Journal of Tropical Ecology (1998) 14:851–864. With 1 figure

Importance of aquatic invertebrates in the diet of rapids-dwelling fish in the Sinnamary River, French Guiana

VÉRONIQUE HOREAU*, PHILIPPE CERDAN*, ANTOINE CHAMPEAU† *and* SANDRINE RICHARD*

** Laboratoire Environnement HYDRECO de Petit Saut B.P. 823, 97388 Kourou Cedex, French Guiana (hydreco-labops@wanadoo.fr)*
† Laboratoire d'Hydrobiologie, Université de Provence, 13331 Marseille Cedex 3, France
(Accepted 3 July 1998)

ABSTRACT. The stomach contents of 683 fishes representing 39 species were examined to determine the diet of fish living in fast-flowing waters (rapids) of the Sinnamary River in French Guiana. Aquatic invertebrates were shown to be an important source of food in the rapids biotopes, in contrast to what has previously been observed for slow-flowing waters. Aquatic insects (e.g., the larval stages of Diptera, Ephemeroptera and Trichoptera) make up 55% of the diet of fish living in rapids. Such prey animals were more common in those biotopes than in slow-flowing waters. Twenty-two species of fish, each represented by at least 10 individuals in all samples, were analyzed for their stomach contents. The spectrum of prey items allowed for an estimation of the similarity of feeding habits. These diets were further compared to those inferred for other rivers of the Amazonian and Guianian regions.

KEY WORDS: diet, fish, rapids, Sinnamary River, French Guiana

INTRODUCTION

The diets of riverine fishes living in Neotropical rainforest lowlands have been well studied (Annibal 1982; Carvalho 1980, 1984; Carvalho *et al.* 1978, Ferreira 1984, Goulding 1980, Goulding & Carvalho 1982; Honda 1972, 1974, Knöppel 1970, 1972; Lowe-McConnell 1987, Marlier 1968, Menezes 1961, Santos 1981, Zaret & Rand 1971). The diets were characterized by the importance of the gallery forest as a source of food for numerous fish species in the Amazonian environment (Almeida 1980, Horeau *et al.* 1996, Knöppel 1970, 1972, Santos 1982, Saul 1975, Soares 1979). Most authors analyzed the stomach contents of fishes inhabiting slow-flowing waters, lakes and ponds in various parts of the Amazonian region. Fish communities have also been studied on the Sinnamary

River in French Guiana where a hydroelectric dam was recently established (Boujard & Rojas-Beltran 1988a, b; Tito de Morais *et al*. 1995). In this river, a recent analysis by Horeau *et al*. (1996) indicated that 47% of the fish diet from slow-flowing waters consisted of terrestrial invertebrates.

Most rivers of the Guianian region show a succession of slow-flowing waters and small rapids. This is the case for the Sinnamary River, with several rapids characterized by granitic blocks emerging above the water's surface. These blocks are commonly colonized by aquatic plants, mainly of the genus *Podostemacea* (Hoff 1995). The vegetation, which flowers during the dry season, provides habitats for an abundant community of aquatic invertebrates (Horeau 1996, Tavares *et al*. 1995).

To the best of our knowledge, there are no studies available on the feeding habits of tropical fishes living in rapids, a community of aquatic vertebrates which might have a special diet with respect to their habitat. This study considered the diet of the various fish species inhabiting rapids. Rapids account for 2% of the length of the Sinnamary channel.

Data on the systematics and ecology of the aquatic invertebrates are beyond the scope of this paper. Here the focus is on their utilization as prey items by fish. As our initial aim was to understand the overall food chain of the fish community, the stomach contents of individuals of very different sizes were analyzed, although it was recognized that some species might shift from one diet to another during their life cycles. In this way, biological data were expected to provide a better description of the general diet of the various species of fish living in rapids.

MATERIALS AND METHODS

Ten different sites in fast-flowing waters were sampled along the Sinnamary River (4°–5°N; 52°50′W) during October and November 1992 (Figure 1). These sites (called 'saut' in French) were characterized by varying densities of *Podostemacea* aquatic plants living among the granitic blocks. However, one locality (site 1, Maïpouri; Figure 1) was devoid of such vegetation. During this scientific expedition, the following environmental variables were measured at all stations: temperature and pH with a meter (Wissenschaftlich-Technische Werkstatten PH 196); conductivity with a conductimeter, WTW LF 196; turbidity with a Hach turbidimeter; transparency with a secchi-disk; dissolved oxygen with a WTW OXY 196 meter; suspended matter through filtration on Whatman GF/C; suspended organic matter and chemical oxygen demand by chromic oxidation; total iron with a UNICAM spectrophotometer; and hardness by titrimetry.

Due to low conductivities it was not possible to employ electro-fishing. Fish were caught by pouring rotenone into the watercourse, allowing for the rapid capture of animals with stomachs full of slightly digested food. One sample was taken per station. The fish were measured, weighed, preserved in 10%

