



## Morphological patterns of five fish species (four characiforms, one perciform) in relation to feeding habits in a tropical reservoir in south-eastern Brazil

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### Summary

Described are the ecomorphological attributes of five abundant fish species and their relationships to the feeding ecology in a tropical reservoir in south-eastern Brazil. A total of 140 individuals were used. All specimens were collected between October 2006 and September 2007. Nine ecomorphological indexes were used and patterns detected by principal components analysis. The carnivorous species (*Oligosarcus hepsetus*) showed higher relative height of mouth to the mouth width aspect. On the other hand, the herbivorous species (*Metynnis maculatus*) had a higher compression index to the relative height. *Geophagus brasiliensis* (perciform) exhibited a larger relative length of the head to the relative length of the caudal peduncle. The two *Astyanax* species (*A. bimaculatus* and *A. parahybae*), although with taxonomic and morphological proximities to each other, exhibited indications of morphological adjustments probably associated to adaptive divergence. Three well-defined trophic groups were confirmed by the cluster analysis. The ecomorphology was effective in predicting feeding habits and aspects of locomotion, and the eventual consequences of the impoundment may be triggering a morphological divergence between closely related species. The authors hope that knowledge with regard to the effects of these man-made ecosystems on ichthyofauna ecomorphology will be further elucidated in the coming years, perhaps providing advice for their implementation in future hydro-power projects.

### Introduction

The ecomorphological paradigm infers that morphological features are adaptive, i.e. they evolve and diversify due to competition, predation or other biotic interactions (Bock, 1990). Using morphological traits to predict species or community patterns of food and habitat use is one possibility of ecomorphological studies (Wainwright and Richard, 1995) which can be accomplished by using morpho-biometric indices known as ecomorphological attributes. Furthermore, changes in morphological traits can be related to environmental changes where species can adapt by changing structure as the result of complex interactions with other species (biotic interactions) or to new environmental constraints.

Because species morphology is somehow linked to habitat use and its performed niche, alterations in the environment such as those resulting from dam construction may restrict the permanence of certain previously existing species. Fish species inhabiting reservoirs are those possessing morphologies that allow behavioural plasticity, or those adapted to cope with new standing water conditions (Cunico and Agostinho, 2006).

Although such restrictions can be related to feeding and reproductive strategies of each species, their morphological characteristics may also influence the selection of those more suited to colonize the new environment.

The damming of rivers around the world is increasing, yet the understanding of these consequences is still in progress. As a result of this change in the watershed landscape, the fish community and other organisms are suffering rearrangements, with the successful colonization of the environment for certain species and the decrease or even loss of others (Agostinho et al., 1999). Nevertheless, few ecomorphological studies contemplate these environments; according to Teixeira and Bennemann (2007), knowledge about the spatial use and its relation to the diet of fish species is limited, especially in recording the occurrence of non-native species. The Paraíba do Sul River is one of the most used lotic systems in Brazil because it is located between large urban-industrial centres (Pinto et al., 2006; Araújo et al., 2009), and presents successive dams on its longitudinal axis. The Funil reservoir is the largest impoundment in this river and represents a strong break in the river flow, altering physical habitats and nutrient input. Understanding morphological diversity of organisms and its use as a tool in the exploitation of natural resources in unusual environments such as reservoirs, which differ from both rivers and lakes, is important because the structural and functional aspects of their communities are still unknown. It is expected that the morphology reflects fish adaptation to the reservoir.

The present study aims to describe the ecomorphological attributes related to ecological differences among the abundant species *Astyanax bimaculatus* (Linnaeus, 1758), *Astyanax parahybae* Eigenmann, 1908, *Oligosarcus hepsetus* (Cuvier, 1829), *Metynnis maculatus* (Kner, 1858) and *Geophagus brasiliensis* (Quoy and Gaimard, 1824) in the Funil reservoir in order to test whether these attributes predict feeding habits and to identify morphological patterns that successfully colonized the reservoirs.

