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Habitat partitioning, habits and convergence among coastal nektonic fish species from the São Sebastião Channel, southeastern Brazil

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Based on a fish survey and preliminary underwater observations, 17 “morphotypes” were identified that characterize the morphological diversity found within 27 nektonic fish species sampled at São Sebastião Channel. Such “morphotypes” were studied using an ecomorphological approach, with the intention to investigate similarities and differences in shape and habits. Underwater field observations were also performed, to verify if the lifestyle of these species, such as vertical occupation of the water column and the habitat use, are in accordance with their distribution in the morphospace. The results, complemented with data from scientific literature on the taxonomy and phylogenies of these species, allowed discussing some of the typical cases of convergent and divergent evolution. Some of the ecomorphological clusters had no phylogenetic support although this is probably due to the environmental conditions in which theirs members have evolved. The body shape and fins positions of a fish clearly influence its ecological performance and habitat use, corroborating the ecomorphological hypothesis on the intimate link between phenotype and ecology.

Com base em um levantamento ictiofaunístico realizado com diversos métodos de captura e em observações subaquáticas preliminares foram selecionados 17 “morfótipos” representativos da diversidade morfológica apresentada dentre 27 espécies de peixes nectônicos amostradas no Canal de São Sebastião. Tais “morfótipos” foram estudados por meio de uma abordagem ecomorfológica com o intuito de investigar semelhanças e diferenças quanto às suas formas e hábitos. Observações diretas no ambiente também foram realizadas para verificar se o modo de vida dessas espécies, assim como a ocupação vertical da coluna d’água e o uso do habitat, condizem com suas distribuições pelo espaço morfológico. Os resultados obtidos, complementados com dados da literatura científica sobre taxonomia e relações de parentesco evolutivo dessas espécies, permitiram discutir alguns típicos casos de convergência e divergência evolutiva. Alguns agrupamentos ecomorfológicos não tiveram qualquer suporte filogenético tendo sido resultantes, provavelmente, das condições ambientais na qual seus membros evoluíram. A forma do corpo e a posição das nadadeiras de um peixe claramente influenciam seu desempenho ecológico e o uso do habitat, corroborando a hipótese ecomorfológica sobre a estreita relação entre fenótipo e ecologia.

Key words: Body form, Fins shape, Fins position, Pelagic fishes, Ecomorphology.

Introduction

“Strong relationships between basic form and ecological function in fishes allow the comparative study of ecological relationships using morphological features” (Winemiller, 1992). Morphology has been used as a predictor of the way-of-life (see Karr & James, 1975; Wainwright & Reilly, 1994); the ecomorphological hypothesis is based on the idea that the morphological attributes of each species should reflect its ecology and, thus, can be used as indicative of its habits and adaptations to different habitats (Van der Klaauw, 1948; Keast & Webb, 1966; Winemiller, 1991, 1992). The central focus of an ecomorphological study (see Karr & James, 1975) is the interaction of morphological and ecological diversity among organisms both in the present and over evolutionary time (Motta & Kotrschal, 1992; Motta *et al.*, 1995b).

Biological convergence is the independent evolution of the same feature within divergent phylogenetic lineage, and the diverse groups of Actinopterygii exhibit numerous examples of ecological convergence (see Winemiller, 1992). As one example, nektonic fishes share many ecological and morphological characteristics; they are basically active and good diurnal swimmers that can form huge schools and feed mostly in the water column where they achieve camouflage

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via three mechanisms: (1) counter shading, (2) silvery sides, and (3) transparency (*cf*. Lagler *et al*., 1977; Helfman *et al*., 1997). In general, the bodies of such fishes are laterally compressed and/or elongated, and their caudal fins, if present, are furcated, with a cylindrical peduncle. Their pectoral fins are also characteristic, being thinner and more elongated when compared to benthic forms. The eyes of a nektonic fish are generally laterally positioned and their mouths are terminal, with a diet composed mainly of other nektonic species or plankton (Helfman *et al*., 1997).

Nektonic fishes have been studied mostly when they are economically relevant or when they belong to high trophic levels, generally for purposes of fisheries management or to characterize food webs structure (see Lowe-McConnell, 1999; Barreiros *et al*., 2003). Otherwise, behavioral studies on such fishes in the wild have revealed some interesting finds on their ecology and/or evolution (*e.g*., Sazima, 1998; Sazima *et al*., 1999).

The main goal of this study is to quantify and compare the similarities and differences in body/fins form and shape, ecology (mainly habitat partitioning) and evolutionary relationships among 17 species of nektonic fish chosen as representative (here called "morphotypes") of the morphological diversity found within 27 nektonic fish species sampled at São Sebastião Channel, to identify and discuss convergence and divergence within such coastal pelagic forms. These "morphotypes" belong to every fish family and order that was registered from the coastal pelagic habitats of the São Sebastião Channel during an unpublished fish survey (from May 1993 to May 1996) that employed several methods of capture (scuba dive with hand nets, spear fishing, angling, hand-line, floating long line, drift nets, trawl nets and manual seine) and also during 133 hours of underwater observations accumulated at the study area by the author since 1995 (Table 1). They are the commonest nektonic species of each higher taxon sampled during such survey and also according to author's personal observations.

In Brazil, the ecomorphological hypothesis has been tested mainly for freshwater fishes (*e.g*., Casatti & Castro, 2006; Ferreira, 2007, but see Gibran, 2007), and the concept of convergent evolution provides and important interface between ecology, morphology, and phylogenetics (Winemiller, 1991).

Material and Methods

Study area. Field work was carried out at São Sebastião Channel, a 25 km long stretch on the coast of São Paulo, southeastern Brazil, and its surroundings (23º41' to 23º54'S and 45º19' to 45º30'W) (Fig. 1). The study area includes rocky shores and reefs as well as sandy and muddy beaches. During the study, water surface temperature varied from 16 to 31°C (average 24.5°C) and horizontal visibility from 0.5 to 8 m (average 2.5 m).

Field-work. Underwater observations were conducted from February 2001 to February 2003 in depths up to 21 m (average of 8 m). A total of 140 hours (118 diurnal, 14 nocturnal and eight twilight), mainly with scuba and snorkeling dive observations (using *ad libitum* and focal animal samplings; *cf*. Altmann, 1974) were conducted, sampling all seasons and habitats (including the swash zones and tide pools). Thirty two sites distributed by the two margins of the São Sebastião Channel and also along its principal axis were explored. During each observation session fishes were visually identified, and then it was recorded the number of individuals of each species found, their respective positions in the water column, feeding

Table 1. The 27 nektonic fish species recorded from the São Sebastião Channel, southeastern Brazil (ordination is based in Nelson, 2006). The "morphotypes" chosen for this study are in bold type.

