



# Ecomorphological patterns in otoliths of tropical fishes: assessing trophic groups and depth strata preference by shape

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**Abstract** The morphology and morphometry of otoliths have emerged as powerful indicators of ecological characteristics of fishes. However, shape descriptors that can accurately predict well-documented functions played by species in tropical ecosystems are either restricted to a few groups or poorly known. Therefore, we evaluated the power of two otolith shape descriptors (ecomorphological indexes and Fourier harmonics) in discriminating trophic and depth strata preference groups of tropical fish species. Differences in otolith shape of ecological groups were visualized by linear discriminant analysis (LDA), and tested by a jack-knife cross-validation method and permutational multivariate analysis of variance (PERMANOVA) for both methods. Visually and statistically, both descriptors were good predictors of trophic groups and depth preference categories (PERMANOVA,  $p < 0.05$ ). Overall jack-knifed classification success between both descriptors were very similar, with harmonics correctly classifying 90.38% of assigned trophic groups and 75.96% of given depth preference categories, against 82% and 56.25% of ecological indexes, respectively. Our results suggest that Fourier descriptors and

ecomorphological indexes of otoliths should be used as functional traits in future studies, as otolith shape provides a wider range of ecological information regarding feeding habitat, mobility, substrate association and water column use.

**Keywords** Ecological indicators · Feeding habit · Functional diversity · *Sagittae* · Surrogate

## Introduction

Many dimensions of a species' niche can be assessed by the identification of relationships between morphological variation and ecological performance of organisms (Williams 1972; Winemiller 1991; Norton et al. 1995). Indeed, ecomorphological patterns found in body structures have provided numerous insights about some of the oldest issues in biology, especially in the understanding of competitive and coevolution mechanisms, and the performance capability of species (Losos 1990; Wainwright and Richard 1995; Tulli et al. 2011). In fishes, for example, the eye size and length of digestive tract have been associated to differences in foraging behavior (Watson and Balon 1984; Soares et al. 2013), the body shape has been used as a predictor of mobility in tropical species (Micheli and Halpern 2005; Passos et al. 2016; Souza et al. 2018), the relative body height is related to the fish ability to move vertically (Pouilly et al. 2003), and otolith morphology have helped to understand water-column use by species and association

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with different types of substrate (Volpedo and Echeverría 2003).

Otoliths, in particular, have been shown as good predictors of ecological characteristics of species due to their variability in shape that may result from - or be associated to - many factors (Schulz-Mirbach et al. 2006). These calcium carbonate structures are found in the inner ear of fishes, being formed and shaped throughout the life history of species by the deposition and interaction of organic matrix fibers and carbonate crystals (Morales-Nin 2000). The layer deposition process results in the formation of translucent and opaque rings as well as microscopic zones – growth increments – (Secor et al. 1992), and the overall shape of otoliths is dually regulated by genetics and the environmental history experienced by species (Lombarte and Leonart 1993). Moreover, since otoliths are metabolically inert, elements and compounds deposited onto their growing surface produce permanent records of fishes' life cycle (Campana 1999), allowing these structures to be used as natural tags.

In Teleostei fishes, otoliths have many functions, mainly related to the sound detection (Fay and Popper 1974), notion of acceleration (Flock and Goldstein 1978) and water column positioning of the fish. The environmental sensorial perception of *sagittae* otoliths in non-ostariophysian fishes and its ecological implications have been vastly discussed in literature (Aguirre and Lombarte 1999; Volpedo and Echeverría 2003; Tuset et al. 2003; Volpedo et al. 2008). For Schulz-Mirbach et al. (2019), otolith mass and overall shape may be associated with the auditory function of fishes as the different otolith shapes may affect the endolymph flow dynamics and how the sensory epithelium functions in the semicircular canals. Therefore, if a fish has simple movements, a more spherical or ellipsoidal otolith is expected, whereas an increase in shape complexity of otoliths may be associated with higher mobility (Schellart and Popper 1992). In addition, the shape and extent of the acoustic sulcus may also play an important role in fish ecology due its close relationship with the auditory ability (Schulz-Mirbach et al. 2010; Lombarte and Tuset 2015; Tuset et al. 2016b). Lombarte and Fortuño (1992) evaluated the ratio between sulcus size (as a proxy for the macula size) and otolith size, finding correlation with the depth of the water column, whereas Aguirre and Lombarte (1999) related sulcus with the type of food and habitat used by fishes.

