

Diet-morphology relationship in a fish assemblage from a medium-sized river of French Guiana: the effect of species taxonomic proximity

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Abstract – We investigated the global relationship between diet and morphology for 42 fish species from a medium-sized river in French Guiana and checked the influence of the species taxonomic proximity on the implication of individual morphological traits in that relation. The 42 species were classified in eight trophic guilds based on analysis of more than 4000 stomach contents. Taxonomic proximity between species was accounted for by an autoregressive model applied to original data of diet and morphology. Original and taxonomic-free data were then submitted to a Canonical Correspondence Analysis in order to detect the relationship between diet and morphology. We compared the results obtained by analyzing the original data and the corrected data. The results confirm the existence of a significant global relationship between diet and morphology. However, morphological traits responsible for that relation were different when considering the taxonomic-free data. Particularly the well known relationship between gut length and detritivory was not observed on the taxonomic free analysis. It is concluded that controlling for phylogeny is essential to the detection of relationships between diet and morphology. It is also concluded that, despite the robustness of some relationships between morphology and diet, many diets cannot be inferred by a ecomorphological approach.

Key words: Freshwater fish / River / Neotropics / Ecomorphology / French Guiana

Résumé – Relation régime alimentaire et morphologie dans un assemblage de poissons d'une rivière de moyenne importance en Guyane française. Effet de la proximité taxonomique entre espèces. Nous avons recherché une relation globale entre le régime alimentaire et la morphologie sur 42 espèces dans une rivière de moyenne importance de Guyane française et vérifié l'influence de la proximité taxonomique sur l'implication de traits morphologiques individuels dans cette relation. A partir de l'analyse de plus de 4000 contenus stomacaux, les 42 espèces ont été classifiées en huit guildes trophiques. La proximité taxonomique entre espèces a été prise en compte par un modèle auto-régressif appliqué sur les données originales de régime alimentaire et de morphologie. Les données originales et les données corrigées ont été ensuite soumises à une analyse canonique des correspondances, en vue de détecter la relation entre régime et morphologie. Nous avons comparé les résultats obtenus par l'analyse des données originales et corrigées. Les résultats confirment l'existence d'une relation globale significative entre régime et morphologie. Cependant, les traits morphologiques responsables de cette relation sont différents pour les données corrigées par rapport aux données originales. En particulier, la relation bien connue, entre la taille de l'intestin et un régime détritivore, n'apparaît pas dans l'analyse des données corrigées. Ainsi, le contrôle de la phylogénie nous paraît essentiel dans les études sur les relations morphologie/régime alimentaire. De plus, en dépit de la robustesse de quelques relations entre la morphologie et le régime alimentaire, de nombreux régimes ne peuvent être déduits de l'approche écomorphologique.

1 Introduction

The trophic position of fish species has been extensively used in the study of fish communities (Hartley 1948;

Wiegert and Owen 1971; Herrera 1976; Roger and Grandperrin 1976; Schlosser 1982; Angermeier and Karr 1983; Grossman 1986; Bowlby and Roff 1986; Schoener 1989; Parrish 1989; Winemiller 1990; Wootton and Oemke 1992; Flecker 1992; Sheldon and Meffe 1993; Chipps et al. 1994;

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Araujo et al. 1995; Adite and Winemiller 1997; Godinho et al. 1998; Maridet et al. 1998). However there are many limitations in accurately determining food regimes of fish. Many species are opportunistic foragers, particularly those inhabiting dynamic river habitats. Some species have long time intervals between two meals, while others crush their food, rendering items in stomach contents difficult to determine. All these make the study of fish communities through diet a very long and arduous task.

One way to avoid these difficulties is to view the fish species' morphology as the expression of an ecological role. The relationship between form and function has long been recognized (see Motta et al. 1995a for an historical overview of the concept), although it has received much more attention in recent years and the term "ecomorphology" has been introduced (Karr and James 1975). This approach states that species occupying similar ecological niches have evolved in such a way that they are close in some key morphological features. Many empirical observations illustrate this hypothesis (Keast 1978; Gatz 1979a,b; Gatz 1981; Wikramanayake 1990; Wainwright 1991; Labropoulou and Marakis 1998; Piet 1998) although few others did not (Grossman 1986; Motta et al. 1995b; Adite and Winemiller 1997). In some occasions this ecomorphological hypothesis has been confirmed by statistical tests (Winemiller and al. 1995; Hugueny and Pouilly 1999; Pouilly et al. 2003; Ibanez et al. 2007). From a statistical point of view, species in an assemblage cannot be considered as independent units as they all originate from a common ancestor (Harvey and Pagel 1991). It is likely that recently diverged species will be morphologically and ecologically similar. Therefore, the detection of a relationship between morphology and diet in an assemblage of species should take into account the phylogenetic relatedness. The result will be to lower the weight of similarities between closely related species and emphasize the convergence of unrelated species.

Earlier studies generated contradictory results. In a study of a fish assemblage from a river in Virginia, Douglas and Matthews (1992) showed that the relationship between diet and morphology turned non-significant when taking into account the phylogeny of the species. Conversely, other studies led to the inverse conclusion, that is, the relation is maintained after removing the effect of phylogenetic (or taxonomic) relatedness (Winemiller et al. 1995; Hugueny and Pouilly 1999; Pouilly et al. 2003). Moreover Ibanez et al. (2007) did not find any phylogenetic influence on morphology or diet in an assemblage of a small creek of the Bolivian Amazon Basin. Biogeographical and ecological factors could explain these contradictory results. In the Neotropical ichthyofauna, morphological diversification is particularly developed (Winemiller 1991) and it is likely that this corresponds to a high level of specialization in functional adaptations of species. In addition, heterogeneous environments exhibiting a predictable variability generate greater diversity and availability of food resources which can favor the development of specialized diets and the evolution of adapted morphologies.