- Actinopterygii
  - Clupeiformes
    - Engraulidae
      - *Anchoa lyolepis* (Evermann & Marsh, 1900)
      - *Anchoa marinii* Hildebrand, 1943
      - ***Anchoa tricolor* (Spix & Agassiz, 1829)**
      - *Anchoviella lepidentostole* (Fowler, 1911)
    - Clupeidae
      - ***Harengula jaguana* Poey, 1865**
      - *Opisthonema oglinum* (Lesueur, 1818)
      - ***Sardinella janeiro* (Eigenmann, 1894)**
  - Mugiliformes
    - Mugilidae
      - ***Mugil curema* Valenciennes, 1836**
      - *Mugil* sp.
  - Atheriniformes
    - Atherinopsidae
      - ***Atherinella brasiliensis* (Quoy & Gaimard, 1825)**
  - Beloniformes
    - Hemiramphidae
      - *Hemiramphus brasiliensis* (Linnaeus, 1758)
      - ***Hyporhamphus unifasciatus* (Ranzani, 1841)**
    - Belonidae
      - ***Strongylura timucu* (Walbaum, 1792)**
  - Gasterosteiformes
    - Fistulariidae
      - ***Fistularia tabacaria* Linnaeus, 1758**
  - Perciformes
    - Pomatomidae
      - ***Pomatomus saltatrix* (Linnaeus, 1766)**
    - Carangidae
      - *Carangoides crysos* (Mitchill, 1815)
      - ***Caranx latus* Agassiz, 1813**
      - ***Chloroscombrus chrysurus* (Linnaeus, 1766)**
      - *Oligoplites saliens* (Bloch, 1793)
      - ***Oligoplites saurus* (Bloch & Schneider, 1801)**
      - ***Selene vomer* (Linnaeus, 1758)**
      - ***Trachinotus carolinus* (Linnaeus, 1766)**
      - *Trachinotus falcatus* (Linnaeus, 1758)
      - *Trachinotus goodei* Jordan & Evermann, 1896
    - Trichiuridae
      - ***Trichiurus lepturus* Linnaeus, 1758**
    - Scombridae
      - ***Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, 1978**
  - Tetraodontiformes
    - Tetraodontidae
      - ***Lagocephalus laevigatus* (Linnaeus, 1766)**

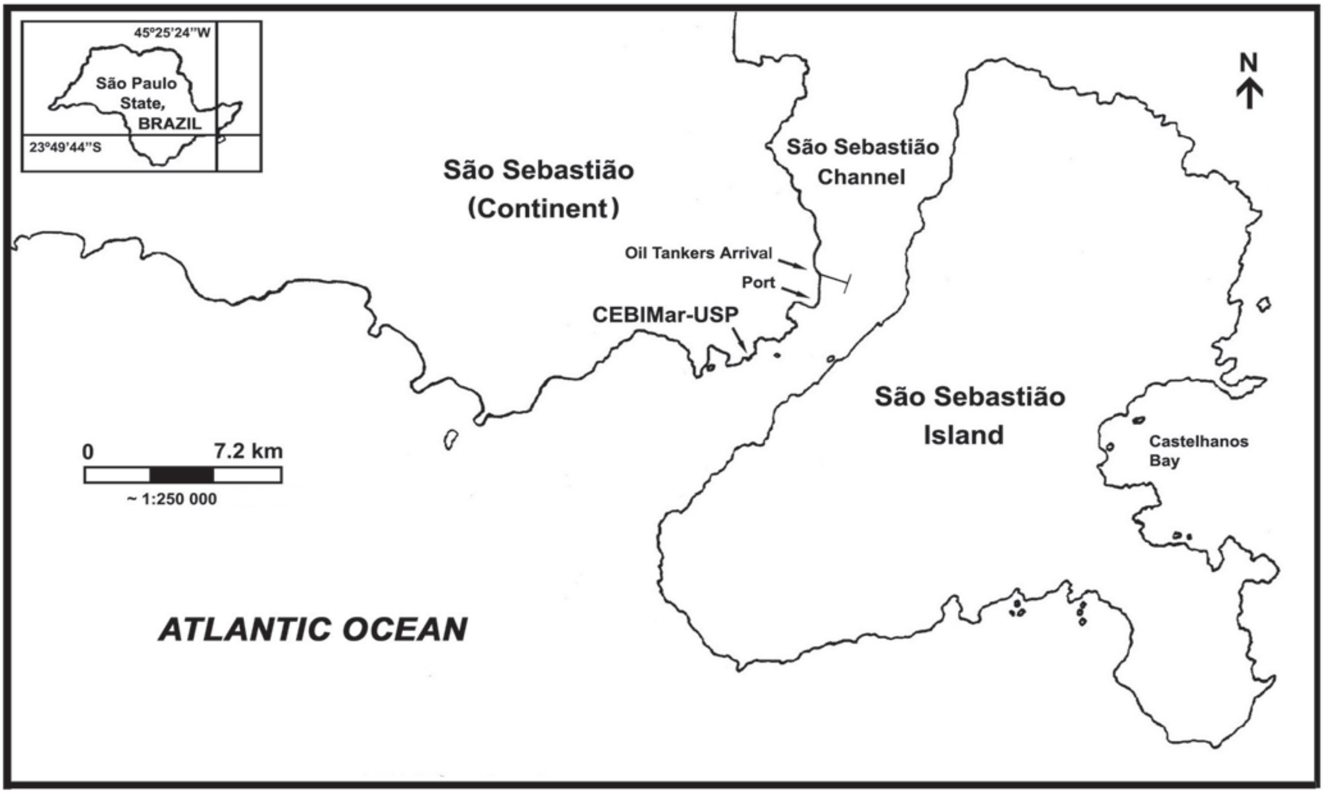

Fig. 1. Map indicating the location of the study area (São Sebastião Channel) and the marine station of the University of São Paulo (CEBIMar-USP) on the coast of São Paulo, southeastern Brazil.

tactics, feeding places, and activity (assessed based on food searching, feeding tactics, and swimming *vs*. inactive; *i.e*., quiescent or "sleeping"; *cf*. Collette & Talbot, 1972).

Ecomorphological analysis. Measures of up to 150 mm were taken with a digital caliper (0.1 mm of precision). Above this size measurements were taken with a plastic rule (1 mm of precision). All measurements were taken on specimens deposited in the Laboratório de Ictiologia de Ribeirão Preto (LIRP), Departamento de Biologia (FFCLRP), Universidade de São Paulo, Ribeirão Preto, Brazil and in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Table 2). All of the voucher specimens from the unpublished fish survey that gave support to this study are available in the fish collection of LIRP (LIRP 835-836; 1103-1119; 1121-1123; 1126-1127; 1139-1146; 1151-1253; 1255-1306; 1313-1415; 1425-1575; 1685-1693; 1706-1718; 1720-1761; 1763-1790; 1792-1812; 1864-1924; 2238-2242; 2977). Fin areas were estimated from their contour outlined on millimetric paper (*cf*. Beaumord & Petrere Jr., 1994). The following 19 ecomorphological attributes, which were chosen based on their biological interpretations, were calculated to each studied species:

a) Compression index (CI): maximum body depth divided by maximum body width (see flatness index in Gatz, 1979). High values indicate a laterally compressed fish. Compression index indicates the fish position in the water column (Watson & Balon, 1984).

b) Relative body depth (RBD): maximum body depth divided by standard length (SL). Low values indicate an elongated fish. It is assumed to be directly related to the capacity for making vertical turns. A fish with a high RBD value has great maneuverability (Gatz, 1979).

c) Relative peduncle length (RPL): caudal peduncle length divided by SL. Long peduncles indicate fishes with good swimming ability (Watson & Balon, 1984).

d) Caudal peduncle compression index (CPC): the depth of the peduncle at its midpoint divided by the width at the same point. High values are typical of less active swimmers (Gatz, 1979).

e) Index of ventral flattening (IVF): maximum midline depth divided by maximum body depth (Watson & Balon, 1984). Low values indicate fishes inhabiting waters with high hydrodynamism, able to maintain their spatial position even when stationary (Hora, 1930).

f) Relative area of dorsal fin (RAD): dorsal fin area divided by body area (Casatti & Castro, 2006). Body area was estimated (standard length times maximum body depth; *cf*. Watson & Balon, 1984). The dorsal fin is mainly a stabilizing plane and in some lineages such as the Tetraodontiformes it also plays an important role for locomotion (Lindsey, 1978).

g) Relative area of pectoral fin (RAPt): measured analogously to RAD. It is generally high among slow swimmers which use pectorals for maneuvering (Watson & Balon, 1984).

