

Early dry-season community structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after hydrodam operation

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Synopsis

We examined fish community structure and habitat use at the start of the dry seasons: (1) in 10 tributaries of the River Sinnamary (French Guiana) before and after the start of dam operation, and (2) in 10 upstream tributaries and at 10 littoral sites in the newly-created reservoir after the start of operation to assess the impact on fish juveniles of a hydroelectric dam built on the river's lower section. After the first year of dam operation, juvenile fish communities downstream of the dam showed an important decrease of the relative abundance of Characiformes, and Perciformes dominated. Principal components analysis revealed a distinct upstream-to-downstream progression in the juvenile fish communities with post-reservoir downstream and reservoir sites representing transitions between the upstream and pre-reservoir downstream sites. Canonical correspondence analysis and electivity indices of fish-habitat associations revealed three relatively distinct groups of sites, corresponding to the downstream, reservoir and upstream taxa. The proportion of juveniles presenting higher-than expected frequencies (Fisher's exact test) towards local environmental variables was higher for taxa more often caught in upstream sites. Inversely, juvenile taxa more frequently observed in downstream and reservoir sites appeared less selective towards local environmental characteristics. In the downstream reaches of the river, hydrodam operation is expected to drive the fish community towards a new biologically accommodated state where tolerant species will dominate and sensitive species will be lacking.

Rationale

Unlike many large tropical rivers, whose seasonal hydrological cycles are more predictable (Bayley 1988), small tropical rivers such as those in French Guiana are subjected to extreme short-term variability in discharge throughout most of the year (Westby 1988). Initial investigations have revealed the important influence of hydrological regime on the density of adult fishes in the floodplain and trib-

utaries of Guianese rivers (Boujard & Rojas-Beltan 1988, Boujard 1992), however there have been no published investigations on any aspect of the life history of larvae and juveniles. In fact, little is known of the reproductive styles, early development, growth, behaviour (Géry 1969, Westby 1988), and indeed the identity of some fish species in rivers of French Guiana. This lack of information is of particular concern with respect to the River Sinnamary, where a hydroelectric dam recently began oper-

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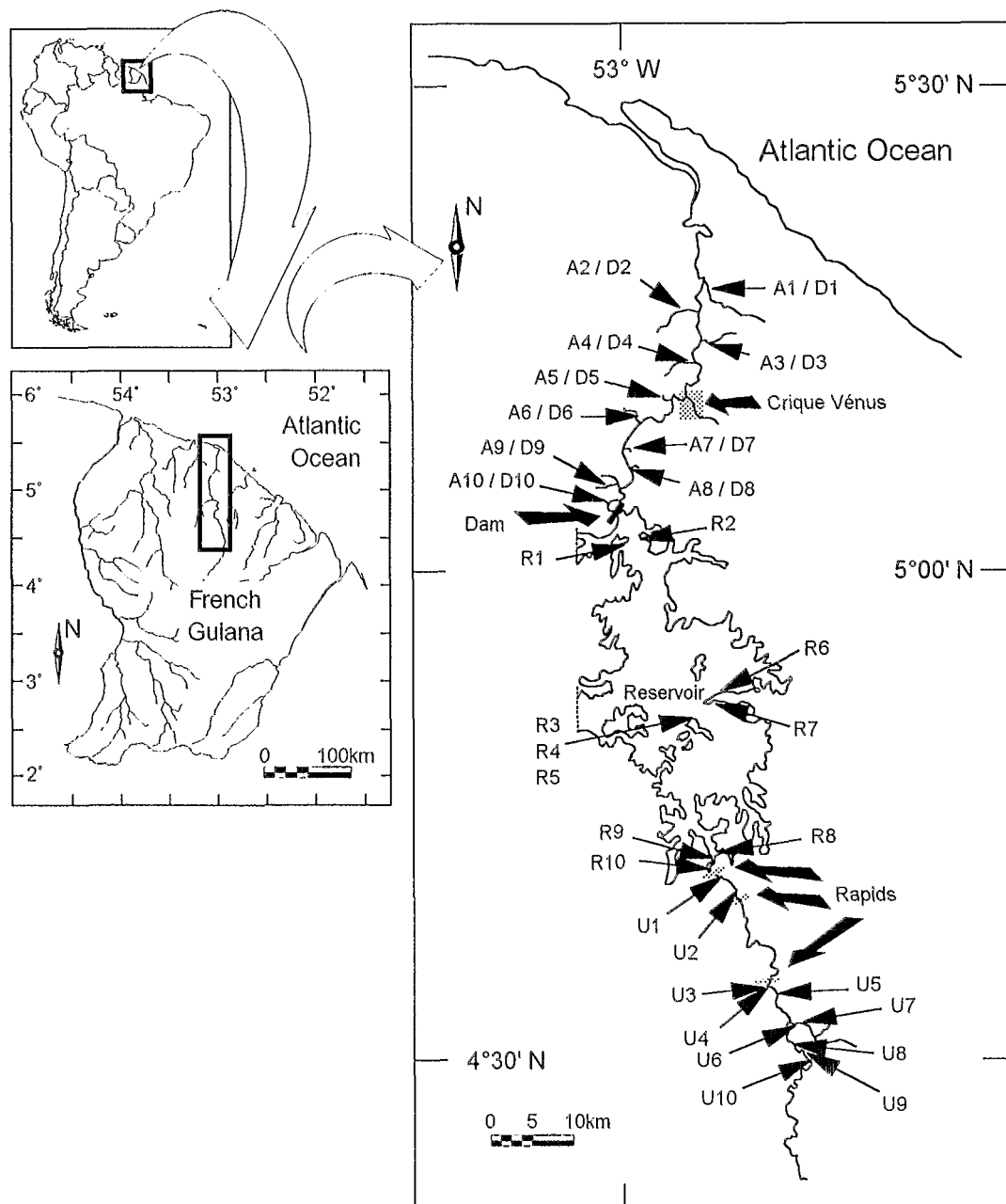


Figure 1. Map of the River Sinnamary (French Guiana, South America), the reservoir at Petit Saut as it appeared in August 1994, and the study sites (A1 to A10: downstream 1993, D1 to D10 downstream 1994, R1 to R7: lower reservoir 1994, R8 to R10: upper reservoir 1994 and U1 to U10: upstream 1994). Only sampled tributaries are presented.

ation in the river's lower section at Petit Saut (Figure 1). As a consequence, assessment of the dam's impact on the success of fish reproduction will be difficult.

Species-environment interactions play an important role in the life-history of freshwater fishes, especially with respect to reproductive and recruitment success. Among the most influential environmental factors in tropical river systems is hydrological regime (Bayley 1988). As reproduction in tropical fishes is often set in motion by wet season floods (Welcomme 1979, Lowe-McConnell 1987, Munro 1990, Boujard 1992, Schwassmann 1992, Val & Almeida-Val 1995), hydroelectric regulation of the Sinnamary's seasonal hydrological regime could have devastating effects on fish populations in the floodplain tributaries downstream of the dam.

The movement of young and small fish between the main channel(s) of large tropical rivers and their flood plains is well known (Welcomme 1985). However, in smaller meander-type rivers such as the River Sinnamary, adult fish migrate between the river and its floodplain via the tributaries (Boujard 1992), which function throughout most, if not all, of the year as feeding, spawning and nursery grounds for fish larvae and juveniles (D. Ponton unpublished observations).

The aims of the present investigation on young fishes in tributaries of the River Sinnamary were twofold: (1) to compare juvenile community structure and fish-habitat associations in the lower Sinnamary before and after the start of the hydrodam's operation; and (2) to develop an empirical model of species-habitat associations in the Sinnamary's tributaries. The beginning of the dry season, July/August was chosen because it is during this period when the young of most species have reached their juvenile period of development (D. Ponton unpublished observations). According to Boujard's (1992) proposed model of the annual cycle in Guianese rivers, July is the sixth interval, when floodplain 'fish are fat and return to the main river'. However, Boujard et al.'s (1990) study on the River Arataye, upon which the temporal aspects of his model appear to be based (Boujard 1992), indicated that young and small fishes still inhabited the floodplain of the trib-

utaries in November, at the end of the dry season. Recent evidence supports this pattern (D. Ponton unpublished observations) and suggests that the dry season in Guianese rivers, similar to that in other South American rivers (Welcomme 1985) and to the end of summer in some European rivers (e.g. Copp 1989, Copp et al. 1994), is a crucial period in the survival of young of the year riverine fishes.

Study sites, material and methods

The River Sinnamary is approximately 260 km in length (Figure 1). It drains an area of 6565 km² with a mean annual precipitation of 3000 mm and has a mean annual discharge of 230 m³ s⁻¹, ranging between 120 and 400 m³ s⁻¹ (for a description of the entire river system, see Boujard 1992 and Tito de Moraes et al. 1995). The river's lower course meanders through a old flat coastal plain dominated by palms *Mauritia flexuosa* and *Euterpe oleracea* as well as 'moutouchis' *Pterocarpus officinalis*. In this section, tidal flows strongly influence the river's level both on a daily and a seasonal basis, with the salt waters of the flood tide pushing up under the river's fresh waters. Upstream, four forest types are associated with the river and its tributaries (Granville 1979): terra firme arborescent assemblage, permanent swamp forest rich in monocotyledons, flooded forests dominated by pteridophytes and palm swamps (for a complete list of plant species associated with the River Sinnamary see Tito de Moraes et al. 1995).

