Freshwater Biology (1999) **42**, 177–198

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APPLIED ISSUES

Spatio-temporal distribution of young fish in tributaries of natural and flow-regulated sections of a neotropical river in French Guiana

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SUMMARY

1. We investigated which environmental parameters control the variation in density, in space and time, of young stages of fish in tributaries of a natural and a flow-regulated section of the Sinnamary River, French Guiana.
2. The density of the progeny in most taxa varied in space and/or time. However, most non-Perciformes responded differently to space and/or time in the two sections.
3. Oxygen, turbidity and habitat structure (i.e. bank length, occurrence of undercut bank, richness in litter, vegetation and substratum) were important, as was the position of the sampling site relatively to the main channel in the downstream tributaries, in explaining the variation of density in space in both sections. Both habitat complexity and distance from the main channel protect young fish against unpredictable flow releases downstream from the Petit Saut dam.
4. Hydrological events played an important role in the temporal variation in densities of many fish taxa. The density of most early life and many juvenile stages (mostly Characiformes) was positively related to hydrological events.
5. Some fish taxa had reproductive habits which were relatively independent of abiotic factors, such as flow variability, and the density of their progeny did not vary with time.
6. The nursery areas of more than 45% of species in the Sinnamary River have been degraded by flow regulation.

Keywords: dam, density variation, hydrology, juvenile fish, local habitat

Introduction

All biological communities vary greatly in space and time (e.g. Wiens, 1986; Southwood, 1988; Morris, 1990). However, the control of abundance and distribution of species in space and time by the abiotic and biotic environment remains a central problem in ecology (Brown, 1984). The importance of these spatial and temporal dimensions is certainly evident for stream communities (e.g. Frissell *et al.*, 1986; Minshall, 1988; Matthews, 1990; Townsend & Hildrew, 1994; Poff & Allan, 1995). In these lotic systems, and within ecological time, habitat features such as depth, current and substratum (e.g. Schlosser, 1982; Bain, Finn & Booke, 1988), water quality (e.g. Matthews, 1998), presence of shelter, or habitat diversity (e.g. Gorman & Karr, 1978; Mérigoux, Ponton & Mérona, 1998) may play a major role in shaping fish communities in space. Flow (e.g. Horwitz, 1978; Resh *et al.*, 1988) and water temperature (e.g. Baltz *et al.*, 1987; Matthews, 1998) are the main physical parameters structuring fish assemblages in time. These physical parameters,

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together with biotic interactions such as competition for food and avoidance of predation (Angermeier, 1987; Govoni, Hoss & Colby, 1989), have strong effects on fish survival, leading to high fluctuations in the abundance of individuals, and thus, in the composition of fish communities in space and time.

The habitat requirements of young fish can determine the structure of adult fish assemblages. Indeed, the survival of larvae and juvenile fish determines the year-class strength of most fish species (e.g. Balon, 1984; Houde, 1987).

Spatial habitat use by young fish, and the factors which induce fluctuations in their density, have been poorly documented in the neotropics. Most studies have been based on observations of adults in large rivers with predictable seasonal flow regimes and extensive floodplains (e.g. Welcomme, 1979; Lowe-McConnel, 1987). In the more variable rivers of the Guiana shield (Covich, 1988; Ouboter & Mol, 1993), studies have focused mainly on (1) the distribution of fish taxa at a large scale in relation to quaternary glacial refugia (Renno *et al.*, 1990; Boujard, 1992) or to physicochemical factors (Mol, 1994), (2) the longitudinal distribution of taxa within drainage basins (Boujard & Rojas-Beltran, 1988; Tito de Morais & Lauzanne, 1994), or (3) taxon–habitat relationships at local scales (Mérigoux, Ponton & Mérona, 1998). The temporal distribution of adult fish was studied in reaches of Guianese rivers by Rojas-Beltran (1986). Only the work of Boujard, Pascal & Meunier (1990) considered both spatial and temporal distribution at the reach scale, but focused on adults. Only recently, Ponton & Copp (1997) documented the habitat requirements of young stages of Guianese fish, and Ponton & Vauchel (1998) tested the strength of the relationship between temporal fish distribution and hydrological parameters.

This lack of information on the spatial and temporal parameters which affect the density of young fish in the neotropics, and thus, shape assemblages of fish, is an essential problem for the Sinnamary River in French Guiana because of the completion of the Petit Saut hydroelectric dam in 1994. Fish are generally well adapted to deal with natural physical and chemical variations (Matthews, 1998), and to select their habitat in a way which maximizes their lifetime reproductive success (Morris, 1990). However, anthropogenic disturbances, such as alteration of the timing, frequency, magnitude or duration of the flood have a strong impact on the aquatic biota (Bain, Finn & Booke, 1988; Bonetto, Wais & Castello, 1989; Richter *et al.*, 1996; Poff *et al.*, 1997). These disturbances may also change physical and chemical conditions in rivers and streams (Collier, Webb & Schmidt, 1996). All these modifications are likely to impact young fish, and thus, have serious long-term consequences for fish assemblages (Welcomme, 1995; Matthews, 1998).

The objectives of the present paper were, firstly, to determine these taxa in the Sinnamary River whose young vary in density over the spatial and temporal scales addressed. The temporal scale corresponded to much of the duration of the young lives of fish in the streams (Ponton & Tito de Morais, 1994). The spatial scale corresponded to the extent of the habitat of young fish (Schiemer *et al.*, 1991; Schiemer & Zalewski, 1992) and was appropriate to the study of multispecies patterns (Poizat & Pont, 1996). Secondly, we examined which local habitat characteristics determined spatial variations in the density of young fish. Thirdly, we tested how hydrological events related to the temporal density variations, and lastly, they compared these patterns in a natural and in a flow-regulated section of the Sinnamary River.

Materials and methods

Study area

The Sinnamary River (Fig. 1) is the fifth largest river of French Guiana, with a length of ≈ 260 km and a mean annual discharge of 230 m3 s–1. Its drainage basin covers about 6565 km2 and receives an annual average precipitation of 3000 mm. The Upper Sinnamary River, upstream from the reservoir (hereafter called the 'upstream section'), crosses different forest types ranging from terra firme arborescent to flooded and permanent swamp forest. Downstream from the dam (the 'downstream section'), the river meanders through an old flat coastal plain (for a description of the entire river system, see Boujard, 1992; Tito de Morais, Lointier & Hoff, 1995). Before the completion of the Petit Saut dam in 1994, the hydrological regime in both sections was dependent on two rainy seasons (November–February and April–July) and a dry season (August–November), accompanied by unpredictable short-term events imposed by sudden heavy rains (Ponton & Copp, 1997).

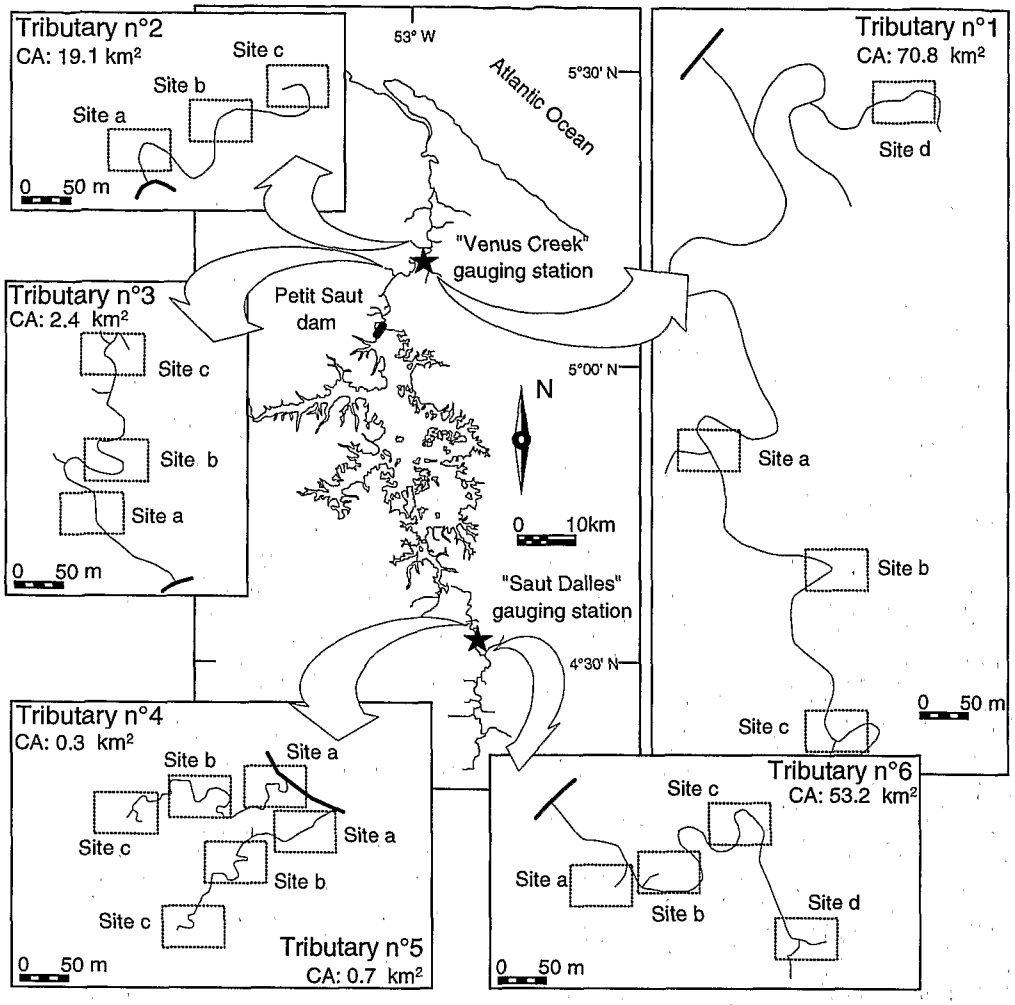

Fig. 1 Study sites (dashed rectangles, $n = 20$) of ≈ 1000 m^2 in the six tributaries under survey in the Sinnamary River, French Guiana. The stars indicate the location of the different gauging stations in the river. During each of the ten campaigns performed in 1995 and 1996, we randomly sampled one area of ≈ 50 m^2 within each site.