Although it has been discussed by many authors that otolith shape is a species-specific feature that results from

the phylogenetic history of species (Wilson 1985), new studies have shown that it may also reflect patterns in the use of resources and habitats by different groups (Aguirre and Lombarte 1999; Nonogaki et al. 2007). This occurs because variability in otolith shape may result from many factors related to fish ecology, such as substrate type (Volpedo and Cirelli 2006), feeding habit (Nonogaki et al. 2007), ontogenetic shifts (Pérez and Fabr e 2013) and environmental conditions – e.g. temperature and depth – (Lombarte and Leonart 1993). Indeed, the morphology of these structures has recently been used as an indicator of roles that organisms play within ecosystems (Tuset et al. 2016a). Nevertheless, the use of otolith morphology as a functional trait – features that strongly influence organismal performance and/or individual fitness (McGill et al. 2006) – has been restricted to a few groups and species (Tuset et al. 2016a; Quinn 2018). For instance, the current knowledge on which descriptors of otolith shape can be related to well-documented functions played by fishes in tropical ecosystems is very scarce (Tuset et al. 2015).

Although there are several tools used to describe external contour and morphological patterns of otoliths – i.e. geodesic methods (Benzinou et al. 2013), wavelet functions (Sadighzadeh et al. 2014), Fourier descriptors (Tracey et al. 2006), ecomorphological indexes (Volpedo and Echeverría 2003) and geometric morphometric analysis (Ramírez-P rez et al. 2010) –, in some cases, the biological interpretations of results may be complex because of their mathematical foundations (Stransky and MacLellan 2005). While a few advances have been achieved in the establishment of relationships between otolith shape and habitat and water column use by species (Galley et al. 2006; Jaramilo et al. 2014), the link of otolith shape to other ecological characteristics, such as feeding behavior is still poorly understood, especially for tropical fish species.

According to Gagliano and McCormick (2004), describing patterns in otoliths that reflect the feeding history of species can be a difficult task due to the intricate processes that influence otolith growth and shape. For instance, many factors that can affect feeding strategies of species – i.e. depth preference and use of substrate type – have also an impact on otoliths (Allen et al. 2006), making necessary to take a closer examination on different features of otolith morphology to identify patterns that can accurately be linked to species' feeding ecology. The identification of such patterns might be a key element in the development of new approaches for

functional ecology (Tuset et al. 2016a), especially for species in tropical regions where studies of feeding ecology are often difficult to be carried out due to the great diversity of prey items consumed by species and high niche differentiation among and within species (Nonogaki et al. 2007; Davis et al. 2012; da Silva and Fabré 2019).

In this context, the present study aims to test whether descriptors of otolith shape can be good predictors of functions performed by fishes in tropical coastal ecosystems. The main question underlying our study is whether or not ecomorphological patterns found in otoliths can be accurately linked to ecological aspects of tropical species expressed by functional guilds. Therefore, we used discriminant and multivariate analysis to comprehend the power of different descriptors of otolith shape in identify the trophic group and depth preference of species.

## Materials and methods

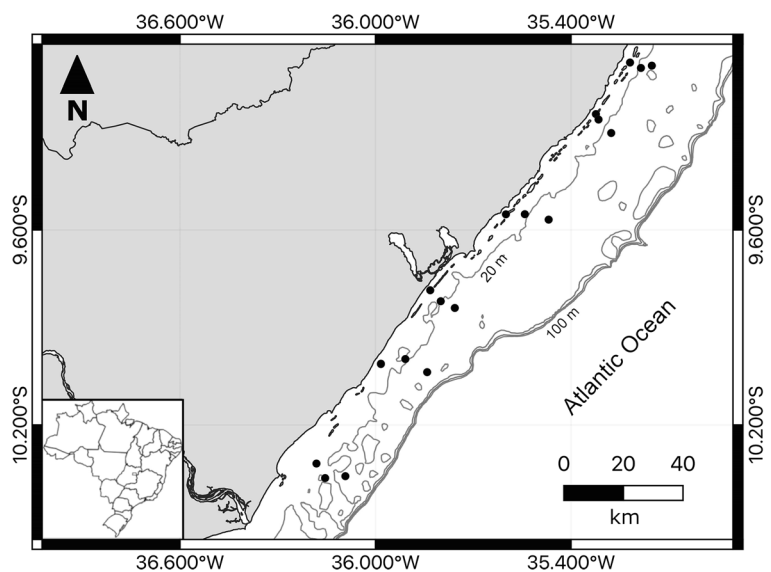
### Sampling and otolith preparation

We sampled 208 otoliths of 33 species collected along the coast of Alagoas (09°47'80.4"S; 35°49'56"W and 10°21'26.8"S; 36°05'32.9"W), located in the tropical south-west Atlantic ecoregion of the north-east Brazil (Fig. 1). This coastline is characterized by a narrow continental shelf (50 km), and it is influenced by the many reef formations, lagoons and estuarine areas

