An Ordination Technique for Fish Diet Comparisons

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ABSTRACT

The frequency of nine food types in the guts of 58 fish species from the Paraná River and its floodplain was compared using similarity definition. A synthetic table ordered on the basis of this definition, with fish species on axis y, and food types on axis x, enabled easy reading numerous kinds of information on feeding ecology of fish in the catchment. For example: 1) which fish species were generalists, specialists or opportunists, 2) those classified as herbivorous species consumed small amounts of animal food, 3) that fish consumed any food type that contained transformed solar energy and matter, 4) what are food preferences dependent on fish taxonomic affinity. The possibility of employing synthetic tables for investigating spatial and temporal variation in fish diet has also been indicated.

Key words: Paraná River, floodplain, fish, feeding, similarity definition, synthetic table

INTRODUCTION

Ordination techniques (or multivariate techniques) have been used commonly in research of plant and animal communities (Krebs, 1989; James & McCulloch, 1990; Diniz-Filho & Bini, 1996), including fish communities (Winemiller & Leslie, 1992; Agostinho et al., 1997). The synthetic diagram proposed by Rominiszyn (1970), constructed on the basis of a similarity definition, has also been used for analyzing fish communities (Penczak, 1972; Balon & Stewart, 1983; Witkowski, 1984; Zalewski et al, 1990; Penczak et al, 1991; Przybylski et al, 1991; Penczak & Agostinho, 1994).

We employed the similarity definition to compare the diet of numerous species of fish from large water bodies published by Hahn *et al* (1997), where fish species were arranged by taxonomic order, and food items randomly in a large table. By employing the synthetic Romaniszyn (1970) method we wanted to check if ecological interpretations of this data was possible.

MATERIAL AND METHODS

Sampling was carried out in the Paraná River and its floodplain (Fig. 1). In the sampled stretch, extending between the mouths of the Paranapanema and Ivai, the Paraná River has a wide braided channel with a low slope (0.09 m km⁻¹) and a great accumulation of sediment in its bed. An extensive alluvial plain (20 km) borders its left margin (Mato Grosso do Sul State), within which lies a complex system of channels and temporary and permanent lagoons.

One fleet of gillnets (mesh size range 3-16 cm knot to knot) was operated monthly between October 1986 to September 1988, and February 1992 to March 1994. Fishes were removed from the nets at 08:00, 18:00 and 22:00 h during each 24 h sampling period.

The material examined consisted of 5713 guts from 58 fish taxa, representing 22 families. The diet of seven fish species was estimated on the basis of one or two guts only, and eight others on the basis of less than 10 fish.

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Fishes were dissected immediately after capture, and guts were fixed in 4% formalin. Diet was analyzed by the frequency of occurrence (fo%) method (Hynes, 1950):

$$fo(\%) = 100 \text{ n}_1/\text{N}$$

where n_1 = numbers of fish containing a particular prey taxon, and N = total number of fish in the sample.

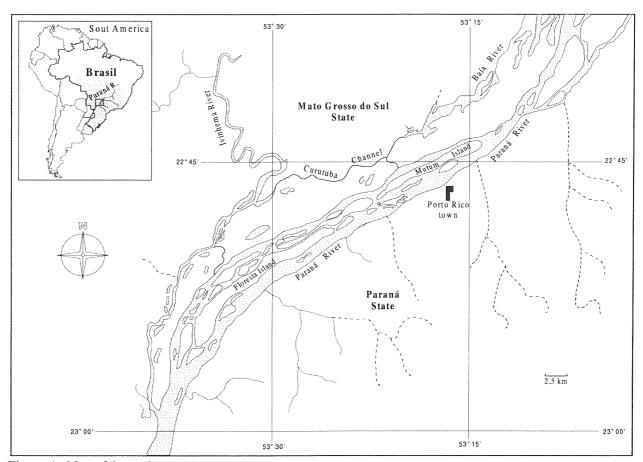


Figure 1. Map of the study area.

The subject of the coenological analysis is a comparison of occurrence frequency of ten diet types in the guts of 58 fish species (Table 1; Hahn *et al*, 1997).

