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Morphological Patterns of Fish and Their Relationships with Reservoirs Hydrodynamics

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ABSTRACT

The aim of this study was to determine morphological patterns of the most abundant fish species found in reservoirs with different hydraulic retention times and stages of colonization, considering habitat strata and feeding strategies. Samplings were carried out in six Paraná State (Brazil) reservoirs, and morphological data were obtained from 15 individuals of 17 fish species. Ecomorphological attributes that best segregated species, were selected using Discriminant Analysis. These selected attributes were later used in a Principal Components Analysis (PCA). Differences among reservoirs concerning occupation of the ecomorphological space were tested through analysis of variance (null models). The six reservoirs differed in the occupation of the fish species ecomorphological space and the first two PCA axes explained 66,3% of the total data variability. Thus alterations in water dynamics could a major factor affecting patterns of fish distribution in reservoirs.

Key words: Ecomorphology, feeding strategies, habitat, reservoir

INTRODUCTION

Morphological diversity of organisms and its use as a tool in the exploitation of natural resources has always arisen great curiosity, with a long historical and evolutionary context of correlations between the form of organisms and ecology. The first commentaries interpreted as "ecomorphological" are found in the Hindu text "Sursuta-sambita" and describe a connection between body form and habitats of freshwater fish (Lindsey, 1978). However, the development of ecomorphology as a field of comparative study (with the objective of demonstrating that variations in ecological characteristics among species are correlated with or caused by congruent morphological, functional or physiological differences) appeared only during the 18th and 19th centuries, when ecological concepts were already better understood.

Because fishes show the highest morphological diversity among vertebrates, they can be an important source of responses to inquiries concerning the relationships between morphology and ecology. This aspect can be emphasized in the neotropical region, which is characterized by high fish diversity and consequently, high morphological types (Winemiller, 1991). The use of ecomorphological approaches in this region may be a relevant tool addressing questions on niches, shared resources and community structure.

Because species morphology is somehow linked to habitat use and its performed niche, alterations in the environment, like those resulted from dam

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constructions may restrict permanence of certain previously existing species. Therefore, we may suppose that fish species inhabiting reservoirs are those possessing morphologies that allow behavioral plasticity, or those adapted to cope with new conditions (i.e. standing water). Although such restrictions can be related to feeding and reproductive strategies of each species, their morphological characteristics may also influence the selection of those more suited to colonize the new environment. Therefore, the main objectives of this study were: (i) characterize the morphology of the numerically most abundant fish species in reservoirs with different hydraulic retention time and age (different stages of colonization) and (ii) identify morphological patterns that successfully colonized the reservoirs, considering distinctly habitats (littoral, bottom and pelagic), and possible effects of feeding strategies influencing colonization.

MATERIALS AND METHODS

Study area

This study was carried out in six hydroelectric reservoirs in the Paraná State (Brazil), located in different basins, with varied ages (more than 32 years old) and morphometries (Table 1).

Mourão and Rio dos Patos reservoirs are located in tributaries of the Ivaí River (Paraná River basin) and situated nearby the cities of Campo Mourão and Prudentópolis, respectively. Alagados (Pitangui River) and Fiú (Apucaraninha River) reservoirs are located in the Tibagi River basin (Rio Paraná basin), in the cities of Ponta Grossa and Tamarana, respectively. Guaricana (Arraial River) and Capivari (Capivari River) reservoirs are located in the Atlantic basin close to the cities of São José dos Pinhais and Campina Grande do Sul, respectively (Fig. 1).

