (1964) Multiple comparisons using rank sums. Technometrics 6:241-252. http://dx.doi.org/10.1080/00401706.1964.10490181
32. Eduardo LN, Frédou T, Lira AS, Ferreira BP, Bertrand A, Ménard F, Frédou FL(2018) Identifying key habitat and spatial patterns of fish biodiversity in the tropical Brazilian continental shelf. Continental Shelf Research 166:108–118. https://doi.org/10.1016/j.csr.2018.07.002
33. Farias GB, Molinero JC, Carré C, Bertrand A, Bec B, Melo PAMC (2022) Uncoupled changes in phytoplankton biomass and size structure in the western tropical Atlantic. Journal of Marine Systems 227:103696. https://doi.org/10.1016/j.jmarsys.2021.103696
34. Farré M, Lombarte A, Recasens L, Maynou F, Tuset VM (2015) Habitat influence in the morphological diversity of coastal fish assemblages. Journal of Sea Research 99:107–117. http://dx.doi.org/10.1016/j.seares.2015.03.002
35. Farré M, Tuset VM, Cartes JE, Massutí E, Lombarte A (2016) Depth-related trends in morphological and functional diversity of demersal fish assemblages in the western Mediterranean Sea. Progress in Oceanography 147:22–37. https://doi.org/10.1016/j.pocean.2016.07.006
36. Ferry-Graham LA, Wainwright PC, Hulsey D, Bellwood DR (2001) Evolution and mechanics of long jaws in butterflyfishes (family Chaetodontidae). Journal of Morphology 248:120-143. https://doi.org/10.1002/jmor.1024
37. Fontes VC, Gomes MP, Vital H, Ferreira BP, Maida M (2020) Reefs distribution and inter reef sedimentation on Tamandaré continental shelf, Northeast Brazil. In: PT Harris and E Baker (eds) Seafloor geomorphology as benthic habitat. Elsevier, pp 561-569. https://doi.org/10.1016/B978-0-12-814960-7.00033-6
38. Foster K, Bower L, Piller K (2015) Getting in shape: habitat-based morphological divergence for two sympatric fishes. Biological Journal of the Linnean Society 114:152–162. https://doi.org/10.1111/bij.12413
39. Fox CH, Gibb AC, Summers AP, Bemis WE (2018) Benthic walking, bounding, and maneuvering in flatfishes (Pleuronectiformes: Pleuronectidae): new vertebrate gaits. Zoology 130:19-29. https://doi.org/10.1016/j.zool.2018.07.002
40. Franssen NR (2011) Anthropogenic habitat alteration induces rapid morphological divergence in a native stream fish. Evolutionary Applications 4:791-804. https://doi.org/10.1111/j.1752-4571.2011.00200.x
41. Froese R, Pauly D (2021) FishBase, version (08/2021). Retrieved from: www.fishbase.org
42. Galili T (2015) dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering. Bioinformatics 31:3718-3720. https://doi.org/10.1093/bioinformatics/btv428

43. Georgakopoulou E, Sfakianakis DG, Kouttouki S, Divanach P, Kentouri M, Koumoundouros G (2007) The influence of temperature during early life on phenotypic expression at later ontogenetic stages in sea bass. Journal of Fish Biology 70:278-291. https://doi.org/10.1111/j.1095-8649.2007.01305.x
44. Gil MA, Hein AM (2017) Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. Proceedings of the National Academy of Sciences 114:4703-4708. https://doi.org/10.1073/pnas.1615652114
45. Habel K, Grasman R, Gramacy RB, Mozharovskyi P, Sterratt DS (2019) geometry: mesh generation and surface tessellation. R package version 0.4.5. https://CRAN.R-project.org/package=geometry
46. Halpern BS, Floeter SR (2008) Functional diversity responses to changing species richness in reef fish communities. Marine Ecology Progress Series 364:147-156. https://doi.org/10.3354/meps07553
47. Harmelin-Vivien ML (2002) Energetic and fish diversity on coral reefs. In: Peter FS (ed) Coral reef fishes: dynamics and diversity on a complex ecosystem, 2nd edn. Academic Pres, San Diego, pp 265-274.
48. Hill W, Mulder HA (2010) Genetic analysis of environmental variation. Genetics Research 92:381-395. https://doi.org/10.1017/S0016672310000546
49. Hugueny B (1990) Richesse des peuplements de poissons dans le Niandan (haut Niger, Afrique) en fonction de la taille de la riviere et de la diversite´ de milieu. Revue d'Hydrobiologie Tropicale 23:351–364
50. Imre I, McLaughlin RL, Noakes DLG (2002) Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. Journal of Fish Biology 61:1171-1181. https://doi.org/10.1111/j.1095-8649.2002.tb02463.x
51. Johansen JL (2014) Quantifying water flow within aquatic ecosystems using load cell sensors: A profile of currents experienced by coral reef organisms around Lizard Island, Great Barrier Reef, Australia. Plos One 9:e83240. https://doi.org/10.1371/journal.pone.0083240
52. Johansen JL, Bellwood DR, Fulton CJ (2008) Coral reef fishes exploit flow refuges in high-flow habitats. Marine Ecology Progress Series 360:219-226. https://doi.org/10.3354/meps07482
53. Johnson RA, Wichern DW (2014) Applied multivariate statistical analysis, 6th edn. Pearson, USA.
54. Kirchheim PD, Goulart E (2010) Ecomorfologia de predação e antipredação em Siluriformes (Osteichthyes). Oecologia Australis 14:550-568.
55. Koop D, Bouchon-Navaro YB, Cordonnier S, Haouisée A, Louis M, Bouchon C (2010) Evaluation of algal regulation by herbivorous fishes on Caribbean coral reefs. Helgoland Marine Research 64:181-190. https://doi.org/10.1007/s10152-009-0177-4
56. Kuhl F, Giardina CR (1982) Elliptic fourier features of a closed contour. Computer Graphics and Image Processing 18:236-258.
57. Langerhans RB (2008) Predictability of phenotypic differentiation across flow regimes in fishes. Integrative and Comparative Biology 48:750-768. https://doi.org/10.1093/icb/icn092

58. Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ (2003) Habitat-associated morphological divergence in two Neotropical fish species. Biological Journal of the Linnean Society 80:689-698.
59. Larouche O, Benton B, Corn KA, Friedman ST, Gross D, Iwan M, Kessler B, et al. (2020) Reef-associated fishes have more maneuverable body shapes at a macroevolutionary scale. Coral Reefs 39:1427–1439. https://doi.org/10.1007/s00338-020-01976-w
60. Lauder GV, Drucker E (2004) Morphology and experimental hydrodynamics of fish fin control surfaces. IEEE Journal of Oceanic Engineering 29:556-571.
61. Leão ZMAN, Kikuchi RKP, Ferreira BF, Neves EG, Sovierzoski HH, Oliveira MDM et al. (2016) Brazilian coral reefs in a period of global change: a synthesis. Brazilian Journal of Oceanography 64:97-116. http://dx.doi.org/10.1590/S1679-875920160916064sp2
62. Lestrel PE (2008) Fourier descriptors and their applications in biology. Cambridge University Press, Cambridge (UK).
63. López-Fernández H, Winemiller KO, Montaña C, Honeycutt RL (2012) Diet-morphology correlations in the radiation of South American Geophagine Cichlids (Perciformes: Cichlidae: Cichlinae). Plos One 7:e33997. https://doi.org/10.1371/journal.pone.0033997
64. Martinez, C.M., Friedman, S.T., Corn, K.A., Larouche, O., Price, S.A. Wainwright, P.C. (2021) The deep sea is a hot spot of fish body shape evolution. Ecology Letters, 24, 1788-1799. https://doi.org/10.1111/ele.13785
65. Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. Ecology 92:2285-2298. https://doi.org/10.1890/11-0037.1
66. Mihalitsis, M. & Bellwood, D.R. (2019) Morphological and functional diversity of piscivorous fishes on coral reefs. Coral Reefs, 38, 945-954. https://doi.org/10.1007/s00338-019-01820-w
67. Mitteroecker P, Gunz P (2009) Advances in geometric morphometrics. Evolutionary Biology 36:235–247. https://doi.org/10.1007/s11692-009-9055-x
68. Mohadasi M, Eagderi S, Shabanipour N, Hosseinzadeh MS, AnvariFar H, Khaefi R (2014) Allometric body shape changes and morphological differentiation of shemaya, *Alburnus chalcoides* (Guldenstadf, 1772), populations in the southern part of Caspian Sea using elliptic fourier analysis. International Journal of Aquatic Biology 2:164-171. https://doi.org/10.22034/ijab.v2i3.80
69. Motta JP, Norton SF, Luczkovich JJ (1995) Perspectives on the ecomorphology of bony fishes. Environmental Biology of Fishes 44:11-20.
70. Muggeo VMR (2008) segmented: an R Package to Fit Regression Models with Broken-Line Relationships. R News 8:20–25.
71. Muir AM, Vecsei P, Krueger CC (2012) A perspective on perspectives: Methods to reduce variation in shape analysis of digital images. Transactions of the American Fisheries Society 141:1161–1170. https://doi.org/10.1080/00028487.2012.685823
72. Muller-Karger FE, Rueda-Roa D, Chavez FP, Kavanaugh MT, Roffer MA(2017) Megaregions among the large marine ecosystems of the Americas. Environmental Development 22:52–62.

https://doi.org/10.1016/j.envdev.2017.01.005

73. Passarone R, Aparecido KC, Eduardo LN, Lira AS, Silva LVS, Justino AKS, Craveiro C, Silva EF, Lucena-Frédou F (2019) Ecological and conservation aspects of bycatch fishes: An evaluation of shrimp fisheries impacts in Northeastern Brazil. Brazilian Journal of Oceanography 67:e19291. http://dx.doi.org/10.1590/S1679-87592019029106713
74. Pauly D, Cheung WWL (2018) Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Global Change Biology 24:e15-e26. https://doi.org/10.1111/gcb.13831
75. Price SA, Friedman ST, Corn KA, Martinez CM, Larouche O, Wainwright PC (2019) Building a body shape morphospace of teleostean fishes. Integrative and Comparative Biology 59:716–730. https://doi.org/10.1093/icb/icz115
76. Price SA, Friedman ST, Wainwright PC (2015) How predation shaped fish: The impact of fin spines on body form evolution across teleosts. Proceedings of the Royal Society B 282:20151428. https://doi.org/10.1098/rspb.2015.1428
77. Price SA, Holzman R, Near TJ, Wainwright PC (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. Ecology Letters 14:462–469. http://dx.doi.org/10.1111/j.1461-0248.2011.01607.x
78. Price SA, Tavera JJ, Near TJ, Wainwright PC (2013) Elevated rates of morphological and functional diversification in reef-dwelling haemulid fishes. Evolution 67:417–428. http://dx.doi.org/10.1111/j.1558-5646.2012.01773.x
79. R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from: http://www.Rproject.org/
80. Robertson DR, Tassell JV (2019) Shorefishes of the Greater Caribbean: online information system (version 2.0). Smithsonian Tropical Research Institute, Balboa, Panamá. Retrieved from: https://biogeodb.stri.si.edu/caribbean/en/pages
81. Rocha LA (2004) Mitochondrial DNA and color pattern variation in three Western Atlantic *Halichoeres* (Labridae), with the revalidation of two species. Copeia 4:770-782. https://doi.org/10.1643/CG-04-106
82. Roisin PL (2005) Computing global shape measures. In CH Chen and PSP Wang (eds), Handbook of pattern recognition and computer vision, 3rd edn. World Scientific, pp 177-196. https://doi.org/10.1142/9789812775320_0010
83. Russo T, Costa C, Cataudella S (2007) Correspondence between shape and feeding habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758. Journal of Fish Biology 71:629-656. https://doi.org/10.1111/j.1095-8649.2007.01528.x
84. Senay C, Boisclair D, Peres-Neto PR (2015) Habitat-based polumorphism is common in stream fishes. Journal of Animal Ecology 84:219-227. https://doi.org/10.1111/1365-2656.12269
85. Shuai F, Yu S, Lek S, Li X (2018) Habitat effects on intra-species variation in functional morphology: evidence from freshwater fish. Ecology and Evolution 8:10902-10913.