### Material and methods

Funil reservoir (Fig. 1) has a 16 800 km<sup>2</sup> catchment and 40 km<sup>2</sup> surface area, mean depth of 22 m and a retention time ranging between 10 and 50 days (Rocha et al., 2002), with a wide variation in water levels that erode the banks substantially. The samples were obtained from vouchers available at the Fish Ecology Laboratory of the University Federal Rural of Rio de Janeiro, from a monthly sampling program carried out from October 2006 to September 2007. Five species were selected (*A. bimaculatus*, *A. parahybae*, *O. hepsetus*, *M. maculatus* and *G. brasiliensis*), considering the abundance and

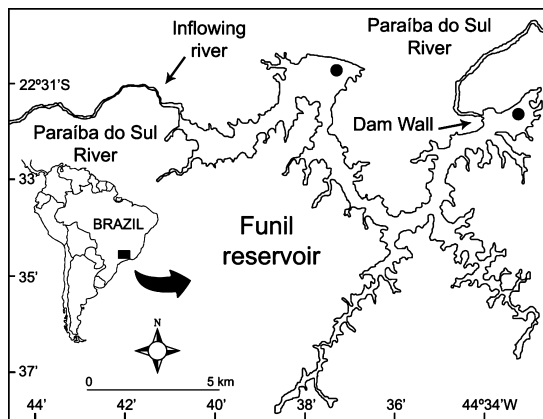


Fig. 1. Map of Funil reservoir showing sampling sites (●)

distribution in this and others Brazilian reservoirs with the intention for future comparisons related to morphological traits to predict species or community patterns or feeding and habitat use. The main diet for each species was identified from the available literature (Table 1).

The morphometric measures – Standard Length; Body Height; Body Width; Head Length; Pectoral Fin Length; Pectoral Fin Width; Caudal Peduncle Length; Caudal Peduncle Height; Caudal Peduncle Width; Mouth Height and Mouth Width – were performed according to the criteria proposed in previous studies (Gatz, 1979a,b; Watson and Balon, 1984; Balon et al., 1986; Freire and Agostinho, 2001) in order to reflect traits associated to habitat use and feeding. Absolute measurements were taken with a calliper accurate to 0.01 mm. Only adults of sizes above  $L_{50}$  (average length of first gonadal maturation, according to data from Vazzoler, 1996) were used in order to avoid eventual allometric effects.

Ecomorphological attributes – Compression Index (CI); Relative Height (RH); Relative Length of the Caudal Peduncle (RLP); Caudal Peduncle Compression Index (CPC); Pectoral Fin Aspect (PFA); Relative Length of the Head (RLH); Relative Width of the Mouth (RWM); Relative Height of the Mouth (RHM) and Mouth Aspect (MA) – were calculated based on morphometric measurements interpreted as indicators of lifestyle or adjustments to the different habitats, as described in studies by Mahon, 1984; Watson and Balon, 1984; Balon et al., 1986; Barrella et al., 1994; Freire and Agostinho, 2001.

The data matrix of ecomorphological attributes was submitted to principal components analysis (PCA) to detect patterns that could clarify the greater part of variation in the original data, allowing understanding of the structure and

changes expressed in the morphological data. To avoid super factorization, only factors with eigenvalues  $> 1.0$  were considered, following the Kaiser-Guttman criteria (Jackson, 1991). This procedure was performed using the Statistica 7.0 package (Statsoft, Tulsa, OK, USA).

A cluster analysis aimed to identify species groups using ecomorphological attributes as descriptors. The Bray-Curtis similarity and UPGMA clustering method was applied, with the analysis performed using the Primer 5.0 software (Clarke and Warwick, 1994).

## Results

Principal component analysis of the ecomorphological attributes yielded two axes with eigenvalues higher than one, explaining 68.9% of the total variance (Table 2): the first component (PC1) explained 48.1%; the second axis (PC2) explained 20.8%. The attributes which most contributed to PC1 were CI and RH, which were directly associated, and RHM and MA, which were negatively associated to this axis. *Metynnis maculatus* was directly related to axis 1 and was characterized as having a laterally compressed body, high body height and relatively small head. *Oligosarcus hepsetus* was inversely correlated to PC1 and characterized as having a relatively low body, large transversal section and large mouth (Fig. 2). A combination of these variables along the PC1 axis allowed identification of two important features for species distinction: hydrodynamic morphology and height of the prey. The PC2 was inversely associated to RLH and RLP, which was closely related to *G. brasiliensis*. This species has a relatively long head and large caudal peduncle.