Similarity between food types (columns) and between fish species (rows) was calculated using the Marczewski & Steinhaus (1958) equation:

$$s = 100w / (a + b - w)$$

where s is similarity of two collections (two food types or two fish species), w is the total of the lower percentage of food types of each pair of species common for two given analyzed food types ('columns') (or the total of the lower percentage of food types of each pair of two given analyzed fish species consuming them ('rows'), a and b are the total percentage of food

types for compared 'columns' (food type) and 'row' (fish species).

Of these two dimensions food types ('columns') and fish species ('rows)) we choose the former to use as an example (Table 2), because the latter would have required presenting a huge (58 columns by 58 rows) table. Because for the calculation of similarity coefficients a given numerical value must be introduced into the equation, we replaced '+', '++' and '+++' from Table 1 by numerical values proportional to them.

The highest values of similarity between pairs of food types were marked by bold numbers and these were used for constructing a two-dimensional dendrite of food types, which, on the same figure, is then transformed into a linear dendrite (Fig. 2).

Table 1. Main food types utilized by fish species from the Upper Paraná River and its floodplain (I=microcrustacea, II= Mollusca, III=insect, IV=other invertebrates, V=fish, VI=algae, VII=plant, VIII=detritus, and IX=sediment). n is the number of investigated guts, No is the species number; frequency of occurrence of prey in the fish gut: + = >0 - 30%; ++ = 31 a 60%; +++ = >60%.

	Family,						Food typ	es			
No	species	n	I	II	III	IV	V	VI	VII	VIII	IX
	Potamotrigonidae										
1	P.motoro	1			+++						
	Characidae										
2	A.bimaculatus	200	+		+++	+	+++	+	++	+	
3	A.lacustris	250			+		+++		+		
4	A.shubarti	293	+		++	+			+++	+	
5	B.orbignyanus	46			+++	+	+		++		
6	G.knerii	6				+	+++				
7	M.intermedia	10	+++		++	+			+	+	
8	R.paranensis	76	+++		+++	+	+++				
9	S.maxillosus	55			+		+++		+		
	Serrasalmidae								·		
10	P.mesopotamicus	18	+		++	+			+++		
11	S.marginatus	728			+	+	+++		+		
12	S.spilopleura	172			+	,	+++		+		
	Anostomidae				·		, , ,		•		
13	L.elongatus	11			+++				+	+	
14	L.friderici	129			++		++		+++	+	
15	L.lacustris	48		+	+		+		+++	+	
16	L.obtusidens	125		+	++		+	+	+++	++	
17	L.vittatus	1		,	+++		,		111	-11-	
18	S.altoparanae	96			1 ()			+++	+++		
19	S.borellii	230	+				++	++	+++		
17	Parodontidae	250	1				77	77	777		
20	A.affinis	24						++			
20	Curimatidae	27						77		++	+++
21	C.modesta	41				1				1.1	
22	C.modesia C.nagelii	148				+		+++		++	+++
23	S.insculpta	94				+		+++		++	+++
23	Prochilodontidae	94				+		+++		++	+++
24	P.lineatus	71									
24		/ 1				+		+		++	+++
25	Erythrinidae H.malabaricus	81									
23		01			+	+	+++		+		
26	Cynodontidae	120									
20	R.vulpinus	138			+	+	+++		+		
27	Gymnotidae	40									
21	G.carapo	40			+++	+	++		+		+
20	Sternopygidae	070									
28	E.trilineata	279	+		+++	+				+++	+
20	Rhamphichthydae	7									
29	R.rostratus	7	+		+++						
20	Doradidae	157									
30	P.granulosus	176	+	++	+	+	+	+	+++	+	+
31	T.paraguayensis	203	+++		++	+++		+	+	+++	+
	Auchenipteridae										
32	A.nuchalis	66	+		+++	+	+				
33	P.galeatus	244			+++	+	++		++		

Cont.

Table 1 – cont.