Fish sampling and spatial habitat characteristics

From March 1995 to October 1996, we sampled fish in three tributaries and their associated floodplains in the upstream section and three others in the downstream section of the Sinnamary River (Fig. 1). During each of the ten sampling campaigns (Fig. 2), we selected an area of about 50 m2 at random (i.e. without previous knowledge of whether fish were present or not) within each of the three (tributaries 2, 3, 4 and 5; Fig. 1) or four (tributaries 1 and 6) 1000-m2 study sites per tributary. Therefore, we sampled each of the ten downstream and ten upstream sites ten times and obtained 200 samples in total. Mérigoux, Ponton & Mérona (1998) gave a complete description of the sampling method. In summary, we first measured temperature, pH and oxygen with a ICM 51000 multiparameter and water turbidity with a LaMotte Model 2008 digital turbidity meter in the undisturbed water. We also measured the current velocity at the water surface by observing the time required for a floating object to traverse 1 m downstream and assigned it to five categories: (1) 0–6 cm s–1; (2) 7–9 cm s–1; (3) 10–14 cm s–1; (4) 15–25 cm s–1; and (5) > 25 cm s–1. Preliminary measurements showed that the categories varied very little, so we measured these only once. Then, we enclosed the sampling area with two or three stop nets (1-mm

mesh) and applied at least two subsequent doses of PREDATOX well mixed with water (6.6% emulsifiable solution of rotenone extracted from Derris elliptica by Saphyr, Antibes, France). We collected fish with dip nets (1-mm mesh) and immediately preserved them in 90% alcohol. After fish sampling, we recorded the depth (in cm) and the presence/absence of organic litter [five categories: leaves, wood diameter ≤ 5 and > 5 cm, and root diameter ≤ 5 and > 5 cm], vegetation (three categories: aquatic, terrestrial herbaceous shrubs or trees), and substratum [six categories: mud, clay, sand, gravel (4–16 mm diameter), stones (16–256 mm) and rocks >256 mm] at each point sample of a 1 × 1 m grid. We recorded bank slope (three categories: shallow to medium ≤ 60°, steep to vertical > 60° and undercut; sensu Gordon, McMahon & Finlayson, 1992) for the point samples closest to the bank. We also measured the distance of the sampling area to the main channel, and determined the total bank length, mean width and surface for each sampling area. Finally, we surveyed between four and ten cross-sections per sampling site for which we measured bankfull width with an horizontal tape, bankfull depth and water surface depth every metre along the horizontal tape (Gordon, McMahon & Finlayson, 1992).

In the laboratory, we sorted and identified all specimens in the 200 samples using keys for adults and juveniles by Géry (1977), Rojas-Beltran (1984), Kullander & Nijssen (1989) and Planquette, Keith & LeBail (1996), and D. Ponton (unpublished data), respectively. The keys for juveniles were based on a series of drawings of specimens of variable size and on meristic parameters, such as number of rays on the anal fin or position of fins. We faced identification problems for a dozen species, which we grouped in the appropriate genera. We referred to species and species groups as taxa.

Hydrology

In the upstream section, a ELSYDE Model CHLOE-E gauging station set upstream from Saut Dalles rapids (Fig. 1) recorded the water level of the Sinnamary River every hour in 1995 and 1996. In the downstream section, water level was recorded hourly with a CR2M model SAB-DBA gauging station set about 25 km downstream from the Petit Saut dam at the entrance of Venus Creek (Fig. 1).

Data analysis

Fish

We measured the standard length of each specimen to the nearest 1 mm. We separated juveniles from adults according to the minimum size at first maturity observed for each species in the Sinnamary River (Mérigoux & Ponton, 1998; Ponton & Mérona, 1998). We classified individual fish, based on their standard length (SL), into early life stages (from ≈ 4 to 15–20 mm SL, depending on species) and juveniles (from > 15 to 20 mm SL; for the exact size limits for each taxon, see Mérigoux & Ponton, 1998). We determined the density of each ontogenetic stage for each sampling area, each sampling site and each sampling campaign by dividing the number of individuals by the corresponding area sampled. Ontogenetic stages of scarce taxa (sum in the 100 up-or 100 downstream samples < 0.4 individuals m–2) were excluded from further analyses.

Spatial habitat parameters

For each site under study, we calculated the mean distance to the Sinnamary River (D_Sin, m) of the ten

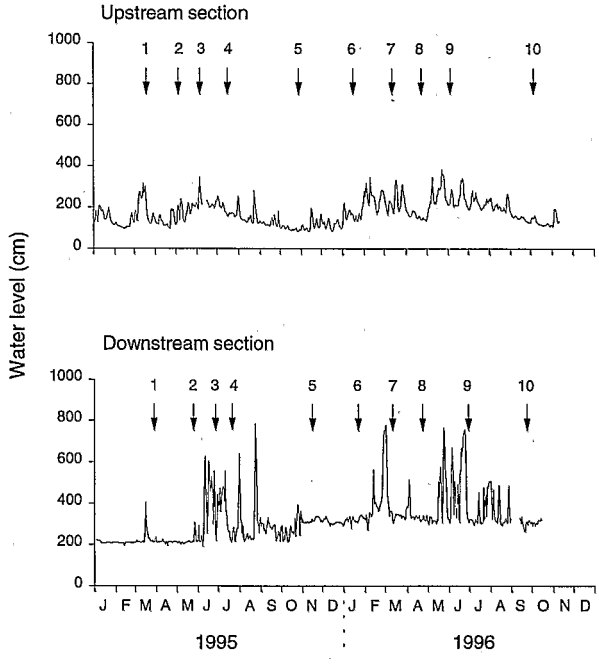

Fig. 2 Water levels recorded at Saut Dalles (upstream) and Petit Saut (downstream) gauging stations from January 1995 to November 1996. The vertical arrows indicate the ten fish sampling campaigns.

areas sampled (from the ten sampling campaigns), the mean of their bank lengths (Ba_Le, m), widths (M_Wi, m), depths (M_De, m), turbidities (TURB, NTU) and oxygen concentrations (OXY, mg L–1). Water temperature (mean = 24.1 and 24.7 °C, respectively, in up- and downstream sites, and SD = 0.3 for both sections) and pH (mean = 4.8 and 4.6, SD = 0.1 and 0.2, respectively, in up- and downstream sites) varied little and were excluded from further analysis. We also omitted water current velocity because 83% of the samples had a velocity ≤ 6 cm s–1. We determined the percentage of the three categories of bank slope (≤ 60°, > 60° and undercut in per cent) at each study site. For each point sample of the 1 × 1 m grid, we merged the occurrences of the categories of litter, vegetation and type of substratum coded 0 (absence) or 1 (presence) (see above for the different categories). We assigned each point sample to one type of habitat which corresponded to a given series of 0 and 1. Then, we counted the different types of chains observed in the ten sampling areas of each site in order to get an index of the richness of litter, vegetation and substrate (LVS).

We related bankfull depth of each of the four to ten surveyed cross-sections to the corresponding water level in the Sinnamary River using the hydrological models defined by Mérigoux *et al.* (1999). In this way, we were able to assess the water level of the Sinnamary River above which flows would overtop the banks for each cross-section. Finally, we counted the number of days during which at least part of each sampling site was flooded during the study period by using the smallest of the four to ten water heights per site. Thereby, we could estimate an 'index of inundation potential' (IP) for each sampling site.

Temporal parameters

Parallel studies (Mérigoux *et al.*, 1999) highlighted the strong influence of the water level of the Sinnamary River on that of the tributaries and their associated floodplains. Therefore, we calculated the minimum, maximum, mean and variance of water level 10, 20, and 30 days before each sampling campaign (DBS) from the Sinnamary water level recorded at the up- and downstream section gauging stations. In the upstream section, we also determined the number of days with water level exceeding 1.0, 2.0 and 3.0 m observed 10, 20 and 30 DBS. Similarly, we calculated downstream water level exceeding 5.0, 6.0, 7.0 and 8.0 m observed 10, 20, and 30 DBS.

Density versus space and time

For each section of the Sinnamary River, we determined how space (i.e. site effect, $n = 10$) and time (i.e. campaign effect, $n = 10$) contributed to the variation in density of the two ontogenetic stages of each taxon using a two-way analysis of variance (ANOVA) (Sokal & Rohlf, 1995).

Fish density versus spatial habitat parameters

We examined the habitat parameters which influenced the densities of taxa in space (i.e. taxa sensible to the site effect detected by the two-way anova). Therefore, fish density and sampling site habitat characteristics were arranged in two data matrices, Sites × Fish Taxa and Sites × Environmental Variables (both rows × columns), separately for the up- and downstream data sets. The Samples × Fish Taxa matrix contained log (x + 1) transformed densities of the fish taxa. We retained eleven environmental variables in the Sites × Environmental Variables matrices of the up- and downstream tributaries (Table 1).

Our next task was to relate the Sites × Fish Taxa matrix to the Sites × Environmental Variables matrix. For this task, co-inertia analysis (Dolédec & Chessel, 1994) is an appropriate method because it serves as a general tool to relate any kinds of standard analysis (e.g. correspondence analysis, principal components analysis or multiple correspondence analysis). Co-inertia analysis is used to demonstrate whether a co-structure exists between faunistic and environmental data sets when many species and several environmental variables are sampled in few sites (Dolédec & Chessel, 1994). Basically, co-inertia analysis is a simultaneous ordination of two data matrices which maximizes, in this case, the co-variance of the score at each sampling site for the taxa and the environmental variables. Co-inertia analysis defines axes which explain the highest possible variation in each of the data matrix, and at the same time, describes the closest possible co-structure of the two data matrices. The generality of the co-inertia analysis is demonstrated by its extensive use in biology (for a review, see Statzner *et al.*, 1997).