https://doi.org/10.1002/ece3.4555

86. Silva MA, Perazzo GX, Kavalco KF, Pasa R (2021) Shape diversity of the fish genus *Astyanax* Baird & Girard, 1854 (Teleostei, Characidae) in adjacent basins. Biologia 76:213–221. https://doi.org/10.2478/s11756-020-00544-5
87. Silva-Júnior CAB, Mérigot B, Lucena-Frédou F, Ferreira BP, Coxey MS, Rezende SM, Frédou T (2017) Functional diversity of fish in tropical estuaries: a traits-based approach of communities in Pernambuco, Brazil. Estuarine, Coastal and Shelf Science 198:413-420. https://doi.org/10.1016/j.ecss.2016.08.030
88. Svanback R, Eklov P (2002) Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131:61–70. https://doi.org/10.1007/s00442-001-0861-9
89. Tegge S, Hall J, Huskey S (2020) Spatial and temporal changes in buccal pressure during prey-capture in the trumpetfish (*Aulostomus maculatus*). Zoomorphology 139:85-95. https://doi.org/10.1007/s00435-019-00470-4
90. Ventura D, Bonhomme V, Colangelo P, Bonifazi A, Lasinio GJ, Ardizzone G (2017) Does morphology predict trophic niche differentiation? Relationship between feeding habits and body shape in four co-occurring juvenile species (Pisces: Perciformes, Sparidae). Estuarine, Coastal and Shelf Science 191:84–95. http://dx.doi.org/10.1016/j.ecss.2017.04.014
91. Vital H(2014) The north and northeast Brazilian tropical shelves. Geological Society London Memoirs 41:35–46. https://doi.org/10.1144/M41.4
92. Webb PW (1984) Form and function in fish swimming. Scientific American 251:72-83.
93. Wiens JJ (2004) The role of morphological data in phylogeny reconstruction. Systematic Biology 53:653-661. https://doi.org/10.1080/10635150490472959
94. Wiley EO, Lieberman BS (2011) Phylogenetics: Theory and practice of phylogenetic systematics, 2nd edn. Wiley-Blackwell, New Jersey.
95. Wilkinson SP, Davy SK (2018) phylogram: an R package for phylogenetic analysis with nested lists. Journal of Open Source Software, 3:790. https://doi.org/10.21105/joss.00790
96. Williams JT, Carpenter KE, Tassel JLV, Hoetjes P, Toller W, Etnoyer P, Smith M (2010) Biodiversity assessment of the fishes of Saba Bank Atoll, Netherlands Antilles. Plos One 5:e10676. http://dx.doi.org/10.1371/journal.pone.0010676
97. Willis SC, Winemiller KO, Lopez-Fernandez H (2005) Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142:284–295. http://dx.doi.org/10.1007/s00442-004-1723-z
98. Yamada T, Sugiyama T, Tamaki N, Kawakita A, Kato M (2009) Adaptive radiation of gobies in the interstitial habitats of gravel beaches accompanied by body elongation and excessive vertebral segmentation. BMC Evolutionary Biology 9:1–14. https://doi.org/10.1186/1471-2148-9-145
99. Zar J H (2010). *Biostatistical analysis*, 5th edn. Pearson Prentice Hall, New Jersey.

100. Zelditch ML, Swiderski DL, Sheets HD, Fink WL (2004) Geometric Morphometrics for Biologists: A Primer, 1st edn. Elsevier Academic Press, USA.