This hypothesis of habitat influence on ecomorphological relationships in communities could not be tested without a multiplication of observations in different habitats. Therefore, the first objective of our study was to investigate the

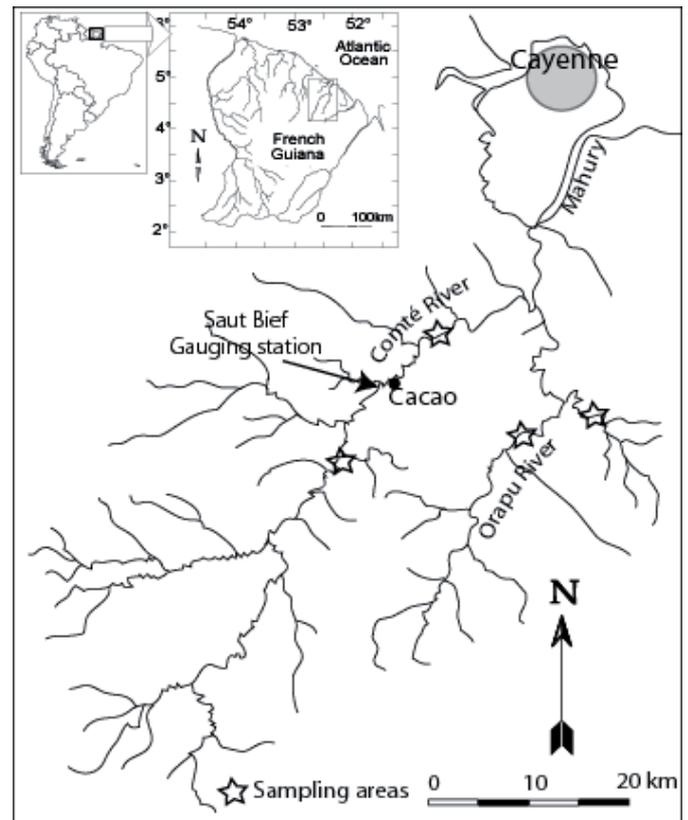


Fig. 1. Situation map. The stars indicate the position of sampling stations sampled during two contrasting seasons. Indicated also is the gauging station where was registered the daily discharge in the basin.

relationship between morphology and diet in a fish assemblage from a tropical river with a highly stochastic hydrological regime. In addition, we explored the influence of the phylogenetic relatedness of species on the variables involved in this relation in order to examine the degree of convergence among these species.

2 Materials and methods

2.1 Study site and sampling procedure

Individual fish for the study were caught in the Mahury basin, a medium-sized basin of French Guiana of about 3000 km² (Fig. 1). The hydrological regime is extremely variable with large daily fluctuations of discharge (Fig. 2). Fish were collected in two contrasting seasons during the years 1998-1999 in 4 stations presenting comparable habitat characteristics: mean width 38 m (± 12 SD), mean depth 4 m (± 1.6 SD), high overhanging marginal vegetation. We used 4 sets of gillnets 25 m long by 2 m height with meshes of 15, 20, 25, 30 and 35 mm, set at 5 p.m., along the banks, on areas of low flows and removed the day after at 7 a.m., following methodology designed by Tejerina Garro and Mérona (2000).

Bray-Curtis similarities between the faunas of the 4 stations were high, always above 50% (range: 54–86). On the field, every fish captured was identified at the species level

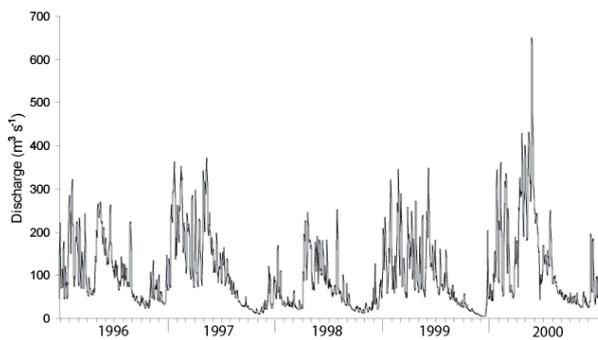


Fig. 2. Mean daily values of discharge recorded in the station “Saut Bief” between 1996 and 2000.

following a recent revision of French Guiana ichthyofauna (Planquette et al. 1996; Keith et al. 2000; Le Bail et al. 2000). One to five well-preserved individual fish were kept in ice and brought to the laboratory for anatomical observations and morphometrical measurements. The remaining fish were dissected in the field and their stomach removed and preserved in alcohol 70% for examination in the laboratory.

2.2 Morphological data

Depending on availability, the number of individual fishes considered for the morphological measurements ranged from 1 to 5. The use of only one specimen is questionable if there is a high intraspecific morphological variance. We conducted an analysis of variance on the table “specimens versus morphological characters” using only the species with 3 or more specimens measured. Overall the within species variance represented 28% of the total variance.

We chose the largest adult individuals in the collection in order to minimize possible allometric effects due to the ontogeny (Gatz 1979b).

The variables chosen were: 1) Body height divided by standard length (BH/SL), 2) Body width divided by standard length (BW/SL), 3) Dorso-ventral flatness: body width divided by body height (BW/BH), 4) Length of the caudal peduncle divided by standard length (CP/SL), 5) Caudal fin area divided by total body area in orthographic projection (measurements made with a planimeter from a photograph: CA/BA), 6) Head length divided by standard length (HL/SL), 7) Head height divided by head length (HH/HL), 8) Eye diameter divided by head height at eye (ED/HHE), 9) Eye position: the proportion of head height under the centre of the eye (EP), 10) Mouth area reported to corporal area, estimated by a planimeter from photographs (MA), 11) Mouth position: the angle formed by a tangent to the mouth and the longitudinal line of the fish. Ventral position = 0°, dorsal position = 180° (MP), 12) Number of gill rakers per mm on the first branchial arch (GR), 13) Length of the longest gill raker on the first branchial arch reported to head length (GR/HL), 14) Intestine length divided by standard length (IL/SL), 15) Number of teeth coded from 0 = none; 10 = less than 30; 40 = more than 30 and less than 50; 80 = more than 50 (TEETH), and 16) Teeth size coded from 0 to 4 (TE/SIZE) see Appendix.

Most of these variables have already been described in previous ecomorphological studies (Gatz 1979b; Watson and Balon 1984; Douglas and Matthews 1992; Wood and Bain 1995; Hugueny and Pouilly 1999) and all are supposed to be linked with species’ diet.

2.3 Stomach contents analysis

Eight categories of food items were identified in the stomachs: 1) higher plants, including roots, leaves, fruits, seeds and wood pieces (HighPl), 2) filamentous algae (Alg), 3) terrestrial invertebrates (Tinv), 4) aquatic invertebrates (Ainv), 5) plankton, including zoo- and phytoplankton (Plk), 6) shellfish, essentially shrimps but occasionally crabs (ShF), 7) fish (Fish), and 8) organic layer, detritus and sediment (OrgL).

The number of stomachs observed ranged from 6 to more than 500. Each stomach content was spread in a Petri dish and items determined using a stereomicroscope. The volumetric percentage of each item was estimated from the space occupied in the dish.

2.4 Data analysis

Characterization of typical diets of species was achieved following a stepwise procedure (Mérona et al. 2001). Specialized species were defined as those having stomachs containing more than 70% of a single food item. The remaining species were classified as carnivores (stomachs with more than 70% of animal food content), herbivores (more than 70% of vegetal or detrital food content) or omnivores (similar amount of animal and vegetal food content). Among the latter we distinguished surface dwelling omnivores as those consuming more than 70% of food of terrestrial origin. Compared to a classical hierarchical clustering method, this procedure allowed a clearer separation of specialized diets. Diet breadth was calculated by using Levin’s standardized index:

$$B_i = \left[\left(\sum_j p_{ij}^2 \right)^{-1} - 1 \right] (n - 1)^{-1}$$

where p_{ij} is the proportion of item j in species i and n is the total number of items considered (Hurlbert 1978).