Table 1 Habitat characteristics for each study site in the upstream and the downstream sections

Tributary	Site	Habitat variables										
		D_Sin (m)	Ba_Le (m)	M_Wi (m)	M_De (cm)	TURB (NTU)	OXY (mg L^{-1})	≤60° (%)	>60° (%)	UND (%)	LVS	IP (days)
Upstream												
4	a	22	22.9	4.9	47	4.0	5.5	54.8	34.1	11.1	64	209
	b	212	28.4	2.8	40	3.3	5.9	47.3	20.2	32.4	68	187
	c	325	28.9	2.4	33	3.1	5.8	37.8	30.8	31.5	45	169
5	a	38	20.4	5.4	42	6.1	5.0	77.9	21.1	1.1	81	187
	b	174	29.8	3.6	28	2.8	5.2	46.1	24.6	29.2	82	220
	c	252	34.9	2.2	27	1.6	5.5	46.3	36.3	17.4	81	132
6	a	130	21.9	4.0	52	2.4	5.0	40.8	57.8	1.3	85	239
	b	209	15.7	5.9	51	3.1	3.6	72.5	21.7	5.8	78	196
	c	402	28.1	4.2	34	3.2	4.7	70.4	25.0	4.6	84	148
	d	607	32.4	3.0	36	4.0	5.4	33.5	50.6	15.8	126	181
Mean		237	26.3	3.8	39	3.3	5.1	52.7	32.2	15.0	79	187
Downstream												
1	a	717	27.3	3.2	48	11.8	4.6	36.6	63.4	0.0	60	18
	b	874	25.3	4.5	31	8.6	5.0	77.0	23.0	0.0	53	38
	c	1068	17.8	4.3	74	7.1	5.1	30.1	34.9	34.9	50	55
	d	373	24.8	5.2	51	11.1	4.2	54.7	36.1	9.2	74	47
2	a	67	17.4	6.0	48	5.9	5.4	66.9	33.1	0.0	74	0
	b	185	26.0	5.9	55	4.6	5.5	53.8	45.3	0.8	70	0
	c	329	23.5	5.5	58	5.0	5.9	51.4	45.9	2.7	74	24
3	a	114	21.2	6.1	51	6.6	5.2	30.2	64.6	5.3	63	19
	b	258	29.3	4.3	59	5.3	5.6	23.2	69.7	7.1	80	70
	c	353	34.3	3.4	59	4.2	5.8	12.5	50.4	37.1	96	23
Mean		434	24.7	4.8	53	7.0	5.2	43.6	46.6	9.7	69	29
P-value		0.083	0.241	0.027	0.002	<0.001	0.449	0.140	0.022	0.108	0.059	<0.001

(D_Sin) mean distance to the Sinnamary River; (Ba_Le) mean bank length; (M_Wi) mean width; (M_De) mean depth; (TURB) mean turbidity; (OXY) mean oxygen content; (≤ 60°) percentage of shallow to medium bank slopes; (> 60°) percentage of steep to vertical bank slopes; (UND) percentage of undercuts; (LVS) richness of litter, vegetation and substratum; (IP) index of inundation potential; (*P*-value) exact probability of the one-sided Wilcoxon rank-sum test (Mehta & Patel, 1995); and (Ho) 'one distribution is not shifted relative to the other'

In preparation for co-inertia analysis, we first submitted the Sites × Fish Taxa matrix to correspondence analysis and the Sites × Environmental Variables to principal components analysis. These ordination techniques respectively elucidate the relationships among taxa and provide the best combinations of environmental variables according to their correlation between each other (Escofier & Pagès, 1990). We then subjected the results from these two analyses to co-inertia analysis to assess the relationship (i.e. the co-structure) between taxa and environmental variables. Finally, we tested the significance of the resulting correlation by a Monte-Carlo method with 10 000 random permutations of the rows of the environmental data set.

Fish density versus temporal parameters

we tested which hydrological factor influenced temporal variations of taxa densities (i.e. those taxa sensitive to the campaign effect detected by the two-way ANOVA). We calculated the exact significance of Spearman's coefficient of rank-order correlation (Mehta & Patel, 1995) between taxon density for each campaign and the different hydrological variables. This method was appropriate since the present data were not normally distributed (Sokal & Rohlf, 1995).

We performed all these analyses separately for the up- and the downstream data set with Systat® 6.01 for Windows (Wilkinson, Blank & Gruber, 1996; regis-

tered trademark of SSPS Inc., Chicago, IL), ADE 4 software (Thioulouse *et al.*, 1997; freeware available at http://pbil.univ-lyon1.fr/ADE-4/) and StatXact® statistical software (CYTEL Software Corporation, Cambridge, MA) for exact distribution-free inference which uses the algorithms developed by Mehta & Patel (1995) to perform permutation tests. Permutation tests are particularly useful in studies based on small samples since these remain as powerful as the corresponding, unbiased parametric test (Good, 1993). The permutation tests can even become more powerful with data from non-standard distributions (Manly, 1997).

Results

Fish

We collected 34 790 young individuals representing seventy taxa from twenty-five families and six orders (Table 2). Characiformes and Perciformes were numerically dominant with 66% and 26%, respectively, of the total individuals. However, Characiformes accounted for 82% and Perciformes for 11% of the total individuals in the upstream section, whereas these accounted for 49% and 43%, respectively, in downstream tributaries. Curimatidae spp., Moenkhausia oligolepis (Günther, 1864) and Hoplias spp. were the most abundant taxa in the upstream sites and Eleotris amblyopsis (Cope, 1870), Krobia guianensis (Regan, 1905), and Moenkhausia hemigrammoides Géry, 1966, dominated downstream. We caught more individuals upstream and nearly the same number of taxa, despite the fact that the total sampled area and volume were greater at downstream sites (Table 2). The early life stages were less abundant than the juveniles, with 44% and 41% of the total number of collected fish in the up- and downstream sections, respectively.

Density variations among sites and/or campaigns

In the upstream section, the density of the early life stage and juveniles varied significantly among sites and/or campaigns in 52% and 79% of taxa, respectively (Table 3). In the downstream section, these values were 70% and 61%, respectively. The density of most Characiformes was particularly variable in time, whatever the section considered. Remarkably, the density of the early life stage and juveniles for most taxa present above or below the reservoir responded inconsistently to site and/or campaigns, depending on the section, most exceptions being found among the Perciformes (Table 3).

Spatial variations in density

Sites in the upstream section were shallower, less frequently had steep banks and were more likely to be inundated. These were also narrower and were less turbid than those downstream from the dam (Table 1). The two matrices, Samples × Fish Taxa and Samples × Environmental Variables were significantly related ($P < 0.001$, Monte-Carlo method with 10 000 permutations) for both upstream and downstream data sets.

In the upstream section, the first two axes of the co-inertia analysis explained 85% of the total co-inertia (Fig. 3a), with the first axis being particularly important. According to the relative contribution of the first two axes on each taxon and each habitat variable (i.e. the percentage of the inertia extracted by, in the present case, a taxon or by a habitat variable; Lebart, Morineau & Piron, 1995), we distinguished four groups of taxa associated with four types of habitats (Fig. 3b, c; Tables 4 & 5). Group 1 (46% of the taxa; Fig. 3c) comprised taxa associated with shallow and narrow sites characterized by long bank length, infrequent shallow to medium bank slopes but a lot of undercuts, clear water with high oxygen concentration, and a low inundation potential. Taxa in group 2 all belonged to the Characiformes. We collected these in habitats with characteristics opposite to those favouring group 1 (Fig. 3b, c). Group 3 consisted of taxa mainly found in habitat with a high diversity of litter, vegetation and substratum and distant from the Sinnamary River. Juveniles of Leporinus spp. (LESP) were the only taxon represented in group 4, and were found in sampling sites with a low diversity of litter, vegetation and substratum near the main river. Finally, juveniles of Pimelodella sp. (PISP) were found in habitat characteristics of groups 1 and 4. The six taxa for which we had enough individuals for both early life and juveniles stages (i.e. CUSP, EERY, ACSP, CFAS, PRAN and HART) presented no ontogenetic shifts between the four types of habitat.

In the downstream section, the first two axes of the co-inertia analysis explained 80% of the total variation

Table 2 List of fish taxa, authority, code, and total number of early life stages (ELS) and juveniles (J) of fish caught in the 200 sampling areas of the upstream and the downstream sites

Order, family and species	Authority	Code	Upstream		Downstream	
			ELS	J	ELS	J
Characiformes						
Hemiodontidae						
Hemiodopsis quadrimaculatus	(Pellegrin, 1908)	HQUA	388	16		
Parodon guyanensis	Géry, 1959	PGUI	186			
Curimatidae						
Chilodus zunevei	Puyo, 1945	CZUN	11	4		
Curimatidae spp.		CUSP	2995	786	62	165
Anostomidae						
Anostomus brevior	Géry, 1960	ABRE		1		
Leporinus despaxi	Puyo, 1943	LDES		35		
Leporinus spp.		LESP	38	63	6	4
Erythrinidae						
Erythrinus erythrinus	(Schneider, 1801)	EERY	53	24	5	
Hoplerythrinus unitaeniatus	(Spix, 1829)	HOUN				20
Hoplias spp.		HOPL	1127	307	880	104
Lebiasinidae						
Copella carsevennensis	(Regan, 1912)	CCAR	24	74	18	86
Nannostomus beckfordi	Günther, 1872	NBEC				79
Pyrrhulina filamentosa	Val. in Cuv., 1846	PFIL	64	216	9	507
Gasteropelecidae						
Gasteropelecus sternicla	(L., 1758)	GSTE			160	27
Characidae						
Acestrorhynchus sp.		ACSP	29	69	32	31
Astyanax bimaculatus	(L., 1758)	ABIM	32	476	6	17
Astyanax cf keithi	Géry, Planquette & LeBail, 1996	AKEI	15	318	145	252
Astyanax meunieri	Géry, Planquette & LeBail, 1996	AMEU			3	
Bryconops spp.		BRSP	14	92	116	122
Characidium fasciadorsale	Fowler, 1914	CFAS	68	108	5	2
Charax pauciradiatus	Günther, 1864	CPAU			35	
Hemigrammus ocellifer	(Steindachner, 1882)	HOCE	58	300	34	473
Hemigrammus unilineatus	(Gill, 1858)	HUNI	5	10	35	145
Hyphessobrycon aff. sovichtys	Schultz, 1944	HSOV			12	28
Melanocharacidium sp.		MESP	62	2		
Microcharacidium eleotrioides	(Géry, 1960)	MELE	52	48	34	33
Moenkhausia chrysargyrea	(Günther, 1864)	MCHR	146	234	376	551
Moenkhausia collettii	(Steindachner, 1882)	MCOL	248	1091	594	301
Moenkhausia georgiae	Géry, 1966	MGEO	14			
Moenkhausia hemigrammoides	Géry, 1966	MHEM	1	1	37	1300
Moenkhausia oligolepis	(Günther, 1864)	MOLI	423	1759	33	315
Moenkhausia sp.		MOSP		3		
Moenkhausia surinamensis	Géry, 1966	MSUR		69	1	
Phenacogaster aff. megalostictus	Eigenmann, 1909	PMEG	214	625	2	2
Piabucus dentatus	(Köhlreuter, 1761)	PDEN			25	14
Poptella brevispina	(Reis, 1989)	PBRE	38	6	461	74
Pristella maxillaris	(Ulrey, 1894)	PMAX	138	502	30	250
Pseudopristella simulata	Géry, 1960	PSIM	161	1049	55	185
Siluriformes						
Doradidae						
Doras carinatus	(L., 1766)	DCAR	1			