h) Relative area of pelvic fin (RAPv): measured analogously to RAD. Pectorals fins are larger in fishes with demersal habitat preference, thus being an indicative of fish position in the water column (Gatz, 1979).

i) Relative area of caudal fin (RAC): measured analogously to RAD. High values are most typical for benthic fishes, indicating ability to produce fast start bursts to ambush prey. Caudal fin area and thrust are related and nektonic fishes with greater relative caudal area swan further per tail beat (Magnuson, 1978).

j) Pectoral fin aspect ratio (PtAR): the maximum length of pectoral fin divided by maximum width. High values indicate long fins that are typical for cruising fishes that swim constantly (Watson & Balon, 1984).

k) Caudal fin aspect ratio (CAR): square of the maximum vertical distance (span) divided by the caudal fin area. High values indicate more active and continuous swimmer fishes (Watson & Balon, 1984).

l) Relative head length (RHL): head length divided by SL. A fish with a relatively larger head is able to handle larger prey (Gatz, 1979; Watson & Balon, 1984).

m) Relative eyes position (EP): depth of the eye midline divided by head depth at this same vertical line. Relative eyes position indicates the vertical habitat preference, since benthic fishes have more dorsally located eyes and nektonic fishes have eyes laterally located (Gatz, 1979; Watson & Balon, 1984).

n) Relative eye size (ES): the diameter of the eye divided by SL. It is directly proportional to the development of visual capabilities in the fish (Protasov, 1970 *apud* Gatz, 1979).

o) Relative mouth width (RMW): interior lateral dimension of the opening when the mouth is fully opened, divided by SL (Gatz, 1979).

p) Relative mouth height (RMH): interior dorsal-ventral dimension of the opening when the mouth is fully opened, divided by SL. Mouth dimensions would indicate, like head length, the relative size of prey (Gatz, 1979).

q) Mouth aspect ratio (MAR): the mouth height divided by mouth width. Mouth aspect ratio is related with the shape of the food, where high values indicate narrow mouths, but large aperture (Beaumord & Petrere Jr., 1994).

r) Index of mouth protrusion (IMP): the ratio of snout length with the mouth open to snout length with the mouth closed. Snout length is the distance from the interior surface of the anterior edge of the bony orbit of the eye to the anterior margin of the upper jaw at its midpoint. High values are common in fishes with the smallest prey (Gatz, 1979).

s) Mouth orientation (MO): the angle of the mouth open and protracted transformed in radians, considering the midpoint between lips and that a dorsal mouth is equal to 0º, a terminal mouth is equal to 90º, and a ventral mouth is equal to 180º. Mouth orientation indicates the position of food relative to the fish, and thereby, the position of the fish in the water column (Gatz, 1979; Watson & Balon, 1984).

Besides the above cited attributes, the general body coloration (as registered during underwater observations and literature data) was also considered for discussion. The feeding ecology and diet of fishes, which is nearly always associated to features such as dentition, dimensions and orientation of the mouth, gill rakers and digestive tube length (*e.g.*, Keast & Webb, 1966; Gatz, 1979; Winemiller, 1992; Wootton, 1994), was investigated in this study by compiling information from literature, conducting field observations on feeding tactics, and also by means of some ecomorphological attributes as relative head length (RHL); relative mouth width (RMW); relative mouth height (RMH); mouth aspect ratio (MAR); index of mouth protrusion (IMP); and mouth orientation (MO). It is important to point out that IMP has a strong phylogenetic component related mostly with the Acanthopterygii lineage (*cf*. Lauder & Liem, 1983).

A rectangular data matrix containing the mean values of the 19 ecomorphological attributes calculated for each 17 studied species (Table 3) was transformed into a cross-products matrix (variance/covariance) and submitted to a Principal Component Analysis (PCA), using the PC-ORD MjM Software (McCune & Mefford, 1999). Such analysis enables the interpretation of species distribution in morphospace. The use of ratios allows the first orthogonal axis from the PCA to be interpreted as a shape determinant rather than a size axis, besides reducing the chance of biasing the analysis due to dominance of a single variable, as body size (*cf*. Winemiller, 1991). The scores obtained from PCA were submitted to a Cluster Analysis (Gauch, 1982; Ludwig & Reynolds, 1988) to better represent the morphological distance (or similarities) among the studied species. A cophenetic coefficient (*i.e*., a measure of distortion) was calculated, using a standard routine of the software NTSYS 2.1 (Rohlf, 2000), to check if the cluster graphic product represented well the original matrix. Because there is always some level of distortion, it is generally considered acceptable a cophenetic coefficient equal or higher than 0.8 (*i.e*., $r \geq 0.8$; Rohlf & Sokal, 1981; Valentin, 2000).

To test the null hypothesis of no significant correlation between phylogeny and morphology a Mantel test was applied (Mantel, 1967), using the Matrix Comparison routine (MXCOMP) of NTSYS 2.1 (Rohlf, 2000). For this, the morphological cross-products matrix cited before was compared to a taxonomic distance matrix following Nelson (2006) in which a value of 1 was coded for species pairs belonging to the same subfamily, 2 for species-pairs belonging to different genera within the same family, 3 for species-pairs belonging to different families within the same suborder, 4 for species-pairs belonging to different suborders within the same order and 5 for species-pairs belonging to different orders within the same class (*cf*. Winemiller, 1991; Douglas & Matthews, 1992). Nowadays, most fish taxonomists consider evolutionary relationships when it is available. Both of these matrixes are symmetric (species *vs*. species), triangular, and diverge only as the type of distance measure between each pair of observations (*i.e*., species). Correlation were considered significant when $p < 0.05$ (see Mantel, 1967; Sokal, 1979; Hubert, 1987; Diniz-Filho, 2000).

Note: (1) the caudal filament of *Fistularia tabacaria* was ignored; (2) in the case of *Trichiurus lepturus*, where the peduncle, a caudal and pelvic fins are absent and *Lagocephalus laevigatus*, where pelvic fins are absent, zero values were applied for these attributes.

Results

With the exception of *F. tabacaria*, all studied species share the basic characteristics of nektonic fishes. *Fistularia tabacaria* diverges only in its disruptive general body coloration that contrasts with the reflective coloration of the other species. Table 4 shows some biological data observed and also compiled from the literature for these species.

The first component (Axis 1) explained 49% of the variance in morphological attributes (Table 5) and the main attributes in this axis were compression index (CI), relative body depth (RBD), caudal fin aspect ratio (CAR), and relative eye size (ES). Such attributes discriminate *Selene vomer* (the species with the most compressed and higher body, larger eyes and more furcated caudal fin) from all of the other nektonic species with a not-so high, more elongate or more fusiform body shape. On the other hand, the second component (Axis 2) explained 24% of the variance (Table 5) and the main attribute in this axis was caudal peduncle compression index (CPC), which discriminate *Harengula jaguana* (the species with the most compressed peduncle among the studied fishes) (Figs. 2-3).

Figures 2 and 3 show the groups A *vs*. B and B1 *vs*. B2 discriminated by the first components of PCA, in which the groups B and B1 are opposite to the groups A and B2, respectively, in relation to ecomorphological attributes CI, RBD, CAR, and ES, while B1 and B2 are also opposite in relation to attribute CPC (the members of group B2 have, in general, a more compressed peduncle than the members of B1). The cumulative variance of these two axes was 73% (Table 5). The leftward species have a higher and more compressed body, larger eyes and a caudal fin configuration typical of more efficient and fast visually oriented swimmers, while the rightward species are, comparatively, more elongate and not so fast/continuous swimmers. The members of group B2 have an intermediate body form compared to the lower and elongated body of the fishes of group A and to the fusiform body of the fishes of group B1.