During the 1992–1993 rainy season, successive flow events of short duration were superimposed on the increase of the river water level from November onwards (Figure 2). Maximum values were observed between March and May, when water levels were about 5 m above those observed at low flow. Starting on 6 January 1994, impoundment immediately induced a rapid increase in the reservoir's water level. For technical reasons, the reservoir water level was kept at 31 m from the beginning of the dry season onwards. During most of the period needed to fill the reservoir, downstream river flow was kept at 100 m³ s⁻¹ except during some short hydrological events. As a consequence, the river level remained low during most of the 1993–1994

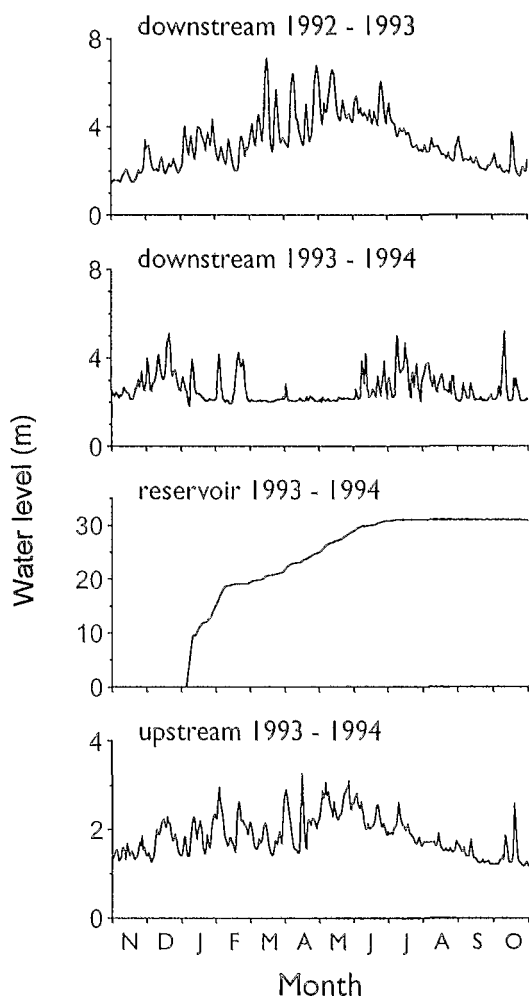


Figure 2. Water levels downstream from the hydroadam in 1992–1993 and 1993–1994, in the reservoir and upstream in 1993–1994, from November (beginning of the rainy season) to October. Note the different scales on the vertical axes.

rainy season. A natural flow regime, including fluctuations, resumed in the river downstream of the dam as soon as the filling of the reservoir stopped in July 1994. Upstream from the reservoir, flow regime presented a natural pattern with water level differences between low and high flow reaching 2 m and the highest water levels being observed between April and May (Figure 2).

The fish were collected from stretches of known length in 10 tributary streams downstream from the dam in 1993 (henceforth, the pre-reservoir downstream) and 1994 (post-reservoir downstream), 10

tributaries upstream from the reservoir in 1994 and 10 stations in the littoral zone of the reservoir in 1994 (Figure 1), seven in the mid-to-lower reservoir (lower reservoir) and three at its upstream end (upper reservoir). The exact locations of sampling sites were chosen at random (i.e. without knowing whether fish were present or not) but were restricted to places where rotenone sampling had been found to be the most efficient for sampling young fish, i.e. sites with maximal depth < 1.5 m and water velocity < 20 cm sec⁻¹. Indeed, deeper sites impede an efficient retrieval of sunken fish and greater water velocities require the use of greater quantities of toxicant, which could have potentially disastrous effects on downstream fishes. At each site, water temperature, pH, oxygen and conductivity were first measured with a ICM 51000 multiparameter analyzer before any disturbance. Then, the extents of the sampling sites were delimited by stop nets (1 mm mesh) carefully set on the bottom in order to avoid fish escapes. Three successive doses of PREDATOX® (6.6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France) were mixed in the water in order to reach the effective contact time¹ (sensu Gilderhus 1972) of the most resistive juveniles taxa of the community with final concentration never exceeding 3 mg l⁻¹. This gradual increase in rotenone concentration allowed the progressive collection of the least resistant (mostly small Characiformes), then the moderately resistant (mostly Siluriformes), and finally the most resistant juvenile fish (mostly Gymnotiformes) at the water surface before they died and sank to the bottom. At each sampling site fish collection was performed by a minimum of 4 persons equipped with 1 mm mesh dip nets. All specimens were immediately preserved in 90% alcohol. The fish not surfacing after rotenone application were retrieved by stirring the water in crevices and under trunks, removing woody debris, and carefully checking for dead fish in leaf litter (total duration of sampling 1–2 hours). No attempt was made to detoxify rotenone outside the sampling area with potassium permanganate because: (1) sampling vol-

¹ Effective contact time refers to the length of time a fish must be exposed to rotenone to result in death.

ume was always small compared to surrounding waters; (2) most fish species outside of the sampling site were found to detect and avoid rotenone; (3) clay, largely represented in our sampling site, is known to reduce rapidly the toxicity of rotenone (Gilderhus 1982); and (4) above 23 °C the half life of this toxicant is less than 1 day (Bettoli & Maceina 1996).

After fish sampling, eleven other environmental variables were measured quantitatively (mean water depth, mean channel width, water velocity), visually estimated (percentage of bottom covered by mud and sand in substrate, by leaf cover on bottom, by branches, tree trunks, etc. within site), and determined by cartographic methods (distance from river, distance from estuary), or assigned by qualitative class (transparency, channel shape). For bottom substrate, at least three or four samples were examined to verify visual estimates. Transparency was judged by eye using visibility of the bottom at a depth of about 0.5 m. Distance from estuary was estimated roughly, as the most recent 1/50 000 maps available to us date from 1966 (sheets NB-22-VI-II-1a, -1c & -2b; Institut Géographique National, Paris), and field experience proved them to be largely approximate.

In the laboratory, all the collected specimens were transferred to 70% alcohol and identified using keys for adults by Géry (1977), Le Bail et al.², Rojas-Beltran³, Lauzanne (unpublished) and keys for young stages by Ponton (unpublished). Standard lengths (SL) were compared to the size at first maturity in order to separate juveniles from adults. Sizes at first maturity were obtained from fish species caught with gill nets (44% of species: L. Lauzanne, L. Tito de Morais & B. de Mérona unpublished-

ed data) or different types of traps (11% of species: A. Bezançon & D. Ponton unpublished data), scientific and aquarium literature (5% of species). When size at first maturity was not available (40% of species), length-frequency distributions were established and specimens belonging to the first modal size group of the population's size distribution were considered as immature. The number of specimens for each taxon and the number of taxa at a given site were then divided by the site's surface area to determine relative densities (individuals m⁻²) and the relative number of taxa per sample (taxa m⁻²).

Comparisons of the mean number of species between site and years were performed on the residuals of the linear regression for species richness vs. sampling area (species richness = 0.075 * sampling area + 14.484, $F = 4.715$, $df = 39$, $p = 0.036$) by using an exact permutation test (Good 1993) with a modified SAS macro (Foster 1995 and personal communication). As the number of individuals was not related significantly to sampling area ($F = 1.4334$, $df = 39$, $p = 0.2386$), comparisons of the mean relative abundance of individuals were directly tested by using the same permutation test. Shannon diversity index and evenness were also calculated for each section of the river in 1993 and 1994. Fish reproductive potential at the various sites was assessed from the presence and absence of fish taxa at the various sites (e.g. Copp 1989) using principal components analysis, which is appropriate for relatively homogeneous data sets with relatively low species turnover (Gauch 1982).

Thirteen environmental variables were retained for analysis. pH (mean = 5.5, SD = 0.446) and conductivity (mean = 26.2, SD = 3.282) varied little and were excluded. Retained environmental data were converted to semi-quantitative categories using reciprocal and natural logarithmic transformations for oxygen content (ppm) and distance from estuary, respectively, and then tested for normality (Liliefors 1967). Using software by Chessel & Dolédec⁴ and Thioulouse (1989), the data on taxa and envi-

² LeBail, P.Y., P. Planquette & J. Géry. 1983. Clé de détermination des poissons continentaux et côtiers de Guyane. Bull. Liaison Groupe Rech. Guyane N° 6 & 8. INRA, 97310 Kourou, French Guiana.

LeBail, P.Y., P. Planquette & J. Géry. 1984. Clé de détermination des poissons continentaux et côtiers de Guyane. Bull. Liaison Groupe Rech. Guyane N° 9. INRA, 97310 Kourou, French Guiana, France.

