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Feeding styles of five species of bottom-feeding fishes of the high Paraná River

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Synopsis

In this study the diets of five species of bottom-feeding fishes (*Prochilodus lineatus, Steindachnerina insculpta, Loricariichthys platymetopon, Trachydoras paraguayensis* and *Iheringichthys labrosus*) were analyzed. Samples were taken in the High Paraná River basin and its floodplain from August 1987 to July 1988 and in February, August and September 1991. The results demonstrated that *P. lineatus* and *S. insculpta* were ileophagous, *L. platymetopon* was detritivorous and *I. labrosus* and *T. paraguayensis* were benthophagous. The feeding activity was higher during the flood period for *P. lineatus* and in dry season for *T. paraguayensis. P. lineatus* and *S. insculpta* fed mainly during the day, while *I. labrosus* and *T. paraguayensis* during the day and dusk, respectively.

Introduction

This study of the diets and feeding activity of the five bottom-feeding fish species adressed question of overlap of habitats, diets and feeding behaviour in relation to feeding sources available. The great variety of benthic food sources in tropical waters includes detritus in different stages of decomposition, periphyton and a rich fauna of benthic invertebrates. These are exploited by a great number of fish species which comprise more than half the fish biomass of the large South American rivers.

Studies on the food consumed by these fishes have rarely been of comparative character, but rather were directed to the biological or ecological aspects of one particular species. Comparative studies, however, were undertaken by Angelescu & Gneri (1949) who analysed the diet and the morphology of the alimentary tract of species of the genera *Loricaria, Plecostomus* and *Prochilodus*, by Sazima & Caramashi (1989) on behaviour and morphological aspects linked to the feeding of Curimatidae and by Fugi & Hahn (1991) on the diet and morphology of the digestive tract of three bottom-feeding species. However, some controversy remains with regard to terminology which best distinguishes the food resources exploited by the fishes.

Study area

We sampled the River Paraná basin and its floodplain in the region of Porto Rico (PR) and Nova Andradina (MS) (22° 40′ and 22° 50′ S and 53° 10′ and 53° 40′ W), 1 560 km from the river source. In