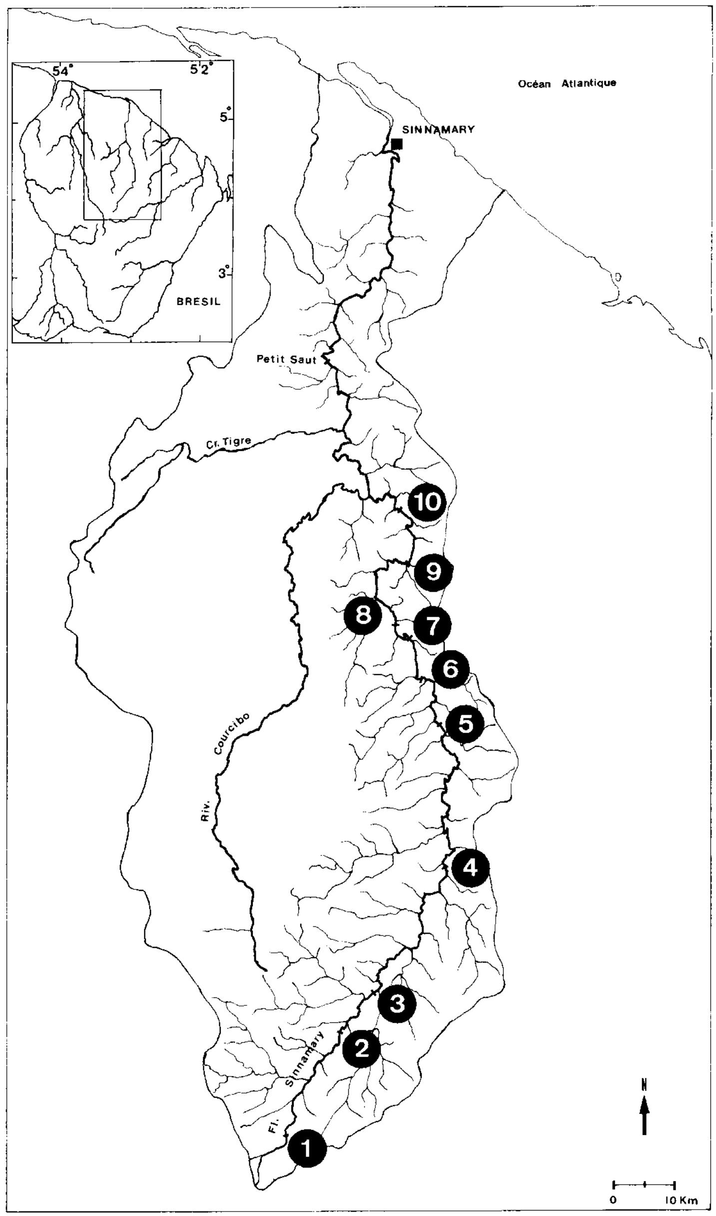

Figure 1. Rapids sampled along the Sinnamary River, French Guiana. 1: Maïpouri, 2: Gérard, 3: Parasol, 4: Deux Roros, 5: Dalles, 6: Takari-Tanté, 7: Aïmara, 8: l'Autel, 9: Patawa, 10: Vata.

formaldehyde, and identified by the ORSTOM ichthyological team at Cayenne (L. Lauzanne & L. Tito de Morais).

The stomach contents of the individuals sampled were identified under a stereomicroscope by comparing them with reference collections of local invertebrates.

In order to have a good notion of diet preferences and to compare these with other observations, the results were analyzed using the occurrence method (Hynes 1950). For each fish species, the proportion of food of aquatic, terrestrial or miscellaneous origin was calculated by summing up the frequencies of the different categories of prey they contained. Items of aquatic or endogenous origin such as all organisms living in water, as well as other elements *in situ* (mud and sand) were considered. Items of terrestrial or exogenous origin came from the forest bordering the river which had fallen into the water. Finally, the miscellaneous category included plant and chitinous remains which could not be clearly identified. Nevertheless, the plant matter was mostly composed of fragments of *Podostemacea*, an aquatic species. Similarly, it was presumed that the major part of the chitinous remains came from the aquatic environment because these non-identifiable items were mostly found in stomachs containing only aquatic invertebrates as other prey items. Consequently, it was estimated that three quarters of these miscellaneous items belonged to the aquatic environment. In the absence of reliable and quantifiable results for this miscellaneous category, they are represented separately in the results.

To group the various fish species according to their feeding preferences, Spearman's rank correlation coefficient was calculated for the 22 different taxa represented by ≥ 10 specimens in all samples. These coefficients were determined by considering 14 different categories of prey (Diptera, Ephemeroptera, Trichoptera, other aquatic insects, other aquatic invertebrates, Hymenoptera, Coleoptera, other terrestrial invertebrates, fishes, plants, sand, chitinous remains, mud and eggs). In this way, the similarity of the diets of different species of fish could be determined (Horeau *et al*. 1996, Fritz 1974, Lauzanne 1976). Then we used the coefficients in order to classify the fish species thanks to clusters obtained with the hierarchical agglomeration method calculated using average linkage (Legendre & Legendre 1984).

RESULTS

The Sinnamary River water is warm, acid, turbid and with a high dissolved oxygen content. Suspended matter is in low concentrations and mostly of organic origin (Table 1). Iron is present, and the water is soft (Richard 1996). Like on the Approuague River (Boujard *et al.* 1997), the equatorial climate includes four seasons: a long dry season (July–December), a short rainy season (January–March), a short dry season 'the short March summer' and a long rainy season (April–July). Also, the water level was low during this study (October–November 1992). The Sinnamary River has a succession of slow-flowing waters (0.2–0.25 m s^{-1}) and small rapids (0.5–1 m s^{-1}) (J. P. Mobèche, *pers. comm.*) where the fish studied were captured.

The size, weight, and number of fishes caught at the 10 sampling sites are

Table 1. Physico-chemical parameters in the rapids of the Sinnamary River, French Guiana.

Parameters	n	Mean ± SD	Minimum	Maximum
Temperature (°C)	29	26.50 ± 1.45	23.8	28.6
pH (pH units)	27	6.23 ± 0.33	5.4	6.7
Conductivity (μS cm^{-1})	29	26.28 ± 1.83	23.4	30.7
Turbidity (NTU)	27	12.26 ± 17.52	5	92
Transparency Secchi (m)	7	1.55 ± 0.53	0.40	2.00
Dissolved oxygen (mgO_2 l^{-1})	27	7.06 ± 0.44	6.3	8
Dissolved oxygen (%)	27	86.22 ± 5.09	78	97
Chemical oxygen demand (mgO_2 l^{-1})	13	25.98 ± 18.43	8.33	77.45
Suspended matter (mg l^{-1})	13	5.92 ± 3.75	3.2	16.4
Organic suspended matter (μC l^{-1})	11	639.03 ± 394.09	115.38	1471.15
Total iron (mg l^{-1})	12	0.68 ± 0.20	0.52	1.23
Hardness (°F)	10	0.52 ± 0.08	0.4	0.65

given in Table 2. Collecting success varied from 23 (Saut Patawa) to 117 (Saut Aïmara) fish per site, yielding 683 individuals representing at least 39 species. Characid fishes (Cypriniformes) were the most diverse taxon with 14 species. Five species were represented by only one specimen: the stomach of an *Acestrorhynchus falcatus* was full of fish; a *Leporinus despaxi* had consumed the aquatic larvae of Diptera and Ephemeroptera and plant matter; an *Imparfinis minutus* and a *Satanoperca aff. leucosticta* had consumed aquatic insects (Diptera and Heteroptera); and the stomach of a *Pseudopristella simulata* was full of mud.

The frequency of the 14 most common prey items found in the analyzed stomach contents are given for each species of fish (Table 3). Aquatic elements predominated in 70% of all the fish examined (Figure 2).