Table 2. Continued

Order, family and species	Authority	Code	Upstream		Downstream	
			ELS	J	ELS	J
Auchenipteridae						
Parauchenipterus galeatus	(L., 1766)	PGAL			5	1
Tatia intermedia	(Steindachner, 1876)	TINT	22	15	181	220
Pimelodidae						
Pimelodella sp.		PISP	6	79	8	13
Pseudopimelodus raninus	(Valenciennes, 1840)	PRAN	25	24	42	41
Rhamdia quelen	(Quoy & Gaimard, 1824)	RQUE		2	1	9
Helogenidae						
Helogenes marmoratus	(Günther, 1863)	HMAR		14		2
Cetopsidae						
Paracetopsis sp.		PASP		2		
Aspredinidae						
Bunocephalus coracoideus	Cope, 1874	BCOR			5	37
Trichomycteridae						
Trichomycterus guianense	(Eigenmann, 1909)	TGUI	29	49	17	4
Callichthyidae						
Callichthys callichthys	L., 1758	CCAL	5	11	2	3
Hoplosternum thoracatum	(Val. in Cuv. & Val., 1840)	HTHO	4		9	20
Loricariidae						
Ancistrus aff. hoplogenys	(Günther, 1864)	AHOP		6	9	9
Farlowella reticulata	Boeseman, 1971	FRET	1			
Gymnotiformes						
Sternopygidae						
Eigenmannia virescens	(Valenciennes, 1847)	EVIR		1		
Sternopygus macrurus	(Bloch & Schneider, 1801)	SMAC	12	5	31	11
Hypopomidae						
Brachyhypopomus beebei	(Schultz, 1944)	BBEE	4	62	3	78
Hypopomus artedi	(Kaup, 1856)	HART	26	36	12	15
Gymnotidae						
Gymnotus spp.		GYSP	126	287	35	197
Cyprinodontiformes						
Aplocheilidae						
Rivulus agilae	Hoedeman, 1954	RAGI	1	51	1	35
Rivulus igneus	Huber, 1991	RIGN		2		
Rivulus xiphidius	Huber, 1979	RXIP	197	282	23	26
Poeciliidae						
Poecilia parae	(Eigenmann, 1894)	PPAR			45	
Tomeurus gracilis	Eigenmann, 1909	TGRA				1
Synbranchiformes						
Synbranchidae						
Synbranchus marmoratus	Bloch, 1795	SMAR	7	15	25	22
Perciformes						
Nandidae						
Polycentrus schomburgkii	Müller & Troschel, 1848	PSCH				72
Cichlidae						
Cleithracara maronii	(Steindachner, 1882)	CMAR	33	74	1	15
Crenicichla saxatilis	(L., 1758)	CSAX	146	131	737	451
Krobia guianensis	(Regan, 1905)	KGUI	676	553	1353	888
Nannacara anomala	Regan, 1905	NANO	91	228	11	205
Eleotridae						
Dormitator macrophtalmus	Puyo, 1944	DMAC			6	9
Eleotris amblyopsis	(Cope, 1870)	EAMB			966	2446

Table 2. Continued

Order, family and species	Authority	Code	Upstream ELS	Upstream J	Downstream ELS	Downstream J
Total number of orders				6		6
Total number of families				19		22
Total number of taxa				56		57
Total number of individuals				18234		16556
Total sampled volume (m^3)				1622		2914
Total sampled area (m^2)				4649		5865

(Fig. 3d). According to the relative contribution of the first two axes on each taxon and each habitat variable, we distinguished four groups of taxa associated with four types of habitat. The taxa in group 1 were associated with large aquatic habitats with a high concentration of oxygen, high diversity of litter, vegetation and substratum, low turbidity, close to the Sinnamary River, and with a low index of inundation potential (Fig. 3e, f). Most taxa in group 2 were non-Characiformes, except juveniles of Moenkhausia chrysargyrea (Günther, 1864) (MCHR), and were collected in sites with characteristics opposite to those of group 1. Early life stages of Poecilia parae (Eigenmann, 1894) (PPAR) were the only representatives of group 3. These preferred shallow water with short bank length, mainly shallow to medium bank slopes and few undercuts. We found taxa of group 4 in habitats with features opposite to those favourable for the early life stages of Poecilia parae. Among the five taxa represented by both early life and juvenile stages (i.e. HOPL, MELE, TINT, RXIP and SMAR), only Microcharacidium eleotrioides (Géry, 1960) (MELE) showed a clear ontogenetic shift in habitat, moving from groups 1 to 4 with age (Fig. 3f). Hoplias spp. (HOPL), Copella carseven-nensis (Regan, 1912) (CCAR) and Bunocephalus coracoideus Cope, 1874 (BCOR) did not show any preference among the studied local habitat parameters.

Among the taxa sensitive to the spatial effects, three at the early life stage and two at the juvenile stage were present in the up- and downstream sections (Fig. 3). In both sections, early life stages of Microcharacidium eleotrioides (MELE) and Pseudopimelodus raninus (Valenciennes, 1840) (PRAN) inhabited sites with a low index of inundation potential, and clear and well-oxygenated water. Early life stages of Rivulus xiphidus Huber, 1979 (RXIP) preferred sites with a long bank length and many undercuts, while juveniles of Nannacara anomala Regan, 1905 (NANO) were mainly found in sampling sites far from the Sinnamary River, whatever the section considered. Habitat preferences of Hoplias spp. (HOPL) juveniles were very different in the two sections studied. Upstream, the juveniles of Hoplias spp. (HOPL) preferred deep large channels characterized by short banks, shallow to medium bank slopes, turbid water with low oxygen and a high index of inundation potential. In the downstream section, Hoplias spp. also preferred deep water, but in contrast to the upstream section, this taxa preferred sites with long banks with lots of undercuts and a steep to vertical bank slope.

Temporal variations in density

In the upstream section, hydrological events explained the temporal variation in density of the early life stages and juveniles in 100% and 72% of taxa, respectively (Table 6). Density in the early life stage was always positively related to hydrological events, among which the mean water level and number of days exceeding 2.0 m were the most influential. The density of most juveniles was also positively correlated with the mean water level and the number of days exceeding 2.0 m. However, the density of Hemigrammus ocellifer (Steindachner, 1882) (HOCE), Phenacogaster aff. megalostictus Eigenmann, 1909 (PMEG), Pristella maxillaris (Ulreys, 1894) (PMAX), Pseudopristella simulata Géry, 1960 (PSIM), Rivulus agilae (RAGI), R. xiphidus (RXIP) and Nannacara anomala (NANO) juveniles decreased with increasing variation in water level measured 10, 20 and/or 30 DBS.

In the downstream section, hydrological events

explained temporal variation in density in 58% (early life stages) and 23% (juveniles) of taxa (Table 7). Density variation in the early life stage of Microcharacidium eleotrioides (MELE) was mainly linked to mean water level, whereas density in the early life stage of Gasteropelecus sternicla (L., 1758) (GSTE) and Moenkhausia hemigrammoides (MHEM) was more sensitive to variation in water level, and the density of the early life stage of Moenkhausia collettii (Steindachner, 1882) (MCOL) and Poptella brevispina (Reis, 1989) (PBRE) was mainly linked to the number of days that the water level in the Sinnamary River exceeded 5.0, 6.0, 7.0 and/or 8.0 m before sampling (Table 7). Density variation in the early life stage of Pseudopristella simulata (PSIM) was equally linked to the mean and variation in water level. Eleotris amblyopsis (EAMB) was the only taxon whose early life stages and juveniles were strongly negatively influenced by hydrological events.

Discussion

The present list of taxa from the tributaries of the Sinnamary River compares well with those established in the same area with the same sampling method by Ponton & Copp (1997) and by D. Ponton, S. Mérigoux & G. H. Copp (unpublished data), having fifty-eight and sixty-four taxa, respectively, in common with these previous works. The tributaries are nursery areas for more than 60% of the fish species inhabiting the Sinnamary River. In the upstream section, the relative abundance of Characiformes and Perciformes was very similar to that found by Ponton & Copp (1997) in unperturbed areas. Downstream from the dam, we found a higher relative abundance of young Characiformes than those observed in 1994 by the above authors, i.e. just after the dam was closed. Therefore, the present results support the prediction of D. Ponton, S. Mérigoux & G. H. Copp (unpublished data) that reproduction by Characiformes would recover rapidly from the failures induced by closure of the dam.

Oxygen concentration and/or turbidity were important parameters in determining the spatial variation in young fish density in both sections. Downstream from the dam, early life and juvenile stages of many taxa were most numerous in well-oxygenated, clear water. It is well known that low oxygen concentration causes stress and limits the distribution and activity of fish (Matthews, 1998). In the neotropics, many fish species respond to declining oxygen by active migration (Lowe-McConnel, 1987). Others display adaptations, such as dermal lip protuberances (Casciotta, 1993) or aerial respiration (Kramer & McClure, 1982), to cope in situ. Young neotropical fish (i.e. taxa belonging to group 2; Fig. 3c, f) may stay in poorly oxygenated tributaries as an evolutionary trade-off between the costs of such adaptations, and a lack of sufficient food, a higher risk of predation or entrainment in the more oxygenated waters of the main channel. Not surprisingly, more than half of the most abundant taxa in clear waters of the downstream tributaries were Characiformes. These diurnal taxa rely on vision for feeding (Goulding, 1980) and are usually abundant in clear water (Rodriguez & Lewis, 1997). However, in the upstream section, some young Characiformes (those belonging to group 2; Fig. 3f) were more abundant in deep and turbid water. Again, these habitat preferences may reflect some trade-off between impeded vision, and for instance, the risk of predation. Indeed, the young stages of some neotropical Characiformes may take refuge from predators in deep turbid water, as do their adult stages (Power, 1984; Schlosser, 1987; Cambray & Bruton, 1994; Lonzarich & Quinn, 1995; Rodriguez & Lewis, 1997).