³ Rojas-Beltran, R. 1984. Clé de détermination des poissons continentaux et côtiers de Guyane. Bull. Liaison Groupe Rech. Guyane N° 7. INRA, 97310 Kourou, French Guiana, France.

⁴ Chessel, D. & S. Dolédec. 1992. ADE Version 3.7: HyperCard® Stacks and Quick Basic MicroSoft® Program library for the Analysis of Environmental Data. 9 fasc. URA CNRS 1451, Université Lyon 1, 69622 Villeurbanne cedex, France. 820 pp.

Table 1. List of fish taxa, authority, abbreviated species code, number of juveniles (Nj), total number of individuals (Nt) and range of standard length (SL) in study stretches from 10 downstream sites in late July – early August 1993 and 30 others in August 1994.

Order family subfamily	Genus/species	Authority	Taxa code	SL Nj/Nt	Min-max (mm)
Characiformes					
Hemiodontidae					
Hemiodontinae	<i>Hemiodopsis quadrimaculatus</i>	(Pellegrin, 1908)	Hq	18/18	11-62
Curimatidae					
Chilodontinae	<i>Chilodus zunevei</i>	Puyo, 1945	Cz	8/9	20-77
Curimatinae	<i>Cyphocharax helleri</i>	Steindachner, 1910	Ch	15/15	57-88
	<i>Cyphocharax</i> spp.		Cy	736/741	10-98
Anostomidae	<i>Anostomus brevior</i>	Géry, 1960	Av	3/7	60-100
	<i>Leporinus friderici</i>	(Bloch, 1794)	Lf	3/9	70-320
	<i>Leporinus gossei</i>	Géry, Planquette & LeBail, 1991	Lg	1/1	87
	<i>Leporinus granti</i>	Eigenmann, 1912	Lr	6/17	50-181
	<i>Leporinus pellegrini</i>	Steindachner, 1910	Lp	1/1	27
	<i>Leporinus</i> spp. (unidentif. juv.)		LS	6/6	40-145
Erythrinidae	<i>Erythrinus erythrinus</i>	(Schneider, 1801)	Fe	10/10	13-88
	<i>Hoplerethrinus unitaeniatus</i>	(Spix, 1829)	HO	2/2	122-130
	<i>Hoplias aimara</i>	(Val. in Cuv. & Val. 1846)	Ha	33/33	8-167
	<i>Hoplias malabaricus</i>	(Bloch, 1794)	Hm	94/95	11-250
Lebiasinidae					
Pyrrhulininae	<i>Copella carsevensensis</i>	(Regan, 1912)	Cc	305/329	13-39
	<i>Nannostomus beckfordi</i>	Günther, 1872	Nb	85/89	13-28
	<i>Pyrrhulina filamentosa</i>	Val. in Cuv., 1846	Pf	130/182	13-63
Gasteropelecidae	<i>Gasteropelecus sternicla</i>	Linnaeus, 1758	Gs	5/5	21-44
Characidae	Characidae sp. (unidentif. juv.)		CS	2/2	10-12
Characidiinae	<i>Characidium</i> gr. <i>fasciatum</i>	Fowler, 1914	Cf	125/125	9-41
	<i>Melanocharacidium blennioides</i>	(Eigenmann, 1909)	Mb	1/1	43-43
	<i>Melanocharacidium</i> sp.		Ms	3/4	16-33
	<i>Microcharacidium eleotrioides</i>	(Géry, 1960)	Me	66/67	11-21
Characinae	<i>Acestrorhynchus falcatus</i>	(Bloch, 1794)	Af	14/17	14-200
	<i>Acestrorhynchus microlepis</i>	(Schomburgk, 1841)	Am	1/1	54-54
	<i>Charax pauciradiatus</i>	Günther, 1864	Cp	1/4	38-132
Cheirodontinae	<i>Pristella maxillaris</i>	(Ulrey, 1894)	Pm	874/874	9-24
	<i>Pseudopristella simulata</i>	Géry, 1960	Ps	1314/1314	9-26
Stethaprioninae	<i>Poptella orbicularis</i>	(Val. in Cuv. & Val., 1849)	Po	3/3	31-42
Tetragonopterinae	<i>Astyanax bimaculatus</i>	(Linnaeus, 1758)	Ab	4/4	39-78
	<i>Astyanax</i> cf. <i>keithi</i>	Géry, Planquette & LeBail, 1996	Ak	151/151	16-71
	<i>Astyanax meunieri</i>	Géry, Planquette & LeBail, 1996	AM	19/19	31-48
	<i>Bryconops</i> sp. 1		B1	44/45	22-114
	<i>Bryconops</i> sp. 2		B2	50/53	28-87
	<i>Bryconops</i> sp. 3		B3	9/9	48-84
	<i>Bryconops</i> spp. (unidentif. juv.)		BS	13/13	13-27
	<i>Hemigrammus boesemani</i>	(Géry, 1959)	Hb	7/12	14/32
	<i>Hemigrammus ocellifer</i>	(Steindachner, 1882)	Ho	675/815	12-31
	<i>Hemigrammus schmardae</i>	(Steindachner, 1882)	Hs	1/1	33
	<i>Hemigrammus unilineatus</i>	(Gill, 1858)	Hu	93/95	11-30
	<i>Hyphessobrycon</i> aff. <i>sovichtys</i>	Schultz, 1944	Hy	6/12	11-23
	<i>Moenkhausia collettii</i>	(Steindachner, 1882)	Mc	2113/2207	13-86
	<i>Moenkhausia chrysargyrea</i>	(Günther, 1864)	MC	74/122	18-87
	<i>Moenkhausia hemigrammoides</i>	Géry, 1966	Mh	171/171	16-35
	<i>Moenkhausia oligolepis</i>	(Günther, 1864)	Mo	670/788	14-98
	<i>Moenkhausia</i> sp.		MO	1/1	55
	<i>Phenacogaster</i> aff. <i>megalostictus</i>	Eigenmann, 1909	Ph	333/408	13-55

Table 1. Continued.

Order family subfamily	Genus/species	Authority	Taxa code	SL N _j /N _i	Min-max (mm)
Siluriformes					
Auchenipteridae	<i>Tatia intermedia</i>	(Steindnacher, 1876)	Ti	18/18	14-45
Pimelodidae	<i>Pimelodella cristata</i>	(Müller & Troschel, 1848)	Pc	42/46	28-120
	<i>Pimelodella gracilis</i>	(Val. in Cuv. & Val., 1840)	Pg	12/14	70-106
	<i>Pimelodus ornatus</i>	(Kner, 1857)	Pt	2/2	130-135
	<i>Pseudopimelodus raninus</i>	(Valenciennes, 1840)	Pr	13/13	11-95
	<i>Pseudopimelodus zungaro</i>	(Humboldt, 1833)	Pz	1/1	28
	<i>Rhamdia quelen</i>	(Quoy & Gaimard, 1824)	Rq	7/7	72-195
Cetopsidae	<i>Hemiketopsis</i> sp.		Hc	1/1	17
Aspredinidae					
Bunocephalinae	<i>Bunocephalus coracoideus</i>	Cope, 1874	Bc	2/3	34-77
Trichomycteridae	<i>Trichomycterus guianense</i>	(Eigenmann, 1909)	Tg	3/3	54-63
Callichthyidae	<i>Corydoras octocirrus</i>	(Nijssen, 1970)	Co	6/6	43-61
	<i>Hoplosternum thoracatum</i>	(Val. in Cuv. & Val., 1840)	Ht	3/3	25-108
Loricariidae	<i>Ancistrus</i> aff. <i>hoplogenis</i>	(Günther, 1864)	Ah	8/10	24-82
	<i>Harttia surinamensis</i>	Boeseman, 1971	Hr	0/1	101
	<i>Lasiancistrus niger</i>	(Norman, 1926)	Ln	2/4	62-112
Gymnotiformes					
Sternopygidae	<i>Eigenmannia virescens</i>	(Valenciennes, 1847)	Ev	18/19	11-147
	<i>Sternopygus macrurus</i>	(Bloch & Schneider, 1801)	Sm	16/26	31/300
Hypopomidae	<i>Brachypomus beebei</i>	(Schultz, 1944)	Bb	76/105	25-196
	<i>Hypopomus artedi</i>	(Kaup, 1856)	HA	4/13	43-257
Gymnotidae	<i>Gymnotus anguillaris</i>	Hoedeman, 1962	Ga	78/78	36-248
	<i>Gymnotus carapo</i>	Linnaeus, 1758	Gc	82/82	42-335
	<i>Gymnotus</i> spp. (unidentif. juv.)		Gy	17/17	15-34
Cyprinodontiformes					
Aplocheilidae	<i>Rivulus agillae</i>	Hoedeman, 1954	Ra	51/66	9-31
	<i>Rivulus igneus</i>	Huber, 1991	Ri	12/34	11-50
	<i>Rivulus xiphidius</i>	Huber, 1979	Rx	147/147	9-25
Poeciliidae					
Poeciliinae	<i>Poecilia parae</i>	(Eigenmann, 1894)	Pp	66/66	6-21
	<i>Poecilia</i> sp.		Pe	4/4	13-14
Synbranchiiformes					
Synbranchidae	<i>Synbranchus marmoratus</i>	Bloch, 1795	Sy	5/5	101-150
Perciformes					
Nandidae Nandinae	<i>Polycentrus schomburgkii</i>	Müller & Troschel, 1848	Pk	44/51	6/56
Cichlidae	<i>Cleithracara maronii</i>	(Steindachner, 1882)	Cm	38/45	17-67
	<i>Cichlasoma bimaculatum</i>	(Linnaeus, 1758)	Cb	1/1	103
	<i>Crenicichla saxatilis</i>	Linnaeus, 1758)	Cs	253/259	9/175
	<i>Kribia guianensis</i>	(Regan, 1905)	Kg	1404/1418	7-120
	<i>Nannacara anomala</i>	Regan, 1905	Na	338/465	7-62
	<i>Satanoperca</i> aff. <i>leucosticta</i>	(Müller & Troschel, 1848)	Sl	79/87	12-158
Eleotridae	<i>Dormitator macrophthalmus</i>	Puyo, 1944	Dm	3/3	19-21
	<i>Eleotris amblyopsis</i>	(Cope, 1870)	Ea	839/1273	9-71
unidentified fish other than larvae				3/3	9-13
unidentified fish larvae				3/3	5

