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Trophic guilds of fishes in sandbank habitats of a Neotropical river

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The objective of this study was to characterize the trophic structure of the community of fishes exploiting riverine sandbank habitats. Collections were carried out during the period of October 1999 to December 2003, on six sand banks in the upper and middle portions of the Tocantins River drainage basin in central Brazil. The availability of food resources was evaluated based on the volume of the items present in the stomachs of all species. A total of 2,127 stomachs of fish belonging to 50 species were analyzed. Nine main trophic guilds grouped the local ichthyofauna according to diet. Aquatic-origin items were the preferred source for 55.5% of the groups analyzed, whereas terrestrial-origin items composed 44.4%. Items of undetermined origin (detritus and sediment), although present in 89% of the guilds, were the predominant food in only one trophic group. Terrestrial insects and fish were the food sources with the largest biomass available in the environment. Sandbank environments are homogeneous, with little shelter and food available; as a rule, the species that occupy these environments are generalists.

O presente estudo teve como objetivo caracterizar a estrutura trófica da comunidade de peixes que exploram ambientes de banco de areia. As coletas foram realizadas no período de outubro de 1999 a dezembro de 2003, em seis bancos de areia das porções superior e média da drenagem do rio Tocantins no Brasil central. A disponibilidade dos recursos alimentares foi avaliada a partir do volume dos itens presentes nos estômagos de todas as espécies. Foram analisados 2.127 estômagos de 50 espécies. Nove guildas tróficas principais agrupam a ictiofauna local quanto a sua dieta. Os itens de origem aquática foram a fonte preferencial para 55,5% dos grupos analisados, os terrestres para 44,4% e os itens de origem indeterminada (detrito e sedimento), apesar de presentes em 89% das guildas, foi o alimento predominante somente em um grupo trófico. Os insetos terrestres e os peixes foram os recursos alimentares com maior biomassa disponível no ambiente. Os ambientes de praia são homogêneos, com baixa oferta de abrigo e de alimento, de modo geral, as espécies que ocupam estes ambientes são generalistas.

Key words: Feeding plasticity, Fish diet, Resource availability.

Introduction

From knowledge of the diet and abundance of the species of fishes in a community, it is possible to identify the different trophic categories, to make inferences about the trophic structure, to evaluate the degree of importance of the different trophic levels, and to understand the interrelations among the components of the community (Payne, 1986; Agostinho *et al.*, 1997).

Sandbank environments are shallow and homogeneous, and because they are relatively unstructured, they offer little shelter or food compared to others, *i.e.*, rocky-shore and vegetated-shore habitats. Lowe-McConnell (1999) described this kind of environment as extensive sandy areas found along riverbanks, which are covered with water during certain times of year. In the Araguaia-Tocantins Basin, the marked seasonality of rains leads to the formation of innumerable sandbank areas, especially during the dry season. The fish communities of these sand banks are little known, in spite of the growing loss of these environments resulting from the construction of hydroelectric reservoirs, which not only permanently floods many of the sand banks but also rearranges the annual river discharge pattern.

The assemblages of fishes on the sand banks are highly important in the dynamics of the environment, because they include a substantial number of benthic organisms, including forage fish, which serve as food for the predators (Lowe-McConnell, 1999). According to Arrington & Winemiller (2003), the fish that occur on river sand banks during the day generally use them for foraging; and fish that occur there during the night take advantage of the shallow water as a refuge from predation.

During this study, a trophic characterization of the species of fishes associated with the sand banks of the upper and middle parts of the drainage basin of the Tocantins River was carried out, with the objective of answering the following questions: (i) what is the food spectrum of the species that occupy the sand banks of the Tocantins River? (ii) how many trophic guilds can be identified in this kind of environment?

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(iii) what is the importance of food of terrestrial and aquatic origin for the guilds present? (iv) what are the proportions of available food resources on the sand banks?

Material and Methods

Paired diurnal and nocturnal samples of fish were collected monthly from October 1999 through December 2003, at six sand banks in the upper and middle portions of the Tocantins River drainage basin: (1) Lake Água Branca (11°49' S; 48°38' W); (2) Lake Dionísio (11°44' S; 48°38' W); (3) Santa Tereza River (11°80' S; 48°63' W); and at three points in the Tocantins River, (4) the first, in the municipality of Peixe (11°47' S; 48°37' W); (5) the second, in the municipality of Ipueiras (10°43' S; 48°25' W); (6) and the third, in the municipality of Lajeado (09°45' S; 48°21' W).

