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Food resource partitioning in a fish community of the central Amazon floodplain

Bernard de Mérona* and Judy Rankin-de-Mérona**

Diets of most of fish species inhabiting a floodplain lake in central Amazonia were studied over a two years and half period. Based on the percentage of relative occurrence of 11 major food categories a classification of species in 11 feeding guilds is proposed. Many species were found to be specialized feeders. Fish, detritus and insects were the most important food resources supporting the fish community in both seasons, but the proportions of fruits, invertebrates and fish were reduced during the low water season. At the community level mean diet overlap between species was low, suggesting efficient resource partitioning within the community. However mean overlap between unspecialized feeders was high. Based on the 23 most abundant species belonging to the different feeding guilds, there was no difference in mean overlap between seasons. Whereas individual species exhibited diet changes between high water and low water seasons, there was no general pattern of seasonal change within feeding guilds.

Os regimes alimentares da maioria das espécies de peixes de um lago de várzea da Amazônia central foram estudados durante dois anos e meio. Baseada nas percentagens de ocorrência relativa de 11 maiores categorias alimentares, uma classificação das espécies em 11 guildas alimentares é proposta. Muitas espécies foram consideradas especializadas em relação aos seus comportamentos alimentares. Peixes, detritos e insetos foram os recursos alimentares mais importantes ao longo do ano, mas as proporções relativas de frutos, invertebrados e peixes foram reduzidas durante a época de águas baixas. A nível de comunidade a sobreposição média entre espécies foi baixa, sugerindo uma partição eficiente dos recursos alimentares. Entretanto, para espécies não especializadas, os valores de sobreposição foram elevados. Baseado em 23 espécies abundantes, pertencentes a diferentes guildas alimentares, não foi observada diferença na sobreposição média entre as estações do ano. Enquanto que certas espécies individuais mostraram mudanças de regime entre épocas de águas altas e baixas, não foi observado nenhuma tendência geral nas modificações sazonais dentro das guildas alimentares.

Key words: varzea lake, fishes, diet, overlap, seasonal variability.

Introduction

Fish diversity in the Amazon basin is the highest ever observed in freshwaters either at a regional (*i.e.* the entire Amazon basin) with more than 1300 species (Lowe-McConnell, 1987; Kullander, 1994) or at a local scale (*i.e.*, within selected lakes, wetlands, streams, and rivers within Amazon basin). For example, Junk *et al.* (1993) captured 132 species in lago Marchantaria, a small floodplain lake in the Solimões near Manaus and Mérona & Bittencourt (1993) recorded 155 species in the nearby lago do Rei about 100 km2 large. High local diversity reflects the problem of species coexistence which, following niche theory (Hutchinson, 1957), is based on resource partitioning (Schoener, 1985). Species share three types of resources: food, space and time (Pianka, 1969). However, trophic separation has been pointed out as the most important mechanism of resource partitioning in fish assemblages (Ross, 1986).

There is an abundant literature on the diets of Amazon fishes. Araujo Lima *et al.* (1995), in a review on trophic aspects of fish communities in Brazil, cite 34 publications dealing directly with diet of Amazonian fish species. However, few of these works consider the entire fish community, which would allow a description of food resource partitioning between species (Marlier, 1968; Knöppel, 1970; Saul, 1975; Ferreira, 1984; Goulding *et al.*, 1988; Mérona *et al.*, 2001; 2003).

The fish community studied here inhabits a floodplain lake in the central Amazon floodplain previously described in Mérona & Bittencourt (1993). It is characterized by high species richness (155 species) and complex temporal dynamics.

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*Institut de Recherches pour le Développement (UR131). Antenne IRD, Lab. Ecol. Hydrosystèmes fluviaux, Univ. Cl. Bernard Lyon 1, 43 Bd. du 11 nov. 1918, 69622 Villeurbanne Cedex, France. e-mail: demerona@univ-lyon1.fr
**INPA - Instituto Nacional de Pesquisa da Amazônia. Present address: 8, place Puvis de Chavannes, 69006 - Lyon, France.

We present the results of a study on the feeding habits of the same fish community.

Our study objectives were to i) document the diet and trophic groups of fishes within an Amazon floodplain lake, ii) quantify the seasonal changes in diet and niche breadth of the most abundant species within the floodplain lake, and iii) examine the degree of resource partitioning of food among fishes within the community.

Material and Methods

The large alluvial island, Ilha do Careiro, is located just southeast of the confluence of the Negro River and the Amazon River (Fig. 1). The island is partly occupied by a permanent floodplain lake, the lago do Rei. This lake is shallow and covers a surface of about 100 km2 during maximum high water. It has a permanent water connection to the Amazon River by a single outlet channel, the parana do Rei. The water level in the lake follows that of the Amazon River; the mean depth is about 1 m in the low water season and can reach 10 m during the high water season. As very flat lands surround the lake, the flood annually inundates large adjacent, mainly forested areas. Most sampling was conducted in the north part: Terra Nova (Fig. 1). In that zone, we sampled all microhabitats available for fish (open waters, border, flooded forest and flooded fields). Additionally we sampled fish from the outlet linking the lake to the Amazon River and in the flooded forest surrounding it.

Fish collections were made by a battery of 13 gillnets (50 m long by 1.5 to 3 m high) each of different mesh size 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 70, 80 and 90 mm between adjacent knots. We sampled fish every two months from February 1986 to May 1988. Gillnets were set out at about 18:00 hours and checked every six hours until 18:00 hours the next day.