Table 2

Factor loads from principal component analysis on ecomorphological attributes of selected fish species

Ecomorphological attributes	CP1	CP2
Compression Index	<b>0.884</b>	0.358
Relative Height	<b>0.953</b>	0.153
Relative Length of the Caudal Peduncle	-0.400	<b>-0.820</b>
Caudal Peduncle Compression Index	-0.053	-0.156
Pectoral Fin Aspect	0.502	-0.194
Relative Length of the Head	0.307	<b>-0.709</b>
Relative Width of the Mouth	0.692	-0.656
Relative Height of the Mouth	<b>-0.892</b>	-0.150
Mouth Aspect	<b>-0.925</b>	0.177
Eigenvalues	4.32	1.87
Percentage of Explained Variance	48.09%	20.80%

Values in bold highlight the most contributing scores to the observed variance.

Table 1

Species list with, scientific name, sampling size (N), trophic guilds and main food

Species	N	Trophic guilds	Main food	References
<i>Astyanax bimaculatus</i>	30	Omnivore	MP; INV; SE; S	Arcifa and Meschiatti (1993); Andrian et al. (2001); Dias et al. (2005)
<i>Astyanax parahybae</i>	30	Omnivore	MP; INV; SE; S	Lowe-McConnell (1975); Lauder and Liem (1983); Esteves and Galetti (1995)
<i>Oligosarcus hepsetus</i>	24	Carnivore	INV; FI; S; F	Lowe-McConnell (1975); Dias et al. (2005); Araújo et al. (2005); Botelho et al. (2007)
<i>Metynnis maculatus</i>	30	Herbivore	MP; AP	Resende et al. (1998); Smith et al. (2003)
<i>Geophagus brasiliensis</i>	26	Omnivore	INV; MUD; SE; FRU	Sabino and Correa-Castro (1990); Aguiaro and Caramaschi (1998); Dias et al. (2005)

AP, algae and periphyton; INV, invertebrates aquatic and terrestrial; MUD, soft substratum; SE, seeds; FRU, fruits; MP, material plant; FI, fins; S, scales; F, flesh fish.

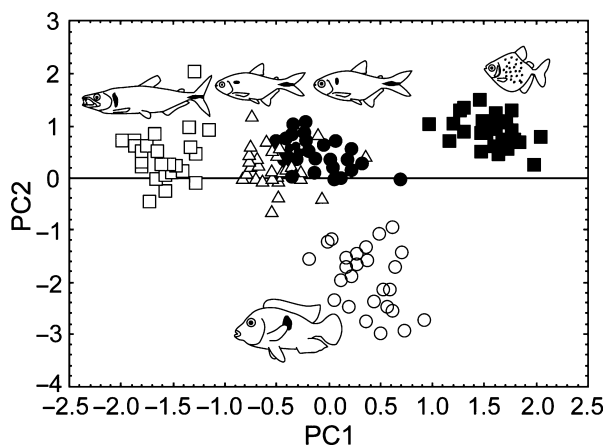


Fig. 2. Ordination diagram, Funil reservoir, from first two principal components on ecomorphological attributes of five studied species: *Astyanax bimaculatus* (●); *A. parahybae* (Δ); *Oligosarcus hepsetus* (□); *Metynnis maculatus* (■); *Geophagus brasiliensis* (○). Sample size (n) for each species indicated in Table 1

The two species of *Astyanax* were located near the centre of the ordination diagram and were characterized as having an intermediate mouth and head size, fusiform body and intermediate caudal peduncle. Despite their taxonomic and morphological proximity, *A. bimaculatus* had a comparatively large mouth opening, whereas *A. parahybae* had a comparatively higher body height.

Cluster analysis of the average values of ecomorphological attributes identified three groups that coincided with fish feeding habits (Fig. 3): one group formed by the omnivorous species *A. bimaculatus*, *A. parahybae* and *G. brasiliensis*; a second group formed by the carnivorous *O. hepsetus*; and a third group formed by the herbivorous *M. maculatus*.