The fish were sampled by means of seines with a mesh size of 5 mm between opposing knots, 20 m long, 2 m high, and fitted with a center bag where the fish concentrated. During seine hauls, one end of the seine was pulled along the shoreline and the other end was pulled in a parallel direction offshore. At the offshore end of the seine the maximum depth was 1.5 m. For most of the year, water velocity ranged from zero in littoral areas to about 0.5 ms^{-1} in some sand banks in the river. During the low-water period (April through September), water transparency was total at the collection localities. During the high-water period (October through March), the mean transparency was 0.50 m. The substrates are dominated by alluvial deposits of fine white sand from the surrounding watershed. The specimens collected were fixed in 10% formalin and transported to the laboratory, where the total length (cm), standard length (cm), and total weight (g) were taken.

Subsamples of the species analyzed were deposited at the Laboratório de Ictiologia e Sistemática of the Universidade Federal do Tocantins, under the numbers listed in Table 2.

The stomachs were stored in 4% formalin. The stomach contents were analyzed under an optical microscope and a stereomicroscope, and the food items were identified to the lowest possible taxonomic level. The food resources identified were grouped as: algae (filamentous and unicellular), aquatic insects (pupae, larvae), terrestrial insects (dipterans, coleopterans, ephemeropterans, hemipterans, homopterans, hymenopterans, lepidopterans, odonates, orthopterans, insect remains), other invertebrates (arachnids, rotifers, nematodes, oligochaetes, bryozoans, poriferans, protozoans and gastropods), fish (characiforms, clupeiforms, fish remains, fish scales, blood), microcrustaceans (cladocerans, copepods, ostracodes), plants (bryophytes, fruits, seeds, plant remains), sediment (mineral particles) and detritus (amorphous organic matter). The item “insect remains” consisted of separated insect parts (wings, legs, heads), and “plant remains” of small plant parts such as roots and leaves.

For the analysis of the stomach contents, the occurrence frequency and volumetric methods were used (Hynes, 1950; Hyslop, 1980). The data for volume were obtained either by compressing the material (food items) under a glass slide on a plate with a one-millimeter grid, to a known height (1 mm), and converting to milliliters based on the area covered; or by placing the items in a graduated cylinder and calculating the displacement of water. The volume of each item was converted to a percentage. We assumed that the results obtained using these two methods were similar.

The possibility of analysis of the data by grouping the sampling localities was evaluated using Kendalls’ Coefficient of Concordance (W) (Siegel, 1975) applied to the volume of the food items (STATISTICA version 5.5; Statsoft, 2000).

In order to classify species into trophic groups, we first ordinated the data using Detrended Correspondence Analysis to remove the arch effect (DCA; Hill & Gauch, 1980; Gauch, 1994). DCA ordination allowed the analysis of the patterns of feeding similarity among the 50 species based on volume values, which were square-root transformed, before analysis, to reduce skewness. Second, we identified trophic groups based on the scores of the first two DCA axes with a non-hierarchical cluster analysis, the k-means method (STATISTICA 5.5; Statsoft, 2000). Non-hierarchical methods maximize intra-group homogeneity, without considering the hierarchy between groups (Valentin, 2000). The formation of the trophic groups was defined using the non-hierarchical grouping analysis (k-means), because in certain cases, the hierarchical classification method does not adequately reflect the similarity relationships among the sampling units. Hierarchical techniques applied to a group of data produce a phenomenon called “*chaining*”, which refers to the tendency for the method to incorporate sampling units into an already existing group, instead of forming a new one (Everitt & Dunn, 1991). Furthermore, when the number of sampling units is large, the dendrograms resulting from the hierarchical techniques are difficult to interpret because of the many groups that are formed. Thus, when the data are not adequately represented by a hierarchical structure and when the objective is to form a number of groups of previously fixed sampling units, the non-hierarchical k-means analysis can be used (Bishop, 1995). Similar methodology to separate trophic guilds was used by Luz-Agostinho *et al*. (2006) and Loureiro-Crippa & Hahn (2006).

The food resources consumed were classified in three groups: items of aquatic origin, items of terrestrial origin, and undetermined, a group that included those items for which it was impossible to determine the origin (*e.g.*, detritus and sediment).

The availability of the food resources was evaluated based on the volume of the items present in the stomachs of all the species combined (Lawlor, 1980; Winemiller & Kelso-Winemiller, 1996). The number of stomachs analyzed per species was not proportional to their participation in the sample, and therefore the volumes were corrected using the equation proposed by Luz-Agostinho *et al.* (2006).