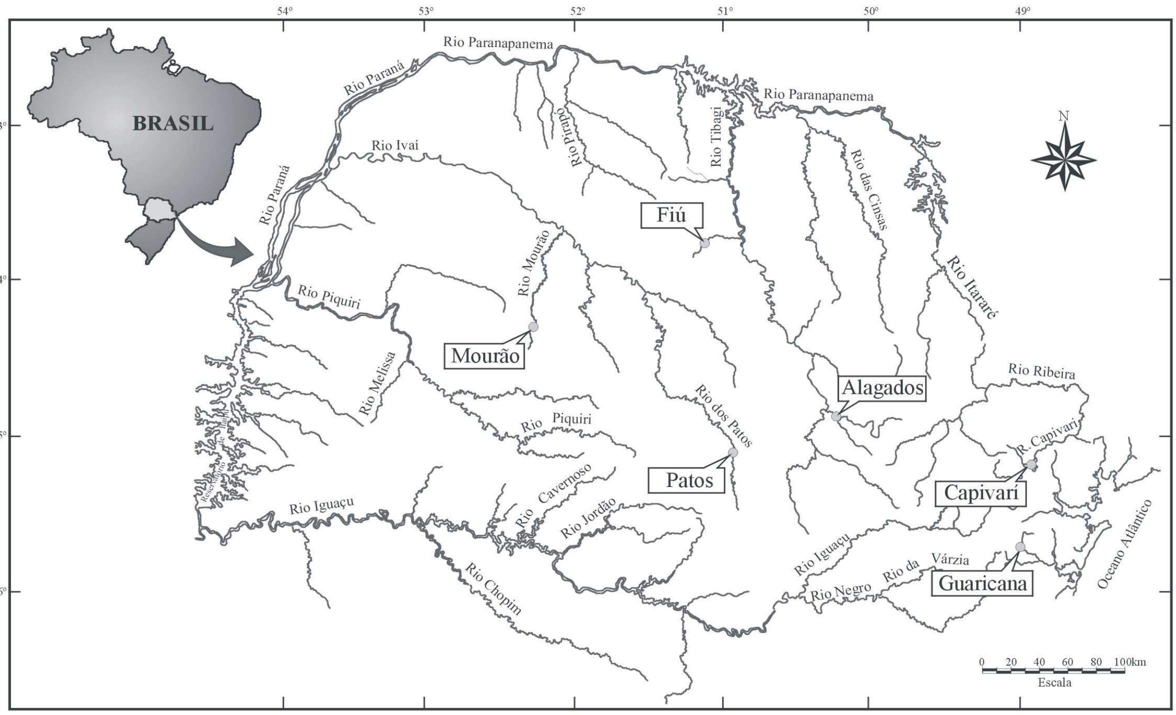

Figure 1 - Location of the six studied reservoirs**.**

In relation to longitudinal distribution, Capivari, Mourão, Guaricana and Rio dos Patos reservoirs are in headwaters, Fiú Reservoir is in the intermediary portion and Alagados Reservoir is near the river's mouth.

Data collection

Morphometric data were obtained from the most abundant fish species of each reservoir (measuring 15 individuals per species, and when not possible, the number of specimens available). Selected species represented more than 90% of total capture in each reservoir The criterion used to determine this abundance rank was the catch per unit of effort (CPUE) data, expressed as the total number of individuals per 1000 m^2 of net in 24 hours. CPUE data from these reservoirs were obtained from Luiz et al. (2003).

Thirty linear measurements were taken from each analyzed individual. Six of them were square (areas) and one was angular (position of the mouth). They were later converted into ecomorphological attributes. A Discriminant Analysis (Johnson, 1998) was used to determine the attributes that best characterized the colonizer species in each reservoir (Table 2).

Table 1 - Morphometric characteristics of the reservoirs.

	Closure year	Area (km^2)	Volume (m^3)	Discharge (m^3/s)	Retention time (days)
Capivari	1970	12.8	$150x10^6$	15.51	48.0
Mourão	1964	10.5	$65x10^6$	24.60	70.0
Alagados	1945	7.1	$29x10^6$	7.18	46.0
Fiú	1957	1.7	$15x10^6$	14.76	12.0
Guaricana	1957	0.4	$6,830x10^3$	5.96	13.0
Rio dos Patos	1901	0.1	800.000	50.00	0.2

Selected attributes were then analyzed by a Principal Components Analysis (PCA), to ordinate the reservoirs according to ecomorphlogical characteristics of 17 fish species, using the method of correlation matrix. To test for differences in the ecomorphological space occupied by each reservoirs, we used null models analysis of variance (one-way ANOVA; EcoSim-Null models, version 7, developed by Gotelli and Entsminger http://homepages.together.net/~gentsmin/ecosim.htm), based on the PCA scores of each reservoir. Significant difference in data distribution between observed and simulated indexes implied an $\alpha < 0.05$. This is a non-parametric technique, with the advantage of requiring neither normal data distribution nor equal variances among groups. Morphological characteristics related to feeding behavior of the species were compared to the trophic structure established by Abelha (2001) for the same reservoirs.

Measurements bellow 150 mm were carried out with a digital pachymeter (resolution - 0.01 mm and average error - 0.02 mm), while an ichthyometer (precision - 1.0 mm) was used for those that exceeded this size. In order to calculate areas, body and fins were projected onto sheets of paper and later digitized, calculating the areas using the software AutoCad R13 (AUTODESK). The angle of the mouth was obtained by projecting the totally open mouth onto paper. All individuals measured are deposited at the Ichthyology Museum of NUPELIA (Center of Research in Limnology, Ichthyology and Aquaculture, Maringá State University). Voucher-specimens (all from State of Paraná, Brazil, collected by Nupélia/COPEL staff):

