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Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America (Petit-Saut Dam, French Guiana)

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Abstract

The closure of a dam and the following inundation of large areas constitute a major perturbation of the river ecosystem. Under tropical conditions, one of the first constraints imposed on organisms in the new ecosystem is the trophic one. This work aims at determining which feeding strategies are the most successful for the development of fish populations in such a transforming environment. In addition, it will examine the change in food resource used by the assemblages. Soon after the closure of the Petit-Saut Dam, French Guiana, higher plants and terrestrial invertebrates constitute the main resources for the fish assemblage but resources of aquatic origin subsequently progressively substituted them. Generalists, already numerous in the river, were the most successful in the first stage of reservoir formation. However, over time, specialist species (detritivores, piscivores, invertivores and herbivores) became more important in the assemblage and the trophic structure became more balanced. These results support the hypothesis of greater colonization ability for generalists and of their decline when competition takes place.

Keywords: Fish; Assemblage; Tropical; Reservoir; Feeding strategies

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1. Introduction

The sequence of ecological changes in a reservoir soon after impoundment has been described and considered on many occasions (Ackermann et al., 1973; Baxter, 1977; Lowe-McConnell, 1973; Petr, 1975; Tundisi and Straskraba, 1999). The cessation or reduction of the stream flow, the increase in water transparency and the liberation of large quantities of nutrients from litter and flooded terrestrial vegetation decomposition, lead to a large increase in productivity. However, this process can be limited by a deficiency in dissolved oxygen, which, in some cases, can provoke fish kills. After this first stage, corresponding to the reservoir filling and its physical stabilization, the system equilibrates with a production value intermediate between that recorded in the undisturbed river and that of the first stage (Balon and Coche, 1974). Less well known, however, is the structure and composition of the fish communities able to develop in the new-formed lake, although this knowledge is fundamental for the management of reservoirs for fishing purposes. In the absence of any introduction of alien species, these communities are formed from the original riverine ichthyofauna. To colonize a reservoir, a fish population must, in the first place, find conditions amenable to its maintenance (basic metabolism, growth) and afterwards for its reproduction. Maintenance is limited by a number of factors, among which change in temperature regime, dissolved oxygen concentration and availability of food resources are the most important. In tropical conditions where temperature is almost constant year around it is unlikely that this parameter will limit the distribution of fish. Oxygen deficiency is frequent in tropical reservoirs in forested areas. However, an oxygenated layer expands rapidly at the lake surface (Richard et al., 1997) and anoxia in the deeper parts does not prevent a rapid colonization by fishes. From these considerations, it could be hypothesized that, under such tropical conditions, trophic limitations are the first to be imposed to the species.

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Some general tendencies in the changes of the trophic structure of fish communities in reservoirs have been detected (Araujo Lima et al., 1995). As could be expected in the transformation of a fluvial environment into a lacustrine one, the main tendency is an increasing importance of autochthonous material in the food regime of fish (Agostinho et al., 1999). In large and deep reservoirs, the predominance of aquatic invertebrates feeders (invertivores), piscivores and planktivores has been noted (Ferreira, 1984; Hahn et al., 1998). However, a recent study of the Tucurui Reservoir on the Tocantins River in Brazil confirms the dominance of piscivores while neither aquatic invertivores nor planktivores show any particular development (Mérona et al., 2001). Furthermore, the diversity of trophic structures in Brazilian reservoirs has been pointed out (Agostinho et al., 1999). It has been suggested that the colonization process in reservoirs is largely determined by the trophic structure soon after impoundment, which, in turn, is dependent on the presence of guild elements with flexible feeding strategies.

In this work, we propose to verify these hypotheses in the case of a large reservoir located in French Guiana in an area covered by primary forest. We propose to address two questions: (1) what are the changes in the food resources used by the assemblage and (2) which feeding strategies are the most successful in colonizing the new environment.

2. Material and methods

2.1. Site description

Petit-Saut Dam is located in French Guiana on the River Sinnamary (Fig. 1). The river itself is 260 km long with a drainage area of 6565 km^2 and a mean annual discharge of 230 m^3 s^{-1} (Tito de Morais and Lauzanne, 1994). The climate in the region is tropical humid with a mean annual precipitation of about 3000 mm distributed in two rainy seasons: one short from mid-December to February and one long from April to July. The mean water temperature in the river before the damming varied between 25 and 26 °C (Richard et al., 1997). The dam, planned for electricity production, was constructed at about 60 km from the estuary and closed in January 1994. It led to the inundation of more than 350 km^2 of pristine tropical forest. The filling period lasted 16 months until May 1995 after which the water level in the lake oscillated seasonally between 30 and 35 m above sea level (Sissakian, 1997) (Fig. 2). Depth is very variable depending on the lateral or longitudinal position and no systematic measure was made. The first months were characterized by a massive deoxygenation of the water column; however, a thin layer of oxygenated water at the surface was always present in most parts of the lake and the oxygen conditions improved rapidly (Richard et al., 1997). The surface water temperature in the reservoir can reach 32 °C in the dry season but most of the time it varied between 28 and 30 °C (Richard et al., 1997). Thermal stratification was rapidly established but was less marked in the beginning of the rains (January– February) (Richard et al., 1997). In the first 2 years after the closure, a large supply of plant material and terrestrial invertebrates was observed falling in the aquatic compartment. This quantity of exogenous material progressively diminished during the subsequent years.