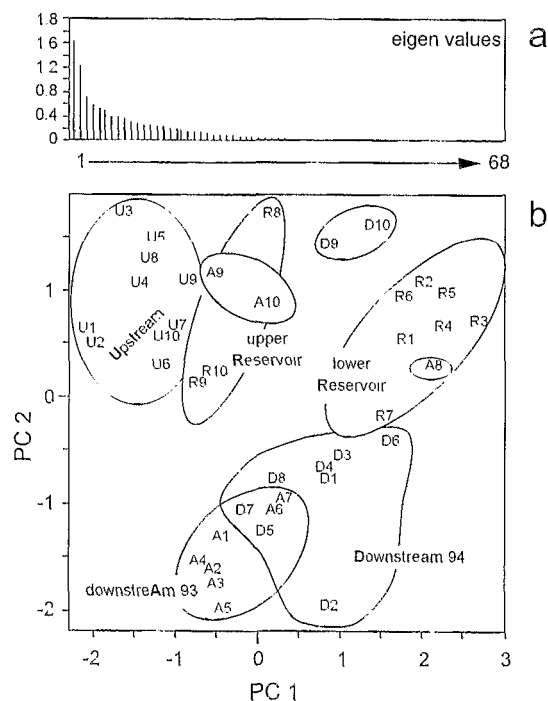


Figure 3. Principal components analysis of the 40 sites by 68 species data matrix in absence/presence, with (a) eigen values and (b) PC1-by-PC2 plot. The first two axes account for 29% of the variability. The upstream (U), reservoir (R), downstream 1993 (A) and downstream 1994 (D) tributaries are indicated.

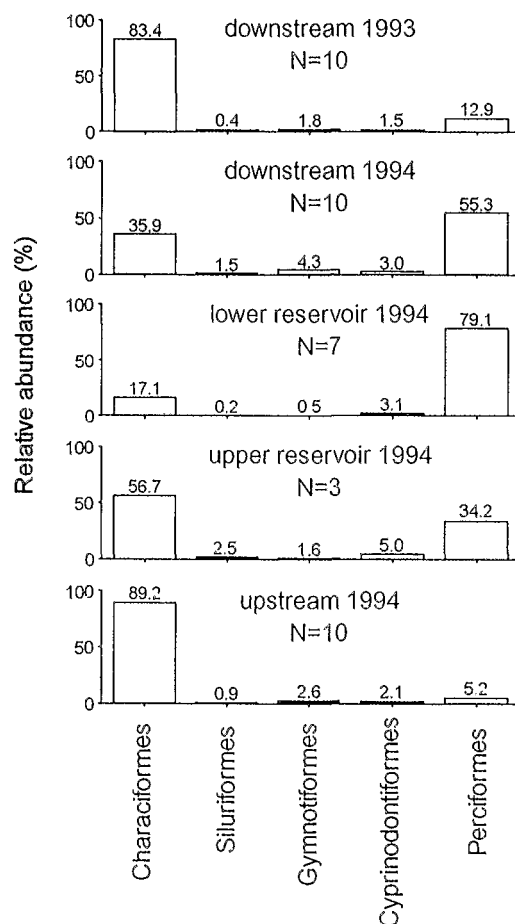


Figure 4. Relative abundance of Characiformes, Siluriformes, Gymnotiformes, Cyprinodontiformes and Perciformes juveniles in the pre-reservoir (1993) downstream and post-reservoir (1994) downstream tributaries, the lower and upper reservoir sites and the upstream (1994) tributaries.

ronmental variables were then subjected to canonical correspondence analysis (CCA), a method of direct gradient analysis that provides an empirically based method of generating both predictive (Ter Braak 1986) and descriptive (Chessel et al. 1987) models of species-habitat associations. CCA is also a powerful alternative to multivariate analysis of variance in the analysis of data from 'before-after-control-impact' studies with and without replication of the impacted site (Ter Braak & Verdonschot 1995).

The samples-by-variables matrix was cross-tabulated with that for samples-by-taxa (converted to absence/presence, 1/0, taxa occurring at less than three sites being eliminated) to determine the frequencies of occurrence and variables-taxa associations (Fisher's exact test, Good 1993), and to generate environmental profiles of habitat use for each taxon. The habitat selectivity profiles were calculated as the difference between the frequency of a tax-

on in the group of samples having a given category of environmental variable and the frequency of that taxon in all samples (non-null).

Results

A total of 13 309 specimens, representing 86 taxa (80 distinct species) from 23 families and 6 orders were collected at the 40 study sites (Table 1). Only *Harttia surinamensis* (Siluriformes, Loricaridae) was represented strictly by adults. The 11 994 juve-

niles were dominated by Characiformes and Perciformes, which accounted for 69.2% and 25% of the individuals, respectively. *Moenkhausia collettii*, *Pseudopristella simulata*, *Pristella maxillaris*, *Cyphocharax* sp. and *Hemigrammus ocellifer* were the most abundant Characiformes. *Krobia guianensis* and *Eleotris amblyopsis* dominated the Perciformes.

Principal components analysis revealed a distinct

upstream-to-downstream progression (Figure 3) in the juvenile fish assemblages of the sites, with post-reservoir downstream tributaries and the reservoir sites representing transitions in the upstream and pre-reservoir downstream sites. Exceptions in this pattern were the two sites just downstream of the dam (A9, A10) and the three sites at the upstream end of the reservoir (R8–10), which had juvenile communities resembling those of the upstream trib-

Table 2. Number (n) and estimated densities (ED, n m⁻²) of individuals, richness (S) and relative richness (RR, S m⁻²) number of taxa, Shannon diversity index and evenness for the different river's sections and year. With SE = standard error.

	Downstream 1993		Downstream 1994		Lower reservoir		Upper reservoir		Upstream 1994	
	n	ED	n	ED	n	ED	n	ED	n	ED
	423	7.83	78	1.04	47	0.42	130	2.17	270	4.50
	411	20.55	197	2.19	55	2.20	399	19.95	489	4.53
	114	2.48	549	14.64	185	7.40	271	5.42	565	9.42
	1703	17.74	269	2.69	23	0.92			756	10.08
	276	4.60	221	5.53	63	2.52			389	11.11
	232	2.90	84	0.93	843	15.33			548	15.22
	153	4.08	188	2.85	61	2.44			357	4.41
	18	1.20	48	1.00					185	4.63
	148	1.97	199	1.99					211	11.72
	123	2.73	25	0.56					667	47.64
Mean	360.10	6.61	185.80	3.34	182.43	4.46	266.67	9.18	443.70	12.33
SE	154.7	2.18	48.0	1.34	11.84	2.00	77.68	5.47	61.17	4.10
	Downstream 1993		Downstream 1994		Lower reservoir		Upper reservoir		Upstream 1994	
	S	RR	S	RR	S	RR	S	RR	S	RR
	19	0.35	16	0.2	10	0.1	20	0.3	28	0.5
	30	1.50	21	0.2	10	0.4	18	0.9	31	0.3
	25	0.54	15	0.4	7	0.3	23	0.5	24	0.4
	25	0.26	15	0.2	5	0.2			25	0.3
	26	0.43	22	0.6	8	0.3			20	0.6
	21	0.26	16	0.2	17	0.3			24	0.7
	16	0.43	21	0.3	13	0.5			22	0.3
	9	0.60	16	0.3					22	0.6
	20	0.27	22	0.2					15	0.8
	18	0.40	8	0.2					20	1.4
Mean	20.9	0.50	17.20	0.28	10.00	0.30	20.33	0.56	23.10	0.58
SE	1.9	0.12	1.39	0.04	1.51	0.05	1.45	0.17	1.41	0.11
	Downstream 1993		Downstream 1994		Lower reservoir		Upper reservoir		Upstream 1994	
	H'	E	H'	E	H'	E	H'	E	H'	E
	3.681	0.659	3.853	0.679	1.996	0.420	3.644	0.694	3.650	0.647

utaries. The pre-reservoir downstream tributary A8 distinguished itself by a higher proportion of Perciformes, as in the lower part of the reservoir (Figures 3, 4).

