

PREDICTING ECOMORPHOLOGICAL PATTERNS FROM MORPHOLOGY OF A TROPICAL ESTUARINE FISH ASSEMBLAGE

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ABSTRACT

Ecomorphological studies generally seek ecological information from a morphological analysis. Based on 12 ecomorphological traits and six coded variables taken from six species of bony fishes (*Anchovia clupeioides*, *Harengula clupeiola*, *Sciades herzbergii*, *Selene vomer*, *Stellifer rastrifer* and *Sphoeroides testudineus*), a principal component analysis and a cluster analysis were made. Three main groups, each sharing similar characteristics, were identified from both analysis: (1) *H. clupeiola* and *A. clupeioides*, cruisers with small heads, big eyes and reduced or absent dentition, indicating the presence of small prey in their diet; (2) *S. herzbergii*, *S. rastrifer* and *S. testudineus* were grouped mainly because of their bottom associated habits, the use of high turbulent microhabitats and for feeding on bigger prey than the first group; (3) *S. vomer* was isolated especially because of the highly compressed and tall body, fast swimming ability and since it has a broader diet than the other species.

Keywords: Brazil, ecomorphology, estuarine fishes, multivariate analysis

PREVENDO PADRÕES ECOMORFOLÓGICOS A PARTIR DA MORFOLOGIA DE UMA ASSEMBLÉIA DE PEIXES ESTUARINOS TROPICAIS

RESUMO

Estudos ecomorfológicos geralmente buscam informações sobre a ecologia das espécies baseada em uma análise morfológica. Baseado em 12 atributos ecomorfológicos e seis variáveis codificadas tomadas em seis espécies de peixes ósseos (*Anchovia clupeioides*, *Harengula clupeiola*, *Sciades herzbergii*, *Selene vomer*, *Stellifer rastrifer* e *Sphoeroides testudineus*), uma análise de componentes principais e uma análise de agrupamento foram feitas. Três grupos principais, cada um compartilhando características similares, foram identificados pelas duas análises: (1) *H. clupeiola* e *A. clupeioides*, espécies migradoras com cabeça pequena, olhos grandes e dentição reduzida ou ausente, indicando a presença de presas pequenas em sua dieta; (2) *S. herzbergii*, *S. rastrifer* e *S. testudineus* foram principalmente agrupadas por possuírem hábitos mais associados ao fundo, pela capacidade de habitarem locais de hidrodinamismo elevado e por se alimentarem de organismos maiores do que no primeiro grupo; (3) *S. vomer* foi isolada principalmente por possuir um alto grau de achatamento lateral e um corpo alto e por ser um nadador veloz com uma dieta mais ampla do que as outras espécies.

Palavras-Chave: análise multivariada, Brasil, ecomorfologia, peixes estuarinos

INTRODUCTION

An ecological approach based on a morphological analysis is considered the major aim of ecomorphological studies. Therefore, ecomorphology is a comparative field that seeks the understanding of

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ecological patterns based in a morphological evaluation (Motta *et al.*, 1995a; 1995b; Norton, 1995; Wainwright & Bellwood, 2002; Winemiller *et al.*, 1995; Wainwright & Richard, 1995). While functional morphology is the study of form relative to function, ecomorphology is especially concerned with form relative to biological roles. These biological roles, which are the species' potential niches, are the result of the constraints of the particular morphological features of each species (i.e. their phenotypes), which were inherited during the course of evolution. Due to its predictive power (see Keast & Webb, 1966; Gatz, 1979a, 1979b; Barel, 1983; Winemiller, 1991; Motta *et al.*, 1995a), ecomorphology is a useful tool for researchers trying to gather information about the many biological aspects of different species.

Bony fishes represent a group of special interest to evaluate ecomorphological relationships, mainly because they exhibit such a high morphological diversity, but also because they are present in so many different environments and have such a long history of evolution. Although the methods used were considerably different, many studies have tried to assess the relationships among morphology, behavior and biological roles within many families of bony fishes (Norton & Brainerd, 1993; Baker *et al.*, 1995; Cech Jr. & Massingill, 1995; Chapman & Liem, 1995; Foster & Baker, 1995; Kotschal, 1995; Long Jr., 1995; Luczovich *et al.*, 1995; Martin, 1995; Motta *et al.*, 1995a; Norton, 1995; Van der Meer *et al.*, 1995; Wainwright & Richard, 1995; Westneat, 1995; Winemiller *et al.*, 1995; Aguirre & Lombarte, 1999; Hulsey & Wainwright, 2002; Wainwright *et al.*, 2002; Huysentruyt *et al.*, 2004).