Figures

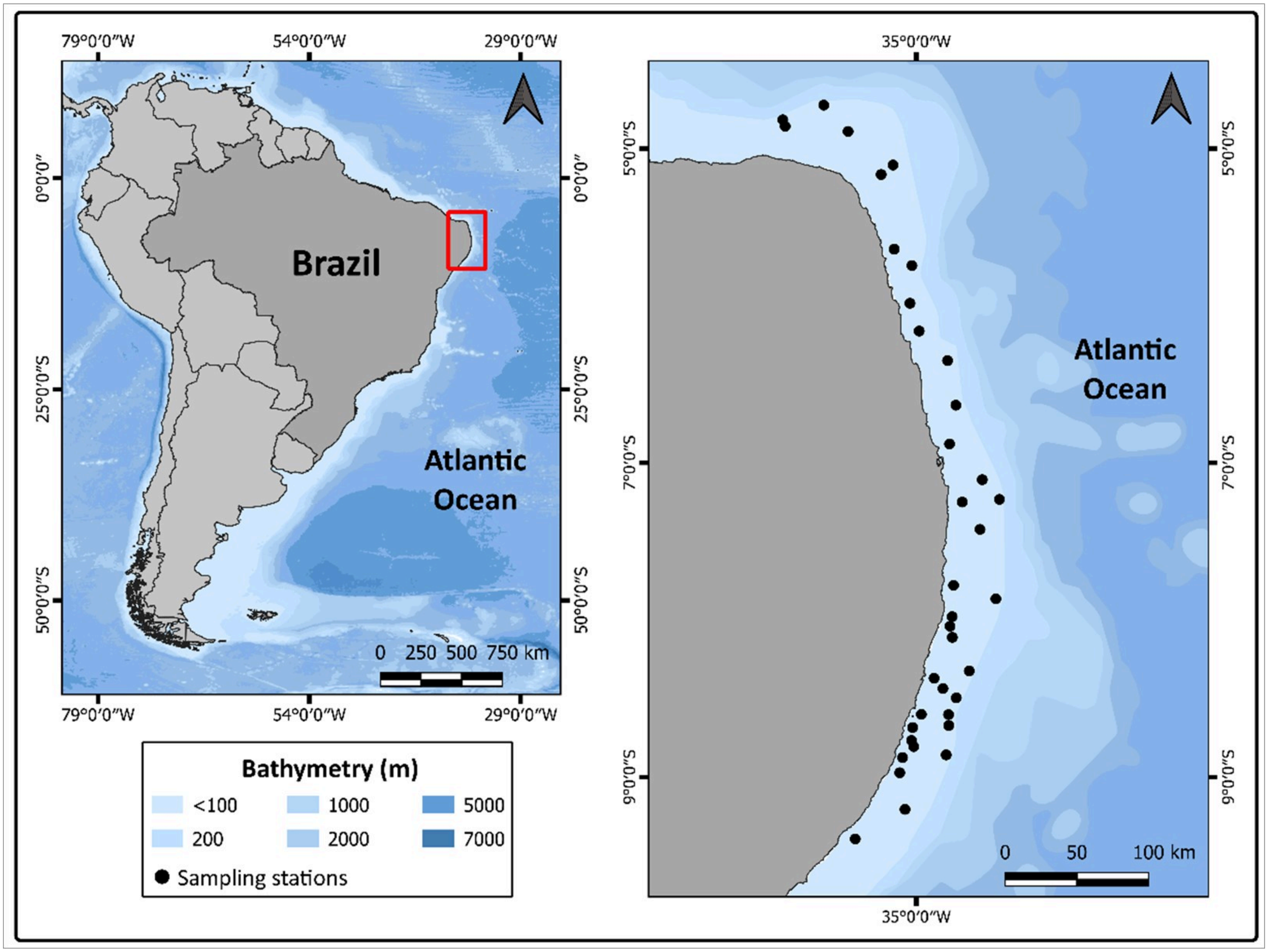

Figure 1

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

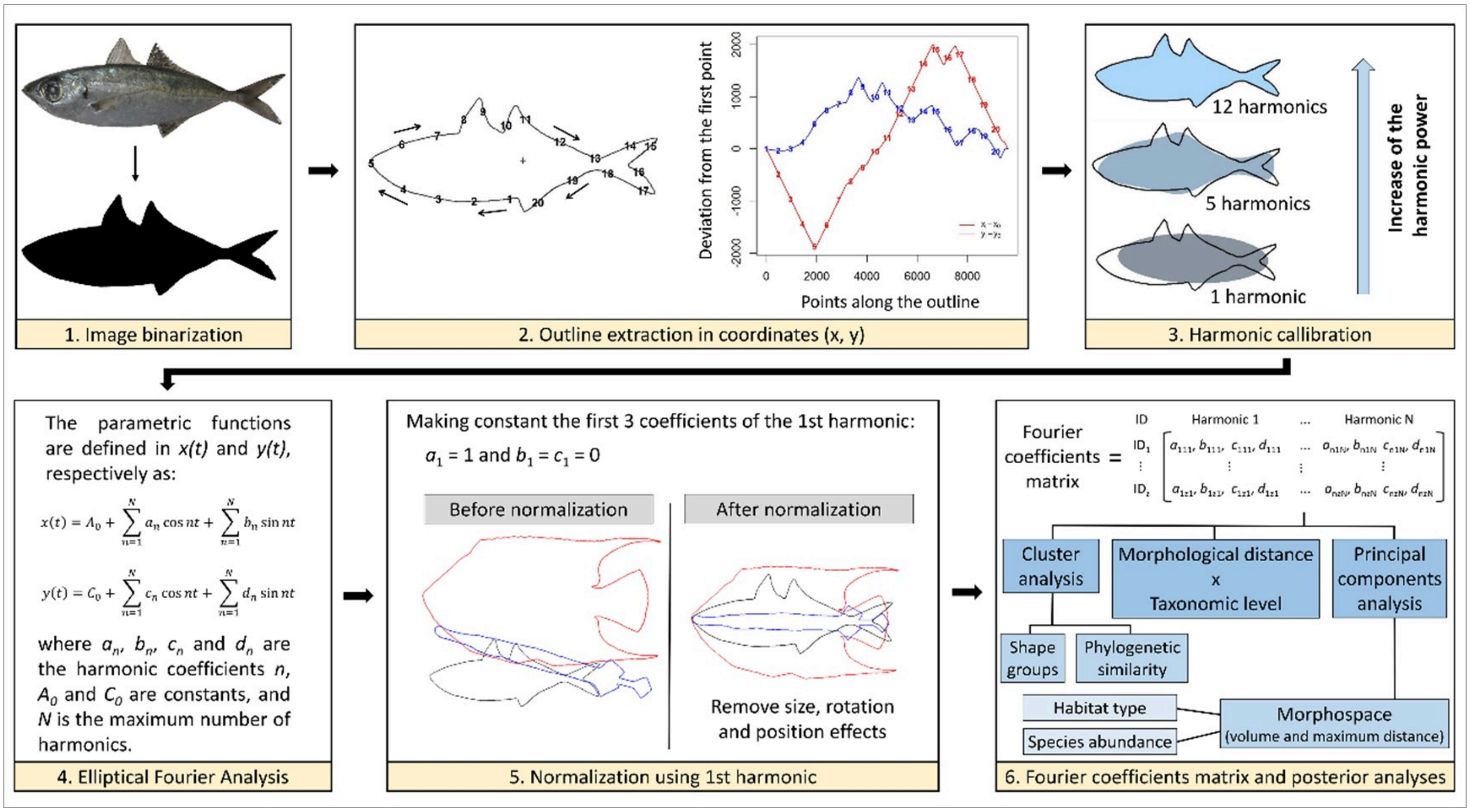

Figure 2

Flowchart of the data analysis process used in this work.

