Journal of Fish Biology
May 2023, Volume 102, Issue 5, Pages 1017-1028
https://doi.org/10.1111/jfb.15350
https://archimer.ifremer.fr/doc/00821/93292/

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

Reis-júnior Josafá [1, 2, *], Bertrand Arnaud [3, 4, 5], Frédou Thierry [4], Vasconcelos-filho Jonas [1, 2],
Aparecido Kátia Cristina [3, 4], Duarte-neto Paulo José [1, 2]

[1] Programa de Pós-graduação em Biometria e Estatística Aplicada (PPG-BEA) Universidade Federal Rural de Pernambuco (UFRPE) Recife Pernambuco (PE), Brazil
[2] Departamento de Estatística e Informática UFRPE Recife PE, Brazil
[3] MARBEC Univ Montpellier, CNRS, Ifremer, IRD Sète, France
[4] Departamento de Pesca e Aquicultura UFRPE Recife PE , Brazil
[5] Departamento de Oceanografia Universidade Federal de Pernambuco Recife PE , Brazil

* Corresponding author : Josafa Reis-Junior, email address : josafajunior13@hotmail.com

---

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 Study area and 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).

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 (Supporting Information 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, Supporting Information Table S2) (Fruciano, 2016).

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 Supporting Information 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 (Supporting Information 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 Supporting Information 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).

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).

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.

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.

Acknowledgements: The authors are grateful to CNPq (National Council for Scientific and Technological Development) for providing research grant to P. J. Duarte Neto (nº 310320/2020-8), T. Frédou (307422/2020-8), and J. Reis-Júnior's scholarship by CAPES (Coordination for the Improvement of Higher Education Personnel) nº 88882.436328/2019-01. We acknowledge the officers and crew of the R/V Antea for their contribution to the success of the operations. This study was funded in part by the "Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco" (APQ AIMMO), and is a contribution to the LMI TAPIOCA (https://tapioca.ird.fr/). The authors are grateful to José Gondin and Anthony Pigot for helping with sample processing.

Author contributions: All authors contributed critically to the drafts and gave final approval for publication. **JRJ**: formal analysis and writing – original draft. **JRJ, AB, JVF, TF** and **PJDN**: conceptualisation, methodology and investigation. **AB, JVF, TF, PJDN** and **KCA**: writing - review and editing.

REFERENCES

Adams, D., Collyer, M., & Kaliontzopoulou, A. (2019). Geomorph: Software for geometric morphometric analyses. R package version 3.1.3.

Aguilar-Medrano, R., Durand, J. R., Cruz-Escalona, V. H., & Moyle, P.B. (2019). Fish functional groups in the San Francisco estuary: Understanding new fish assemblages in a highly altered estuarine ecosystem. *Estuarine, Coastal and Shelf Science*, 227, 106331. https://doi.org/10.1016/j.ecss.2019.106331

Aguirre, W., & Prado, P. J. (2018). *Guía prática de morfometria geométrica: Aplicaciones em la Ictiología.* Ecuador: Pontificia Universidad Católica del Ecuador Sede Esmeraldas (PUCESE).

Akin, S., & Winemiller, K. O. (2008). Body size and trophic position in a temperate estuarine food web. *Acta Oecologica*, 33, 144–153. https://doi.org/10.1016/j.actao.2007.08.002

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

Assunção, R. V., Silva, A. C., Roy, A., Bourlès, B., Silva, C. H. S., Ternon, J. F., 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

Astudillo-Clavijo, V., Arbour, J. H., & López-Fernández, H. (2015). Selection towards different adaptive optima drove the early diversification of locomotor phenotypes in the radiation of Neotropical geophagine cichlids. *BMC Evolutionary Biology*, 15, 1–13. https://doi.org/10.1186/s12862-015-0348-7

Auster, P. J. (2008). Predation tactics of trumpetfish in midwater. *Neotropical Ichthyology*, 6, 289–292. http://dx.doi.org/10.1590/S1679-62252008000200018

Batista, V. S., & Fabré, N. N. (2001). Temporal and spatial patterns on Serra, *Scomberomorus brasiliensis* (Teleostei, Scombridae), catches from the fisheries on the Maranhão coast, Brazil. *Brazilian Journal of Biology*, 61, 541–546. http://dx.doi.org/10.1590/S1519-69842001000400003

Bejarano, S., Jouffray, J. B., Chollett, I., Allen, R., Roff, G., Marshell, A., Steneck, R., Ferse, S. C. A, & Mumby P. J. (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

Benevides, L. J., Nunes, J. A. C. C., Costa, T. L. A., & Sampaio, C. L. S. (2016). Flight response of the barber surgeonfish, *Acanthurus bahianus* Castelnau, 1855 (Teleostei: Acanthuridae), to spearfisher presence. *Neotropical Ichthyology*, 14, e150010. https://doi.org/10.1590/1982-0224-20150010