In 1993, the juvenile fish communities downstream of the dam were dominated by Characiformes (>83% of the individuals), with Perciformes accounting for only 12.9% (Figure 4). In 1994, the same sites showed a significant (Fisher exact test, $p < 0.001$) decrease of the relative abundance of Characiformes (35.9%) when compared to the relative abundance of Perciformes (55.3%). After dam operation, communities in the lower reservoir contained a very high proportion of Perciformes, whereas those in the upper reservoir resembled more those of upstream reaches. Juveniles of Siluriformes, Gymnotiformes and Cyprinodontiformes never exceeded 9% of the sample regardless of the river section. Assuming that the character of the upstream tributaries in 1994 is typical of the tributaries of the entire Sinnamary system prior to dam construction, operation of the hydrodam seems to have effected a decrease in the relative reproductive success of Characiformes in the downstream tributaries (Figures 3, 4).

Juvenile species richness and density varied among sites (Table 2). In 1994, the mean numbers of individuals per unit of sampling were significantly lower in the lower reservoir (exact permutation test, $p \leq 0.05$) and the downstream tributaries ($p \leq 0.05$) than those upstream. Maximum values observed upstream were four times those obtained downstream. The mean number of species per sample reached minimum values in the lower reservoir and maximal values upstream. When compared by permutation tests, mean residuals of the regression for numbers of species verse sample area were high-

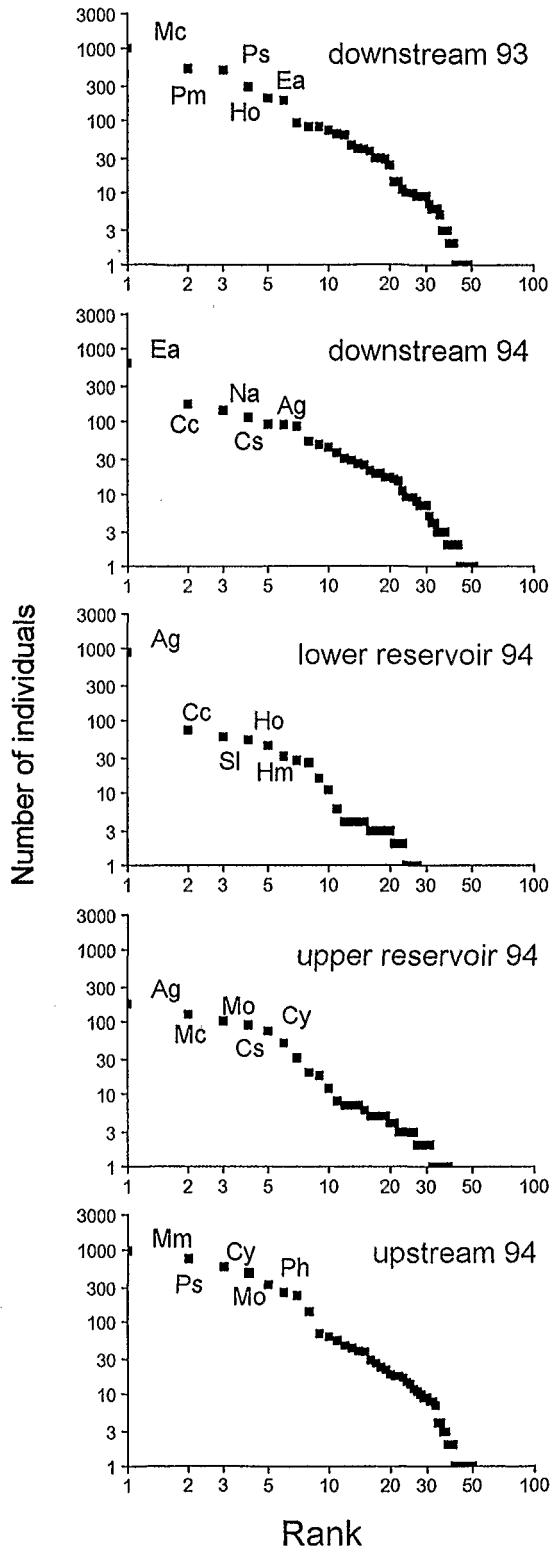
er for the pre-reservoir downstream tributaries, the upper reservoir and the upstream tributaries than post-reservoir downstream and lower reservoir sites (Table 3). It indicates that independently of sampling size the numbers of fish species are lower than expected in the post-reservoir downstream and lower reservoir sites.

The most abundant taxa also varied between river sections and years (Figure 5). Downstream of the dam, the five most abundant juvenile taxa sampled in 1993 were *Moenkhausia collettii*, *Pristella maxillaris*, *Pseudopristella simulata*, *Hemigrammus ocellifer* and *Eleotris amblyopsis*. In 1994, juveniles of the Perciformes Eleotridae *E. amblyopsis* remained dominant in downstream tributaries, followed in abundance by one Lebiasinidae, *Copella carsevegnensis*, and three Cichlidae, *Nannacara anomala*, *Crenicichla saxatilis*, and *Kribia guianensis*. Young *K. guianensis* dominated in the lower reservoir along with *Copella carsevegnensis*, *Satanoperca* sp. aff. *leucosticta*, *Hemigrammus ocellifer* and *Hoplias malabaricus*; these taxa were also amongst the most abundant taxa in the upper reservoir with *Moenkhausia collettii*, *M. oligolepis*, *Crenicichla saxatilis* and *Cyphocharax* spp. The five most abundant juveniles caught in the upstream tributaries are all Characiformes (*Moenkhausia chrysargyrea*, *Pseudopristella simulata*, *Cyphocharax* spp., *M. oligolepis*, and *Phenacogaster* aff. *megalostictus*).

Only nine species of juveniles were collected in at least three downstream sites in 1993 and 1994, respectively (Table 4). For some of them, their association with environmental variables differed between years and when differences occurred, associations were often more significant after dam completion than before. As an example, association between *Eigenmannia virescens* and the type of

Table 3. Comparisons of the residuals of regression for the number of species versus sampling area performed using an exact permutation test (Good 1993) with a modified SAS macro (Foster 1995 and personal communication). Only probabilities for significant differences are given.

	Downstream 1993	Downstream 1994	Lower reservoir	Upper reservoir
Upstream 1994	—	0.0003	0.0001	—
Reservoir (head) 1994	—	0.0279	0.0080	
Reservoir (body) 1994	0.0008	0.0133		
Downstream 1994	0.0197			



←

Figure 5. Ranked abundances of fish juveniles taxa in the pre-reservoir (1993) downstream and post-reservoir (1994) downstream tributaries, the lower and upper reservoir sites and the upstream (1994) tributaries. Only the codes (Table 1) of the five most abundant species are presented.

substrate changed from non significant in 1993 to highly significant in 1994 (Table 4). As potential differences in habitat selection were detected before and after dam closure, analysis of fish-habitat relationships was restricted to 1994 samples.

In the canonical correspondence analysis of fish-habitat associations (Figure 6), distance from the estuary, channel shape and water temperature were the most important environmental variables, i.e. the longest vectors (Ter Braak & Verdonschot 1995). Three relatively distinct groups of sites were revealed by the CCA, corresponding to the downstream, reservoir and upstream tributaries. Although a compromise of the numerous taxa-variables interactions measured, the CCA summarises well the main interacting factors that define habitat of the various taxa. Upstream taxa, such as *Cyphocharax* spp., *Characidium* gr. *fasciatum*, *Pseudopristella simulata*, *Astyanax* cf. *keithi*, *Moenkhausia collettii*, *Moenkhausia oligolepis*, *Phenacogaster* aff. *megalostictus*, *Pimelodella cristata*, and *Rivulus xiphius*, generally preferred asymmetrical channels (mainly two-stage) with moderate water velocities, elevated oxygen levels, and equal proportions of mud and sand (Figures 6, 7a–b).

Downstream taxa, such as *Nannostomus beckfordi*, *Bryconops* sp3, *Hemigrammus unilineatus*, *Eigenmannia virescens* and *Eleotris amblyopsis*, also preferred asymmetrical channels, though mainly narrower 1-stage, as well as slow-to-elevated water velocities, lower oxygen concentrations and water transparencies, and greater proportions of sand in the bottom substrate (Figure 6, 7c). *Crenicichla saxatilis* (Cs), though ordinated amongst the reservoir taxa, is probably a remnant of the Sinnamary's original middle stretches, occurring in high numbers both at the upper reservoir sites and in tributaries downstream of the reservoir (Figure 5), but observed less often than expected in the reservoir (last depth category, Figure 7d). Cs's ordination amongst reservoir taxa is probably due to its preferences for

Table 4. Comparison of the total frequency (fc) of environmental variables and juvenile taxa (ft) present at downstream tributaries in 1993 and 1994. Only significant associations between taxa and variables (Fisher exact test) are presented for each taxa year and variable. See Table 1 for taxa codes.

