

Don p. Au (1/3/00)
(Ponton)
Pole 3

Impact of a dam in the neotropics: what can be learned from young-of-the-year fish assemblages in tributaries of the River Sinnamary (French Guiana, South America)?

DOMINIQUE PONTON^{a,*}, SYLVIE MÉRIGOUX^{b,1} and GORDON H. COPP^{c,2}

^a IRD (formerly ORSTOM), Université Montpellier II,

Laboratoire d'Hydrobiologie Marine et Continentale UMR-CNRS 5556, Case 093, 34095 Montpellier Cedex 5, France

^b Université Lyon 1, Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, 69622 Villeurbanne, France

^c Landscape and Ecology Research Group, Department of Environmental Sciences, University of Hertfordshire, College Lane, Hatfield, Herts AL10 9AB, UK

ABSTRACT

1. The aim of this paper is to assess the usefulness of surveying young fish assemblages in tributaries of the Sinnamary River (French Guiana, South America) as a means of assessing fish species diversity and monitoring environmental change in a neotropical river subjected to hydrodam operations.

2. This work confirms that the tributaries of the Sinnamary River are nurseries for more than half the fish species present in the river.

3. It shows that in natural conditions the young fish assemblages at the beginning of the dry season are overwhelmingly dominated by Characiformes, but that species of other orders are favoured in the impacted sections.

4. This study confirms that the evaluation of the reproductive success of the different fish species over large river stretches at the end of the rainy season appears to be an appropriate method for detecting the immediate effects of flow disturbances on fish communities.

5. The results suggest that it is more informative and less time-consuming to consider the abundance of juveniles only, and to group them at the order level instead of calculating diversity indices.

6. The relative abundance of Characiformes juveniles at the end of the rainy season seems a cost-efficient way of assessing the hydrological impact of the dam on the Sinnamary River, and this may be the case for other neotropical rivers where these methods may be generally applicable. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: fish conservation; fish species diversity; hydropower; reproductive success; South America

* Correspondence to: IRD (formerly ORSTOM), Université Montpellier II, Laboratoire d'Hydrobiologie Marine et Continentale UMR-CNRS 5556, Case 093, 34095 Montpellier Cedex 5, France. Fax: + 33 4 67143719; e-mail: Dominique.Ponton@mpl.ird.fr

¹ Fax: + 33 4 72431141; e-mail: merigoux@cismun.univ-lyon1.fr

² Fax: + 44 1707 285258; e-mail: g.h.copp@herts.ac.uk



INTRODUCTION

The damming of rivers is considered as 'one of the most dramatic and widespread deliberate impacts of humans on the natural environment' (Dynesius and Nilsson, 1994). Dams interrupt within-channel patterns and processes (Ward and Stanford, 1983) as well as modify lateral interactions between the main channel and its floodplain (Ward and Stanford, 1995). In downstream reaches, flow regulation modifies the river-bed morphology (Ligon *et al.*, 1995; Collier *et al.*, 1996), alters the retention of suspended material (Plumstead, 1990), provokes phytoplankton blooms (Mérona *et al.*, 1987), and decreases food-chain diversity (Power *et al.*, 1995).

Flow regulation, as induced in river reaches downstream of dams, is recognized as the most disruptive factor for fish assemblages, independent of latitude. In temperate streams, flow variations strongly influence fish assemblage structure as well as the use of microhabitats by adult fish (Grossman *et al.*, 1998). The sensitivity of fish to discharge variations is strongly age dependent (Schlosser, 1987; Schlosser and Angermeier, 1990); young fish are more affected by variations in discharge (Schlosser, 1985) or water velocity (Harvey, 1987; Gozlan, 1998) than older ones. This important relationship between discharge and the frequency of occurrence and the abundance of young-of-the-year (YOY) fish suggests that human impact should be monitored more closely through surveys of YOY rather than adult fish (Copp *et al.*, 1991). Moreover, as the year-class strength of most fish species is determined by the survival rates of their larvae and juveniles (e.g. Snyder, 1983; Balon, 1984; Schlosser, 1985; Houde, 1987; Grosberg and Levitan, 1992; Schiemer and Zalewski, 1992), the determination of how flow regulation affects young-of-the-year fish is essential for predicting the structure of adult fish assemblages (Gozlan, 1998).

In the last few years, the effects of river regulation on various aspects of the early life history of fish have been studied in temperate streams (Copp, 1990; Mastroiello *et al.*, 1996; Mann and Bass, 1997; Gozlan, 1998). However, studies of the effects of South American dams have until recently referred only to adult fish and especially those important for fisheries (Mérona *et al.*, 1987; Ribeiro *et al.*, 1995).

In the late 1980s, Electricité de France obtained the mandate to construct a dam at 'Petit-Saut', the first set of rapids (moving upstream) on the River Sinnamary, French Guiana, with the legal obligation to fund studies aimed at documenting the impact of the dam on water quality (Richard *et al.*, 1997), the aquatic flora (Vaquer *et al.*, 1997) and fauna (Horeau *et al.*, 1997) and especially the fish (Tito de Morais and Lauzanne, 1994; Mérona and Tito de Morais, 1997; Tito de Morais and Raffray, 1999). Studies on the early life stages of fish in the Sinnamary began at the end of 1992, providing information on taxon-habitat relationships (Ponton and Copp, 1997; Méricoux and Ponton, 1999; Méricoux *et al.*, 1999), on changes in morphology and diet during ontogeny (Méricoux and Ponton, 1998), and on the immediate impact following dam closure that took place in January 1994 (Ponton and Vauchel, 1998).

The present work has three main aims: (1) to describe changes in YOY fish assemblages downstream of the dam and in the reservoir during the three years following dam closure, (2) to compare YOY fish assemblage structure in affected tributaries with those of unaffected tributaries, and (3) to assess the usefulness of surveying YOY fish assemblages as a means of assessing fish species diversity and monitoring environmental changes in a neotropical river subjected to hydrodam operations.

THE RIVER SINNAMARY AND THE PETIT-SAUT DAM

With a length of approximately 260 km and a mean annual discharge of $230 \text{ m}^3 \text{ s}^{-1}$, the River Sinnamary is the fifth largest river of French Guiana (Figure 1). Its drainage basin covers about 6570 km² and receives annual precipitation that averages 3000 mm (for a description of the entire river system, see Boujard, 1992; Tito de Morais *et al.*, 1995). In 1989, Électricité de France (EDF) started to build a 111 MW, 750 m long, 44 m high dam at the Petit-Saut rapids (Figure 1).

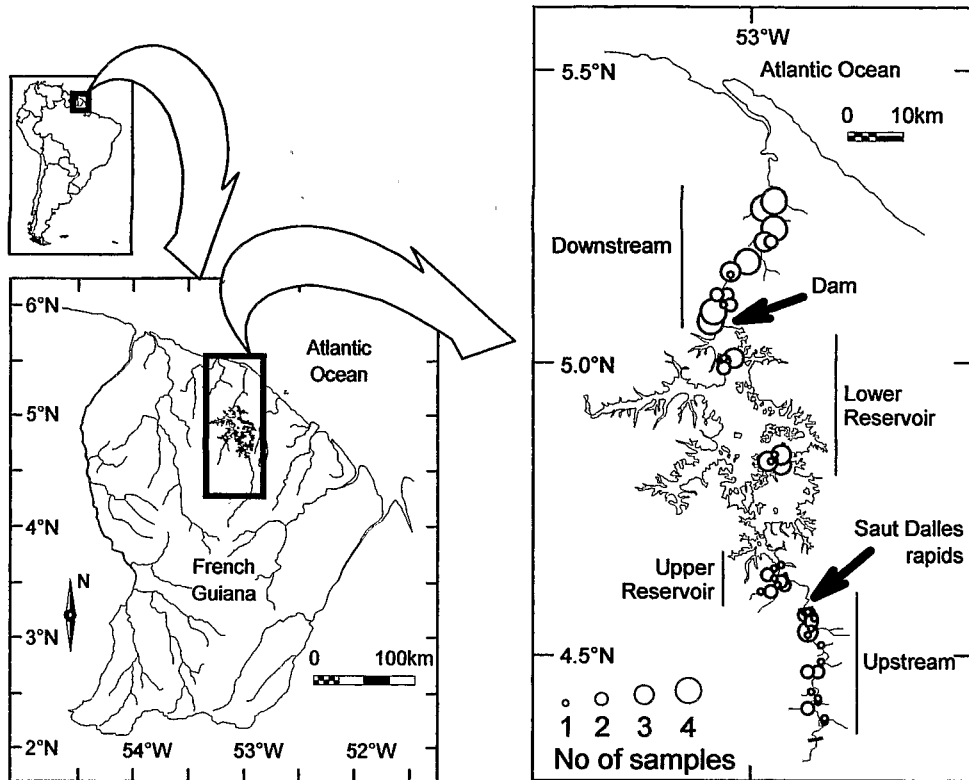


Figure 1. Map of the River Sinnamary (French Guiana, South America), the reservoir at Petit-Saut as it appeared in 1995–1996, and the sampling sites in the downstream, reservoir and upstream sections from 1993 to 1996. The circles are proportional to the number of samples taken at the same place during the 4 years. Only sampled tributaries are presented.

Operation of the dam created three different parts (hereafter referred to as sections) of the River Sinnamary in which water level fluctuations differed strongly (Figure 2). The downstream section meanders through an old flat coastal plain where water levels are influenced by the tides. Before the dam was constructed, each excessive rise in water level in the river backed up the tributaries, which spilt over and inundated the floodplain. When the dam gates were first closed on 5 January 1994, river discharge downstream of the dam was reduced to $100 \text{ m}^3 \text{ s}^{-1}$ during most of the rainy season (November–June in French Guiana) in order to fill the reservoir. As a consequence, water levels downstream of the dam remained at about 200 cm (Figure 2) and no flooding occurred during the entire 1994 rainy season (for a complete description of the downstream effects of the first year of impoundment see Ponton and Vauchel, 1998). The filling phase extended over two successive rainy seasons and was completed in June 1995; from this moment onwards, increasing quantities of water were released through the generators. Water levels during the first part of the 1996 rainy season (February–March) were higher than the two previous years, but no seasonal patterns were detectable and unpredictable flow events of huge amplitude prevailed. In the reservoir, the water level increased dramatically in 1994 and 1995, flooding more than 350 km^2 of pristine Guianese rain forest. In 1996, water levels fluctuated a few metres within the range imposed by dam operations (Figure 2). The upper course of the River Sinnamary traverses different forest types, from dry land arborescent assemblages to flooded or permanent swamp forest. In this upstream section, flow patterns and