This paper discusses the behaviors and biological roles of an assemblage of tropical estuarine fishes based on their morphological particularities. Therefore, the aim of this study was 1) to assess biological information based on the morphological individualities of each species and 2) to identify relationships between these species that may indicate similar biological roles.

MATERIALS AND METHODS

Fishes used on this study belong to the scientific collection of the Departamento de Sistemática e Ecologia of the Universidade Federal da Paraíba and were collected on the estuary of the Mamanguape River (located between lat 06°43' and 06°51' S, and long 35°07' and 34°54' W), northeastern Brazil. The estuary is about 24 Km long (east-west) and about 2.5 Km wide and sustains a well preserved mangrove forest composed mainly of *Rhizophora mangle*, *Avicennia germinans*, *A. schaueriana*, *Laguncularia racemosa* and *Conocarpus erectus* (Alves *et al.*, 2005, p. 2).

The studied species were (family and standard length range indicated): *Anchovia clupeioides* (Engraulidae, 69.8 – 117.2mm), *Harengula clupeiola* (Clupeidae, 31.1 – 96.5mm), *Sciades herzbergii* (Ariidae, 51.7 – 245.0mm), *Selene vomer* (Carangidae, 26.2 – 97.6mm), *Stellifer rastrifer* (Scianidae, 51.3 – 123.6mm)

and *Sphoeroides testudineus* (Tetraodontidae, 47.8 – 132.3mm). For each species, 25 individuals were analyzed, with the exception of *S. herzbergii* with 20 individuals analyzed. These are common species of fishes found in the northeastern region of Brazil and were chosen mainly because they live together in the same habitat, sharing the same resources (Carvalho-Filho, 1999; Menezes *et al.*, 2003; Araújo *et al.*, 2004). Although range of the size classes differed considerably, all individuals examined were adults and prior to the beginning of the study, a one way analysis of variance (ANOVA) was used to verify differences among different size classes. No significant differences were detected (in every case $P > 0.05$) and since the indexes used are proportional (i.e. relative to standard or to head length), no distinctions between the size classes were considered.

The following morphological measurements were taken: standard length (SL), head length (HL), head length with mouth open (HLO), head depth (HD), body depth (BD), body width (BW), body depth below midline (BDM), caudal peduncle length (CPL), caudal peduncle height (CPH), caudal peduncle width (CPW), pectoral fin length (PL), pectoral fin width (PW), mouth height (MH), mouth width (MW), eye diameter (ED) and eye height (EH). From these measures, a total of 12 ecomorphological traits were estimated: (1) index of compression (Watson & Balon, 1984): $IC = BH/BW$, (2) relative depth of the body (Gatz, 1979a): $RDB = BH/SL$, (3) caudal peduncle relative length (Watson & Balon, 1984): $CPRL = CPL/SL$, (4) caudal peduncle index of compression (Gatz, 1979a): $CPIC = CPH/CPW$, (5) index of ventral flattening (Mahon, 1984): $IVF = BDM/BD$, (6) pectoral fin aspect ratio (Keast & Webb, 1966): $PAR = PL/PW$, (7) relative position of the eyes (Gatz, 1979a): $RPE = EH/HD$, (8) relative size of the eyes (this study): $RSE = ED/HL$, (9) relative length of the head (Watson & Balon, 1984): $RLH = HL/SL$, (10) relative height of the mouth (Watson & Balon, 1984): $RHM = MH/SL$, (11) relative width of the mouth (Gatz, 1979a): $RWM = MW/SL$ and (12) mouth aspect (Beaumont, 1991): $MA = MH/MW$. Additionally, six coded variables were estimated and scored as integer values for the seven species: (1) pectoral fin shape (PS), where 1 = rounded, 2 = intermediate and 3 = pointed, (2) caudal fin shape (CS), where 1 = absent, 2 = rhomboidal, 3 = trunked and 4 = forked, (3) eye position (EP), where 1 = lateral, 2 = dorso-lateral and 3 = dorsal, (4) mouth position (MP), where 1 = supra-terminal, 2 = terminal, 3 = sub-terminal and 4 = ventral, (5) dentition type (DT), where 1 = villiform, 2 = canine, 3 = fused and 4 = absent and (6) presence or absence of barbells (B), where 0 = absence and 1 = presence.