found in the region (Medeiros et al. 2007). Fishes were collected by ten nylon gillnets linked by ropes in a chain arrangement in 18 sampling sites distributed along the coast (Federal Scientific Fish Sampling License 1,837,810). The chain of 10 nets was 100 m long and 2.9 m high with mesh sizes that ranged from 20 to 80 mm randomly located along the chain. Four sampling surveys were undertaken in January, April, May and July 2013, encompassing the two well-established seasons of the study area (dry and wet seasons).

In laboratory, fishes were identified at level species using regional taxonomic keys (Figueiredo and Menezes 1978, 1980; Menezes and Figueiredo 1980, 1985), measured to the nearest mm (total length) and sexed. Otoliths were removed using the open-the-hatch technique as described by Secor et al. (1992), cleaned from tissues with 5% NaOH, washed with distilled water, dried and stored in labeled vials. To avoid the effect of ontogenetic variability, only otoliths from sexually mature specimens were used in this study (Stransky and MacLellan 2005), hence, maturity stage of individuals was assigned using macroscopic gonadal examination following Vazzoler (1996). A digital picture of the left *sagittae* from each individual was taken using a stereoscopic binocular microscope Leica S8-APO equipped with a camera Leica EC3. Otoliths were always positioned with their respective dorsal margin to the top of the image, anterior (rostral) region to the left and sulcus-side-up.

**Fig. 1** Map of study area showing sampling sites (•) and depth strata (grey lines) where sampling surveys were carried out



The morphology of otoliths was described by two different approaches. First, we calculated four ecomorphological indexes (see Table 1 for details) to identify patterns in otolith form: the E, R and S indexes which describe otolith shape and dimensions (Volpedo and Echeverría 2003; Volpedo et al. 2008), and an edge complexity index (EC) based on Kalff's shoreline development factor (SFD) which was used to describe irregularities on otoliths' edge (Kalff 2002). These indexes were calculated using the following morphometrical measurements, which were record in millimeters (mm) for all otoliths using the shapeR package in the R statistic software (Libungan and Pálsson 2015)– otolith length (OL), otolith width (OW), otolith area (OA) and otolith perimeter (OP) – and the image processing system ImageJ (Rasband 2012): rostrum length (RL) and sulcus area (SA). All measurements were size-corrected before analysis to ensure unbiased comparisons between groups (Reist 1985). Second, we retrieved the elliptic Fourier descriptors (EFD) for each otolith using the shapeR package in the R statistics software (Kuhl and Giardina 1982; Lestrel 1997). This method is considered one of the best techniques for capturing the entire shape variation and small-scale individual differences (Campana and Casselman 1993), allowing the deconstruction of otolith shape in orthogonal series, which are called harmonics. Harmonics represent a series of sine and cosine curves that are generated by a Fourier expansion, taking the elliptic shape as reference (Younker and Ehrlich 1977; Bird et al. 1986).

#### Data analysis

Prior to analysis, studied species were categorized according to a trophic group and a depth strata preference

category (see Table 2 for species' classification), which are two ecological features of species commonly related to functions performed by them in ecosystems. Fishes were assigned to a trophic group based on the main diet of adults according to existing published data. To promote uniformity in the trophic group classification of species, the categories used herein followed Ferreira et al. (2004): carnivorous (fishes that feed predominately on sessile invertebrates, but may also feed on other organisms, including fishes); mobile invertebrate feeders (fishes that only feed on mobile invertebrates); omnivorous (fishes that feed on a variety of food items, including planktonic, benthic and nektonic organisms) and piscivorous (fishes that feed mainly on other fish species). Depth preference was assigned using data found in online databases such as FishBase, taking in consideration three depth strata: shallow (0–40 m), medium (41–60 m) and deep (61–150 m).