Bertrand, A. (2015). ABRACOS cruise, RV Antea. https://doi.org/10.17600/15005600

Bertrand, A. (2017). ABRACOS 2 cruise, RV Antea. https://doi.org/10.17600/17004100

Blake, R. W. (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

Bonhomme, V., Picq, S., Gaucherel, C., & Claude, J. (2014). Momocs: outline analysis using R. *Journal of Statistical Software*, 56(13), 1–24. https://doi.org/10.18637/jss.v056.i13

Bozdogan, H. (1987). Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52, 345–370. https://doi.org/10.1007/BF02294361

Brandl, S. J., & Bellwood, D. R. (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

Brandl, S. J., & Bellwood, D. R. (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

Brandl, S. J., Robbins, W. D., & Bellwood, D. R. (2015). Exploring the nature of ecological specialisation 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

Breda, L., Oliveira, E. F., & Goulart, E. (2005). Ecomorfologia de locomoção de peixes com enfoque para espécies neotropicais. *Acta Scientiarum Biological Sciences*, 27, 371-381. https://doi.org/10.4025/actascibiolsci.v27i4.1271

Burns, J. G., Di Nardo, P., & Rodd, F. H. (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

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

Carpenter, K. E. (2002a). *The living marine resources of the Western Central Atlantic - Volume 3: Bony fishes part 2* (Opistognathidae *to* Molidae*), sea turtles and marine mammals.* Rome: FAO.

Carpenter, K. E. (2002b). *The living marine resources of the Western Central Atlantic - Volume 2: Bony fishes part 1 (*Acipenseridae *to* Grammatidae*).* Rome: FAO.

Carrassón, M., & Cartes, J. E. (2002). Trophic relationships in a Mediterranean deep-sea fish community: Partition of food resources, dietary overlap and connections within the benthic boundary layer. *Marine Ecology Progress Series*, 241, 41–55. https://doi.org/10.3354/meps241041

Claverie, T., & Wainwright, P. C. (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

Collar, D. C., O'Meara, B. C., Wainwright, P. C., & Near, T. J. (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

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

Dantas, D. V., Barletta, M., & Costa, M. F. (2015). Feeding ecology and seasonal diet overlap between *Stellifer brasiliensis* and *Stellifer stellifer* in a tropical estuarine ecocline. *Journal of Fish Biology*, 86, 707-733. https://doi.org/10.1111/jfb.12592

Dias, T. L. P., Rosa, I. L., & Feitoza, B. M. (2001). Food resource and habitat sharing by the three western south Atlantic surgeonfishes (Teleostei: Acanthuridae: Acanthurus) off Paraíba Coast, North-eastern Brazil. *Journal of Ichthyology and Aquatic Biology*, 5, 1–10.

Dossa, A. N., Silva, A. C., Hernandez, F., Aguedjou, H. M. A., Chaigneau, A., Araujo, M., & Bertrand, A. (2022). Mesoscale eddies in the southwestern tropical Atlantic. *Frontiers in Marine Science*, 9, 886617. https://doi.org/10.3389/fmars.2022.886617

Eduardo, L. N., Bertrand, A., Frédou, T., Lira, A. S., Lima, R. S., Ferreira, B. P., Menard, F., & Lucena-Frédou, F. (2020). Biodiversity, ecology, fisheries, and use and trade of Tetraodontiformes fishes reveal their socio-ecological significance along the tropical Brazilian continental shelf. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30, 761–774. https://doi.org/10.1002/aqc.3278

Eduardo, L. N., Frédou, T., Lira, A. S., Ferreira, B. P., Bertrand, A., Ménard, F., & Frédou, F. L. (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

Farias, G. B., Molinero, J. C., Carré, C., Bertrand, A., Bec, B., Melo, P. A. M. C. (2022). Uncoupled changes in phytoplankton biomass and size structure in the western tropical Atlantic. *Journal of Marine Systems*, 27, 103696. https://doi.org/10.1016/j.jmarsys.2021.103696

Farré, M., Tuset, V. M., Cartes, J. E., 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

Fonseca, M. S., Araújo, F. G., Teixeira-Neves, T. P, Corrêa, G., Pereira-Filho, G. H., & Neves, L. M. (2021) Drivers of distribution of the parrotfish *Sparisoma frondosum* (Agassiz, 1831) in Southwest Atlantic rocky reefs: Insights for management and conservation. Ocean and Coastal Management, 209, 105642. https://doi.org/10.1016/j.ocecoaman.2021.105642

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

Freire, K. M. F., & Pauly, D. (2010). Fishing down Brazilian marine food webs, with emphasis on the east Brazil large marine ecosystem. *Fisheries Research*, 105, 57–62. https://doi.org/10.1016/j.fishres.2010.02.008

Froese, R. & Pauly, D. (2022). FishBase, version (02/2022). Available at www.fishbase.org (last accessed 13 October 2022).