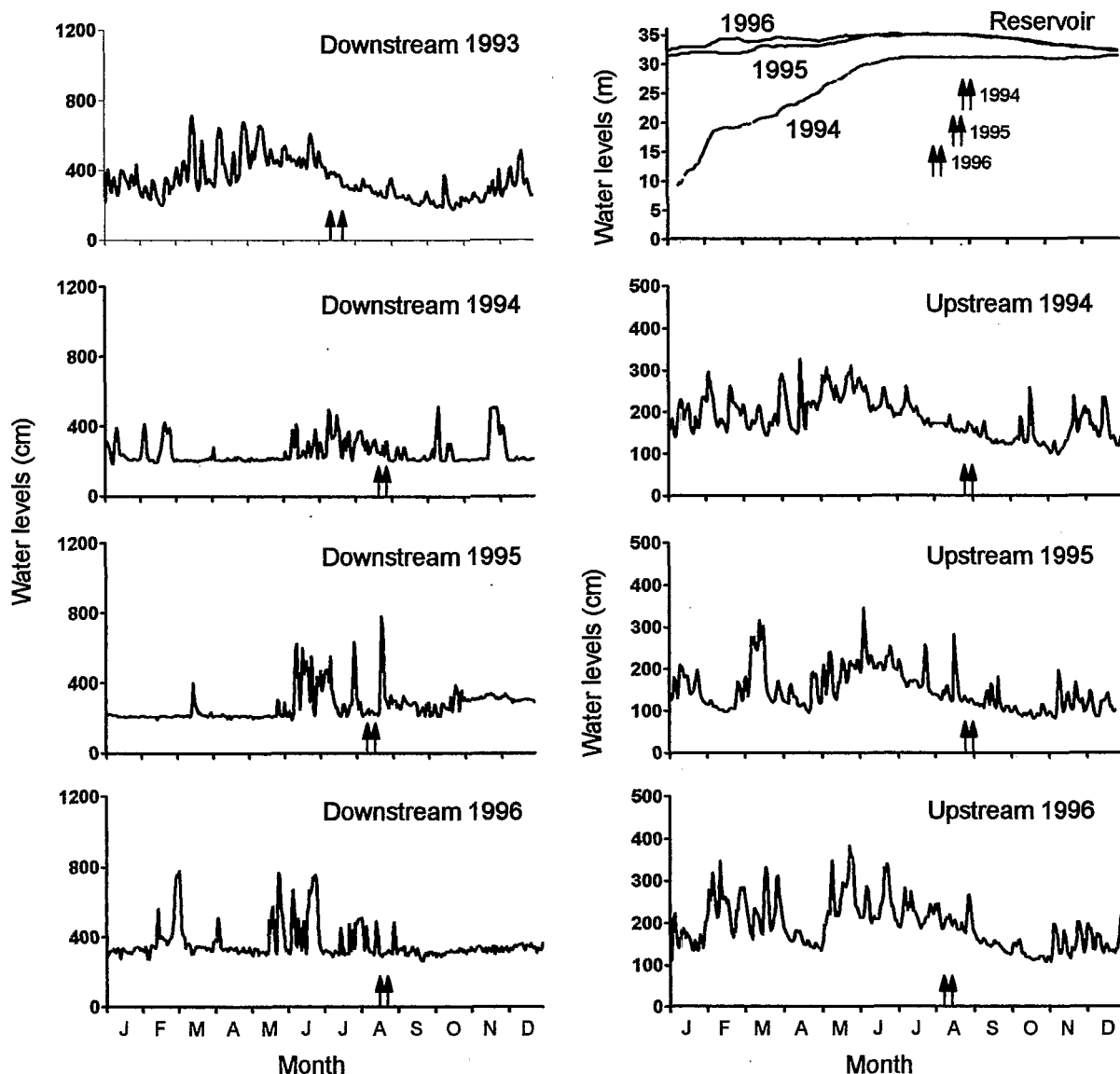


Figure 2. Daily water levels observed in the downstream, reservoir and upstream sections of the River Sinnamary in 1993 (downstream section only), 1994, 1995 and 1996. River water levels were recorded by Hydrological Section ORSTOM Cayenne with ELSYDE Model CHLOE-E gauging stations that were set 300 m downstream from the Petit-Saut dam and upstream from Saut Dalles rapids. Downstream from the dam, water levels correspond to daily minimum values in order to remove the effect of tide; upstream from the reservoir, they correspond to mean daily values. Water levels in the reservoir were provided by Electricité de France. Vertical arrows indicate the beginning and end of sampling periods.

flooding processes remained unperturbed, with predictable long-term variations in water level due to alternate rainy and dry seasons accompanied by unpredictable short-term events imposed by sudden heavy rains (Figure 2).

THE FISH COMMUNITY OF THE RIVER SINNAMARY

A total of 126 freshwater fish species were recorded in the River Sinnamary before dam closure (Tito de Morais and Lauzanne, 1994). None of them seemed to exhibit large upstream spawning migrations similar to those performed by *Prochilodus* species (Lowe-McConnell, 1987) or large pimelodid catfish (Barthem *et al.*, 1991) in the Amazon. However, longitudinal movements, such as those observed in *Hoplias aimara* (Tito de Morais and Raffray, 1999), may have been impeded by the Petit-Saut dam. Most fish communities in French Guiana, those of the River Sinnamary excluded, are in an almost pristine state (Planquette *et al.*, 1996) and no Guianese fish species has a specific conservation status. Although many small-sized characids and some catfishes, gymnotids and cichlids are of potential interest for the aquarium trade, none is collected for export (N. Brehm, Sté Ecobios, Cayenne, personal communication).

MATERIAL AND METHODS

Study sites

Fish were collected at different sampling sites in 10 tributary streams downstream from Petit-Saut dam in 1993 (i.e. before dam closure) and in 1994, 1995 and 1996; 10 tributaries upstream from the reservoir in 1994, 1995 and 1996; and 10 sites in the littoral zone of the Petit-Saut reservoir in 1994, 1995 and 1996 (Figure 1). Seven (in 1994) or six reservoir sites (in 1995 and 1996) were located in the reservoir's mid-to-lower part and the remaining sites were in the reservoir's upstream end. The sites of the lower and upper reservoir were grouped and considered separately, as previous work demonstrated that the composition of their young fish assemblages differed spatially in this section (Ponton and Copp, 1997).

Fish sampling and habitat descriptions

Sampling sites were selected without knowing whether YOY fish were present or not and within types of habitat where rotenone had previously been efficient for sampling young fish, i.e. sites with low water speed and a maximum depth ≤ 1.5 m. A complete description of the sampling technique, its limitations, and the precautions used have been published elsewhere (Ponton and Copp, 1997; M rigoux *et al.*, 1998). Briefly, at each site prior to any disturbance, measurements were made of water temperature, pH, oxygen and conductivity with an ICM 51000 multiparameter analyzer and turbidity with a LaMotte Model 2008 digital turbidity meter. An area of about 50 m² was enclosed with two or three 1 mm mesh stop nets and applied at least two successive doses of Predatox (6.6% emulsifiable solution of rotenone extracted from *Derris elliptica*), which had been well mixed with water. A minimum of four persons equipped with dip nets (1 mm mesh) collected the specimens and preserved them immediately in 90 % alcohol. After fish sampling, additional environmental variables were measured quantitatively (total length of study site, bank length, mean width, etc.), visually estimated (water velocity) and determined by cartographic methods (distance from river, distance from estuary). Percentages of the substrate covered by mud and sand, leaf cover, branches, tree trunks, etc., were visually estimated in 1993 and 1994 or (in 1995 and 1996) calculated from the information recorded at each point of a 1 × 1 m grid covering the whole area (Table 1).

In the laboratory, all fish specimens were sorted and identified using keys for adults (G ry, 1977; Rojas-Beltran, 1984; Kullander and Nijssen, 1989; Planquette *et al.*, 1996) and for juveniles (D. Ponton, unpublished), and measured for standard length (SL) to the nearest 1 mm. The key for juveniles was based on specimens of different size and on characters such as the number of branched rays on the anal fin or position of the fins. Non-adults were separated from adults of each species according to values used by M rigoux and Ponton (1998), which were based on the observed minimum sizes at first maturity of

Table 1. Minimum and maximum values of habitat variables recorded from 1993 to 1996 at sites in the downstream, lower reservoir, upper reservoir, and upstream sections

Section	Downstream				Lower reservoir			Upper reservoir			Upstream		
Variable	1993	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Distance from estuary (km) ^a	20–64	16–64	16–64	16–64	72–87	72–87	72–87	106–112	115–118	118	115–137	133–146	133–164
Distance from river (m) ^b	5–1000	0–600	4–290	4–600	—	—	—	0–300	—	—	0–200	2–10	10–200
Distance from nearest creek (m) ^c	0	0	0–3	0–150	—	—	—	0	—	—	0	0	0–5
Water velocity ^d	0–1	1	0–1	0	0	0	0	0	0	0	0–1	0–1	0
Temperature (°C) ^e	23.7–26.8	24.6–25.4	25.0–27.0	23.6–26.3	27.5–31.3	29.0–32.5	28.8–33.3	25.2–27.2	25.8–28.0	24.8–26.8	23.9–26.1	23.3–26.8	23.8–26.0
pH ^e	5.1–6.1	4.8–5.6	4.3–5.3	4.2–5.2	5.3–6.4	5.2–5.7	5.1–5.4	5.2–5.5	4.5–5.9	4.8–5.2	5.0–5.6	5.3–5.9	4.5–5.2
Conductivity (µS cm ⁻¹) ^e	22.0–31.0	23.3–37.8	19.2–32.6	NA	24.0–29.5	19.7–23.9	NA	26.6–27.9	NA	NA	21.1–30.0	NA	NA
Oxygen (mg L ⁻¹) ^e	4.7–6.9	2.8–6.8	2.9–6.0	3.1–7.4	3.9–5.3	3.5–6.5	4.3–7.3	7.1–7.5	3.8–7.6	2.0–7.5	4.1–7.5	6.0–7.3	2.6–7.0
Turbidity (NTU) ^f	NA	NA	4.1–21.4	1.6–11.1	NA	2.0–5.7	2.7–6.1	NA	4.5–6.9	3.9–15.5	NA	1.7–5.0	1.2–10.6
Canopy cover ^d	4	4	3–4	4	2	2	1–2	4	3–4	1–4	4	1–4	3–4
Surface area (m ²) ^b	15–96	38–100	42–81	30–82	25–112	29–55	35–55	20–60	36–84	63–77	14–108	73–136	45–95
Volume (m ³) ^g	10–93	19–126	10–47	14–49	20–101	13–27	19–31	16–48	13–45	17–37	7–65	29–71	16–71
Bank length (m) ^b	20–50	25–50	18–43	19–38	8–30	7–13	7–13	20–30	9–11	11–17	14–35	19–43	10–42
Total length (m) ^b	10–24	12–25	9–21	10–19	NA	7–11	6–12	10–15	7–12	10–13	7–18	9–22	9–21
Mean width (m) ^b	1.0–5.0	0.5–7.0	2.8–5.5	2.0–6.3	NA	2.6–6.2	4.4–6.0	2.0–5.0	3.4–9.2	5.3–6.9	1.5–9.0	4.1–11.4	3.1–7.8
Maximum depth (m) ^h	NA	0.5–1.6	0.7–1.3	0.8–1.5	0.8–1.5	1.1–1.3	0.9–1.3	1.0–1.5	0.7–1.5	0.6–1.3	0.5–1.2	0.9–1.4	0.4–1.4
Mean depth (m) ⁱ	0.4–1.2	0.4–1.4	0.3–0.7	0.4–0.9	0.6–1.0	0.5–0.7	0.4–0.7	0.8	0.4–0.8	0.3–0.6	0.4–1.0	0.4–0.6	0.3–0.9
% Leaves ^j	20–100	10–80	15–60	30–83	60–90	51–100	48–90	20–80	10–100	3–92	10–80	25–84	25–99
% Wood ^j	0–30	5–40	17–32	8–67	10–40	5–52	20–89	10–60	16–36	40–64	5–60	3–47	10–26
% Submerged vegetation ^j	NA	NA	0–11	0–18	NA	21–33	6–20	NA	14–33	6–26	NA	0–1	8–90
% Mud ^j	20–100	0–100	40–100	42–100	100	0–100	85–91	40–100	0–100	0–91	20–95	16–45	26–100
% Sand ^j	0–80	0–100	0–60	0–57	0	0–95	0	0–60	0–97	0–87	5–80	53–84	0–60