Hypostomus plecostomus consumed only items of aquatic origin. Others, such as *Lithoxus planquetti*, *Pimellodela gracilis*, *Cyphocharax helleri*, *Leporinus friderici*, *Parupygus savannensis*, *Characidium fasciatum*, *Hemiodopsis quadrimaculatus*, *Melanocharacidium blennioides*, *Characidium aff. fasciadorsale* and *Corydoras octocirrus* consumed aquatic and miscellaneous items. Even though none of the diets of the fish living in rapids consisted exclusively of terrestrial items, many individuals consumed those of aquatic and terrestrial origin. This was the case for *Poptella orbicularis*, *Moenkhausia oligolepis*, *Astyanax polylepis*, *Astyanax bimaculatus*, *Bryconops* sp.3, *Knodus aff. moenkhausia*, *Bryconops* sp.2, *Bryconops* sp., *Bryconops caudomaculatus*, *Parodon guianensis*, *Crenicichla saxatilis* and *Hoplias aimara*.

When considering the entire community of fish living in rapids, it appears (Table 3) that their diet is highly diverse, with a predominance of aquatic invertebrates which are abundant in this biotope (Horeau 1996, Tavares *et al*. 1995).

Fishes from rapids consumed mainly aquatic items. Minerals (or sand) (2%) of no nutritional value were ingested by certain species, and mud (5%) by some fish species. However, aquatic invertebrates made up the largest part of the diet (56%). These consisted mainly of aquatic insects: Diptera (20%), Ephemeroptera (15%), Trichoptera (10%), Coleoptera (2.5%), Lepidoptera

Table 2. Size, weight and number of fishes caught and analysed from 10 rapids of the Sinnamary River.

Species	n	Standard length (mm) min.-max.	Weight (g) min.-max.
Order Cypriniformes			
Anastomidae			
Leporinus friderici (Bloch, 1794)	6	33–49	0.58–1.91
Leporinus granti Eigenmann, 1912	24	36–137	0.92–55.4
Cherodontinae			
Phenacogaster megalostictus Eigenmann, 1909	17	20–43	0.10–0.75
Stechaprioninae			
Poptella orbicularis (Valenciennes in C. et V., 1849)	5	43–72	1.63–8.55
Tetragonopterinae			
Astyanax bimaculatus (Linnaeus, 1758)	33	24–120	0.38–13.70
Astyanax polylepis (Günther, 1864)	12	26–68	0.38–7.35
Astyanax sp.	5	27–39	0.30–0.88
Bryconops caudomuculatus (Günther, 1869)	10	24–56	0.21–2.43
Bryconops sp.	64	12–55	0.02–2.58
Bryconops sp. 2	20	23–64	0.21–3.42
Bryconops sp. 3	10	23–43	0.14–1.07
Deuterodon sp.	49	30–82	0.45–11.75
Knodus aff. moenkhausia	18	23–43	0.16–1.38
Moenkhausia oligolepis (Günther, 1864)	7	24–74	0.37–11.98
Characidiidae			
Characidium aff. fasciadorsale	10	33–49	0.34–1.23
Characidium fasciadorsale Fowler, 1914	6	63–70	2.67–3.70
Characidium fasciatum Reinhardt, 1866	30	32–60	0.22–2.47
Melunocharacidium blennoides (Eigenmann, 1909)	67	29–63	0.20–4.06
Curimatidae			
Cyphocharax helleri (Steindachner, 1910)	29	28–85	0.39–12.00
Erythronididae			
Hoplias aimara (Valenciennes, 1846)	6	68–165	3.84–47.70
Hemiodidae			
Hemiodopsis quadrimaculatus (Pellegrin, 1908)	8	36–73	0.67–3.74
Parodon guianensis Géry, 1959	34	27–90	0.18–9.91
Hypopomidae			
Parupygus savannensis Hoedeman, 1962	3	50–310	0.18–24.79
Order Siluriformes			
Callichthyidae			
Corydoras octocirrus Nijssen, 1970	11	28–60	0.64–5.50
Loricaridae			
Harttia surinamensis Boeseman, 1971	23	42–92	0.42–4.87
Hypostomus plecostomus (Linnaeus, 1758)	3	94–134	11.90–47.70
Lasiancistrus niger (Norman, 1926)	47	27–103	0.35–60.24
Lithoxus planquetti Boeseman, 1982	5	34–64	0.74–5.00
Pimellodidae			
Heptapterus longior (Eigenmann, 1912)	35	35–106	0.24–6.27
Heptapterus tapanahoniensis Mees, 1974	29	40–138	0.34–26.5
Pimelodella cristata (Müller et Troschel, 1848)	3	66–98	2.94–9.73
Pimelodella gracilis (Valenciennes in C. el V., 1840)	8	60–143	1.51–29.88
Order Perciformes			
Cichlidae			
Aequiderns aff. guianensis	18	17–105	0.14–43.16
Crenicichla saxatilis (Linnaeus, 1758)	23	28–142	0.30–43.70
Total	678		

Five species were analysed by only one specimen [standard length/weight]:
Leporinus despaxi Puyo, 1960 [100 / 15.6]
Acestrorhynchus falcatus (Bloch, 1794) [130 /16.6]
Pseudopristella simulata Géry, 1960 [51 / 2.94]
Imparfmis minutus (Lütken, 1874) [72 / 2.98]
Satanoperca aff. leucosticta [36 / 0.94]

Table 3. The relative occurrence of various items in the stomach of 34 species of fishes caught in rapid-flowing waters of ten localities along the Sinnamary River.