The Mantel test revealed a non-significant correlation between phylogeny and morphology among the studied fishes ($r = 0.12$, $p = 0.22$; $p > 0.05$). Based on this find, the clusters A, B1 and B2 from figures 2 and 3 were used to illustrate and discuss some cases of convergence and divergence.

Discussion

The majority of species studied here share some important features presented on most nektonic fishes, as a body color that blend with the surrounding water and also with the pattern of light underwater, besides a hydrodynamic and relatively fusiform shape. One exception was *F. tabacaria*, that shows a color patter that can be considered disruptive and shared with benthic and nektobenthic fishes, which blends them with the

Table 2. List of the examined material from Laboratório de Ictiologia de Ribeirão Preto (LIRP, FFCLRP-USP) and from Museu de Zoologia da USP (MZUSP), São Paulo, Brazil.

Taxa	Range of standard length (mm)	Material examined and number of specimens by lot (n) when n > 1
Engraulidae		
Anchoa tricolor	66.65-102.25	LIRP 1162(4); LIRP 1163; LIRP 1164; MZUSP 10632(2); MZUSP 11555; MZUSP 18664
Clupeidae		
Harengula jaguana	69.93-79.16	LIRP 1199(10)
Sardinella janeiro	81.10-158.00	LIRP 1237; LIRP 833(3); MZUSP 11410(2); MZUSP 46177; MZUSP 47126(3)
Mugilidae		
Mugil curema	122.14-200.00	LIRP 1490; LIRP 1492; LIRP 1494; LIRP 1495; LIRP 1496; MZUSP 67383(2); MZUSP 67393(3)
Atherinopsidae		
Atherinella brasiliensis	90.88-109.60	LIRP 1440(2); LIRP 1441(2); LIRP 1444(2); LIRP 1446(2); LIRP 1447; LIRP 1449
Hemiramphidae		
Hyporhamphus unifasciatus	188.00-250.00	LIRP 1889(2); LIRP 1890; LIRP 1892(2); LIRP 1897; LIRP 1899; LIRP 892(3)
Belonidae		
Strongylura timucu	351.00-467.00	LIRP 1909(4); LIRP 1910(2); LIRP 1911(3); LIRP 842
Fistulariidae		
Fistularia tabacaria	185.00-429.00	LIRP 832(2); MZUSP 66442; MZUSP 66449; MZUSP 66450; MZUSP 66453; MZUSP 66454; MZUSP 66455(2); MZUSP 66458
Pomatomidae		
Pomatomus saltatrix	175.00-260.00	MZUSP 14248; MZUSP 14249; MZUSP 14250; MZUSP 47116; MZUSP 69772; MZUSP 69774(2); MZUSP 69778; MZUSP 69780; MZUSP 69781
Carangidae		
Caranx latus	98.00-157.20	LIRP 1404(3); LIRP 1405(2); LIRP 1410; LIRP1411; LIRP1412; MZUSP 44654(2)
Chloroscombrus chrysurus	85.50-103.00	LIRP 1226; MZUSP 64446(9)
Oligoplites saurus	74.61-148.30	LIRP 1282: MZUSP 10121; MZUSP 64592(2); MZUSP 64593(2); MZUSP 64594; MZUSP 64601; MZUSP 64608(2)
Selene vomer	76.30-98.10	LIRP 1245; LIRP 1246; LIRP 1247(2); MZUSP 3302; MZUSP 65391; MZUSP 65392; MZUSP 65471; MZUSP 8783(2)
Trachinotus carolinus	114.40-160.00	MZUSP 14263(3); MZUSP 14265-6(2); MZUSP 42367; MZUSP 5192(2); MZUSP 65503; MZUSP65514
Trichiuridae		
Trichiurus lepturus	735.00-1300.00	LIRP 1714; LIRP 1715; MZUSP 81100; MZUSP 81101; MZUSP 81102(2); MZUSP 81103; MZUSP 81104; MZUSP 81105(2)
Scombridae		
Scomberomorus brasiliensis	178.00-435.00	LIRP 1713; MZUSP 68822; MZUSP 13340; MZUSP 68823; MZUSP 79264
Tetraodontidae		
Lagocephalus laevigatus	177.00-310.00	LIRP 1717; LIRP 1718; MZUSP 72042(3); MZUSP 72043; MZUSP 72044; MZUSP 72057(2); MZUSP 7668

background (FZG unpublished data), thus indicating that, in nature, the limits between the ecological groups and any generalization should be treated very carefully. The trumpetfish is a stalking predator that lurks near plants or other reef habitats and stealthily approach prey, striking from close quarters. Thus, such coloration contributes to the success of this feeding tactic.

In this study, the main ecomorphological attributes influencing species distribution in the morphospace were those that indicate the position of fish in the water column (*i.e.*, those associated with habitat use), swimming capacity, and visual orientation. The morphological attributes related to feeding or prey size/diet were less important. Body shape and fins configuration/positions clearly influence the ecological performance (*e.g.*, hydrodynamics, swimming speed, maneuverability etc.) and habitat use in fishes (see Motta, 1988; Gibran, 2007). Previous studies show that external morphology is not a good predictor of diet (a result in opposition to the ecomorphological hypothesis), but it enables to infer how a fish can eat and where it can feed; morphological similarities observed among species generally reflects similar patterns in habitat use and/or feeding mode (*e.g.*, Motta, 1988; Gibran, 2007). Thus, foraging behavior, rather than external morphology, is the critical variable accounting for interspecific differences in diet (*e.g.*, Schmitt & Coyer, 1982). The two species of Beloniformes studied herein are a good example of similarities in body design but with marked differences in diet, as discussed below.

As a function of the physics of movement through a fluid medium, basic body shape and fins strongly influences

Table 3. Mean (M) and standard deviation (SD) values for the 19 ecomorphological attributes calculated for the 17 nektonic fish species analyzed. The last column (*n*) is the number of individuals measured (only five specimens of *Scomberomorus brasiliensis* were available in the fish collections examined). CI = compression index; RBD = relative body depth; RPL = relative peduncle length; CPC = caudal peduncle compression index; IVF = index of ventral flattening; RAD = relative area of dorsal fin; RAPt = relative area of pectoral fin; RAPv = relative area of pelvic fin; RAC = relative area of caudal fin; PtAR = pectoral fin aspect ratio; CAR = caudal fin aspect ration; RHL = relative head length; EP = relative eyes position; ES = relative eye size; RMW = relative mouth width; RMH = relative mouth height; MAR = mouth aspect ratio; IMP = index of mouth protrusion; MO = mouth orientation. *Anc tri = Anchoa tricolor*; *Ath bra = Atherinella brasiliensis*; *Car lat = Caranx latus*; *Chl chr = Chloroscombrus chrysurus*; *Fis tab = Fistularia tabacaria*; *Har jag = Harengula jaguana*; *Hyp uni = Hyporhamphus unifasciatus*; *Lag lae = Lagocephalus laevigatus*; *Mug cur = Mugil curema*; *Oli sau = Oligoplites saurus*; *Pom sal = Pomatomus saltatrix*; *Sar jan = Sardinella janeiro*; *Sco bra = Scomberomorus brasiliensis*; *Sel vom = Selene vomer*; *Str tim = Strongylura timucu*; *Tra car = Trachinotus carolinus*; *Tri lep = Trichiurus lepturus*.