2.2. Fish sampling

Fish sampling was done by surface gillnets 25 m long by 2 m height of mesh size 10, 15, 20, 25, 30, 35, 40, 50, 60, and 70 mm between knots. Two sets of 10 nets were set at about 05:00 p.m. and removed between 07:00 and 10:00 a.m. the next day. In the river, the nets were positioned along the banks in areas of low water current whereas in the reservoir the former canal of the river and the marginal areas were sampled.

Two zones of the reservoir were sampled: one in the lower part, at about 5 km from the dam, and the other in the medium part at about 50 km from the dam. In the river, sampling took place in an area immediately above the upper limit of the reservoir until December 1996 and after that in three stations localized at increasing distances upstream from the lake (Fig. 1).

Sampling was done on an approximately monthly basis between February 1994 and December 1996 and twice a year in the subsequent years (Fig. 2). For the river we treated samples separately during high water periods and low water ones, based on the mean monthly discharge in the river. There are 13 samples in high water and 22 in low water periods. In the reservoir three periods are considered: the filling phase between February 1994 and December 1995 (36 samples), the physical stabilization between January 1996 and December 1997 (24 samples) and the ecological stabilization from January 1998 to December 2000 (12 samples) when the thickness of the oxygenated epilimnion remained stable (Richard, personal communication).

Gillnet sampling to study fish communities has some shortcomings because of the highly selective nature of this fishing method (Hamley, 1975). However, the use of a large range of meshes, the multiplicity of samples, and the care taken in the investigation to sample every habitat in a zone can reduce the bias associated with gillnet sampling (Tejerina-Garro and Mérona, 2000) and were adopted in this study. In wide tropical rivers, where other sampling methods are difficult or impossible to utilize, gillnet sampling has been shown to be efficient in detecting changes in fish community structure (Mérona et al., 2001; Tejerina-Garro et al., 1998).

2.3. Stomach content analysis

The analysis of stomach contents started in 1994. In the field, after identification of the species (Keith et al., 2000; Le Bail et al., 2000; Planquette et al., 1996), individual fishes were measured and weighed and a maximum of 10 specimens of adult size of each species were taken at random, their

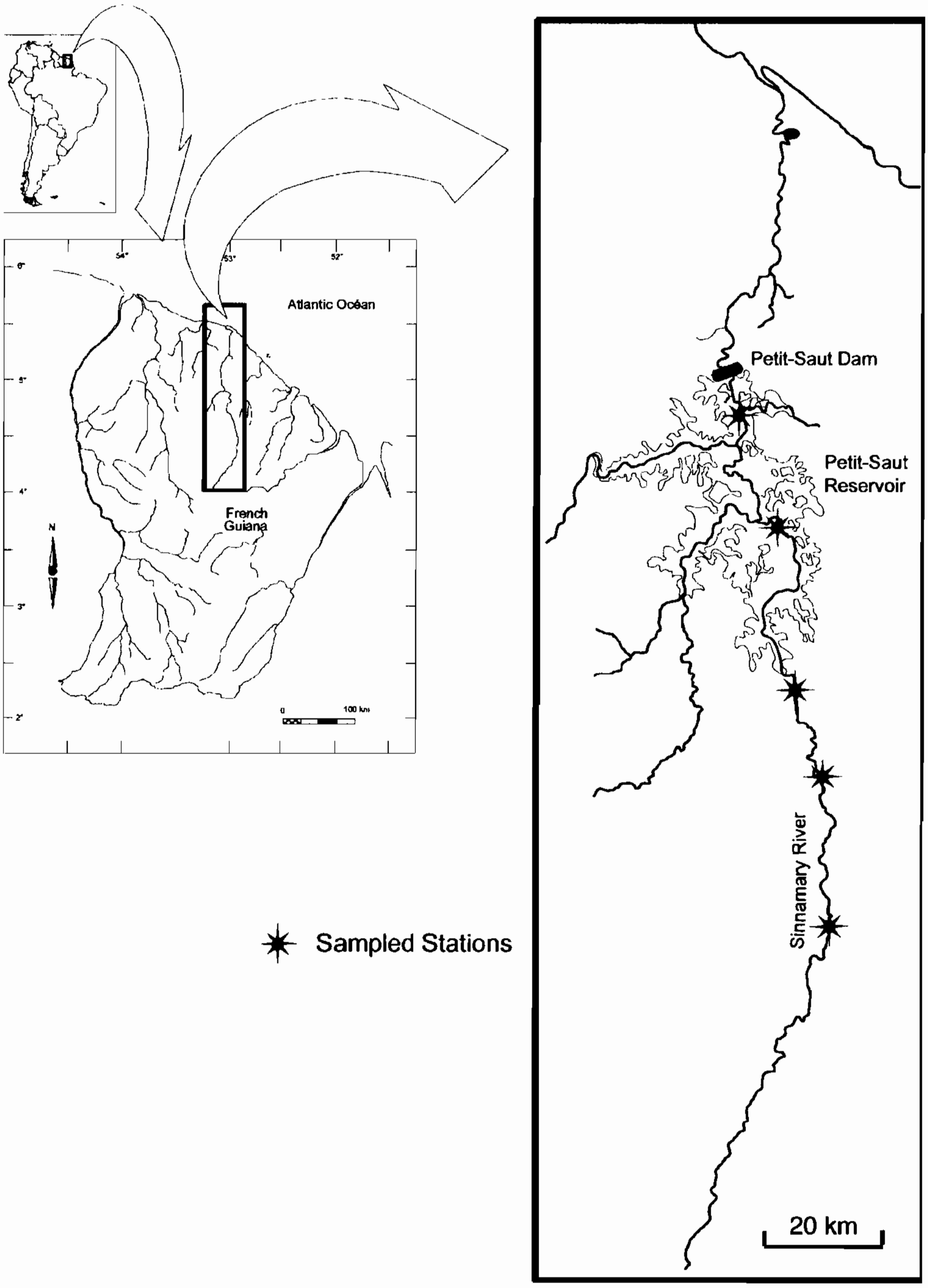

Fig. 1. Location of study site.