Categories for water speeds are: 0, null; and 1, 0.07–0.09 m s⁻¹; and for canopy cover 1, 0–25%; 2, 25–50%; 3, 50–75%; and 4, 75–100%. With leaves: percentage of leaves and leaf litter; wood: wood diameter >5 cm and <5 cm; submerged vegetation: terrestrial herbaceous vegetation or shrubs, or trees. NA, not available. Methods used to measure environmental variables: ^a 1/50 000 maps of Institut Géographique National; ^b thread distance measurer; ^c thread distance measurer (values >0 indicate that sampling occurred in a flooded area adjacent to a creek); ^d visual estimation; ^e ICM 51000 multiparameter analyzer; ^f LaMotte Model 2008 digital turbidity meter (1995 and 1996 only); ^g surface × mean depth (1993 and 1994) or integration of volumes between transects (1995 and 1996); ^h maximum value of about 10 measurements (1993 and 1994) or maximum value of all the measurements along the 1 × 1 m grid (1995 and 1996); ⁱ mean of *ca* 10 measurements (1993 and 1994) or mean of all the measurements along the 1 × 1 m grid (1995 and 1996); ^j visual estimation (1993 and 1994) or % of occurrence on the 1 × 1 m grid (1995 and 1996). See Ponton and Copp (1997) and Méricoux *et al.* (1998) for further details.

females (Ponton and Mérona, 1998). Non-adults were classified, based on their SL, into early life-stages (*ca* 4 to 15–20 mm SL, depending on species), young juveniles (*ca* 15–20 to 30–50 mm SL), and older juveniles (*ca* >30–50 mm SL) (see Appendix A for the exact size limits for each taxon). Problems were encountered in identifying 12 species, which were grouped with the genus to which they belong. Species and species groups are referred to as taxa.

Almost a third of the samples were obtained from sites in the reservoir where lentic conditions prevailed. Thus, to reduce any potential biases in the structure of young fish assemblages related to high water velocity in some habitats, five sites in the downstream section and five others upstream from the reservoir with water velocities $\geq 10 \text{ cm s}^{-1}$ were ignored, leaving 90 sites for further analyses.

Data analysis

The total number of fish taxa (hereafter referred to as richness) as well as the number of samples in which each taxon occurred (hereafter referred to as frequency of occurrence) were determined for each life-history stage and separately for Characiformes and non-Characiformes taxa. Four indices of young fish diversity were calculated: the traditional Shannon diversity index H' , and evenness E (Magurran, 1988) as well as Δ and Δ^* , two indices of taxonomic distinctness (Warwick and Clarke, 1995). Δ and Δ^* have been developed by these authors in order to detect changes in the composition of marine benthos communities following human impacts. Δ is defined as the average (weighted) path length between every pair of individuals:

$$\Delta = \frac{\sum_{i < j} w_{ij} x_i x_j + \sum_i 0.5 x_i (x_i - 1)/2}{\sum_{i < j} x_i x_j + \sum_i x_i (x_i - 1)/2}, \quad (1)$$

with x_i , abundance of the i th species ($i = 1, \dots, S$) and w_{ij} , weight given to the path length linking species i and j in the hierarchical classification ($w_{ij} = 1$ if i and j belong to the same genera, $w_{ij} = 2$ if they belong to the same family, etc.).

Δ is thus a taxonomic index empirically related to H' (Warwick and Clarke, 1995) but with an added component of taxonomic separation, which takes into account the path length linking species in the hierarchical Linnean classification. A taxonomic classification (Appendix A) was used based mostly on Nelson (1984) and partially on Géry (1977). Δ^* is an index of taxonomic distinctness defined as Δ divided by the value it takes when all the species belong to the same genus:

$$\Delta^* = \frac{\sum_{i < j} w_{ij} x_i x_j}{\sum_{i < j} x_i x_j} \equiv \frac{\sum_k w_k f_k}{\sum_k f_k}, \quad (2)$$

with x_i and w_{ij} as in Equation (1), f_k , sums of cross-products of counts from all pairs of species connected at the same hierarchical level, and w_k , the corresponding path weights. The sums are over $k = 1, \dots, K$, where K is the number of hierarchical taxonomic levels.

Jack-knifed estimates (Manly, 1997) of these four indices were calculated for each year within each section. Differences in occurrences of taxa were tested with Fisher's exact test for 2×2 tables or Pearson's Chi-Square test for $R \times C$ tables with StatXact®, a statistical software package for exact distribution-free inference that uses the algorithms developed by Metha and Patel (1995) for performing permutation tests.

RESULTS

Habitat characteristics

Within each river section, most of the habitat variables remained in the same range of values for that section (Table 1). Although no statistical test was attempted because some habitat characteristics were recorded with techniques that differed between years, a few discrepancies were apparent. Some sampling sites were situated further upstream in the creeks of the downstream section in 1996; turbidity varied between years in most sections; sampled volumes also differed between downstream and lower reservoir sites; and the percentages of submerged vegetation were higher in upstream sites in 1996. At sites in the lower reservoir section, the percentage of wood covering the bottom and the water temperature increased each year in relation to the decay of the dead flooded forest and the subsequent lower percentage of canopy cover.

Except in the reservoir, the differences in habitat characteristics between sites were strongly linked to variations in River Sinnamary water levels. Indeed, year-to-year variations in water depth made it impossible to sample exactly the same locations each year. In 1994 and 1995, the discharges released downstream by the dam were lower (Figure 1). As a consequence, it was necessary to choose different places within large tributaries or to sample tributaries where water depth was greater. In 1996, sampling was performed earlier in the upstream section due to logistical constraints (Figure 1). At that time of the year, the water levels in the upstream reaches were about 0.5 and 0.8 m higher than in 1994 and 1995, respectively. In some tributaries, flooded areas with abundant submerged vegetation were the only places that could be sampled.

Richness and abundance of young fish

At the 90 sites, 29250 fish were collected, of which 23308 (79.7%) were young stages of different age groups (Appendix A). Overall, early life stages, young and older juveniles represented 10.3, 57.7, and 32.0% of the total number of individuals, respectively. Of the 70 taxa, 25 occurred infrequently in the samples ($n \leq 5$), but they were nevertheless retained in the analyses. All taxa except *Parodon guyanensis* were present as young or older juveniles.

Young and older juveniles always dominated the YOY assemblages numerically and comprised almost all the taxa (Figure 3). YOY fish assemblages were very similar in downstream sites in 1993 and upstream sites each year: young juveniles represented $> 70\%$ of the individuals and $> 70\%$ of the taxa; in contrast early life stages were rare and comprised few taxa. After dam completion, the age structures of the young fish assemblages varied from year to year in downstream sites.

Downstream from the dam, the number of taxa of young and older juvenile Characiformes per 100 m² varied significantly with time from 1994 onwards ($p < 0.05$, Kruskal–Wallis test, Figures 4 and 5, respectively). Marginally significant differences ($p \leq 0.10$) were also observed for Characiformes in the lower reservoir section, but not in its upper part. Significant variations in the number of taxa per 100 m² of young and older juvenile Characiformes were also observed in the upstream area, but the values of richness always remained greater than those observed in the downstream section from 1994 onwards. Numbers of taxa and individuals per 100 m² of non-Characiformes juveniles did not vary significantly over time except in the upstream section, where values observed in 1994 were always significantly greater than the following years. Abundance and richness of early life stages were characterized by great variability over time, whereas the abundance and richness of young and older juveniles varied identically with time within a given section. As a consequence, the data obtained for young and older juveniles were grouped and maintained as a category 'juveniles', separate from 'early life stages' in subsequent analyses.

The four diversity indices calculated for juveniles varied differently between years within each river section (Table 2). The Shannon species diversity index H' did not vary significantly with time in each

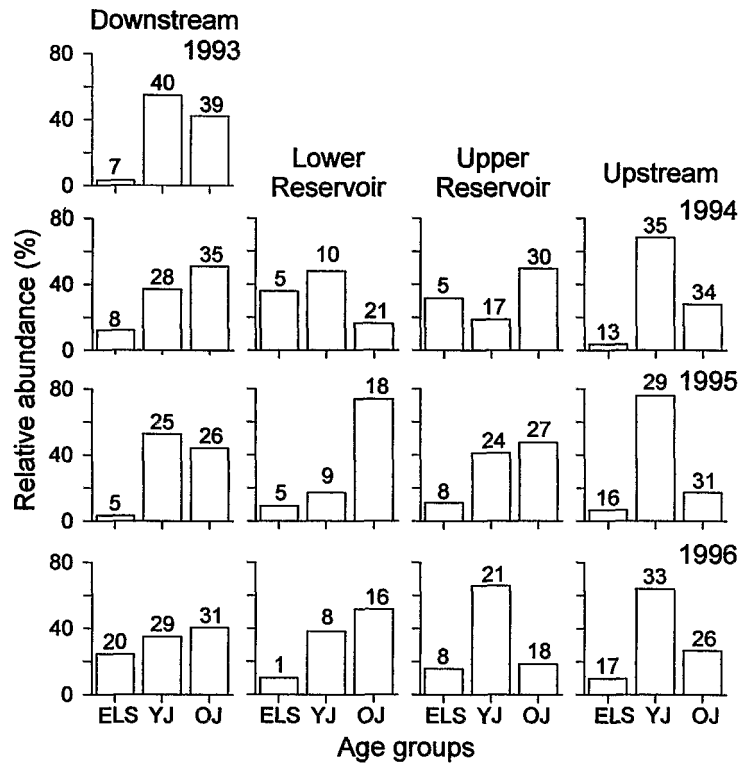


Figure 3. Relative abundance of early life stages (ELS), young juveniles (YJ), and older juveniles (OJ) caught in the different river sections and years. The corresponding number of taxa is presented above each bar.

section, whereas evenness E , and taxonomic index Δ increased significantly after dam completion in downstream sites. The index of taxonomic distinctness Δ^* varied from year to year in both downstream and upstream sections.

Comparisons between sections and years of the percentages of Characiformes juveniles taxa and individuals (Table 3) provided more information than the diversity indices. In downstream sites (1993 only), upper reservoir, and upstream sites, the juvenile assemblages of the tributaries were dominated both taxonomically and numerically by Characiformes as they represented approximately > 60% of the taxa and > 80% of the individuals. In these assemblages, the progeny of *Moenkhausia collettii*, *Pseudopristella simulata*, *Pristella maxillaris*, *Moenkhausia oligolepis*, and *Hemigrammus ocellifer* dominated (Appendix A). Downstream of the dam in 1994, and in the lower reservoir section each year, Characiformes juveniles represented only half of the taxa and one third (downstream section) or one fifth (lower reservoir) of the individuals. At these sites, Perciformes juveniles such as *Eleotris amblyopsis* in the downstream section, or *Krobia guianensis* in the lower reservoir section dominated the assemblages (Appendix A). The relative abundance of Characiformes juveniles increased slightly in 1995 and 1996 in downstream reaches, although these values remained lower than they were before dam closure.