	Family,	Food types												
No	species	n	I	II	III	IV	V	VI	VII	VIII	IX			
	Ageneiosidae				,									
34	A.brevifilis	2					+++							
35	A.ucayalensis	17			+	++	+++							
36	A.valenciennesi	2			+	+	++							
	Pimelodidae													
37	H.platyrhynchos	90				+	+++		+					
38	I.labrosus	338	++	++	+++	+++		+		++	++			
39	P.corruscans	57				+	+++		+					
40	P.gracilis	6	+		+++	+		+		+				
41	P.luetkeni	1					+++							
42	P.maculatus	300	+	++	++	+++	+++	+	++	+				
43	P.pirinampu	10					+++							
44	Rhamdia sp.	2					+++							
45	S.lima	22				++	+++							
	Hypophthalmidae													
46	H.edentatus	36	+++			+		++						
	Callichthyidae													
47	C.callichthys	5	++		++	+				++	+			
48	H.littorale	322	+++	+	+++	++			+	+++	+			
	Loricariidae													
49	Hypostomus sp.	15						+		+++	+			
50	L.platymetopon	116			++	+		+		+++	++			
51	L.prolixa	9				+		+		+++	++			
52	Loricariichthys sp.	23			++	+		+		+++	++			
53	M.aculeatus	7						+		+++	++			
54	R.aspera	11				+		+		+++	++			
	Sciaenidae													
55	P.squamosissimus	206			++	++	+++		+					
	Soleidae													
56	C.jenynsii	5			++		+++							
	Cichlidae													
57	C.ocellaris	5					+++							
58	S.pappaterra	2		+	+		+		+	++	+			

Table 2. Similarity of food types (I-IX). Bold numbers signify the highest similarities used for fractional dendrite's connections. Symbols explanations as in Table 1.

	Food type										
Food type	I	II	III	IV	V	VI	VII	VIII	IX		
I	100	12.82	25.00	31.75	7.20	14.75	11.25	24.36	10.45		
II		100	9.78	11.32	5.77	9.52	14.04	12.31	11.11		
III			100	29.63	21.66	7.63	26.96	24.19	11.02		
IV				100	19.20	21.43	20.93	27.27	21.92		
V					100	4.62	19.23	4.49	2.19		
VI						100	13.75	28.57	46.15		
VII							100	12.38	5.56		
VIII								100	39.19		
IX									100		

To transform a branched dendrite into a linear one, a technique of encircling groups of elements connected by decreasing similarity values was applied. The technique proceeded from the highest similarity (s = 46.15, circle no. 1) to the lowest one (s = 14.04, circle no. 8), which ensured against mistakes. Then, the linear dendrite was drawn starting from food types IX and VI, connected within circle no. 1, and ending by appending food type II within circle no. 8. This technique of proceeding from circle to circle was useful, because when transforming a branched dendrite into a linear one, weaker connections must be 'broken' to insert between respective food types, with similarities higher than those that have been 'broken away'. For example, food type I could be inserted between food types IV and VIII (similarity 27.27), but not between III and IV, because similarity between the latter pair was 29.63 (Fig. 2). More examples on how/where a dendrite may be 'broken' to insert elements with higher values of similarity are shown in Fig. 4.

Ouotients calculated between decreasing similarities of neighbouring food types and fish species (Figs. 2 and 4), except the border ones, differed slightly between them and if a quotient differing from the neighbouring ones (Fig. 2: 1.09, Fig. 4: 1.07 and 1.05) happened to lie between their series, then its similarity (Fig. 2: 29.63, Fig. 4: 77.78 and 70.00) constituted the lower bound of similarity for distinguishing clusters (Romaniszyn, 1970). In the following analysis, all elements (food types, fish species) below that value of similarity have been treated separately.

The dendrite for 58 species as well as a table with similarity values between fish species that was its source were too large to be presented here in their entirety. However, clusters and 'separate species' within them (quotient values 1.07 and 1.05) are presented in linear form (Fig. 3), as well as species compositions within single clusters (Fig. 4). According to Magurran (1988), a dendrogram of 30 elements or more could be difficult to interpret.

The lengths of lines connecting elements in Fig. 2 and 4 represented distance (1-s) rather than similarity.