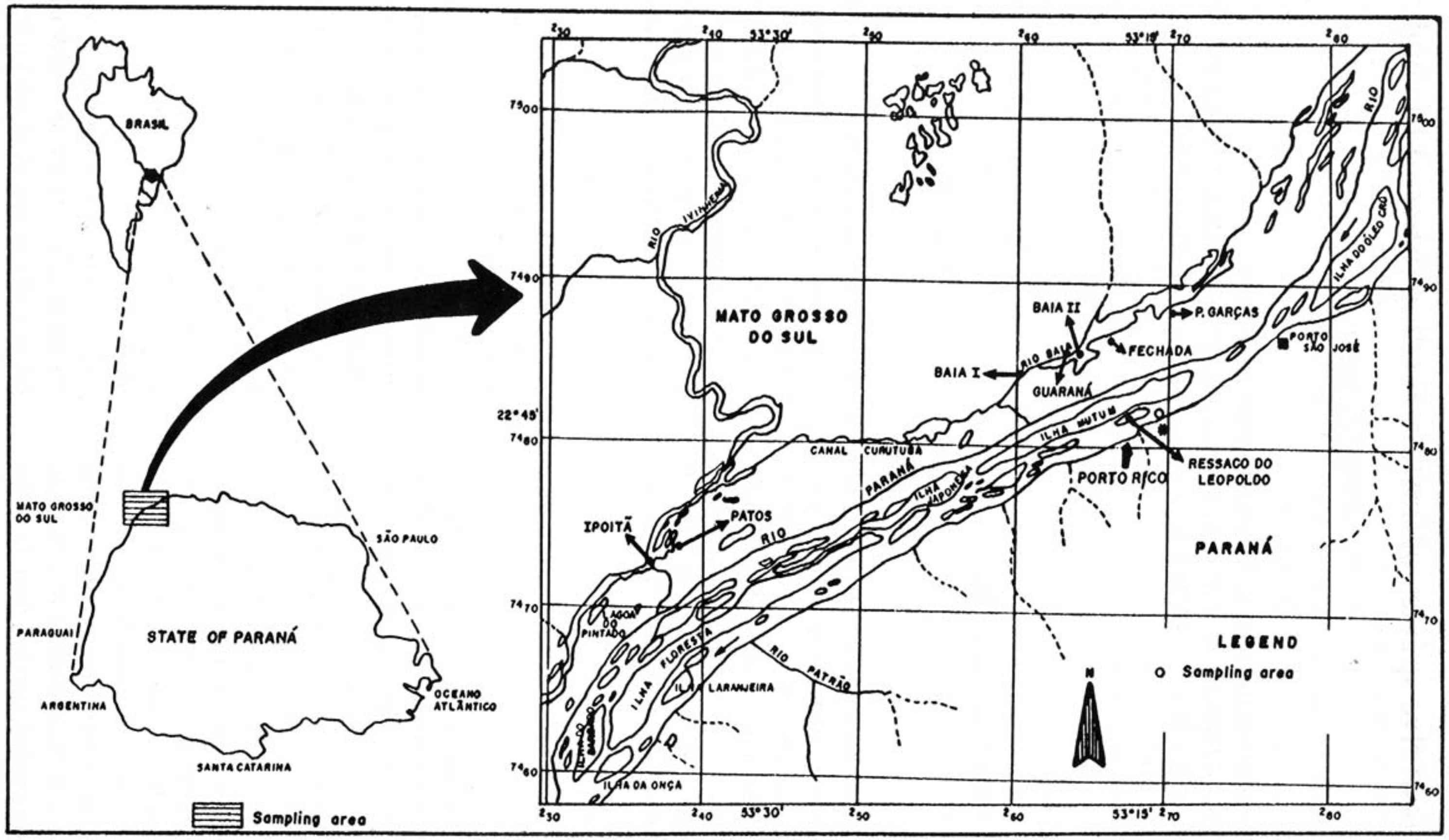

Fig. 1. Study area showing sampling locations.

this region, the Paraná River has a large braided channel with low gradient. An extensive alluvial floodplain on its right margin is ca. 20 km wide, with many permanent and seasonal lakes. The lowest part of the floodplain is formed by a varzea zone occupying a 5 km margin, with complex draining system. Ten collecting stations were established including lake environments (Fechada, Guaraná, Pousada das Garcas and Patos), backwater (Leopoldo), channels (Baía I and II, Corutuba) and rivers (Paraná and Ivinheima) (Fig. 1).

Materials and methods

The diet and the feeding activity of five bottom-feeding fishes, curimba, *Prochilodus lineatus* (Prochilodontidae), saguiru, *Steindachnerina insculpta* (Curimatidae), cascudo-chinelo, *Loricariichthys platymetopon* (Loricariidae), mandi, *Iheringichthys labrosus* (Pimelodidae) and armadinho, *Trachydoras paraguayensis* (Doradidae) were analysed. To determine the diet of the species, samples were obtained from stations Baía II and Leopoldo backwater in the high water (February 1991) and the dry periods (August and September 1991). These data were later pooled due to the absence of seasonal variations. Samples were taken monthly between August 1987 and July 1988 at all the stations so that seasonal variations in the feeding activity (dry, flooding increase, high water and drying periods) could be tested. To evaluate diel variations in feeding activity four special samples (in different phases of the hydrological cycle) were taken in the lakes Pousada das Garças and Patos.

Gillnets with different meshes (3, 4, 6, 8, 10, 12, 14 and 16 cm) were set throughout the 24 hours of each day. Catches were at 7:30, 17:30 and 22:30 h for the determination of seasonal variations in feeding activity and every 3 hours for diel variations. To establish diet, fish were collected from the nets at 4 hour intervals.

All fish were measured for routine biometric data, then their viscera were removed. A stomach fullness degree was assigned to each fish: 0 (completely empty stomach); 1 (partially empty stomach: 25%); 2 (partially full stomach: 25%–75%); 3 (completely full stomach: 75%–100%).

Feeding activity was calculated according to average stomach fullness (Santos 1978): $Gr = \Sigma if_{ri}/\Sigma f_{ri}$, where: f_{ri} = absolute frequency of degree 'i' fullness ($i = 0, 1, 2, 3$).

Stomach contents were analysed by stereo- and compound light microscopes and items identified to the least taxonomic level using descriptions and keys of Edmondson (1959) and Bourelly (1972, 1981, 1985). Methods of occurrence frequency and of points (Hynes 1950, Hyslop 1980) were applied to the resulting data. The latter is used as an indicator of relative volume. Both were combined to obtain the feeding index (Kawakami & Vazzoler 1980).

For the study of the diet of *L. platymetopon* the anterior third of the intestine was examined since its small stomach is always without food. Because of this characteristic this species was not been analysed in the study of alimentary activity.

The diet similarity of these species was obtained by applying a grouping analysis to a matrix of 47 (food items) × 5 (species), using the following algorithms: Euclidian distance as a coefficient of similarity and UPGMA (non-ponderable link to pairs by using arithmetical averages) as a linking method. The dendrogram was evaluated by cophenetical correlation (Rohlf 1989).

Results

Prochilodus lineatus: This species (7.9 cm to 26.0 cm SL) fed on inorganic sediments, organic detritus, algae, Testacea and nematodes. The first element was the principal item representing 52.8% of the feeding index (Fig. 2). Among the algae were Bacillariophyceae of the genera *Aulacoseira, Navicula, Eunotia, Pinnularia, Cyclotella, Cymbella, Gomphonema* and *Surirella* which were the most frequent (Table 1). Among the Testacea, *Difflugia* was conspicuous.