Taxa	Hm		Pf		B2		Mc		Mh		Ev		Ga		Rx		Pp			
Year	93	94	93	94	93	94	93	94	93	94	93	94	93	94	93	94	93	94		
	fc	ft	7	5	8	7	6	3	9	6	7	6	5	4	4	6	5	4	5	7
Depth (m)																				
0-0.4	3	2	2	0	3	2	1	1	3	1	3	1	2	2	1	2	1	2	0	2
0.41-0.84	4	6	3	3	2	4	3	0	3	4	2	3	3	2	2	2	2	2	3	4
> 0.8	3	2	2	2	3	1	2	2	3	1	2	2	0	0	1	2	2	0	2	1
	0.033																			
Width (m)																				
0-2	3	1	2	0	2	1	1	0	2	1	2	1	1	0	0	0	2	0	0	0
2.1-4	6	5	5	1	5	4	5	1	6	2	5	2	4	3	3	4	2	4	4	4
4.1-10	1	4	0	4	1	2	0	2	1	3	0	3	0	1	1	2	1	0	1	3
reservoir	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0.048																			
Velocity (cm sec ⁻¹)																				
0	2	0	1	0	1	0	2	0	2	0	1	0	1	0	1	0	2	0	2	0
1-5	3	9	3	4	3	6	3	3	3	6	3	6	1	4	0	6	1	4	1	7
6-10	3	1	2	1	2	1	1	0	2	0	1	0	2	0	2	0	1	0	2	0
11-20	2	0	1	0	2	0	0	0	2	0	2	0	1	0	1	0	1	0	0	0
Temperature (°C)																				
23-23.9	2	0	2	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0
24-24.9	4	3	3	1	3	2	3	0	4	0	3	0	2	1	2	2	2	2	3	2
25-25.9	2	7	1	4	2	5	1	3	2	6	2	6	0	3	0	4	2	2	0	5
26-26.9	2	0	1	0	2	0	1	0	2	0	1	0	2	0	2	0	1	0	1	0
≥ 27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0.033																			
Oxygen (ppm)																				
≤ 4	0	3	0	2	0	2	0	0	0	3	0	2	0	1	0	0	0	0	0	2
4.1-5	5	2	3	1	5	2	3	1	5	1	4	1	4	1	3	1	2	1	2	1
5.1-6	3	2	2	2	3	1	2	2	3	1	2	2	0	0	1	2	2	0	2	1
6.1-7	2	3	2	0	0	2	1	0	1	1	1	1	1	2	0	3	1	3	1	3
> 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0.022																			
Transparency																				
Low	2	0	2	0	1	0	2	0	2	0	2	0	0	0	0	0	1	0	2	0
Moderate	2	2	1	1	2	1	1	1	2	2	2	1	0	1	0	1	2	1	0	2
High	6	8	4	4	5	6	3	2	5	4	3	5	5	3	4	5	2	3	3	5
Channel shape																				
Symetrical	2	1	1	0	1	0	2	0	2	0	1	0	1	0	1	1	2	1	2	1
As. meander	4	8	4	5	3	6	3	2	3	5	3	5	3	3	1	4	0	2	2	5
As. 2-stages	4	1	2	0	4	1	1	1	4	1	3	1	1	1	2	1	3	1	1	1
Mud (%)																				
0-33	1	3	0	0	1	3	1	1	1	2	0	2	1	3	1	3	1	3	1	3
34-66	2	1	1	1	2	0	1	1	2	0	1	1	1	0	2	1	1	0	2	0
67-100	7	6	6	4	5	4	4	1	6	4	6	3	3	1	1	2	3	1	2	4
	0.003																			

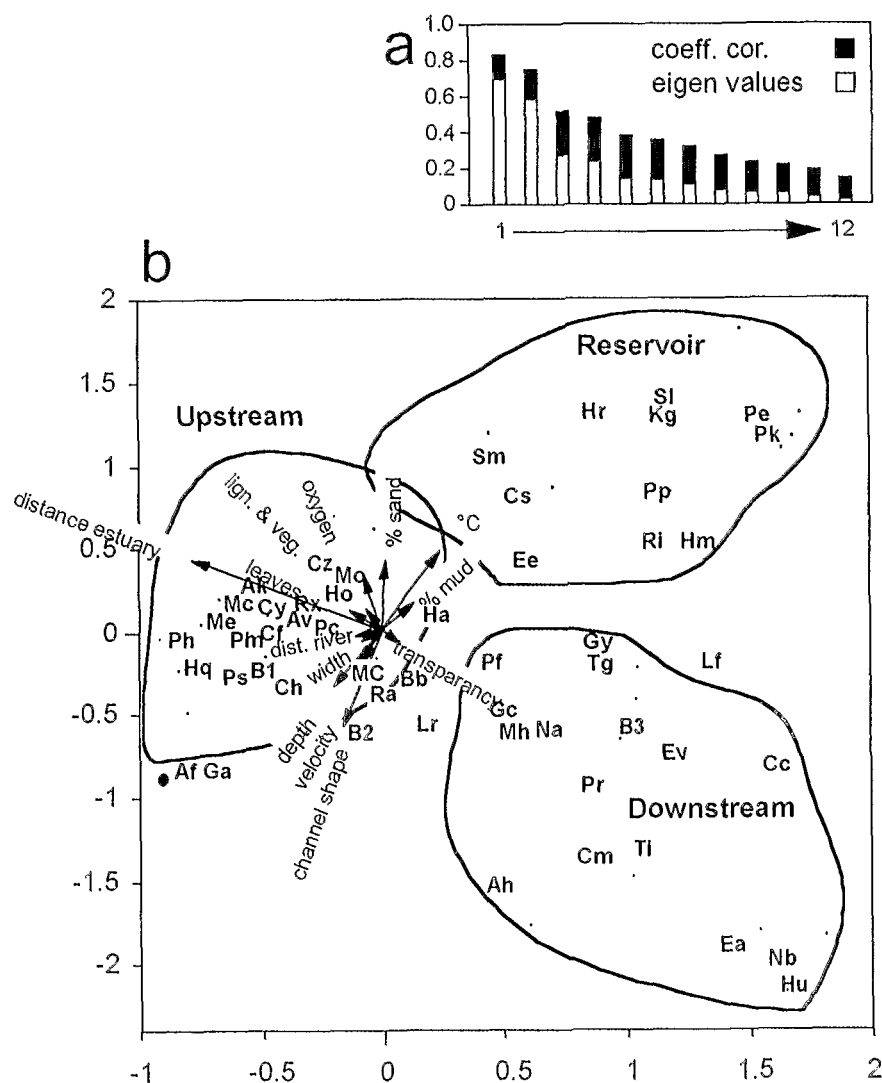


Figure 6. Canonical correspondence analysis (Chessel et al. 1987) biplot for the 42 fish taxa of (see Table 1 for codes) and 13 environmental variables (see Table 4 for variables and categories). The eigen values (a) and correlation coefficients are illustrated graphically to facilitate evaluation. For clarity, the sites are indicated by points (b), their ordination scores reflecting their geographical origins (upstream, reservoir, downstream 1994 as labelled). The fish taxa were grouped according to ordination to aid interpretation.

Discussion

Juvenile fish community structure

The range of taxa captured during our investigations (Table 1) compare well with the juvenile taxa caught in the Crique Vénus (Figure 1) by light traps (Ponton 1994) and other sampling methods (D. Pon-

ton unpublished) but differ from other published lists of fish species represented in the River Sinnamary. More than 60 taxa reported by Boujard & Rojas-Beltan (1988) for that river were not observed as juveniles in the tributaries we sampled, whereas 26 additional taxa were captured. Superimposed on potential erroneous identifications, which are common in south American freshwater fish studies (Va-