All specimens were identified to species level from Géry (1977), Burgess (1989) and from consultation of specialists (see acknowledgments). Specimens of each species were deposited in the collections of the Instituto Nacional de Pesquisa da Amazônia (INPA, Manaus, Brazil).

The fish were counted and weighed and the capture per unit of effort (the weight of fish captured by 100 m2 of net during 24 h = CPUE) was computed for each net and summed for the whole battery. Capture per unit of effort is an index of fish density in the environment. Since large variations in the volume of water in the lake were observed during the hydrological cycle, we corrected the CPUE by an estimation of that volume at the time of sampling. The detailed description of the methodology can be found in Mérona & Bittencourt (1993). This procedure enabled us to sum up the different samples in order to get an average assemblage for a period.

We examined the stomachs of fish captured from all sampling dates. We only examined the stomachs of adult specimens because juveniles are seldom captured by the sampling methodology adopted. The occurrence of the main food items in the stomachs (i.e. those representing more than about 10% of the main bulk) was recorded in the field at the time of capture. When identification was impossible in the field, the stomachs were preserved in 10% formaldehyde and examined in the laboratory under a stereomicroscope. Due to the large number of fish captured (more than 800 specimens per sample on average) every stomach could not be examined and priority was given to omnivorous species whose feeding habits are more difficult to establish. The diets of some abundant fish species have been well established and we only examined 1 to 3 stomachs of these fishes for control. Specifically, fishes with well known diets were curimatids, *Curimata cyprinoides*, *Psectrogaster amazonica*, *Potamorhina latior*, two loricariids, *Hypostomus plecostomus* and *Glyptoperichthys joselimaianus*, some famous large predators like *Hydrolycus scomberoides* and *Rhaphiodon gibbus* and three planktivores (*Hypophtalmus edentatus*, *H. fimbriatus* and *H. marginatus*). Data on the diet composition for these species

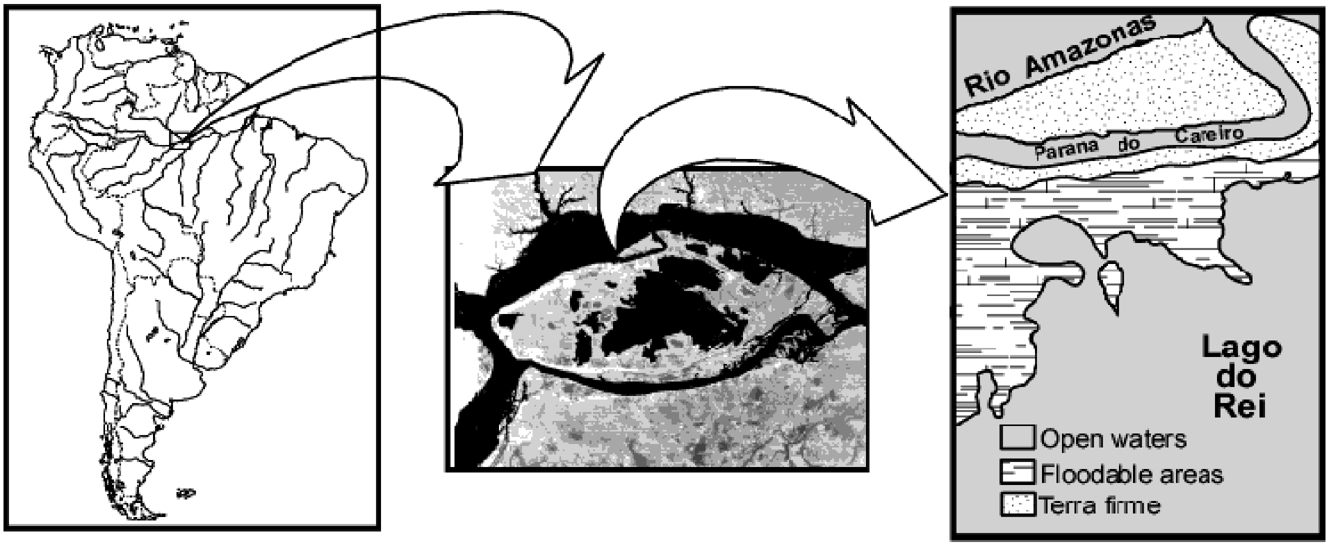

Fig. 1. Localization of the lago do Rei and detail of the study site in the northern part.

Table 1. Relative abundance (percent) of food items observed in stomachs of 74 species captured in lago do Rei, Brazil, February 1986 to May 1988, and attribution to guilds.