Data on daily feeding periodicity revealed that this species has its feeding peak between 3 and 9 hours after sunrise. Six hours after sunset all the individuals had empty stomachs (Fig. 3a). Considering the different phases of the hydrological cycle,

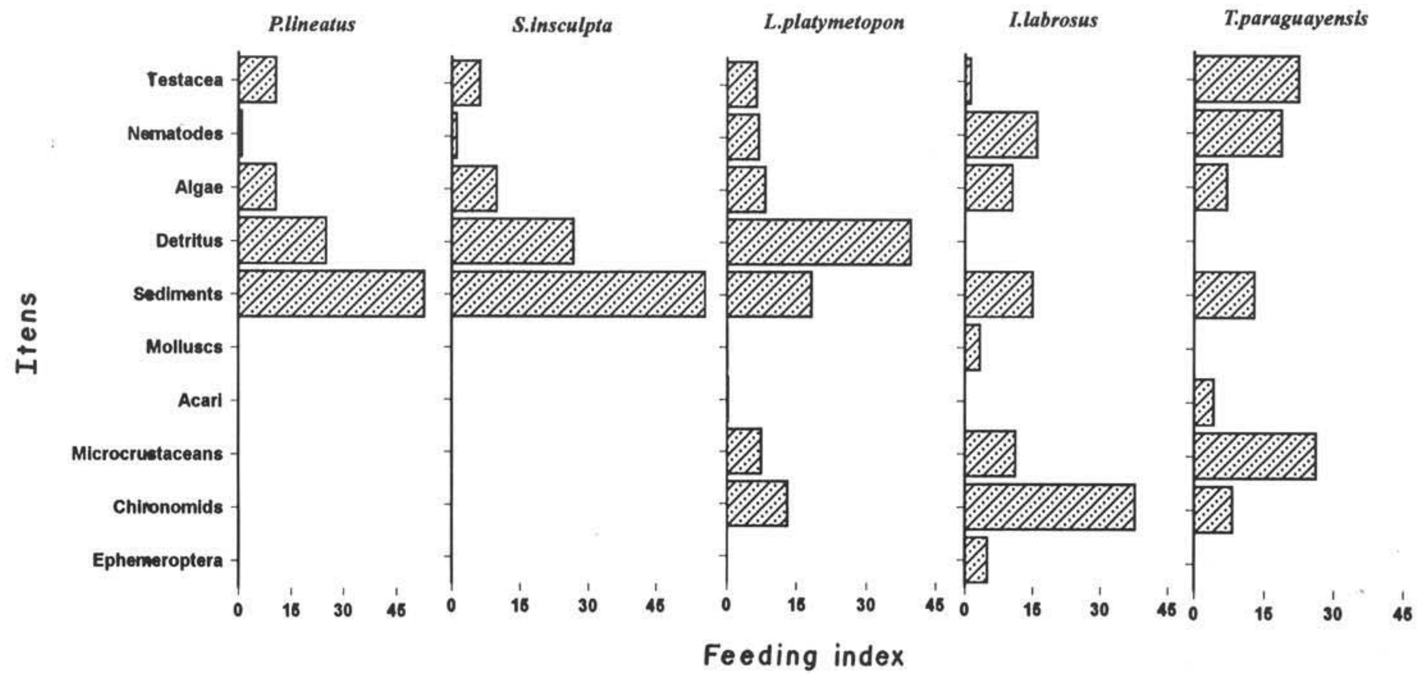

Fig. 2. Relative contribution of food items in the diet of bottom-feeding species in the floodplain of the Paraná River, based on the combination of occurrence and points methods (feeding index).

Table I. Feeding spectrum or species represented by the occurrence frequency of the alimentary items. Pli = *P. lineatus*, Sin = *S. insculpta*, Lpl = *L. platymetopon*, Tpa = *T. paraguayensis*, Ila = *I. labrosus*.