Results

A total of 2,473 stomachs from 124 fish species contained some type of food. However, diet characterization was carried out only for species for which we found more than ten stomachs with identifiable food items, resulting in a data set of 2,127 stomachs representing 50 species.

Kendall's coefficient of concordance ($W = 0.7481$ and $p < 0.05$) showed that there was a correlation between the food items at the six sampling points, and therefore they were treated together.

Analysis of the DCA results showed that axis 1 accumulated the greatest variability of species, with an eigenvalue of 0.3229, followed by axis 2 with an eigenvalue of 0.0356 (Fig. 1).

Nine trophic groups with similar diets could be discriminated through the K-means analysis of the scores derived from DCA axes 1 and 2. The R statistic showed that adding new groups would not significantly reduce the value of the sum of squares within the groups, indicating that nine appeared to be the most parsimonious number of groups for the data set (Table 1). The nine trophic groups are shown in Table 2. The species scores along DCA axes 1 and 2 (Fig. 1) are circled, so as to visualize more easily the nine groups formed by the K-means analysis.

The nine trophic groups were characterized as follows:

Group 1: seven species (14% of the species analyzed) preferentially consumed terrestrial and aquatic insects, together with fish, sediment, plant matter, and algae. The exceptions were *Myleus* cf. *torquatus* and *Pimelodus blochii*, which ate mainly fish.

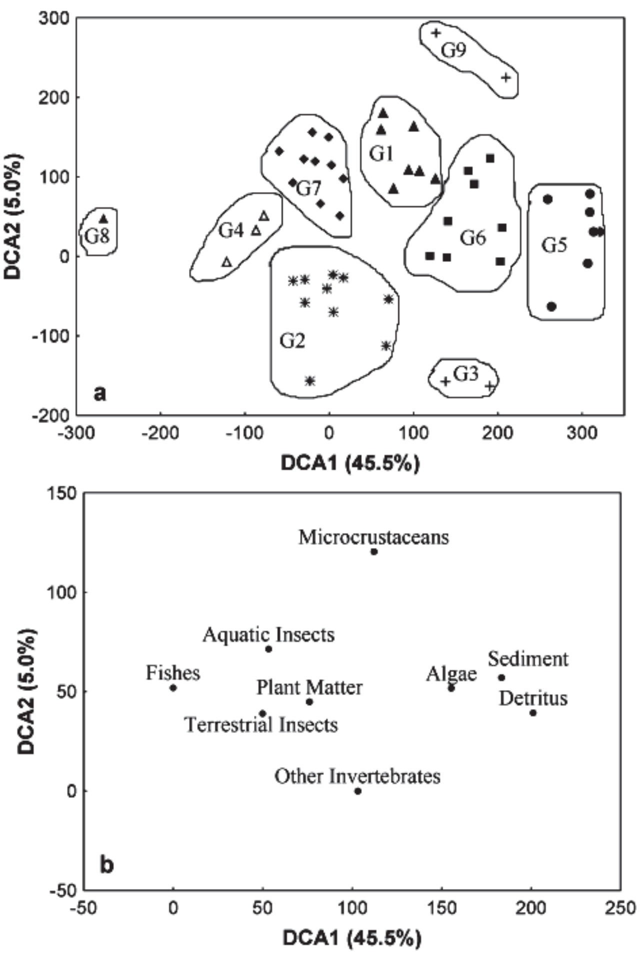

Fig. 1. Scores for the fish species (a) and their food items (b) along Axes 1 and 2, derived from detrended correspondence analysis (DCA). The circles in (a) indicate the groups determined by the k-means analysis.

Group 2: ten species (20%) ingested a large quantity of terrestrial insects (>50%). However, *Acnodon normani*, in addition to consuming a large amount of terrestrial insects, ate mainly plant matter (38%).

Group 3: two species (4%) fed mainly on terrestrial insects. They also ate significant amounts of other invertebrates and detritus.

Group 4: three species (6%) consumed a large amount of terrestrial insects and fish. *Exodon paradoxus* consumed mainly fish (scales), whereas the other species consumed terrestrial insects and fish in equal proportions.

Group 5: seven species (14%) basically exploited the bottom, consuming a large amount of detritus and sediment, together with algae.

Group 6: eight species (16%) fed on a wide variety of items, such as algae, detritus, aquatic insects, terrestrial insects, microcrustaceans, other invertebrates, fish, sediment, and plant matter. Terrestrial insects predominated in the diet of most of the species, except for *Hemiodus unimaculatus* for which the most prominent item was sediment.