Species	Number analyzed	Fruit/ Flower	Other plant matter	Insect	Terrestrial Invertebrate	Aquatic Invertebrate	Shrimp	Eggs & scales	Fish	Plankton	Detritus	Other	Trophic guild
Acaronia nassa	6	-	-	17	-	-	-	-	83	-	-	-	piscivore
Acestrorhynchus microlepis	13	-	-	-	-	-	-	-	100	-	-	-	piscivore
Acestrorhynchus falcirostris	74	-	-	1	-	-	11	-	88	-	-	-	piscivore
Ageneiosus aff. dentatus sp1	6	-	-	-	-	-	67	-	33	-	-	-	shrimp eater
Ageneiosus aff. dentatus sp.2	13	-	-	-	-	-	100	-	-	-	-	-	shrimp eater
Ageneiosus sp.1	6	-	-	83	-	-	-	-	17	-	-	-	insectivore
Ageneiosus ucayalensis	4	-	-	25	-	-	75	-	-	-	-	-	shrimp eater
Anadoras weddellii	14	19	24	19	14	24	-	-	-	-	-	-	omnivore
Anodus elongatus	3	-	-	-	-	-	-	-	-	100	-	-	planktivore
Anodus sp.	9	-	-	22	-	-	-	-	-	78	-	-	planktivore
Astronotus ocellatus	5	60	-	40	-	-	-	-	-	-	-	-	omnivore
Auchenipterus nuchalis	46	-	-	77	-	21	-	-	2	-	-	-	insectivore
Brycon carpophagus	122	63	6	9	9	1	1	2	7	1	1	-	frugivore
Brycon melanopterus	9	53	7	7	33	-	-	-	-	-	-	-	omnivore
Calophysus macropterus	8	11	-	11	-	-	-	-	78	-	-	-	piscivore
Chaetobranchus flavescens	5	-	17	17	-	67	-	-	-	-	-	-	aquatic invert
Chalceus macrolepidotus	67	49	-	30	15	1	-	3	2	-	-	-	omnivore
Cichla monoculus	34	-	-	-	-	-	26	-	74	-	-	-	piscivore
Cichlassoma amazonarum	3	-	-	-	-	-	-	-	-	-	100	-	detritivore
Colossoma macropomum	151	59	19	6	4	5	-	2	1	5	-	-	unsp. herbivore
Curimata cyprinoides	3	-	-	-	-	-	-	-	-	-	100	-	detritivore
Curimatella meyeri	10	-	-	-	-	9	-	-	-	-	91	-	detritivore
Eigenmannina melanopogon	12	-	25	8	-	-	-	-	-	67	-	-	planktivore
Electrophorus electricus	5	-	-	40	20	-	-	-	40	-	-	-	unsp. carnivore
Glyptoperichthys joselimaianus	2	-	-	-	-	-	-	-	-	-	100	-	detritivore
Hemiodopsis microlepis	13	7	14	14	-	-	-	50	-	7	7	-	omnivore
Hemiodus immaculatus	88	-	1	9-	-	4	-	-	1	-	3	-	insectivore
Heros severum	7	-	31	15	-	8	-	15	-	-	31	-	omnivore
Hoplerythrinus unitaeniatus	89	55	-	9	7	-	-	6	24	-	-	-	omnivore
Hoplias malabaricus	49	-	2	-	-	-	4	2	92	-	-	-	piscivore
Hoplosternum littorale	7	-	10	10	10	60	-	10	-	-	-	-	aquatic invert
Hydrolycus scomberoides	3	-	-	-	-	-	-	-	100	-	-	-	piscivore
Hypophthalmus edentatus	3	25	-	-	-	-	-	-	-	75	-	-	planktivore
Hypophthalmus fimbriatus	3	-	-	-	-	-	-	-	-	100	-	-	planktivore
Hypophthalmus cf. marginatus	2	-	33	-	-	-	-	-	-	67	-	-	planktivore
Hypostomus plecostomus	3	-	-	-	-	-	-	-	-	-	100	-	detritivore
Leporinus friderici	42	50	24	5	6	8	2	2	3	-	-	-	omnivore
Leporinus trifasciatus	9	89	11	-	-	-	-	-	-	-	-	-	frugivore
Loricariichthys acutus	4	14	-	43	-	29	-	-	-	-	14	-	omnivore
Lycengraulis grossidens	35	-	-	-	-	-	3	-	97	-	-	-	piscivore
Mylossoma aureum	13	81	13	-	-	6	-	-	-	-	-	-	frugivore
Mylossoma duriventre	60	70	4	4	6	15	-	-	-	-	-	-	frugivore
Osteoglossum biccirhosum	132	3	18	54	4	4	4	1	10	-	-	1	unsp. carnivore
Parauchenipterus galeatus	37	25	10	46	8	4	-	2	2	-	2	-	omnivore
Parauchenipterus sp.2	168	14	10	41	7	6	1	2	19	-	-	-	unsp. carnivore
Pellona castelneana	45	-	-	2	-	4	19	-	74	-	-	-	piscivore
Pellona flavipinnis	119	-	1	31	-	8	36	-	24	-	-	-	unsp. carnivore
Piaractus brachypomus	14	52	22	-	13	9	-	-	-	-	4	-	unsp. herbivore
Pimelodus blochii	32	17	7	39	4	22	4	2	4	-	-	-	unsp. carnivore
Plagioscion montei	88	-	-	14	5	3	43	-	35	-	-	-	unsp. carnivore
Plagioscion squamosissimus	90	-	-	6	-	2	58	-	33	-	-	-	unsp. carnivore
Potamorhina altamazonica	18	-	5	-	-	-	-	-	-	-	95	-	detritivore
Potamorhina latior	1	-	-	-	-	-	-	-	-	-	100	-	detritivore
Prochilodus nigricans	14	13	33	-	-	7	-	-	-	-	47	-	unsp. herbivore
Psectrogaster amazonica	3	-	-	-	-	-	-	-	-	-	100	-	detritivore
Psectrogaster sp.1	6	-	-	-	14	-	-	-	-	-	86	-	detritivore
Pseudodoras niger	7	30	10	-	-	60	-	-	-	-	-	-	aquatic invert
Pseudostylosurus sp.	7	-	-	-	-	-	-	-	100	-	-	-	piscivore
Pterodoras granulosus	35	40	58	-	-	2	-	-	-	-	-	-	unsp. herbivore
Pygocentrus nattereri	190	2	17	7	-	1	1	3	67	-	-	1	piscivore
Rhaphiodon gibbus	2	-	-	-	-	-	-	-	100	-	-	-	piscivore
Rhaphiodon vulpinus	17	-	-	-	-	-	18	-	82	-	-	-	piscivore
Rhytiodus argenteofuscus	5	40	20	40	-	-	-	-	-	-	-	-	omnivore
Rhytiodus microlepis	99	2	96	-	-	1	-	1	-	-	-	-	leaf eater
Schizodon fasciatum	100	13	80	1	3	2	-	2	-	-	-	-	leaf eater
Semaprochilodus theraponura	4	-	20	-	-	-	-	-	-	-	80	-	detritivore
Serrasalmus elongatus	47	-	4	4	-	-	-	4	85	-	-	2	piscivore
Serrasalmus rhombeus	5	-	17	17	-	-	17	-	50	-	-	-	unsp. carnivore
Serrasalmus sp.3	61	13	9	29	-	4	3	3	38	-	-	-	unsp. carnivore
Serrasalmus spilopleura	94	20	8	16	-	2	2	9	42	-	-	-	omnivore
Sorubim lima	31	-	-	94	-	-	-	-	6	-	-	-	insectivore
Sternopygus macrurus	31	-	11	66	-	9	11	3	-	-	-	-	insectivore
Triportheus albus	23	-	-	78	-	22	-	-	-	-	-	-	insectivore
Triportheus angulatus	434	37	6	34	13	5	-	4	1	-	-	1	omnivore
Triportheus elongatus	211	37	3	33	20	4	-	2	-	-	-	1	omnivore