Species items	Pli		Sin		Lpl		Tpa		Ila	
	n	%	n	%	n	%	n	%	n	%
Difflugia	55	5.9	43	6.8	95	7.3	61	9.1	19	3.7
Euglypha	10	1.1	–	–	23	1.8	38	5.7	12	2.2
Centropyxis	–	–	–	–	10	0.8	–	–	5	1.0
Nematoda	13	1.4	20	3.2	75	5.8	62	9.3	63	12.3
Bivalvia	–	–	–	–	–	–	2	0.3	21	4.1
Gastropoda	–	–	–	–	9	0.7	–	–	–	–
Acarina	–	–	–	–	17	1.3	50	7.5	6	1.2
Cyclopoida	–	–	–	–	77	5.9	46	6.9	35	6.8
Harpacticoida	–	–	–	–	12	0.9	52	7.8	3	0.7
Cladocera	–	–	–	–	66	5.1	53	7.9	21	4.1
Ostracoda	–	–	–	–	55	4.2	55	8.2	46	9.0
Chironomidae	–	–	–	–	100	7.7	61	9.1	61	11.9
Ephemeroptera	–	–	–	–	–	–	–	–	23	4.5
Org detritus	55	5.9	62	9.8	116	8.9	–	–	–	–
Inorg. sediment	55	5.9	62	9.8	116	8.9	62	9.3	60	11.7
Cyanophyceae	–	–	–	–	2	0.2	–	–	–	–
Phacus	–	–	8	1.3	3	0.3	–	–	–	–
Scenedesmus	9	1.0	19	3.0	18	1.4	2	0.3	–	–
Pediastrum	–	–	1	0.2	5	0.4	–	–	–	–
Staurastrum	14	1.5	10	1.6	6	0.5	3	0.4	–	–
Cosmarium	13	1.4	17	2.7	6	0.5	–	–	–	–
Xanthidium	5	0.5	–	–	–	–	–	–	–	–
Achnanthes	41	4.4	14	2.3	10	0.8	–	–	–	–
Amphora	22	2.4	2	0.3	10	0.8	–	–	–	–
Anomoeoneis	6	0.6	–	–	–	–	–	–	–	–
Aulacoseira	55	5.9	62	9.8	115	8.8	60	9.0	58	11.4
Caloneis	13	1.4	3	0.5	–	–	–	–	–	–
Capartograma	8	0.9	5	0.8	2	0.2	–	–	–	–
Cocconeis	3	0.3	–	–	3	0.3	–	–	–	–
Cycotella	49	5.3	23	3.6	–	–	–	–	–	–
Cymbella	49	5.3	10	1.6	66	5.1	3	0.4	10	2.0
Diploneis	24	2.6	8	1.3	–	–	–	–	–	–
Eunotia	51	5.5	31	4.9	25	1.9	–	–	–	–
Fragilaria	49	5.3	11	1.7	–	–	–	–	–	–
Frustulia	29	3.1	18	2.8	–	–	–	–	–	–
Gomphonema	43	4.6	14	2.2	3	0.3	–	–	–	–
Gyrosigma	3	0.3	–	–	–	–	–	–	–	–
Hantzchia	8	0.9	6	0.9	–	–	–	–	–	–
Navicula	52	5.6	45	7.2	65	5.0	13	1.9	4	0.8
Neidium	13	1.4	3	0.5	3	0.3	–	–	–	–
Nitzschia	27	2.9	25	3.9	–	–	–	–	–	–
Pinnularia	52	5.6	45	7.2	65	5.0	13	1.9	4	0.8
Rhopalodia	3	0.3	–	–	–	–	–	–	–	–
Stauroneis	27	2.8	16	2.5	7	0.5	–	–	–	–
Surirella	46	5.0	31	4.9	82	6.3	30	4.5	15	2.9
Synedra	9	1.0	7	1.1	–	–	–	–	–	–
Thalassiosira	13	1.4	1	0.2	–	–	–	–	–	–