The physical structure of the habitat also explained some variation in the density of young fish. In the upstream section, the longer the bank length, the higher the densities of the young of many taxa. This observation confirms the importance of the riparian zone for the progeny of neotropical fish (Mérigoux, Ponton & Mérona, 1998). In these zones, these fish may find shelter from predators or flow variability, and a wide range of food (Schiemer & Zalewski, 1992; Tito de Morais, Lointier & Hoff, 1995). The positive relationship between the density of some young fish and the percentage of undercut bank also supports this hypothesis. Moreover, the density of the early life stage of Acestrorhynchus sp. (ACSP) and of juveniles of Cleithracara maronii (Steindachner 1882) (CMAR) in the upstream section, as well as those of numerous taxa downstream from the dam, increased with increasing richness in litter, vegetation and substratum (LVS; Fig. 3). Habitat diversity is known to enhance fish species diversity in temperate-(e.g. Gorman & Karr, 1978) and tropical rivers (Mérigoux,

Table 3 Significance of sites (space) and campaigns (time) for explaining the variations of taxon density of early life stages (ELS) and juveniles (J) in up- and downstream sections by two-way analysis of variance (ANOVA)

		Upstream								Downstream							
		ELS				J				ELS				J			
		Space		Time		Space		Time		Space		Time		Space		Time	
Order	Code	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Characiformes	HQUA		NS†		NS		–		–		–		–		–		–
	PGUI		NS		NS		–		–		–		–		–		–
	CUSP	4.54	***		NS	3.43	***	2.01	*		NS		NS		NS		NS
	LDES		–		–		NS		NS		–		–		–		–
	LESP		NS	2.85	**	2.00	*		NS		–		–		–		–
	EERY	4.70	***	2.36	*	4.21	***		NS		–		–		–		–
	HOUN		–		–		–		–		–		–		–		–
	HOPL		NS		NS	2.74	**	5.79	***	2.52	*	3.06	**	2.06	*		NS
	CCAR		NS		NS		NS		NS		–		–	2.32	*	3.32	**
	NBEC		–		–		–		–		–		–		NS	4.63	***
	PFIL		NS	2.16	*		NS	5.13	***		–		–		NS	2.31	*
	GSTE		–		–		–		–		NS	2.56	*	2.19	*		NS
	ACSP	2.11	*	3.15	**	2.1	*	5.73	***		NS	3.75	***		NS		NS
	ABIM		NS	4.51	***		NS	2.89	**		–		–		–		–
	AKEI		–		–	2.37	*		NS		NS		NS		NS	2.79	**
	BRSP		–		–		NS		NS		5.81	***	NS		NS		NS
	CFAS	3.27	**	2.93	**	2.59	*	2.87	**		–		–		–		–
	CPAU		–		–		–		–		2.08	*	NS		–		–
	HOCE		NS		NS		NS	2.37	*		NS		NS		NS	2.75	**
	HUNI		–		–		–		–		NS		NS		NS	2.18	*
	HSOV		–		–		–		–		–		–		NS		NS
	MESP		NS	2.83	**		–		–		–		–		–		–
	MELE		2.19	*	NS		NS		NS	2.30	*	4.01	***	4.18	***		NS

	MCHR		NS	6.09	***		NS	13.97	***		NS		NS		2.18	*	NS
	MCOL		NS		NS	3.53	***	3.81	***		NS	2.19	*		NS		NS
	MHEM		–		–		–		–	2.11	*	2.20	*		NS	2.46	*
	MOLI		NS	4.08	***	2.23	*	3.21	**		NS	3.42	***		NS		NS
	MSUR		–		–	2.61	*		NS		–		–		–		–
	PMEG		NS		NS		NS	2.06	*		–		–		–		–
	PBRE		NS	2.93	**		–		–	2.04	*	8.32	***		NS		NS
	PMAX		NS		NS		NS	2.04	*		NS		NS		NS		NS
	PSIM		NS		NS		NS	2.98	**		NS	2.05	*		NS	3.49	***
Siluriformes	TINT		NS		NS		–		–	2.76	**	2.49	*		2.25	*	NS
	PISP		–		–	2.09	*	3.20	**		–		–		–		–
	PRAN	3.16	**		NS	4.39	***		NS	2.24	*		NS		NS	4.54	***
	BCOR		–		–		–		–		–		–	2.18	*		NS
	TGUI		NS		NS	3.83	***		NS		–		–		–		–
Gymnotiformes	SMAC		–		–		–		–	8.99	***		NS		–		–
	BBEE		–		–		NS		NS		–		–		NS		NS
	HART	2.61	*		NS		6.51	***	NS		–		–		–		–
	GYSP		NS	5.03	***	4.30	***	3.14	**		NS	2.69	**		NS		NS
Cyprinodontiformes	RAGI		–		–	2.47	*	5.72	***		–		–		NS		NS
	RXIP	3.31	**	2.07	*		NS	5.19	***	3.44	***		NS		2.71	**	NS
	PPAR		–		–		–		–	2.67	**		NS		–		–
Synbranchiformes	SMAR		–		–		–		–	2.75	**		NS	7.56	***	2.13	*
Perciformes	PSCH		–		–		–		–		–		–	3.05	**	2.18	*
	CMAR		NS		NS	2.64	*		NS		–		–		–		–
	CSAX		NS		NS		NS		NS		NS		NS		NS		NS
	KGUI		NS		NS		NS		NS		NS		NS		NS		NS
	NANO		NS		NS	2.1	*	2.02	*		–		–	6.66	***	2.26	*
	EAMB		–		–		–		–		NS	27.84	***		NS	8.54	***

The F-value is indicated only if $P \leq 0.05$. We omitted taxa with low density (sum of densities in the 100 µp- or 100 downstream samples < 0.4 individuals m^{-2}). See Table 2 for taxon codes

*$0.01 < P \leq 0.05$.

**$0.001 < P \leq 0.01$.

***$P \leq 0.001$.

(NS) not significant.

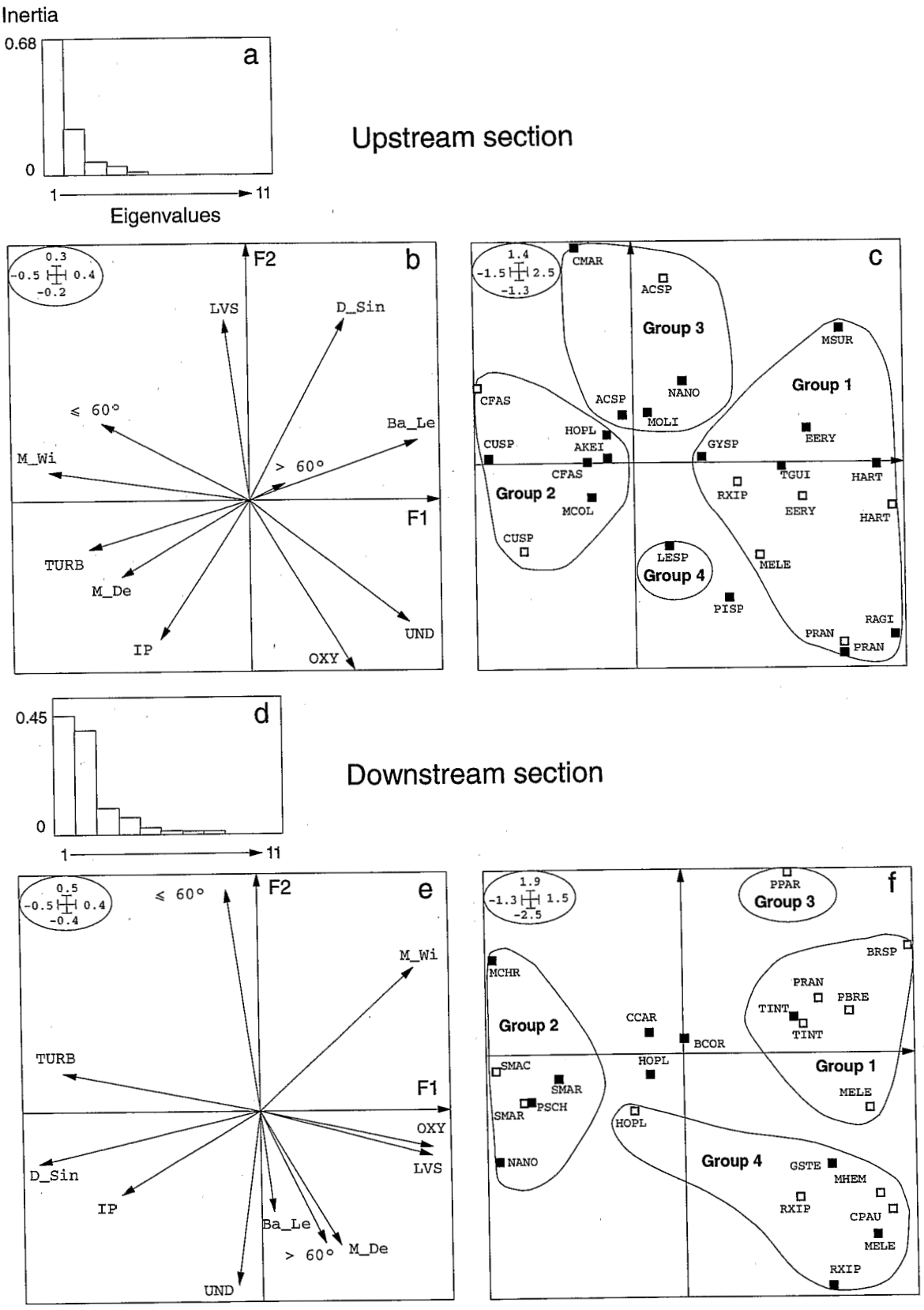
3 Inertia
0.68
a
0
1
11
Eigenvalues
Upstream section
0.3
-0.5
0.4
-0.2
F2
b
LVS
D_Sin
≤ 60°
Ba_Le
M_Wi
> 60°
F1
TURB
M_De
IP
UND
OXY
1.4
-1.5
2.5
-1.3
CMAR
c
ACSP
Group 3
MSUR
NANO
Group 1
CFAS
ACSP
MOLI
HOPL
EERY
CUSP
AKEI
GYSP
CFAS
TGUI
HART
RXIP
Group 2
EERY
MCOL
HART
CUSP
LESP
MELE
Group 4
PISP
RAGI
PRAN
PRAN
0.45
d
0
1
11
Downstream section
0.5
-0.5
0.4
-0.4
≤ 60°
F2
e
M_Wi
TURB
F1
OXY
LVS
D_Sin
IP
Ba_Le
> 60°
M_De
UND
1.9
-1.3
1.5
-2.5
PPAR
Group 3
f
BRSP
MCHR
PRAN
PBRE
TINT
Group 2
CCAR
TINT
BCOR
SMAC
HOPL
Group 1
SMAR
MELE
SMAR
PSCH
HOPL
NANO
Group 4
GSTE
MHEM
RXIP
CPAU
MELE
RXIP