Table 2. Relative abundance (percent) of food items observed in stomachs of selected species and niche breath during low (LW) and high water (HW) seasons in lago do Rei, Brazil.

Species		Number analyzed	Fruit/ Flower	Other plant matter	Insect	Terrestrial Invertebrate	Aquatic Invertebrate	Shrimp	Eggs & scales	Fish	Plankton	Detritus	Other	Niche breadth
Piscivore														
Acestrorhynchus falcirostris	HW	26	-	-	-	-	-	-	-	100	-	-	-	1.00
	LW	35	-	-	-	-	-	23	-	77	-	-	-	1.54
Cichla monoculus	HW	10	-	-	-	-	-	-	-	100	-	-	-	1.00
	LW	21	-	-	-	-	-	43	-	57	-	-	-	1.96
Hoplias malabaricus	HW	14	-	-	-	-	-	7	7	86	-	-	-	1.34
	LW	30	-	3	-	-	-	3	-	93	-	-	-	1.15
Pellona castelneana	HW	26	-	-	4	-	7	18	-	71	-	-	-	1.82
	LW	14	-	-	-	-	-	21	-	79	-	-	-	1.51
Serrasalmus elongatus	HW	26	-	4	4	-	-	-	4	89	-	-	-	1.26
	LW	18	-	6	6	-	-	-	6	78	-	-	6	1.62
Pygocentrus nattereri	HW	139	1	15	7	-	1	1	3	69	-	-	1	1.97
	LW	26	-	28	14	-	3	3	3	48	-	-	-	3.01
Frugivore														
Mylossoma duriventris	HW	27	79	-	11	-	11	-	-	-	-	-	-	1.56
	LW	9	56	33	-	-	11	-	-	-	-	-	-	2.31
Leaf eater														
Rhytiodus microlepis	HW	58	2	98	-	-	-	-	-	-	-	-	-	1.03
	LW	22	-	100	-	-	-	-	-	-	-	-	-	1.00
Schizodon fasciatum	HW	42	16	80	2	-	2	-	-	-	-	-	-	1.50
	LW	17	-	100	-	-	-	-	-	-	-	-	-	1.00
Insectivore														
Hemiodus immaculatus	HW	83	-	1	96	-	-	-	-	1	-	1	-	1.08
	LW	5	-	-	40	-	40	-	-	-	-	20	-	2.78
Sternopygus macrurus	HW	13	-	7	64	-	21	7	-	-	-	-	-	2.13
	LW	17	-	11	74	-	-	16	-	-	-	-	-	1.73
Unsp. herbivore														
Colossoma macropomum	HW	42	88	7	-	2	-	-	2	-	-	-	-	1.28
	LW	28	15	41	29	-	12	-	-	3	-	-	-	3.42
Unsp. carnivore														
Osteoglossum biccirhosum	HW	50	7	18	49	1	6	1	1	15	-	-	-	3.26
	LW	66	1	20	57	3	1	8	-	8	-	-	2	2.67
Parauchenipterus sp.2	HW	98	23	13	46	6	5	1	1	4	-	-	-	3.50
	LW	28	-	6	56	3	13	-	3	19	-	-	-	2.68
Serrasalmus sp.3	HW	43	15	6	35	-	2	4	-	38	-	-	-	3.41
	LW	13	-	21	21	-	14	-	-	43	-	-	-	3.38
Pellona flavipinnis	HW	39	-	-	60	-	16	9	-	16	-	-	-	2.40
	LW	80	-	1	17	-	4	49	-	29	-	-	-	2.83
Plagioscion montei	HW	53	-	-	11	4	2	43	-	41	-	-	-	2.77
	LW	31	-	-	22	-	5	41	-	32	-	-	-	3.13
Plagioscion squamosissimus	HW	49	-	-	11	-	2	53	-	34	-	-	-	2.45
	LW	36	-	-	-	-	3	68	-	30	-	-	-	1.83
Omnivore														
Leporinus friderici	HW	11	46	23	15	-	-	-	-	15	-	-	-	3.19
	LW	16	71	18	-	-	-	6	6	-	-	-	-	1.86
Serrasalmus spilopleura	HW	28	-	10	23	-	3	-	13	52	-	-	-	2.90
	LW	57	30	8	16	-	2	3	5	36	-	-	-	3.93
Triportheus angulatus	HW	278	42	7	46	2	2	-	-	1	-	-	-	2.57
	LW	38	2	10	76	-	10	-	2	-	-	-	-	1.69
Triportheus elongatus	HW	129	42	2	49	2	4	-	1	-	-	-	-	2.38
	LW	18	-	14	76	-	10	-	-	-	-	-	-	1.64