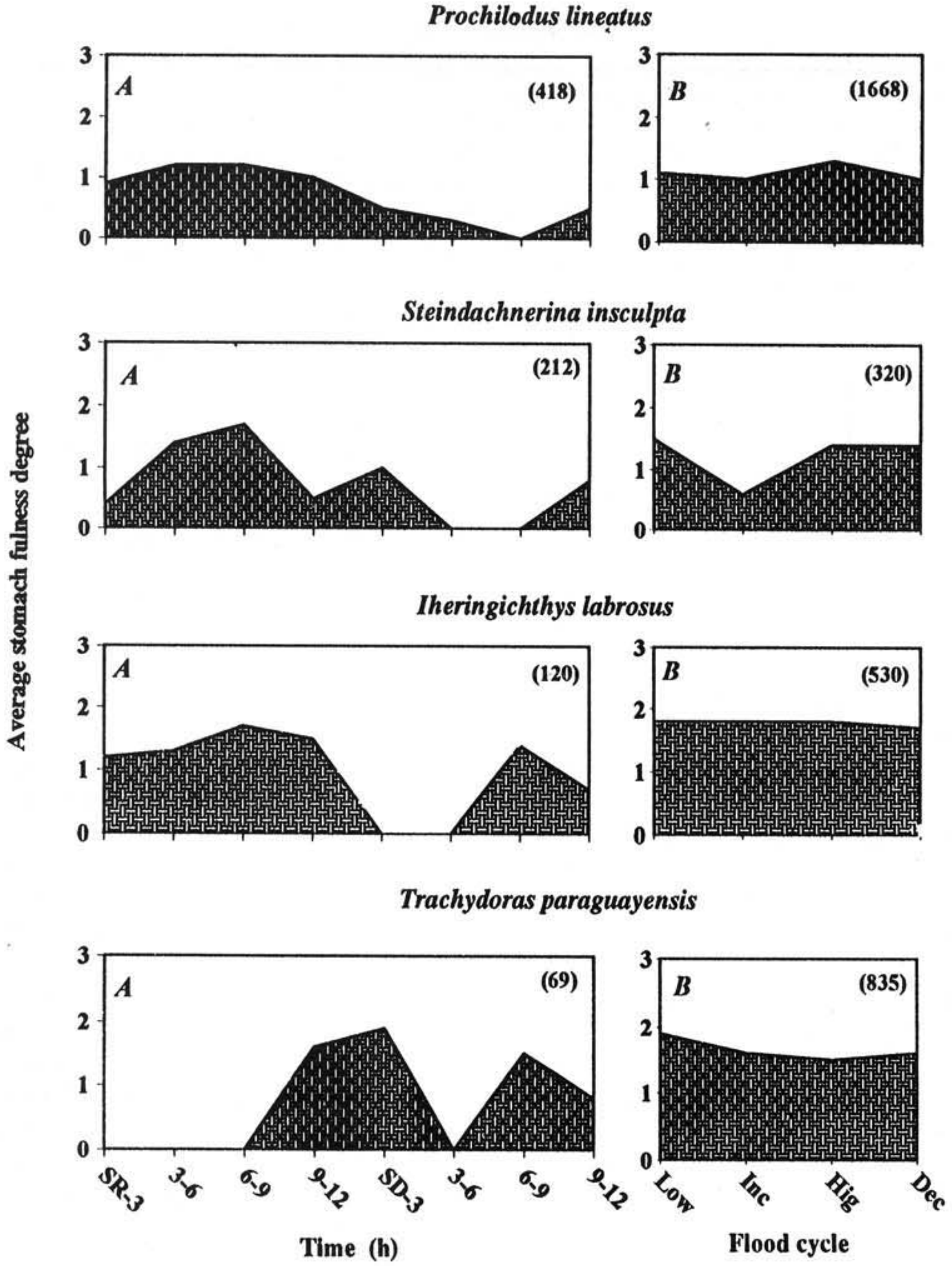

Fig. 3. Diel and seasonal variations in average stomach fullness index of bottom-feeding species of the Paraná River floodplain (SR = sunrise, SS = sunset, Low = low water, Inc = increasing water level, Hig = high water, Dec = decreasing water level). () = samples size; A = diel variation, B = seasonal variation.

the intake of food was slightly higher in the high water period (Fig. 3b).

Steindachnerina insculpta: Gastric contents of individuals of this species (4.9 cm to 9.8 cm SL) revealed (as in *P. lineatus*) that diet consists of inorganic sediments, organic detritus, algae, Testacea and nematodes. Inorganic sediments made up 55.9% of the feeding index (Fig. 2). Baccilariophycea was the

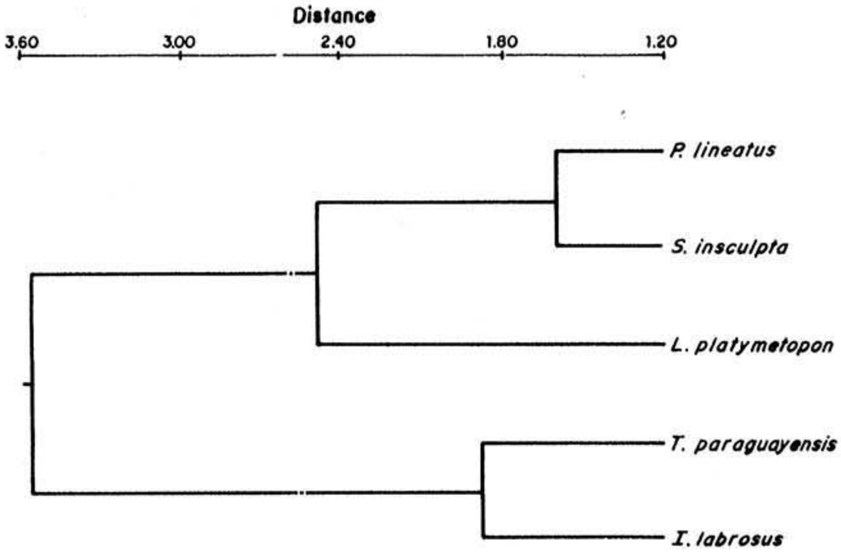

Fig. 4. Similarity between diets (occurrence methods) as measured by Euclidian distance.

predominant group among the algae. The genera *Aulacoseira, Navicula, Surirella, Pinnularia* and *Eunotia* were the most frequent (Table 1).

Although it was absent in the samples gathered between 3 and 9 hours after sunset, the species was a diurnal feeder with an activity peak between 6 and 9 hours after sunrise (Fig. 3a). Food intake was high throughout the year. The flooding increase period was an exception and even catches were low (Fig. 3b).

Loricariichthys platymetopon: The diet of this species (11.0 cm to 23.8 cm SL) is composed of organic detritus, inorganic sediments, chironomids, Testacea, microcrustaceans, nematodes, acari, molluscs and algae. Organic detritus was the most important item, representing 40% of the feeding index. Inorganic sediments and chironomids were common (Fig. 2).