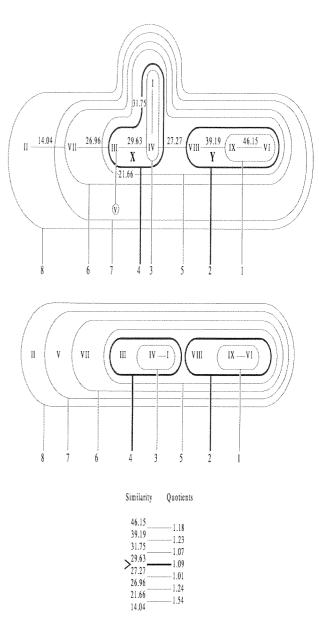


Figure 2. The two-dimensional dendrite of food types with two distinguished clusters of food types (X, Y) on the basis of a quotient 1.07 (similarity $s \ge 29.63$). Circles numbered from 1 to 8, starting their drawing from the largest and ending with the lowest similarity value between food types, served for drawing the linear dendrite (below).

The linearly arranged dendrites of food types and fish species were used to derive a synthetic table (Romaniszyn, 1970), in which the plus and minus values were again used for symbolizing items, i.e. as in the original table by Hahn *et al* (1997). The entire procedure of how to construct a branched and a linear dendrite starting from the initial table has been described by Romaniszyn (1970).

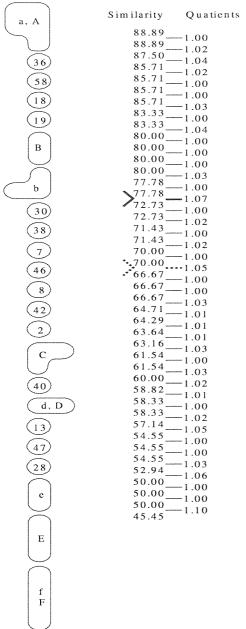


Figure 3. Simplified pattern of a two-dimensional dendrite, in which distinguished clusters and separated species are marked. Clusters of species were distinguished on the basis of two quotients, 1.07 and 1.05, representing similarities ≥ 77.78 and ≥ 70.00 , respectively. All similarity indices and quotients from the two-dimensional dendrite are included in the picture.

RESULTS

Based on the linear composition of elements (food types and fish species), a synthetic table distinguished the following elements: species characterized by s = 100%, two types of clusters

of fish species (the stronger with s = 77.78% and a weaker one with s = 70.00%) and food type clusters with s = 29.63. As a result, the dendrite for fish species contained 6 'strong' clusters (A-F), 5 'weaker' ones (a-b, d-f) and 15 separate species. The dendrite for food types contained two clusters (X, Y), and 3 prey with no pronounced connections (Table 3).

Before starting the analysis of the synthetic table, some technical problems connected with the interpretation of the species' clusters have to be explained. Clusters distinguished by stronger (big letters) and weaker (small letters) similarity values either only border one another, or the 'weaker' clusters envelope the 'stronger' clusters. The former case occurred when s < 70.00%. Hence, clusters b and B as well as E and e were separated because their similarities were 63.64% and 61.54%, respectively. The latter case occurred between clusters a and A, d and D and f and F, because their similarities were 70.00% (Fig. 4).

The synthetic table (Table 3) enabled an easier interpretation of ecological information hidden in Table 1. At the beginning of Table 3, a large cluster of piscivores (A + a) is visible, yet fishes were consumed exclusively by five species, whereas the others also consumed: plants, insects and other invertebrates, but never food types I, VIII, IX and VI. In the connected clusters A + a (18 fish species), as many as nine are represented, yet families only (Pimelodidae) is represented by six taxons, whereas the others are represented by 1-2 taxa. Moving down the table we also can see three species with frequent consumption (No. 8, 42 and 2) and five with intermediate (++) frequency of food consumption.

At the opposite end of the table (clusters E, F and f) are 11 species that always consumed detritus, sediment and algae (cluster Y), but never food types II, V, VII and I. In spite of distinct taxonomic affinity, these species belong now to the same trophic guild. The following families entered the above clusters as a group: Loricaridae (6 taxa), Curimatidae (13 taxa) and single representatives of the families: Parodontidae and Prochilodontidae.