can be found in Marlier (1968), Saul (1975), Santos *et al.* (1984), Soares *et al.* (1986), Goulding *et al.* (1988), Planquette *et al.* (1996), LeBail *et al.* (2000), Mérona *et al.* (2001), and Mérona *et al.* (2003). Many rare species yielded no information either because the few collected stomachs were empty or because they were kept in the systematic collections of INPA and therefore were excluded from the analyses.

The 11 food items considered were Fruit/Flower - fruits, seeds and flowers, Vege - vegetative parts of higher plants, predominantly leaves, Inse - unidentifiable insect fragments (In many stomachs the macroscopic examination was unable to identify the terrestrial or aquatic origin of the insect remains), Invt - terrestrial invertebrates, including winged insects, ants, termites, snails and centipedes, Inva - aquatic invertebrates, including insect larvae and pupae, worms and aquatic snails, Shrimp - shrimps (Shrimps were considered separately from other aquatic invertebrates because of their great abundance in the lake and the presence of fish species selecting this type of prey (Goulding & Ferreira, 1984)), Plankton - zooplankton or phytoplankton, Egg/Scale - fish scales or undetermined eggs (separated from the resource fish because consuming this type of food is associated to a different feeding behavior), Fish - fish flesh, fins or bones, Detritus - detritus, organic layer, periphytic algae and mud, Other - pieces of terrestrial vertebrates, feathers, wood fragments.

We computed the percentage of relative occurrence for each item, i.e. for each species, the number of occurrences of each food item divided by the total number of occurrences of all the items. Given that the method adopted focused on the main food items in the stomach, that is those that occupy a significant volume in the stomach, no more precise estimation of volume was made.

The placement of species in feeding guilds was determined by successively separating groups of species with stomach contents composed of more than 60% of a single food item, and leaving at the end those omnivorous species with no marked dominance of a given food category (see Table 1).

A broad estimation of the relative importance of the resources supporting the fish community was obtained by distributing the captured biomass of each species over the different food categories based on their relative contribution in the stomachs (Mérona *et al.*, 2001; 2003). According to Winemiller (1989) this procedure permits to take into account only the food resources that the fish can effectively access. Seasonal change in the pattern of relative contributions of resources was tested by a chi-square test. To perform the test, items with low contribution values were grouped together: insects, terrestrial invertebrates, aquatic invertebrates and plankton in invertebrates; other and unknown in unknown.

For some species we compared the efficiency of resource partitioning in the low water season when only open water is available to fish (October and December 1986, September, October and December 1987) and high water season when forest and marginal fields are inundated (June and August 1986, April and June 1987). Data from intermediate hydrological stages (February 1986, 1987 and 1988) were excluded from this comparison. The mean percentage of relative occurrence of each food category was computed separately for the two seasons and symmetric overlaps between species diet were calculated using the formula of Morisita (1959). Morosita's index and its relatives (Horn, 1966; Pianka, 1973) generate overlap values ranging form zero to one, and are the most frequently used overlap indices (Linton *et al.*, 1981). Generally values equal or greater than 0.60 are assumed to represent high dietary overlap (Zaret & Rand, 1971). Differences in mean overlap between seasons were tested by a t-test. Diet composition was compared between the two seasons. Niche breadth was calculated as the inverse sum of the squared proportions of the relative occurrences of the food items in the stomachs (Levins, 1968).

Results

We were able to examine the stomach contents and determine the diets of 74 of 140 fish species captured in the lago do Rei (Table 1). These species represented 94% of the total fish biomass captured during the period February 1986 to May 1988.

Examination of fish diets (Table 1) suggested the presence of 11 trophic groups within the fish community. Only 27 of the 74 species had a diversified diet and were classified either in the omnivore feeding guild, when animal and vegetal food are consumed in approximately equal parts, or in the unspecialized herbivore or carnivore guilds when only food of vegetal or animal origin was found in the stomachs. The 47 other species had a diet dominated by a single food item. Planktivores had more than 65% relative occurrence of plankton in their stomachs. Detritivores' stomachs were full of a mushy substance with few recognizable items at a macroscopic level. This was apparently either mud of a brown color, or a green paste made of periphyton. Piscivores consumed fish for more than 65% relative occurrence of their diet. Shrimp eaters were also predatory fishes but with a marked preference for shrimps which composed 65 to 100% relative occurrence in their diet depending on the species. Frugivores were specialized in consuming fruits or seeds, items that represented more than 60% of the mean relative occurrence in their stomachs. Leaf eaters ate predominantly vegetative parts of vascular plants. Stomachs of insectivores contained undetermined insect remains. Species grouped in this guild are very heterogeneous in their morphology and their preys are probably of diverse origin, either aquatic or terrestrial. In some cases nevertheless aquatic insect larvae were easily recognizable and, together with other benthic animals, allowed the definition of a guild of aquatic invertebrate predators.