A general phylogenetic pattern of fish species from South America is not yet available. Thus, in this study we use the taxonomic proximity resulting of the recent fish systematic revision of Reis et al. (2003) to determine the phylogenetic proximity between species. We elaborated a taxonomic distance matrix (T) giving the value 1 for congeneric species, 2 for consubfamilial species, 3 for confamilial species, 4 for species belonging to the same order and 5 otherwise.

Data of the two tables, “species by food items” and “species by morphological characters”, were normalized by a transformation Box Cox (Box and Cox 1964)

Normalized tables of diet and morphology were adjusted to an autoregressive model of the form (Cheverud et al. 1985):

$$Y = p \times W \times Y + \text{error} \quad (1)$$

where Y is the vector of values (food items or morphological variable), p is the coefficient of taxonomic autocorrelation estimated by maximum likelihood (see Cheverud et al. 1985,

Table 1. Diet composition of 42 fish species from the Mahury River in French Guiana expressed as the volumetric percentage of 8 food items.

Guild Species	Sample size	Food items								Diet breadth
		Higher plants	Algae	Terrest. Invert.	Aquatic Invert.	Plankton	Shellfish	Fish	Org. layer/ Sedim/ Detrit	
Detritivores										
<i>Anostomus brevior</i>	7	0	0	0	0	0	0	0	100	0.000
<i>Hypostomus gymnorhynchus</i>	14	0	0	0	0	0	0	0	100	0.000
<i>Chilodus zunevei</i>	23	0	0	0.9	1.7	0	0	0	97.4	0.008
<i>Curimata cyprinoides</i>	145	2.1	0	1.4	0	1.2	1.1	0	93.6	0.020
<i>Cyphocharax</i> sp.	40	2.5	0	1	1.5	0	0	0	95	0.015
<i>Cyphocharax spilurus</i>	81	9.6	0.5	0	0	0	0	1.2	88.6	0.037
Macrocarinivores										
<i>Acestrorhynchus falcatus</i>	82	0	0	0	0	0	0	100	0	0.000
<i>Acestrorhynchus guianensis</i>	140	0	0	4.1	0	0	1.4	94.1	0.4	0.018
<i>Hoplias aimara</i>	24	0	0	0	0	0	16.7	83.3	0	0.055
<i>Plagioscion squamosissimus</i>	21	0	0	0	0	0	23.8	76.2	0	0.081
<i>Pterengraulis atherinoides</i>	9	0	0	0	0	0	33.3	66.7	0	0.114
<i>Ageneiosus brevifilis</i>	29	6.9	0	3.4	0	0	10.3	64.8	14.5	0.169
<i>Hoplias malabaricus</i>	22	1.8	0	7.3	4.5	0	22.7	63.6	0	0.165
<i>Lycengraulis batesii</i>	16	0	0	5	0	0	18.8	61.3	15	0.185
Macrophytivores										
<i>Myleus ternetzi</i>	295	95.9	0.1	2.6	0.1	0	0.7	0	0.5	0.012
<i>Leporinus granti</i>	26	75	0	14.6	0.8	0	0	3.8	5.8	0.100
<i>Leporinus friderici</i>	284	74.1	0.5	9.7	0.7	0	0.5	7.9	6.1	0.108
<i>Leporinus fasciatus</i>	10	70	0	10	0	0	0	0	20	0.122
Terrestrial invertivores										
<i>Bryconops affinis</i>	300	6.6	0.3	87.3	4	0	0	0.7	0.9	0.043
<i>Bryconops caudomaculatus</i>	592	9.7	0.2	86.8	0.7	0	0	0.2	2.2	0.044
<i>Auchenipterus nuchalis</i>	572	3.9	0.2	84.3	6.8	0.9	0	0.6	3.1	0.056
Unspecialized carnivores										
<i>Charax pauciradiatus</i>	64	2.3	0	20.5	5.2	0	23	43.8	5.3	0.345
<i>Anchovia surinamensis</i>	38	0	0	2.6	54.2	25.8	5.3	0	12.1	0.235
<i>Eigenmania virescens</i>	45	4.4	0	39.1	36.4	2.2	0.7	0	14.4	0.320
<i>Pachypops fourcroyi</i>	23	6.5	2.6	57.4	7.8	0	6.1	0	17.8	0.237
<i>Loricaria cataphracta</i>	21	0	0	13.3	45.7	12.9	0	0	28.1	0.301
<i>Ageneiosus dentatus</i>	13	0	0	10.8	0	0	44.6	27.7	16.9	0.309
Unspecialized herbivores										
<i>Hemiodus unimaculatus</i>	138	18.3	14.5	4.1	0.7	0.7	0	1.4	60.3	0.197
<i>Hemiodus quadrimaculatus</i>	103	24	27.4	1.2	15.5	0	0	1	29.9	0.437
<i>Piabucus dentatus</i>	22	30	35.5	2.7	0	0	0	4.5	27.3	0.344
Surface dwelling omnivores										
<i>Astyanax bimaculatus</i>	20	35.5	0	61	0	0	0	0	3.5	0.143
<i>Moenkhausia chrysargyrea</i>	6	66.7	0	33.3	0	0	0	0	0	0.114
<i>Moenkhausia surinamensis</i>	78	60.2	0.8	34.2	0.3	0	0	1	3.6	0.154
<i>Moenkhausia oligolepis</i>	42	31.8	2.4	63.4	0	0	0	0	2.4	0.140
<i>Moenkhausia georgiae</i>	40	49.5	2.5	43.3	1.3	0	0	0	3.5	0.186
<i>Moenkhausia grandisquamis</i>	26	49.7	0.5	44.2	0.4	0	0.7	0.7	3.5	0.179
<i>Poptella brevispinna</i>	261	25.1	0.5	66.7	4	0.2	0	0.9	2.5	0.137
<i>Jubiaba keithi</i>	23	43.5	0	44.3	0.4	0	0	4.3	7.4	0.221
<i>Parauchenipterus galeatus</i>	283	44.7	0.3	46.7	1.5	0	1.9	2.8	1.8	0.198
Other omnivores										
<i>Serrasalmus humeralis</i>	36	31.7	0	1.7	0	0	3.3	52.8	10.6	0.222
<i>Doras carinatus</i>	56	3.6	5.4	8.9	45.4	0.9	0	1.1	31.9	0.303
<i>Satanoperca jurupari</i>	38	0	0	9.7	15	8.9	0	4.7	61.6	0.196