To evaluate whether ecomorphological indexes and harmonics could be used as a tool for distinguishing trophic and depth preference groups, linear discriminant analysis (LDA) were carried in the PAST statistics software. The LDA reduces the ratio of within-class variance and maximizes the ratio of between-class variance, seeking directions on space that have maximum discriminability among given classes (Rezzi et al. 2007), making this analysis a powerful tool in the identification of groups. In addition to graphic visualization, to evaluate the effective discriminant power of both descriptors (harmonics and ecomorphological indexes), we first used a jack-knife method for the estimation of the classification error, and statistically test differences among and within groups by permutational multivariate analysis of variance – PERMANOVA – (Anderson 2017).

Additionally, the mean contour of each group (trophic and depth preference) was reconstructed by the

**Table 1** Ecomorphological indexes used to identify patterns in otoliths of tropical fishes collected in the south-west Atlantic

Indexes	Meaning	Formula	Reference
EC	Describes edge irregularities in otoliths	$EC = \frac{OP}{2 \cdot \sqrt{OA \cdot \pi}}$	Kalff (2002)
E	Expresses the tendency in the shape of the sagittae (circular or elongate)	$E = \frac{OA}{OL}$	Volpedo and Echeverría (2003)
R	Expresses how much of the otolith length that corresponds to the rostrum	$R = \frac{RL}{OL}$	Volpedo and Echeverría (2003)
S	Tendency of macula nervosa to have a greater surface area of information uptake to transmit to the fish brain	$S = \frac{SA}{OA}$	Gauldie (1988)

**Table 2** Average ecomorphological indexes values for species collected in the south-west Atlantic and their respective trophic groups “TG” (Carn – carnivorous, MIF – mobile invertebrate

feeders, Omn – omnivorous, Pisc – piscivorous) and depth preference categories “DP” (shallow, medium and deep)

Family / Species	N	Ecomorphological indexes				TG	DP
		EC	E	R	S		
<b>Albulidae</b>							
<i>Albula nemoptera</i> <sup>1</sup>	3	1.19	0.43	0	0.40	Carn	Medium
<i>Albula vulpes</i> <sup>2</sup>	16	1.18	0.55	0	0.40	Carn	Shallow
<b>Bothidae</b>							
<i>Bothus ocellatus</i> <sup>3</sup>	1	1.05	0.63	0	0.30	Carn	Deep
<b>Carangidae</b>							
<i>Caranx crysos</i> <sup>4</sup>	9	1.39	0.40	0.29	0.29	Pisc	Deep
<i>Chloroscombrus chrysurus</i> <sup>5</sup>	18	1.26	0.46	0.31	0.22	Omn	Deep
<i>Oligoplites saurus</i> <sup>6</sup>	6	1.23	0.58	0.19	0.33	Carn	Medium
<b>Clupeidae</b>							
<i>Opisthonema oglinum</i> <sup>7</sup>	30	1.45	0.47	0.36	0.37	Omn	Medium
<b>Cynoglossidae</b>							
<i>Symphurus tessellatus</i> <sup>8</sup>	2	1.02	1.08	0	0.15	MIF	Medium
<b>Gerreidae</b>							
<i>Diapterus rhombeus</i> <sup>9</sup>	30	1.15	0.64	0.21	0.24	Carn	Deep
<i>Eucinostomus argenteus</i> <sup>9</sup>	19	1.16	0.57	0	0.24	Carn	Medium
<b>Haemulidae</b>							
<i>Conodon nobilis</i> <sup>10</sup>	7	1.09	0.66	0.12	0.26	Carn	Deep
<i>Haemulon aurolineatum</i> <sup>11</sup>	16	1.07	0.68	0.17	0.24	MIF	Shallow
<i>Haemulon steindachneri</i> <sup>12</sup>	2	1.07	0.69	0.13	0.26	MIF	Medium
<i>Haemulopsis corvinaeformis</i> <sup>13</sup>	30	1.08	0.71	0.14	0.22	MIF	Medium
<i>Orthopristis ruber</i> <sup>14</sup>	10	1.09	0.61	0.21	0.28	MIF	Deep
<b>Lutjanidae</b>							
<i>Lutjanus analis</i> <sup>3</sup>	2	1.11	0.56	0.18	0.29	Carn	Medium
<i>Lutjanus synagris</i> <sup>11</sup>	11	1.12	0.60	0.19	0.30	Carn	Medium
<b>Mullidae</b>							
<i>Pseudupeneus maculatus</i> <sup>3</sup>	1	1.18	0.74	0.15	0.30	Carn	Deep
<b>Paralichthyidae</b>							
<i>Syacium micrurum</i> <sup>15</sup>	10	1.08	0.70	0	0.42	MIF	Deep
<b>Sciaenidae</b>							
<i>Cynoscion jamaicensis</i> <sup>16</sup>	2	1.13	0.61	0	0.51	Carn	Deep
<i>Larimus breviceps</i> <sup>17</sup>	31	1.07	0.67	0	0.48	MIF	Medium
<i>Macrodon ancylodon</i> <sup>18</sup>	2	1.18	0.74	0	0.49	Carn	Medium
<i>Menticirrhus americanos</i> <sup>19</sup>	11	1.24	0.38	0	0.57	Carn	Medium
<i>Micropogonias furnieri</i> <sup>20</sup>	34	1.07	0.78	0	0.43	MIF	Medium
<i>Paralonchurus brasiliensis</i> <sup>21</sup>	1	1.15	0.46	0	0.54	MIF	Medium
<i>Stellifer brasiliensis</i> <sup>22</sup>	2	1.12	0.64	0	0.33	MIF	Medium
<i>Umbrina coroides</i> <sup>14</sup>	3	1.05	0.68	0	0.50	MIF	Shallow
<b>Scombridae</b>							
<i>Scomberomorus brasiliensis</i> <sup>23</sup>	5	1.21	0.51	0.32	0.33	Pisc	Medium
<i>Scomberomorus cavalla</i> <sup>24</sup>	3	1.35	0.50	0.33	0.40	Pisc	Shallow