There was a significant difference in the relative contribution of the food categories supporting the fish community between seasons (chi-square=86.99; df=6; p<0.001). In both seasons, fish, detritus and insects were the most abundant food resources exploited by the Terra Nova fish community (Fig. 2). Higher plant vegetative parts appeared to be a constant resource whereas the relative proportion of fruits or seeds and, to a lesser extent, invertebrates and fish, were reduced from the high water to the low water season. In the low water season, detritus composed a greater proportion of the resources when other resources were apparently in short supply.

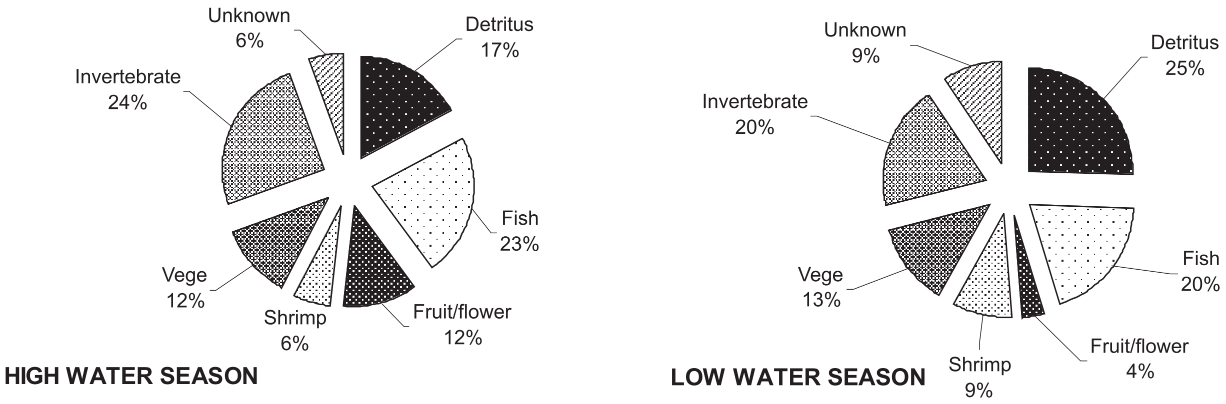

Fig. 2. Relative importance of food categories in supporting the community's biomass of fish species inhabiting a floodplain lake (lago do Rei) in Central Amazonia in the two seasons.

When considering the whole community in Terra Nova, the mean overlap between diets was very low (0.238) showing a high degree of food partitioning between species (Fig. 3A). However, among the generalist species, the mean overlap was much greater (Fig. 3 B). On the 23 species where stomach content data were sufficient we observed no difference between mean overlaps in the two contrasted seasons (n=253; t=-0.109; p=0. 913) (Fig. 3 C). However, some individual species showed modifications in their feeding habits (Table 2). Four out of six piscivores enlarge their niche breath in the low water season, part of their fish food being substituted by shrimps or even plant matter. Consumption of fruits in *Mylossoma duriventris* and *Colossoma macropomum* was much reduced in the low waters and substituted by plant vegetative parts plus invertebrates. Conversely *Leporinus friderici* ate a greater proportion of seeds during the low water season. Omnivore species generally narrowed their dietary niche breadth in the low water season with the exception of a piranha species, *Serrasalmus spilopleura*, which increased its consumption of fruits and seeds.

Discussion

Specialists *versus* generalists

It is an accepted generalization that riverine fish species are mostly opportunistic in their feeding habits because of the ephemeral character of habitats and resources (Lowe-McConnell, 1987; Araujo Lima *et al.*, 1995). Nevertheless, many Amazonian fish species exhibit marked morphological adaptations to a particular type of food (Pouilly *et al.*, 2003). In this study we were able to differentiate eight types of specialized feeding behaviors, based on plankton, detritus, leaves, insects, aquatic invertebrates, fruits, fish and shrimp. This could be the expression either of opportunistic species occasionally sharing the great diversity of food resources of the floodplain, or of adaptive selection of specialist species able to feed only upon one particular type of prey because of morphological, anatomical or physiological attributes. If truly specialized, then these species might be expected to have the same diet in different environments (i.e. show a low flexibility in their diet).

Carvalho & Goulding (1985) observed a high consistency in the planktivorous diet of *Hypophthalmus fimbriatus*, and their result suggested that a decrease in plankton abundance resulted in a decrease in food intake rather than an increase in niche breath. In a different environment, Carvalho (1978) and Carvalho *et al.* (1978) described a phytoplanktophagous diet for *Hypophthalmus perporosus* (probably a synonym of *Hypophthalmus marginatus*, see Santos *et al.*, 1984) in the lower Tocantins River. The species lives in the pelagic compartment of a large clear-water river where phytoplankton production is high (Schmidt, 1982). Planktophagous diets were also reported in other floodplain lakes of central Amazonia for *Anodus laticeps* (probably a synonym of one of the *Anodus* species captured in the present study) (Marlier, 1968) and for *Hypophthalmus edentatus* (Carvalho, 1980). In reservoirs *Hypophthalmus marginatus*, *H. edentatus* and *Anodus elongatus* are also planktivores (Hahn *et al.*, 1998; Mérona *et al.*, 2001). These data show that plankton represents the obligatory food resource for these species. This specialization explains why the distributions of these species are limited to environments including a large pelagic compartment allowing the development of plankton.