Table 4 Relative contributions of the first two axes on each taxon expressed in percentages (i.e. the square cosines of the angle between each axis and vectors joining the gravity centre of the whole data set to each taxon; Lebart, Morineau & Piron, 1995). A relative contribution of 100% means a square cosines of 1, and therefore, a high correlation with the considered axis. The 'remains' (variation remaining) are the sum of the relative contributions of the remaining axes to the taxon

	Upstream					Downstream				
Order	Code	Stage	F1	F2	Remains	Code	Stage	F1	F2	Remains
Characiformes	CUSP	ELS	72	20	8	HOPL	ELS	22	69	9
	CUSP	J	98	0	2	HOPL	J	22	18	61
	LESP	J	12	31	57	CCAR	J	12	12	76
	EERY	ELS	89	2	10	GSTE	J	18	26	56
	EERY	J	85	2	14	BRSP	ELS	58	33	9
	HOPL	J	58	28	14	CPAU	ELS	36	53	10
	ACSP	ELS	5	79	16	MELE	ELS	71	16	13
	ACSP	J	9	67	25	MELE	J	27	61	12
	AKEI	J	44	1	55	MCHR	J	57	34	9
	CFAS	ELS	70	7	23	MHEM	ELS	36	48	16
	CFAS	J	44	0	56	PBRE	ELS	83	14	3
	MELE	ELS	74	19	7					
	MCOL	J	51	14	35					
	MOLI	J	9	64	27					
	MSUR	J	78	15	7					
Siluriformes	PISP	J	48	47	5	TINT	ELS	68	11	21
	PRAN	ELS	63	22	14	TINT	J	59	17	24
	PRAN	J	63	25	12	PRAN	ELS	33	14	53
	TGUI	J	95	0	5	BCOR	J	0	4	96
Gymnotiformes	HART	ELS	90	1	9	SMAC	ELS	34	1	65
	HART	J	90	0	10					
	GYSP	J	52	0	47					
Cyprinodontiformes	RAGI	J	76	15	9	RXIP	ELS	12	47	41
	RXIP	ELS	73	1	25	RXIP	J	10	66	24
						PPAR	ELS	9	71	20
Synbranchiformes						SMAR	ELS	36	8	56
						SMAR	J	46	4	50
Perciformes	CMAR	J	11	67	22	PSCH	J	54	12	33
	NANO	J	26	34	39	NANO	J	41	33	26

Fig. 3 Results of co-inertia analyses expressing the relationships between fish taxa with a significant site (space) effect (see Table 3) and habitat, respectively, in the up- and downstream sections. (a & d) Histograms of the relative inertia of each axis. (b & e) Habitat variable coordinates on the F1 × F2 plane of the co-inertia analyses. The vector length and direction of each habitat variable illustrate the correlation between each variable and the axes. See Table 1 for habitat variable codes. (c & f) Fish taxa coordinates on the F1 × F2 plane of the co-inertia analyses. See Table 2 for taxon codes: (◇) early life stages; and (◆) juveniles. We determined the groups of taxa according to the relative contributions of the first two axes on each taxon (i.e. Lebart, Morineau & Piron, 1995; see Tables 4 & 5 for details and values). A taxon was considered as well represented by an axis if its relative contribution was more than 25%. If each of the relative contributions of the two first axes was higher than 25%, we chose the highest relative contribution for assigning the taxon to a group. In the upstream section, we did not assign the juveniles of PISP to any group since their correlations with both axes were similar (see Table 4 for the relative contribution values). In the downstream section, correlations of juveniles of HOPL, CCAR and BCOR with both axes were low. Therefore, we did not assign them to any group (see Table 4 for the relative contribution values). The four ellipses in the upper-left corners represent the scale of the factorial scores.

Table 5 Relative contributions of the first two axes on each variable expressed in percentages (i.e. the square cosines of the angle between each axis and vectors joining the gravity centre of the whole data set to each variable; Lebart, Morineau & Piron, 1995). A relative contribution of 100% means a square cosines of 1, and therefore, a high correlation with the considered axis. The 'remains' (variation remaining) are the sum of the relative contributions of the remaining axes to the variables. See Table 1 for variable names

	Upstream			Downstream		
Habitat variables	F1	F2	Remains	F1	F2	Remains
D_Sin	40	44	16	87	5	8
Ba_Le	95	4	2	1	36	63
M_Wi	98	1	1	50	42	8
M_De	72	8	20	14	42	44
TURB	87	3	11	88	3	9
OXY	50	43	7	79	4	18
£ 60°	78	7	15	2	94	4
> 60°	11	1	88	12	52	37
UND	78	14	7	2	79	19
LVS	4	65	31	76	5	19
IP	42	30	27	58	20	22

Ponton & Mérona, 1998). One possible explanation is that a diverse habitat provides numerous refugia against environmental fluctuations (Pearson, Li & Lamberti, 1992). The highest number of taxa associated with high values of LVS in the downstream section supports the hypothesis of Lonzarich & Quinn (1995) that habitat complexity is especially important to stream fish exposed to anthropogenic disturbances. Indeed, dam operations strongly modified the seasonal pattern of the Sinnamary River flow in the downstream reaches in 1995 and 1996 (Fig. 2). Fluctuations in water level in the main channel are the main factor driving those observed in the tributaries (Mérigoux *et al.*, 1999) and Ponton & Vauchel (1998) emphasized how artificially low water in the main channel during the rainy season may increase the water speed in the tributaries. Thus, it can be hypothesized that vegetation, roots, wood, litter or large rocks might be more crucial in providing refugia for young fish inhabiting unpredictable downstream environments.

Interestingly, the position of the sampling sites relatively to the main channel (D_Sin; Fig. 3) was a more discriminatory variable downstream than upstream. In downstream tributaries, the influence of dam operations and of the tide which regularly raises the level of freshwater (Ponton & Copp, 1997) induces maximal variations at the confluence of the tributaries with the main channel and decreases with the distance from the river (Mérigoux *et al.*, 1999). Sternopygus macrurus (Bloch & Schneider, 1801) (SMAC), Synbranchus marmoratus Bloch, 1795 (SMAR), Polycentrus schomburcki Müller & Troschel, 1848 (PSCH) or Nannacara anomala (NANO) occurred at sites distant from the main channel. These species have parental care for relatively few large offspring (Winemiller, 1989; Ponton & Tito de Morais, 1994; Ponton & Mérona, 1998). Their reproductive habits correspond well to the definition of the equilibrium strategy (Winemiller, 1989), i.e. to the use of stable environments. Thus, the restriction of the progeny of these species to sites distant from the river may be a consequence of their reproductive strategy.

The present findings suggest that hydrological events play an important role in the population dynamics of young Characiformes. In temperate rivers, the peak density of eggs and larval fish is often related to temperature and river discharge (Holland, 1986), or to photoperiod (Billard & Gillet, 1984). In the neotropics, where temperature and photoperiod vary little through the year, rising waters at the beginning of the rainy season is the main cue for reproduction of many fish species, especially among the Characiformes (Lowe-McConnel, 1987; Menezes & de Vassoler, 1992). With increasing water level, medium to large species of this order usually colonize the adjacent floodplains where they are supposed to find suitable spawning sites, and where their progeny

Table 6 Exact significance of Spearman's coefficient of rank-order correlation (Mehta & Patel, 1995) between the hydrological variables and the density of each taxon sensitive to the time effect at early life (ELS) and juvenile (J) stages in the upstream section (see Table 3): (o) non-significant; (+ or –) $0.01 < P \leq 0.05$; (++ or — —) $0.001 < P \leq 0.01$; (+++ or — — —) $P \leq 0.001$; $n = 10$; symbols indicate a positive or negative relationship. The results are given only for mean and variance of water levels, as well as the number of days during which water levels exceeded 2.0 m (ND > 2) 10, 20, and 30 days before sampling (DBS) since the analysis with closely related variables such as minimum and maximum, or ND > 1 and ND > 3 gave similar results. See Table 2 for taxon codes

		DBS								
		Mean			Variance			ND > 2		
Code	Stage	10	20	30		20	30	10	20	30
Characiformes										
CUSP	J	o	o	o	o	o	o	o	o	o
LESP	ELS	+	+	++	o	o	o	++	++	++
EERY	ELS	o	o	o	o	o	o	o	o	+
HOPL	J	o	o	+	o	o	o	o	o	o
PFIL	ELS	++	++	++	+	+	o	++	++	+
PFIL	J	o	o	o	o	o	o	o	o	o
ACSP	ELS	+	+	++	o	o	o	++	+	+
ACSP	J	+	+	++	o	o	o	+	+	+
ABIM	ELS	+	+	+	++	+	+	+	o	o
ABIM	J	++	++	++	o	o	o	++	+	++
CFAS	ELS	+	++	++	o	o	o	+	+	++
CFAS	J	o	o	o	+	o	o	o	o	o
HOCE	J	+	o	o	— — —	–	–	o	o	o
MESP	ELS	o	+	+	o	o	o	+	+	+
MCHR	ELS	+	+	++	o	o	o	o	o	+
MCHR	J	o	o	o	o	o	o	o	o	o
MCOL	J	–	o	o	o	o	o	o	o	o
MOLI	ELS	++	+++	+++	+	+	+	++	+	++
MOLI	J	o	o	+	o	o	o	o	o	o
PMEG	J	o	o	o	–	o	o	o	o	o
PBRE	ELS	+++	+++	++	+	+	+	+++	+++	+++
PMAX	J	–	–	o	o	–	— — —	o	o	–
PSIM	J	— —	–	o	–	— —	–	–	–	–
Siluriformes										
PISP	J	o	o	o	o	o	o	o	o	o
Gymnotiformes										
GYSP	ELS	o	o	o	o	o	+	o	o	o
GYSP	J	o	o	o	o	o	o	o	o	o
Cyprinodontiformes										
RAGI	J	–	o	o	–	–	o	–	–	o
RXIP	ELS	o	o	+	o	o	o	o	o	o
RXIP	J	o	o	o	–	–	o	o	o	o
Perciformes										
NANO	J	–	o	o	— —	— —	–	o	o	o

will find food and shelter (Bayley, 1988; Junk, Bayley & Sparks, 1989). Among the taxa which have such a seasonal strategy (Winemiller, 1989), and in accord with our results in upstream tributaries, Acestrorhynchus sp. (ACSP), Astyanax bimaculatus (L., 1758) (ABIM), Moenkhausia chrysargyrea (MCHR), Moenkhausia oligolepis (MOLI) and Poptella brevispina (PBRE) are the best representatives in the Sinnamary River (Ponton & Mérona, 1998). However, the high density of juveniles observed during periods of high