Group 7: ten species (20%) had diets with a strong predominance of terrestrial and aquatic insects. However, *Hyphessobrycon* sp. B and *Moenkhausia* sp. E consumed a high proportion of plant matter and fish respectively.

Group 8: one species (2%), *Vandellia* sp. 3, which fed exclusively on fish blood.

Group 9: two species (4%) with food habits ranging from algae to plant matter, or from invertebrates to fish. However, these species preferentially ingested microcrustaceans or detritus, respectively.

Terrestrial and aquatic insects, plant matter, and sediment were the food items consumed most often by the fish assemblage (Table 2). Aquatic-origin items were present in 55.5% of the groups analyzed. These consisted mainly of aquatic insects such as larvae and pupae, followed by fish and microcrustaceans. Terrestrial resources, consisting mainly of terrestrial insects and plants, were the preferred source for 44.4% of the groups. The items of undetermined origin, detritus and sediment, were present in 89% of the guilds; however, they were the predominant food only in guild 5 (Fig. 2).

Table 1. Results used to calculate the R-statistic (R), to assess whether the increase from k to k+1 groups was significant. Sum of SQ-within = sum of sum of squares within; n-k-1 = degrees of freedom; P = probability of Type 1 error.

K	SQ-within	n-k-1	Number of groups	R	P
2	473800.7	47	2 for 3	21.8966	0.0000
3	331275.3	46	3 for 4	18.5000	0.0000
4	283237.7	45	4 for 5	6.9537	0.0025
5	209043.22	44	5 for 6	13.8420	0.0000
6	174067.6	43	6 for 7	7.4345	0.0019
7	134687.98	42	7 for 8	10.2332	0.0003
8	112035.76	41	8 for 9	6.6722	0.0037
9	103714.98	40	9 for 10	2.4870	0.0996

Table 2. Food resources used by the fish species, estimated by volume. N = number of stomachs examined; 1 = Algae; 2 = Detritus; 3 = Aquatic Insects; 4 = Terrestrial Insects; 5 = Microcrustaceans; 6 = Other Invertebrates; 7 = Fishes; 8 = Sediment; 9 = Plant Matter; – = absence of specimens.