Taxonomy / Food	Aquatic																Terrestrial						Miscellaneous	
	Diptera	Ephemeroptera	Trichoptera	Coleoptera	Plecoptera	Lepidoptera	Odonata	Heteroptera	Others invertebrates	Decapoda	Hydracarina	Snails	Fishes	Sand	Mud	Eggs	Coleoptera	Diptera	Hymenoptera	Lepidoptera	Arachnidae	Others invertebrates	Plant matter	Chitinous remains
Leporinus friderici	21.4	7.1	3.6	–	–	3.6	–	–	–	–	14.3	–	–	7.1	14.3	–	–	–	–	–	–	–	21.4	7.1
Leporinus granti	23	15	13	2	–	4	3	–	2	–	5	1	–	3	2	1	1	–	–	–	–	2	6	17
Phenacogaster megalostictus	23.9	8.7	12	2.2	–	2.2	–	–	3.3	–	1.1	–	–	1.1	–	–	–	–	1.1	–	1.1	–	29.3	14.1
Poptella orbicularis	12.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37.5	–	–	–	50	–
Astyanax bimaculatus	10.4	11.7	1.3	5.2	–	–	1.3	–	2.6	–	1.3	–	–	2.6	1.3	–	2.6	–	9.1	–	–	2.6	36.4	11.7
Astyanax polylepis	7.1	3.6	–	7.1	–	–	3.6	3.6	–	–	–	3.6	–	–	3.6	–	–	–	14.3	–	3.6	3.6	21.4	25
Astyanax sp.	27.8	11.1	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.6	–	–	–	–	22.2	22.2
Bryconops caudomaculatus	14.3	8.6	8.6	8.6	–	–	5.7	5.7	2.9	–	–	–	–	–	–	–	–	–	5.7	–	–	–	14.3	25.7
Bryconops sp.	17.6	16	8.8	4.4	0.4	2.8	1.6	0.4	0.8	–	0.8	–	–	–	–	–	2.4	1.6	7.2	–	2	2.8	4.8	25.6
Bryconops sp. 2	15.4	3.8	3.8	7.7	–	1.9	1.9	–	1.9	–	–	–	–	–	1.9	–	–	1.9	11.5	–	–	5.8	5.8	36.5
Bryconops sp. 3	18.2	4.5	9.1	4.5	–	–	–	–	4.5	–	–	–	–	–	–	–	–	–	36.4	4.5	9.1	–	–	9.1
Deuterodon sp.	19.5	16.4	4.7	0.8	–	3.9	1.6	–	–	–	–	–	–	1.6	–	0.8	–	–	0.8	–	–	2.3	37.5	10.2
Knodus aff. moenkhausia	12.8	19.1	6.4	6.4	–	4.3	21	–	–	–	–	–	–	2.1	–	–	–	2.1	17	–	–	2.1	–	25.5
Moenkhausia oligolepis	5	10	–	–	–	–	–	10	–	–	–	–	–	–	–	–	5	–	30	–	–	5	10	25
Characidium aff. fasciadorsale	21.1	26.3	13.2	7.9	–	–	–	–	7.9	–	–	–	–	5.3	–	–	–	–	–	–	–	–	–	18.4
Characidium fasciadorsale	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100	–
Characidium fasciatum	26.2	22.4	11.2	2.1	0.9	8.4	1.9	1.9	–	–	1.9	–	–	–	–	–	–	–	–	–	–	–	–	22.4
Melanocharacidium blennioides	25.3	26.2	15.8	–	–	5	1.4	–	1.4	–	1.8	–	–	–	0.5	–	–	–	0.5	–	–	–	–	22.2
Cyphocharax helleri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	100	–	–	–	–	–	–	–	–	–
Hoplias aimara	8.3	8.3	8.3	–	–	–	–	–	16.7	16.7	–	–	16.7	–	–	–	–	–	8.3	–	–	–	8.3	8.3
Hemiodopsis quadrimatulatus	27.4	13.6	–	–	–	–	–	4.5	–	–	–	–	–	4.5	4.5	–	–	–	4.5	–	–	–	36.5	–
Parodon guianensis	25.9	12.1	12.1	–	–	3.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7	–	44.8	–
Parupygus savannensis	25	–	12.5	12.5	–	–	–	–	12.5	–	–	–	–	12.5	–	–	–	–	–	–	–	–	–	25
Corydoras ortociirrus	38.5	11.5	3.8	–	–	–	–	–	7.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	38.5
Harttia surinamensis	–	–	3.2	–	–	–	–	–	–	–	–	–	–	19.4	58.1	–	–	–	–	–	–	–	–	19.4
Hypostomus plecostomus	–	–	–	–	–	–	–	–	–	–	–	–	–	50	50	–	–	–	–	–	–	–	–	–
Lasiancistrus niger	17.6	1.5	1.5	–	–	–	–	–	1.5	–	–	–	–	11.8	55.9	1.5	–	1.5	–	–	2.9–		0.9	23.3
Lithoxus planquetti	16.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	83.3	–
Heptapterus longior	19	19.8	15.5	1.7	0.9	0.9	3.4	–	4.3	–	–	1.7	–	5.2	0.9	–	–	2.6	–	–	–	–	2.9	1.5
Heptaptetus tapanahoniensis	17.9	20.3	18.7	24	0.8	0.8	2.4	–	2.4	1.6	–	3.3	0.8	–	–	–	0.8	–	1.6	1.6	0.8	0.8	2.4	20.3
Pimelodella cristata	20	20	13.3	–	6.7	–	6.7	–	–	–	–	–	–	–	–	–	–	–	6.7	–	–	6.7	–	20
Pimelodella gracilis	14.3	14.3	7.1	–	–	7.1	–	–	–	7.21	–	–	–	–	–	–	–	–	–	–	–	–	28.6	21.4
Aequidens aff. guianensis	10.2	8.2	8.2	6.1	2	2	2	–	–	–	–	10.2	–	12.2	8.2	–	–	–	–	–	2	–	4.1	24.5
Crenicichla saxatilis	12.8	29.8	8.5	2.1	2.1	–	2.1	–	2.1	–	2.1	6.4	2.1	–	–	–	–	–	2.1	–	–	2.1	2.1	23.4