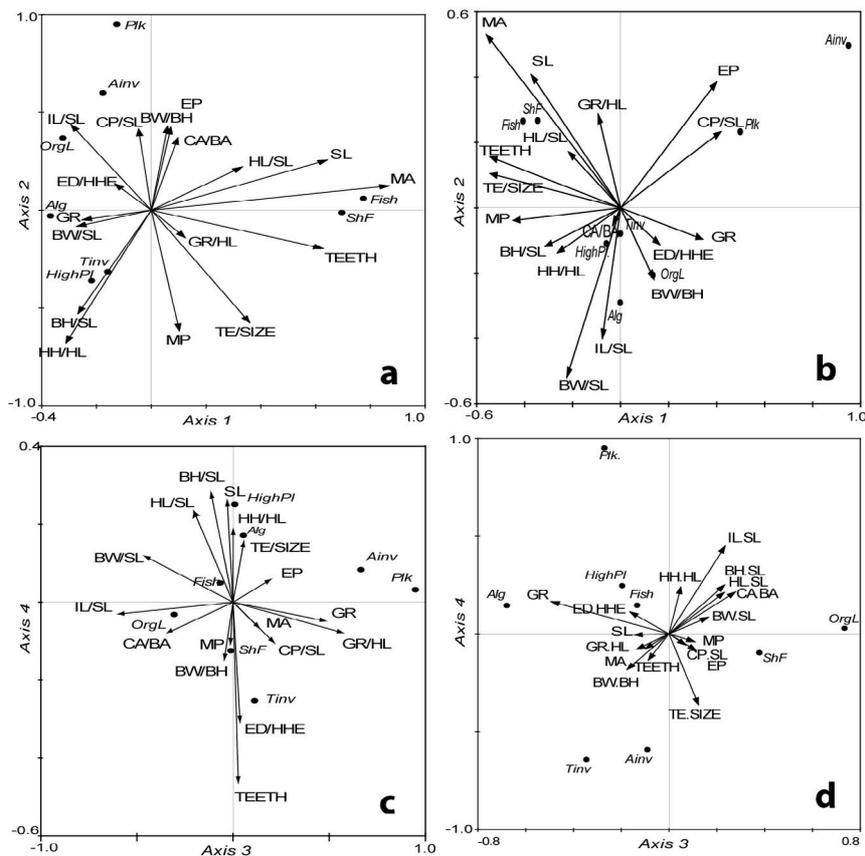


Fig. 3. Projection of food items and morphological variables on the Canonical Correspondence Analysis axes. a and c original data; b and d residual data.

for details), W is a matrix of weights increasing with the taxonomic similarity between species, in our case $W = 1/T$.

The error corresponds to the residual values of the model, i.e., values of diet or morphology independent of taxonomical relatedness. Under the hypothesis of phylogenetic inertia we expect a positive taxonomic autocorrelation. That means that taxonomically related species tend to be more similar for the trait Y than unrelated species. In this case we considered the residuals (error) in (1) as a taxonomic free variable. Negative values suggest some kind of morphological convergence and in this case using methods to “remove” the phylogenetic effect tended to erase this signal we were looking for in the data. As a result data in subsequent analyses were kept untransformed if $p < 0$. In the following text the transformed values of traits will be called “residual data” as opposed to “original data”.

To explore the relationship between diet and morphology we used the Canonical Correspondence Analysis (CCA, Ter Braak 1986). This analysis is a correspondence analysis of trophic data in which the axes are a linear combination of explanatory variables (morphological variables).

3 Results

Information on stomach contents and morphology data was obtained for 42 species among the most abundant of the assemblages. Overall these species represented 98% of the total

number of fishes captured but only 51% of the species' richness because of the great number of rare species in our collections. Studied species belong to 31 genera, 15 families and 5 orders (Table 1 and Appendix).

We identified 8 groups of species exhibiting similar diets (Table 1). Four of them are specialized in their feeding habits. Detritivores had their digestive tract generally full of a green or brown paste. Macrocarivores consumed mainly fish but also shrimps and crabs. Macrophytivores fed upon leaves, fruits, flowers and even wooden pieces. Insects, and particularly ants, constituted the main food of terrestrial invertivores. The 4 remaining feeding groups showed more generalized diets. The group of unspecialized carnivores is heterogeneous, including 2 species consuming relatively large prey like fishes and shrimps (*Charax pauciradiatus* and *Ageneiosus dentatus*) and other feeding preferentially on insects. Unspecialized herbivores ingested a large quantity of sediment in a diet based on higher plants and algae. Surface dwelling omnivores had a relatively narrow diet breadth with higher plant and terrestrial invertebrates composing the main bulk of their stomach contents. Finally the three species classified as other omnivores showed very different diets. *Serrasalmus humeralis* consumed fish pieces and fruits, *Doras carinatus* ingested many aquatic invertebrates along with sediment and *Satanoperca jurupari* completed a diet based on sediment with a great variety of prey.

Table 2. Results of Canonical Correspondence Analyses (CCA) between diet and morphology of 42 fish species from the Mahury basin in French Guiana. Orig. = original data; Resid. = taxonomic-free data.

	Axis 1		Axis 2		Axis 3		Axis 4	
	Orig.	Resid.	Orig.	Resid.	Orig.	Resid.	Orig.	Resid.
Cumulative % of dietary data	26.9	30.4	44.2	47.0	57.1	52.2	63.1	56.0
Cumulative % of diet/morphology relationship	38.4	48.9	63.1	75.6	81.5	83.9	90.1	90.0
Diet/morphology relationship (r^2)	87.7	78.1	69.9	73.1	71.7	44.1	53.7	62.4

Table 3. Fraction of variance of food items explained by the 4 first axes of Canonical Correspondence Analyses on original and residual data. In bold, fraction > 20% of variance explained by the model. Terr invert: terrestrial invertebrates; Aquat invert: aquatic invertebrates; Organic layer: detritus or sediment.

Item	Axis 1		Axis 2		Axis 3		Axis 4		% Expl.	
	Orig.	Resid.	Orig.	Resid.	Orig.	Resid.	Orig.	Resid.	Orig.	Resid.
Higher plants	0.113	0.034	0.309	0.116	0.001	0.029	0.197	0.045	63.53	48.01
Algae	0.052	0.000	0.000	0.256	0.002	0.109	0.015	0.005	39.84	47.75
Terr invert	0.064	0.000	0.249	0.053	0.046	0.081	0.220	0.280	58.49	53.54
Aquat invert	0.024	0.584	0.275	0.160	0.463	0.000	0.001	0.018	79.43	78.07
Plankton	0.005	0.309	0.274	0.067	0.369	0.007	0.000	0.088	76.76	50.79
Shellfish	0.452	0.411	0.000	0.244	0.000	0.038	0.021	0.003	73.67	77.44
Fish	0.808	0.391	0.005	0.167	0.007	0.003	0.004	0.004	84.92	62.10
Organic layer	0.203	0.099	0.265	0.233	0.239	0.230	0.003	0.000	71.06	57.40

Table 4. Contributions of morphological variables in Canonical Correspondence Analyses of original and residual data. E = additional fit (increase in eigenvalue in %); P = probability from 199 random permutations. In bold, variables selected by a stepwise forward model (see methods for abbreviations).