		CI	RBD	RPL	CPC	IVF	RAD	RAPt	RAPv	RAC	PtAR	CAR	RHL	EP	ES	RMW	RMH	MAR	IMP	MO	*n*
Anc tri	M	1.92	0.19	0.17	3.38	0.58	0.04	0.02	0.01	0.11	3.42	1.74	0.26	0.54	0.07	0.07	0.14	1.94	1.00	1.57	10
	SD	0.11	0.01	0.01	0.77	0.08	0.01	0.01	<0.01	0.02	1.21	0.42	<0.01	0.03	<0.01	<0.01	0.01	0.19	0.00	0.00	-
Ath bra	M	1.57	0.19	0.16	2.76	0.55	0.03	0.05	0.03	0.15	2.76	1.35	0.24	0.53	0.07	0.06	0.07	1.17	0.70	1.57	10
	SD	0.14	0.01	0.01	0.22	0.04	<0.01	0.01	<0.01	0.01	0.13	0.15	0.01	0.03	<0.01	<0.01	<0.01	0.12	0.03	0.00	-
Car lat	M	2.70	0.43	0.08	0.75	0.40	0.06	0.04	0.02	0.10	3.70	2.58	0.32	0.55	0.09	0.11	0.14	1.24	0.69	1.57	10
	SD	0.13	0.01	0.01	0.08	0.06	0.01	<0.01	<0.01	0.01	0.23	0.44	0.01	0.03	0.01	0.01	0.02	0.11	0.03	0.00	-
Chl chr	M	4.14	0.47	0.07	1.62	0.66	0.05	0.04	0.01	0.08	3.58	2.82	0.28	0.61	0.09	0.07	0.11	1.51	0.60	1.13	10
	SD	0.16	0.01	0.01	0.13	0.05	0.01	<0.01	<0.01	<0.01	0.30	0.34	0.01	0.04	0.01	0.01	0.01	0.16	0.04	0.00	-
Fis tab	M	0.73	0.03	0.12	0.61	0.47	0.03	0.02	<0.01	0.04	1.34	1.37	0.37	0.54	0.03	0.02	0.03	1.48	1.00	1.57	10
	SD	0.13	0.01	<0.01	0.20	0.10	0.01	0.01	<0.01	0.01	0.27	0.46	0.01	0.07	<0.01	<0.01	0.01	0.21	0.00	0.00	-
Har jag	M	2.50	0.35	0.10	4.52	0.66	0.04	0.02	0.01	0.10	4.50	1.32	0.29	0.70	0.10	0.07	0.11	1.60	1.00	1.61	10
	SD	0.11	0.01	0.01	0.45	0.05	0.01	<0.01	<0.01	0.01	0.23	0.61	0.01	0.02	<0.01	<0.01	0.01	0.12	0.00	0.00	-
Hyp uni	M	1.37	0.11	0.05	1.71	0.61	0.03	0.03	0.01	0.11	2.62	1.57	0.35	0.59	0.05	0.04	0.04	1.00	1.00	1.05	10
	SD	0.13	0.01	0.01	0.17	0.05	<0.01	<0.01	<0.01	0.01	0.25	0.45	0.02	0.03	<0.01	<0.01	0.01	0.10	0.00	0.00	-
Lag lae	M	1.27	0.27	0.24	0.99	0.40	0.04	0.07	0.00	0.12	1.02	1.25	0.32	0.69	0.08	0.09	0.06	0.69	1.00	1.57	10
	SD	0.13	0.02	0.01	0.11	0.06	0.01	0.01	0.00	0.01	0.16	0.32	0.01	0.02	0.01	0.01	0.01	0.05	0.00	0.00	-
Mug cur	M	1.71	0.25	0.16	2.26	0.40	0.04	0.04	0.03	0.17	2.61	1.62	0.26	0.51	0.07	0.08	0.08	1.00	0.55	2.32	10
	SD	0.15	0.01	0.01	0.22	0.10	0.01	0.01	0.01	0.02	0.31	0.44	0.02	0.06	0.01	<0.01	0.01	0.07	0.05	0.00	-
Oli sau	M	3.40	0.29	0.06	1.64	0.56	0.05	0.02	0.01	0.10	2.35	2.21	0.24	0.56	0.07	0.07	0.12	1.58	0.74	1.22	10
	SD	0.40	0.02	0.01	0.18	0.08	0.01	0.01	<0.01	0.01	0.31	0.53	0.02	0.04	0.01	0.01	0.02	0.20	0.06	0.00	-
Pom sal	M	2.27	0.28	0.09	2.03	0.53	0.08	0.03	0.02	0.13	2.41	1.97	0.30	0.60	0.05	0.10	0.09	0.93	0.75	1.57	10
	SD	0.34	0.02	0.01	0.18	0.05	<0.01	<0.01	<0.01	0.01	0.19	0.42	0.01	0.03	<0.01	0.02	0.02	0.10	0.03	0.00	-
Sar jan	M	1.97	0.24	0.09	2.65	0.60	0.04	0.03	0.01	0.11	3.19	1.90	0.27	0.66	0.07	0.05	0.09	1.98	1.00	1.57	10
	SD	0.15	0.02	0.01	1.02	0.06	0.01	0.01	<0.01	0.03	0.91	0.51	0.04	0.05	0.01	0.01	0.01	0.38	0.00	0.00	-
Sco bra	M	2.18	0.21	0.04	1.23	0.73	0.07	0.03	0.01	0.10	2.12	3.47	0.24	0.62	0.04	0.07	0.10	1.56	1.00	1.57	5
	SD	0.36	0.03	0.01	0.25	0.07	0.03	<0.01	<0.01	0.01	0.29	0.73	0.01	0.02	0.01	0.01	0.02	0.12	0.00	0.00	-
Sel vom	M	6.86	0.74	0.05	1.84	0.24	0.05	0.04	0.01	0.08	3.35	4.25	0.42	0.57	0.09	0.06	0.12	2.23	0.78	1.05	10
	SD	0.45	0.03	0.01	0.11	0.08	0.01	<0.01	<0.01	0.01	0.41	1.21	0.02	0.05	0.01	0.01	0.02	0.40	0.05	0.00	-
Str tim	M	1.10	0.06	0.04	1.15	0.50	0.02	0.03	0.01	0.06	2.87	0.84	0.34	0.60	0.03	0.03	0.13	4.47	1.00	1.57	10
	SD	0.05	0.01	0.01	0.12	0.09	<0.01	<0.01	<0.01	0.01	0.32	0.36	0.01	0.02	<0.01	<0.01	0.02	0.78	0.00	0.00	-
Tra car	M	3.27	0.52	0.07	1.79	0.34	0.04	0.03	0.01	0.12	4.24	2.79	0.27	0.44	0.07	0.09	0.08	0.91	0.63	1.79	10
	SD	0.28	0.01	0.01	0.16	0.05	0.01	<0.01	<0.01	0.01	6.43	0.51	0.01	0.05	0.01	<0.01	<0.01	0.04	0.03	0.00	-
Tri lep	M	2.70	0.06	0.00	0.00	0.53	0.25	0.01	0.00	0.00	2.49	0.00	0.13	0.68	0.02	0.02	0.04	2.49	1.00	1.57	10
	SD	0.25	<0.01	0.00	0.00	0.05	0.05	<0.01	0.00	0.00	0.33	0.00	0.01	0.05	<0.01	<0.01	0.01	0.13	0.00	0.00	-

ecological performance (Winemiller, 1992). Such attributes are directly related to swimming speed, swimming constancy, and maneuverability linked, thus, to the spatial resources partition (*i.e.*, body design, peduncles and fins shape indicate the mode of spatial utilization in aquatic habitats; *e.g.*, Keast & Webb, 1966; Gatz, 1979; Mahon, 1984; Winemiller, 1991, 1992). The seizing and manipulation of food depend on the individual swimming ability and maneuverability, with a strong evolutionary pressure on the interactions between feeding and locomotion (see Keenleyside, 1979; Pough *et al.*, 2005). The finds presented herein support that the specific use of space is clearly linked to the functional morphology (see *e.g.*, Winemiller, 1991).