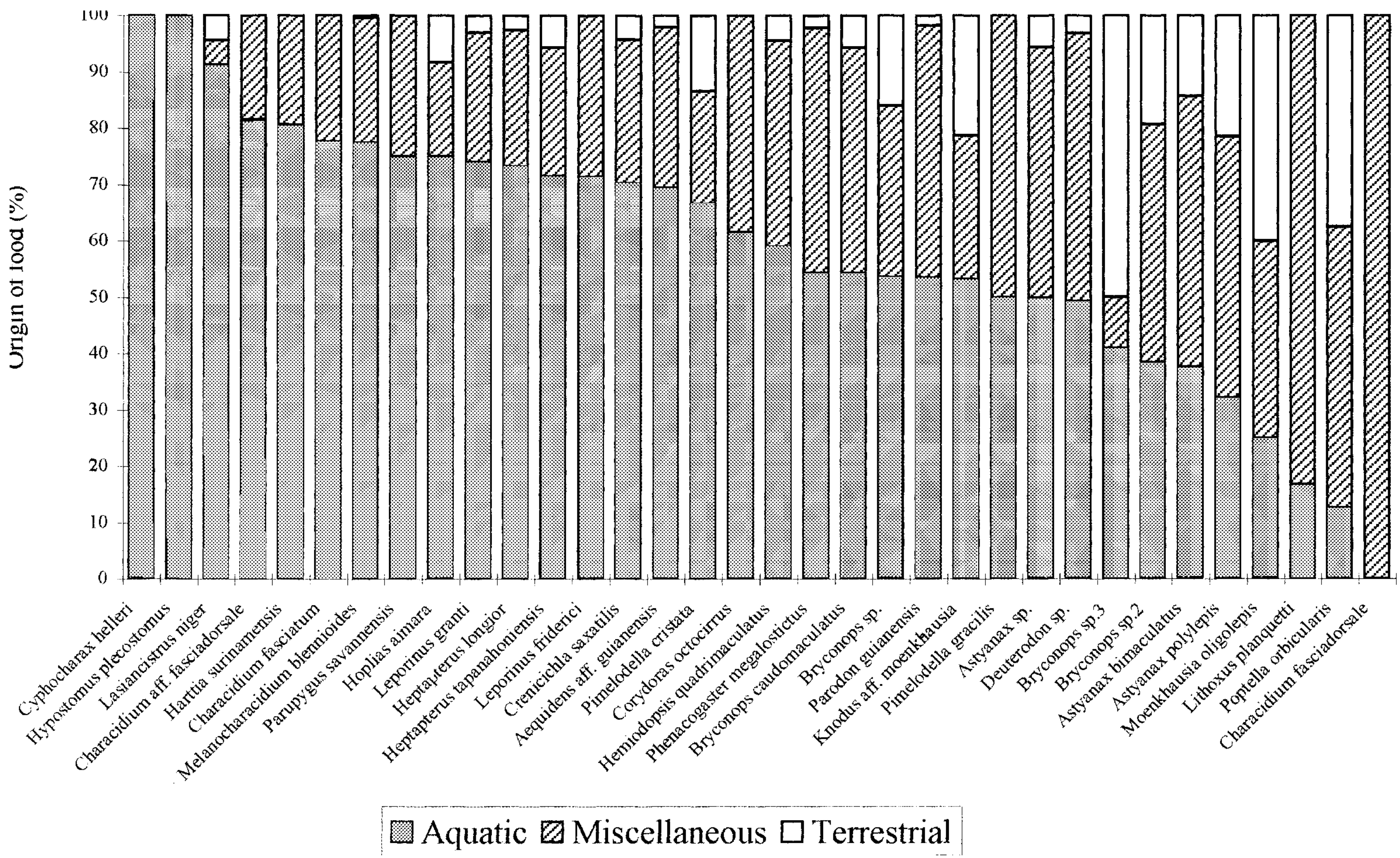

Figure 2. Food origin (aquatic – terrestrial – mixed items) for each species studied in the Sinnamary River, French Guiana.

(2.5%), Odonata (1.5%), and several other aquatic insects. Water mites (1%), Decapoda (0.3%) and molluscs (0.8%) were also found in some fishes. Terrestrial elements were relatively scarce (7%). They consisted mainly of Hymenoptera or ants (4%), the other elements being Coleoptera, Arachnida, Diptera, and other terrestrial invertebrates.

The dendrogram (Figure 3) classifies the fish species according to the similarity of their diets. In the Sinnamary River, the following categories can be distinguished. (i) Insectivores whose prey comes exclusively from the aquatic environment (*Characidium fasciatum* and *Characidium aff. fasciadorsale*). (ii) Insectivores whose prey comes mainly from the aquatic environment (*Melanocharacidium blennioides*, *Heptapterus longior*, *Leporinus granti*, *Corydoras octocirrus*, *Crenicichla saxatilis*, *Heptapterus tapanahoniensis* and *Aequidens guianensis*); the latter species differed slightly from the other fishes of its group in that it also consumed mud. (iii) Fish that consume plants and aquatic invertebrates (*Bryconops caudomaculatus*, *Phenacogaster megalostictus*, *Deuterodon* sp. and *Astyanax bimaculatus*). (iv) Insectivores for which the invertebrates consisted of numerous terrestrial elements (*Bryconops* sp., *Knodus aff. moenkhausia* and *Bryconops* sp.3). *Bryconops* sp.2 and *Astyanax polylepis* overlap two groups (iii and iv) because they consume aquatic and terrestrial invertebrates, as well as plants. *Parodon guianensis* also belongs to this case (iii + iv). It is somewhat different, however, because it consumed a considerable amount of plant matter (>45%) and chitinous remains were absent. (v) Detritivores were represented by *Harttia surinamensis, Cyphocharax helleri* and *Lasiancistrus niger*.

DISCUSSION

As indicated in Table 3, the fishes of the rapids show very dissimilar types of diets. Frequently, some species (for example, *Hoplias aimara*: see below) have different diets as they age. As juveniles, they mostly consume small aquatic invertebrates, whereas, as adults, they shift to a piscivorous diet. With or without food of terrestrial origin, insectivorous fish species are well represented in the rapids, as are omnivorous. The recognition of herbivorous species is difficult because their food intake, primarily plants, also includes small aquatic invertebrates. Lastly, we emphasize the presence of several mud-eating species. The family Loricariidae can consume algae (Power 1984). In this study, they feed on mud as do species of the family Curimatidae which has one detritivorous species (Planquette *et al.* 1996). The following discussion attempts to characterize the fishes caught in the Sinnamary rapids in relation to their dietary preferences, and to compare these data with those concerning the same taxa studied in other Amazonian or Guianian biotopes by various authors.