stomach removed from the general cavity and preserved in 70% alcohol. In the laboratory, the contents (if any) were spread in a petri dish and the different items separated under a stereomicroscope. All analyses were supervised by the first author. Due to the large number of fish species, we limited to a few individuals the examination of those having constant and homogenous stomach content. The volumetric percentage of each item was estimated visually. Items recognized in the stomachs were leaves, fruits and seeds, plant remains, algae, terrestrial insects, aquatic insects (within which we distinguished the Chaoboridae), other terrestrial invertebrates, plankton, decapods, other aquatic invertebrates, fish, sediment and detritus. Due to their poor representation in the stomachs, some of these items were subsequently grouped together for the determination of diets and for the comparison of trophic structures (see next section).

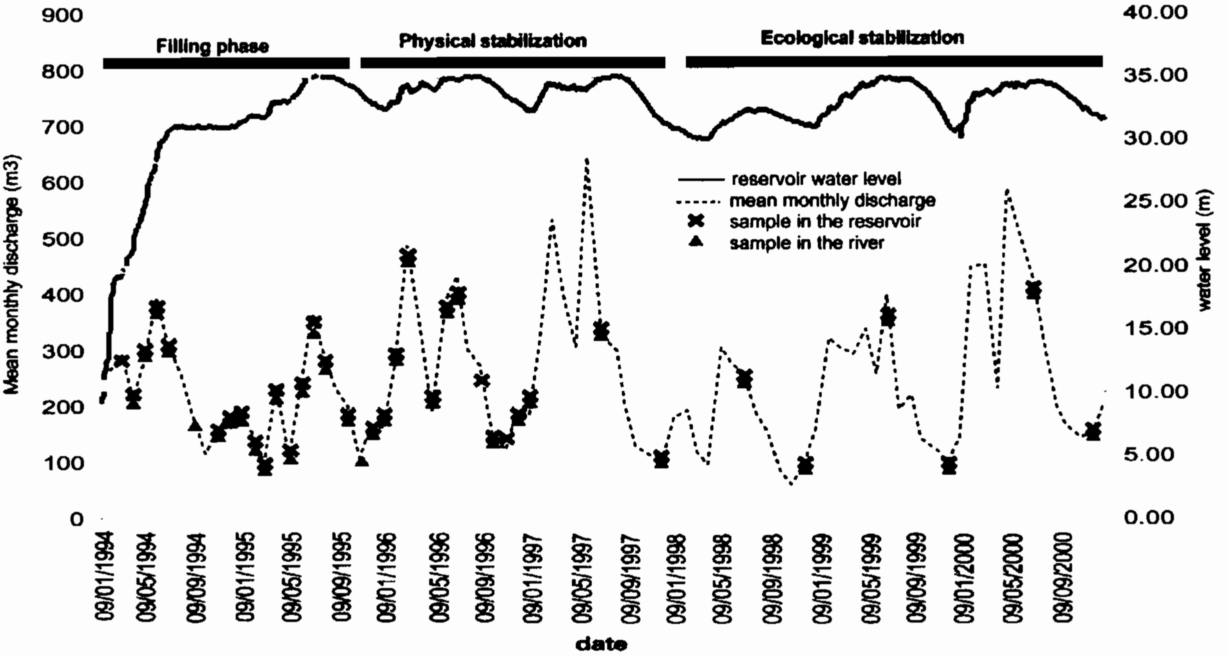

Fig. 2. Water level fluctuations in the reservoir and discharge in the river upstream during the study with indication of the sampling occasions.

2.4. Data treatments

Data were organized in 10 matrixes:

- five matrixes of capture data species × sample one for each of the groups defined previously (i.e. river in the high water period, river in the low water period, reservoir period 1, reservoir period 2 and reservoir period 3).
- five matrixes of stomach contents species × food item, two for the river high and low water periods and three for the three periods in the reservoir. Species mean stomach content was obtained by calculating the mean of individual percentages for each item.

Feeding guilds were determined from the matrix of stomach contents in the river by an adapted stepwise procedure (Mérona et al., 2001), that is:

- Step 1: more than 70% of detritus or sediment in the stomachs: detritivores.
- Step 2: more than 70% of plankton in the stomachs: planktivores.
- Step 3: more than 70% of fish and decapods in the stomachs: piscivores.
- Step 4: more than 70% of invertebrates in the stomachs: invertivores.
- Step 5: more than 70% of plant material in the stomachs: herbivores.
- Step 6: none of the above statements: omnivores.

The relative importances of resources used by the assemblage were assessed in summing the percentages of each item across all the species (Winemiller, 1989). This procedure, originally aimed at estimating resource availability in the environment, is based on the hypothesis that the fish is the best sampler of the resource available (or at least those that are used) because it focuses on the resource it can effectively access. The method is more reliable when based on many species assemblages containing a great diversity of morphotypes, because any single species would have a relatively small influence on estimates of resource.

The trophic structure of the assemblage is defined here by the proportion in biomass of each feeding guild identified.