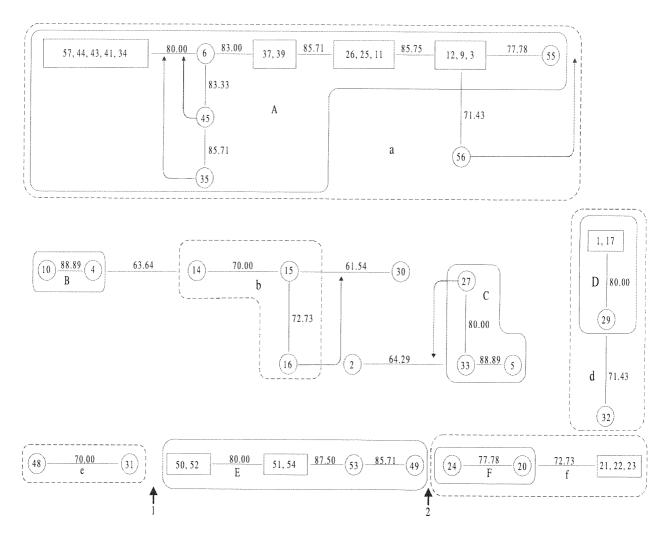


Figure 4. Connections of fish species within the distinguished clusters marked with lines representing by their length the distance definition (s-1). Arrows indicate the only feasible places of inserting fish species, always 'breaking' lower similarity values. Arrow no. 1 represents s = 6.54, arrow no. 2 s = 60.00. Solid line indicates a cluster distinguished for $s \ge 77.78$, dotted line for $s \ge 70.00$.

Except cluster D, with species consuming insects almost exclusively, the middle of the synthetic table is occupied by omnivores with species consuming insects almost exclusively. This part also includes: 1) individual taxa; 2) cluster B with a domination of plants in its diet; 3) cluster b encompassing the family Anostomidae, also with a domination of plants in its diet, but also consuming additionally fishes, insects and detritus; 4) cluster C, located near the center of the synthetic table, characterized by the domination of insects in its diet, with a

contribution of fish and plants; and 5) taxa from cluster D consume, with minor exceptions, insects.

At first sight, eight of nine food types distinguished in Table 3 were consumed with the highest frequency (+++) in the Paraná River floodplain. Because 57 of 58 fish species captured occurred in all sampled habitats (Hahn *et al*, 1997), no attempt was made to examine fish diets relative to capture site (river, stagnant water).

Table 3. Synthetic table showing ordered with the similarity coefficient (s) nine food types (I- IX) for 58 fish species in the Paraná river and its floodplain, according to prey frequency of occurrence in their guts. Clusters of species distinguished for $s \ge 77.78\%$ are marked by capital letters and surrounded with a solid line; for s > 70.00%, by small letters and dotted line. The fish species names are framed when s is equal 100%. Clusters of food types distinguished for $s \ge 29.63$ are marked by capital letters (X,Y) and double line. Symbols explanations as in Table 1 (see text for further explanations).