The dominant taxa (*M. collettii*, *P. maxillaris*, *P. simulata*, *K. guianensis* and *E. amplyopsis*) presented contrasting variations in the abundance of their juveniles among sampling sites between years in the different sections (Figure 6), whereas their frequencies of occurrence did not vary within each section except for *K. guianensis* in the lower reservoir ($p = 0.0168$, exact Pearson's Chi Square test). Interestingly, even dominant taxa in the downstream section, such as *P. simulata* and *P. maxillaris*, were present at only

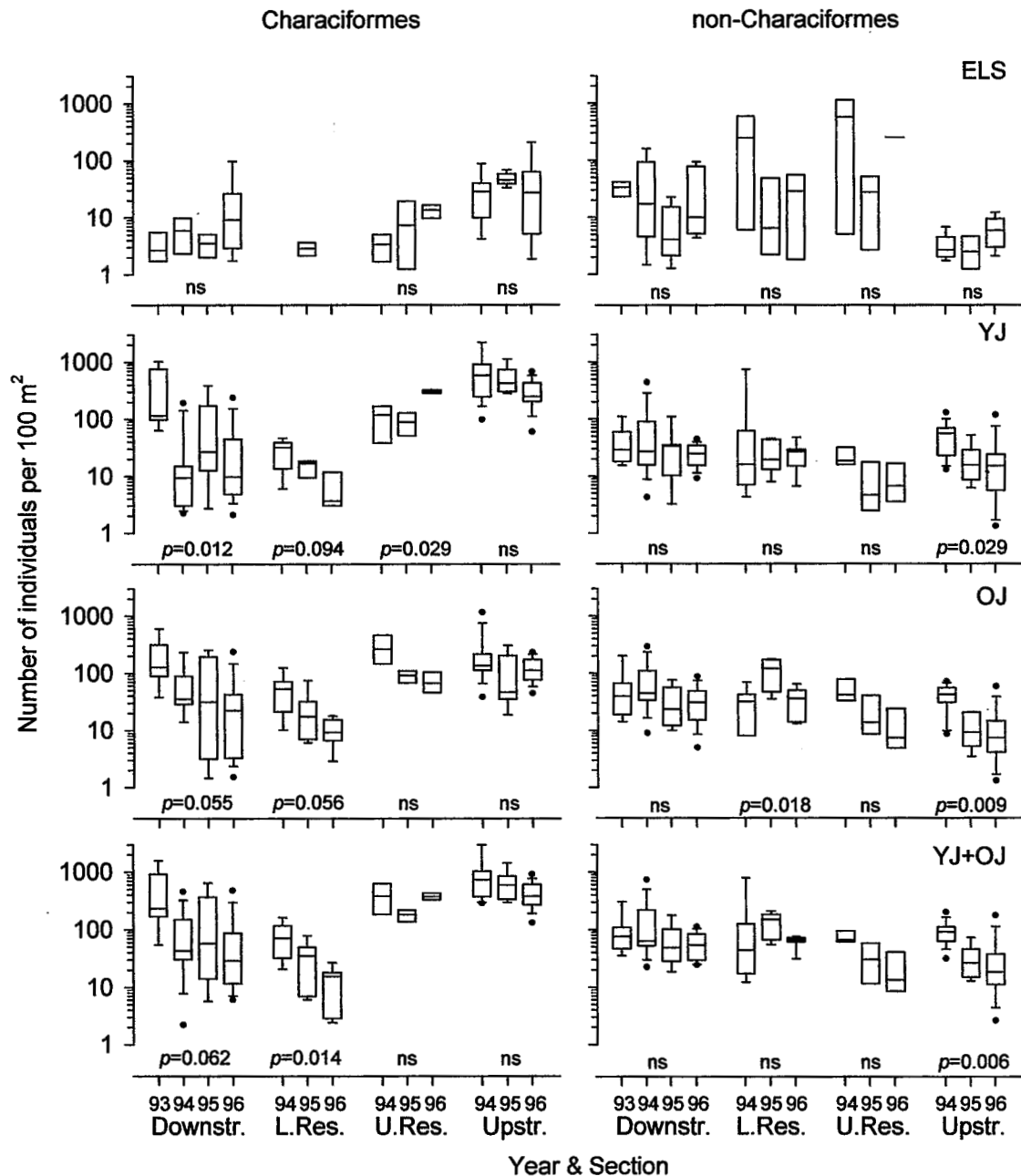


Figure 4. Number of Characiformes and non-Characiformes early life stages (ELS), young (YJ) and older (OJ) juveniles per 100 m² caught each year in each section. Probabilities of significant differences between any of the means within a section (Kruskal–Wallis test) are given when $p < 0.10$. Boxes represent 50% of the data (lower limit = first quartile and upper limit = third quartile), the horizontal bar corresponds to the median value, the whiskers extend to the 5th and 95th percentiles, and the dots represent values outside this range (Downstr., downstream; L.Res., lower reservoir; U.Res., upper reservoir; and Upstr., upstream section).

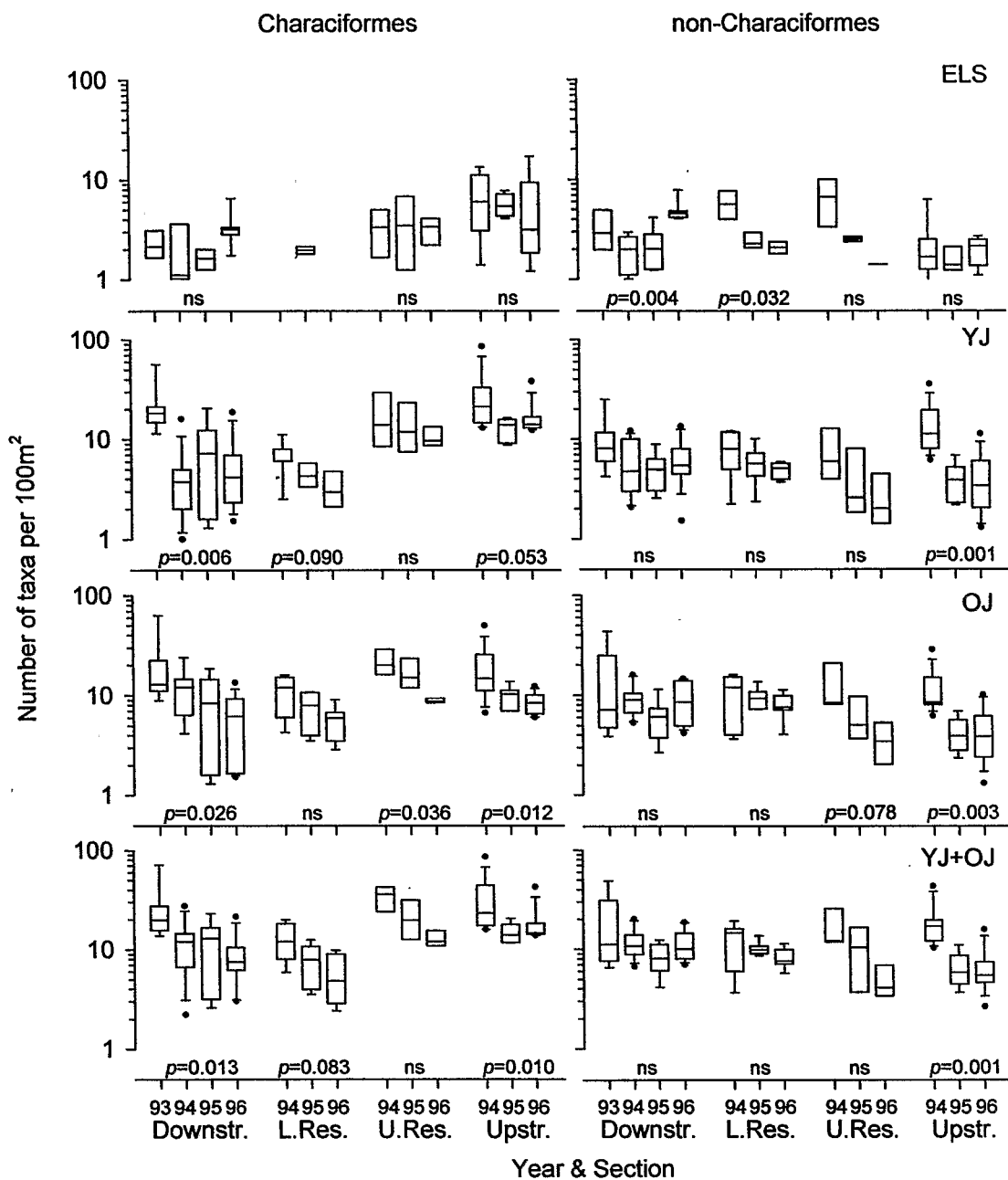


Figure 5. Number of taxa of Characiformes and non-Characiformes for early life stages (ELS), young (YJ) and older (OJ) juveniles per 100 m² obtained each year and in each section. Legend as in Figure 4.

half the studied sites. Similarly, juvenile *K. guianensis* overwhelmingly dominated young fish assemblages in lower reservoir sites in 1994, but they were present in < 50% of the sites. Although the densities of every taxon at upstream sites were variable, their frequencies of occurrence were significantly higher than in the downstream sites ($p < 0.05$ for each taxon, Fisher Exact test).

Table 2. Jack-knifed estimates of the mean and standard deviation (S.D.) of Shannon fish juveniles diversity index (H'), evenness (E), taxonomic diversity index (Δ), and measure of taxonomic distinctness (Δ^*) in river/reservoir sections of the River Sinnamary for each year within each section

Section	Year	<i>n</i>	H'	E	Δ	Δ^*
Downstream	1993	8	1.039 (0.508) A	0.017 (0.009) A	2.094 (1.151) A	2.502 (0.829) A
	1994	10	1.195 (0.276) A	0.025 (0.010) B	3.119 (0.470) B	3.580 (0.133) B
	1995	7	1.158 (0.108) A	0.026 (0.010) B	2.809 (0.715) B	3.145 (0.630) A
	1996	10	1.286 (0.379) A	0.029 (0.010) B	3.036 (1.109) B	3.321 (0.702) B
Lower reservoir	1994	7	0.697 (0.612) A	0.015 (0.055) A	1.953 (2.260) A	3.397 (0.392) A
	1995	6	0.806 (0.173) A	0.031 (0.023) A	2.201 (0.700) A	2.929 (0.493) B
	1996	6	0.874 (0.192) A	0.037 (0.010) A	2.309 (0.491) A	2.862 (0.300) B
Upper reservoir	1994	3	1.238 (0.231) A	0.022 (0.003) A	2.637 (0.505) A	2.924 (0.345) A
	1995	4	1.212 (0.171) A	0.023 (0.010) A	2.538 (0.587) A	2.719 (0.567) A
	1996	4	0.964 (0.237) A	0.028 (0.011) A	2.300 (0.230) A	2.833 (0.379) A
Upstream	1994	10	1.106 (0.132) A	0.021 (0.006) A	2.354 (0.493) A	2.650 (0.454) A
	1995	5	0.987 (0.122) A	0.019 (0.005) A	1.956 (0.238) A	2.256 (0.204) B
	1996	10	1.098 (0.171) A	0.025 (0.004) B	2.255 (0.353) A	2.540 (0.400) A

Δ and Δ^* were calculated following Warwick and Clarke (1995) and the hierarchical Linnean classification presented in Appendix A (see details in text). Identical letters indicate no significant difference between mean estimates compared two by two within each section by a *t*-test at 95% significance (*n* = number of samples).

Table 3. Relative number (in %) of Characiformes juveniles (taxa and individuals) each year within each section

Section	Year	<i>n</i>	Relative abundance of Characiformes juveniles	
			Taxa	Individuals
Downstream	1993	8	61.5 A	87.4 A
	1994	10	54.3 A	37.8 B
	1995	7	56.7 A	68.2 C
	1996	10	54.5 A	63.1 D
Lower reservoir	1994	7	47.4 A	21.6 A
	1995	6	55.6 A	20.7 A
	1996	6	56.3 A	19.6 A
Upper reservoir	1994	3	67.7 A	80.3 A
	1995	4	65.5 A	87.7 B
	1996	4	68.2 A	94.3 C
Upstream	1994	10	61.1 A	88.8 A
	1995	5	61.8 A	95.9 B
	1996	10	64.7 A	91.5 C

Identical letters indicate no significant difference between relative abundance of Characiformes taxa or individuals (comparisons made two by two, Fisher exact test, $\alpha = 0.05$). *n*, number of samples.