Astyanax altiparanae - NUP 773; 30 ex. (15 measured); Fiú Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Tamarana city; viii.1995-v.1999; - NUP 739; 24 ex. (15 measured); Mourão Reservoir, tributary of the Rio Mourão; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999; - NUP 759; 24 ex. (15 measured); Fiú Reservoir, tributary of the Rio Tibagi; upper Rio Paraná basin; Tamarana city; viii. 1995-v.1999; *Astyanax eigenmanniorum* - NUP 765; 43 ex. (15 measured); Fiú Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Tamarana city; viii.1995-v.1999. *Astyanax janeiroensis* - NUP 2360; 21 ex. (15 measured); Guaricana Reservoir, tributary to Rio Arraial; Atlantic basin; Guaratuba city; vii.2001. *Astyanax paranae* - NUP 657; 105 ex. (15 measured); Alagados Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Ponta Grossa city; viii.1995-v.1999. *Astyanax scabripinnis* - NUP 738; 41 ex. (15 measured); Mourao Reservoir, tributary to Rio Ivaí; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999. *Astyanax* sp. I - NUP 652; 83 ex. (15 measured); Patos Reservoir, tributary to Rio Ivaí; upper Rio Paraná basin; Prudentópolis city; viii.1995-v.1999. *Astyanax* sp. K - NUP 2068; 6 ex. (6 measured); Capivari Reservoir, tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; vii.2001; - NUP 2420; 12 ex. (4 measured); Capivari Reservoir, tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; 2000-2001. *Bryconamericus iheringi* - NUP 308; 17 ex. (15 measured); Fiú Reservoir, tributary to Rio Apucaraninha; upper Rio Paraná basin; Apucarana city; 10.viii.1999. *Deuterodon* sp. A - NUP 2358; 20 ex. (15 measured); Capivari Reservoir, tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; vii.2001. *Deuterodon* sp. B - NUP 644; 21 ex. (15 measured); Guaricana Reservoir, tributary to Rio Arraial; Atlantic basin; Guaratuba city; viii.1995-v.1999. *Oligosarcus paranensis* - NUP 740;66 ex. (15measured); Mourão Reservoir, tributary to Rio Mourão;upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999; - NUP 303; 6 ex. (6 measured); Fiú Reservoir; tributary to Rio Apucaraninha; upper Rio Paraná basin; Apucarana city; 09.viii.1999; - NUP 658; 17 ex. (15 measured); Capivari Reservoir; tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; viii.1995-v.1999. *Hoplias malabaricus* - NUP 753; 3 ex. (3 measured); Alagados Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Ponta Grossa city; viii.1995-v.1999; - NUP 726; 5 ex. (5 measured); Mourão Reservoir, tributary to Rio Mourão; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999. *Hoplias lacerdae* - NUP 857; 11 ex. (11 measured); Mourão Reservoir, tributary to Rio Mourão; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999; - NUP 727; 6 ex. (4 measured); Mourão Reservoir, tributary to Rio Mourão; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999. *Rhamdia quelen* - NUP 731; 7 ex. (3 measured); Mourão Reservoir, tributary to Rio Mourão; upper Rio Paraná basin; Campo Mourão city; viii.1995-v.1999; - NUP 772; 8 ex. (3 measured); Fiú Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Tamarana city; viii.1995-v.1999; - NUP 752; 3 ex. (3 measured); Alagados Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Ponta Grossa city; viii.1995-v.1999; - NUP 761; 9 ex. (3 measured); Patos Reservoir, tributary to Rio Ivaí; upper Rio Paraná basin; Prudentópolis city; viii.1995-v.1999; - NUP 748; 8 ex. (3 measured); Guaricana Reservoir, tributary to Rio Arraial; Atlantic basin; Guaratuba city; viii.1995-v.1999. *Hypostomus* cf. *Aspilogaster* - NUP 850; ex. 7 (7 measured); Patos Reservoir, tributary to Rio Ivaí; upper Rio Paraná basin; Prudentópolis city; x.1995-i.1999; - NUP 848; 13 ex. (8 measured); Patos Reservoir, tributary to Rio Ivaí; upper Rio Paraná basin; Prudentópolis city; x.1995-i.1999. *Geophagus brasiliensis* - NUP 2002; 3 ex. (3 measured); Capivari Reservoir, tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; 1999; - NUP 578; 9 ex. (8 measured); Guaricana reservoir; tributary to rio Arraial; Atlantic basin; Guaratuba city; ix.1999; - NUP 754; 15 ex. (4 measured); Alagados Reservoir, tributary to Rio Tibagi; upper Rio Paraná basin; Ponta Grossa city; viii.1995-v.1999. *Tilapia rendalli* - NUP 783; 23 ex. (13 measured); Capivari Reservoir, tributary to Rio Ribeira do Iguape; Atlantic basin; Campina Grande do Sul city; viii.1995-v.1999.