Iheringichthys labrosus: In the stomachs of individuals of this species (7.0 cm to 20.4 cm SL) were chironomids, nematodes, microcrustaceans, ephemeropteras, molluscs, Testacea, acari, algae and inorganic sediments. Chironomids were the most important item representing 37.7% of the feeding index, followed by nematodes (15.9%), microcrustaceans (11.3%) and algae (11.3%). Sediments were also common (Fig. 2). The most representative microcrustaceans were ostracods and harpacticoids. Among the Testacea *Difflugia* was conspicuous (Table 1).

Feeding of this species occured during a prolonged period. It reaches its peak between 6 to 12 hours after sunrise. Between 6 and 9 hours after sunset the quantity of food in the stomach was still high. It should, however, be emphasized that no individual was caught from sunset until 6 hours later (Fig. 3a). The intensity of food intake was high during the whole period under analysis (Fig. 3b).

Trachydoras paraguayensis: The food of this species (4.1 cm to 9.4 cm SL) included microcrustaceans, Testacea, nematodes, chironomids, inorganic sediments, algae and acari. The principal items were microcrustaceans (26.3%), Testacea (22.5%), nematodes (18.7%) and sediments (13%) (Fig. 2). Among the Testacea, the most common was *Difflugia* (Table 1).

Analysis of daily variations in feeding activity was not possible due to the absence of this species in catches made during the day. However, feeding peak may be noted during dusk, between sunset and 3 hours later (Fig. 3a). This species fed more during the dry season (Fig. 3b).

Grouping analysis undertaken as to the similarity of gastric contents of species revealed three distinct groups: (1) *P. lineatus* and *S. insculpta*, (2) *L. platymetopon* and (3) *I. labrosus* and *T. paraguayensis* (Fig. 4). The coefficient of cophenetical correlation was 0.8, showing that there was no significant deviation from the original similarity matrix.

Discussion

In this study an analysis of stomach contents showed that the resources exploited by the abovementioned fishes were different, although all the species studied fed on substratum. *Prochilodus* and *Steindachnerina* (= *Curimata*) showed the greatest similarities in diet composition and have been the object of various studies in different places (for *Prochilodus*: Gneri & Angelescu 1951, Bowen 1983, Fugi & Hahn 1991, Almeida et al. 1993; for *Steindachnerina*: Nomura & Taveira 1979, Carvalho 1984, Sazima & Caramashi 1989, Fugi & Hahn 1991).

Inorganic sediments, detritus and algae in the gastric contents of *P. lineatus* and *S. insculpta*, recorded in this study, have been reported earlier. The high proportion of sediments and organic detritus in their diets shows the benthic feeding habit of the two species, while the presence of periphytical diatoms shows that periphyton is also important. However, though both species feed on periphyton, they may use different substrata. *P. lineatus* can exploit not only the periphyton which colonizes aquatic macrophytes (epiphyton) but also that which lies over the sediment (epipelon) while the mouth morphology of *S. insculpta* makes it difficult to feed on epiphyton.

The components of the complex mixture which constitute mud and which are actually digested and assimilated have not been identified. Although inorganic sediment is quantitatively the most important item for these species, its dietary value is questionable. However, these particles might work to break up the cellular walls of the algae (Payne 1978). Furthermore, the material adsorbed on sedimentary particles should be relevant in the diet (Odum 1968).

The importance of algae in the feeding of fish is questionable. Many fish digest only some groups of algae, chiefly Diatomaceae, since these have apertures in their walls and allow the entrance of gastric juice (Prowse 1964). The use of this food source in various species of fish is associated with the presence of cellulasic activity (Stichney & Shumway 1974; Prejs & Blaszczyk 1977).

Among the components of the diet of these species, detritus has been widely discussed and, among the most problematic questions, is its nutritional value. Bowen (1987) showed that different approaches have been used to describe it, the most important being the density of microorganisms, energetic content and aminoacids concentration. Even though it includes animal food, the diet of *L. platymetopon* was mostly organic detritus. This result was not recorded by Py-Daniel (1984) in the Amazon region. On the other hand, detritus figures as an important item for other representatives of Loricariidae (Angelescu & Gneri 1949, Saul 1975). The detritus consumed by this species is different from that taken by *P. lineatus* and *S. insculpta* with regard to the size of the particles. Detritus ingested by *L. platymetopon* is an agglomerate of big particles. Its ventral mouth with wide, thin movable lips (Fugi & Hahn 1991) presupposes feeding by suction, aspirating the loose detritus which has been recently deposited on the sediment. Such behaviour has been observed directly in this species (Winemiller personal cummunication).

Although *I. labrosus* and *T. paraguayensis* take food from the bottom, they utilize selective styles and essentially consume benthic invertebrates. Although the food spectrum of both species is similar, *T. paraguayensis* preferentially fed on microcrustaceans and Testacea, while *I. labrosus* fed on larvae of chironomids. Further differences in size of swallowed organisms suggest that there is trophic segregation between these species.