**Table 2** (continued)

Family / Species	N	Ecomorphological indexes				TG	DP
		EC	E	R	S		
Serranidae							
<i>Diplectrum formosum</i> <sup>25</sup>	2	1.22	0.46	0.24	0.22	MIF	Deep
Sparidae							
<i>Calamus pennatula</i> <sup>25</sup>	1	1.22	0.43	0.20	0.38	MIF	Shallow
Sphyraenidae							
<i>Sphyraena guachancho</i> <sup>26</sup>	5	1.25	0.36	0.13	0.36	Pisc	Deep
Stromateidae							
<i>Peprilus paru</i> <sup>19</sup>	1	1.11	0.61	0.21	0.32	Carn	Medium

<sup>1</sup> Adams et al. (2012); <sup>2</sup> Crabtree et al. (1998); <sup>3</sup> Randall (2002); <sup>4</sup> Sley et al. (2009); <sup>5</sup> Chaves and Umbria (2003); <sup>6</sup> Duque-Nivia et al. (1996); <sup>7</sup> Vega-Cendejas et al. (1997); <sup>8</sup> Guedes et al. (2004); <sup>9</sup> Denadai et al. (2012); <sup>10</sup> Pombo et al. (2014); <sup>11</sup> Ferreira et al. (2004); <sup>12</sup> Estrada (1986); <sup>13</sup> Denadai et al. (2013); <sup>14</sup> Zahorcsak et al. (2000); <sup>15</sup> Marques et al. (2009); <sup>16</sup> Kehrig et al. (2013); <sup>17</sup> Bessa et al. (2014); <sup>18</sup> Castro et al. (2015); <sup>19</sup> Bowman et al. (2000); <sup>20</sup> Mendoza-Carranza and Vieira (2008); <sup>21</sup> Santos et al. (2016); <sup>22</sup> Sabinson et al. (2015); <sup>23</sup> Begg and Hopper (1997); <sup>24</sup> DeVane (1978); <sup>25</sup> Gómez-Canchong et al. (2004); <sup>26</sup> Akadje et al. (2013)

sum of the harmonics using the SHAPE software (Iwata and Ukai 2002) to visualize patterns in otolith shape. The Fourier harmonics were normalized in relation to the first harmonic – represented by a displacement circle with barely no information about the original shape (Kuhl and Giardina 1982; Iwata and Ukai 2002) –, and the mean contour as well as its standard deviation were formed by the outline reverse Fourier transform. All statistical analyses were performed at a significance level of  $p < 0.05$ .