Morphological variables	Original data		Residual data	
	P	E	P	E
SL	0.130	3.409	0.078	4.878
BH/SL	0.322	1.705	0.372	2.439
BW/SL	0.920	0.568	0.034	7.317
BW/BH	0.592	1.136	0.068	4.878
CP/SL	0.488	1.705	0.704	2.439
CA/BA	0.132	2.841	0.242	2.439
HL/SL	0.794	0.568	0.718	2.439
HH/HL	0.002	12.500	0.098	4.878
ED/HHE	0.084	3.409	0.116	4.878
EP	0.030	4.545	0.002	17.073
MA	0.002	30.114	0.002	21.951
MP	0.230	2.273	0.476	2.439
GR	0.164	2.841	0.158	4.878
GR/HL	0.012	9.091	0.180	2.439
IL/SL	0.002	11.364	0.734	0.000
TEETH	0.008	6.250	0.208	2.439
TE/SIZE	0.006	5.682	0.010	12.195

Canonical Correspondence Analyses of the two data sets (original and residual) both revealed significant relationships between diet and morphology ($p = 0.002$). In both cases the 4 first factors of the analysis explained more than 90% of the total variability of the data sets (Table 2). However the correlations of diet versus morphology on the 4 axis were slightly higher for the original data as compared to those for the residual data. The fraction of variance of each food item explained by morphology was generally lower for the residual data with the exception of algae (48% vs. 40%) and shellfish (77% vs.

74%) (Table 3). For the other items this value varies from 64 to 85% for the original data and from 48 to 78% for the residual data. The main differences between the two analyses concerned the morphological variables involved in the explanatory model. A stepwise forward selection of these variables gave a model with 7 variables explaining 79.55% of the total variability of the original data set, whereas the same method applied to the residual data gave a model with 4 variables explaining 58.54% of the total variability of the data set (Table 4). Three variables were common in the two models: the mouth area and the teeth size, both showing a strong association with items fish and shellfish and eye position with aquatic invertebrates and plankton (Fig. 3a–d). Gut length was associated with organic layer, teeth number and size with fish and shellfish (Fig. 3a), gill raker size with plankton, head height with higher plants (Fig. 3c), when considering original data. Body width was associated with higher plants in the residual data model (Fig. 3b).

The projection of species on the ordination plot of the CCAs showed large differences between original and residual data analyses (Fig. 4). For the original data, the position of species at the centroid of their morphological attributes showed a good similarity with their diets (Fig. 4a,c). Species with specialized diets are clearly grouped together and isolated, whereas generalist feeders are dispersed through the morphological space. Conversely, the figure obtained from the residual data analysis showed large overlaps in the distribution of groups of specialists (Fig. 4b,d).

4 Discussion

The forty two analyzed species were classified in eight trophic guilds. Four of them were specialists (detritivore, macrocarnivore, macrophytivore and terrestrial invertivore) and four, generalists (unspecialized carnivore or herbivore, surface dwelling omnivore and other omnivore). This pattern

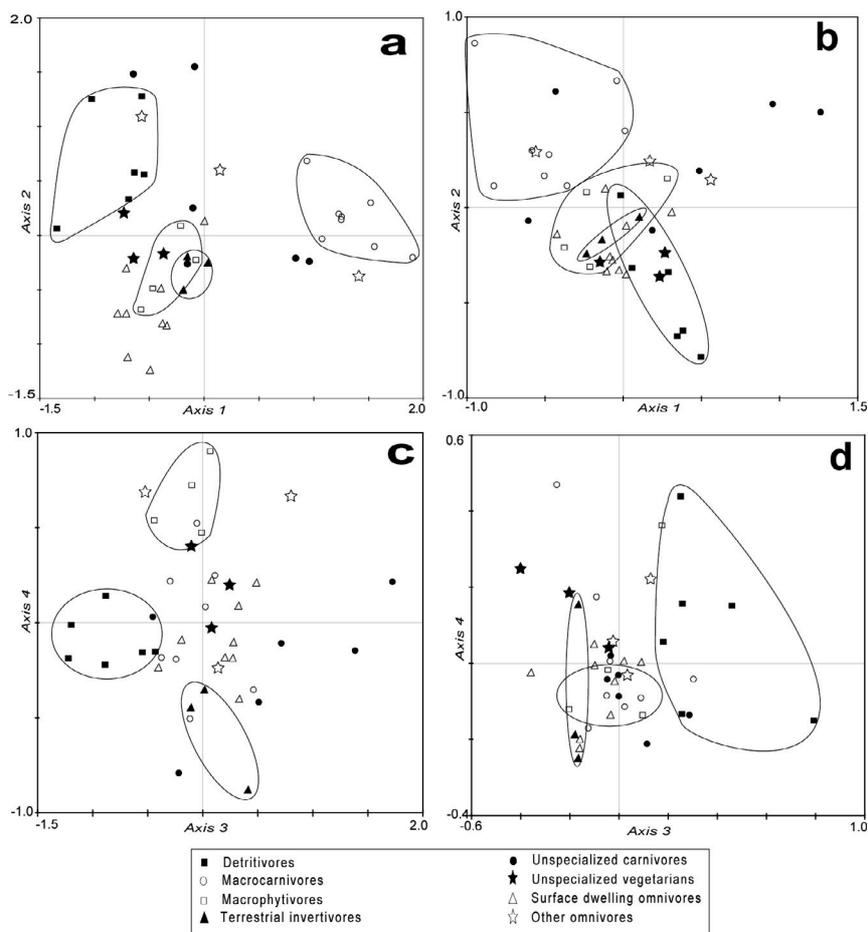


Fig. 4. Projection of species, positioned at the centroid of their morphological attributes, on the four first axes of the Canonical Correspondence Analyses for original (a and c) and residual (b and d) data.

is broadly in agreement with other studies of trophic structure of fish communities in the Amazon region (Mérona et al. 2001; Pouilly et al. 2003, 2006; Mérona et al. 2003; Mérona and Rankin-de Mérona 2004; Mérona and Vigouroux 2006; Ibanez et al. 2007). However, some discrepancies exist, which seem to be related to the type of environment sampled. In small forested streams, fish assemblages are dominated by invertebrates' feeders (Angermeier and Karr 1983; Horeau et al. 1996; Bojsen and Barriga 2002; Silva 1993; Pouilly et al. 2006; Ibanez et al. 2007), attesting the importance of allochthonous source of energy in these systems. In much larger systems autochthonous food sources are equally important and piscivores, detritivores and omnivores form the main bulk of the fish assemblages (Pouilly et al. 2003; Mérona et al. 2001; Mérona and Rankin 2004). In addition specialized planktivores, algivores or aquatic invertivores are often present in these systems. The situation of the medium-sized river from French Guiana studied here appears intermediate between small forested streams and large systems with no neat dominance of one or a few number of guilds.