Vo_	Species	II	V	VII	Ш	IV	I	VIII	IX	VI	Clus
				Veimmennen en en	de estados como	the Control of the State of Lorent Lo			SEEDINGS CONTROL OF CONTROL	SEMERAL LANGE KO	
7	C.ocellaris		+++								
4	Rhamdia sp.		+++								
3	P.pirinampu		+++								
1	P.luetkeni		+++								
4	A.brevifilis	J	+++								l
5	A.ucayalensis		+++		+	++					
5	S.lima		+++			++					
0	G.knerii	7	+++			+					1,
9 7	P.corruscans		+++	+		+					Α
	H.platyrhynchos	-	+++	+		+					
6 5	R.vulpinus H.malabaricus		+++	+	+	+					
) [E .		+++	+	+	+					
	S.marginatus	-	+++	+	+	+					
2	S.spilopleura		+++	+	+						
	S.maxillosus		+++	+	+						
~	A.lacustris		+++	+	+						
5	P.squamosissimus		+++	+	++	++		-		and the construction of	
5	C.jenynsii		+++		++			~~~=====			
5	A.valenciennesi		++		+	+					
8	S.pappaterra	+	+	+	+			++	+		
8	S.altoparanae			+++						+++	
9	S.borellii		++	+++	*************		+	*****		++	
9	P.mesopotamicus			+++	++	+	+				В
	A.schubarti			+++	++	+	+	+			
1	L.friderici		++	+++	++			+			_
5	L.lacustris	+	+	+++	+			+			
6	L.obtusidens	+	+	+++	++			++		+	
)	P.granulosus	++	+	+++	+	+	+	+	+	+	~~~~~~~~
3	I.labrosus	++			+++	+++	++	++	++	. +	
	M.intermedia			+	++	+	+++	+			
5	H.edentatus					+	+++			++	
	R.paranensis		+++		+++	+	+++				
2	P.maculatus	++	+++	++	++	+++	+	+		+	
	A.bimaculatus		+++	++	+++	+	+	+		+	
7	G.carapo		++	+	+++	+	aran de la companya d		+		1
3	P.galeatus		++	++	+++	+					C
	B.orbignyanus		+	++	+++	+					
0	P.gracilis		*********		+++	+	+	+		+	ad .
2	A.nuchalis		+		+++	+	+				
)	R.rostratus		***************************************	***************************************	+++	***************************************	+				1
,		7					т.				
7	P.motoro				+++						D
7	L.vittatus				+++						
3	L.elongatus			+	+++			+			
7	C.callichthys				++	+	++	++	+		
3	E.trilineata				+++	+	+	+++	+		
3	H.littorale	+		+	+++	++	+++	+++	+		
1	T.paraguayensis			+	++	+++	+++	+++	+	+	
)	L.platymetopon				++	+		+++	++	+	
?	Loricariichthys sp.]			++	+		+++	++	+	
1	L.prolixa					+		+++	++	+	E
t	R.aspera]				+		+++	++	+	
3	M.aculeatus							+++	++	+	1
7	Hypostomus sp.							+++	+	+	1
4	P.lineatus					+		++	+++	+	F
)	A.affinis							++	+++	++	
l	C.modesta					+		++	+++	+++	
ı 2						+					1
3	C.nagelii S insculpta					+		++	+++	+++	
	S.insculpta	L				T		TT		+++	
				X			Y	<u> </u>			1

DISCUSSION

More information can be read from Table 3 than from Table 1. Table 1 contains the Hahn *et al.*, (1997) 'frequency' data (i.e. how many species consume separately insects, fish, plants, algae, microcrustacea and mollusca). Table 3 separated some species that consumed some of these diet elements separately, yet it is clear that food types V, VIII, IX and VI constituting cluster Y, cooccurred with species clusters E, F and f with no exception.

Synthetic tables allow one to 1) distinguish species or clusters belonging to generalist, specialist or opportunist species (Gerking, 1994), 2) distinguish predatory, omnivorous and herbivorous species plus intermediate forms and outliers, and 3) determine the extent to which herbivorous species require sometimes small amounts of animal food (Kamler, 1992; Gerking, 1994). Our analysis suggested that a large majority of families have trophic specialists. Exceptions were the family Loricaridae, which formed cluster E, Curimatidae, (all of which entered cluster f), and a large group of pimelodids, belonging to piscivores.

The synthetic table has limitations also. For example, a food web shows consumer-resource interactions among a group of organisms, or aggregates trophic units, including their shifts in space and time (Winemiller & Polis, 1996), but Table 3 contains a composite of samples from various months. If similar tables were developed separately for fish samples from successive months, seasons or size groups, then temporal diet shifts could be discerned. Dietary variation in space also would be visible if data collected from different habitats were analysed as separate tables.

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RESUMO

As frequência de ocorrência de nove tipos de itens alimentares em estômagos de 58 espécies de peixes do rio Paraná e sua planície alagável são comparadas com base nas definições de similaridade. É proposta uma tabela sintética baseada nessas definições, com as espécies de peixes no eixo y e os tipos de alimento no eixo x, permitindo uma visualização mais clara de diversos tipos de informações sobre a ecologia alimentar de peixes na bacia. Entre as informações, destacam-se (i) quais espécies são generalistas, especialistas ou oportunistas; (ii) que espécies classificadas como herbívoras consomem também itens de origem animal; (iii) que os peixes consomem qualquer tipo de alimento que contenha energia; (iv) que a preferência alimentar depende das afinidades taxonômicas. A possibilidade de empregar tabelas sintéticas na investigação de variações espaciais e temporais na dieta de peixe é também indicada.