Species	Voucher specimens	N	1	2	3	4	5	6	7	8	9
GROUP 01											
Colomesus asellus	UNT565	49	0.413	2.110	32.148	31.187	0.060	1.139	11.343	10.710	10.890
Myleus cf. *torquatus*	UNT6545	25	23.301	0.181	7.156	13.070	–	–	33.105	2.213	20.974
Moenkhausia sp. H	UNT4476	28	–	–	33.576	46.354	0.906	0.324	0.324	8.319	10.197
Pimelodus blochii	UNT3460	34	0.005	5.137	11.461	23.630	3.777	0.085	29.004	10.667	16.233
Pimelodella cristata	UNT3667	13	–	–	27.031	44.614	–	0.582	1.456	26.317	–
Phenacogaster sp. A	UNT3303	49	–	1.655	43.640	43.349	5.304	4.877	–	0.784	0.392
Satanoperca jurupari	UNT4929	20	0.089	6.178	3.223	30.043	2.136	0.209	25.707	8.057	24.357
GROUP 02											
Acnodon normani	UNT2901	20	–	–	4.553	37.176	–	0.955	19.105	0.637	37.574
Brycon sp.1	UNT3927	40	–	0.199	3.890	56.285	–	1.177	29.460	2.297	6.693
Bryconops sp. A	UNT3837	33	0.535	0.535	4.173	80.166	–	3.355	1.873	3.478	5.886
Jupiaba polylepis	UNT7258	43	–	2.464	12.850	72.435	0.198	5.700	4.275	–	2.077
Moenkhausia loweae	UNT3515	85	0.236	2.871	7.619	69.998	0.364	4.039	1.392	0.768	12.714
Moenkhausia sanctaefilomenae	UNT3720	68	–	–	7.818	70.541	0.118	14.118	2.674	0.110	4.622
Moenkhausia sp. I	UNT3561	73	0.126	–	11.505	65.402	0.259	2.939	2.484	1.365	15.920
Tetragonopterus argenteus	UNT2801	77	–	2.535	10.871	65.484	0.765	4.688	8.361	0.216	7.079
Triportheus trifurcatus	UNT1614	47	0.054	0.508	4.442	82.570	0.382	0.458	8.611	0.196	2.780
Tetragonopterus sp. A	UNT3522	25	–	–	8.989	58.093	–	1.685	5.417	2.274	23.542
GROUP 03											
Bryconops sp. D	UNT6297	42	0.034	15.291	5.007	64.205	0.049	10.090	0.000	0.000	5.325
Moenkhausia sp. A	UNT7345	26	–	34.604	1.583	49.353	0.432	12.302	0.000	0.288	1.439
GROUP 04											
Exodon paradoxus	UNT2347	42	–	–	0.805	8.639	–	0.204	87.690	1.231	1.430
Moenkhausia sp. C	UNT4284	15	0.270	–	9.939	48.745	–	–	39.089	0.809	1.148
Roeboides affinis	UNT2576	50	–	0.390	11.767	43.113	–	–	42.057	0.624	2.048
GROUP 05											
Apareiodon argenteus	UNT1162	28	3.132	33.221	0.071	1.883	–	3.998	0.017	46.785	10.894
Curimatella immaculata	UNT3759	20	0.398	31.180	0.021	0.077	–	0.042	–	68.116	0.166
Caenotropus labyrinthicus	UNT2488	28	0.470	30.419	0.944	4.214	0.839	0.879	0.395	58.731	3.109
Cyphocharax plumbeus	UNT3780	10	0.623	30.982	0.342	–	0.214	0.499	–	67.197	0.143
Cyphocharax spilurus	UNT6281	16	0.553	28.850	0.028	0.115	0.000	0.735	–	68.847	0.872
Prochilodus nigricans	UNT3055	12	0.455	30.945	–	–	0.060	0.080	–	65.745	2.717
Steindachnerina gracilis	UNT4524	24	0.456	33.846	0.015	0.024		0.039	–	64.084	1.536
GROUP 06											
Bivibranchia velox	UNT1342	48	0.559	22.417	9.804	30.435	0.375	1.376	1.035	28.501	5.497
Ctenobrycon hauxwellianus	UNT6611	73	1.987	3.645	2.957	51.021	0.586	1.018	8.050	12.467	18.269
Geophagus altifrons	UNT7201	69	0.140	0.407	16.540	48.133	4.647	13.148	0.264	16.129	0.592
Hemiodus unimaculatus	UNT4509	46	1.352	8.037	4.714	24.339	1.531	8.134	0.013	36.155	15.724
Knodus sp. D	UNT2435	92	1.750	12.926	11.148	55.104	1.476	0.131	0.738	6.326	10.402
Moenkhausia gr. dichroura	UNT2734	103	0.187	8.893	8.536	54.328	1.152	3.568	11.960	5.936	5.439
Retroculus lapidifer	UNT7277	74	0.439	12.025	18.314	34.654	2.087	1.883	0.016	23.849	6.733
Serrapinus sp. A	UNT1815	36	7.370	7.152	9.752	40.739	6.554	7.865	1.573	11.289	7.707
GROUP 07											
Aphyocharax sp. A	UNT2346	60	–	–	17.403	71.291	1.682	–	2.994	3.200	3.429
Creagrutus britskii	UNT2875	37	0.095	–	11.622	59.291	0.338	–	1.655	2.811	24.189
Hemigrammus sp. B	UNT6602	32	–	–	27.554	66.290	0.126	–	–	–	6.030
Hyphessobrycon sp. B	UNT4617	44	0.122	–	6.593	42.698	2.271	2.133	1.828	–	44.355
Jupiaba sp. B	UNT3307	43	–	–	13.158	72.491	2.667	–	8.579	2.895	0.211
Knodus sp. C	UNT6903	84	0.434	–	24.371	57.763	–	0.500	4.847	3.916	8.170
Microschemobrycon sp.	UNT4235	26	–	–	39.021	55.490	0.148	1.187	–	0.593	3.561
Moenkhausia sp. E	UNT6786	85	0.001	3.033	29.748	30.875	0.056	0.334	35.121	0.298	0.535
Moenkhausia sp .F	UNT4357	12	–	–	37.262	45.120	–	0.552	7.673	5.709	3.683
Poptella compressa	UNT3615	16	–	–	13.734	80.694	0.440	–	0.391	0.244	4.497
GROUP 08											
Vandellia sp. 3	UNT5665	19	–	–	–	–	–	–	100.000	–	–
GROUP 09											
Anchoviella cf. *carrikeri*	UNT1262	50	0.113	12.429	7.869	17.048	35.312	1.170	17.247	1.728	7.085
Bivibranchia fowleri	UNT1388	36	0.556	26.030	11.581	8.748	15.228	1.132	0.553	25.131	11.042

The analysis of the proportions of food items suggested that terrestrial insects and fish were the main food resources available to fish in the environment (Fig. 3).