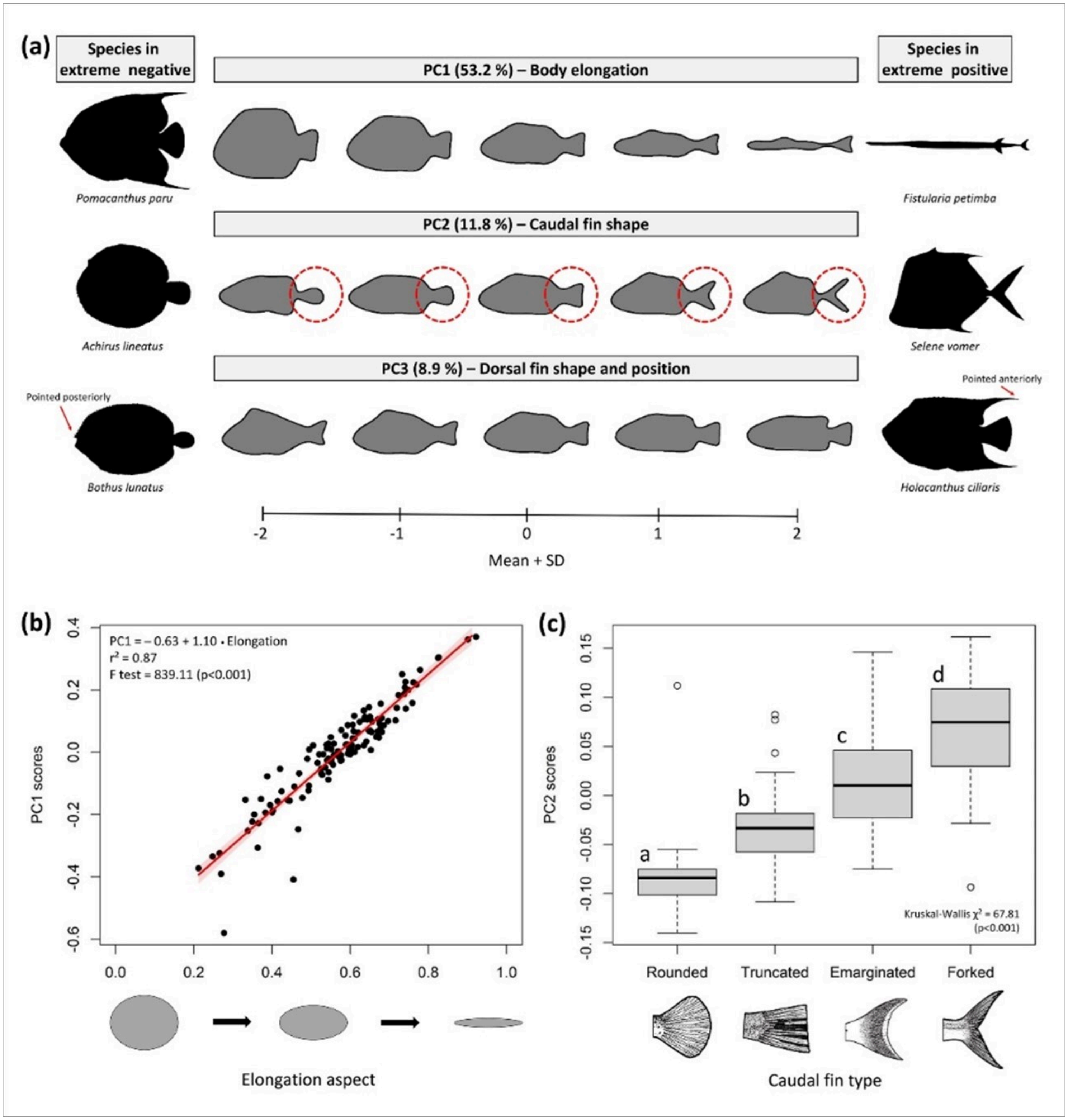

Figure 3

Variation of fish body shape in the 3 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 differences (Dunn test, p<0.01) (c).