Previous works have demonstrated relationships between diet and morphology in fish based on data not corrected by the phylogeny of the fish species studied (Gatz 1979b; Wikramanayake 1990; Adite and Winemiller 1996;

Hugueny and Pouilly 1999; Pouilly et al. 2003; Ibanez et al. 2007; Teixeira and Bennemann 2007). Our data confirm this significant correlation in fish assemblages (Probability of 0.002 for the correlation between morphology and diet). Two main associations emerge consistently from these previous studies. The first one is a relationship between standard length and mouth size with consumption of large prey like fishes or shrimps (Gatz 1979b; Winemiller 1989; Piet 1998; Hugueny and Pouilly 1999; Winemiller et al. 1995). This association was clearly confirmed by our analysis on original data. Given that we used the relative mouth size, the relation with macrocarnivory was independent of the size of the fish. This observation is in contradiction with the conclusion of Hugueny and Pouilly (1999) who stated that for an assemblage of African fishes the absolute size of the mouth is a better index of piscivory. In the South American fauna however, many large species are frugivores (Goulding 1980) like *Colosoma* spp. or detritivores (e.g., *Prochilodus* spp., or *Pterygoplichthys* spp.) and small ones are exclusively piscivores like many Engraulidae or small species of piranhas (*Serrasalmus* spp.). Fish as a prey presents a large range of sizes and the piscivore behavior does not depend on the predator size. In a study of ontogenetic diet shifts in piscivorous fishes from Venezuela Winemiller (1989) shows that these species start to feed on fish at very

small sizes 40 to 80 mm SL. Number and size of teeth are two other characters that have been linked to the capture of large prey such as crayfish or fish (Gatz 1979b) and could be another good index of a macrocarnivorous diet.

The second important association pointed out by previous works, and also detected in the analysis of our original data, is that of the relative gut length with consumption of detritus (Kapoor et al. 1975; Reifel and Travill 1978; Paugy 1994; Kramer and Bryant 1995; Huguény and Pouilly 1999; Pouilly et al. 2003; Ibanez et al. 2007). Herbivory was also sometimes reported as linked to gut length in the literature and this is apparently related to the quantity of indigestible material in the diet (Kapoor et al. 1975). Indeed species like *Myleus* spp. have a long intestine generally full of leaf debris. However, at the community level, the relation macrophytes/gut length has never been proved (Gatz 1979; Huguény and Pouilly 1999; Pouilly et al. 2003) and was not found in our data either. This is probably due to the position of many omnivores, which consume large amount of vegetal material but have a relatively short intestine. Herbivorous diet was instead associated with head height (for the original data) and body width (for the residual data). Generally, herbivorous species are poor swimmers, inhabiting preferentially the still waters of pools. An evolution towards a high or large body could have the adaptive significance of avoiding predation and increasing maneuverability.

Long and numerous gill rakers are generally associated with a filtering feeding behavior and as a consequence with small prey (Kliewer 1970). However, Gatz 's results (1979b) did not strongly support this hypothesis: for the set of species, he analyzed, the taxonomic component seemed to be determinant in the relationship. Gill raker number and size have been shown to be associated with planktivory in the Mamoré floodplain (Pouilly et al. 2003). Our data weakly support this conclusion. Number and size of gill rakers were somehow correlated ($r = 0.4377$) and were associated to plankton and aquatic invertebrates. The weakness of this relation in the Mahury basin was probably due to the fact that plankton is a relatively rare resource in that environment and, as a consequence, there is no specialist planktivore in our assemblage. These results suggest that the number and size of gill rakers are not strong predictive characters for attributing a diet to a morphological feature in our context. In our data, an eye in an upward position was apparently linked to aquatic invertebrates. This observation supports Gatz 's assumption that a dorsal position of eye could be associated, along with other characters, to a benthic habitat preference, compatible with a diet based on aquatic invertebrates (Gatz 1979a).

We found a strong taxonomic influence on both diet and morphology. For most of the variables (morphology and food item) the taxonomic proximity of species was correlated to proximity in morphology and/or diet. This result is in contradiction with the situation observed in the Chipiriri River where no relation has been detected between morphology or diet and phylogenetic proximity (Ibanez et al. 2007). The specific composition of the assemblages under study is probably responsible for this contradiction. In the Chipiriri River, only 2 genera out of 28 contained more than one species (actually two) whereas 7 out of 31 included more than one species in the

Mahury assemblage. Although, our sample was partial, due to gillnets' selectivity, it could be hypothesized that habitat plays a fundamental role in the evolution of fish assemblages leading to different faunistic compositions. Indeed, large habitats harbor more niches and allow the coexistence of more species.

Because of the strong influence of taxonomic relatedness on diet and morphology in our set of data, it has been accounted for in the correlation between morphology and diet. The result suggests that unrelated species having similar diets display similar morphological adaptations, and thus display convergence. However some correlations between morphological traits and diet have been altered by considering taxonomic-free variables instead of raw data.

Two main associations between morphology and diet were maintained after removing the taxonomic proximity between species: mouth area and teeth size with fish and shellfish consumption, and eye position with aquatic invertebrates and plankton. Because macrocarnivores and consumers of aquatic invertebrates included species belonging to distantly related families, the relation should be, indeed, relatively phylogenetically independent and the results evidenced an evolutionary process based on convergence.

Conversely the association between gut length and detritivory was not demonstrated in our analysis of taxonomic-free data. This is probably due to the fact that gut morphology and length have a strong taxonomic component. This has been shown in the African ichthyofauna (Kouamélan et al. 1997), and this is probably also the case for the Neotropical ichthyofauna. Indeed, detritivory is closely related to the phylogeny of species as every studied species from the families or sub-families Curimatidae, Prochilodontidae or Hypostominae are mud-feeders (Kramer and Bryant 1995; Bowen 1988; Goulding et al. 1988; Mérona et al. 2001; Mérona and Rankin-de Mérona 2004). Ideally correlations between variables should be preserved when taxonomy (phylogeny) is accounted for. However when entire taxa (e.g. families) are homogeneous in their morphology and ecology the removal of the taxonomic component leads to weakness the initial ecomorphological relationships as observed in our data with the relationship between detritivory and gut length.

Thus, for this character, we could hypothesize an evolutionary process based on parallelism, that is a convergence within relatively close evolutionary lines (Winemiller et al. 1995).