DISCUSSION

The impact of Petit-Saut dam on young fish assemblages

The present study confirms that tributaries of the River Sinnamary are inhabited at the end of the rainy season by the progeny of more than half of the approximately 130 species present in the river. Notable exceptions are representatives of the Serrasalminae and the large Siluriformes, whose nurseries still remain unknown. The main advantages to young fish of the lower reaches of tributaries and their associated flooded areas are the lentic 'retention' conditions that occur during the rainy season and protect them from being flushed downstream into the main river. The lower part of the tributaries correspond to the 'igapó' zone of the Amazon system (Lowe-McConnell, 1987; Henderson, 1990), where water velocity decreases with the river's rise in water level (Ponton and Vauchel, 1998). Thus, protection of the tributaries' natural character (biotic, hydrologic, physical), or 'intactness' (Maitland and Lyle, 1991), as well as the natural hydrological regime of the main river, is essential to the conservation of at least half of the fish species occurring in the Sinnamary.

Under natural conditions, i.e. downstream from the dam in 1993 and upstream from the reservoir in all years, the YOY fish assemblages observed at the beginning of the dry season were overwhelmingly dominated by Characiformes (Table 3). In the entire fish assemblage inhabiting the Venezuelan Llanos, Winemiller (1989) observed that: (1) large-bodied Characiformes usually undergo synchronized reproduction during a short period in the rainy season, have high fecundity, and provide no parental care; and (2) smaller Characiformes are characterized by early maturation and continuous production of small clutches during the entire rainy season. In the River Sinnamary, most Characiformes belong to this second group (Ponton and Mérona, 1998), which corresponds to opportunistic reproductive strategies (*sensu* Winemiller and Rose, 1992). Temperate zone equivalents are the European minnow *Phoxinus phoxinus* (Mills, 1987; Mastrotillo *et al.*, 1996) and three-spined stickleback *Gasterosteus aculeatus* (see Wootton, 1984).

Immediately after dam closure, Characiformes juveniles were no longer dominant in either the downstream or the lower reservoir sections (Table 3). Although modifications to the structure of YOY fish assemblages appear similar in these two sections, they may originate from different causes. Downstream from the dam, Ponton and Vauchel (1998) demonstrated how the reduced quantity of water released in the main channel during the 1994 rainy season decreased the mean water depths and increased the mean water velocities at the mouth of one of the largest tributaries in this section. They concluded that: (1) the lack of flooding of areas adjacent to the tributary during the entire rainy season may have impeded adults of Characiformes to find suitable reproduction sites; or (2) if reproduction of some Characiformes species occurred, then their progeny were less likely to cope with the increased water velocities in the tributaries. In the lower reservoir sites, young Cichlidae such as *K. guianensis*, *Satanoperca* sp. aff. *leucosticta*, *Cichlasoma bimaculatum*, and *Crenicichla saxatilis* and Erythrinidae of the genus *Hoplias* (most likely mainly *H. malabaricus*) were very abundant each year (Appendix A). Interestingly, these species take extensive care of their young (see Ponton and Tito de Morais, 1994 for a review) and thus are representative of the equilibrium life history strategy (Winemiller and Rose, 1992). The lentic conditions of the Petit-Saut reservoir are possibly better for fish species with small clutch size and parental care, confirming the prediction of Winemiller (1995) that fish species of the equilibrium life history strategy are favoured within assemblages that have not undergone disturbances for a long time.

At the end of the rainy seasons 1995 and 1996, the percentages of young Characiformes in the fish assemblages sampled in downstream reaches increased slightly (Table 3), indicating that some kind of recovery followed the alteration of fish species densities due to dam closure. It supports the hypothesis of Poff and Ward (1990) that the rate of recovery following human disturbance is greater in systems with elevated natural temporal heterogeneity. The recovery rates of stream taxa subjected to human

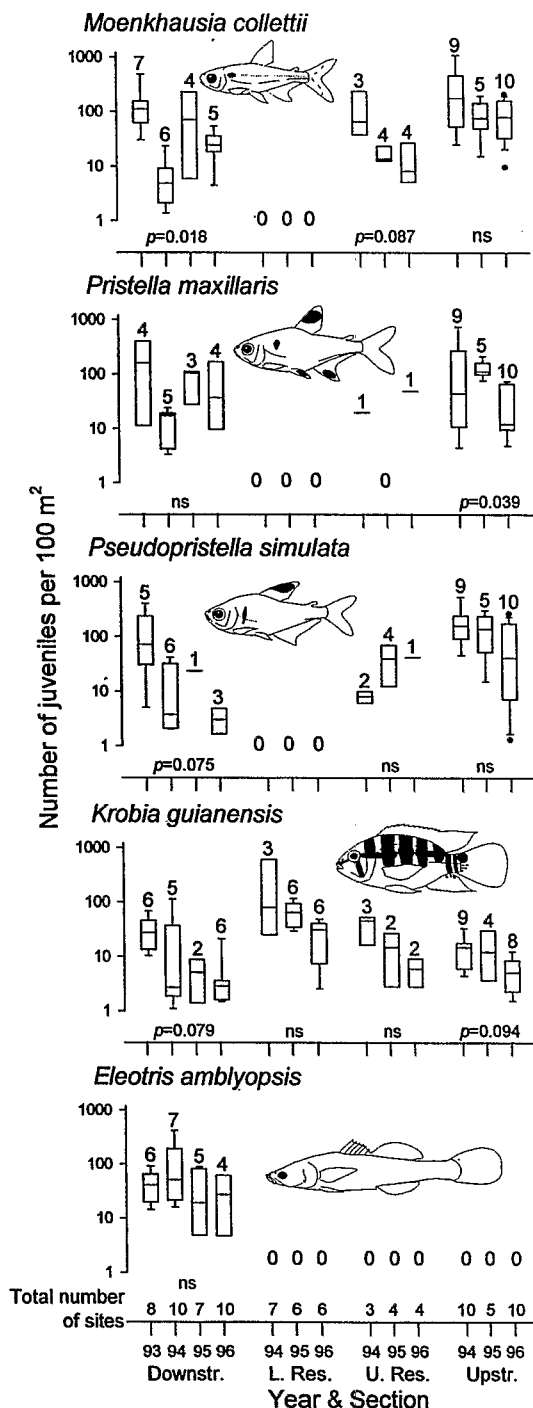


Figure 6. Densities of young and older juveniles per 100 m² for some of the most abundant taxa caught each year in the different sections (null values excluded). The number above each box indicates the number of sites at which the taxa were observed. Probabilities from Kruskal–Wallis test are given when $p < 0.10$. Boxes described in Figure 4. Illustrations (not to scale) of the species based on the modified drawings by L. Lauzanne (ORSTOM, unpublished).

disturbances are affected by abiotic and biotic factors (Grossman *et al.*, 1990). Abiotic factors correspond mainly to hydrological conditions—for example, how long the effects of the disturbances persist. Biotic factors are physiological and ecological abilities of the species to survive the disturbances. In a recent work, Ponton and Mérona (1998) suggested that the stochastic flow regimes of Guianese rivers may have favoured the reproductive traits of the small Characiformes with small eggs and extended periods of reproduction. In the River Sinnamary, these traits may have allowed those taxa able to survive as adults through the 1994 period of impoundment to recover from flow perturbations induced by dam closure. Alternatively, the progeny of small characids such as, for example, *M. collettii*, *P. maxillaris*, and *P. simulata*, did not achieve their pre-dam densities in downstream tributaries at the end of the 1995 and 1996 rainy seasons despite their opportunistic reproductive strategy (Figure 6). Thus, although a recovery pattern was discernible in the composition of young fish assemblages at the order level, the densities of some taxa did not seem to corroborate this trend.

YOY fish assemblages for richness assessment and impact monitoring in the neotropics

Sampling methods affect the precision of any fish surveys (Pepin and Shears, 1997), thus adequate capture methods are required when using young fish assemblages to assess fish species diversity and to document human impacts in tropical rivers. Electrofishing, which is very efficient for sampling young fish in temperate rivers (Copp and Garner, 1995), is ineffective in Guianese waters where water conductivity is very low (Table 1). Light-traps can produce useful results (see Ponton and Vauchel, 1998) but they are very selective (Ponton, 1994). In this context, Rotenone appears to be the only practical alternative, even though its extreme toxicity requires cautious use (Bettoli and Maceina, 1996), and its efficiency is limited to shallow habitats with no or low water movement and not heavily clogged with fallen trees or dead branches.

The choice of sampling time is also important when surveying YOY fishes. In temperate waters, late summer/early autumn has been suggested as the best time for the inventory of YOY fishes because virtually all species have passed through the high mortality of larval development but have not yet entered that of the overwinter period (Copp *et al.*, 1991). In European rivers, the reproduction of most fish species is driven by increases in water temperature and day length in spring and early summer (Welcomme, 1985), though the onset of spawning in some species (pike *Esox lucius*, sofie *Chondrostoma toxostoma*) is linked to rain events or changes in water level (Welcomme, 1985; Gozlan, 1998). In tropical rivers, numerous fish species reproduce in accordance with water level increases (see the reviews by Welcomme, 1985 or Munro, 1990), and in the River Sinnamary most of the fish species breed during a large part of the rainy season (Ponton and Mérona, 1998). Then, at the beginning of the dry season, from late July to early September, their progeny concentrate in the tributaries as water levels decrease. If the aim of the survey is to obtain an impression of fish species richness, and more precisely the reproductive effort of the different fish species, then sampling should take place before biotic interactions that influence the structure of tropical fish become too intense (see Winemiller, 1996). In this context, it is suggested that the best time to survey YOY fish assemblages in Guianese rivers is the transition period from the wet- to the dry-season. In river sections with very different hydrological conditions, and thus potentially different timing in reproduction, the YOY fish assemblages should be better surveyed at regular intervals in time than at a given period (see Sogard, 1997). Indeed, mortality rates are generally higher for the smaller (i.e. younger) individuals (e.g. Miller *et al.*, 1988) and vary among fish taxa and from year to year as demonstrated for marine species (Houde, 1997). Our survey was limited by logistic reasons to sampling at given, and somewhat different, times in each year, and part of the observed variability in the abundance of the youngest stages (Figure 3) might thus reflect this limitation.

In some parts of the temperate zones, YOY fish require less effort in the field to count and identify at the species level than most other animal groups (Copp *et al.*, 1991), but this is not the case in the

neotropics. South America is famous for the richness of its fish communities (Lowe-McConnell, 1987), but some species are difficult to identify as adults and some ecological studies have been published using some misidentifications (Vari and Weitzman, 1990). In this context, it is understandable that few descriptions and no key for identifying the young stages of neotropical fish have been published so far. The identification of young specimens requires extensive series of drawn specimens of variable size for which meristic characters have been recorded (Nakatani *et al.*, 1997; D. Ponton, unpublished). This time-consuming process is rarely possible within the period allocated for documenting impacts. Fortunately, the identifications are much easier at high taxonomic levels and when young individuals have entered the juvenile period, i.e. when they have acquired all the characteristics of adults (Copp and Kováč, 1996; Kováč and Copp, 1999).