## Results

Among the 45 Fourier harmonics extracted to describe otolith shape, the first 12 harmonics explained more than 99.99% of variation and were thus used for the multivariate analysis. Although harmonics were able to visually discriminate both trophic and depth preference groups better than ecomorphological indexes (Figs. 2 and 3), overall jack-knifed classification success between both descriptors were very similar, with harmonics correctly classifying 90.38% of assigned trophic groups and 75.96% of given depth preference categories, against 82% and 56.25% of ecological indexes, respectively (Tables 3 and 4). In both descriptors, misclassification percentages among trophic groups were particularly high between mobile invertebrate feeders and carnivorous species, while considering

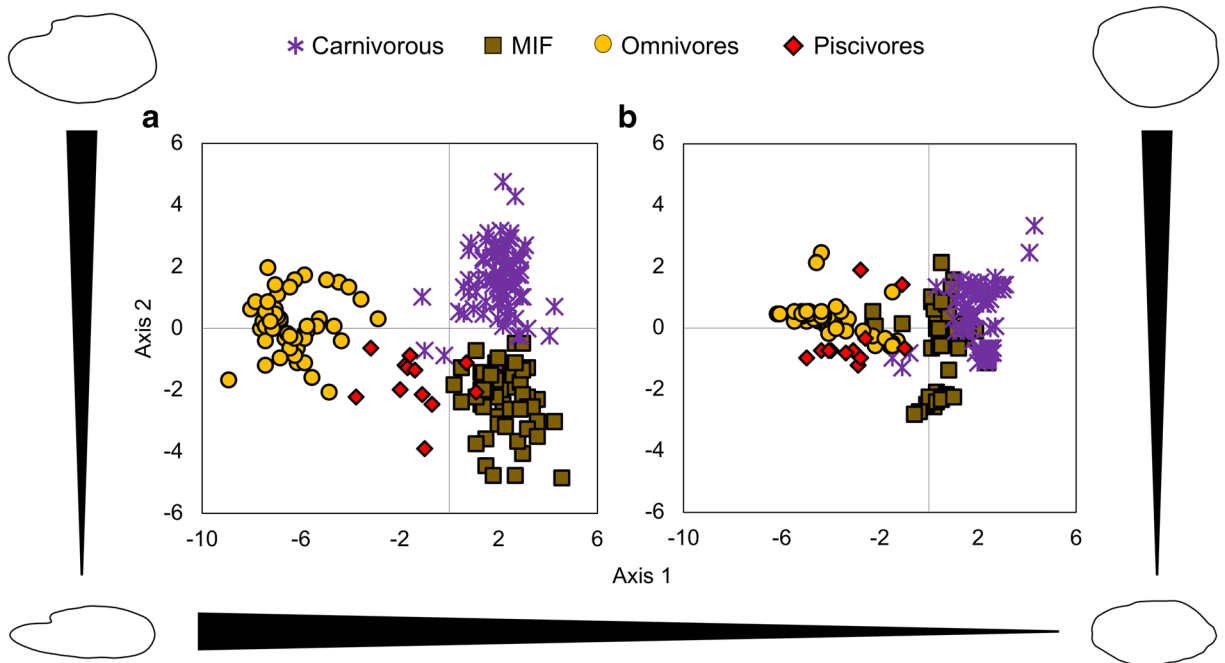
depth preference categories greater similarity was found among species from medium and deep depths (Tables 3 and 4).

Statistically, both descriptors were good predictors of trophic groups and depth preference categories (PERMANOVA, Pseudo-P < 0.05), however no interactions between these two factors were found (Pseudo-P = 0.998). Differences in average shapes between trophic groups and depth preference categories could be observed by the reconstructed outlines of the mean Fourier harmonics. The main shape difference between trophic groups occurred in otolith elongation due to rostrum development and complexity, with piscivorous and omnivorous species presenting a more developed rostrum and elongated otolith with high complexity, while carnivorous and mobile invertebrate feeders individuals showed a tendency towards a rounded shape (Fig. 2). Considering the depth preference categories, otoliths of species living in deeper depths showed a rounded shape in comparison to otoliths of the ones from shallow waters (Fig. 3).