Discussion

Although in tropical environments there are species of fishes with marked trophic specializations, the majority of species show broad flexibility in feeding (Agostinho *et al.*, 1995; Araújo-Lima *et al.*, 1995; Lowe-McConnell, 1999). Feeding flexibility is a reflection of the interaction between the quality or quantity of the available food, and the degree of morphological and behavioral limitations exhibited by the species, the latter with ontogenetic variations (Luz *et al.*, 2001). Therefore, determination of the trophic guilds of tropical fishes is often hampered by the broad feeding overlap of the species. Separation of the guilds by visual analysis of the dominant items in the stomachs often results in a high degree of subjectivity.

The 50 species of fishes caught along sand banks of the Tocantins system were grouped in nine trophic guilds. Melo *et al.* (2004), studying 71 species of the Araguaia River basin, and Luz-Agostinho *et al.* (2006), analyzing 64 species in the basin of the Paraná River, both using clustering methods and working in different habitats, also found nine trophic guilds. Mérona & Rankin-de-Mérona (2004) analyzed 74 species in a floodplain lake in central Amazonia, and separated 11 trophic guilds based on the dominant food items. Pouilly *et al*. (2003) analyzed the diets of 48 species from lakes in the Bolivian Amazon, and separated eight trophic guilds using hierachical methods. However, the number of guilds established for different environments in the Paraná River basin varied from 7 to 10 (Hahn *et al.,* 1997, 2004; Peretti & Andrian, 2004; Loureiro-Crippa & Hahn, 2006; Luz-Agostinho*,* 2006). Understanding of the ecological meaning of the variation in the number of trophic guilds is impeded by the use of different methods to separate the guilds. Therefore, studies are needed to compare the accuracy of these methods and eventually to standardize the methodology.

The number of trophic groups and the similarity in the diet of the species of different groups, a result of the range of diet, made it difficult to assign names to the guilds. The dietary similarity results in part from the hydrological instability and homogeneity of the sandbank environment. According to Poff & Allan (1995), trophic generalism is greater in hydrologically variable environments. The shallowness of the sand banks makes them susceptible to random environmental variations caused by the winds and daily fluctuations of the water level, especially in areas influenced by reservoirs.

The sandbank environments are shallow and homogeneous; the sediment is composed of sand and a smaller quantity of organic detritus carried in by the water. It is expected that in environments with these characteristics, terrestrial-origin food sources will be important food sources for the fish assemblage. Analysis of the origin of food items revealed that aquatic-origin resources, composed mainly of aquatic insects (larvae and pupae) were the main food sources for 55.5% of the trophic guilds; whereas allochthonous items, mainly terrestrial insects and plant matter, were the main constituents of the diet for 44.4% of the guilds. However, the importance of terrestrial-origin items to the sandbank fishes can be seen in the large volume of terrestrial insects, which represented more than 40% of the total volume of the items used by the fish. The relative importance of terrestrial- and aquatic-origin food varies according to the composition of the fish assemblage, and also the habitat (Casatti, 2002; Gurgel *et al.,* 2002; Melo *et al.*, 2004; Dias *et al.,* 2005).

Terrestrial and aquatic insects, plants, and sediments were present in the diet of more than 80% of the fish species analyzed. Luz *et al.* (2001), working with ponds on the Upper Paraná River floodplain, observed that insects were the most available resource in two of the three ponds in the study. Insects are the principal invertebrates in the food of fish. In general, we can state that nearly all species of fishes consume insects at some stage of their lives (Goulding *et al.*, 1988). These arthropods function trophically as a bridge between the inaccessible or indigestible forms of primary production and the fish communities (Goulding *et al.*, 1988). Luz-Agostinho *et al.* (2006), studying fishes of the Corumbá Reservoir, established that the availability of resources varied in the affluent streams, and that terrestrial insects were the most important resource.

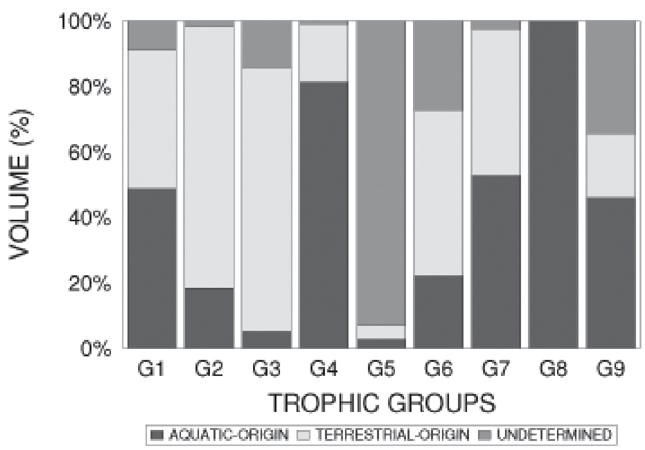

Fig. 2. Proportions of terrestrial, aquatic, and undetermined resources used by the fish trophic groups.