Table 7 Exact significance of Spearman's coefficient of rank-order correlation (Mehta & Patel, 1995) between the hydrological variables and the density of each taxon sensitive to the time effect at the early life (ELS) and juvenile (J) stages in the downstream section (see Table 3): (o) non-significant; (+ or –) $0.01 < P \leq 0.05$; (++ or — —) $0.001 < P \leq 0.01$; (+++ or – – –) $P \leq 0.001$; $n = 10$; symbols indicate a positive or negative relationship. The results are given only for mean and variance of water levels, as well as the number of days during which water level exceeded 5.0 m (ND > 5) 10, 20 and 30 days before sampling (DBS) since the analysis with closely related variables such as minimum and maximum, or ND > 6, ND > 7 and ND > 8 gave similar results. See Table 2 for taxon codes

		DBS								
		Mean			Variance			ND > 2		
Code	Stage	10	20	30	10	20	30	10	20	30
Characiformes										
HOPL	ELS	o	o	o	o	o	o	o	o	o
CCAR	J	o	o	o	o	o	o	o	o	o
NBEC	J	o	o	o	o	o	o	o	o	o
PFIL	J	o	o	o	o	o	o	o	o	o
GSTE	ELS	o	+	+	o	++	++	o	o	+
ACSP	ELS	o	o	o	o	o	o	o	o	o
AKEI	J	o	o	o	o	o	o	o	o	o
HOCE	J	o	o	o	o	o	o	o	o	o
HUNI	J	o	o	o	o	o	o	o	o	o
MELE	ELS	+	++	+++	o	+	o	o	++	++
MCOL	ELS	o	+	+	o	+	+	o	+	++
MHEM	ELS	o	o	+	o	++	++	o	o	+
MHEM	J	o	o	o	o	o	o	o	o	o
MOLI	ELS	o	o	o	o	o	o	o	o	o
PBRE	ELS	++	+	o	+	o	o	+	+	++
PSIM	ELS	o	+	+	o	+	+	o	o	o
PSIM	J	o	o	o	o	o	o	o	o	o
Siluriformes										
TINT	ELS	o	o	o	o	o	o	o	o	o
PRAN	J	++	+	+	o	o	o	+	++	o
Gymnotiformes										
GYSP	ELS	o	o	o	o	o	o	o	o	o
Synbranchiformes										
SMAR	J	o	o	o	o	o	o	o	o	o
Perciformes										
PSCH	J	o	o	o	o	o	o	o	o	o
NANO	J	o	o	+	o	o	o	o	o	o
EAMB	ELS	o	— —	— —	o	o	o	o	— —	— —
EAMB	J	— —	— —	— —	–	o	o	–	— —	–

water may also result from their foraging habits. Juveniles of Hoplias spp. (HOPL), Acestrorhynchus sp. (ACSP) or Pseudopimelodus raninus (PRAN) may congregate in the inundated areas in order to find the small fish which are their prey (Mérigoux & Ponton, 1998). Similarly, juveniles of Moenkhausia oligolepis (MOLI) (which occurred at high density after periods of high water) feed on terrestrial insects (Mérigoux & Ponton, 1998) which are numerous in freshly flooded areas (Welcomme, 1979).

Eleotris amblyopsis (EAMB) was the only taxon for which density was negatively related to high water level in the Sinnamary at early life stages. This species is known to reproduce at the end of the rainy season (Ponton & Copp, 1997), and therefore, the density of the early life stage would be greatest after periods of low water.

The early life stage of some taxa was present the all year round in the tributaries of the Sinnamary River and without significant variations in density. This

suggests that reproduction in some fish is relatively independent of abiotic factors such as flow. Early life stages of the erythrinids Hoplias malabaricus (Bloch, 1794) [grouped at the genus level with H. aimara (Valenciennes, 1840) in the present study] and those of all the cichlids did not vary with time in upstream tributaries. These species are known to be nest spawners (Breder & Rosen, 1966; Ponton & Tito de Morais, 1994), and thus, are the representatives of the equilibrium strategy (Winemiller, 1989). On the other hand, in upstream tributaries, Hemigrammus ocellifer (HOCE), Microcharacidium eleotrioides (MELE), Moenkhausia collettii (MCOL), Phenacogaster aff. Megalostictus (PMEG), Pristella maxillaris (PMAX) and Pseudopristella simulata (PSIM) also had stable densities of their early stages over time. However, in contrast to erythrinids and cichlids, these small-sized characids present all the characteristics associated with the opportunistic strategy: short generation time, small eggs, low fecundity and multiple bouts of reproduction (Winemiller, 1989; Ponton & Mérona, 1998). Thus, different reproductive strategies may result in the same temporal stability in the abundance of offspring. Interestingly, the density of the early life stages of Microcharacidium eleotrioides (MELE), Moenkhausia colletti (MCOL), Pseudopristella simulata (PSIM) and Hoplias spp. (HOPL) did not vary in time in the upstream sites, but did so downstream. It remains to be tested whether these variations in downstream tributaries originated from cycles of reproduction induced by the unstable conditions in this section or by variations in mortality superimposed on a constant reproductive output.

More generally, the relationship between hydrological events and the density of many young fish in the Sinnamary River confirmed that human impact is best monitored by surveys of young fish rather than adults (see also Copp *et al.*, 1991; D. Ponton, S. Mérigoux & G. H. Copp, unpublished data). Moreover, the present results support those of Scheidegger & Bain (1995) in Central Alabama, U.S.A., which showed differences in the composition, distribution and microhabitat use of young fish in natural and flow regulated rivers. These authors stressed the fact that flow regulation and the associated degradation of nursery habitat are potential threats to the conservation of fish. Indeed, the availability of suitable nurseries is a major factor which affects the survival of young fish (e.g. Hyslop, 1988). Ponton & Vauchel (1998) hypothesized that, in future, downstream tributaries of the Sinnamary River will develop deeper channels which will require higher discharge in the river to overspill their banks and inundate their floodplains. Thus, if their hypothesis is sustained, dam operations will lead to shorter periods through the year of favourable conditions for young fish.

Over the last decade, a great deal of knowledge has been accrued on the adult fish assemblages of the Sinnamary River (Tito de Morais & Lauzanne, 1994; Tito de Morais, Lointier & Hoff, 1995), on their reproductive strategies (Ponton & Tito de Morais, 1994; Ponton & Mérona, 1998) and on the ecology of their young stages (Ponton & Copp, 1997; Mérigoux & Ponton, 1998; Ponton & Vauchel, 1998; present study). These different works constitute a unique framework in the neotropics for investigating the long-term consequences of damming on the young stages of freshwater fish, and therefore, on fish communities.

Acknowledgments

We thank A. Amezi, N. Brehm, J. C. Bron, G. Elfort, P. Lhopital, J. Raffray, M. Tarcy and others for help in the field, J. P. Maubèche and P. Vauchel for providing hydrological data, D. Chessel and B. Hugueny for help in data analyses, B. Statzner for his useful comments, and two anonymous referees and Professor A. Hildrew for their helpful comments on a previous version of the manuscript. Electicité De France (contract numbers GP 7572 and 7585) and ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération) funded this study.

References

Angermeier P.L. (1987) Spatiotemporal variation in habitat selection by fishes in small Illinois streams. *Community and Evolutionary Ecology of North American Stream Fishes* (eds W. J. Matthews & D. C. Heins), pp. 52–60. University of Oklahoma Press, Norman, OK.

Bain M.B., Finn J.T. & Booke H.E. (1988) Streamflow regulation and fish community structure. *Ecology*, **69**, 182–192.

sup;Balon E.K. (1984) Reflections on some decisive events in the early life of fishes. *Transactions of the American Fisheries Society*, **113**, 178–185.

Baltz D.M., Vondracek B., Brown L.R. & Moyle P.B. (1987) Influence of temperature on microhabitat choice by fishes in a California stream. *Transactions of the American Fisheries Society*, **116**, 12–20.

Bayley P.B. (1988) Factors affecting growth rates of young tropical floodplain fishes, seasonality and density-dependence. *Environmental Biology of Fishes*, **21**, 127–142.

Billard R. & Gillet C. (1984) Influence de quelques facteurs de l'environnement sur la fonction de reproduction chez les poissons. *Cahiers du Laboratoire de Montereau*, **15**, 45–54.

Bonetto A.A., Wais J.R. & Castello H.P. (1989) The increasing damming of the Parana Basin and its effects on the lower reaches. *Regulated Rivers*, **4**, 333–346.

Boujard T. (1992) Space-time organization of riverine fish communities in French Guyana. *Environmental Biology of Fishes*, **34**, 235–246.

Boujard T., Pascal M. & Meunier F.J. (1990) Micro-répartition spatio-temporelle du peuplement ichthyologique d'un haut bassin fluvial de Guyane, l'Arataye. *Revue d'Ecologie (Terre Vie)*, **45**, 357–373.