Among the carnivores, *Hoplias aimara* is known as the supreme predator of the Sinnamary River. We have found various parts of consumed fishes in almost all the stomachs of adult individuals of this species. Nevertheless, the young *Hoplias* individuals do not eat only fish. The six juveniles from four rapids

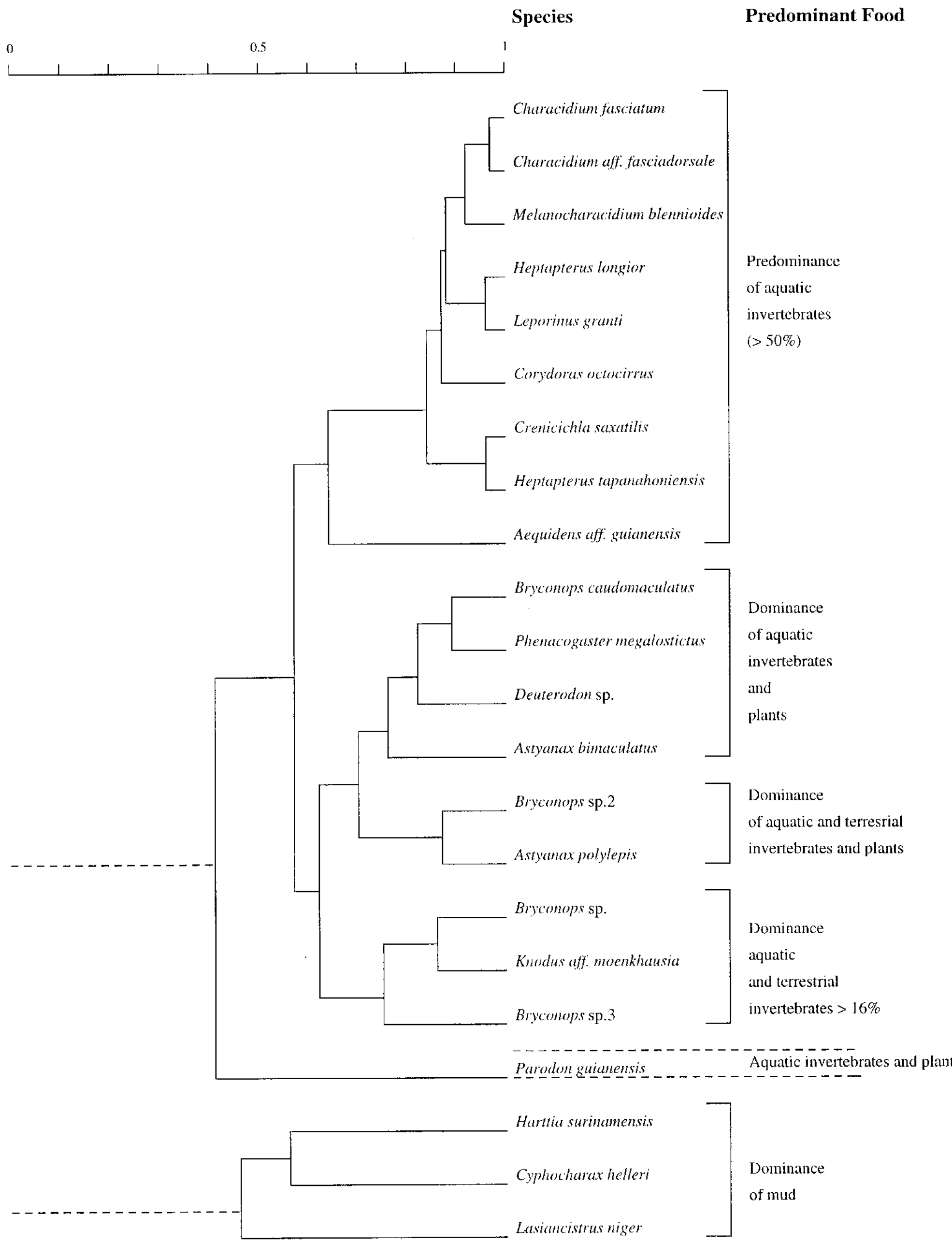

Figure 3. Spearman coefficient: correlation matrix dendogram for 22 fish species represented by at ≥ 10 specimens.

analyzed were relatively small (65 to 168 mm) and presented 75% of aquatic elements among which were Decapoda, other invertebrates, and some fish. Terrestrial elements as well as plant matter were also present. Thus, this species seems to be omnivorous early in its life before becoming exclusively piscivorous. *Hoplias aimara* also occasionally consumes crabs, iguanas or birds (P. Cerdan, *pers. obs*.). Published data on the diet in this genus mainly concerns *Hoplias malabaricus* (Bloch 1974) of which the young are also omnivores (Arcifa & Meschiatti 1993, Knöppel 1970, Saul 1975, Soares 1979).

Acestrorhynchus falcatus, locally named 'dent-chien', is known as being piscivorous in other biotopes such as in the Igarapé Barro (Knöppel 1970) or in the Curúa-Una Reservoir (Ferreira 1984) in Brazil. In our study, it also consumed only fishes. Finally, the small *Crenicichla saxatilis* (28 to 142 mm) caught in these rapids, fed mainly upon aquatic invertebrates (79%) and fishes. This confirms the observations of Soares (1979), who mentioned for this species only indigenous food consisting of aquatic insects and chitinous remains. Knöppel (1970) found plants (25%), chitinous remains (15%), fishes (15%), but mainly aquatic insects (45%) in the stomachs of the *C. saxatilis* caught in Lago Calado (Brazil). In this study and in all cases cited, the individuals analyzed were small in size (18–142 mm), and while the adults are piscivorous, the young are mainly insectivorous.

Among the fish that consume aquatic and/or terrestrial invertebrates, *Aequidens aff. guianensis* preys upon aquatic insects and molluscs. *Characidium fasciatum*, *C. aff. fasciadorsale*, *Melanocharacidium blennioides* as well as *Parupygus savannensis*, *Satanoperca aff. leucosticta*, *Phenacogaster megalostictus*, *Heptapterus tapanahoniensis* and *Corydoras octocirrus* apparently eat mainly aquatic invertebrates. A sample of the latter species analyzed by Marlier (1968) in Lake Redondo contained algae (diatoms, Desmidiacea and Oocystacea) as well as Cladocera.

In this study, most of the fish species were omnivorous which consumed mainly aquatic elements. These species included *Pimelodella gracilis* and *Leporinus despaxi*, which fed on the larvae of aquatic invertebrates (Diptera and Ephemeroptera) as well as on plants (33%). Three samples of *L. despaxi* analyzed by Knöppel (1972) from the slow-flowing sections of the Mana and Maroni rivers in French Guiana, had only plant remains in their stomachs. In the rapids, *L. friderici* consumed plants (21%) and aquatic invertebrates (50%) as well as mud (14%) and sand (7%). The diet of this fish was first studied in Brazil by Knöppel (1970), then by Santos (1982), and most recently by Boujard *et al*. (1988, 1990) in French Guiana where the results were very similar. This species has a rather opportunistic diet, tending towards fruits, but also including insect larvae (Ephemoptera and Diptera). *Hemiodopsis quadrimaculatus* is also an omnivore (larvae of aquatic Diptera, sand, mud and plants). Knöppel (1972) listed the presence of plants and chitinous remains in the stomachs of two of these fish caught in the Tumatumari and Potaro rivers in Guyana.