## Discussion

The five abundant species studied in Funil reservoir had clear differentiated ecomorphological traits with low within-group variation and a clear between-group separation, suggesting that selection could be operating on their morphologies to adapt and cope with new standing water conditions by food partition and different habitat use, thus avoiding competition.

*Metynnis maculatus* had higher CI and RH compared with the others examined species. These attributes are associated with the use of structured habitats, where fish with a high and

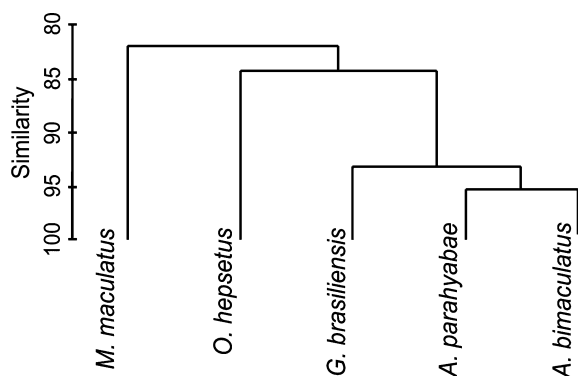


Fig. 3. Dendrogram from cluster analysis on ecomorphological attributes of five fish species, Funil reservoir

laterally compressed body find less resistance when performing manoeuvres such as pitch or yaw (Alexander, 1967). Experimental data have shown that short and compressed fish have higher manoeuvrability (Werner, 1977; Webb et al., 1996), therefore it is reasonable to hypothesize that the close association between these two ecomorphological attributes with *M. maculatus* is an indication of how this species is adapted to their original habitat (Amazon rivers), where the systematic forest floods provide an increase in the habitat heterogeneity. This species, characterized by herbivorous feeding habits, presented the highest differentiation from other species, as demonstrated by the ordination and clustering analysis, indicating the influence of shape on the diet. The morphology suggests it is a herbivore associated mainly with fruits and seeds that are crushed by its strong molariform teeth. The body shape is more closely related to taxonomic groups of other Serrasalminae species such as *Colossoma* spp. and *Piaractus* spp., which are also herbivorous, since other herbivores can have differentiated shapes such as those species of *Brycon* spp. and *Leporinus* spp. that have long and hollow body shapes.

*Oligosarcus hepsetus* showed higher RHM and MA, indicating the other extreme of the trophic niche, exploring lotic environments and having carnivorous feeding habits. A carnivorous fish of the Acestrorhynchinae subfamily, it is characterized by a wide mouth opening that allows with a single bite ingestion of an entire prey (Casatti et al., 2001). In the present study this pattern was corroborated by the high values of these two attributes in the ACP and also by the form of a single branch in the cluster analysis. *O. hepsetus* is common in many reservoirs of the Paraíba do Sul River and preys on smaller species such as *Astyanax* spp. (Araújo et al., 2005; Dias et al., 2005; Botelho et al., 2007). In common with other carnivorous species it has a relatively large head, caudal peduncle and mouth, indicating that they feed on large prey and have a good swimming capacity. The large terminal mouth with a broad opening and sharp, conical teeth is suitable for grabbing and biting the prey.

A third group detected in the cluster analysis and occupying an intermediate position in the PCA was formed by two species of *Astyanax* and *G. brasiliensis*, the latter distinguishing itself with the highest RLH and RLP. *Astyanax* spp. are midwater-surface foraging characins and *G. brasiliensis* is a benthic cichlid (Géry, 1977; Taphorn, 1992). Yet despite typical foraging niches, many fishes consume abundant prey when available, even outside their speciality (Lowe-McConnell, 1975, 1987; McKaye and Marsh, 1983; Winemiller, 1989, 1990; Robinson and Wilson, 1994). Because a reservoir typically contains more zooplankton than the inflowing river (Saunders and Lewis, 1988, 1989; Hamilton et al., 1990), it might be expected that *Astyanax* spp. and *G. brasiliensis* forage more frequently on these midwater prey items. The relatively compressed body and height, as well as terminal mouth and multicuspoid teeth in *G. brasiliensis* indicate preference for low dynamism and calm waters at the margins and structured littoral zones, with some capacity to perform vertical movements.