Froese, R., Garthe, S., Piatkowski, U., & Pauly, D. (2004). Trophic signatures of marine organisms in the Mediterranean as compared with other ecosystems. *Belgian Journal of Zoology*, 134, 31–36.

Fruciano, C. (2016) Measurement error in geometric morphometrics. *Development Genes and Evolution*, 226, 139–158. https://doi.org/10.1007/s00427-016-0537-4

Georgakopoulou, E., Sfakianakis, D. G., 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

Giachini-Tosetto, E., Bertrand, A., Neumann-Leitão, S., & Nogueira-Júnior, M. (2022). The Amazon River plume, a barrier to animal dispersal in the Western Tropical Atlantic. *Scientific Reports*, 12, 537. https://doi.org/10.1038/s41598-021-04165-z

Gibran, F. Z. (2007). Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil. *Neotropical Ichthyology*, 5, 387–398. https://doi.org/10.1590/S1679-62252007000300018

Grubich, J. R., Rice, A. N., & Westneat, M. W. (2008). Functional morphology of bite mechanics in the great barracuda (*Sphyraena barracuda*). *Zoology*, 111, 16–29. https://doi.org/10.1016/j.zool.2007.05.003

Itoh, T., Tsuji, S., & Nitta, A. (2003). Migration patterns of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags. *Fishery Bulletin*, 101, 514–534.

Jackson, D. A. (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*, 74, 2204–2214. https://doi.org/10.2307/1939574

Johansen, J. L. (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

Keppeler, W. F., Montana, C. G., & Winemiller, K. O. (2020) The relationship between trophic level and body size in fishes depends on fuctional traits. *Ecological Monographs*, 90, e01415. https://doi.org/10.1002/ecm.1415

Kirchheim, P. D., & Goulart, E. (2010). Ecomorfologia de predação e antipredação em Siluriformes (Osteichthyes). *Oecologia Australis*, 14, 550–568.

Klingenberg, C. P. (2013). Visualizations in geometric morphometrics: How to read and how to make graphs showing shape changes. *Hystrix, the Italian Journal of Mammalogy*, 24, 15–24. https://doi.org/10.4404/hystrix-24.1-7691

Knoppers, B., Ekau, W., & Figueiredo, A. G. (1999). The coast and shelf of east and northeast Brazil and material transport. *Geo-Marine Letters*, 19(3), 171-178. https://doi.org/10.1007/s003670050106

Langerhans, R. B. (2008). Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology*, 48, 750–768. https://doi.org/10.1093/icb/icn092

Lauder, G. V., & Drucker, E. (2004). Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE Journal of Oceanic Engineering*, 29, 556–571.

Liao, J. C. (2002). Swimming in needlefish (Belonidae): Anguilliform locomotion with fins. *The Journal of Experimental Biology*, 205, 2875–2884.

Linde, M., Palmer, M., & Gómez-Zurita, J. (2004). Differential correlates of diet and phylogeny on the shape of the premaxilla and anterior tooth in sparid fishes (Perciformes: Sparidae). *Journal of Evolutionary Biology*, 17, 941–952. https://doi.org/10.1111/j.1420-9101.2004.00763.x

López-Fernández, H., Winemiller, K. O., Montaña, C., & Honeycutt, R. L. (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

Marcil, J., Swain, D. P., & Hutchings, J. A. (2006). Countergradient variation in body shape between two populations of Atlantic cod (*Gadus morhua*). *Proceedings of the Royal Society B*, 273, 217–223. https://doi.org/10.1098/rspb.2005.3306

Mehta, R. S., Ward, A. B., Alfaro, M. E., & Wainwright, P. C. (2010). Elongation of the body in eels. *Integrative and Comparative Biology*, 50, 1091–1105. https://doi.org/10.1093/icb/icq075

Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology*, 36, 235–247. https://doi.org/10.1007/s11692-009-9055-x

Muggeo, V. M. R. (2008). segmented: An R package to fit regression models with broken-line relationships. *R News*, 8, 20–25.

Muir, A. M., Vecsei, P., & Krueger, C. C. (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

Muschick, M., Indermaur, A., & Salzburger, W. (2012). Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology*, 22, 2362–2368. https://doi.org/10.1016/j.cub.2012.10.048

Nash, K. L., Welsh, J. Q., Graham, N. A. J., & Bellwood, D. R. (2015). Home-range allometry in coral reef fishes: Comparison to other vertebrates, methodological issues and management implications. *Oecologia*, 177, 73–83. https://doi.org/10.1007/s00442-014-3152-y

Novakowski, G. C., Hahn, N. S., & Fugi, R. (2008). Diet seasonality and food overlap of the fish assemblage in a Pantanal pond. *Neotropical Ichthyology*, 6, 567–576. https://doi.org/10.1590/S1679-62252008000400004