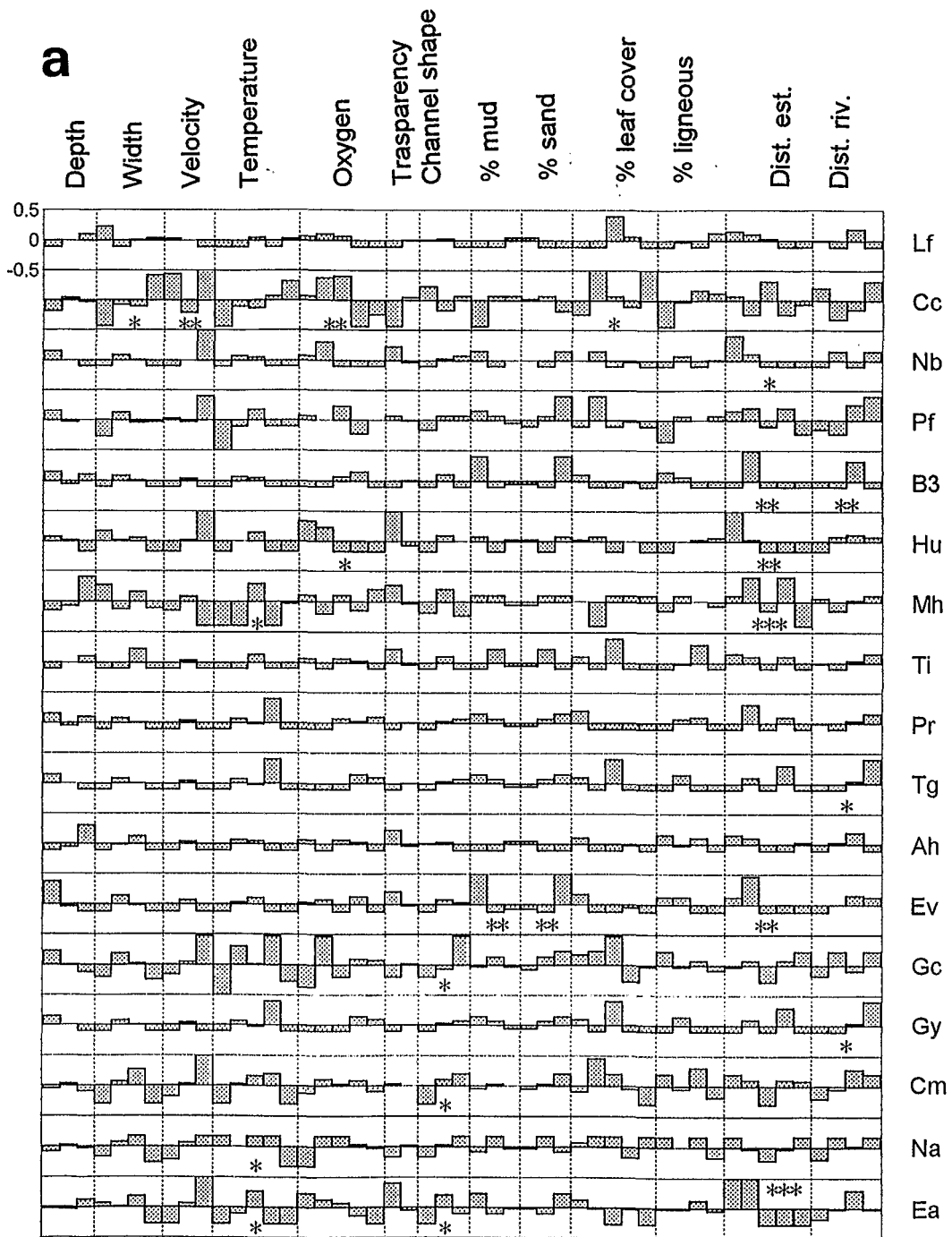


Figure 7. Habitat electivities and Fisher's exact test associations (* = $0.01 < p \leq 0.05$; ** = $0.001 < p \leq 0.01$; *** = $p < 0.001$) for fish taxa in tributaries and the Petit Saut reservoir of the River Sinnamary (see Table 1 for codes). Each histogram represents the difference between the frequency of that taxon in the group of samples having that category of environmental variable and the frequency of that taxon in all samples for fish species representative of upstream tributaries (a-b), downstream tributaries (c), and reservoir sites (d). See Table 4 for categories of each environmental variable.

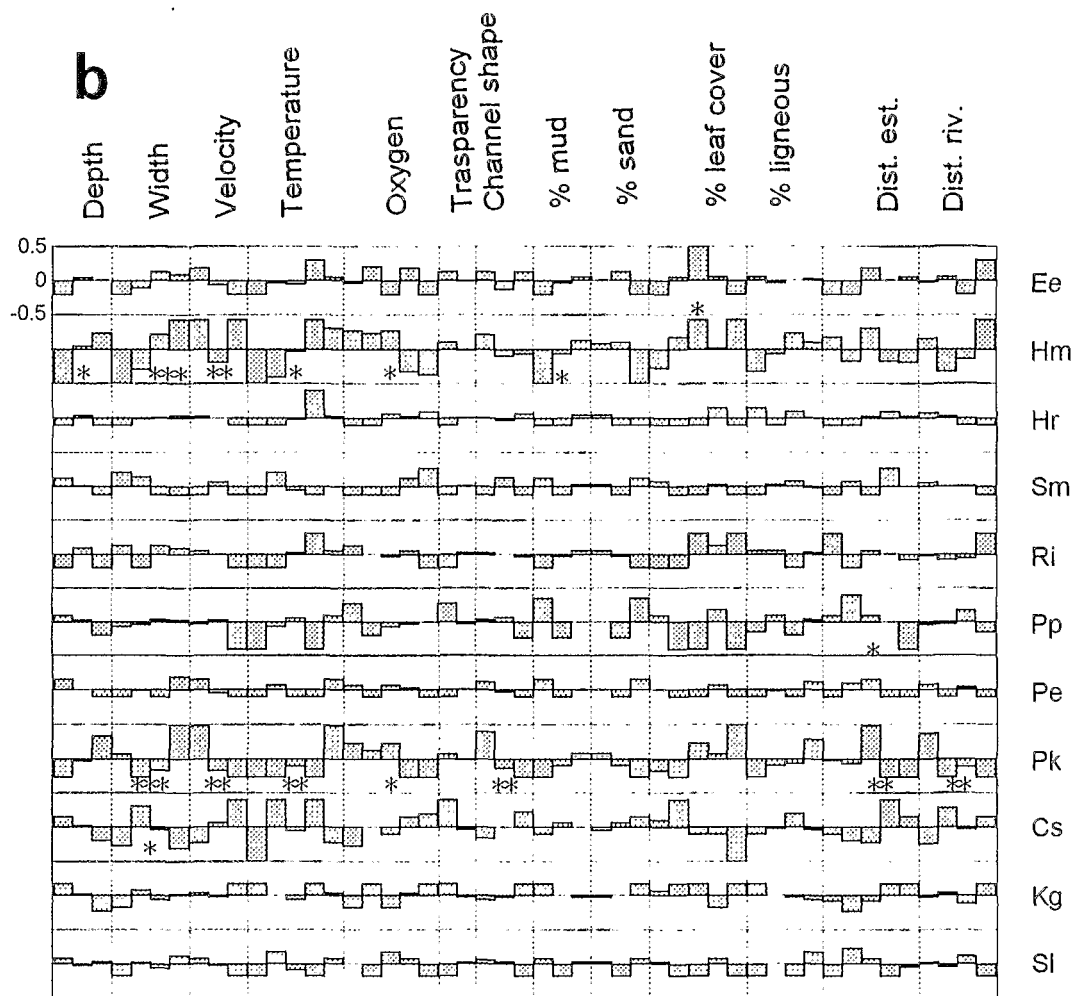


Figure 7. Continued.

ri & Weitzman 1990), two points may explain the observed discrepancies.

Firstly, the zone referred to by Boujard & Rojas-Beltan (1988) as the upper (haut) Sinnamary is in fact part of the current lower section of the reservoir. The accessibility of the upstream section of the Sinnamary was very difficult prior to the start of dam construction, which opened up an area originally accessible only by helicopter or boat + portage. Secondly, most of the species listed by Boujard & Rojas-Beltan (1988), and unreported in our samples, are of estuarine origin. Boujard (1992) estimated that about 60 fish species of the River Sinnamary can be found in the river's estuary.

Amongst the 14 most important estuarine taxa listed by Boujard (1992, Table 2, p. 237), only individuals of the synbranchiform *Synbranchus marmoratus* were also observed as juveniles and adults in lower and upper reaches of the river (S. Mériçoux & D. Ponton unpublished). Thus, it seems unlikely that juveniles of estuarine fish species use freshwater tributaries and their associated areas as nurseries.

On the other hand, the taxa we observed compare well with those Tito de Morais et al. (1995) found in the true upper reaches of the River Sinnamary. Taxa we did not collect correspond mainly to Serrasalmidac and large Siluriformes, whose



Figure 7. Continued.