## Discussion

In our study, both studied descriptors of otolith morphology were good predictors of features related to tropical species' ecology, such as trophic groups and depth strata preference. In both methods, species in the same group clustered together regardless variability in

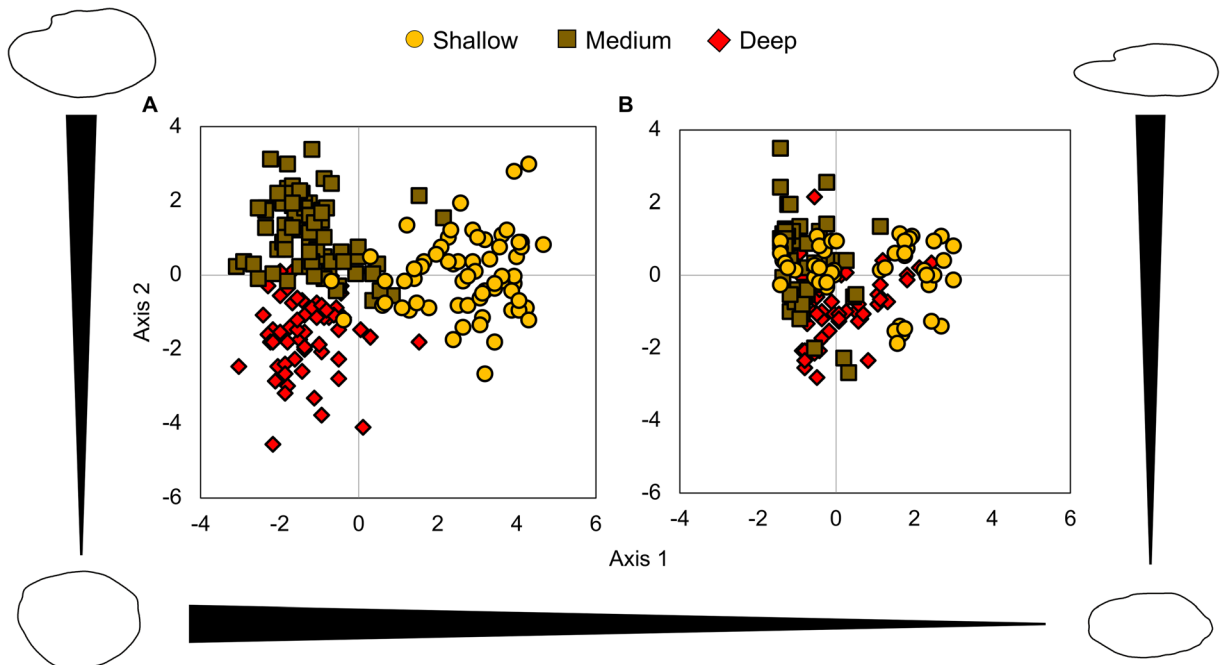




**Fig. 2** Linear discriminant analysis scores for the classification of trophic guilds of studied species based on Fourier descriptors (a) and ecomorphological indexes (b)

body shape and phylogenetic relationships, indicating that otoliths can retain a wider range of ecological information in their shape, which can be retrieved from

simpler analysis such the use of ecomorphological indexes, or more complex methods like the use of geomorphometric analysis.



**Fig. 3** Linear discriminant analysis scores for the classification of depth strata preference of studied species based on Fourier descriptors (a) and ecomorphological indexes (b)

**Table 3** Jack-knifed classification matrix – in percentage – for the LDA analysis of studied fish trophic groups with ecomorphological indexes and elliptic Fourier descriptors (Carn – carnivorous; MIF – mobile invertebrate feeders; Omn – omnivorous; Pisc – piscivorous)

Groups	Ecomorphological indexes (%)				Fourier descriptors (%)			
	Cam	MIF	Pisc	Omn	Cam	MIF	Pisc	Omn
Carn	71	23	4	2	86	7	5	2
MIF	6	93	1	0	4	94	2	0
Pisc	0	0	67	33	33	0	67	0
Omn	2	0	20	78	2	0	2	96

Although ecomorphological indexes were not able to visually distinguish trophic groups or depth strata categories as Fourier harmonics did (Figs. 2 and 3), both methods can clearly indicate differences between different ecological groups as shown by PERMANOVA and jack-knifed cross-validation results. In general, harmonics have been considered a powerful method to describe otolith shapes comprehensively (Lestrel 1997), especially when it come to understand ecological features of species since this method captures the entire shape variation and small-scale individual differences (Gagliano and McCormick 2004). However, our results show that ecomorphological indexes can also be good descriptors of ecological functions, despite being simpler indicators of morphology (Mahe et al. 2016).