Taking as a basis diet similarity, three trophic groups were found: (1) ileophagous: *P. lineatus* and *S. insculpta*, (2) detritivorous: *L. platymetopon* and (3) benthophagous: *I. labrosus* and *T. paraguayensis*. The terminology used to catalogue the food habit of these species has not been consistent. The same species is variously called ileophagous, phytophagous, detritivorous or benthophagous by different authors. Differences in nomenclature for species which have similar diets may also originate from differences in food supply in distinct environments. However, it has been verified that detritus, sediments and algae are the predominant food items of *P. lineatus, S. insculpta* and other species of the same genera, independently of the places where they were collected. A criterion which may be useful in the classification of the feeding habits of this group is the predominance of detritus and minute sediment particles. Angelescu & Gneri (1949) describe ileophagy as the habit of eating mud which consists of organic detritus and associated organisms. To exploit these resources the species have a special digestive apparatus, which distinguish them from other detritivores. These species should be classified as ileophagous and not detritivorous.

L. platymetopon and other Loricariidae have been classified as omnivorus (Angelescu & Gneri 1949, Py-Daniel 1984) or herbivorous (Hamilton et al. 1992). However, in our analysis, detritus was the principal dietary component. Welcomme (1985) states that deposits on the river bed constitute two distinct sources of food: detritus comprised of decomposing vegetation, associated with microorganisms and animal communities, and mud composed of the transformation of large particles into minute ones.

I. labrosus and *T. paraguayensis* which consumed a third food source by selecting benthic organisms, were called benthophagous.

P. lineatus and *S. insculpta* were diurnal feeders. These results are in conflict with the hypothesis that species that eat detritus or mud take food continuously, which is supposedly justified by the low nutritional values of these food sources. Diurnal feeding activity was also described by Mochek et al. (1991) for *Prochilodus nigricans*.

The daily feeding rhythm was not uniform for benthophagic species. Differences in diel feeding may have reflected a reduction in searching for food, because gillnet samples were passive. *I. labrosus* fed chiefly during the day and *T. paraguayensis* at dusk.

The literature reports a tendency for greater feeding activity during the day by fishes which eat benthic invertebrates (Cordes & Page 1980, Scrimgeour & Winterbourn 1987, Sagar & Glova 1988, Walsh et al. 1988). In our study species the presence of relatively large eyes suggest visual orientation in searching for food. *T. paraguayensis*, however, feeds predominantly in the evening. This fact may be related to the activity of its predators and is consequently a reflection of predatory pressures.

The most intense feeding activity of *P. lineatus* during high water must be related to food abundance. The flooding of extensive areas with large amounts of organic matter and an increase in the substratum area, would contribute to the production of organic detritus and periphyton. Furthermore, during high water less energy and time would be required to avoid predators. This must produce more feeding activity since an increase in shelter and a reduction in the relative density of piscivores occur during this period. Although *S. insculpta* has the same feeding habits, its pattern of feeding activity was different from that of *P. lineatus*. With the exception of the flooding increase period, when the sample size was small, feeding activity was more or less continuous during the year. Thus it seems this species would probably not use the periphyton which colonizes vertical substrata, which would be more abundant in high water, as does *P. lineatus*. The continous feeding by *I. labrosus* is probably related to the availability of chironomids, its principal food. On the other hand, *T. paraguayensis* feeds intensely during the dry season. This may be related to alterations in the availability of the benthic microcrustaceans that are predominant under low water conditions (Takeda et al. 1991).

Conclusion

Although they all feed from the superficial layers of the substratum, these species form three trophic groups which exploit distinct fractions of the substratum. *Prochilodus lineatus* and *Steindachnerina insculpta* consume particularly minute particles of matter composed of the inorganic sediment, fine detritus and diatoms. They should be considered ileophagous. *Loricariichthys platymetopon*, on the other hand, feeds on organic detritus in earlier stages of decomposition. In this case, inorganic particles are less important in the diet. Thus, it may be classified as detritivorous. Lastly, *Iheringichthys la-*

brosus and *Trachydoras paraguayensis* which essentially feed on meso- and macrozoobenthic elements together with a small proportion of inorganic matter, should be classified as benthophagous.

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References cited

Almeida, V.L.L., E. Kawakami-Resende, M.S. Lima & C.J.A. Ferreira. 1993. Dieta e atividade alimentar de *Prochilodus lineatus* (Characiformes, Prochilodontidae) no Pantanal do Miranda-Aquidauana, Mato Grosso do Sul, Brasil. Revista Unimar 14: 125–139.

Angelescu, V. & F.S. Gneri. 1949. Adaptaciones del aparato degestivo al regimen alimentício en algunos peces del rio Uruguay y del rio de La Plata. Revista del Instituto Nacional de Investigacion de las Ciências Naturales 1: 161–281.

Bourrelly, P. 1972. Les algues d'eau douce: initiation a la systématique. vol. 1. Édition N. Boubée & Cie, Paris. 572 pp.