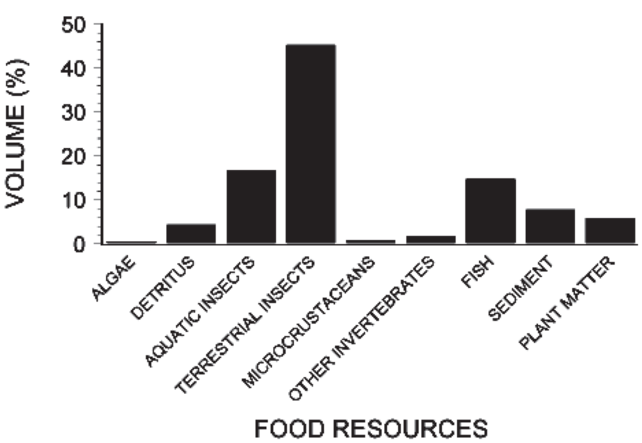

Fig. 3. Food resource availability, inferred from the volume of items in the stomachs analyzed for all species combined.

There are few tropical species with specialized feeding habits (Abelha *et al.*, 2001). Most species are generalists, using available foods, although with a certain degree of preference. Riverine sandbank environments are markedly homogeneous and afford little food or shelter, leading to increased sharing of the limited variety of available resources. Nine main trophic guilds grouped the local ichthyofauna in respect to diet. However, the wide overlap in consumption of these resources makes these guilds very heterogeneous, even considering that this number has been recorded in samples from other kinds of habitat, as previously mentioned. The food resources responsible for sustaining the fish community in the environment were principally terrestrial and aquatic insects.

Acknowledgments

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Literature Cited

Abelha, M. C. F., A. A. Agostinho & F. Goulart. 2001. Plasticidade trófica em peixes de água doce. Acta Scientiarum, 23(2): 425-434.

Agostinho, A. A., A. E. A. de M. Vazzoler & S. M. Thomaz. 1995. The High River Paraná basin: limnological and ichthyological aspects. Pp. 59-103. In: Tundisi, J. G., C. E. M. Bicudo & T. Matsumura-Tundisi (Eds). Limnology in Brazil. São Paulo, Brazilian Academy of Sciences/ Brazilian Limnological Society, 376p.

Agostinho, A.A., C. M. L. Ferreti, L. C. Gomes, N. S. Hahn, H. I. Suzuki, R. Fugi & F. Abujanra. 1997. Ictiofauna de dois reservatórios do rio Iguaçu em diferentes fases de colonização: Segredo e Foz do Areia. Pp. 275-292. In: Agostinho, A.A. & L.C. Gomes (Eds). Reservatório de Segredo: bases ecológicas para o manejo. Maringá, Eduem, 387p.

Araújo-Lima, C. A. R. M., A. A. Agostinho & N. N. Fabre. 1995. Trophic aspects of fish communities in Brazilian rivers and reservoirs. Pp. 105-136. In: Tundisi, J. G., Bicudo, C. E. M. & T. Matsumura-Tundisi (Eds). Limnology in Brazil. São Paulo, Brazilian Academy of Sciences/ Brazilian Limnological Society, 376p.

Arrington, D. A. & K. O. Winemiller. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. Journal of Fish Biology, 63: 442-459.

Bishop, C. M. 1995. Neural networks for pattern recognition. New York, Oxford University Press, 482p.

Casatti, L. 2002. Alimentação dos peixes em um riacho do Parque Estadual Morro do Diabo, Bacia do Alto Rio Paraná, sudeste do Brasil. Biota Neotropica, 2(2): 1-14.

Dias, A. C. M. I., C. W. C. Branco & V. G. Lopes. 2005. Estudo da dieta natural de peixes no reservatório de Ribeirão das Lajes, Rio de Janeiro, Brasil. Acta Scientiarium, Maringá, 27(4): 355-364.

Everitt, B. S. & G. Dunn. 1991. Applied multivariate data analysis. London, Edward Arnold, 304p.

Gauch, H. G. 1994. Multivariate analysis in community ecology. Cambridge, Cambridge University Press, 298p. (Cambridge Studies in Ecology, 1).