The environmental and biological pressures to the nektonic or pelagic life are so limitative and shaper that every aquatic vertebrate, alive or extinct, can show convergent features with the others vertebrates that share the same habitat (see *e.g.*, Helfman *et al.*, 1997; Lowe-McConnell, 1999; Levinton, 2001; Pough *et al.*, 2005). Adaptation is the most important concept to understand the linkage between morphology and ecology (Peres-Neto, 1999). An adaptation is "a feature having properties of form and function which permit the organism to maintain successfully the synergy between a biological role of that feature and a stated selection force" (*cf.* Bock, 1980). When there is independent evolution of the same feature within distant phylogenetic lineages (*i.e.*, convergence) or when closely related lineages present dissimilar traits (*i.e.*, divergence) such feature/trait should be adaptive (see Bock, 1980; Brooks & McLennan, 1991; Winemiller, 1992; Ricklefs & Miles, 1994).

In this context, ecomorphological convergences among divergent taxa provide powerful evidence for determinism in the evolution of species traits (see Motta & Kotrschal, 1992; Winemiller, 1992; Motta *et al.*, 1995a; Winemiller *et al.*, 1995). One of the most exciting conceptual advances in recent ecomorphological studies has been the incorporation of phylogenetic hypotheses (Motta & Kotrschal, 1992; Losos & Miles, 1994; Motta *et al.*, 1995b). This is considered as an

Table 4. Synthesis of the results obtained during the field observations at study site complemented with data on the feeding habits from Figueiredo & Menezes (1978, 1980, 2000), Menezes & Figueiredo (1980, 1985), and Carvalho-Filho (1999). Species were organized according to the cluster results of Fig. 3. For the definition of the feeding tactics see Keenleyside (1979) and Sazima (1986). Schools could be with just a few individuals, by tens (medium) or by the hundred (large). With the exception of the feeding habits, all other data with no reference were recorded during direct field observations of the present study and mainly for individuals belonging to the range of standard length of Table 2. In bold type there is the only species that were not observed underwater, and the interrogation marks (?) mean unknown information

Species	Feeding activity	Position in the water column and/or feeding places	Feeding habits (obtained from the literature above)	Feeding tactics or feeding categories	Group formation
Anchoa tricolor	diurnal	mid water	carnivore	particulate feeding	medium to large schools
Atherinella brasiliensis	diurnal	water surface	omnivore	surface picker (present study and Sazima, 1986)	small to medium schools
Mugil curema	diurnal	mid water and water surface, but feeding at bottom	detritivore	mud-eater (present study and Sazima, 1986)	small to large schools
Sardinella janeiro	diurnal	mid water	planktivore	filter feeding	medium to large schools
Pomatomus saltatrix	diurnal	mid water and water surface	carnivore	chasing (see Carvalho-Filho, 1999)	medium to large schools
Caranx latus	diurnal and crepuscular	mid water	carnivore	roving predation or patrolling (present study and Sazima, 1986)	solitary or small to medium schools
Oligoplites saurus	diurnal	mid water	carnivore	roving predation or patrolling (present study); mutilator (*cf.* Sazima, 1986)	small to medium schools
Scomberomorus brasiliensis	?	mid water	carnivore	chasing (see Carvalho-Filho, 1999)	solitary or small to medium schools (see Carvalho-Filho, 1999)
Chloroscombrus chrysurus	diurnal	mid water	carnivore/planktivore	particulate feeding and roving predation or patrolling	solitary or small to medium schools
Trachinotus carolinus	diurnal	mid water	carnivore	?	small schools
Fistularia tabacaria	diurnal	mid water	carnivore	stalking predation	solitary
Lagocephalus laevigatus	?	mid water or over the bottom	carnivore	?	solitary
Trichiurus lepturus	nocturnal and crepuscular	mid water	carnivore	?	solitary or small to medium schools
Hyporhamphus unifasciatus	diurnal	water surface	omnivore	surface picker (present study and Sazima, 1986)	small schools
Strongylura timucu	diurnal	water surface	carnivore	stalking predation	small schools
Harengula jaguana	diurnal	mid water	carnivore/planktivore	particulate feeding	medium to large schools
Selene vomer	diurnal and crepuscular	mid water	carnivore	?	small to medium schools