RESULTS

Taxonomic positions of the 17 fish species analyzed are shown in Table 3. Initial analyses were restricted to 14 ecomorphological attributes derived from the morphometric data (Table 2).

Only the first two principal components presented eigenvalues higher than those estimated by the Broken-stick model. Principal component 1 explained 46.7% of the variability in the morphometric data and Principal component 2 explained 19.6%. Attributes index of ventral flattening (IVF), eye position (EP), relative width of the mouth (RWM), relative opening of the mouth (ROM) and relative area of the mouth (RAM) correlated positively with the first principal component, while compression index (CI), relative height of the body (RH) and pectoral fin aspect (PFA) correlated negatively. The attribute caudal fin aspect (CFA) correlated positively with the second principal component, while attributes relative height of the mouth (RHM) and proportional width of the mouth (PWM) correlated negatively (Table 4).

Position in the ecomorphological space differed among the six studied reservoirs (Observed index = 12.57; p ($I_{obs} > I_{exp}$) = 0.001). Rio dos Patos Reservoir appeared distinct from the others, having a fish assemblage (most abundant species) characterized by high indices of ventral flattening and caudal fin aspect and low indices of attributes correlated with mouth morphology. In addition, this was the only reservoir showing high captures of *Hypostomus aspilogaster*, species characterized by a body strongly ventral-flattened (Table 5).

Table 2 - Ecomorphological attributes selected by the Discriminat Analysis (Wilks' λ=0.0000; F=26.262; p<0.0001), to be used in the principal components analysis.

ATTRIBUTES	Wilks-λ Parcial	CODE	SIGNIFICANCE
Compression Index	0.66	CI	Body height divided by body width. High indices indicate laterally long fish that inhabit lentic environments (WATSON & BALON, 1984).
Relative Height	0.40	RH	Body height divided by standard length. Attribute inversely related to high hydrodynamism environments and directly related to the capacity for vertical movement (GATZ, 1979a).
Caudal Peduncle Compression Index	0.71	PCI	Caudal peduncle height divided by its width. Long peduncles indicate slow-swimming individuals with little maneuverability (GATZ, 1979a).
Index of Ventral Flattening	0.81	IVF	Average body height (Vertical distance from midline to ventrum, midline defined as a imaginary line crossing the eye pupil towards the center of the ultimate vertebra) divided by body height. Low indices are associated with individuals from high hydrodynamic environments, allowing benthic individuals to maintain position without the need to swim.
Pectoral Fin Aspect	0.69	PFA	Pectoral fin length divided by its width. High indices indicate long narrow fins, which are present in fish that swim for long distances.
Relative Area of the Caudal Fin	0.77	RACF	Caudal fin area divided by body area. Large tails indicate rapid starts, which is typical of most benthic fish.
Caudal Fin Aspect	0.32	CFA	Square of the caudal fin height divided by the fin area. High indices indicate active swimmers. (GATZ, 1979a).
Eye Position	0.72	EP	Height of the average eye line divided by the height of the head. Benthic fish possess eyes located dorsally, while nektonic ones tend to have lateral eyes (GATZ, 1979a).
Relative Width of the Mouth	0.60	RWM	Mouth width divided by standard length. Attribute related to the size of the mouth, suggesting relatively large prey for high indices (GATZ, 1979a).
Relative Height of the Mouth	0.55	RHM	Mouth height divided by standard length. Attribute also related to mouth size. Attributes associated to mouth size are also related to the hydrodynamic form of the fish. (WATSON & BALON, 1984).
Mouth Aspect	0.82	MA	Mouth height divided by its width. Attribute related to food shape , where high indices indicate fish with narrow mouths (but a large opening), suggesting piscivory.
Relative Area of the Mouth	0.73	RAM	Product of mouth width multiplied by its height and divided by body area. Attribute related to food size, where high indices indicate large-sized food (BEAUMORD & PETRERE, 1994).
Proportional Width of the Mouth	0.85	PWM	Mouth width divided by body width. High values indicate large prey.
Relative Opening of the Mouth	0.81	ROM	Mouth height (totally open) divided by body height. High values indicate large prey.

Table 3 - Fish species analyzed in this study. Reservoir's codes: Mourão (M); Alagados (A); Patos (P); Fiú (F); Capivari (C); Guaricana (G).