Other omnivores consuming more terrestrial elements were *Poptella orbicularis*, *Moenkhausia oligolepis*, *Bryconops* sp.3, *B.* sp.2, *B.* sp. (frequency in all rapids = 21.5%; L. Tito de Morais, *pers. comm.*), *B. caudomaculatus*, *Pimelodella cristata* and *Astyanax polylepis*. These species also prey upon aquatic invertebrates consisting of Coleoptera, Diptera, Ephemeroptera, Odonata, Heteroptera larvae, and molluscs, as well as plants. The stomach contents of some *Astyanax* have also been described. Arcifa & Meschiatti (1993) have suggested that *A. bimaculatus*, from Lake Monte Alegre near São Paulo, is an insectivore (aquatic and terrestrial). *A. fasciatus* (Cuvier 1819), in Lake Redondo consumed some crustaceans (Decapoda, Cladocera and Cyclopoda), but also some Coleoptera larvae (Marlier 1968). The latter taxon, studied in the Igarapé Porto (Aripuana, Brazil) ate insects and plants of which 60% were allochthonous items (for example, fallen from the tree canopy) (Soares 1979). The genus *Astyanax* is generally considered to be composed of insectivores eating mostly (up to 95%) endogenous elements (Soares 1979). *Astyanax bimaculatus*, of which this study included 33 individuals caught at four different sites, can be considered as an important element in the fish population of rapids (8.6% of all fishes caught in the rapids; L. Tito de Morais, *pers. comm.*). Its food consisted mainly of aquatic invertebrates (34.3%), plants (35.2%) and some terrestrial invertebrates such as ants and beetles. Some minerals and mud were also present.

Among the fishes considered as herbivorous, *Characidium fasciadorsale* does not eat only plants. *Lithoxus planquetti* consumed mainly plants but also small aquatic invertebrates (17% of Diptera larvae) living in the plants. *Parodon guianensis* consumed mainly plants (*c*. 60%). We must note that this fish is present at Saut Maïpouri (site 1 on Figure 1) where *Podostemacea* are not found. In this rapid, *Parodon* individuals eat aquatic invertebrates (Ephemeroptera, Diptera, Trichoptera and Lepidoptera larvae) whereas elsewhere this species is herbivorous.

Deuteron sp. (frequency among the fish population in the rapids = 13.8%; L. Tito de Morais, *pers. comm.*) and *Astyanax* sp. also consumed considerable amounts of plant matter, accompanied by some aquatic invertebrates.

Detritivorous species included *Pseudopristella simulata* and *Cyphocharax helleri* which were exclusively mud-eating. *Harttia surinamensis* and *Lasiancistrus niger* consumed mainly mud mixed with a few other elements. *Hypostomus plecostomus* is also a detritivore in the Sinnamary River, whereas it was considered omnivorous in Lake Monte Alegre, near São Paulo in Brazil (Arcifa & Meschiatti 1993).

Unlike several studies carried out in the Amazon region where the fish diet is derived for a large part from the forest, this study of the rapids-dwelling fishes emphasizes the importance of river-produced materials in their diet and the opportunistic, omnivorous diet of the majority. Indeed, many species of teleosts consume aquatic invertebrates (e.g., Diptera, Ephemoptera and Trichoptera larvae) which are particularly common in those biotopes of fast-flowing water (Horeau 1996). It would be of considerable interest to compare the diet of these same species in the lake formed behind the Petit Saut dam, a new biotope of more stagnant water having quite a different aquatic entomofauna.

ACKNOWLEDGEMENTS

We would like to thank all of the people who helped with the field work, specially L. Lauzanne and L. Tito de Morais (ORSTOM) for the identification of the fish, B. Brun and R. Chappaz (Université de Provence), F. Catzeflis, Y. Collos and A. Vaquer (CNRS), L. Tito de Morais (ORSTOM) and Andrea Dejean for their valuable suggestions. Financial support was provided by EDF-CNEH (Electricité de France, Centre National d'Equipement Hydrologique).

LITERATURE CITED

ALMEIDA, R. G. 1980. Aspectos taxonomicos e habitos alimentares de tres especies de *Triportheus* (Pisces:Characoidei, Characidae) do lago de Castanho, Amazonas, *Tese de Mestrado, INPA, Manaus,* AM, Brasil. 104 pp.

ANNIBAL, S. R. P. 1982. Avaliaçao bio-ecológica e pesqueira das 'pescadas' *Plagioscion squamosissimus* Heckel, 1840 e *Plagiscion montei* Soares, 1978 no 'sistema lago do Rei', Ilha do Careiro*, INPA, Manaus, AM, Brasil. Dissertaçao Mestrado, INPA/FUA*. 113 pp.

ARCIFA, M. S. & MESCHIATTI, A. J. 1993. Distribution and feeding ecology of fishes in a Brazilian reservoir: Lake Monte Alegre. *Interciencia* 18:302–313.

BOUJARD, T., LE BAIL, P. Y. & PLANQUETTE, P. 1988. Données biologiques sur quelques espèces continentales de Guyane française d'intérêt piscicole. *Aquatic Living Resource* 1:107–113.

BOUJARD, T., PASCAL, M., MEUNIER, J. F. & LE BAIL, P. Y. 1997. *Poissons de Guyane. Guide écologique de l'Approuague et de la réserve des Nouragues*. INRA, Paris. 219 pp.

BOUJARD, T. & ROJAS-BELTRAN, R. 1988a. Zonation longitudinale du peuplement ichtyque du fleuve Sinnamary (Guyane française). *Revue d'Hydrobiologie Tropicale* 21:47–61.

BOUJARD, T. & ROJAS-BELTRAN, R. 1988b. Description des captures au filet tramail sur le cours supérieur du Sinnamary (Guyane française). *Revue d'Hydrobiologie Tropicale* 21:349–356.

BOUJARD, T., SABATIER, D., ROJAS-BELTRAN, R., PRÉVOST, M. F. & RENNO, J. F. 1990. The food habits of three allochthonous feeding characoids in French Guiana. *Revue d'Ecologie (Terre et Vie)* 45:247–258.

CARVALHO, F. M. 1980. Alimentaçao do mapará (*Hypophthalmus edentatus* Spix, 1829) do lago do Castanho, Amazonas (Siluriformes, Hypophthalmidae). *Acta Amazonica* 10:545–555.