5 Conclusion

Our results based on the original data (i.e. those not corrected by the taxonomic relatedness of species) confirm former works on tropical rich ichthyofauna (Wikramanayake 1990; Winemiller 1995; Huguény and Pouilly 1999; Pouilly et al. 2003; Ibanez et al. 2007). Three main specialized diets, macrocarnivory (especially ichthyophagy), detritivory and planktivory were associated to some morphological features. Generally the authors confirmed that the overall correlation between diet and morphology was still significant when controlling the effect of the phylogeny (or failing that, the taxonomy) of the analyzed group of species in the model and inferred the reality of the associations between individual morphological

traits and diet. The analysis conducted here shows that significant overall correlations between morphology and diet both in raw data and data corrected by the phylogeny does not necessarily imply similar individual associations between morphological traits and food items. Although considering taxonomic distance as a surrogate of true phylogenetic distance, our results suggest that phylogeny has indeed a significant influence on the relationship between diet and morphology in our set of data. The results presented also suggest that the habitat in which the study is conducted has an influence on the relationships found between morphology and diet via the taxonomic composition of its fauna. However many more observations in different habitats are necessary to test this hypothesis. Overall, it appears that a few associations morphology/diet are robust but are not sufficient to infer a trophic structure of an entire fish assemblage as a number of diets are not clearly associated with morphological features.

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Appendix: Mean values of morphological parameters for 42 species of the Comté River. SL: standard length (in mm), BH/SL: Body height on standard length, BW/SL: body width on standard length, BW/BH: body width on body height, CP/SL: caudal peduncle length on standard length, CA/BA: caudal fin area, HLSL: head length on standard length, HH/HL: head height on head length, ED/HHE: eye diameter on head height, EP: eye position, MA: mouth area, MP: mouth position, GR: number of gill rakers, GR/HL: length of gill rakers on head length, IL/SL: intestine length on standard length, TE: teeth number, TE/SIZE teeth size.

Order	Code	SL	BH/SL	BW/SL	BW/BH	CP/SL	CA/BA	HLSL	HH/HL	ED/HHE	EP	MA	MP	GR	GR/HL	IL/SL	TE	TE/SIZE	
Family																			
Species																			
Characiforme																			
Acestrorhynchidae																			
<i>Acestrorhynchus falcatus</i> (Bloch, 1794)	AFAL	202.8	0.23	0.13	0.56	0.10	0.31	0.29	0.66	0.42	0.73	0.52	79.50	2.28	0.02	0.79	80	1	
<i>Acestrorhynchus guianensis</i> Menezes, 1969	AGUI	183.2	0.20	0.11	0.57	0.10	0.16	0.28	0.58	0.50	0.78	0.55	51.00	0.43	0.01	0.86	80	4	
Anostomidae																			
<i>Anostomus brevior</i> Géry, 1960	ABRE	90.5	0.25	0.13	0.51	0.11	0.18	0.23	0.65	0.49	0.65	0.12	143.00	0.38	0.03	1.52	10	3	
<i>Leporinus fasciatus</i> (Bloch, 1794)	LFAS	207.5	0.26	0.14	0.53	0.09	0.19	0.22	0.96	0.40	0.64	0.17	50.00	0.75	0.05	0.55	10	3	
<i>Leporinus friderici</i> (Bloch, 1794)	LFRI	215	0.31	0.18	0.59	0.11	0.15	0.25	0.93	0.45	0.55	0.24	73.00	0.75	0.04	1.55	10	3	
<i>Leporinus granti</i> Eigenmann, 1912	LGRA	156.9	0.34	0.19	0.56	0.12	0.11	0.22	1.17	0.35	0.50	0.18	71.00	0.92	0.06	1.57	10	3	
Characidae																			
<i>Charax pauciradiatus</i> Günther, 1864	CPAU	110.8	0.42	0.13	0.31	0.09	0.16	0.26	1.26	0.42	0.62	0.69	121.75	0.55	0.19	0.63	80	3	
<i>Piabucus dentatus</i> (Koelreuter, 1761)	PDEN	139.8	0.21	0.10	0.50	0.09	0.10	0.17	0.93	0.51	0.47	0.13	86.00	1.67	0.02	1.00	10	2	
<i>Astyanax bimaculatus</i> (Linnaeus, 1758)	ABIM	109.8	0.38	0.16	0.45	0.12	0.14	0.20	1.47	0.38	0.57	0.13	115.00	1.50	0.09	0.66	10	3	
<i>Bryconops affinis</i> (Günther, 1864)	BAFF	99	0.26	0.15	0.57	0.11	0.16	0.22	0.99	0.60	0.52	0.31	92.00	1.52	0.07	0.70	40	3	
<i>Bryconops caudomaculatus</i> (Günther, 1869)	BCAU	98.8	0.27	0.14	0.53	0.12	0.13	0.22	0.93	0.60	0.68	0.27	101.20	1.03	0.07	0.81	40	3	

Appendix: Continued.

Order Family Species	Code	SL	BH/SL	BW/SL	BW/BH	CP/SL	CA/BA	HLSL	HH/HL	ED/HHE	EP	MA	MP	GR	GR/HL	IL/SL	TE	TE/SIZE
<i>Jubiaba keithi</i> (Géry, Planquette and Le Bail, 1996)	JKEI	73.2	0.54	0.15	0.28	0.12	0.14	0.26	1.40	0.40	0.69	0.13	115.50	1.36	0.09	1.27	40	3
<i>Moenkhausia chrysargyrea</i> (Günther, 1864)	MCHR	80.7	0.51	0.18	0.36	0.07	0.14	0.24	1.64	0.39	0.58	0.16	93.00	1.59	0.08	1.21	40	3
<i>Moenkhausia georgiae</i> Géry, 1966	MGEO	71	0.49	0.15	0.32	0.10	0.15	0.25	1.37	0.46	0.51	0.24	120.00	1.36	0.05	0.66	40	3
<i>Moenkhausia grandisquamis</i> (Müller and Troschel, 1845)	MGRA	101.4	0.46	0.14	0.31	0.11	0.12	0.25	1.09	0.52	0.60	0.19	89.50	1.49	0.08	0.97	80	3
<i>Moenkhausia oligolepis</i> (Günther, 1864)	MOLI	77.4	0.46	0.18	0.40	0.10	0.10	0.25	1.42	0.34	0.46	0.16	114.00	1.13	0.07	0.89	40	3
<i>Moenkhausia surinamensis</i> Géry, 1965	MSUR	85.7	0.47	0.16	0.35	0.10	0.11	0.27	1.43	0.58	0.69	0.19	120.00	1.18	0.09	1.66	40	3
<i>Myleus ternetzi</i> (Norman, 1929)	MTER	132.5	0.64	0.16	0.24	0.07	0.12	0.27	1.59	0.43	0.58	0.14	89.00	0.90	0.09	3.68	10	3
<i>Serrasalmus humeralis</i> Cuvier and Valenciennes, 1849	SHUM	118.7	0.57	0.13	0.23	0.12	0.17	0.33	1.40	0.40	0.70	0.73	124.00	0.00	0.00	2.57	40	4
<i>Poptella brevispina</i> Reis, 1989	PBRE	80.3	0.61	0.15	0.25	0.11	0.14	0.24	1.73	0.43	0.55	0.19	122.67	1.75	0.08	0.88	40	3
Chilodontidae <i>Chilodus zunevei</i> Puyo, 1945	CZUN	81.4	0.39	0.18	0.48	0.11	0.13	0.27	1.06	0.50	0.54	0.11	121.5	0.89	0.02	1.82	0	0

Appendix: Continued.