OSTEICHTHYES
- *OSTARIOPHYSI*
  - *CHARACIFORMES*
    - *CHARACIDAE*
      - *Astyanax altiparanae Garutti & Britski, 2000.*[M; F; P.]
      - *Astyanax eigmanniorum (Coupe, 1894)* [F.].
      - *Astyanax janeiroensis Eigenmann, 1908*[G.].
      - *Astyanax cf. paranae Eigenmann, 1914* [A.]
      - *Astyanax scabripinnis (Jenyns, 1842).*[M.]
      - *Astyanax sp. I* [P.]
      - *Astyanax sp. K* [C.]
      - *Bryconamericus iheringii (Boulenger, 1887)* [F.].
      - *Deuterodon sp. A* [C.]
      - *Deuterodon sp. B* [G.]
      - *Oligosarcus paranensis Menezes & Géry, 1983.* [M;C;F]
    - *ERYTHRINIDAE*
      - *Hoplias lacerdae (Miranda-Ribeiro, 1908).* [M.]
      - *Hoplias malabaricus (Bloch, 1794)* [A].
  - *SILURIFORMES*
    - *HEPTAPTERIDAE*
      - *Rhamdia quelen (Quoy & Gaimard, 1824).* [F;A;M;G;P.]
    - *LORICARIIDAE*
      - *Hypostomus cf. aspilogaster (Cope, 1894).*[P.]
  - *PERCIFORMES*
    - *CICHLIDAE*
      - *Geophagus brasiliensis (Quoy & Gaimard, 1824).*[G;A;C.]
      - *Tilapia rendalli (Boulenger, 1897)* [C.].

Table 4 - Result of the principal components analysis. Coefficients were obtained using Pearson correlations.

	PCA Axes	
	1	**2**
Percentage variance	46.7	19.6
Accumulated variance	------	66.3
Index of ventral flattening	.810	.214
Eye Position	.692	.149
Relative width of the mouth	.748	-.290
Relative opening of the mouth	.814	-.496
Relative area of the mouth	.774	-.431
Compression index	-.960	-.018
Relative height of the body	-.892	.163
Pectoral fin aspect	-.697	.104
Caudal fin aspect	.321	.695
Relative height of the mouth	-.096	-.822
Proportional width of the mouth	-.032	-.841

Rhamdia quelen also contribute to characterize some reservoirs, because it showed higher abundances in those with lower hydraulic retention time (Patos, Fíu and Guaricana; Tables 1 and 5). Guaricana and Capivari reservoirs also showed higher values for the attribute CFA; however, they were characterized (most abundant species) by individuals laterally longer. Mourão and Alagados also presented significant values of CFA; however, morphological aspects related to mouth morphology were more detached.