Boujard T. & Rojas-Beltran R. (1988) Zonation longitudinale du peuplement ichtyque du fleuve Sinnamary (Guyane Française). *Revue d'Hydrobiologie Tropicale*, **21**, 47–61.

Breder C.M., Jr & Rosen D.E. (1966) *Modes of Reproduction in Fishes*. Natural History Press, New York, NY.

Brown J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Cambray J.A. & Bruton M.N. (1994) Evolutionary trade-off between egg size and egg number in a sister species pair of refin minnows, *Pseudobarbus afer* and *P. asper* (Osteichthyes: Cyprinidae). *Ichthyological Explorations of Freshwaters*, **5**, 305–320.

Casciotta J.R. (1993) New record of the dermal lip protuberance in Characiforms from Rio de La Plata basin in Uruguay. *Ichthyological Explorations of Freshwaters*, **4**, 79–80.

Collier M., Webb R.H. & Schmidt J.C. (1996) *Dams and rivers – primer on the downstream effects of dams*. U.S. Geological Survey Circular, **1126**, 94 pp.

Copp G.H., Olivier J.M., Penaz M. & Roux A.L. (1991) Juvenile fishes as functional describers of fluvial ecosystem dynamics: applications on the river Rhône, France. *Regulated Rivers*, **6**, 135–145.

Covich A.P. (1988) Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. *Journal of the North American Benthological Society*, **7**, 361–386.

Dolédec S. & Chessel D. (1994) Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology*, **31**, 277–294.

Escofier B. & Pagès J. (1990) *Analyses Factorielles Simples et Multiples: Objectifs, Méthodes et Interprétation*. Dunod, Paris.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Géry J. (1977) *Characoids of the world*. T. F. H. Publications, Neptune City, NJ.

Good P. (1993) *Permutation Tests – A Practical Guide to Resampling Methods for Testing Hypotheses*. Springer-Verlag, Berlin.

Gordon N.D., McMahon T.A. & Finlayson B.L. (1992) *Stream Hydrology. An Introduction for Ecologists*. John Wiley & Sons, Chichester.

Gorman O.T. & Karr J.R. (1978) Habitat structure and stream fish communities. *Ecology*, **59**, 507–515.

Goulding M. (1980) *The Fishes and the Forest: Explorations in Amazonian Natural History*. California University Press, Berkeley, CA

Govoni J.J., Hoss D.E. & Colby D.R. (1989) The spatial distribution of larval fishes about the Mississippi River plume. *Limnology and Oceanography*, **34**, 178–187.

Holland L.E. (1986) Distribution of early life history stages of fishes in selected pools of the Upper Mississippi River. *Hydrobiologia*, **136**, 121–130.

Horwitz R.J. (1978) Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs*, **48**, 307–321.

Houde E.D. (1987) Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, **2**, 17–29.

Hyslop E.J. (1988) A comparison of the composistion of the juvenile fish catch from the Sokoto-Rima floodplain, Nigeria, in years preceding and immediately after upstream dam completion. *Journal of Fish Biology*, **32**, 895–899.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publications Fisheries Aquatic Science*, **106**, 110–127.

Kramer D.L. & McClure M. (1982) Aquatic surface respiration, a widespread adaptation to hypoxia in tropical freshwater fishes. *Environmental Biology of Fishes*, **7**, 47–55.

Kullander S.O. & Nijssen H. (1989) *The Cichlids of Surinam*. E. J. Brill, Leiden.

Lebart L., Morineau A. & Piron M. (1995) *Statistique Exploratoire Multidimensionnelle*. Dunod, Paris.

Lonzarich D.G. & Quinn T.P. (1995) Experimental evidence for the effect of depth and structure on the

distribution, growth, and survival of stream fishes. *Canadian Journal of Zoology*, **73**, 2223–2230.

Lowe-McConnell R.H. (1987) *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge.

Manly B.F.J. (1997) *Randonization, Bootstrap and Monte-Carlo Methods in Biology*. Chapman & Hall, London.

Matthews W.J. (1990) Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. *American Midland Naturalist*, **124**, 31–45.

Matthews W.J. (1998) *Patterns in Freshwater Fish Ecology*. Chapman & Hall, London.

Menezes N.A., de Vassoler A.E.A. & M. (1992) Reproductive characteristics of characiformes. *Reproductive Biology of South American Vertebrates*, **4**, 60–70.

Mehta C. & Patel N. (1995) *Statxact 3 for Windows – Statistical Software for Exact Nonparametric Inference – User Manual*. CYTEL Software Corporation, Cambridge, MA.

Mérigoux S., Hugueny B., Ponton D., Statzner B. & Vauchel P. (1999) Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks, *Oecologia*, **118**, 503–576.

Mérigoux S. & Ponton D. (1998) Body shape and ontogenetic diet shifts in young fish of the Sinnamary River, French Guyana, South America. *Journal of Fish Biology*, **52**, 556–569.

Mérigoux S., Ponton D. & de Mérona B., (1998) Fish richness and species-habitat relationships in two coastal streams of French Guyana, South America. *Environmental Biology of Fishes*, **51**, 25–39.

Minshall G.W. (1988) Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263–288.

Mol J.H. (1994) Effects of salinity on distribution, growth and survival of three neotropical armoured catfishes (Siluriformes-Callichthyidae). *Journal of Fish Biology*, **45**, 763–776.

Morris D.W. (1990) Temporal variation, habitat selection and community structure. *Oikos*, **59**, 303–312.

Ouboter P.E. & Mol J.H.A. (1993) The Fish Fauna of Suriname. *Freshwater Ecosystems of Suriname* (ed. P. E. Ouboter), pp. 133–154. Kluwer Academic Publishers, Amsterdam, Netherlands.

Pearson T.N., Li H.W. & Lamberti G.A. (1992) Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society*, **121**, 427–436.

Planquette P., Keith P. & Le Bail P.Y. (1996) *Atlas Des Poissons d'Eau Douce de Guyane*, Tome 1. IEBG, MNHN, INRA, CSP, Ministère de l'Environnement, Paris.

Poff N.L. & Allan J.D. (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, **76**, 606–627.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime, a paradigm for river conservation and restoration. *Bioscience*, **47**, 769–784.

Poizat G. & Pont D. (1996) Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshwater Biology*, **36**, 611–622.

Ponton D. & Copp G.H. (1997) Early dry-season assemblage structure and habitat use of young fish in tributaries of the River Sinnamary (French Guyana, South America) before and after hydrodam operations. *Environmental Biology of Fishes*, **50**, 235–256.

Ponton D. & de Mérona B. (1998) Fish life-history tactics in a neotropical river with a highly stochastic hydrological regime: the Sinnamary river, French Guyana, South America. *Polskie Archivum Hydrobiologii*, **45**, 189–212.

Ponton D. & Tito de Morais L. (1994) Stratégies de reproduction et premiers stades de vie des poissons du fleuve Sinnamary (Guyane Française): analyses de données bibliographiques. *Revue d'Hydrobiologie Tropicale*, **27**, 441–465.

Ponton D. & Vauchel P. (1998) Immediate downstream effects of the Petit-Saut dam on young neotropical fish in a large tributary of the Sinnamary River (French Guyana, South America). *Regulated Rivers*, **14**, 227–243.

Power M.E. (1984) Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology*, **65**, 523–528.

Renno J.F., Berrebi P., Boujard T. & Guyomard R. (1990) Intraspecific genetic differentiation of *Leporinus friderici* (Anostomidae, Pisces) in French Guyana and Brazil: a genetic approach to the refuge theory. *Journal of Fish Biology*, **36**, 85–95.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.

Richter B.D., Baumgartner J.V., Powell J. & Braun D.P. (1996) A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, **10**, 1163–1174.

Rodriguez M.A. & Lewis W.M. (1997) Structure of fish assemblages along environmental gradients in floodplain lakes of the Oronico River. *Ecological Monographs*, **67**, 109–128.

Rojas-Beltran R. (1984) *Clé simplifiée des espèces de Siluriformes*. Bulletin de Liaison, Groupe de Recherche de Guyane, 63 pp.

Rojas-Beltran R. (1986) Evolution du peuplement ichtyologique d'un petit cours d'eau temporaire de la savane littorale de Guyane. *Cybium*, **10**, 263–277.

Scheidegger K.J. & Bain M.B. (1995) Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia*, **1**, 125–135.

Schiemer F. & Zalewski M. (1992) The importance of riparian ecotones for diversity and productivity of riverine fish communities. *Netherlands Journal of Zoology*, **42**, 323–335.

Schiemer F., Spindler T., Wintersberger H., Schneider A. & Chovanec A. (1991) Fish fry associations: important indicators for the ecological status of large rivers. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewante Liminologie*, **24**, 2497–2500.

Schlosser I.J. (1982) Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs*, **52**, 395–414.

Schlosser I.J. (1987) The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, **68**, 651–659.

Sokal R.R. & Rohlf F.J. (1995) *Biometry*, 3rd edn. W. H. Freeman, New York, NY.

Southwood T.R.E. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3–18.

Statzner B., Hoppenhaus K., Arens M.F. & Richoux P. (1997) Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biology*, **37**, 463–472.

Thioulouse J., Chessel D., Dolédec S. & Olivier J.M. (1997) ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, **7**, 75–83.

Tito de Morais L. & Lauzanne L. (1994) Zonation longitudinale des peuplements ichtyques avant mise en eau de la retenue de Petit-Saut (Guyane française). *Revue d'Hydrobiologie Tropicale*, **27**, 467–483.

Tito de Morais L., Lointier M. & Hoff M. (1995) Extent and role for fish populations of riverine ecotones along the Sinnamary River (French Guyana). *Hydrobiologia*, **303**, 163–179.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265–275.

Welcomme R.L. (1979) *Fisheries Ecology of Floodplain Rivers*. Longman Inc., New York, NY.

Welcomme R.L. (1995) Relationships between fisheries and the integrity of river systems. *Regulated Rivers*, **11**, 121–136.

Wiens J.A. (1986) Spatial scale and temporal variation in studies of Shrubsteppe birds. *Community Ecology* (eds J. Diamond & T. J. Case), pp. 154–172. Harper and Row, New York, NY.

Wilkinson L., Blank G. & Gruber C. (1996) *Desktop Data Analysis with Systat*. Prentice Hall, Upper Saddle River, NJ.

Winemiller K.O. (1989) Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, **81**, 225–241.

(Manuscript accepted 24 February 1999)