REFERENCES

Agostinho, A.A.; Bini, L.M.; Gomes, L.C. (1997), Ecologia de comunidade de peixes da área de influência do reservatório de Segredo. In- *Reservatório de Segredo:bases ecológicas para o manejo*, Eds. A.A. Agostinho & L.C. Gomes, EDUEM, Maringá, PR, Brazil. pp.97-111 (in Portuguese)

Balon, E.K. & Stewart, D.J. (1983), Fish assemblages in a river with unusual gradient (Luongo, Africa - Zaire system), reflections on river zonation, and description of another new species. *Envir. Biol. Fish.*, **9**, 225-252.

Diniz-Filho, J.A.F. & Bini, L.M. (1996), Assessing the relationship between multivariate community structure and environmental variables. *Mar. Ecol. Prog. Ser.*, **143**, 303-306.

Gerking, S.D. (1994), Feeding ecology of fish. Academic Press, San Diego.

Hahn, N.S.; Andrian, I.F.; Fugi, R. & Almeida, V.L.L. (1997), Ecologia trófica. In- A planície de inundação do alto rio Paraná: Aspectos fisicos, químicos, biológicos e sócioeconômicos, Eds. A.E.A.M. Vazzoler; A.A.

- Agostinho. & N.S. Hahn, EDUEM, Maringá, PR, Brazil. pp. 205-224 (in Portuguese).
- Hynes, H.B.N. (1950), The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.*, **19**: 36-58.
- James, F.C. & McCulloch, C.E. (1990), Multivariate analysis in ecology and systematics: panacea or Pandora's box. Ann. Rev. Ecol. Syst., 21, 29-66.
- Kamler, E. (1992), Early life history of fish: an energetics approach. Chapman and Hall, London.
- Krebs, C. (1989), *Ecological methodology*. Harper & Row, New York.
- Magurran, A.E. (1988), *Ecological Diversity and its Measurement*. Crom Helm, Sydney.
- Marczewski, E. & Steinhaus, H. (1958), On a certain distance of sets and the corresponding distance of function. *Coll. Math.*, **6**, 319-327.
- Penczak, T. (1972), Structure of fish groupings in the rivers and streams of the Nida drainage basin. *Ekol. pol.*, **20**, 327-344.
- Penczak, T.; Forbes, I.; Coles, T.F.; Atkin, T. & Hill, T. (1991), Fish community structure in the rivers of Lincolnshire and South Humberside, England. *Hydrobiologia*, **211**, 1-9.
- Penczak, T.; Agostinho, A.A. & Okada, E.K. (1994): Fish diversity and community structure in two small tributaries of the Paraná River, Paraná State, Brazil. *Hydrobiologia*, **294**, 243-251.

- Przybylski, M.; Biro, P.; Zalewski, M.; Tatrai, I. & Frankiewicz, P. (1991), The structure of fish communities in streams of the northern part of the catchment area of Lake Balaton (Hungary). *Acta Hydrobiol.*, 33, 135-148.
- Romaniszyn, W. (1970), An attempt at interpreting agglomerative tendencies of animals based on definition of similarity and distance. *Wiad. ekol.*, **16**, 306-321.
- Winemiller, K.O. & Leslie, M.A. (1992), Fish assemblages across a complex, tropical freshwater/marine ecotone. *Envir. Biol. Fish.*, **34**, 29-50.
- Winemiller, K.O. & Polis, G.A. (1996), Food webs: what can they tell us about the world. In: Food webs: integration of patterns and dynamics, Eds. K.O. Winemiller & G.A. Polis, Chapman and Hall, New York, pp. 1-22.
- Witkowski, A. (1984), Structure of communities and biomass of ichthyofauna in the Biebrza River, its old river beds and affluents. *Pol. ecol. Stud.*, **10**, 447-474.
- Zalewski, M.; Frankiewicz, P.; Przybylski, M.; Banbura, J. & Nowak, M. (1990), Structure and dynamics of fish communities in temperate rivers in relation to the abiotic-biotic regulatory continuum concept. *Pol. Arch. Hydrobiol.*, **37**, 151-176.

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