To determine the degree of jaw protrusion, the following variable based on Motta *et al.* (1995a) was calculated: $(HLO-HL/SL) \times 100$. The results are expressed as percent of jaw protrusion relative to head length.

All measurements < 150.0mm were made with vernier calipers and estimated to the nearest 0.05 mm. Measurements > 150.0mm were taken with a clear plastic ruler and estimated to the nearest millimeter.

A principal components analysis (PCA) was used to identify ecomorphological patterns between the species. To detect the degree of association between the species, a cluster analysis with the standard Euclidean distance measure was conducted with the use of the ecomorphological traits and the coded variables. All statistical analyses were performed with the use of Statistica® version 5.1.

RESULTS

The eigenvalues obtained from the first two principal components were greater than one and accounted for 53% of the cumulative variance (PC1 = 34%; PC2 = 19%). Variables that scored high in the first component were index of compression (IC = 0.853032), relative depth of the body (RDB = 0.708810), mouth aspect (MA = 0.884556), pectoral fin shape (PS = 0.756711) and dentition type (DT = 0.765559) with positive correlation values and caudal peduncle relative length (CPRL = -0.756417) and relative width of the mouth (RWM = -0.778514) with negative correlation values. For the second component, pectoral fin aspect ratio (PAR = 0.501229) and pectoral fin shape (PS = 0.603292) scored high with positive correlation values while index of ventral flattening (IVF = -0.773626) scored high with negative correlation values. A summary of the ecomorphological traits and the coded variables results are shown in Table 1.

For the first component, three groups were obtained. *Harengula clupeiola* and *Anchovia clupeioides* grouped close sharing a moderately compressed and tall body with reduced or absent dentition and intermediate pectoral fins. *Stellifer rastrifer*, *Sciades herzbergii* and *Sphoeroides testudineus* also grouped close and formed a single group sharing rounded bodies, large mouths with specialized dentition and rounded to intermediate pectoral fins. *Selene vomer* was separated from the preceding species in morphospace and was characterized by a highly compressiform and tall body with a large mouth gape, reduced or absent teeth and pointed pectoral fins. For the second component, species were separated into two groups. The first included *S. herzbergii*, *S. rastrifer* and *S. vomer* which shared longer, slender and intermediate to pointed pectoral fins. The second included *A. clupeioides*, *H. clupeiola* and *S. testudineus*, which shared rounded to intermediate pectoral fins and moderately depressed bodies (Figure 1).

Cluster analysis of the ecomorphological traits along with the coded variables resulted in the same three groups obtained on the first analysis. *Anchovia clupeioides* and *Harengula clupeiola* formed the first group clustering at the 2.3 level and *Stellifer rastrifer*, *Sciades herzbergii* and *Sphoeroides testudineus* formed the second group clustering at the 3.6 level. *Selene vomer*, the outlier species, was joined together with the other species at the 4.4 level (Figure 2).

Of the species that protrude the jaws during mouth opening, *Selene vomer* protruded between 4.4 and 7.83% (mean \pm SL: 5.45% \pm 2.05%) of head length while

Harengula clupeiola protruded between 0.7 and 2.37% (1.2% \pm 0.55%) of head length. The other species protruded less than 1% or showed no protrusion whatsoever.

DISCUSSION

The analyses used for this study showed that some particular ecomorphological features of each species was responsible for their separation in morphospace. In general, the ecomorphological traits that scored higher were mainly indicative of habitat and microhabitat utilization. However, some generalizations about diet can be made based on these features. Overall, three groups sharing similar morphological characteristics were apparent from both analyses.

Anchovia clupeioides and *Harengula clupeiola*, the first group obtained, shared moderately tall and compressed fusiform bodies, short and compressed caudal peduncles, forked caudal fins, relatively small head with big lateral eyes, reduced or absent teeth and intermediate pectoral fin shape. In freshwater fishes, these features are characteristic of mid-water inhabiting fishes, which are specialized for cruising (Gatz, 1979a, 1979b; Watson & Balon, 1984), but have also been found on estuarine and marine fishes (Motta *et al.*, 1995a). Also, the presence of a small head, reduced or absent teeth and relatively large eyes, clearly shows the importance of small prey items on the diet of these species. In fact, zooplanktonic organisms are the main items on the diet of these two species (Sierra *et al.*, 1994; Ortaz *et al.*, 1996).