Global differences between the groups of samples (river in high water periods, river in low water periods, reservoir in the three successive periods) were tested by a non-parametric analysis of similarity (Anosim) (Clarke, 1993). This analysis compares groups of samples from a distance matrix transformed to ranks. It gives a global index called global R, which is tested by permutations of the objects. The method also allows pairwise comparisons of the samples. To compare the contributions of each feeding guild between pair of samples, non-parametric Kolmogorov–Smirnov tests were performed using the software Systat 9®.

3. Results

We were able to analyze 1485 stomachs of 43 abundant fish species captured in the river, representing more than 99% of the total capture (Tables 1 and 2). Among them the omnivores were dominant (16 of 43 species) while the other species were herbivores (nine species), detritivores (seven species), piscivores (six species) and invertivores (five species).

In the reservoir we analyzed 2093 stomachs (743 in the first period, 858 in the second and 492 in the third) pertaining

Table 1
Capture (kg) of the species analyzed for stomach content in the Sinnamary River and in the reservoir

Order	Family	Species and authority	River		Reservoir		
			High water	Low water	Period 1	Period 2	Period 3
Characiformes	Hemiodontidae	*Bivibranchia bimaculata* Vari, 1985	0.154	3.888	0.097	0.000	0.000
		Hemiodopsis quadrimaculatus (Pellegrin, 1908)	35.712	64.318	4.179	1.922	7.200
		Hemiodus unimaculatus (Bloch, 1794)	24.716	52.481	5.868	30.551	22.344
	Curimatidae	*Chilodus zunevei* Puyo, 1945	0.268	2.890	0.826	0.285	0.138
		Curimata cyprinoides (Linné, 1758)	6.459	86.313	34.670	29.446	54.472
		Cyphocharax helleri (Steindachner, 1910)	0.153	5.723	1.360	0.216	0.000
		Cyphocharax sp.	5.437	17.602	2.967	0.086	2.299
		Cyphocharax spilurus (Günther, 1864)	33.772	130.096	36.640	1.825	0.372
	Anostomidae	*Anostomus brevior* Géry, 1960	0.498	2.192	0.516	0.029	0.000
		Leporinus fasciatus (Bloch, 1794)	7.075	64.318	4.179	1.922	7.200
		Leporinus friderici (Bloch, 1794)	155.268	498.337	103.830	106.486	38.033
		Leporinus gossei Géry, Planquette and Le Bail, 1991	1.261	3.328	4.544	10.246	1.219
		Leporinus granti Eigenmann, 1912	7.303	13.472	7.512	4.187	0.962
		Leporinus maculateus Müller and Troschel, 1844	0.204	0.804	0.271	0.000	0.037
	Erythrinidae	*H. aimara* (Valeneiennes, 1840)	189.136	838.031	10.607	18.995	39.800
		Hoplias malabaricus (Bloch, 1794)	4.158	8.071	102.430	43.672	0.499
	Characidae	*Acestrorhynchus falcatus* (Bloeh, 1794)	94.972	265.427	109.422	59.642	0.288
		Acestrorhynchus guianensis Menezes, 1969	38.294	101.316	66.617	105.501	32.884
		Astyanax bimaculatus (Linné, 1758)	1.137	10.257	23.046	13.172	1.572
		Bryconops affinis (Günther, 1864)	11.468	20.614	0.653	0.122	2.751
		Byconops caudomaculatus (Günther, 1869)	23.053	119.966	60.025	121.192	21.809
		Bryconops melanurus (Bloch, 1795)	9.836	31.928	1.392	2.622	0.019
		Charax pauciradiatus Günther, 1864	1.182	13.240	105.860	90.629	15.234
		Jubiaba keithi (Géry, Planquette and Le Bail, 1996)	1.347	3.460	2.839	1.800	0.007
		Jubiaba meunieri (Géry, Planquette and Le Bail, 1996)	0.691	2.826	0.525	0.040	0.034
		Moenkhausia chrysargyrea (Günther, 1864)	0.576	1.675	2.757	4.305	1.013
		Moenkhausia georgiae Géry, 1966	0.498	2.276	1.581	1.804	0.316
		Moenkhausia oligolepis (Günther, 1864)	3.522	7.624	2.039	0.985	0.119
		Moenkhausia surinamensis Géry, 1965	6.081	11.239	1.639	0.710	0.100
		Poptella brevispina Reis, 1989	13.810	41.147	6.640	13.244	18.759
		Triportheus rotundatus (Schomburk, 1841)	83.129	266.146	709.322	926.166	95.947
	Serrasalmidae	*Myleus rhomboidalis* (Cuvier, 1818)	1.458	28.263	7.837	26.255	12.389
		Myleus ternetzi (Norman, 1929)	32.113	169.774	16.519	36.756	11.677
Siluriformes	Auchenipteridae	*Auchenipterus nuchalis* (Spix, 1829)	27.613	78.806	87.575	77.879	36.030
		Parauchenipterus galeatus (Linné, 1766)	5.213	7.307	429.800	77.537	12.728
	Pimelodidae	*Pimelodella cristata* (Müller and Troschel, 1848)	5.490	6.574	0.737	0.000	0.000
		Pimelodella geryi (Hoedeman, 1961)	0.078	0.296	1.044	0.000	0.000
		Pimelodus ornatus Kner, 1858	0.304	7.351	0.937	0.019	0.013
	Loricariidae	*Hypostomus gymnorhynchus* (Norman, 1926)	1.562	4.744	99.348	22.009	5.385
	Doradidae	*Doras carinatus* (Linné, 1766)	0.029	4.081	0.387	0.038	0.111
Gymnotiformes	Sternopygidae	*Eigenmania virescens* (Valenciennes, 1847)	0.101	0.817	0.302	0.000	0.046
Perciformes	Cichlidae	*Geophagus surinamensis* (Bloch, 1791)	0.013	0.980	0.000	0.000	0.062
		Krobia guianensis Regan, 1905	0.092	1.806	0.542	0.000	0.111
Total capture			840.632	3016.405	2085.444	1838.615	447.769

to the same species already analyzed in the river, which also represented more than 99% of the total capture in the reservoir (Table 1).