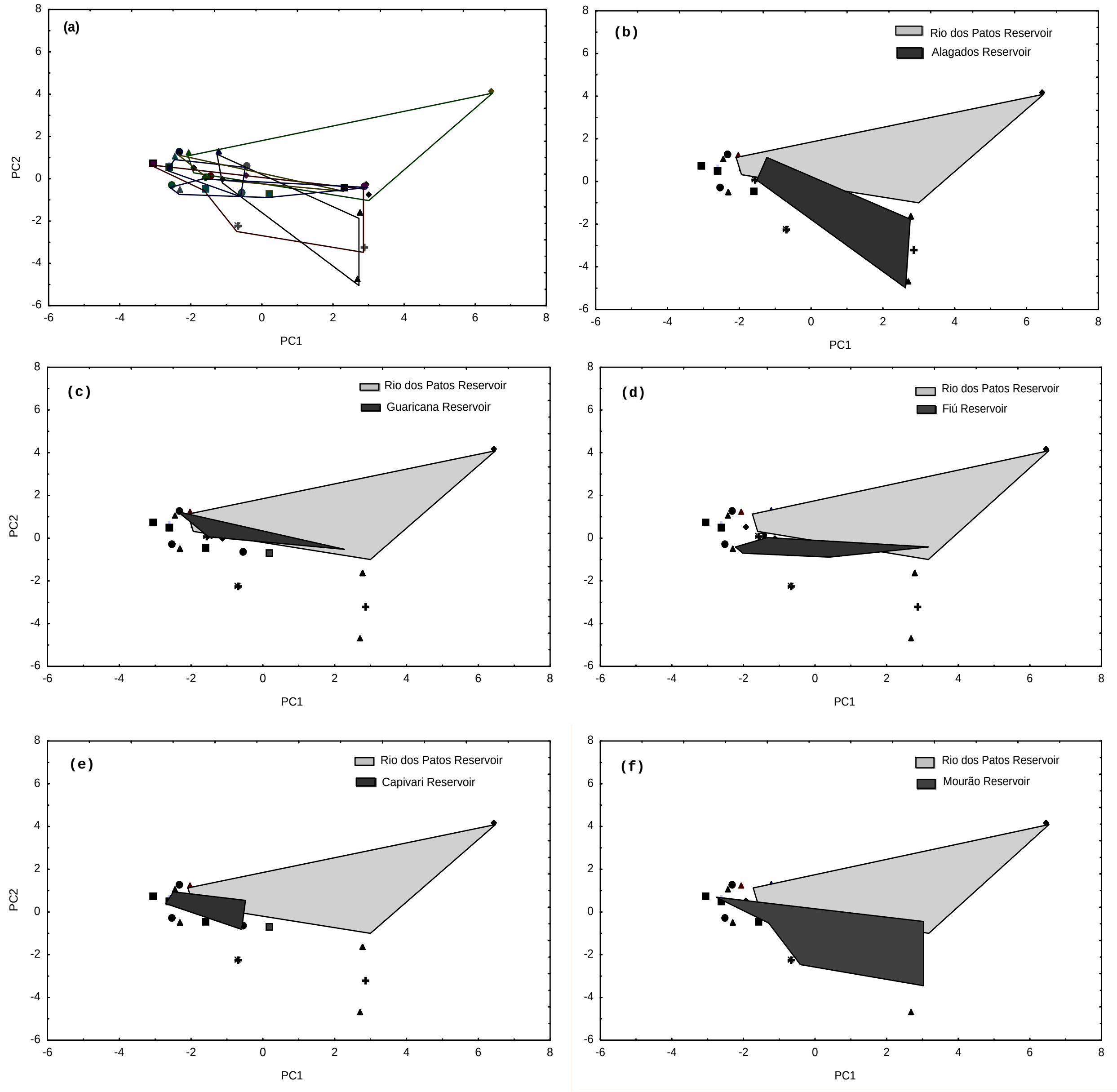

Figure 2 - Projection of the ecomorphological space occupied by fish species in six reservoirs (a). Additionally, we compared the space of each reservoir to the space occupied by the reservoir having the highest hydrodynamism (Rio dos Patos Reservoir) (b, d, e, f).

In relation to the body compression index, diversified morphological types characterized Fiú Reservoir, with species showing both low and high values of CI. Occupation of the ecomorphological space by these reservoirs is presented in Table 4 and Fig. 2.

DISCUSSION

Alterations in physical characteristics of natural environments due to reservoir construction were evident, affecting mainly the water flow regime of fluvial systems. Hydrodynamic modification may cause severe habitat alterations, consequently facilitating the colonization of lentic-adapted species.

Table 5 - Values of catch per unit of effort, PCA scores and mean values of ecomorphological attributes for species.