Although *Sciades herzbergii*, *Stellifer rastrifer* and *Sphoeroides testudineus* show some remarkable differences within their morphotypes, the morphological characteristics shared by these species herein were sufficient to group them in morphospace. The presence of rounded bodies, long caudal peduncles, rounded to intermediate pectoral fin shape, large terminal or ventral mouths, big heads with relatively small lateral or dorso-lateral eyes and specialized dentition type were observed among these species. These related features are mainly indicative of an epibenthic microhabitat use or, otherwise, a sedentary life-style (Keast & Webb, 1966; Motta *et al.*, 1995a). Also, in freshwater fishes, these were previously related to the use of turbulent microhabitats with high current action (Gatz, 1979b; Watson & Balon, 1984; Freire & Agostinho, 2001). Thus, the presence of rounded bodies and long caudal peduncles enable these fishes to use these highly dynamic and unstable areas. The presence of big heads, large mouths and specialized dentition are indicative of a diet composed of bigger prey items than that of the preceding group, and also of a specialized diet (Keast & Webb, 1966; Gatz, 1979b; Watson & Balon, 1984). For example, the diet of *S. testudineus* is mainly composed of hard-shelled prey like crabs, bivalves and gastropods (Pauly, 1991; Turingan, 1994) and their fused teeth seem well suitable for crushing these organisms. The presence of small eyes and barbells in the ariid *S. herzbergii* suggests that sight is not

the main sensory modality used to catch prey. Moreover, this may also be related to the use of dynamic habitats, where sight is less important than chemical reception. Also, the presence of a ventrally flattened body in this species indicates the use of epibenthic habits. Like the preceding species of this group, *S. rastrifer* is also thought to feed on bottom-dwelling organisms, particularly benthic crustaceans (Keith *et al.*, 2000).

Selene vomer, the outlier species, was distantly separated from the preceding groups mostly because of its highly compressed and tall body. This species also exhibits a short, but laterally broad, caudal peduncle with a forked caudal fin, pointed pectoral fins with a high aspect ratio (long and slender). These features are mainly present in good swimmers which frequently migrate between distant areas (Motta *et al.*, 1995a). Also, this species possesses lateral eyes, a rounded terminal mouth with a large gape, big head and absent or reduced teeth. These features, plus the striking ability to protrude the jaws, suggests that this species feeds on evasive prey (ram feeding) that dwell in the water column, but may also feed on epibenthic species by picking them from the substrate with their highly protrusible jaws. The diet of this species consists mainly of small bony fishes, shrimps, crabs and polychaetes (Sierra *et al.*, 1994).

The analysis made on the present study focused on six species of four phylogenetic groups: Clupeiformes (*Anchovia clupeioides* and *Harengula clupeiola*), Siluriformes (*Sciades herzbergii*) Tetraodontiformes (*Sphoeroides testudineus*) and Perciformes (*Stellifer rastrifer* and *Selene vomer*). A phylogenetic review of these groups is available in Lauder & Liem (1983). Based on the morphometric data herein obtained, the species were grouped according to their ecomorphological similarities. The first group obtained (*A. clupeioides* and *H. clupeiola*) share similar morphological characteristics that were inherited during the course of evolution from a common ancestor. Consequently, it is reasonable to say that these species have not specialized to an extent as to be morphologically disparate. Moreover, they are closer to the more primitive teleost body form sharing, with these, ancestral characters such as lateral eyes, and intermediate sized, forked caudal fins (Motta *et al.*, 1995a). On the other hand, *S. herzbergii*, *S. testudineus* and *S. rastrifer*, the second group, showed remarkable morphological similarities, despite of the fact that these are three distantly related taxa (Lauder & Liem, 1983). This suggests a case of morphological convergence between these species, which is related to the use of similar ecological roles. The carangid *S. vomer* showed no similarities with any of the studied species.