The trophic structure of the assemblage in the river did not vary significantly seasonally (Table 3). Two feeding guilds dominated the assemblage: the piscivores and the herbivores (Fig. 3). Conversely, all comparisons between the river and the reservoir showed significant differences (Table 3). The most significant differences are a greater contribution of the omnivores and a lower contribution of herbivores and piscivores in the reservoir as compared to the river (Table 4). However, piscivores remained the second guild by order of importance in the lake. The trophic structure did not differ from the first to the second period in the reservoir, although some feeding guilds showed significant differences in their relative contribution. The second period was marked by an increase of invertivores mirroring a decrease of detritivores. The third period was statistically different from the precedent ones and during it the relative importance of omnivores was balanced by an increase of detritivores and herbivores.

Table 2
Results of stomach contents analysis on the fish species in the Sinnamary River. Data are the mean percentages by volume of each food item in the stomachs

Species	NB analyzed	Vegetal material	Algae	Terrestrial invertebrates	Plankton	Chaoboridae	Decapodes	Other aquatic invertebrates	Fish	Detritus and sediment	Guild
A. brevior	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	Detritivore
C. cyprinoides	16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	Detritivore
Cyphocharax sp.	14	0.00	0.00	0.00	0.00	0.00	0.00	4.29	0.00	74.29	Detritivore
C. spilurus	21	23.81	0.00	0.00	0.00	0.00	0.00	0.00	4.76	71.43	Detritivore
C. zunevei	20	0.00	0.00	1.00	0.00	0.00	0.00	2.00	0.00	97.00	Detritivore
H. unimaculatus	12	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	98.33	Detritivore
H. gymnorhynchus	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	Detritivore
A. falcatus	32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	Piscivore
A. guianensis	22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	Piscivore
C. pauciradiatus	13	0.00	0.00	7.69	0.00	0.00	15.38	0.00	76.92	0.00	Piscivore
H. aimara	10	0.00	0.00	0.00	0.00	0.00	10.00	0.00	90.00	0.00	Piscivore
H. malabaricus	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	Piscivore
P. ornatus	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	Piscivore
A. bimaculatus	5	30.00	0.00	70.00	0.00	0.00	0.00	0.00	0.00	0.00	Invertivore
A. nuchalis	147	10.54	0.00	81.61	0.00	3.17	0.00	4.12	0.54	0.00	Invertivore
B. affinis	60	5.17	0.00	90.61	0.00	0.00	0.00	4.22	0.00	0.00	Invertivore
B. caudomaculatus	118	21.80	0.00	76.26	0.00	0.00	0.00	0.75	0.85	0.34	Invertivore
E. virescens	7	0.00	0.00	70.00	0.00	0.00	0.00	15.71	0.00	14.29	Invertivore
J. meunieri	5	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	Herbivore
C. helleri	2	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	50.00	Herbivore
H. quadrimaculatus	35	28.57	19.43	0.00	0.00	0.00	0.00	1.14	0.00	48.00	Herbivore
L. fasciatus	4	50.00	0.00	25.00	0.00	0.00	0.00	0.00	0.00	25.00	Herbivore
L. friderici	139	75.18	0.29	8.59	0.00	0.00	0.14	1.37	8.53	5.47	Herbivore
L. gossei	2	50.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	30.00	Herbivore
L. granti	14	60.71	0.00	21.43	0.00	0.00	0.00	0.00	7.14	10.71	Herbivore
M. rhomboidalis	6	96.67	0.00	0.00	0.00	0.00	0.00	3.33	0.00	0.00	Herbivore
M. ternetzi	145	97.40	0.00	1.45	0.00	0.00	0.00	0.19	0.00	0.97	Herbivore
K. guianensis	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	40.00	60.00	Omnivore
J. keithi	12	43.33	0.00	48.33	0.00	0.00	0.00	0.00	8.33	0.00	Omnivore
B. bimaculata	3	0.00	0.00	0.00	66.67	0.00	0.00	0.00	0.00	33.33	Omnivore
B. melanurus	136	29.74	0.00	66.24	0.00	0.49	0.00	1.48	0.00	2.06	Omnivore
D. carinatus	11	9.09	3.64	9.09	0.00	0.00	0.00	32.12	0.00	42.42	Omnivore
G. surinamensis	3	0.00	0.00	33.33	0.00	0.00	0.00	33.33	0.00	33.33	Omnivore
L. maculatus	2	50.00	0.00	40.00	0.00	0.00	0.00	0.00	0.00	0.00	Omnivore
M. chrysargyrea	4	50.00	0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	Omnivore
M. georgiae	32	46.56	0.00	47.60	0.00	0.00	0.00	1.46	0.63	3.75	Omnivore
M. oligolepis	33	35.66	0.00	61.31	0.00	0.00	0.00	0.00	0.00	3.03	Omnivore
M. surinamensis	64	62.32	0.94	32.99	0.00	0.00	0.00	0.31	0.00	3.44	Omnivore
P. brevispinna	112	35.25	0.00	60.80	0.00	0.00	0.08	0.89	1.52	1.46	Omnivore
P. cristata	4	12.50	0.00	25.00	0.00	0.00	0.00	12.50	0.00	50.00	Omnivore
P. galeatus	5	5.00	0.00	65.00	0.00	0.00	10.00	0.00	20.00	0.00	Omnivore
P. geryi	2	60.00	0.00	20.00	0.00	0.00	0.00	10.00	0.00	0.00	Omnivore
T. rotundatus	201	63.81	0.30	30.34	0.00	0.00	0.14	1.08	3.57	0.76	Omnivore