	Species	PC1	PC2	CPUE	CI	RH	PCI	IVF	PFA	RACF	CFA	EP	RWM	RHM	MA	RAM	ROM	PWM
					Ecomorphological attributes													
Alagados	*A. paranae*	-0.923	-0.085	553.27	2.86	0.33	2.45	0.53	2.37	0.21	1.70	0.61	0.07	0.08	1.09	0.03	0.25	0.65
	G. brasiliensis	-1.30842	1.26084	52.88	2.58	0.44	3.25	0.60	2.70	0.18	0.56	0.69	0.09	0.08	0.89	0.02	0.17	0.51
	H. malabaricus	3.43101	-4.42649	23.17	1.60	0.24	2.48	0.59	1.99	0.23	0.81	0.63	0.12	0.11	0.97	0.07	0.48	0.79
	R. quelen	3.10788	-1.07349	2.88	1.12	0.20	2.78	0.56	1.69	0.21	0.89	0.69	0.11	0.08	0.75	0.04	0.40	0.60
Capivari	*Deuterodon* sp.*A*	-2.58269	0.42368	326.09	3.00	0.39	2.93	0.47	2.24	0.19	1.71	0.57	0.07	0.09	1.29	0.02	0.22	0.51
	G. brasiliensis	-0.41857	0.78828	117.89	2.54	0.42	3.09	0.60	2.15	0.18	0.62	0.71	0.09	0.08	0.80	0.02	0.18	0.57
	O. paranensis	-0.29218	-0.81013	21.95	2.56	0.29	2.48	0.55	2.74	0.24	1.23	0.64	0.08	0.09	1.13	0.03	0.31	0.69
	T. rendalli	-2.49302	0.73582	15.05	2.79	0.46	3.03	0.54	3.22	0.20	0.82	0.62	0.08	0.09	1.10	0.02	0.19	0.49
	Astyanax sp.*K*	-2.58928	0.48191	13.44	2.84	0.37	2.83	0.48	2.57	0.16	3.56	0.56	0.07	0.09	1.33	0.02	0.24	0.51
Fiú	*O. paranensis*	0.53221	-0.69656	201.96	2.59	0.33	2.23	0.61	2.22	0.24	1.28	0.71	0.08	0.10	1.24	0.03	0.30	0.63
	A. altiparanae	-2.44084	-0.3552	123.10	3.21	0.44	3.68	0.51	2.50	0.20	1.42	0.50	0.09	0.08	0.83	0.02	0.18	0.69
	A. eigmanniorum	-2.09637	-0.67765	52.31	3.02	0.40	3.26	0.50	2.41	0.24	1.41	0.56	0.08	0.10	1.26	0.03	0.24	0.58
	B. iheringii	-1.42832	0.22827	38.21	2.81	0.34	3.17	0.48	1.79	0.23	1.79	0.56	0.07	0.08	1.10	0.03	0.23	0.59
	R. quelen	3.19649	0.25583	16.35	1.16	0.19	2.30	0.66	1.59	0.20	0.86	0.70	0.09	0.08	0.84	0.03	0.40	0.55
Guaricana	*Deuterodon* sp.*B*	-2.34367	1.0564	258.51	2.91	0.38	2.70	0.53	2.78	0.20	1.73	0.53	0.07	0.08	1.17	0.02	0.21	0.52
	G. brasiliensis	-0.3293	0.26138	81.94	2.52	0.43	3.03	0.59	2.26	0.19	0.72	0.71	0.10	0.09	0.89	0.03	0.20	0.57
	A. janeiroensis	-1.3162	0.34782	53.66	2.81	0.36	3.53	0.49	2.09	0.22	3.02	0.54	0.09	0.07	0.84	0.02	0.20	0.68
	R. quelen	2.53336	0.02746	7.98	1.26	0.25	2.58	0.60	2.13	0.24	1.09	0.60	0.10	0.08	0.79	0.05	0.32	0.51
Mourão	*A. altiparanae*	-3.10803	0.51299	343.30	3.08	0.45	3.18	0.51	2.81	0.16	2.76	0.49	0.08	0.08	1.05	0.02	0.19	0.55
	O. paranensis	-0.24361	-2.28775	230.44	2.70	0.30	2.54	0.55	2.08	0.20	1.58	0.65	0.08	0.11	1.39	0.04	0.35	0.68
	A. scabripinnis	-1.38004	-0.45889	41.77	2.76	0.33	3.43	0.55	2.16	0.24	1.57	0.55	0.07	0.09	1.25	0.03	0.27	0.60
	H. lacerdae	3.37092	-2.76502	9.31	1.32	0.22	2.47	0.57	1.69	0.19	0.67	0.71	0.11	0.10	0.90	0.06	0.46	0.67
	R. quelen	3.07961	0.27888	5.16	1.11	0.20	3.19	0.65	1.83	0.24	1.15	0.68	0.10	0.07	0.76	0.04	0.37	0.55
Patos	*Astyanax* sp.*I*	-2.051	1.19105	145.43	2.88	0.39	2.77	0.53	2.35	0.18	2.17	0.55	0.07	0.08	1.09	0.02	0.20	0.52
	A. altiparanae	-1.88533	0.43607	50.26	3.09	0.45	3.59	0.55	2.57	0.20	1.24	0.68	0.09	0.08	0.94	0.02	0.18	0.60
	H. aspilogaster	6.72518	5.65426	26.99	0.73	0.19	1.31	0.70	1.67	0.39	11.22	0.80	0.10	0.06	0.63	0.04	0.33	0.37
	R. quelen	3.25345	-0.30421	10.23	1.18	0.21	2.87	0.63	2.45	0.26	1.42	0.62	0.10	0.08	0.74	0.07	0.36	0.58

However, many species do not have adaptations that allow them to inhabit lentic environments, and may be locally extinct (Lowe-McConnell, 1975). According to Sagnes et al. (2000) and Wikramanayake (1990), other factors are involved in fish habitat selection; however, the study of body hydrodynamics and swimming ability of fish species has a promising perspective for the understanding and prediction of relationships between habitat use and water flow.

The influence of water flow structuring reservoir fish assemblages could be easily observed in Mourão and Rio dos Patos Reservoirs: Mourão presented a long water retention time (Table 1) and, consequently, was the most lentic of the studied environments, whereas Rio dos Patos (Fig. 2.f) presented the highest hydrodynamism and is more similar to the original undammed fluvial environment. Considering the species numerically more abundant, Mourão showed values of the index of ventral flattening lesser pronounced and values of the compression index more pronounced when compared to Patos reservoir. Therefore, Mourão was inclined to be occupied by nektonic fishes, having the ability to swim vertically and horizontally and were better suited to occupy environments of low hydrodynamism (Tables 2 and 4). On the other hand, the fish assemblage of Rio dos Patos Reservoir included species with lower indices of body compression and body height than Mourão: characteristics related to species from high hydrodynamic environments

(Watson and Balon, 1984; Gatz, 1979a, Gatz, 1979b; Beaumord and Petrere, 1994). Some species showing higher captures in reservoirs with hydrodynamic similar to Mourão, showed ecomorphological attributes related to lentic-habitat species.