Multivariate techniques, particularly principal components analysis, have been successfully used on many fish studies that tried to assess information of ecomorphological patterns. For example, Motta *et al.* (1995a), studying an assemblage of distantly related subtropical seagrass fishes, obtained similar groups of fishes as in the present study. He also found a poor correspondence between morphology and diet for most of the species of the fish assemblage. Therefore, morphological similarities observed by Motta *et al.*

(1995a), as in the present study, were mostly reflective of microhabitat utilization and, to a less extent, feeding behavior. Winemiller (1991), studying five freshwater fish assemblages from five widely separated regions, successfully used an ecomorphological approach, among others, to evaluate information about similar species belonging to different lowland freshwater fish assemblages from distant places, and found that tropical fish assemblages exhibited higher levels of niche diversification than temperate assemblages.

Based on the results obtained on the present study, it is possible to state that studies using an ecomorphological approach are important to predict ecological patterns based on morphological characteristics. Future ecomorphological studies with fish assemblages should gather morphological, behavioral and ecological information from the many different aquatic environments and, whenever possible, make laboratory experiments in order to further support their hypothesis.

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Table 1. Mean ± standard length of 12 ecomorphological traits plus the scores of six coded variables taken from six species of estuarine fishes. Refer to Material and Methods for legends

	Species					
	<i>Anchovia clupeioides</i>	<i>Harengula clupeiola</i>	<i>Sciades herzbergii</i>	<i>Selene vomer</i>	<i>Stellifer rastrifer</i>	<i>Sphoeroides testudineus</i>
IC		2.26 ± 0.26	0.95 ± 0.06	7.02 ± 0.75	1.68 ± 0.13	0.95 ± 0.14
RDB		0.29 ± 0.04	0.2 ± 0.01	0.74 ± 0.04	0.3 ± 0.02	0.28 ± 0.02
CPRL	3.17 ± 0.27	0.10 ± 0.01	0.18 ± 0.02	0.14 ± 0.01	0.26 ± 0.02	0.24 ± 0.01
CPIC	0.26 ± 0.02	3.99 ± 1.12	1.75 ± 0.15	1.79 ± 0.24	2.24 ± 0.28	0.99 ± 0.11
IVF	0.15 ± 0.01	0.71 ± 0.05	0.32 ± 0.05	0.4 ± 0.07	0.52 ± 0.06	0.5 ± 0.05
PAR	3.3 ± 0.47	2.79 ± 0.33	2.81 ± 0.72	2.81 ± 0.45	3.01 ± 0.52	1.16 ± 0.2
RPE	0.6 ± 0.04	0.67 ± 0.11	0.63 ± 0.11	0.7 ± 0.04	0.55 ± 0.13	0.77 ± 0.06
RSE	2.52 ± 0.25	0.36 ± 0.03	0.25 ± 0.07	0.26 ± 0.02	0.26 ± 0.03	0.26 ± 0.03
RLH	0.6 ± 0.05	0.29 ± 0.01	0.26 ± 0.01	0.42 ± 0.02	0.3 ± 0.01	0.35 ± 0.02
RHM	0.3 ± 0.01	0.06 ± 0.01	0.06 ± 0.02	0.09 ± 0.01	0.08 ± 0.03	0.05 ± 0.01
RWM	0.27 ± 0.01	0.05 ± 0.01	0.11 ± 0.01	0.05 ± 0.02	0.1 ± 0.02	0.08 ± 0.01
MA	0.07 ± 0.01	1.28 ± 0.5	0.6 ± 0.22	1.97 ± 0.44	0.85 ± 0.17	0.63 ± 0.12
PS	0.05 ± 0.02	2	2	3	2	1
CS	1.34 ± 0.19	3	3	3	1	2
EP	2	1	1	1	1	2
MP	3	1	4	2	2	2
DT	1	4	1	4	1	3
B	3	0	1	0	0	0
	4					
	0					