Many fish species classified as detritivores exhibit the same kind of diet in other habitats. Detritus constitutes the main food source for *Potamorhina latior* along the beaches and into the inundated forest of the Negro River (Goulding *et al.*, 1988) *Semaprochilodus theraponura* feeds on detritus

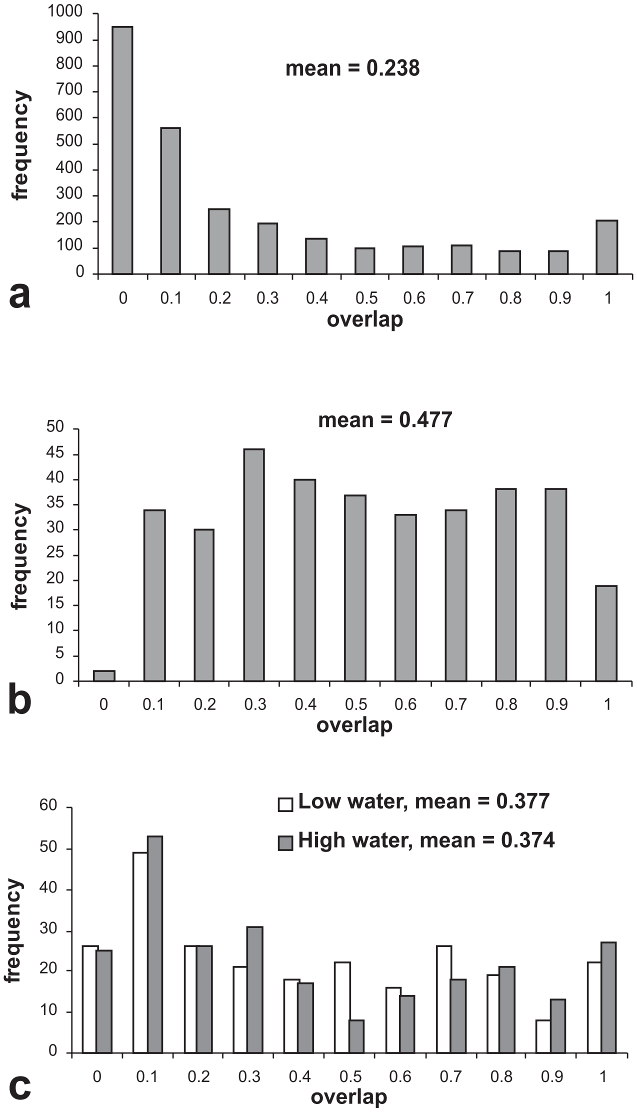

Fig. 3. Distribution of overlaps values between diets of fish species inhabiting a floodplain lake (lago do Rei) in Central Amazonia. a: whole community all seasons (74 species); b: generalist species all seasons (27 species); and c: seasonal differences (23 species).

mixed with sand in the different habitat types of Curuá-Una reservoir (Ferreira, 1984) and a small forested creek in Central Amazon (Knöppel, 1970). The diet of *Glyptoperichthys joselimaianus* (=*Pterygoplichthys multiradiatus*) consists of mud or fine sediment in Central Amazonia (Marlier, 1968). Regardless the food type ingested, the feeding behavior of these detritivore species, scraping of the benthic layer, appears to be a fixed character that goes with morphological adaptations.

Two species are considered here as exclusive leaf eaters. *Schizodon fasciatum* and *Rhytiodus microlepis* were studied in the Madeira River (Goulding, 1980), other rivers in the state of Rondônia (Santos, 1991) and another floodplain lakes (Santos, 1981) and were always reported to consume vegetative parts of higher plants sometimes supplemented by algae.

Frugivory in Amazonian fishes is a well-recognized phenomenon since the works of Gottsberger (1978) and Goulding (1980). Species of the sub-family Serrasalminae (genus *Piaractus*, *Colossoma*, *Mylossoma*, and *Myleus*) and of the genus *Brycon* have already been described as fruit and seed eaters (Honda, 1974; Goulding, 1980; Goulding *et al.*, 1988). Fruit eating is evidently much reduced during the low water period when the fruit sources in the forests are not accessible to fish. In these periods the frugivores ingest more seeds than fruits supplementing their diet with other kind of food such as plankton, detritus or leaves. This change in feeding behavior associated with reduced availability of fruits during periods of low water explains why we did not classify *Colossoma macropomum* as frugivore. Furthermore, Goulding (1980) found that overall food intake is much lower during this period than in the high water period.

Piscivores formed the largest guild in the lago do Rei with 14 species thus classified in our analysis. The diets of most piscivores from our study area have been examined in other geographic locations and typically exhibited a piscivorous diet in those locations. In the upper Madeira River, *Pellona castelneana* and *Cichla ocellaris* (=*C. monoculus*?) consume only fish (Goulding 1980). The same feeding regime is described in different Rio Negro habitats for *Acestrorhynchus falcirostris* and *A. microlepis* (Goulding *et al.*, 1988). *Hoplias malabaricus* is also an exclusive piscivore in the Tocantins River and in the Sinnamary River in French Guiana (Mérona *et al.*, 2001; 2003) although its diet is more diverse in the Venezuela Llanos but always dominated by fish (Winemiller, 1989). Conversely, *Pygocentrus nattereri* seems to be able to feed on alternative food sources. In the Pantanal of Mato Grosso in Brazil, this species consumes plant matter, crabs and insects as frequently as fish (Sazima & Machado, 1990).

In contrast to the guilds mentioned above whose species are in the majority true specialists, three guilds encountered in lago do Rei contain species with apparently more flexible diets.

Species classified here as insectivores are of two types. *Auchenipterus nuchalis* and *Triportheus albus* are surface feeders that have already been reported to feed preferentially upon terrestrial insects associated with allochthonous plant material (Horeau *et al.*, 1996; Mérona *et al.*, 2001). The other species form a heterogeneous group. *Sternopygus macrurus* and *Hemiodus immaculatus* are predators of aquatic invertebrates and/or aquatic plants (Knöppel, 1970; 1972; Goulding *et al.*, 1988). *Sorubim lima* was considered as a shrimp-eating specialist in the Rio Madeira floodplain by Goulding & Ferreira (1984).