CARVALHO, F. M. 1984. Aspectos biológicos e ecofisiológicos de *Curimata (Potamorhina) pristigaster*, um Characoidei Neotropico. *Amazoniana* VIII:525–539.

CARVALHO, J. L. DE, CHAVES COELHO, A. & TODA, E. 1978. Hábito alimentar do mapará, *Hypophthalmus perporosus*, Cope, 1878 (Pisces Hypophthalmidae). *Boletim de la Faculdad de Ciencias Agrarias do Pará* 10:17–35.

FERREIRA, E. J. G. 1984. A ictiofauna da represa hidreléctrica de Curúa-Una, Santarém, Pará. II, Alimentação e Hábitos alimentares das principais espécies. *Amazoniana* 9:1–16.

FRITZ, E. S. 1974. Total diet comparison in fishes by Spearman rank correlation coefficients. *Copeïa* 1:210–214.

GOULDING, M. 1980. *The fishes and the forest*: *explorations in Amazonian natural history*. University of California Press, Berkeley. 280 pp.

GOULDING, M. & CARVALHO, M. L. 1982. Life history and management of the tambaqui (*Colossoma macropomum, Characidae*): an important Amazonian food fish. *Revista Brasilera da Zoologia* 1:107–133.

HOFF, M. 1995. Les berges du fleuve Sinnamary (Guyane française): géomorphologie et groupements végétaux. *Hydroécologie Appliquée* 7:151–183.

HONDA, E. M. S. 1972. Contribuçao ao conhecimento da biologia de peixes do Amazonas. I, Alimentaçao de *Geophagus*. *Acta Amazonica* 2:81–88.

HONDA, E. M. S. 1974. Contribuçao ao conhecimento da biologia de peixes do Amazonas. II, Alimentaçao de tambaqui, *Colossoma bidens* (Spix). *Acta Amazonica* 4:47–53.

HOREAU, V. 1996. La mise en eau de la retenue hydroélectrique de Petit Saut (Guyane). Hydrobiologie 1 Du Fleuve Sinnamary avant la mise en eau. 2 De la retenue pendant la mise en eau. 3 Du fleuve en aval. *Thèse de l'Université de Marseille I*. 250 pp.

HOREAU, V., CERDAN, P., CHAMPEAU, A. & RICHARD, S. 1996. Importance des apports exogènes dans le régime alimentaire de quelques poissons de 'criques' du bassin versant du fleuve Sinnamary (Guyane Française). *Revue d'Ecologie (Terre et Vie)* 51:29–41.

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. *Journal of Animal Ecology* 19:36–58.

KNÖPPEL, H. A. 1970. Food of central Amazonian fishes. Contribution to the nutrient-ecology of Amazonian rain-forest-streams. *Amazoniana* 2:257–352.

KNÖPPEL, H. A. 1972. Zür Nahrung tropischer Süsswasserfische aus Südamerika. *Amazoniana* 3:231–246.

LAUZANNE, L. 1976. Régimes alimentaires et relations trophiques des poissons du lac Tchad. *Les Cahiers de l'O.R.S.T.O.M., série Hydrobiologie* 10:267–310.

LEGENDRE, L. & LEGENDRE, P. 1984. *Collection d'écologie. No. 13: Ecologie numérique, Vol. 2. La structure des données écologiques*, Masson, Paris & Presses de l'Université du Québec, Canada. 335 pp.

LOWE-McCONNELL, R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge. 382 pp.

MARLIER, G. 1968. Etudes sur les lacs de l'Amazonie centrale. III, Les poissons du lac Redondo et leur régime alimentaire; les chaînes trophiques du lac Redondo; les poissons du rio Preto da Eva. *Cadernos da Amazonia* 11:21–57.

MENEZES, R. S. DE 1961. Nota sôbre alimentaçao do jacundá, *Crenicichla saxatilis* (L., 1758). *Boletim de la Sociedad Ceara Agronomia* 2:51–53.

PLANQUETTE, P., KEITH, P. & LE BAIL, P. Y. 1996. *Atlas des poissons d'eau douce de Guyane (tome 1)*. Collection du Patrimoine Naturel. Vol 22. Institut d'Écologie et de Gestion de la Biodiversité, Muséum National d'Histoire Naturelle, Institut National de la Recherche Agronomique, Conseil Supérieur de la Pêche, Ministrière de l'Environnement. 429 pp.

POWER, M. 1984. Habitat quality and the distribution of algal-grazing catfish in a Panamanian stream. *Journal of Animal Ecology* 53:357–374.

RICHARD, S. 1996. La mise en eau de la retenue hydroélectrique de Petit Saut (Guyane). Hydrochimie 1 Du fleuve Sinnamary avant la mise en eau. 2 De la retenue pendant la mise en eau. 3 Du fleuve en aval. *Thèse de l'Université de Marseille I*. 278 pp.

SANTOS, G. M. DOS 1981. Estudos de alimentaçao e hábitos alimentares de *Schizodon fasciatus* Agassiz, 1829, *Rhytiodus microlepis* Kner, 1859 e *Rhytiodus argenteofuscus* Kner 1859, do lago Januaca, AM (Osteichthyes, Characoidei, Anostomidae). *Acta Amazonica* 11:267–283.

SANTOS, G. M. DOS 1982. Caracterizaçao, habitos alimentares e reprodutivos de quatro espécies de *aracus* e consideraçoes ecologicas sobre o grupo no lago Janaucá-AM. (Osteichthyes, Characoidei, Anostomidae). *Acta Amazonica* 12:713–739.

SAUL, W. G. 1975. An ecological study of fishes at a site in upper Amazonian Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 127:93–134.

SOARES, M. G. M. 1979. Aspectos ecológicos (alimentaçao e reproduçao) dos peixes do igarapé do Porto, Aripuana, MT. *Acta Amazonica* 9:325–352.

TAVARES, A. S., ENRICONI, A. & ODINETZ COLLART, O. 1995. Insect communities associated with aquatic macrophytes Podostemaceae in amazonian waterfalls. XXVI SIL International Congress. 23–29 July 1995, São Paulo, Brésil 1.

TITO DE MORAIS, L., LOINTIER, M. & HOFF, M. 1995. Extent and role for fish populations of riverine ecotones along the Sinnamary River (French Guiana). *Hydrobiologia* 303:163–179.

ZARET, T. M. & RAND, A. S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52:336–342.