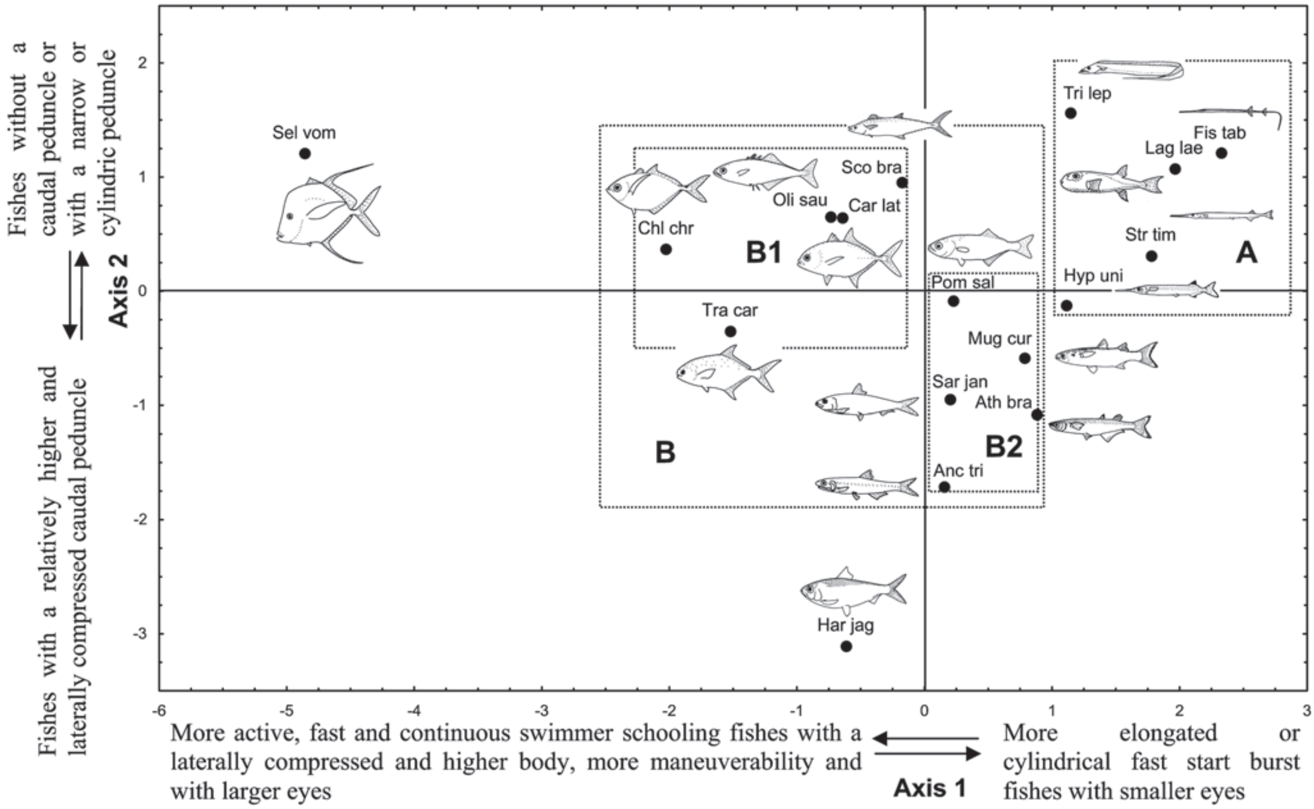

Fig. 2. Distribution of the 17 nektonic fish species in ecomorphological space. Ordination is by the first two axes of PCA (cumulative % of variance = 73) (see Table 5). Anc tri = *Anchoa tricolor*; Ath bra = *Atherinella brasiliensis*; Car lat = *Caranx latus*; Chl chr = *Chloroscombrus chrysurus*; Fis tab = *Fistularia tabacaria*; Har jag = *Harengula jaguana*; Hyp uni = *Hyporhamphus unifasciatus*; Lag lae = *Lagocephalus laevigatus*; Mug cur = *Mugil curema*; Oli sau = *Oligoplites saurus*; Pom sal = *Pomatomus saltatrix*; Sar jan = *Sardinella janeiro*; Sco bra = *Scomberomorus brasiliensis*; Sel vom = *Selene vomer*; Str tim = *Strongylura timucu*; Tra car = *Trachinotus carolinus*; Tri lep = *Trichiurus lepturus*. There is no scale among the fishes (see Table 2 for standard length range) (illustrations: Alexandre C. Ribeiro).

objective way to identify cases of convergence and/or divergence (see *e.g.*, Motta *et al.*, 1995b; Winemiller *et al.*, 1995; Casatti & Castro, 2006). In this study, the Mantel test showed that some of the ecomorphological groups found had no phylogenetic support, what means that such similarities in morphology are probably due to evolutionary convergence for the nektonic life style and to the vertical distribution of species in the water column. Based on these results, complemented with data from the scientific literature about the taxonomy and phylogenies of such taxa (*e.g.*, Helfman *et al.*, 1997; Nelson, 2006), it was possible to discuss some of typical cases of convergence and divergence, as follows:

The letter A (Figs. 2-3) indicates a cluster of Beloniformes, Gasterosteiformes, Perciformes, and Tetraodontiformes that share a low and elongated body in which theirs caudal fins (if present) allow fast start burst. This cluster illustrates examples of morphological convergence among species from different orders of Actinopterygii. The species *Hyporhamphus unifasciatus* and *Strongylura timucu* were placed together probably by their phylogenetic proximity; *i.e.*, their similarities in morphology can be explained by the fact that they share a close evolutive ancestral. These studied Beloniformes show similarities in morphology, habitat use and foraging activity (*i.e.*, life associated to water surface and diurnal habits) due to their close evolutionary relationship, but *S. timucu* is a piscivore while *H. unifasciatus* is an omnivore (*i.e.*, a divergent feature). All other members of this latter group are convergent regarding their elongate bodies. In addition, *T. lepturus* and *S. timucu* constitute a typical case of convergence also regarding their habitats and habits. Both are piscivores and explore the resources available at the water column, although they use different resources: *T. lepturus* inhabits mid water (staying stationary in a vertical posture), having crepuscular/nocturnal feeding activity while *S. timucu* swims very close to the water surface and feeds during the day-time, as *H. unifasciatus*. Another convergence showed by all of these nektonic elongated fishes is that their dorsal and anal fins are positioned at the same vertical line of their bodies, besides posterior positioned, near of the caudal region (*T. lepturus* is an exception because it does not have an anal fin and the dorsal fin follows all its slender body).

In is important to note that *F. tabacaria* and *L. laevigatus*, for example, look like very different each other, but in spite of

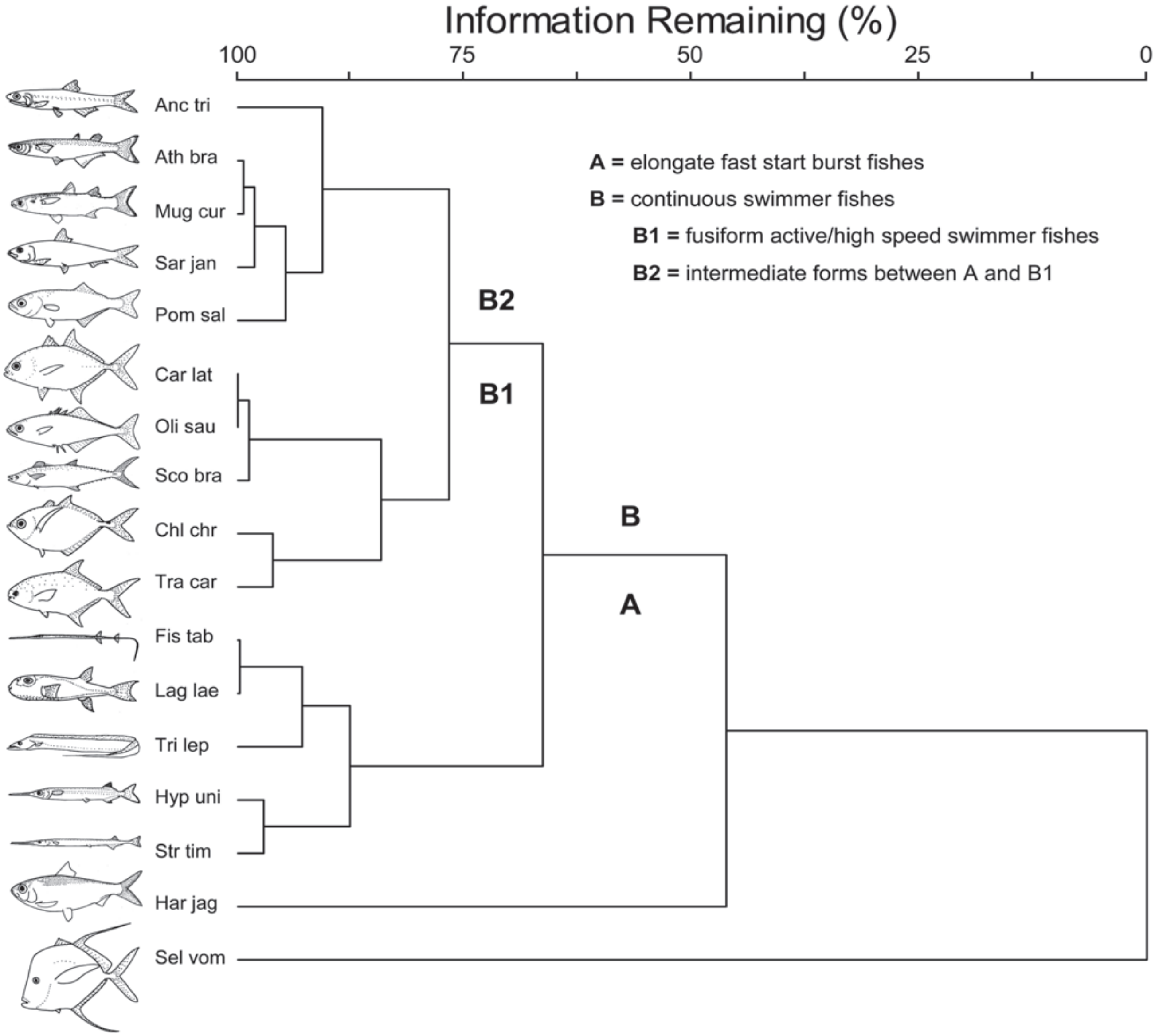

Fig. 3. Dendrogram of ecomorphological relationships (similarity) for the 17 nektonic fish species studied. Cluster analysis is by the Euclidean distance measure and Group Average linkage method using the same scores (*i.e.*, coordinates) calculated for PCA and plotted in Fig. 2 (cophenetic coefficient *r* = 0.86). Anc tri = *Anchoa tricolor*; Ath bra = *Atherinella brasiliensis*; Car lat = *Caranx latus*; Chl chr = *Chloroscombrus chrysurus*; Fis tab = *Fistularia tabacaria*; Har jag = *Harengula jaguana*; Hyp uni = *Hyporhamphus unifasciatus*; Lag lae = *Lagocephalus laevigatus*; Mug cur = *Mugil curema*; Oli sau = *Oligoplites saurus*; Pom sal = *Pomatomus saltatrix*; Sar jan = *Sardinella janeiro*; Sco bra = *Scomberomorus brasiliensis*; Sel vom = *Selene vomer*; Str tim = *Strongylura timucu*; Tra car = *Trachinotus carolinus*; Tri lep = *Trichiurus lepturus*. There is no scale among the fishes (see Table 2 for standard length range) (illustrations: Alexandre C. Ribeiro).

this tridimensional discrepancy they were placed together in the graphics of PCA and cluster analysis (see Figs. 2-3). If *L. laevigatus* was to be compared with any other Tetraodontiform fish it would be evident that it is an elongated form of puffer.