O'Toole, A. C., Danylchuk, A. J., Goldberg, T. L., Suski, C. D., Philipp, D. P., Brooks, E., & Cooke, S. J. (2011). Spatial ecology and residency patterns of adult great barracuda (*Sphyraena barracuda*) in coastal waters of The Bahamas. *Marine Biology*, 158, 2227–2237. https://doi.org/10.1007/s00227-011-1728-1

Pauly, D., & Palomares, M. L. (2000). Approaches for dealing with three sources of bias when studying the fishing down marine food web phenomenon. In Briand F. (ed), *Fishing down the Mediterranean food webs? vol. 12* (pp. 61–66). Greece: CIESM Workshop Series.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres-Jr, F. (1998). Fishing down marine food webs. *Science*, 279, 860–863. https://doi.org/10.1126/science.279.5352.860

Pessanha, A. L. M., Araújo, F. G., Oliveira, R. E. M. C. C., Silva, A. F., & Sales, N. S. (2015). Ecomorphology and resource use by dominant species of tropical estuarine juvenile fishes. *Neotropical Ichthyology*, 13, 401–412. https://doi.org/10.1590/1982-0224-20140080

Portner, H. O., Schulte, P. M., Wood, C. M., & Schiemer, F. (2010), Niche dimensions in fishes: An integrative view. *Physiological and Biochemical Zoology*, 83, 808–826. https://doi.org/10.1086/655977

Pratchett, M. S., & Berumen, M. L. (2008). Interspecific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). *Journal of Fish Biology*, 73, 1730–1747. https://doi.org/10.1111/j.1095-8649.2008.02062.x

Price, S. A., Friedman, S. T., & Wainwright, P. C. (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

Pusey, B. J., & Bradshaw, S. D. (1996). Diet and dietary overlap in fishes of temporary waters of southwestern Australia. *Ecology of Freshwater Fish*, 5, 183–194. https://doi.org/10.1111/j.1600-0633.1996.tb00132.x

R Development Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org/

Rohlf, F. J. (2015). The tps series of software. *Hystrix, the Italian Journal of Mammalogy*, 26, 9–12. https://doi.org/10.4404/hystrix-26.1-11264

Rohlf, F. J., & Slice, D. E. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, 39, 40–59. https://doi.org/10.2307/2992207

Roisin, P. L. (2005) Computing global shape measures. In C. H. Chen & P. S. Wang (Eds.), Handbook of pattern recognition and computer vision (pp. 177-196). London (UK): World Scientific Publishing.

Romanuk, T. N., Hayward, A., & Hutchings, J. A. (2011). Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography*, 20, 231–240. https://doi.org/10.1111/j.1466-8238.2010.00579.x

Schlager, S., Jefferis, G., & Ian, D. (2019). Morpho: Calculations and visualizations related to geometric morphometrics. R package version 2.7.

Sfakianakis, D. G., Leris, I., Laggis, A., & Kentouri, M. (2011). The effect of rearing temperature on body shape and meristic characters in zebrafish (*Danio rerio*) juveniles. *Environmental Biology of Fishes*, 92, 197–205. https://doi.org/10.1007/s10641-011-9833-z

Souza, A. T., Ilarri, M. I., & Rosa, I. L. (2011). Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish *Stegastes rocasensis* (Actinopterygii: Pomacentridae). *Environmental Biology of Fishes*, 91, 133–144. https://doi.org/10.1007/s10641-010-9765-z

Stergiou, K. I., & Karpouzi, V. S. (2002). Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*, 11, 217–254. https://doi.org/10.1023/A:1020556722822

Stramma, L., & Schott, F. (1999). The mean flow field of the tropical Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 46(1-2), 279-303. https://doi.org/10.1016/S0967-0645(98)00109-X

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

Van Wassenbergh, S., van Manen, K., Marcroft, T. A., Alfaro, M. E., & Stamhuis, E. J. (2015). Boxfish swimming paradox resolved: Forces by the flow of water around the body promote manoeuvrability. *Journal of the Royal Society Interface*, 12: 20141146. https://doi.org/10.1098/rsif.2014.1146

Ventura, D., Bonhomme, V., Colangelo, P., Bonifazi, A., Lasinio, G. J., & 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

Wainwright, P. C., & Bellwood, D. R. (2002). Ecomorphology of feeding in coral reef fishes. In P. F. Sale (Ed.), *Coral Reef Fishes: Dynamics and diversity in a complex ecosystem* (pp. 33–56). San Diego: Academic Press.