Finally, the choice of pertinent indicators for monitoring long-term changes in abundance of animal species has always been challenging. Fish surveys are confronted with incomplete sampling frameworks (for example, our sampling scheme excluded the species that do not use tributaries as nursery areas), measurement errors in the estimations of taxa densities, and modifications of the location of sampling sites (see Thomas, 1996 for identical comments on bird surveys). In our study, some local habitat characteristics varied between years within a section (Table 1) and may have induced some variability in species' abundance. This may explain why the four indices of diversity which were calculated were not very successful for detecting the impact (Table 2) and as such would be of limited use in assessing the conservation value of a particular site or the success of mitigation measures aimed to protect species richness.

CONCLUSIONS

The conservation of the rich array of biotic resources of tropical countries, and thus the possibility to exploit them in a sustainable way, is increasingly threatened by technological advances and social changes (Furtado, 1991). The growing needs to produce electricity have induced the construction of an ever-increasing number of large dams in the tropics (IUCN, 1997). As a consequence, the proportion of rivers presenting altered flow presently exceeds 20% in Africa, 15% in Asia, and 5% in South America (Bravard and Petts, 1993). A recent study conducted by the World Bank Group concluded that only a quarter of the large dams completed several years ago in different parts of the world would meet the present more demanding impact mitigation and management policies (IUCN, 1997). This number should be even lower in the tropics where the relationships between river flow regime and aquatic communities are usually poorly known and where the tools for assessing and monitoring the impacts of dams are scarce or non-existent.

The first environmental studies that preceded the construction of Petit-Saut dam, one of the 40000 large dams of the world (IUCN, 1997), confirmed this need for a better knowledge, and thus better assessment tools, of dam impacts on rivers in general (e.g. O'Keeffe and Davies, 1991), and neotropical rivers in particular. This lack of data was especially obvious when taking into consideration the relationships between river flow regime and the environmental biology of neotropical fish. This is perhaps not surprising as 'many fish biologists equate the state of ichthyological knowledge in the Neotropics with that of North America during the early nineteenth century' (Winemiller, 1996).

In this context, our study of temporal variations of young neotropical fishes in the River Sinnamary over the few years after Petit-Saut dam closure aimed at providing some tools for assessing the medium term impact of hydrodam operations on the fish assemblages. The authors are fully aware that: (1) the approach was mainly descriptive; (2) the study was short when compared with the generation time of some large species; (3) the conceptual model of the ecological function of the tributaries (Ponton and Vauchel, 1998) needs to be tested in other rivers; and (4) our sampling sites gave only a partial view of

the impact of a dam on the early life stages of Guianese fish. Nevertheless, the work demonstrated that YOY fish assemblages in tributaries downstream of the dam reacted immediately to dam operations, emphasizing the importance of protecting the natural character of rivers at the catchment scale (i.e. small and large tributaries as well as the main river and hydrological interactions thereof) as a base-level approach to species conservation. That the YOY fish assemblages later presented some kind of recovery in tributaries of the downstream section confirms that, following Poff and Ward (1990), the evaluation of the reproductive success of the different fish species over large river stretches appears to be an appropriate scale for detecting the immediate effects of flow disturbances on fish communities. Moreover, amongst the different groups of fish, young Characiformes seemed to be the most sensitive to the impact and thus appear to be good functional descriptors (*sensu* Bournaud and Amoros, 1984; Copp *et al.*, 1991) of the dynamics of the River Sinnamary.

It may be concluded that the use of the relative abundance of Characiformes juveniles at the end of the rainy season can be a cost-efficient way to document the impact of flow regulation on neotropical fish populations. This simple indicator should ensure that the conservation of the whole fish community is more effective by allowing dam operators to adapt flow releases to reproductive success of these sensitive taxa on a year-to-year basis. In the future, basic environmental prudence should dictate that the construction of future dams in this area is deferred until Guianese fish phylogenetics and vicariance biogeography (Brooks *et al.*, 1992) are better documented. Only the combination of systematic and ecological information will allow the identification of rivers where human impact is potentially less disruptive.

ACKNOWLEDGEMENTS

This investigation was funded by Electricité de France (Contracts No GP 7530 and 7572) and ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, which also graciously provided GHC with travel to and subsistence in French Guiana in 1993 and 1994. Water levels in the River Sinnamary and in the reservoir were provided, respectively, by Ph. Vauchel, Hydrological Section, ORSTOM Cayenne and Electricité de France, Centre National d'Équipement Hydraulique, Aménagement de Petit-Saut. A. Amési, N. Brehm, J.-C. Bron, L. Coste, G. Elfort, J. Grimaud, A. Mallet, S. Papet, J. Raffray, M. Suaudeau, M. Tarcy helped at various times in the field. We thank P.J. Boon, L. Greenberg, T. Moulton and an anonymous referee for their reviews and constructive comments on this manuscript.

REFERENCES

- Balon, E.K. 1984. 'Reflections on some decisive events in the early life of fishes', *Transactions of the American Fisheries Society*, **113**, 178–185.
- Barthem, R.B., de Brito Ribeiro, M.C. and Petrere, M.J. 1991. 'Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon basin', *Biological Conservation*, **55**, 339–345.
- Bettoli, P.W. and Maceina, M.J. 1996. 'Sampling with toxicants', in Murphy, B.R. and Willis, D.W. (Eds), *Fisheries Techniques*, American Fisheries Society, Bethesda, 303–333.
- Boujard, T. 1992. 'Space-time organization of riverine fish communities in French Guiana', *Environmental Biology of Fishes*, **34**, 235–246.
- Bournaud, M. and Amoros, C. 1984. 'Des indicateurs biologiques aux descripteurs de fonctionnement: quelques exemples dans un système fluvial', *Bulletin d'Écologie*, **15**, 57–66.
- Bravard, J.P. and Petts, G.E. 1993. 'Interférences avec les interventions humaines', in Amoros, C. and Petts, G. E. (Eds), *Hydrosystèmes Fluviaux*, Masson, Paris, 234–274.
- Brooks, D.R., Mayden, R.L. and McLennan, D.A. 1992. 'Phylogeny and biodiversity: conserving our evolutionary legacy', *Trends in Ecology and Evolution*, **7**, 55–59.
- Collier, M., Webb, R.H. and Schmidt, J.C. 1996. 'Dams and rivers—primer on the downstream effects of dams', *U.S. Geological Survey Circular*, **1126**, 1–94.
- Copp, G.H. 1990. 'Effect of regulation on 0+ fish recruitment in the Great Ouse, a lowland river', *Regulated Rivers: Research and Management*, **5**, 251–263.

- Copp, G.H. and Garner, P. 1995. 'Evaluating the microhabitat use of freshwater fish larvae and juveniles with Point Abundance Sampling by electrofishing', *Folia Zoologica*, **44**, 145–158.
- Copp, G.H. and Kováč, V. 1996. 'When do fish with indirect development become juveniles?', *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 746–752.
- Copp, G.H., Oliver, J.M., Penaz, M. and Roux, A.L. 1991. 'Juvenile fishes as functional describers of fluvial ecosystem dynamics: applications on the River Rhône, France', *Regulated Rivers: Research and Management*, **6**, 135–145.
- Dynesius, M. and Nilsson, C. 1994. 'Fragmentation and flow regulation of river systems in the northern third of the world', *Science*, **266**, 753–762.
- Furtado, J.I. dos 1991. 'Ecologically-based strategies for conservation and development in the tropics', *Ecological Research*, **6**, 157–174.
- Géry, J. 1977. *Characoids of the World*, T.F.H. Publications, Neptune City.
- Gozlan, R. 1998. 'Environmental biology and morphodynamics of the sofie, *Chondrostoma toxostoma* (Cyprinidae) with emphasis on early development', Unpublished PhD Thesis, University of Hertfordshire, UK.
- Grosberg, R.K. and Levitan, D.R. 1992. 'For adults only? Supply-side ecology and the history of larval biology', *Trends in Ecology and Evolution*, **7**, 130–133.
- Grossman, G.D., Dowd, J.F. and Crawford, M. 1990. 'Assemblage stability in stream fishes: a review', *Environmental Management*, **14**, 661–671.
- Grossman, G.D., Ratajczak, R.E. Jr., Crawford, M. and Freeman, M.C. 1998. 'Effects of environmental variation and interspecific interactions on assemblage structure and microhabitat use by stream fishes', *Ecological Monographs*, **68**, 395–420.
- Harvey, B.C. 1987. 'Susceptibility of young-of-the-year fishes to downstream displacement by flooding', *Transactions of the American Fisheries Society*, **116**, 851–855.
- Henderson, P.A. 1990. 'Fish of the amazonian Igapo: stability and conservation in a high diversity–low biomass system', *Journal of Fish Biology*, **37**(Suppl. A), 61–66.
- Horeau, V., Cerdan, P. and Champeau, A. 1997. 'La mise en eau du barrage hydroélectrique de Petit-Saut (Guyane): ses conséquences sur les peuplements d'invertébrés aquatiques et sur la nourriture des poissons', *Hydroécologie Appliquée*, **9**, 213–240.
- Houde, E.D. 1987. 'Fish early life dynamics and recruitment variability', *American Fisheries Society Symposium*, **2**, 17–29.
- Houde, E.D. 1997. 'Patterns and trends in larval-stage growth and mortality of teleost fish', *Journal of Fish Biology*, **51**, 52–83.
- IUCN—The World Conservation Union and the World Bank Group. 1997. *Large Dams: Learning from the Past, Looking at the Future. Workshop Proceedings*. IUCN, Gland, Switzerland and Cambridge, UK and the World Bank Group, Washington, DC.
- Kováč, V. and Copp, G.H. 1999. 'Looking at early development in fishes', *Environmental Biology of Fishes*, **56**, 7–14.
- Kullander, S.O. and Nijssen, H. 1989. *The Cichlids of Suriname*, E.J. Brill, Leiden.
- Ligon, F.K., Dietrich, W.E. and Trush W.J. 1995. 'Downstream ecological effects of dams', *BioScience*, **45**, 183–192.
- Lowe-McConnell, R.H. 1987. *Ecological Studies in Tropical Fish Communities*, Cambridge University Press, Cambridge.
- Magurran, A.E. 1988. *Ecological Diversity and its Measurement*, Croom Helm Ltd, London.
- Maitland, P.S. and Lyle, A.A. 1991. 'Conservation of freshwater fish in the British Isles: the current status and biology of threatened species', *Aquatic Conservation: Marine and Freshwater Ecosystems*, **1**, 25–54.
- Mann, R.H.K. and Bass, J.A.B. 1997. 'The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management', *Regulated Rivers: Research and Management*, **13**, 295–301.
- Manly, B.F.J. 1997. *Randomization, Bootstrap and Monte-Carlo Methods in Biology*, Chapman and Hall, London.
- Mastrorillo, S., Dauba, F. and Beland, A. 1996. 'Utilisation des microhabitats par le vairon, le goujon, et la loche franche dans trois rivières du sud-ouest de la France', *Annales de Limnologie*, **32**, 75–85.
- Mérigoux, S. and Ponton, D. 1998. 'Relationship between body shape and diet of young fish in the Sinnamary River, French Guiana, South America', *Journal of Fish Biology*, **52**, 556–569.
- Mérigoux, S. and Ponton, D. 1999. 'Spatio-temporal distribution of young fish in tributaries of natural and flow-regulated sections of a neotropical river in French Guiana, South America', *Freshwater Biology*, **42**, 177–198.
- Mérigoux, S., Ponton, D. and Mérona, B. de 1998. 'Fish richness and species–habitat relationships in two coastal streams of French Guiana, South America', *Environmental Biology of Fishes*, **51**, 25–39.
- Mérigoux, S., Hugué, B., Ponton, D., Statzner, B. and Vauchel, P. 1999. 'Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks', *Oecologia*, **118**, 503–516.