The two *Plagioscion* species were intensively studied in Amazonian floodplain lakes (Annibal, 1982; Wortmann, 1982) and some data also exist on their food habits in other habitats (Goulding & Ferreira, 1984; Mérona *et al.*, 2001). Despite a marked preference for shrimp, it appears that these species, as is also true for *Ageneiosus* species, are better described as unspecialized carnivores rather than shrimp eating specialists. Depending on the availability of shrimp in the environment these species are also able to prey on fish or insects (Hahn *et al*., 1997).

Only three species have a diet largely restricted to aquatic invertebrates in the Lago do Rei. One, *Chaetobranchus flavescens* is a cichlid, a family whose members generally have a very diverse diet (Ferreira, 1981). Two other species are bottom-dwelling siluriforms and their food is poorly known. In the flooded forest of the Madeira basin the diet of *Pseudodoras niger* (synonym of *Oxydoras niger*) is composed of aquatic insect larvae mixed with detritus (Goulding, 1980). The same feeding regime is observed in the Tocantins River (Mérona *et al.*, 2001). Therefore, consuming aquatic invertebrates does not seem to be, for these species, a feeding specialization. They are rather benthic feeders, which select their food from what is available on the bottom.

The food resource

Fish and the organic layer together represent the majority of the resources used by the adult fish community in the Lago do Rei. A number of data suggest that many migratory species in the Amazon River basin reproduce in the main stream of the white water rivers and that their larvae and juveniles are passively transported to the floodplain at the time of the rising of the waters (Schwassmann, 1978; Cox-Fernandes & Mérona, 1988; Petry, 1989; Araujo Lima, 1994; Cox-Fernandes, 1997). Therefore fish constitutes a large and probably non-limiting resource in the floodplain, even more available in the high water season, which corresponds to the growing season for most of the species. The organic layer that in our definition includes detritus, mud and epiphytic algae, is also an extremely abundant resource. Detritus and mud originate from the deposition of material brought by the river and from the total or partial decomposition of the forest litter incorporated in the aquatic environment during flooding. Epiphytic production is boosted by the great quantity of nutrients (Kern & Darwich, 1997; Weber, 1997). In the low water period, the organic layer compensates for the shortage in other resources. Insects, either terrestrial or aquatic, support a large biomass of the fish community. During the high water, when the forest is inundated, a number of terrestrial insects fall in the water and are preyed upon by fish. The relative importance of insects and fruits, two resources that are for a large part derived from the flooded forest, is reduced in the dry season when the only habitat available for fish is the open water. The contribution of shrimp is higher in the low water season. *Macrobrachium amazonicum* was the most abundant species of shrimp in lago do Rei during our study. *M. amazonicum* reproduces all year, but its maximum reproductive output occurs during the low water season (Odinetz-Collart, 1991). Plankton provides only a small part of the available resource. Its development in the floodplain is limited by the low transparency (Schmidt, 1973; Brandorff, 1977).

Resource partitioning

The analysis of dietary overlaps shows that resource partitioning is well defined with low overlap overall at the community level in both seasons. Not surprising, overlaps are much higher for the unspecialized feeding guilds. In a study on a tropical stream fish community in Panama, Zaret & Rand (1971) observed reduced diet overlaps between species during the dry season, which they attributed to a shortage in food resources. They stated that this observation supported the competitive exclusion principle arguing that a reduction in niche dimensions lowers the level of competition between species. These findings are in contradiction with Lowe McConnell's (1964) observations on fish communities in the Rupununi River. Her conclusion was that diets are more specialized during the high water season when foods are varied and plentiful than in the dry season where fish share the little food available. Goulding (1980) and Goulding *et al.* (1988) based on observations on fish communities from Rio Machado and Rio Negro agreed with Lowe McConnell's hypothesis, although they showed that many species share the same items during the flood. Nevertheless our findings, based on 23 species belonging to various different feeding guilds, do not show any general tendency in the seasonal pattern of overlaps between species. It appears that the response to a shortage in food supply can be different depending on the species and not on the guild. On the four omnivores studied, three narrowed their diet in the low water season either in preying more on insect (*Triportheus* spp.) or in concentrating on seeds (*Leporinus friderici*) and just one enlarged it. This suggests that other mechanisms must exist which allow the co-existence of species in very complex fish communities. Lowe-McConnell (1964) and Goulding (1980) suggested that the fact that many species reduce their food intake during the dry season, consuming the fat accumulated during the wet season, play a role in lowering the level of competition. Partitioning of space at different times could be another way to enhance co-existence (Pianka, 1969; Ross, 1986).

Conclusions

The Amazon floodplain with its diverse fish fauna represents a unique opportunity to understand how species coexist. According to classical niche theory (Hutchinson, 1957) one way to achieve co-existence is to use separate resources of the environment. Food, space and time are resources likely to be partitioned by fish. The data presented here lead to three main conclusions:

- many fish species (41 out of 74 studied here) exhibit a specialized diet in the diverse fish community of central Amazonia which leads to an overall efficient food partitioning in this community,
- there is a large seasonal variation in the food resource supporting the fish community related to the accessibility of flooded terrestrial areas,
- individual species generally change their feeding habits in the low water season when some food resources are scarce but there is no general tendency observed at the community or at the feeding guild levels.

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