The group B could be divided in two subgroups, B1 and B2. The first one represents the Carangidae and Scombridae families, while the other group, B2, clusters Clupeiformes, Atherinidae, Mugilidae, and Pomatomidae (Figs. 2-3; Table 1).

The B1 group includes more fusiform and active/high speed swimmer fishes in comparison with the others species studied. *Selene vomer* was probably not included in this cluster due to its very high and compressed body, which diverges from the other carangids studied. This cluster also shows convergent traits between Carangidae and Scombridae (Figs. 2-3). The B2 group includes convergent forms among species from different orders of Actinopterygii that are intermediate among the forms of A and B1, being neither so elongated nor fusiform and, in spite of being active swimmers, they are more capable to execute maneuvers than the other

Table 5. Eigenvalues, eigenvectors, and variance extracted for the two principal axes of PCA. The correlation index values in bold type (*i.e.*, $r \geq 0.6$; negatives or positives) between each ecomorphological attribute and the correspondent axis were used to interpret the distribution of the 17 nektonic fish species in the graphic of PCA (see Fig. 2). CI = compression index; RBD = relative body depth; RPL = relative peduncle length; CPC = caudal peduncle compression index; IVF = index of ventral flattening; RAD = relative area of dorsal fin; RAPt = relative area of pectoral fin; RAPv = relative area of pelvic fin; RAC = relative area of caudal fin; PtAR = pectoral fin aspect ratio; CAR = caudal fin aspect ratio; RHL = relative head length; EP = relative eyes position; ES = relative eye size; RMW = relative mouth width; RMH = relative mouth height; MAR = mouth aspect ratio; IMP = index of mouth protrusion; MO = mouth orientation.

	PCA axes			
	1		2	
Eigenvalue	47.874		23.621	
% of variance	48.912		24.134	
Cumulative % of variance	48.912		73.046	
	Eigenvectors and *r* values for each axis			
CI	-0.7971	**-0.955**	0.2347	0.198
RBD	-0.0982	**-0.916**	-0.0013	-0.009
RPL	0.0120	0.344	-0.0145	-0.294
CPC	-0.1376	-0.218	-0.8445	**-0.940**
IVF	0.0194	0.264	-0.0349	-0.333
RAD	0.0010	0.033	0.0160	0.378
RAPt	0.0002	0.027	0.0007	0.065
RAPv	0.0001	0.027	-0.0023	-0.330
RAC	-0.0009	-0.041	-0.0171	-0.522
PtAR	-0.3148	-0.593	-0.4471	-0.592
CAR	-0.4784	**-0.815**	0.1380	0.165
RHL	-0.0086	-0.230	0.0058	0.108
EP	0.0079	0.196	-0.0001	-0.002
ES	-0.0089	**-0.647**	-0.0077	-0.390
RMW	-0.0050	-0.321	-0.0044	-0.199
RMH	-0.0106	-0.536	-0.0073	-0.259
MAR	0.0191	0.037	0.0786	0.108
IMP	0.0448	0.448	-0.0018	-0.013
MO	0.0698	0.403	-0.0668	-0.271

fishes studied. This fact was confirmed during the underwater observations of Clupeiformes which, when surprised by a predator, such as juvenile barracudas *Sphyraena* sp. (Sphyraenidae), performs the so called "confusion effect" behavior (*cf.* Keenleyside, 1979: 56-57), the most commonly proposed mechanism by which schooling fish gain protection against predation. On the other hand, *A. brasiliensis* swims near the water surface in groups and uses its maneuverability to get food items distributed through the entire water column, while *M. curema* uses such ability to swim near the bottom and scoop up, to ingest portions of substrate containing diatoms and plant detritus (Figs. 2-3; Table 4).

The isolation of *H. jaguana* from the other Clupeiformes of the B2 group is another case of divergence. In addition, among all of the studied members of this order there are two carnivorous species that uses the particulate feeding tactic (*H. jaguana* and *A. tricolor*; members of Clupeidae and Engraulidae families, respectively), and one species of planktonic filter feeding (*S. janeiro*; a clupeid that has numerous and long gill rakers to filter plankton; see Table 4 and Figueiredo & Menezes, 1978). Thus, despite belonging to the same morphological cluster, both clupeid species diverge in terms of feeding modes.

In conclusion, results presented herein showed that similarities in morphology reflected similarities in habitat use and/or feeding tactics. There were covariations concerning habitat use and/or feeding modes and body forms, corroborating the ecomorphological hypothesis that differences in body form and shape (*i.e.*, phenotype) lead to differences in biological roles (*i.e.*, ecology). However, similarities in morphology are not always in agreement with similarities in diet, as observed in *H. unifasciatus* and *S. timucu*. As they belong to closely related lineages, such divergences in diet may be due to evolutionary events that minimize interspecific competition. As more data on phylogeny become available, it is also possible to map the changes in the biological characters of interest and to better apply the comparative method (see Brooks & McLennan, 1991; Losos & Miles, 1994; Westneat, 2001). Further studies like this may include a set of performance data to test if morphology and performance are better correlated than morphology and phylogeny; this approach has a lot of promise and avoids only inferring ecological performance based on ecomorphological attributes (P. C. Wainwright, pers. comm.). A detailed study involving closely related species, as only the Carangidae or Clupeiformes fishes, will better clarify their ecomorphological relationships and shifts in resource use. Performance influences on the individual's fitness and it is the crucial link between an organism's morphology and its ecology (see Reilly & Wainwright, 1994; Wainwright, 1994).

Acknowledgements

This paper contains some of the main findings of my Doctoral's thesis on habits and ecomorphology of 68 coastal marine fish species chose as "morphotypes" from the morphological diversity found during an unpublished fish survey realized at São Sebastião Channel, southeastern Brazil (including benthic, nektobenthic and nektonic species). I am very grateful to Ricardo M. C. Castro for advice; Alexandre C. Ribeiro, Flávia B. Santos, Hertz F. dos Santos, Leandro M. de Souza, and Luis Fernando Netto for assistance in the field; Eleonora Trajano, Lilian Casatti, Marcelo R. de Carvalho, and Rodrigo L. de Moura for useful suggestions on my thesis; Pitágoras da C. Bispo for helping with statistical software; Peter C. Wainwright for useful suggestions on this manuscript; Gisele Y. Kawauchi and João P. Barreiros for useful suggestions and English reviews; CEBIMar-USP, FFCLRP-USP and LIRP-USP for logistical support; FAPESP (grants 00/06722-8, 05/51856-6 and 05/51855-0), for essential financial support.

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