- Mérona, B. de, Carvalho, J.L. de and Bittencourt, M.M. 1987. 'Les effets immédiats de la fermeture du barrage de Tucuruí (Brésil) sur l'ichtyofaune en aval', *Revue d'Hydrobiologie Tropicale*, **20**, 73–84.
- Mérona, B. de and Tito de Morais, A. 1997. 'Les études ichtyologiques liées à la construction du barrage de Petit-Saut: un premier bilan et des recommandations', *Hydroécologie Appliquée*, **9**, 241–262.
- Metha, C., Patel N. 1995. *StatXact 3 for Windows—Statistical Software for Exact Nonparametric Inference—User Manual*, CYTEL Software Corporation, Cambridge.
- Miller, T.J., Crowder, L.B., Rice, J.A. and Marschall, E.A. 1988. 'Larval size and recruitment mechanisms in fishes: toward a conceptual framework', *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 1657–1670.
- Mills, C.A. 1987. 'The life history of the minnow *Phoxinus phoxinus* (L.) in a productive stream', *Freshwater Biology*, **17**, 53–67.
- Munro, A.D. 1990. 'Tropical freshwater fish', in Munro, A.D., Scott, A.P.S. and Lam, T.J. (Eds), *Reproductive Seasonality in Teleosts: Environmental Influences*, CRC Press, Boca Raton, Florida, 145–239.
- Nakatani, K., Baumgartner, G. and Cavicchioli, M. 1997. 'Ecologia de ovos e larvas de peixes', in Vazzoler, A.E.A.M., Agostinho, A.A. and Hahn, N.S. (Eds), *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos*, Editora da Universidade Estadual de Maringá, Maringá, 281–306.
- Nelson, J.S. 1984. *Fishes of the World*, John Wiley and Sons, New York.
- O'Keeffe, J.H. and Davies, B.R. 1991. 'Conservation and management of the rivers of the Kruger National Park: suggested methods for calculating instream flow needs', *Aquatic Conservation: Marine and Freshwater Ecosystems*, **1**, 55–71.
- Pepin, P. and Shears, T.H. 1997. 'Variability and capture efficiency of bongo and Tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton', *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 765–773.
- Planquette, P., Keith, P. and Le Bail, P.-Y. 1996. *Atlas des poissons d'eau douce de Guyane (Tome 1)*, IEBG-M.N.H.N., INRA, CSP, Ministère de l'Environnement, Paris.
- Plumstead, E.E. 1990. 'Changes in ichthyofaunal diversity and abundance within the Mbashe estuary, Transkei, following construction of a river barrage', *South African Journal of Marine Sciences*, **9**, 399–407.
- Poff, N.L. and Ward, J.V. 1990. 'Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity', *Environmental Management*, **14**, 629–645.
- Ponton, D. 1994. 'Sampling neotropical young and small fishes in their microhabitats: an improvement of the quatrefoil light-trap', *Archiv für Hydrobiologie*, **131**, 495–502.
- Ponton, D. and Copp, G.H. 1997. 'Early dry-season assemblage structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after hydrodam operations', *Environmental Biology of Fishes*, **50**, 235–256.
- Ponton, D. and Mérona, B. de 1998. 'Fish life-history tactics in a neotropical river with a highly stochastic hydrological regime: the Sinnamary river, French Guiana, South America', *Polskie Archiwum Hydrobiologii*, **45**, 201–224.
- Ponton, D. and 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. and Vauchel, Ph. 1998. 'Immediate downstream effects of the Petit-Saut dam on young neotropical fish in a large tributary of the Sinnamary River (French Guiana, South America)', *Regulated Rivers: Research and Management*, **14**, 227–243.
- Power, M.E., Sun, A., Parker, G., Dietrich, W.E. and Wootton, J.T. 1995. 'Hydraulic food-chain models', *BioScience*, **45**, 159–167.
- Ribeiro, M.C.L.D., Petrere, M. and Juras, A.A. 1995. 'Ecological integrity and fisheries ecology of the Araguaia Tocantins River Basin, Brazil', *Regulated Rivers: Research and Management*, **11**, 325–350.
- Richard, S., Arnoux, A. and Cerdan P. 1997. 'Évolution de la qualité physico-chimique des eaux de la retenue et du tronçon aval depuis le début de la mise en eau du barrage de Petit-Saut', *Hydroécologie Appliquée*, **9**, 57–83.
- Rojas-Beltran, R. 1984. 'Clé simplifiée des espèces de Siluriformes', *Bulletin de Liaison Groupe de Recherches de Guyane*, **7**, 1–63.
- Schiemer, F. and Zalewski, M. 1992. 'The importance of riparian ecotones for diversity and productivity of riverine fish communities', *Netherlands Journal of Zoology*, **42**, 323–335.
- Schlosser, I.J. 1985. 'Flow regime, juvenile abundance, and the assemblage structure of stream fishes', *Ecology*, **66**, 1484–1490.
- Schlosser, I.J. 1987. 'A conceptual framework for fish communities in small warmwater streams', in Matthews, W.J. and Heins, D.C. (Eds), *Community and Evolutionary Ecology of North American Stream Fishes*, University of Oklahoma, Norman, 17–24.

- Schlosser, I.J. and Angermeier, P.L. 1990. 'The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes', *Polskie Archiwum Hydrobiologii*, **37**, 265–284.
- Snyder, D.E. 1983. 'Fish eggs and larvae', in Nielsen, L.A. and Johnson, D.L. (Eds), *Fisheries Techniques*, American Fisheries Society, Bethesda, 165–197.
- Sogard, S.M. 1997. 'Size-selective mortality in the juvenile stage of teleost fishes: a review', *Bulletin of Marine Sciences*, **60**, 1129–1157.
- Thomas, L. 1996. 'Monitoring long-term population change: why are there so many analysis methods?', *Ecology*, **77**, 49–58.
- Tito de Morais, L. and 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, A. and Raffray, J. 1999. 'Movements of *Hoplias aimara* during the filling phase of the Petit-Saut dam, French Guyana', *Journal of Fish Biology*, **54**, 627–635.
- Tito de Morais, L., Lointier, M. and Hoff, M. 1995. 'Extent and role for fish populations of riverine ecotones along the Sinnamary River (French Guiana)', *Hydrobiologia*, **303**, 163–179.
- Vaquer, A., Pons, V. and Lautier, J. 1997. 'Distribution spatio-temporelle du phytoplancton dans le réservoir de Petit-Saut (Guyane française)', *Hydroécologie Appliquée*, **9**, 169–193.
- Vari, R.P. and Weitzman, S.H. 1990. 'A review of the phylogenetic biogeography of the freshwater fishes of South America', in Peters, G. and Hutterer, R. (Eds), *Vertebrates in the Tropics*, Museum Alexander Koenig, Bonn, 381–393.
- Ward, J.V. and Stanford, J.A. 1983. 'The serial discontinuity concept of lotic ecosystems', in Fontaine, T.D. and Bartell, S.M. (Eds), *Dynamics of Lotic Ecosystems*, Ann Arbor Science, Ann Arbor, 347–356.
- Ward, J.V. and Stanford, J.A. 1995. 'The serial discontinuity concept: extending the model to floodplain rivers', *Regulated Rivers: Research and Management*, **10**, 159–168.
- Warwick, R.M. and Clarke, K.R. 1995. 'New "biodiversity" measures reveal a decrease in taxonomic distinctness with increasing stress', *Marine Ecology and Progressive Series*, **129**, 301–305.
- Welcomme, R.L. 1985. 'River fisheries', *FAO Fisheries Technical Paper*, **262**, 1–330.
- Winemiller, K.O. 1989. 'Patterns of variation in life history among South American fishes in seasonal environments', *Oecologia*, **81**, 225–241.
- Winemiller, K.O. 1995. 'Factors driving temporal and spatial variation in aquatic floodplain food webs', in Polis G.A. and Winemiller K.O. (Eds), *Food Webs: Integration of Patterns and Dynamics*, Chapman and Hall, New York, 298–312.
- Winemiller, K.O. 1996. 'Dynamic diversity in fish assemblages of tropical rivers', in Cody, M.L. (Ed.), *Long-term Studies of Vertebrates Communities*, Academic Press, London, 99–134.
- Winemiller, K.O. and Rose, K.A. 1992. 'Patterns of life-history diversification in North American fishes: implications for population regulation', *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2196–2218.
- Wootton, R.J. 1984. *A Functional Biology of Sticklebacks*, Croom Helm Ltd, London.

APPENDIX A

List of fish taxa, authority, taxa codes, and number of individuals caught per age group and corresponding range of standard lengths (SL) for different years in each section. Taxa occurring infrequently ($n \leq 5$) in the samples whatever their size are indicated with an asterisk (*). ELS, early life stages; YJ, young juveniles; and OJ, older juveniles.

Order	Age group	SL (mm)	Downstream				Lower reservoir			Upper reservoir			Upstream		
			1993	1994	1995	1996	1994	1995	1996	1994	1995	1996	1994	1995	1996
Family	Species and authority														
Characiformes															
Hemiodontidae															
<i>Hemiodopsis quadrimaculatus</i> (Pellegrin 1908)	ELS	–13]								1		1	6		6
	YJ	[14–23]	12								2		1		7
	OJ	[24–89]	10							1	3				
<i>Parodon guyanensis</i> * Géry 1959	ELS	–15]												3	3
Curimatidae															
<i>Chilodus zunevei</i> Puyo 1945	ELS	–12]										1			2
	YJ	[13–29]	1							2	1	4	2	3	6
	OJ	[30–64]								1	2		1	3	
Curimatidae spp.	ELS	–13]				1					3	8	85	133	146
	YJ	[14–29]	68	3	28	23			1	50	37	362	494	154	437
	OJ	[30–74]	1	1					1	28	3	62	5	9	
<i>Cyphocharax helleri</i> * Steindachner 1910	OJ	[30–89]								7			8	14	
Anostomidae															
<i>Anostomus brevior</i> * Géry 1960	ELS	–13]													3
	YJ	[14–29]													2
	OJ	[30–75]								2				2	
<i>Leporinus despaxi</i> * Puyo 1943	YJ	[13–59]									1	6			
	OJ	[60–89]												7	1
<i>Leporinus pellegrini</i> * Steindachner 1910	YJ	[13–44]	1												