Resources use in the river was comparable from one season to the other. The only apparent difference was the reduction of detritus in the high water periods when fish, vegetal matter and terrestrial invertebrates increased in importance (Fig. 4). In the reservoir, aquatic organisms are much more important than in the river. Plankton and Cha-

Table 3
Probabilities associated with the ANOSIM test on the distributions of guilds biomass in the fish assemblages. HW: river high water season; LW: river low water season; PER1: reservoir 1994–1995; PER2: reservoir 1996–1997; PER3: reservoir 1998–2000. In bold: significant differences

Samples	HW	LW	PER1	PER2
LW	0.162			
PER1	**0.001**	**0.001**		
PER2	**0.001**	**0.001**	0.206	
PER3	**0.002**	**0.005**	**0.001**	**0.001**

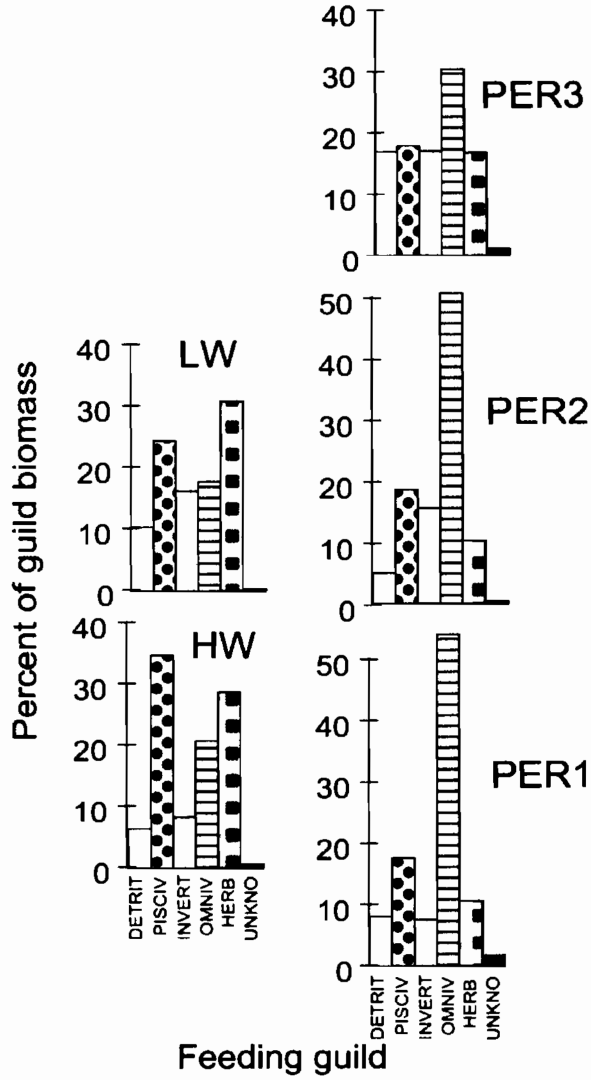

Fig. 3. Distribution of fish biomass by feeding guilds in the fish assemblages of the Sinnamary River in high (HW) and low (LW) water seasons and of Petit-Saut Reservoir at three consecutive periods (PER1, PER2, PER3). DETRIT, detritivore; PISCIV, piscivore; INVERT, invertivore; OMNIV, omnivore; HERB, herbivore; UNKNO, species with diet not determined.