In previous works, ecomorphological indexes have been widely used to describe water column use and associations to different types of substrate (Volpedo and Echeverría 2003; Volpedo et al. 2008), but in the present study, their combination with Fourier harmonics allowed us to identify relationships with other aspects of species' ecology. For example, piscivorous and omnivorous species presented otoliths with a tendency towards a more elongated shape, pronounced rostrum and high complexity which enhance fishes' swimming capability and help in prey detection and capture due to

specialization in acoustic communication (O'Toole et al. 2010; Ferguson et al. 2015; Schrandt et al. 2015). Moreover, as preys consumed by these groups are often found in the middle of the water column, some adaptive aspects, such as a well-developed rostrum, are required to support a high luminosity and noisy pelagic environment near the sea surface (Begg and Hopper 1997; Paxton 2000; Lombarte and Cruz 2007). This feature allow species to process information faster than sedentary species, making them quicker swimmers and enhancing its ability to capture preys (Lyachakov and Redbane 1993; Popper et al. 2005). Additionally, higher edge complexity found for piscivorous and omnivorous species may be associated to greater levels of food consumption, as it has been shown by studies that otolith lobes' formation depends on the protein accretion process (Hüssy 2008).

On the other hand, carnivorous and mobile invertebrate feeders were characterized by otoliths with rounded shape, regular edges and smaller or not-developed rostrum. Fish species in these groups feed mainly on organisms associated with the substrate – e.g., crustaceous, polychaetas –, which do not require them to move up in the water column (Crabtree et al. 1998; Marques et al. 2009), neither a great swimming performance to capture their preys (Freitas et al. 2011;

**Table 4** Jack-knifed classification matrix – in percentage – for the LDA analysis of depth preference strata for studied fish with ecomorphological indexes and elliptic Fourier descriptors

Groups	Ecomorphological indexes (%)			Fourier descriptors (%)		
	Shallow	Medium	Deep	Shallow	Medium	Deep
Shallow	57	34	9	83	8	9
Medium	4	63	33	7	72	21
Deep	18	28	54	1	25	74



Denadai et al. 2015). Our results agree with Volpedo et al. (2008) which found that not active swimmers exhibit tendency towards a rounded otolith.

In relation to patterns found in otoliths associated to depth strata preference of species, the presence of fishes with elongated otoliths in coastal and shallow areas goes against the expected. According to Lombarte and Cruz (2007), otolith size tends to increase with depth as a compensatory response to the reduction of light. However, the pattern found in our study may be explained by the narrow extension of the oceanic shelf in the studied region (50 km), which allows pelagic species to undertake migratory movements to coastal and estuarine areas for feeding or reproduction (Kadison et al. 2010). One reason for this investment in migratory movements may be associated to the estuarization process that occurs in the tropical region (Passos et al. 2016) which creates a highly productive zone that attracts species from deeper regions.

Furthermore, it is important to notice that otolith morphology was able to identify trophic groups despite body shape similarities and phylogenetic relationships among studied species. For example, although the three studied carangid species in our paper have a close phylogenetic relationship and resembling body structures, they were all clustered separately, being placed near to species that share similar feeding habits with them. Comparable results were found for Gagliano and McCormick (2004) that showed that otolith shape embodies a sensitive record of individual recent feeding histories independently of their size or age. Factors that allow morphological patterns in otoliths to accurately reflect ecological characteristics of species include their lack of extreme morphologies – which strongly influence ecomorphological indexes – (Tuset et al. 2016a), and the fact that otolith shape is a species-specific feature formed throughout fish life-history (Wilson 1985) which allows the retaining of information regarding habitat use, locomotion, mobility and feeding behavior (Volpedo and Echeverría 2003; Lombarte and Cruz 2007; Volpedo et al. 2008).

In summary, our results show that ecomorphological patterns and Fourier harmonics are good predictors of ecological groups of tropical fishes, providing a wider range of information regarding the feeding strategies and habitat use by species. Such information is of great importance to estimate the functional structure of assemblages and help us to understand more about the role played by species in the ecosystems (da Silva et al.

2019). Therefore, we conclude that Fourier descriptors and ecomorphological indexes that are associated to the shape, rostrum length and sulcus area of otoliths can be included in future studies as functional traits in order to obtain a more realistic picture of how functionally diversity the studied communities are. Besides that, in our work we had an approach exploring 2D data (e.g., linear measures), for the future, we intend to add 3D data, which may provide new insights about functional characteristics of otoliths.

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