<i>Leporinus</i> spp.	YJ	[13–44]										11				
	OJ	[45–115]	1	3	1		1			5			1	4	6	
Erythrinidae																
<i>Erythrinus erythrinus</i> (Schneider 1801)	ELS	–15]		3									1	1		
	YJ	[16–49]										3	2		1	
	OJ	[50–149]					3						1			
<i>Hoplerythrinus</i> <i>unitaeniatus</i> * (Spix 1829)	OJ	[30–209]	2													
<i>Hoplias</i> spp.	ELS	–19]	7	8	5	76		2		1	8	14	10	24	79	
	YJ	[20–49]	5	1	10	2	36	21	11	4	11	15	10	1	14	
	OJ	[50–159]	10	15		7	11	9	7		3	8	5	4	9	
Lebiasinidae																
<i>Copella</i> <i>carsevegnensis</i> * (Regan 1912)	ELS	–11]				2					1			1	2	
	YJ	[12–18]	3	49	5	16	16				6		6	2	8	
	OJ	[19–24]	5	82	2	23	31			3	2		1	1		
<i>Nannostomus beckfordi</i> Günther 1872	YJ	[13–19]	10	11	2	1		1	1							
	OJ	[20–24]	34	8		3		3	3							
<i>Pyrrhulina filamentosa</i> Val. in Cuv. 1846	ELS	–13]									1		1			
	YJ	[14–29]	26	15	7	9	5	1		3	3	5	14	3	24	
	OJ	[30–49]	14	43	17	12	23	2	5	5		1	4	1	3	
Characidae																
<i>Acestrorhynchus</i> spp.	ELS	–14]	1			2										
	YJ	[15–39]	1								1				4	
	OJ	[40–119]	3			1		3	2	1	2	2	3	1		
<i>Astyanax bimaculatus</i> * (Linnaeus 1758)	YJ	[14–29]	4													
	OJ	[30–79]					1									
<i>Astyanax</i> cf <i>keithi</i> Géry, Planquette & Le Bail 1996	ELS	–10]				7									19	
	YJ	[11–24]	24		19					3	1	3	27	52	90	
	OJ	[25–54]	57		1					15	8		21	94	47	
<i>Astyanax meunieri</i> * Géry, Planquette & Le Bail 1996	OJ	[25–64]					16			3						
<i>Bryconops</i> spp.	ELS	–14]				1					1	11	3	2		
	YJ	[15–34]	2			6					103	123	20	13	9	
	OJ	[35–79]	35	12	1	3		1	2	2	11	7	38	21	26	

<i>Characidium fasciadorsale</i> Fowler 1914	ELS	−13]	2										1				
	YJ	[14–29]	59								1	23	28	79	60		
	OJ	[30–44]	2					4	3	8	1	5	1	1			
<i>Charax pauciradiatus</i> * Günther 1864	OJ	[20–79]	1														
<i>Hemigrammus aff. schmardae</i> * (Steindachner 1882)	OJ	[25–34]								1							
<i>Hemigrammus boesemani</i> * (Géry 1959)	YJ	[12–18]	2				1										
	OJ	[19–24]	5			1	19										
<i>Hemigrammus ocellifer</i> (Steindachner 1882)	ELS	−11]													1	4	
	YJ	[12–18]	80	2	15	5			3		3	2	13	145	161	138	
	OJ	[19–24]	154	35	13	26	31		8	4	8	7	13	89	13	30	
<i>Hemigrammus unilineatus</i> (Gill 1858)	ELS	−11]		1													
	YJ	[12–18]	1	75	2										1		
	OJ	[19–29]	3	14	4										1		
<i>Hyphessobrycon aff. sovichtys</i> Schultz 1944	YJ	[10–14]	1						1	2							
	OJ	[15–19]	2			11			2	2							
<i>Melanocharacidium</i> sp.	ELS	−12]	1										1		1	10	
	YJ	[13–21]	2	2		1								1	3	4	
<i>Microcharacidium eleotrioides</i> (Géry 1960)	YJ	[9–13]								1				16	16	7	
	OJ	[14–15]		1										6	4	5	
<i>Moenkhausia chrysargyrea</i> (Günther 1864)	YJ	[14–29]	14		38	8				2	1	7	8	39	11		
	OJ	[30–44]	7	7	62	36		4		2	1	4	12			3	
<i>Moenkhausia collettii</i> (Steindachner 1882)	ELS	−11]				3		1							1		
	YJ	[12–24]	551	5	169	43				3	2	39	791	319	345		
	OJ	[25–34]	262	24	80	48				106	43	6	162	85	333		
<i>Moenkhausia georgiae</i> * Géry 1966	YJ	[13–19]														2	
	OJ	[20–59]									2						
<i>Moenkhausia hemigrammoides</i> Géry 1966	YJ	[13–24]	83	15	23	7							15				

	OJ	[25–34]	5	29	5	12	4		12	2		3			
<i>Moenkhausia oligolepis</i> (Günther 1864)	ELS	–12]								2				1	
	YJ	[13–29]	32			1			23	9	181	66	31	155	
	OJ	[30–64]	25	6	2	5		36	77	40	99	322	12	181	
<i>Moenkhausia</i> <i>surinamensis</i> * Géry 1966	OJ	[30–59]		1					3						
<i>Phenacogaster</i> aff. <i>megalostictus</i> Eigenmann 1909	ELS	–11]											3	16	
	YJ	[12–18]	1									215	725	130	
	OJ	[19–29]	1				1		10	1		161	223	86	
<i>Poptella brevispina</i> * Reis 1989	ELS	–12]				17									
	YJ	[13–29]			3	4			1						
	OJ	[30–64]	1	1						1					
<i>Pristella maxillaris</i> (Ulrey 1894)	ELS	–9]										6	35	12	
	YJ	[10–14]	219	6	33	160			4		34	248	638	219	
	OJ	[15–18]	178	44	100	93					1	2	59	8	
<i>Pseudopristella</i> <i>simulata</i> Géry 1960	ELS	–10]									1	31	52	10	
	YJ	[11–16]	241	9	5	3			4	21	29	540	701	491	
	OJ	[17–21]	244	29	14	4			1	80	1	107	77	142	
<i>Triportheus</i> <i>rotundatus</i> * (Schomburgk 1841)	YJ	[15–24]												3	
Siluriformes															
Auchenipteridae															
<i>Tatia intermedia</i> (Steindachner 1876)	ELS	–13]				1								1	
	YJ	[14–24]	4	1								2			
	OJ	[25–59]	4	6	3	2							2		
Pimelodidae															
<i>Pimelodella</i> spp.	YJ	[20–39]			3							2	4	1	
	OJ	[40–99]							18	1		34	1	1	
<i>Pimelodus ornatus</i> (Kner 1857)	OJ	[50–194]		1								1			
<i>Pseudopimelodus</i> <i>raninus</i> (Valenciennes 1840)	ELS	–12]		1											
	YJ	[13–29]	1	1											
	OJ	[30–64]		5					1				2	2	

<i>Rhamdia quelen</i> * (Quoy & Gaimard 1824)	OJ	[50–99]		1															
Cetopsidae																			
<i>Hemicetopsis</i> sp.*	YJ	[12–18]															1		
Aspredinidae																			
<i>Bunocephalus coracoideus</i> * Cope 1874	YJ	[14–38]	1					1											
	OJ	[39–69]	1					3											
Trichomycteridae																			
<i>Trichomycterus guianense</i> * (Eigenmann 1909)	YJ	[14–28]																1	1
	OJ	[29–49]																1	2
Callichthyidae																			
<i>Callichthys callichthys</i> Linnaeus 1758	YJ	[13–49]						3					2						
	OJ	[50–89]											1						
<i>Megalechis thoracata</i> * Reis 1996	YJ	[13–49]						2							1				
	OJ	[50–109]	1																
Loricariidae																			
<i>Ancistrus</i> aff. <i>hoplogenyss</i> * (Günther 1864)	YJ	[13–29]						1											
	OJ	[30–64]						5											1
<i>Lasiancistrus niger</i> * (Norman 1926)	OJ	[50–89]						1							1				
Gymnotiformes																			
Sternopygidae																			
<i>Sternopygus macrurus</i> (Bloch & Schneider 1801)	ELS	–19]	4					3										2	
	YJ	[20–59]	4			9		2									1		
	OJ	[60–144]	4					3				7					1		1
Hypopomidae																			
<i>Brachyhypopomus beebei</i> (Schultz 1944)	ELS	–19]											2						
	YJ	[20–49]	6			7							3		2		1		
	OJ	[50–99]	16			29		7	10	2			18		3		26	12	3

<i>Hypopomus artedi</i> (Kaup 1856)	ELS	−19]				7											
	YJ	[20–49]				6						1	4	4			
	OJ	[50–129]		1		1						2		2			
Gymnotidae																	
<i>Gymnotus</i> spp.	ELS	−18]			2	4	1										
	YJ	[19–49]	2	13	1	1						9	2				
	OJ	[50–184]	13	30	10	29	3			3	1	2	73	12	6		
Cyprinodontiformes																	
Aplocheilidae																	
<i>Rivulus agillae</i> Hoedeman 1954	ELS	−9]				1	6						1	1	3		
	YJ	[10–14]	3	4	14	17				2			13	1	14		
	OJ	[15–19]	5	12	9	16	1	1	1		2		8		10		
<i>Rivulus igneus</i> * Huber 1991	YJ	[10–19]											1				
<i>Rivulus xiphidius</i> Huber 1979	ELS	−9]				6							4	3	31		
	YJ	[10–14]	9	5	2	13				8	2		44	13	59		
Poeciliidae																	
<i>Poecilia parae</i> (Eigenmann 1894)	ELS	−7]			3	6	4										
	YJ	[8–10]	2	4	16	32	4			1							
	OJ	[11–12]		4	10	24	6			2							
Synbranchiformes																	
Synbranchidae																	
<i>Synbranchus</i> <i>marmoratus</i> Bloch 1795	ELS	−58]				1											
	YJ	[59–99]			1												
	OJ	[100–199]			1	1	3		1		1	1	2	3	4		
Perciformes																	
Nandidae																	
<i>Polycentrus</i> <i>schomburgkii</i> Müller & Troschel 1848	ELS	−12]					5										
	YJ	[13–18]	2		2	1	19										
	OJ	[19–29]	1	3	4	3	7	1									
Cichlidae																	
<i>Cichlasoma</i> <i>bimaculatum</i> (Linnaeus 1758)	ELS	−12]						3									

	YJ	[13–28]						11	1						
	OJ	[29–94]	2		1			112	8						
<i>Cleithracara maronii</i> (Steindachner 1882)	YJ	[13–33]		3							1	1	4	1	3
	OJ	[34–51]		13		12		1					2		3
<i>Crenicichla saxatilis</i> (Linnaeus 1758)	ELS	–19]	1	89		72				87					
	YJ	[20–49]	21	19	88	8	3	4	29		2	6	9	8	5
	OJ	[50–140]	7	6	6	9	1	35	27	3	3	6	6	5	3
<i>Krobia guianensis</i> (Regan 1905)	ELS	–12]	74	3		42	427	40	24	138	42	175	2	5	
	YJ	[13–28]	94	73	6	17	438	39	35	21	6	6	43	54	23
	OJ	[29–74]	12	16	2	2	20	153	38	20	5	3	11	11	13
<i>Nannacara anomala</i> Regan 1905	ELS	–11]				3	1			2			5		
	YJ	[12–18]	14	31	2	16	8				1	11	93	3	42
	OJ	[19–29]	9	124	1	39	29	2	1	4	12	23	53	3	38
<i>Satanoperca</i> aff. <i>leucosticta</i> (Müller & Troschel 1848)	ELS	–12]					1	1							
	YJ	[13–28]	3	3			57	8	11				11		
	OJ	[29–89]	3				1	9	20						
Eleotridae															
<i>Dormitator</i> <i>macrophthalmus</i> * Puyo 1944	YJ	[14–24]		4											
	OJ	[25–49]				1									
<i>Eleotris amblyopsis</i> (Cope 1870)	ELS	–14]		94	20	49									
	YJ	[15–19]	10	248	38	30									
	OJ	[20–24]	106	241	88	46									
Total number of samples			8	10	7	10	7	6	6	3	4	4	10	5	10
Total surface sampled			428	691	435	605	292	269	287	130	84	281	527	501	731
Total number of taxa			46	41	32	37	22	19	16	36	32	26	41	41	40
Total number of individuals			2955	1673	1010	1247	1225	521	238	723	538	1341	4213	3992	36