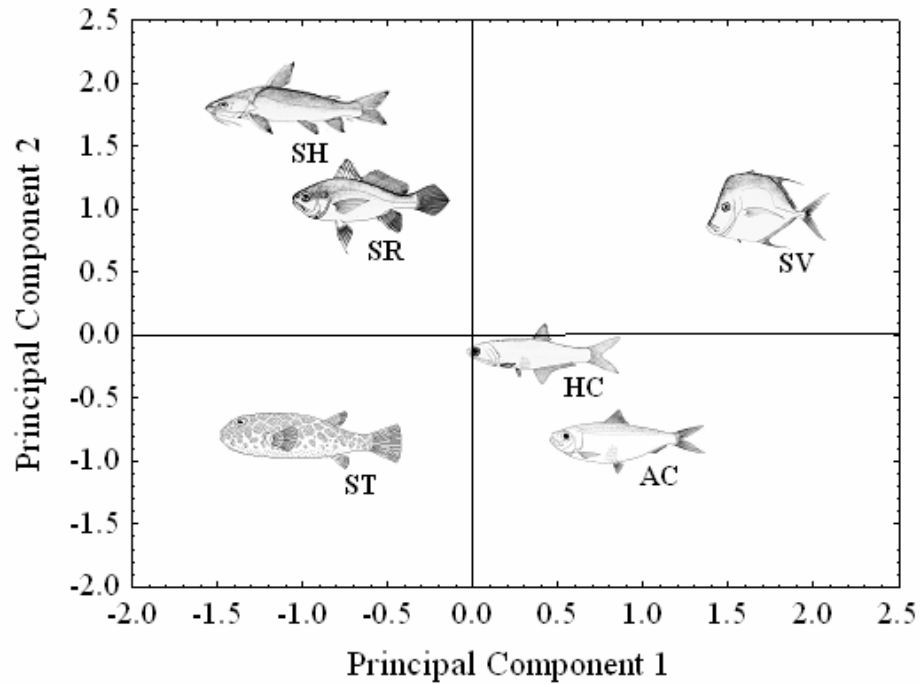


Figure 1. Principal components analysis made from 12 ecomorphological traits and six coded variables taken from six species of estuarine fishes. Each fish represents the central position of all individuals of the respective species sampled. AC: *Anchovia clupeoides*; HC: *Harengula clupeola*; SH: *Sciades herzbergii*; SV: *Selene vomer*; SR: *Stellifer rastrifer*; ST: *Sphoeroides testudineus*.

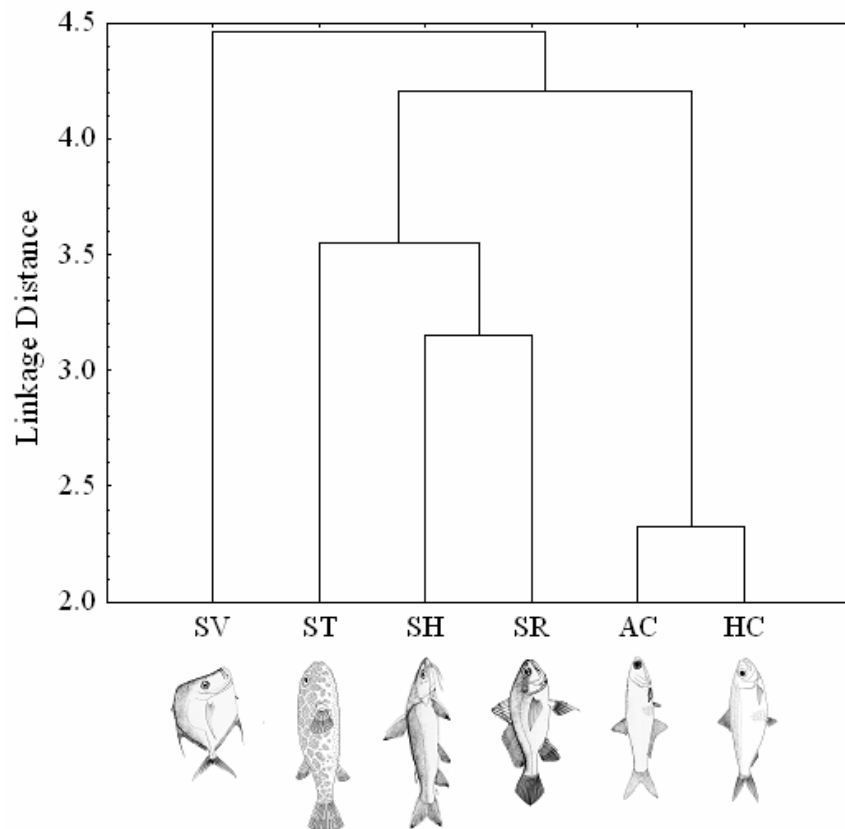


Figure 2. Cluster analysis based in 12 ecomorphological traits and six coded variables taken from six species of estuarine fishes. Refer to Fig. 1 for legends.