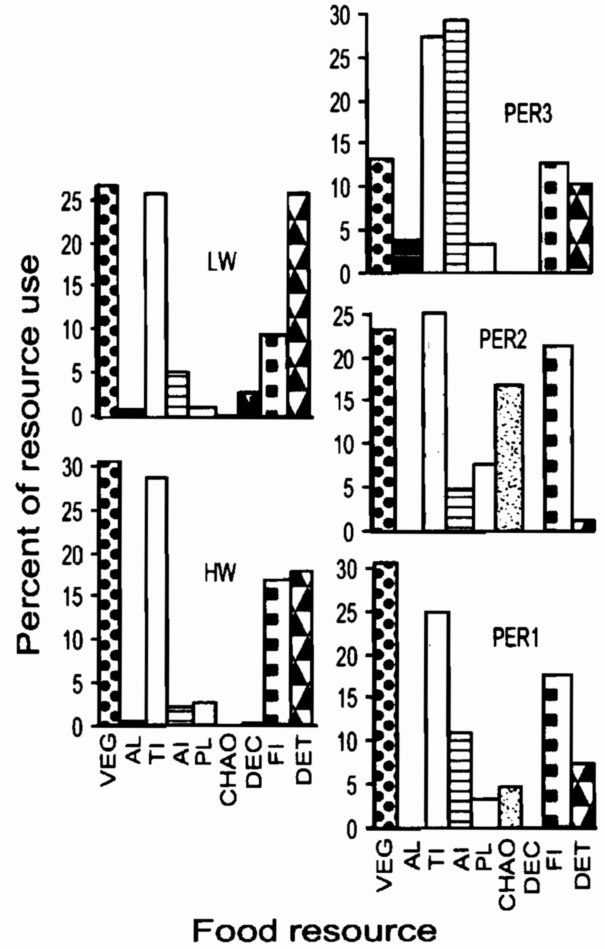

Fig. 4. Distributions of resource use by the fish assemblages of the Sinnamary River in the high (HW) and low (LW) water seasons and of the Petit-Saut Reservoir at three consecutive periods (PER1, PER2, PER3). VEG, higher plant matter; AL, algae; TI, terrestrial invertebrates; AI, aquatic invertebrates; PL, plankton; CHAO, chaoboridae larvae; DEC, decapodes; FI, fish; DET, detritus.

oborid larvae reached a peak in the physical stabilization period when other aquatic invertebrates (mainly Dipterids and Ephemeropterids) were dominant in the ecological stabilization phase. Higher plants were the main resource used by the assemblages in the filling phase, and its importance diminished as the time passed. Terrestrial invertebrates remained an important food resource until the end of the observation period.

4. Discussion

Species diets in the Sinnamary River were, for most of them, similar to diets reported in previously published data. The only noticeable discrepancies were for some invertivores

Table 4
Probabilities associated with Kolmogorov–Smirnov tests between groups of samples for each of the guilds composing the assemblages. HW: river high water season; LW: river low water season; PER1: reservoir 1994–1995; PER2: reservoir 1996–1997; PER3: reservoir 1998–2000. In bold: significant difference

Guild	HW/LW	HW/PER1	HW/PER2	HW/PER3	LW/PER1	LW/PER2	LW/PER3	PER1/PER2	PER1/PER3	PER2/PER3
Detritivores	0.461	0.320	0.411	**0.038**	0.594	**0.004**	0.101	**0.028**	**0.023**	**<0.001**
Piscivore	0.163	**<0.001**	**0.006**	**0.010**	0.071	0.145	**0.010**	0.774	**0.027**	0.125
Invertivore	0.101	0.148	**0.038**	**0.010**	0.125	0.325	0.195	**0.001**	**0.005**	0.523
Omnivore	0.673	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	0.598	**<0.001**	**<0.001**
Herbivore	0.540	**<0.001**	**<0.001**	0.109	**<0.001**	**<0.001**	**<0.001**	**0.007**	**<0.001**	**<0.001**

and omnivores. *Eigenmmania* species are known to be benthic feeders, picking aquatic insect larvae on the bottom (Ellis, 1913; Goulding et al., 1988). In the Sinnamary River, aquatic invertebrates are rare because of the strong current and so this species completes its diet with terrestrial insects. The same cause makes the dominant food items for omnivores to be of an exogenous origin, a fact that has already been noted in French Guiana rivers (Boujard et al., 1990; Horeau et al., 1996).

The trophic structure of the fish assemblage in the Sinnamary River appears to be poorly diversified. Specialized guilds are few; there are no planktivores, a few exclusive aquatic invertebrates feeders and many omnivores. As a comparison, eight feeding guilds were recognized using the same methodology in the fish communities of the Tocantins River (Mérona et al., 2001). The Sinnamary situation seems to be intermediary between small streams where most of the species are omnivorous (Knöppel, 1970; Saul, 1975; Soares, 1979) and large rivers or floodplains where the food partitioning is very fine (Marlier, 1958; Mérona et al., 2001). The relative importance of generalist species could be related to the high level of disturbance of the environment (Southwood, 1988), which also contributes to the maintenance of the system in a "juvenile" state (Frontier and Pichod-Viale, 1991). Although the hydrological regime in the Sinnamary River has a general seasonal pattern, it is marked by numerous unpredictable abrupt changes in water level and discharge (Ponton and Mérona, 1998). This fact can also explain the similarity in trophic structure in the river in different seasons. It is also hypothesized that the physical features of the Sinnamary River, which has a steep-sided bed, contribute to the availability of allochthonous resources over the whole year.

When a river is dammed, there is a rapid transformation in the type of the food resource available to fish. The filling of the reservoir makes large quantities of food of terrestrial origin accessible, either as parts of higher plants or invertebrates (Lowe-McConnell, 1973; Petr, 1975). Later on, autotrophic production becomes established (Baxter, 1977) which includes a pelagic compartment with the development of phytoplankton and zooplankton and a benthic compartment on the bottom or on the submerged substrates. The data presented here show that, although riverine species are not necessarily adapted to use these new resources, the assemblage as a whole is able to exploit them. Resources of terrestrial origin (higher plant products and terrestrial invertebrates) are the first to be exploited by fish already adapted to their consumption. The great decline of higher plant resource in the last stage of the reservoir formation is evidently related to the death of the flooded vegetation and the concomitant interruption of the falling of leaves and fruits in the water. Conversely, terrestrial invertebrates maintained their dominant position as a resource until the end of the observation period, 7 years after the closure. The fact that many species in the river are pre-adapted for preying on terrestrial insects (Horeau et al., 1996) together with the great abundance of termites (*Nasutitermes* sp.) falling in the water with the dead branches can explain this relative importance.