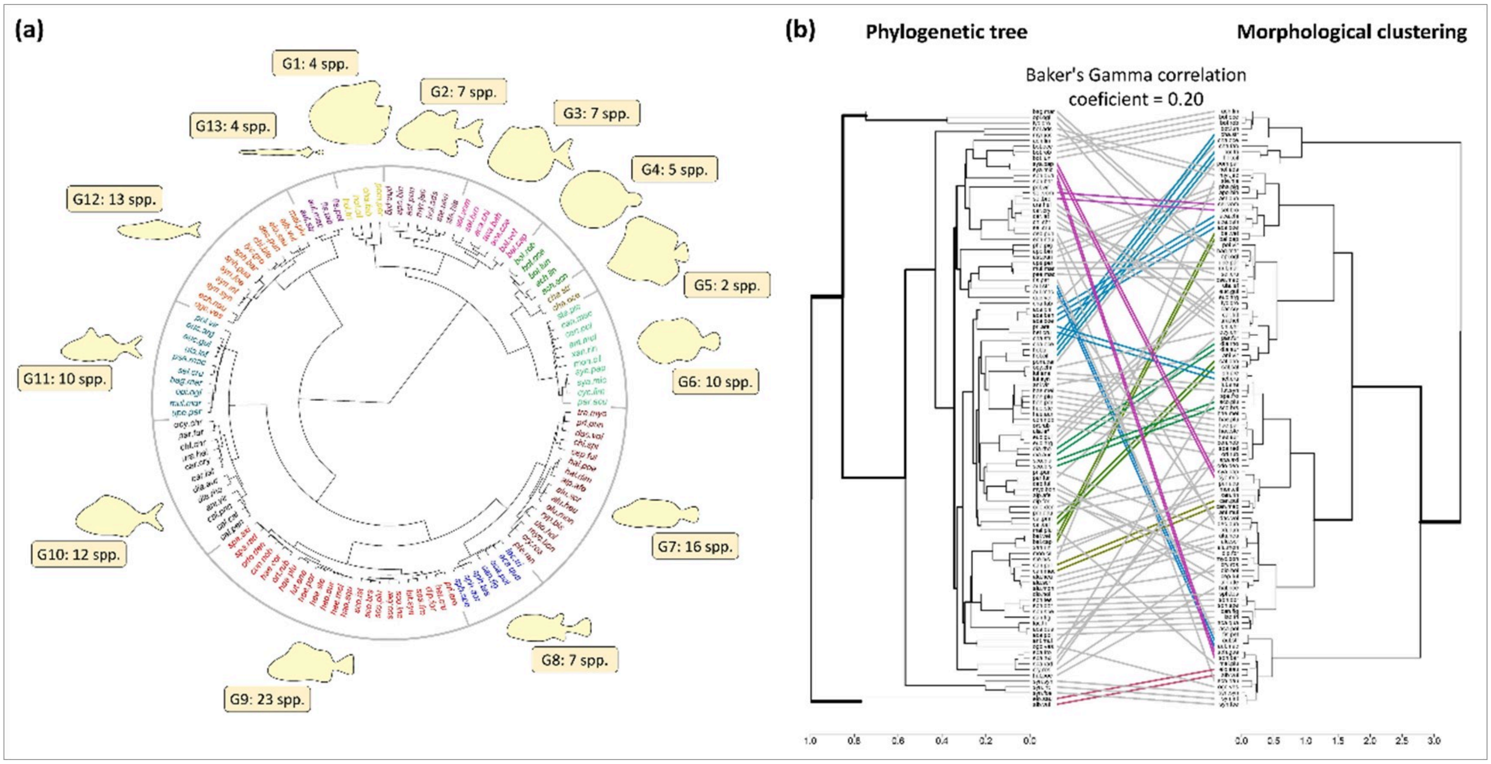

Figure 4

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 analysed 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).

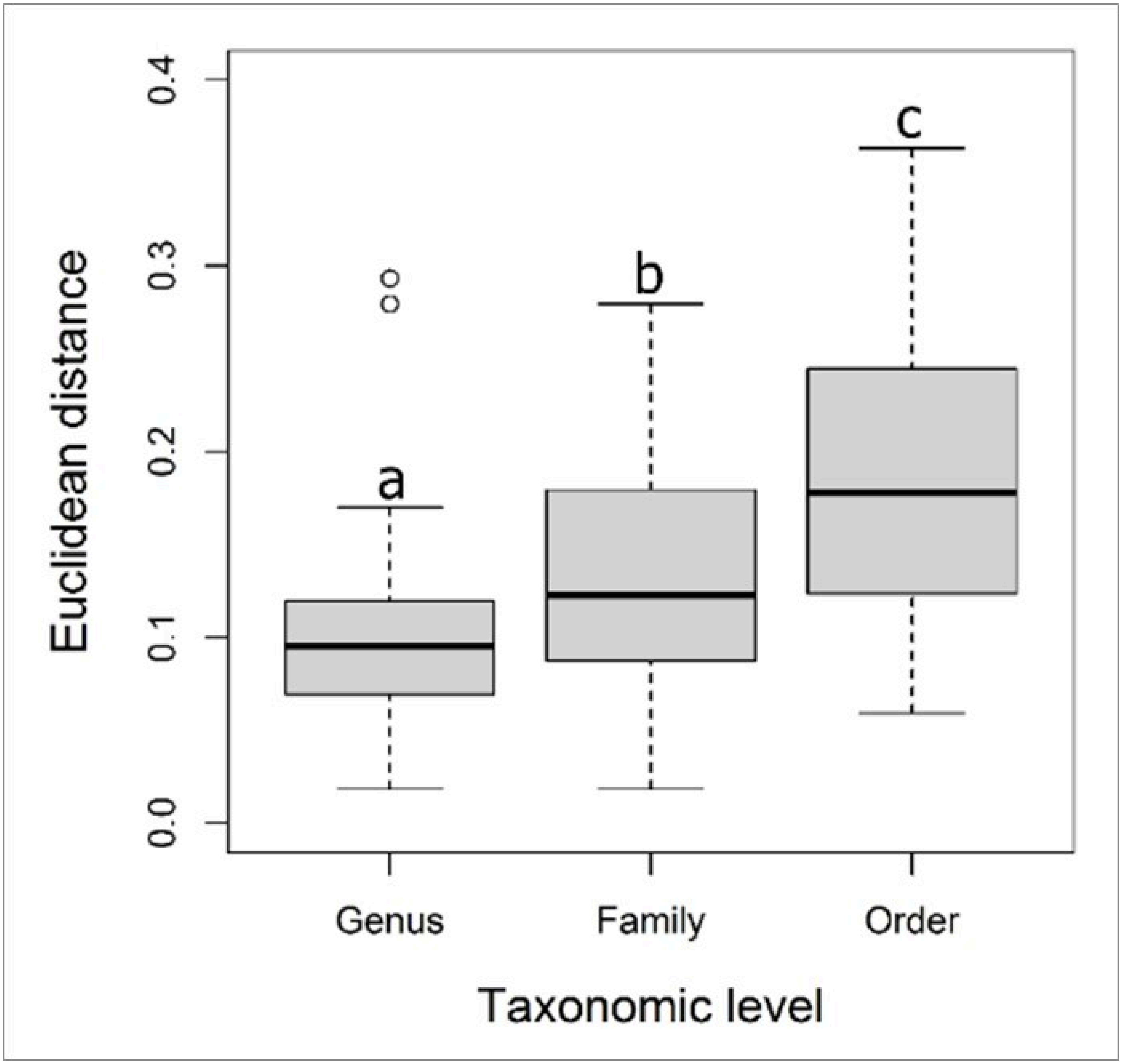

Figure 5

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, $p<0.05$).