Goulding, M., M. L. Carvalho & E. J. G. Ferreira. 1988. Rio Negro, Rich Life in Poor Water. Amazonian diversity and foodchain ecology as seen through fish communities. The Hague, SPB Academic Publishing, 200p.

Gurgel, H. de C. B., F. D. Lucas & L. de L. G. Souza. 2002. Dieta de sete espécies de peixes do semi-árido do Rio Grande do Norte, Brasil. Revista de Ictiologia, 10(1/2): 7-16.

Hahn, N. S., R. Fugi, V. L. L. Almeida, M. R. Russo & V. E. Loureiro. 1997. Dieta e atividade alimentar de peixes do reservatório de Segredo. Pp. 141-162. In: Agostinho, A. A. & C. G. Gomes. Reservatório de Segredo: bases ecológicas para o manejo. Maringá, Eduem, 387p.

Hahn, N. S., R. Fugi & I. de F. Andrian. 2004. Trophic ecology of the fish assemblages. Pp. 247-269. In: Thomaz, S. M., A. A. Agostinho & N. S. Hahn. (Eds.). The Upper Paraná River and its Floodplain: physical aspects, ecology and conservation. Leiden, Backhuys Publishers, 393p.

Hill, M. O. & H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio, 42(1-3): 47-58.

Hynes, H. B. N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pigosteus pungitius*), with a review of methods used in studies of the food of fishes. Journal of Animal Ecology, 19(1): 36-56.

Hyslop, E. J. 1980. Stomach contents analysis, a review of methods and their application. Journal of Fish Biology, 17: 411-429.

Lawlor, L. R. 1980. Overlap, similarity, and competition coefficients. Ecology, 61(2): 245-251.

Loureiro-Crippa, V. E. & N. S. Hahn. 2006. Use of food resources by the fish fauna of a small reservoir (rio Jordão, Brazil) before and shortly after its filling. Neotropical Ichthyology, 4(3): 357-362.

Lowe-McConnell, R. H. 1999. Estudos ecológicos de comunidade de peixes tropicais. Translated by Vazzoler, A. E. A. de M., A. A. Agostinho & P. T. M. Cunningham. São Paulo, EDUSP, 535p. Original title: Ecological Studies in Tropical Fish Communities.

Luz, K. D. G. da., F. Abujanra, A. A. Agostinho & L. C. Gomes. 2001. Caracterização trófica da ictiofauna de três lagoas da planície aluvial do alto rio Paraná, Brasil. Acta Scientiarum, 23(2): 401-407.

Luz-Agostinho, K. D.G., L. M. Bini, R. Fugi, A. A. Agostinho & H. F. Júlio Jr. 2006. Food spectrum and tropic structure of the ichthyofauna of Corumbá Reservoir, Paraná River Basin, Brazil. Neotropical Ichthyology, 4(1): 61-68.

Mérona, B. de & J. Rankin-de-Mérona. 2004. Food resource partitioning in a fish community of the central Amazon floodplain. Neotropical Ichthyology, 2(2): 75-84.

Melo, C. E., F. A. Machado & V. Pinto-Silva. 2004. Feeding habits of fish from a stream in the savanna of Central Brazil, Araguaia Basin. Neotropical Ichthyology, 2(1): 37-44.

Payne, A. I. 1986. The ecology of tropical lakes and rivers. Chichester, J. Wiley & Sons, 301 p.

Peretti, D. & I. de F. Andrian. 2004. Trophic structure of fish assemblages in five permanent lagoons of the high Paraná River floodplain, Brazil. Environmental Biology of Fishes, 71(1): 95-103.

Poff, N. L. & J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology, 76(2): 606-627.

Pouilly, M., F. Lino, J. G. Bretenoux & C. Rosales. 2003. Dietary-morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. Journal of Fish Biology, 62: 1137-1158.

Siegel, S. 1975. Estatística não-paramétrica: Para as ciências do comportamento. São Paulo, MacGraw-Hill, 350p.

Stasoft, Inc. 2000. STATISTICA for Windows (Computer Program Manual). Version 5.5, Tulsa, OK.

Valentin, J. L. 2000. Ecologia numérica: uma introdução à análise multivariada de dados ecológicos. Rio de Janeiro, Interciência, 117p.

Winemiller, K. O. & L. C. Kelso-Winemiller. 1996. Comparative ecology of catfishes of the Upper Zambezi River floodplain. Journal of Fish Biology, 49(6): 1043-1061.

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