Fish as a resource is relatively more important in the reservoir as compared to the river but the relative contribution of piscivore species is lower. Some observations on large reservoirs in the tropics reveal a great development of piscivores. That was the case in Tucurui Reservoir where the resource "fish" is the most important and piscivores dominate the assemblage (Mérona et al., 2001), and in Itaipu (Hahn et al., 1998). In many other reservoirs piscivores, although surpassed by other guilds, are also abundant. This fact was reported in Guri (Novoa et al., 1991), Kainji (Ita, 1984), Kariba (Marshall, 1984), and Bukit Mehra (Siaw-Yang, 1988). Fishes are supposed to be an abundant resource in the beginning of the lake formation because of the reproduction success of many forage species expected in that period. The high contribution of this guild in the Sinnamary River is the consequence of the relative abundance of a large predator species: *Hoplias aimara* whose individual weight can reach 30 kg. Nonetheless, this species remains rare in the lake where the piscivore species are medium sized.

The most marked differences in resources used by the fish assemblage between the river and the reservoir are those of aquatic origin. In large man-made lakes, where the pelagic compartment is extremely expanded, plankton constitutes an abundant resource easily available to fish (Fernando, 1994; Popp et al., 1996). In Petit-Saut Reservoir, it appears that plankton abundance (including chaoborid larvae) is highly variable as it also is in other man-made lakes (Hanna and Schiemer, 1993; Horeau et al., 1998). Although it is present in all periods, its relative importance as a resource reaches a peak in the physical stabilization phase. Conversely, aquatic invertebrates, whose importance in the river is insignificant, became the second resource by order of importance in the ecological stabilization phase. These new resources are exploited by omnivore and invertivore species. Two omnivore species dominated the fish assemblage: *Triportheus rotundatus* and *Parauchenipterus galeatus* (Mérona, 2002). Omnivores are generally dominant in relatively small reservoirs (Agostinho et al., 1997; Arcifa et al., 1988; Ferreira, 1984; Hahn et al., 1997; Viera, 1982; Zarate et al., 1991). However, during the filling stage of Volta Lake (Ghana), the largest tropical reservoir established in a forested area, omnivore species were also very abundant (Petr, 1969). Finally, detritus, which in our definition include sediment, mud and organic layer on substrates, increased in the third period of formation of the lake and detritivores follow the same tendency. A great development of detritivores was also observed in Salto Grande, Argentina (Delfino and Baigun, 1991), Guri, Venezuela (Novoa et al., 1991), Kainji, Nigeria (Ita, 1984), Bukit Mehra, Malaysia (Siaw-Yang, 1988) and Itaipu, Brazil (Agostinho et al., 1994). The quantity of detritus and its nutritional value is indeed favored by the flooding of a reservoir because of the great amount of nutrients sedimenting on the bottom (Horn and Horn, 1998). Furthermore, in reservoirs established in forested areas, there is a great increase in the number of substrates available for the development of periphyton.

As a whole, omnivory, generally associated with an opportunistic feeding behavior, was the most successful strategy in colonizing the new-formed reservoir. This observation confirms the hypothesis that seasonal and stochastic fluctuations in the environment favor generalists because of their capacity to reduce the time dedicated to food searching and so to optimize the gain of energy in the feeding process (Schoener, 1971; Wilson and Yoshimura, 1994). When the environment stabilizes, some species develop feeding specializations and it could be hypothesized that competition processes tend to limit the development of generalist species. However, this hypothesis is not verified in other reservoirs in South America. In Tucurui and Itaipu reservoirs specialist feeders dominated the community as soon as the first stages of formation (Hahn et al., 1998; Mérona et al., 2001). These two reservoirs are established in very large hydrographic basins, including floodplains (i.e. lacustrine habitats) and house very diversified fish faunas with species already adapted to life in standing waters.

Another observation supported by the data presented here is the increase in the relative importance of resources of aquatic origin during the ageing process of the reservoir. However, this increase is still limited. In Itaipu reservoir resources of terrestrial origin remained important 6 years after the closure of the dam (Agostinho and Zalewski, 1995). In Petit-Saut the percentage of higher plant material and terrestrial invertebrates was 55.8% in the river and 42.5% in the reservoir during the third period. This suggests that the process of stabilization of the new ecosystem is far from complete.

5. Conclusions

Four general conclusions can be drawn from our observations.

- The fish assemblage is able to use the new resources generated in the lake environment. This phenomenon reveals itself early in the process of reservoir formation.
- In the process of transformation of a river into a lake, there is an increase of autochthonous production, which translates in an increase in the contribution of food of aquatic origin available to the fish assemblage. However, this process can be very slow for reservoirs established in forested areas where the decomposition of trees takes a long time.
- Omnivorous species, able to take advantage of a large variety of foods, are favored by the abrupt change in the environment. This adaptive advantage declines when the environment stabilizes and competition takes place with species specializing on a definite kind of food.
- The trophic structure of the community in a reservoir depends on the ichthyofauna composition in the original river. In reservoirs established in large hydrographic basins, omnivores are seldom dominant because of the existence of species already specialized in consuming the lake resources.

The results of this study, conducted as part of a broader project on the environmental impacts of the Petit-Saut Dam, improve our knowledge on fish communities in tropical reservoirs, a scientific field where data are scarce. From the perspective of a multi-purpose use of reservoirs and particularly the development of fisheries, the ability to predict the type of fish species likely to develop in these environments is essential. However, the factors determining the ultimate composition of a fish community are numerous and the multiplication of empirical observations is the only way to determine general patterns.

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