Ward, A. B, & Brainerd, E. L. (2007). Evolution of axial patterning in elongate fishes. *Biological Journal of the Linnean Society*, 90, 97–116. https://doi.org/10.1111/j.1095-8312.2007.00714.x

Ward, A. B., & Mehta, R. S. (2010). Axial elongation in fishes: Using morphological approaches to elucidate developmental mechanisms in studying body shape. *Integrative and Comparative Biology*, 50, 1106–1119. https://doi.org/10.1093/icb/icq029

Webb, P. W. (1982). Locomotor patterns in the evolution of Actinopterygian fishes. *American Zoologist*, 22, 329–342. https://doi.org/10.1093/icb/22.2.329

Webb, P. W. (1984a). Form and function in fish swimming. *Scientific American*, 251, 72–83.

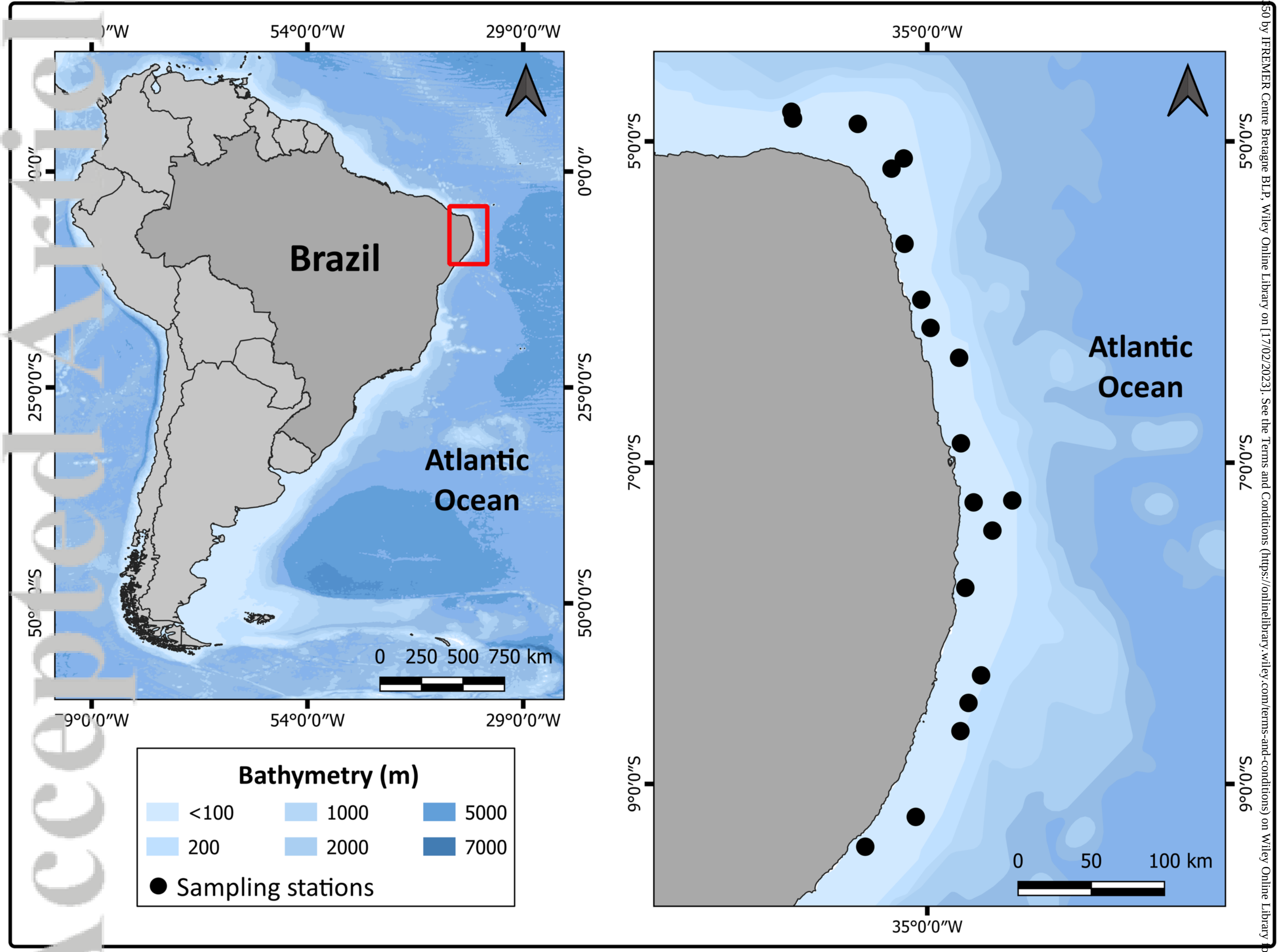
Webb, P. W. (1984b). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist*, 24, 107–120. https://doi.org/10.1093/icb/24.1.107

Welsh, J. Q., & Bellwood, D. R. (2014). Herbivorous fishes, ecosystem function and mobile links on coral reefs. *Coral Reefs*, 33, 303–311. https://doi.org/10.1007/s00338-014-1124-7