The long caudal peduncle in *Geophagus brasiliensis* is an ecomorphological attribute that was not expected to match its general behaviour because it is not an active swimmer, and not even a predator of potentially large species. *G. brasiliensis* is one of the most common species in Brazilian rivers, with a high capacity for adaptation to lentic environments, and is abundant in lakes and reservoirs in Rio de Janeiro state

(Santos et al., 2004; Araújo et al., 2009). This is an omnivorous fish that uses the feeding tactic of picking up substrate and sorting prey (Sabino and Correa-Castro, 1990). When ecomorphological relationships are barely in evidence, other inferences may be taken from a more detailed morphological analysis. Such as fish with rounded caudal fins (e.g. *G. brasiliensis*), which have lower values for the ratio index (ratio of the squared height of a fin divided by its area) and which are generally not good swimmers (Pauly, 1989). Some fish having these characteristics exhibit a better performance in habitats that are spatially heterogeneous; often their fins are flexible, allowing fine position adjustments (Gosline, 1971), as occurs in this and other species of Perciformes.

*Astyanax* spp. generally are classified as omnivorous and opportunist species, which display a great ability to change their prey according to environmental variations and shortages of their principal food (Lobón-Cerviá and Bennemann, 2000). *Astyanax* species apparently have few morphological, ecological and behavioural differences, suggesting their being a group in recent speciation (Gurgel, 2004). According to Horn (1998), omnivores have broad morphologic variations, probably related to the lack of specialization that characterizes this trophic group.

A clear separation in ecomorphological traits between the two *Astyanax* species was found according to PCA, with *A. paraguayae* having comparatively higher RHM and MA allowing the ingestion of large-sized prey in the water column; *A. bimaculatus*, however, had comparatively higher CI and RHW that enable use of more structured habitats in the margins, where fish with high and laterally compressed bodies find less resistance when performing manoeuvres. Such differentiation may be an indication that these two species are experiencing morphological diversification in order to explore different habitat and feeding resources, thus avoiding competition. Morphological divergence at the intraspecific level associated with habitat use was found for two conspecific populations of neotropical fish [(*Bryconops caudomaculatus*, Characidae; *Biotodoma warrini*, Cichlidae (Langerhans et al., 2003)]. For both species, maximum body depth was positioned more anteriorly (i.e. fusiform) in the river channel than in lagoons and also exhibited a relatively terminal mouth in the lagoons compared to the main river channel. Piorski et al. (2005) examined the ecomorphological index of two species of piranha in a tropical marginal lagoon and found that the species were discriminated by swimming ability, water column position and relative prey size.

The 'confined' nature of a reservoir can lead to selective pressure in functional redundancy among fish species favouring the niche filtering hypothesis, *sensu* Zobel (1997), which prevents species too dissimilar from one another to co-occur (i.e. abiotic properties of the habitat) and acts as a filter allowing only a narrow spectrum of species to survive. Environmental factors certainly limit the presence of certain functional traits, thus decreasing functional diversity of local communities under environmental pressure and leading to a simplification of ecosystem processes in such areas. This pattern was also found for fish communities in coastal lagoons, another kind of 'confined' system, as reported by Mouillot et al. (2007).

It can be concluded that the studied species followed patterns reported by Pianka (2000) in that morphological changes among species reflect, at least in part, the differentiated use of resources, and finally, ecological differences with a parallel between morphological and ecological similarity. It is believed that a given set of morphological characters indicates delimitation of trophic groups (Hugueny and Pouilly, 1999; Pouilly et al., 2003). Within this context, the segregation of species in the cluster confirms the interaction between morphology and feeding habits. Moreover, the ordination analysis brings out possible consequences related to impoundments of species with similar morphology. According to the above, the ecomorphology was effective in predicting feeding habits and aspects of locomotion; the eventual consequences of the impoundment may be triggering some morphological divergence between closely-related species.

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