Bourrelly, P. 1981. Les algues d'eau douce: initiation a la systématique. vol. 2. Sociéte Nouvelle Des Éditions Boubée, Paris. 517 pp.

Bourrelly, P. 1985. Les algues d'eau douce: initiation a la systématique. vol. 3. Sociéte Nouvelle Des Éditions Boubée, Paris. 606 pp.

Bowen, S.H. 1983. Detritivory in neotropical fish communities. Env. Biol. Fish. 9: 137–144.

Bowen, S.H. 1987. Composition and nutritional value of detritus. pp. 192–216. *In:* D.J.W. Moriart & N.R.S.V. Pullin (ed.) Detritus and Microbial Ecology in Aquaculture, ICLARM Conference Proceedings, Manila.

Carvalho, F.M. 1984. Aspectos biológicos e ecofisiológicos de *Curimata* (*Potamorhina*) *pristigaster*, um Characoidei neotropico. Amazoniana 8: 525–539.

Cordes, L.E. & L.M. Page. 1980. Feeding chronology and diet composition of two darters (Percidae) in the Iroquois River Sistem, Illinois. Amer. Midl. Nat. 104: 202–206.

Edmondson, W.T. 1959. Fresh-water biology. 2 ed. John Wiley & Sons, New York. 1248 pp.

Fugi, R. & N.S. Hahn. 1991. Espectro alimentar e relações morfológicas com o aparelho digestivo de três espécies de peixes comedoras de fundo do rio Paraná, Brasil. Rev. Brasil. Biol. 51: 873–879.

Gneri, F.S. & V. Angelescu. 1951. La nutricion de los peixes iliofagos. Revista del Instituto Nacional de Investigacion de las Ciencias Naturales 2: 1–44.

Hamilton, S.K., W.M. Lewis & S.J. Sippel. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia 89: 324–330.

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. J. Anim. Ecol. 19: 36–56.

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

Kawakami, E. & G. Vazzoler. 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. Bolm. Inst. Oceanogr., São Paulo 29: 205–207.

Mochek, A.D., A.I. Pyanov & S.I. Saranchov. 1991. Results of telemetric tracking of *Prochilodus nigricans* in a Forest Reservoir (Peru, Ucayali, Department). J. Ichthyology 31: 115–119.

Nomura, H. & A.C. D. Taveira. 1979. Biologia do saguirú, *Curimatus elegans* STEINDACHNER 1874, do rio Mogi Guaçu São Paulo (Osteichthyes, Curimatidae). Rev. Brasil. de Biol. 39: 331–339.

Odum, H.E. 1968. The ecological significance of fine particle selection by the striped mullet *Mugil cephalus*. Limnol. Oceogr. 13: 92–97.

Payne, A.I. 1978. Gut pH and digestive strategies in estuarine grey mullet (Mugilidae) and tilapia (Cichlidae). J. Fish Biol. 13: 627–630.

Prejs, A. & M. Blaszcyk. 1977. Relationship between food and cellulase activity in freshwater fishes. J. Fish Biol. 11: 447–452.

Prowse, G.A. 1964. Some limnological problems in tropical fish ponds. Verh. Intern. Verein. Limnol. 15: 480–484.

Py-Daniel, L.H.R. 1984. Sistemática dos Loricariidae (Ostariophysi, Siluroidei) do Complexo de lagos do Janaucá, Amazonas, e aspectos de sua biologia e ecologia. Master Thesis, Universidade de Amazonas, Manaus. 278 pp.

Rohlf, F.J. 1989. NTSYS: Numerical taxonomy and multivariate analysis system. Department of Ecology and Evolution, State of New York, Stony Brook. 190 pp.

Sagar, P.M. & G.J. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). J. Fish Biol. 33: 643–653.

Santos, E.P. dos. 1978. Dinâmica de população aplicada a pesca e piscicultura. Universidade de São Paulo, São Paulo. 129 pp.

Saul, W.G. 1975. An ecological study of fishes at a site in upper Amazonian Ecuador. Proc. Acad. Nat. Sci. hil. 12: 93–134.

Sazima, I. & E.P. Caramaschi. 1989. Comportamento alimentar de duas espécies de *Curimata*, sintópicas do Pantanal do Mato Grosso (Osteichthyes, Characiformes). Rev. Brasil. Biol. 49: 325–333.

Scrimgeour, G.J. & M.J. Winterbourn. 1987. Diet, food resource partitioning and feeding periodicity of two riffle-dwelling fish species in a New Zealand river. J. Fish Biol. 31: 309–324.

Stichney, R.R. & S.E. Shumway. 1974. Occurrence of cellulase activity in the stomachs of fishes. J. Fish Biol. 6: 719–790.

Takeda, A.M., G.Y. Shimizu, G.M. Shulz & A.C.M. Silva. 1991. Zoobentos de quatro lagoas de várzea do alto rio Paraná (MS-