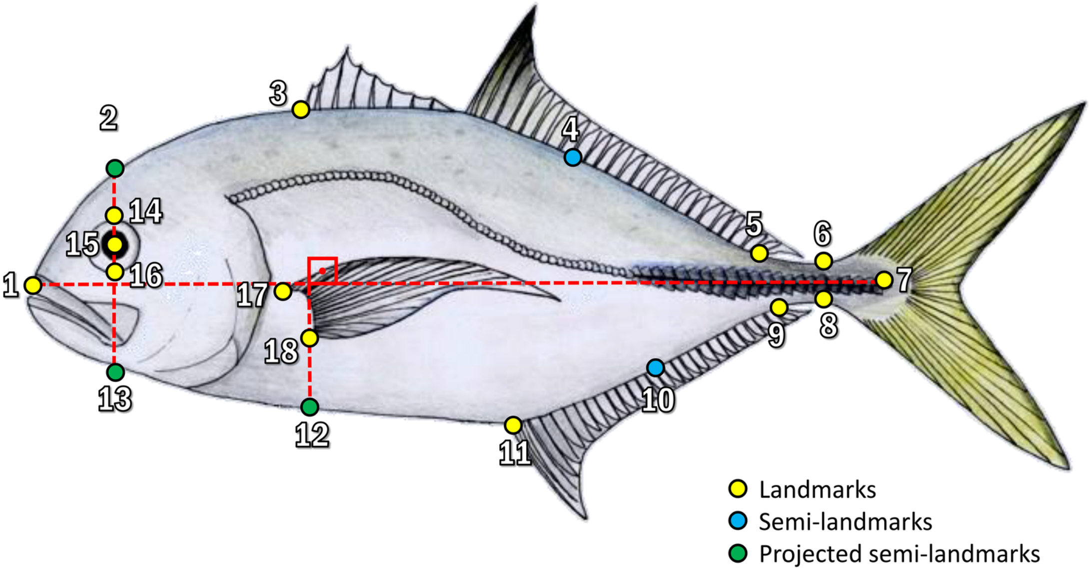
Winemiller, K. O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs*, 61, 343–365. https://doi.org/10.2307/2937046

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

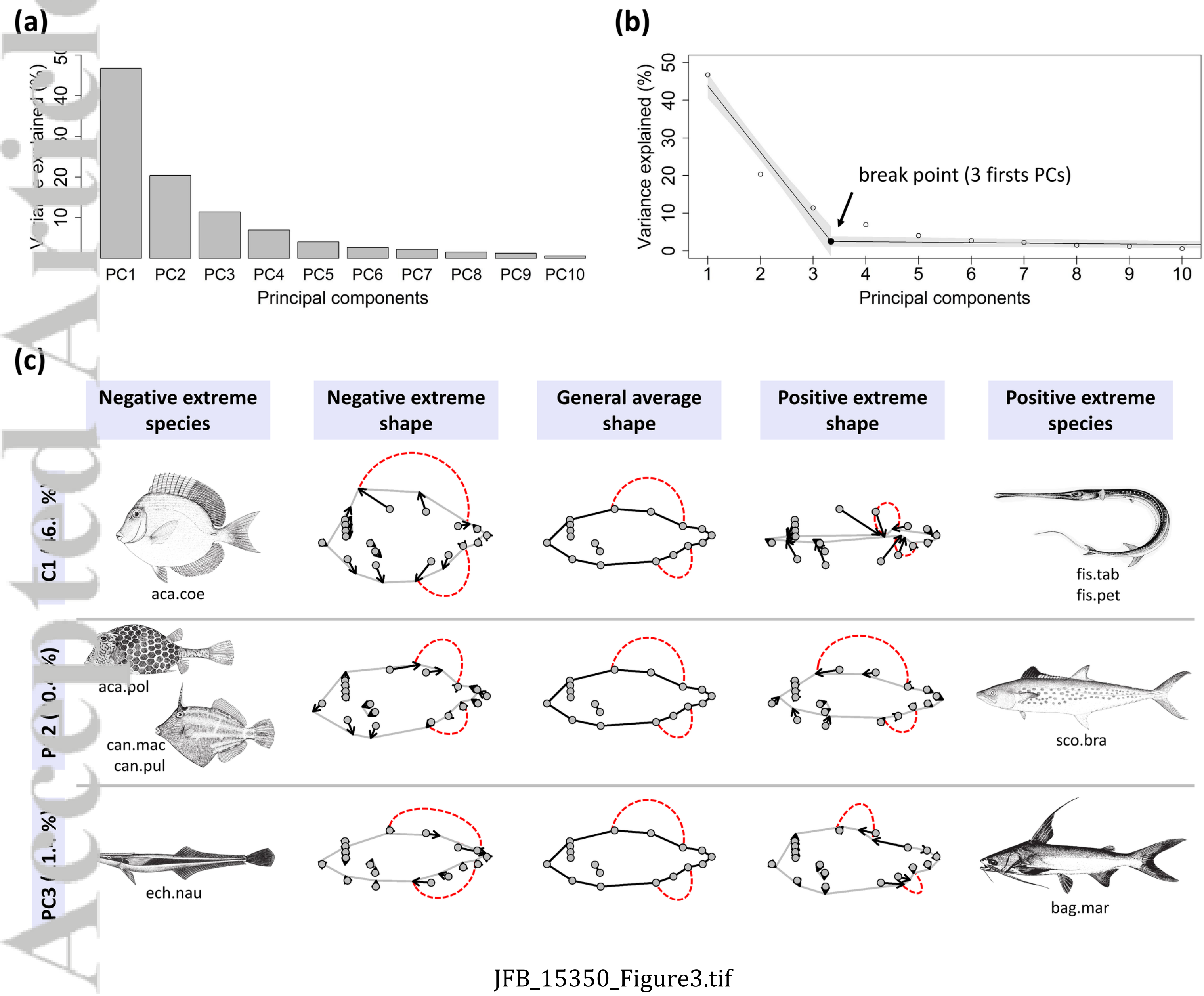
Zelditch, M. L., Swiderski, D. L., Sheets, H. D., & Fink, W. L. (2004). *Geometric Morphometrics for Biologists: A Primer* (1st edition). USA: Elsevier Academic Press.