Most abundant species of Alagados Reservoir (Fig. 2.b) presented low occupation of the ecomorphological space, possibly due to the shorter hydraulic retention time in the main reservoir body (24 days shorter than Mourão). Capivari, with hydrodynamic characteristics similar to Alagados Reservoir, presented the lowest and most restricted occupation of the ecomorphological space (Fig. 2.e). This could be related to the distinct evolutionary history of the Capivari River, which belongs to the Atlantic basin.

After Rio dos Patos Reservoir, Fiú and Guaricana (Figs. 2.c and 2.d) showed the shortest hydraulic retention time. These reservoirs presented some similarities in the size and position of the ecomorphological space, besides a wide hydrodynamic diversity of forms.

The morphological characteristics of the mouth can indicate the predominant trophic structure in the assemblage. Hugueny and Pouilly (1999) obtained satisfactory results relating fish diet to the form of the species in a West Africa fish assemblage. The species analyzed in Rio dos Patos Reservoir presented distinct attributes related to mouth morphology. Abelha (2001) reported that this reservoir presented a trophic structure characterized mainly by detritivorous species, and following this information, we would expect species with low indices of relative width of mouth (RWM) and relative opening of the mouth (ROM). However, the most abundant species in this reservoir showed a diverse morphologic configuration possibly due to the fact that the dammed portions presented an ichthyofauna composed predominantly of food-flexible species (post-damming diet alterations).

The other reservoirs had fish species characterized by mouth morphologies denoting their respective trophic niches. Mourão, Fiú and Guaricana included species with mouth characteristics related to the ingestion of small-sized food items (low indices of RWM, ROM and RAM) to possibly piscivorous species ingesting large-sized food items (high values of RWM, ROM e RAM) (Tables 2 and 4). This corroborate with the feeding plasticity found in species of this reservoir, composed predominantly of omnivores (Abelha, 2001).

In relation to the occupation of habitats by fish species, Gatz (1979a) recognized and supported the evidence that eyes position reflected the stratum occupied by a species in the water column. The most abundant species of Patos Reservoir tended to show the highest indices related to eye position (EP) that characterized them as benthonic-pelagic habits, more adapted to high water flows, as the case of this reservoir. In reservoirs with lower water flows, these indices showed different tendencies, indicating the presence of nektonic species, which could occupy both littoral and surface regions.

In addition to obstructing fish migratory routes, dammings transforms lotic environments into lentic ones, altering physical and chemical characteristics of aquatic environments and, consequently, altering the abundance and distribution of species in the water column (Júlio Jr. et al., 1997). Barrella et al. (1994) related the ichthyofaunistic modifications to the lack of species (in the original fauna) adapted to exploit new pelagic-habitats imposed by the damming of a Tietê River tributary. The absence of pelagic species in fluvial systems has been considered a determining factor of low species richness and abundance observed in open areas of reservoirs in South America. Thus, fish species in neotropical reservoirs are concentrated mainly in littoral areas and near the mouth of tributaries (Agostinho *et al*., 1999 and Fernando and Holcík, 1982; Gomes and Miranda, 2001).

This study showed that, among others factors, water dynamics in reservoirs had a major role selecting which fish species will occupy these environments, imposed basically by ecomorphological constraints.

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RESUMO

Neste estudo, são analisados as restrições na ocupação de peixes em reservatórios com diferentes tempos de retenção da água e estágios de colonização de acordo com características morfológicas das espécies. Busca-se padrões morfológicos mais adaptados na ocupação dos reservatórios considerando diferentes habitats e estratégias alimentares. Os dados morfológicos foram obtidos em 10 indivíduos das espécies mais abundantes em seis reservatórios do estado do Paraná. Os atributos ecomorfológicos que melhor segregaram as espécies foram determinados através de uma Análise Discriminante, sendo estes posteriormente utilizados em uma Análise de Componentes Principais (PCA). Diferenças entre os reservatórios na ocupação do espaço ecomorfológico foram testados através de Análise de Variância (modelo nulo). Os seis reservatórios diferiram na ocupação do espaço ecomorfológico com os dois primeiros eixos da PCA explicando 66,3% variabilidade total dos dados. Conclui-se então que alterações na dinâmica da água também afetam os padrões de distribuição das espécies de peixes em reservatórios.

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