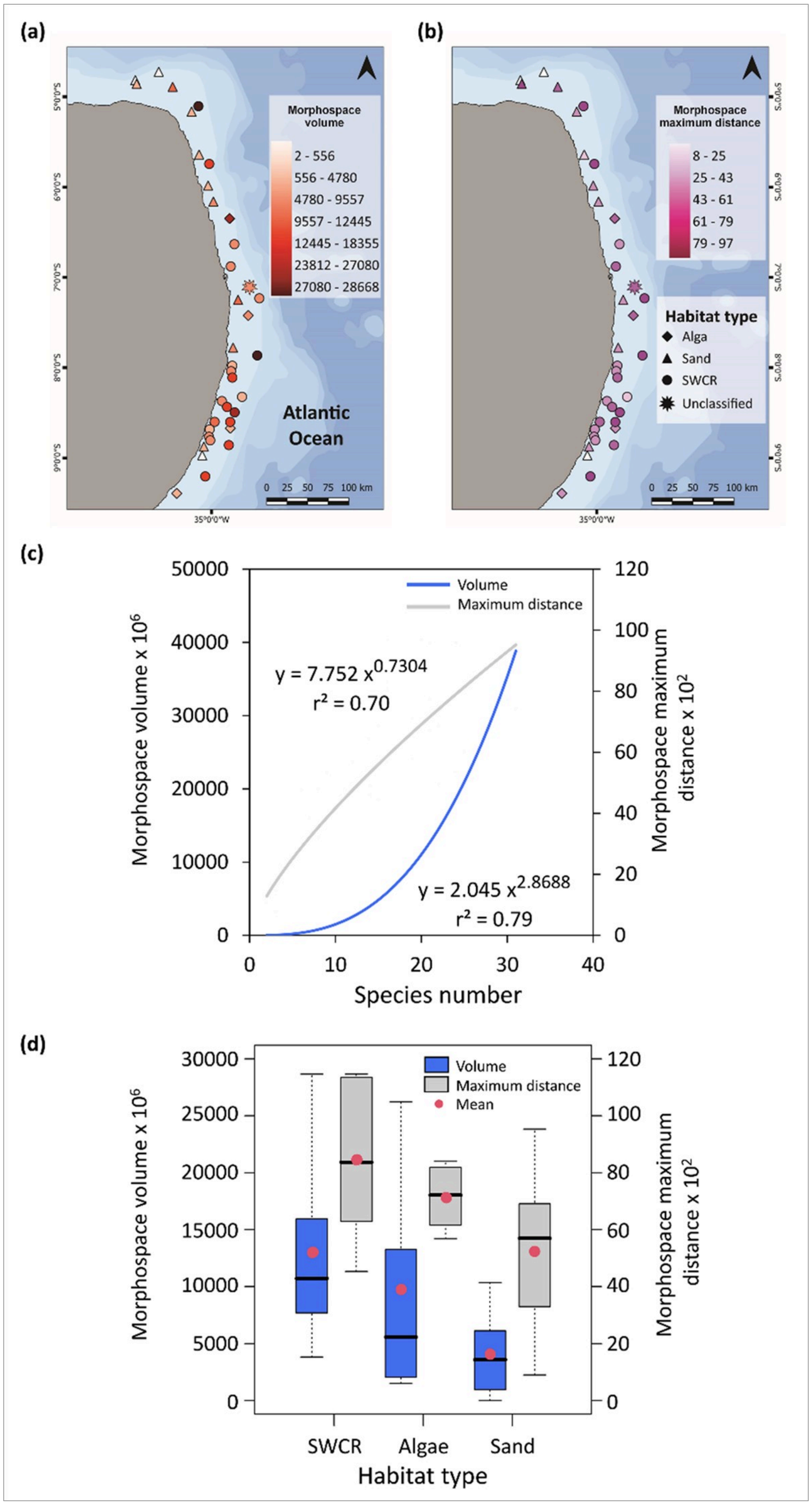

Figure 6

Variation of morphospace volume (a) and maximum distance (b) at each bottom station type. Relationship of volume and maximum distance with species number composing the morphospace (c). Variation of volume and maximum distance of morphospace in each habitat type (d).