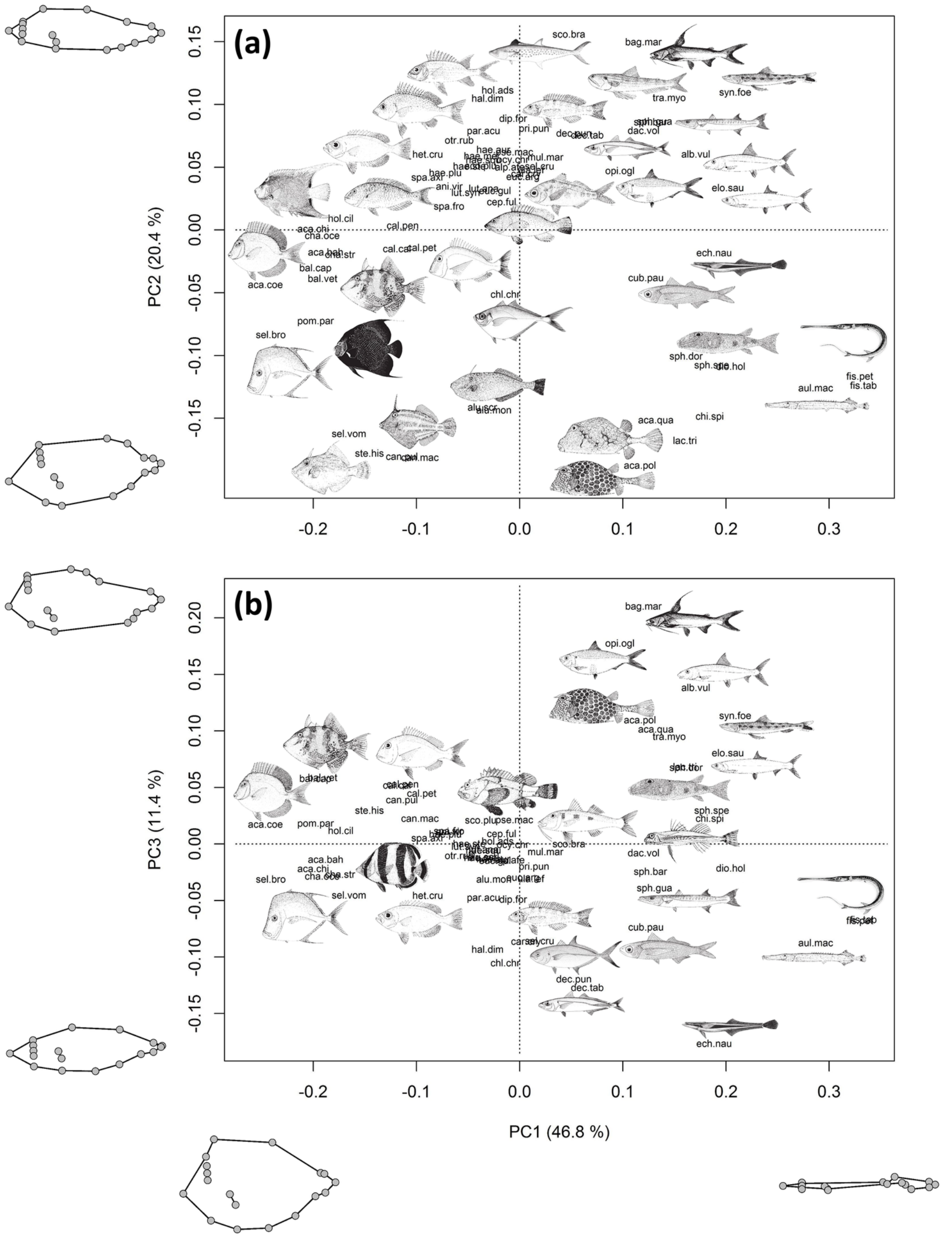
JFB_15350_Figure1.tif



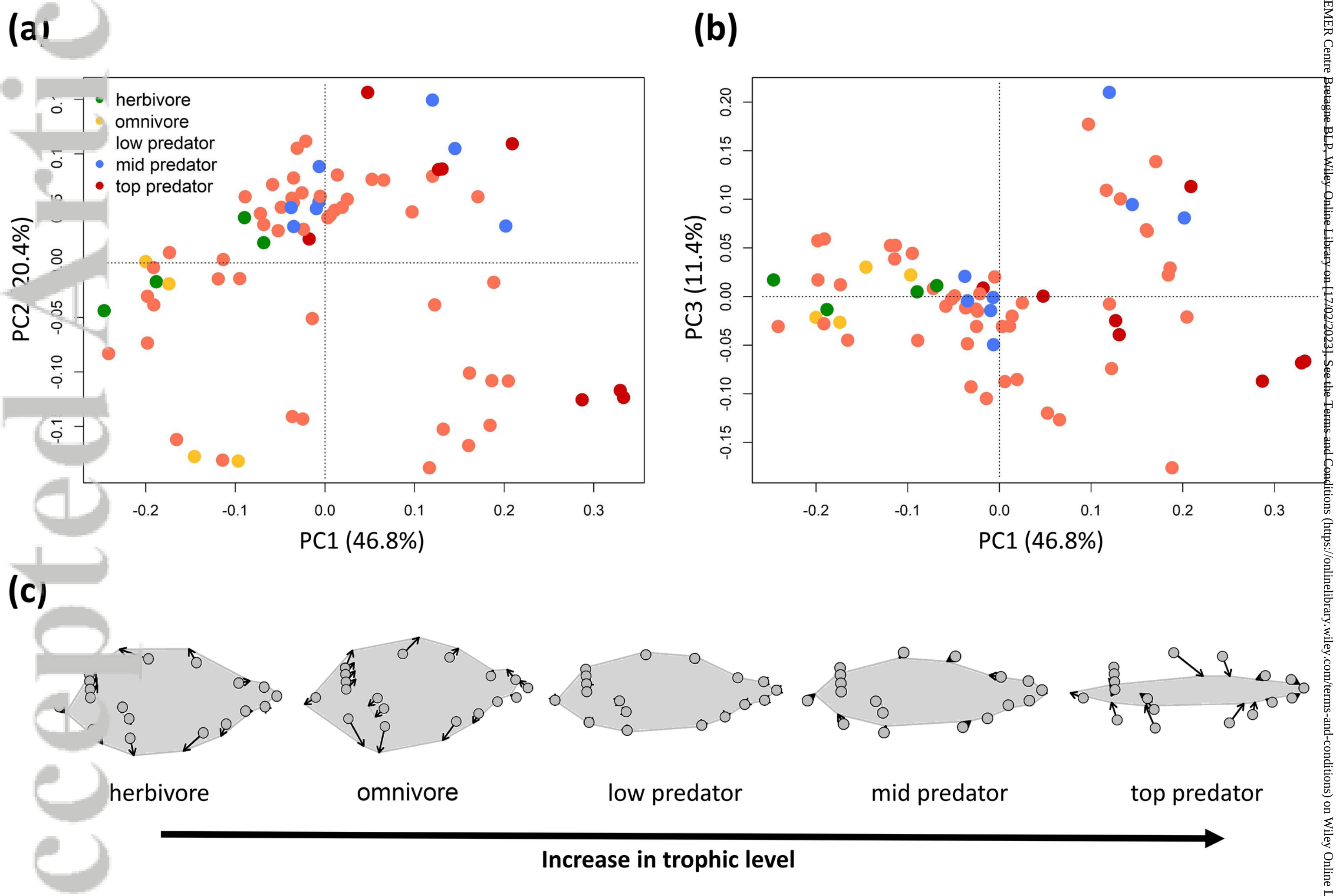
JFB_15350_Figure2.tif



JFB_15350_Figure3.tif



JFB_15350_Figure4.tif



JFB_15350_Figure5 new.tif

FIGURE CAPTIONS

Figure 1. Study area off Northeast Brazil Shelf.

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.

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 Supporting Information 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).

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 Supporting Information 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.

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. R² = Multiple determination coefficients.

Model	**Intercept**	**PC1**	**L_{max}**	**PC2**	**PC3**	**F test**	**AIC**	**R²**
				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.