Order	Code	SL	BH/SL	BW/SL	BW/BH	CP/SL	CA/BA	HLSL	HH/HL	ED/HHE	EP	MA	MP	GR	GR/HL	IL/SL	TE	TE/SIZE
Family																		
Species																		
Curimatidae																		
<i>Curimata cyprinoides</i> (Linnaeus, 1758)	CCYP	158.4	0.39	0.16	0.42	0.11	0.19	0.31	1.04	0.54	0.52	0.26	50.75	0.48	0.03	12.26	0	0
<i>Cyphocharax</i> sp.	CYP1	98.7	0.37	0.18	0.49	0.13	0.16	0.24	0.96	0.54	0.66	0.12	34.33	0.00	0.00	30.78	0	0
<i>Cyphocharax spilurus</i> (Günther, 1864)	CYSP	107.7	0.35	0.17	0.48	0.13	0.15	0.27	0.93	0.58	0.61	0.16	40.50	0.00	0.00	32.15	0	0
Erythrinidae																		
<i>Hoplias aimara</i> (Valenciennes, 1840)	HAIM	477	0.23	0.17	0.76	0.13	0.16	0.32	0.58	0.52	0.67	0.48	116.00	0.44	0.05	0.77	80	4
<i>Hoplias malabaricus</i> (Bloch, 1794)	HMAL	259.4	0.21	0.16	0.79	0.13	0.25	0.30	0.62	0.43	0.71	0.46	118.50	0.36	0.04	0.97	80	4
Hemiodontidae																		
<i>Hemiodopsis quadrimaculatus</i> (Pellegrin, 1908)	HQUA	122.5	0.25	0.15	0.62	0.11	0.20	0.23	0.76	0.56	0.63	0.16	50.50	2.32	0.04	1.49	10	2
<i>Hemiodus unimaculatus</i> (Bloch, 1794)	HEUN	170.6	0.24	0.15	0.62	0.12	0.17	0.23	0.77	0.62	0.59	0.16	43.40	3.47	0.04	1.39	40	2
Clupeiforme																		
Engraulidae																		
<i>Anchovia surinamensis</i> (Bleeker, 1866)	ASUR	103.5	0.28	0.10	0.37	0.12	0.17	0.28	0.81	0.56	0.63	0.73	42.00	3.57	0.27	0.38	0	0
<i>Lycengraulis batesii</i> (Günther, 1868)	LBAT	162.8	0.20	0.08	0.42	0.16	0.14	0.21	0.76	0.54	0.59	0.61	65.67	0.55	0.07	0.35	80	3
<i>Pterengraulis atherinoides</i> (Linnaeus, 1766)	PATH	180.5	0.23	0.08	0.33	0.10	0.13	0.22	0.90	0.50	0.62	0.82	58.00	0.74	0.12	0.30	80	2

Appendix: Continued.

Order	Code	SL	BH/SL	BW/SL	BW/BH	CP/SL	CA/BA	HLSL	HH/HL	ED/HHE	EP	MA	MP	GR	GR/HL	IL/SL	TE	TE/SIZE
Family																		
Species																		
Gymnotiforme																		
Sternopygidae																		
<i>Eigenmania virescens</i> (Valenciennes, 1847)	EVIR	172.9	0.16	0.06	0.36	0.00	0.00	0.10	0.84	0.40	0.64	0.10	93.00	0.00	0.00	0.32	80	2
Perciforme																		
Cichlidae																		
<i>Satanoperca jurupari</i> Heckel, 1840	SJUR	114.7	0.36	0.15	0.43	0.16	0.26	0.31	1.03	0.32	0.80	0.35	79.67	0.72	0.03	1.27	80	2
Sciaenidae																		
<i>Pachypops fourcroi</i> (Lacépède, 1802)	PFUR	118.2	0.25	0.16	0.63	0.25	0.24	0.30	0.76	0.56	0.63	0.31	35.00	1.27	0.03	0.65	80	1
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	PSQU	337	0.30	0.16	0.55	0.27	0.12	0.26	1.10	0.30	0.66	0.63	94.00	0.22	0.10	0.80	40	3
Siluriforme																		
Ageneiosidae																		
<i>Ageneiosus dentatus</i> Kner, 1857	ADEN	193.7	0.20	0.13	0.66	0.11	0.18	0.24	0.56	0.49	0.40	0.46	27.00	0.78	0.05	1.12	80	4
<i>Ageneiosus brevifilis</i> (Cuvier and Valenciennes, 1857)	AGBR	261.5	0.17	0.19	1.14	0.13	0.16	0.30	0.54	0.32	0.31	0.80	75.00	0.51	0.04	1.25	80	1
Auchenipteridae																		
<i>Auchenipterus nuchalis</i> (Spix, 1829)	ANUC	108.8	0.16	0.11	0.69	0.12	0.17	0.19	0.73	0.65	0.46	0.38	98.00	3.19	0.11	1.04	80	1
<i>Parauchenipterus galeatus</i> (Linnaeus, 1766)	PGAL	164.9	0.25	0.19	0.78	0.13	0.22	0.23	0.83	0.22	0.53	0.38	122.00	0.31	0.02	1.86	80	1
Doradidae																		
<i>Doras carinatus</i> (Linnaeus, 1766)	DCAR	133.5	0.21	0.17	0.82	0.15	0.17	0.31	0.59	0.42	0.73	0.16	0.00	0.76	0.04	1.56	10	2
Loricariidae																		
<i>Hypostomus gymnorhynchus</i> (Norman, 1926)	HGYM	113.4	0.22	0.29	1.34	0.34	0.41	0.23	0.82	0.26	0.69	0.06	0.00	1.09	0.04	19.43	80	3
<i>Loricaria cataphracta</i> Linnaeus, 1758	LCAT	180.3	0.08	0.12	1.42	0.81	0.15	0.20	0.37	0.47	0.92	0.12	0.00	1.50	0.01	1.26	10	2