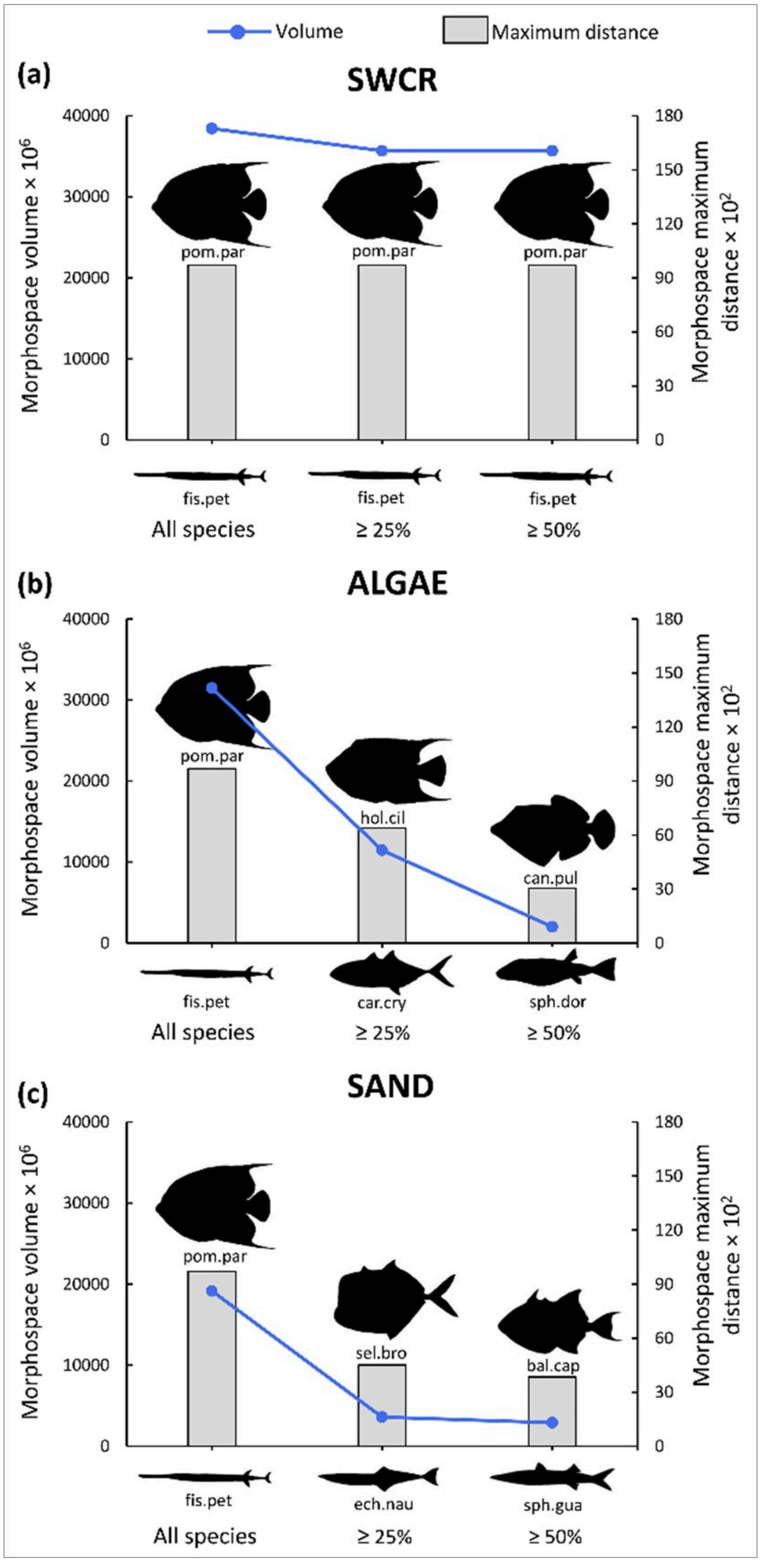

Figure 7

Variation of morphospace volume and maximum morphological distance 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 distance.

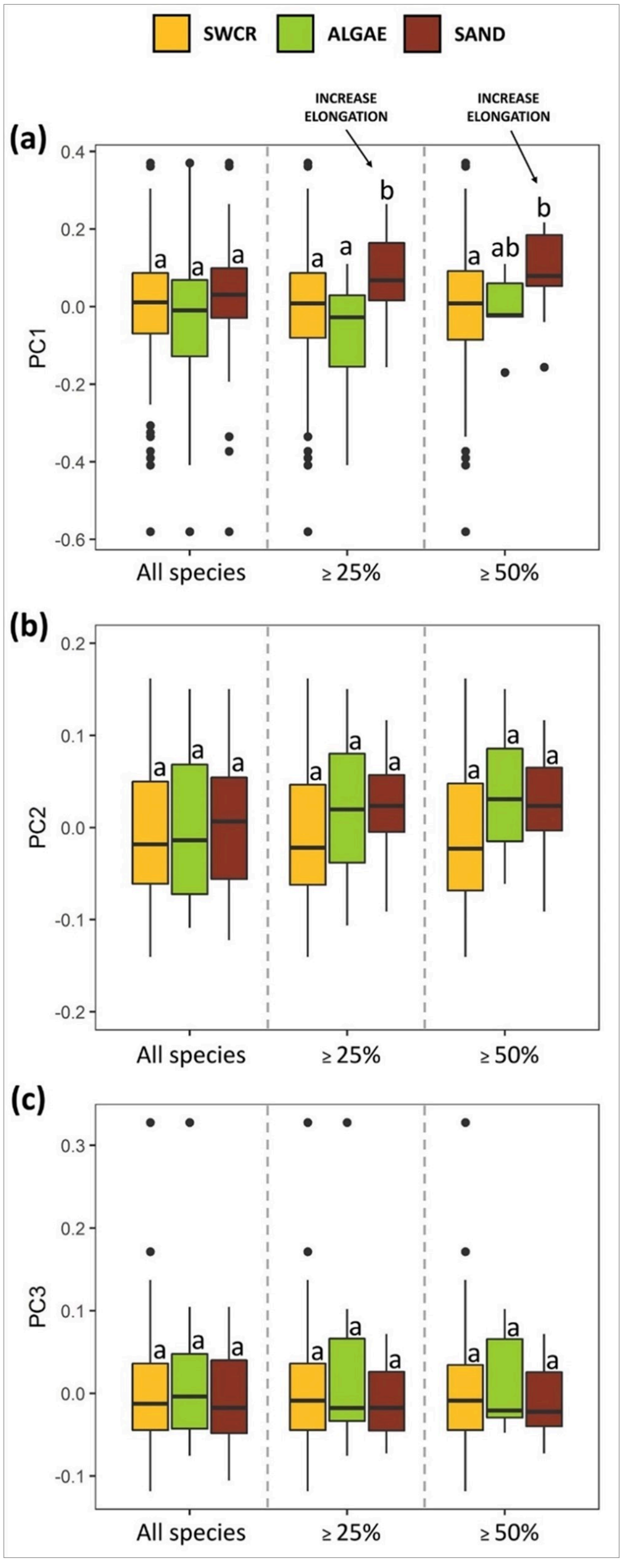

Figure 8

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).

Supplementary Files

- SupportingInformationR1.docx