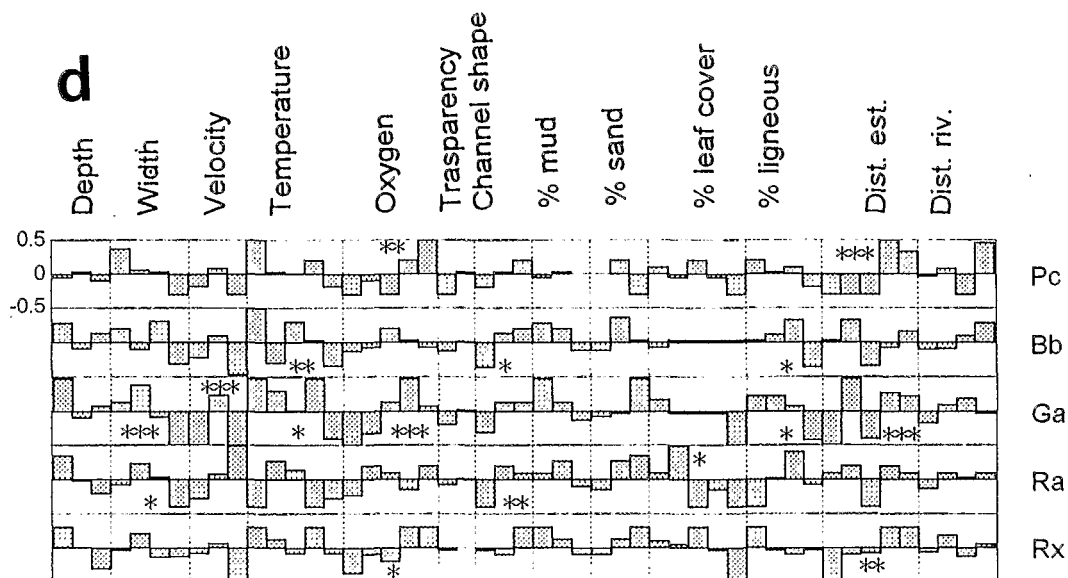


Figure 7. Continued.

adults occupy the main channel of the river; juveniles of these species are rarely or never found in tributaries even during surveys covering extended periods of time (D. Ponton unpublished). Thus, the nurseries of the young of at least some large Guianese fish species remain to be found and our study provides a partial view only of the juveniles that inhabit the Sinnamary River.

Effects of Petit-Saut dam impoundment

To our knowledge, our work is the first to document the effects of a hydroelectric dam on juvenile fish communities in the tropics. Studies aimed at documenting the effects of dams on fish in tropical areas usually focus only on the adults of large species caught by gill nets (see Petr 1978 for a review and Mérona et al. 1987 for an example in the Amazon basin). Similarly, studies on the effects to fish young are restricted mainly to specific taxa that are of commercial interest as larvae, such as large migratory catfishes in the Amazon (Barthem et al. 1991) or young *Tilapia* in Africa (Dudley 1974).

Downstream of the dam, water levels remained

low during a large part of the 1993–1994 rainy season and this strong disturbance (sensu Resh et al. 1988) induced important modifications to the juvenile communities found in the tributaries at the end of the rainy season. In July 1993, downstream tributaries were dominated by Characiformes and 80% of the most abundant taxa were Characidae. Dominance of young Characiformes at the end of the rainy season appears to be a recurrent phenomenon from year to year before dam closure. When re-analysing data obtained at that period of the year in 1991 and 1992 in the Venus Creek with a similar sampling protocol (Tito de Moraes unpublished data), we found that Characiformes accounted for 79.3% of the young fishes in July 1991 and 83.2% at the end of June 1992. Contrastingly, after the first year of dam operation, the young Characiformes were no more dominant at the downstream sampling sites: their relative abundance decreased from 83.4% to 35.9%. More precisely, of the five most abundant taxa caught in 1993, the four abundant Characiformes taxa were replaced by one Lebiastinidae and three Cichlidae species and only the perciform Eleotridae *Eleotris amblyopsis* remained abundant.

The habitat requirements of the progeny of the four characids found to be abundant in downstream reaches before dam completion (*Moenkhausia collettii*, *Pristella maxillaris*, *Pseudopristella simulata* and *Hemigrammus ocellifer*) seem unlikely to explain by themselves the decrease in abundances of Characiformes. None of the variables for which deviations from expected frequencies were found (Figure 7a) are likely to have been modified by dam operation. The drastic modifications in the richness and relative composition of the juvenile communities must most likely result from the differential rate of reproduction success and/or of survival during early life among species in relation to the low water levels induced by dam operation. Miniature or small-sized Characiformes taxa found in the Sinnamary River are mostly phytophils (Ponton & Tito de Moraes 1996) and most of them reproduce during the period of highest water levels (Breder & Rosen 1966, Munro 1990, D. Ponton unpublished). Low downstream flow during impoundment reduced the intensity and duration of flooding events during most of the 1993–1994 rainy season. As a consequence, adults of small-sized characids may have encountered difficulties in accessing suitable spawning grounds and/or their young may have been unable to benefit from food and shelter usually found in flooded areas.

Despite alteration of flow regime, the progeny of some species remained very abundant in all the downstream sites. For example, the high reproductive success of *Eleotris amblyopsis* (Figure 5) may be explained by the fact its young first occur at the end of the dry season (D. Ponton unpublished observations), thus this species had already reproduced before dam closure. Moreover, the reproductive guild (sensu Balon 1981) to which the species belongs may also bring some advantages towards flow alterations. *Eleotris oxycephala*, another species of this bottom dwelling genus, is a nest spawning speleophil (Breder & Rosen 1966). *E. amblyopsis* may behave in a same manner and this reproductive habits on the bottom of streams may confer a certain independence from flow variations. The cichlids *Nannacara anomala*, *Crenicichla saxatilis* and *Krobia guianensis* are also nest spawners (Sterba 1963, Breder & Rosen 1966, Werner 1982), and all of them

maintained high numbers of juveniles in downstream sites after dam operation.

The juvenile fish communities we observed in the reservoir differ strongly from those of the river's tributaries. The progeny of Characiformes represented only 17.1 and 56.7% of the individuals in the body and head parts of the reservoir, respectively (Figure 4). Mean values of density and richness were also lower especially in the lower part of the reservoir where lentic characteristics prevailed (Tables 2, 3). These lentic environments, characterised by high temperatures and low oxygen concentrations, appear to be especially detrimental to the juveniles that prefer lotic conditions (Figure 7a–b). The progeny of taxa more frequently observed in the reservoir's littoral zone appear to be less selective of local habitat characteristics (Figure 7c) confirming that eurytopic species cope with environmental change better than do stenotopic species (see review in Poff & Ward 1990). For example, young stages of *Krobia guianensis* dominated largely the upper and lower reservoir samples but were also present in tributaries from other sections of the Sinnamary. The generalist tendencies of *K. guianensis* (Figure 7c) provides them a great ubiquity in the River Sinnamary and may explain their wide distribution in the black water rivers of Surinam (Ouboter & Mol 1993).

Perspectives

Impoundment imposed a 'press disturbance' (sensu Yount & Niemi 1990, Niemi et al. 1990) on a large section of the River Sinnamary. In the next years, this disturbance is expected to drive the fish community towards a new biologically accommodated state where tolerant species will dominate and sensitive species will be lacking. This succession will take years, as many biological processes are involved. For example, it is likely that some species or taxa of the juvenile community observed in the littoral zone of the reservoir have been favoured by abundant new food resources. Indeed, impoundment has induced the rapid death of flooded trees, and large amounts of leaves have accumulated. This leaf litter is known to provide cover (Lowe-McCon-

nell 1964) and a source of food for fish (Henderson & Walker 1990, Walker 1995). On the long term, this value is expected to decrease in the future as the leaves will decompose and will not be renewed as long as riparian vegetation does not develop. Thus, taxa for which early survival had been increased following impoundment may encounter harsher conditions as the reservoir evolve (Balon 1974).

The other main question remains whether and how the downstream fish community will recover from the perturbation induced by impoundment. Little published information is available on the effects of river damming on the early life of neotropical fishes, and no data exist on the resiliency of fish communities in these geographical areas. The rate of recovery is expected to depend strongly on the duration of downstream flow modifications (e.g. Kingsolving & Bain 1993). A long period of flow alteration, i.e. a press disturbance (*sensu* Kingsolving & Bain 1993), will slow down recovery and even impede it. As a consequence, the first step towards restoring the capacity of downstream tributaries to sustain a rich community of juveniles, and thus fish species, is to require dam operators to simulate natural discharge fluctuations as soon as impoundment will be completed. Water level oscillations in the River Sinnamary will re-create the flooded areas where phytophil species can reproduce and other juveniles can feed and find shelter from predation.

A large part of the fish community resiliency would also depend on whether short flow increases, such as those during the 1993–1994 rainy season (Figure 2), are sufficient to act as a refugium from the long lasting perturbation. Many South American fish species are of small or very small size and most miniature species present a life span of 1 year or less (Weitzman & Vari 1988). Thus, poor reproductive success of these species or low survival of their early life stages due to successive periods of drastic flow regulations may impede their ability to persist downstream of the dam. On the other hand, small Characiformes and Cyprinodontiformes present traits such as early maturation, continuous reproduction and small brood size, which reflects rapid colonisation abilities (Winemiller 1989). Moreover, fish species of the River Sinnamary have evolved in a system that possesses high flow varia-

tions from year to year, a characteristic shared by most of the rivers of French Guiana (Ph. Vauchel, personal communication). This high natural environmental variability may have given fish communities inhabiting these rivers a great persistence, resistance, and rate of recovery (e.g. Poff & Ward 1990). Future investigations will demonstrate whether Guianese fish communities show a greater resiliency than those of more predictable systems.

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