

Sylvie Mérioux · Bernard/Hugué · Dominique/Ponton
Bernhard Statzner · Philippe/Vauchel

Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks

Received: 6 July 1998 / Accepted: 16 November 1998

Abstract The species richness of communities should largely depend on habitat variability and/or on habitat state. We evaluated the ability of habitat variability and habitat state to predict the diversity of juvenile neotropical fish communities in creeks of a river floodplain. The young-fish fauna consisted of 73 taxa, and samples were well distributed over a wide range of relevant temporal and spatial habitat variability. We were unable to demonstrate clear patterns of richness in relation to temporal and spatial habitat variability (if habitat state variables were not included), regardless of the temporal variability scale, the grouping of sites (up- and downstream sites differed in temporal variability patterns), taxonomic units or life stages considered. Using stepwise multiple regression, 36% of the variance in species richness was explained for all data, and at best 47% was explained for all taxonomic units at upstream sites using temporal and spatial habitat variability and habitat state (bank length, mean width, mean water level before fishing and/or water turbidity). Using Monte Carlo simulations, we blindly predicted 31% (all data) and at best 37% (all upstream taxa) of the observed variance in species richness from these model types. This limited precision is probably because rare species produced most of the richness patterns in our creeks. The prediction of these rare species is generally difficult for various reasons, and may be a problem in many ecosystem types.

Key words Species richness · Habitat diversity · Hydrological variability · Young fish

Introduction

Predicting diversity or species richness of communities is one of the central aims of much current ecological research (Heywood and Watson 1995). Two elements play a role in such predictions. Firstly, temporal habitat variability is viewed as a measure of disturbance and affects species richness (e.g., *intermediate disturbance hypothesis*, Connell 1978). Secondly, spatial habitat variability is viewed as a buffer against such disturbance, providing refugia and spatial diversity (Townsend and Hildrew 1994). In addition to habitat variability, species richness should depend on habitat state (i.e., the mean conditions, Resh et al. 1994). Therefore, evaluating the ability of habitat variability and habitat state to predict the diversity of communities is an important exercise. This paper assesses that ability for juvenile neotropical fish communities in creeks (small tributaries) of a river floodplain.

In running waters, abiotic factors strongly structure freshwater animal communities (e.g., Grossman et al. 1982; Statzner et al. 1988; Palmer and Poff 1997). The frequency of disturbance by floods or droughts is usually high, and competitive or predator-prey interactions are often marginal factors in determining the composition of lotic assemblages (Resh et al. 1988). Therefore, abiotic factors, i.e., temporal and spatial habitat heterogeneity, are currently considered to be of major importance in stream ecology (e.g., Pringle et al. 1988; Townsend 1989).

Temporal variability is usually viewed as frequency and/or severity of disturbance (Hildrew and Townsend 1987; Poff and Ward 1990), and is often described as stream flow variability (Resh et al. 1988). Lotic fish diversity responds to such temporal variation of discharge by (1) reduction of diversity if unpredictable disturbances through discharge increase (Horwitz 1978;

S. Mérioux (✉) · B. Hugué · B. Statzner
CNRS/ORSTOM, Laboratoire d'Ecologie des
Eaux Douces et des Grands Fleuves, Université Lyon 1,
69622 Villeurbanne Cedex, France
email: merigoux@cismsun.univ-lyon1.fr

D. Ponton
ORSTOM-HEA, Université Montpellier II,
Laboratoire Hydrobiologie Marine et Continentale,
Case Postale 093,
F-34095 Montpellier Cedex 5, France

P. Vauchel
ORSTOM, BP 1386,
Dakar, Senegal



Fonds Documentaire ORSTOM
Cote: B* 17669 Ex: 1

Schlosser 1985), and (2) reduction of diversity through biotic interactions when discharge patterns are stable (Meffe 1984). These patterns correspond to predictions made by the intermediate disturbance hypothesis (Connell 1978).

Spatial habitat variability is often viewed as availability of physical niche space and refugia that modifies competitive exclusion and the effect of disturbances (Townsend 1989; Townsend and Hildrew 1994). Correspondingly, the highest species richness of lotic fish occurs in spatially more diverse habitats (e.g., Gorman and Karr 1978; Mérigoux et al. 1998). These patterns of fish diversity correspond to predictions of the *patch dynamics concept*, i.e., highest species richness occurs at intermediate levels of temporal and at highest levels of spatial habitat variability (Townsend 1989). Thus, evidence from fish suggests that the patch dynamics concept can be applied for mobile organisms (see Frid and Townsend 1989; Downes 1990 for discussion of this point).

However, the only study that has tested the patch dynamics concept for lotic fish failed to support it (Persat et al. 1994). The authors suggested that separate studies of juveniles and adults as ontogenetic niche shifts could explain why the patch dynamics concept predictions were not supported. In addition, long-lived organisms such as fish should be disturbed by only a small fraction of events (Townsend and Hildrew 1994). However, we suggest that juveniles and adults respond differently to a given event, and that young fish are affected by shorter-term events than adults. Moreover, Resh et al. (1994) suggested the inclusion of variables that describe the state of habitats in studies relating species richness to habitat variability.

A study of lotic young fish in diverse neotropical communities on a short temporal scale (weeks) and a small spatial scale ($< 100 \text{ m}^2$) appeared to be appropriate for evaluating the power of habitat variability and state in diversity predictions. Our temporal scale corresponded to a large part of the life span of the young fish in the creeks studied (Ponton and Tito de Morais 1994). Our spatial scale corresponded well to the space used as habitat by young fish (Schiemer et al. 1991; Schiemer and Zalewski 1992), and was appropriate for the study of multi-species patterns (Poizat and Pont 1996). In addition, the studied creeks of the neotropical Sinnamary River (French Guiana) act as nurseries for fish larvae and juveniles throughout most, if not all, of the year (Ponton and Copp 1997; Ponton and Vauchel 1998). The upper Sinnamary River has extreme, unpredictable natural hydrological variations in relation to local rains, like the majority of Guianese watercourses (Westby 1988). The lower Sinnamary River is now under the impact of the Petit Saut dam, which changes the natural hydrological regime (Ponton and Vauchel 1998). In addition, the tidal rhythm of the Atlantic affects the lower Sinnamary, which adds hydrological variability (Ponton and Copp 1997). Habitats in the creeks should be more or less affected by that hydrological variability of the Sinnamary according to their longitudinal distance from the main

river. Therefore, habitats in the creeks should cover a large range of temporal variability patterns, and hydrological instability provides a measure of disturbance for fish (Poff and Allan 1995). The morphology of the creeks and the surrounding floodplain forest are natural, i.e., humans have not yet changed the spatial variability of the creeks (which is not the case in most running waters in temperate regions). Thus, these creeks were ideal for studying the effect of the variability and the state of abiotic factors on young fish species richness.

Our objectives were to (1) examine young-fish species richness in the framework of temporal and spatial variability to test the patch dynamics concept predictions made by Townsend (1989), i.e., that species richness will be highest at intermediate levels of temporal and at highest levels of spatial variability; (2) evaluate the relative importance of habitat variability and state variables in predictions of fish species richness; and (3) examine how this relative importance changed with spatial location (upstream or downstream from the dam), taxonomic units (Characiformes and non-Characiformes) and with developmental stages.

Materials and methods

Study area

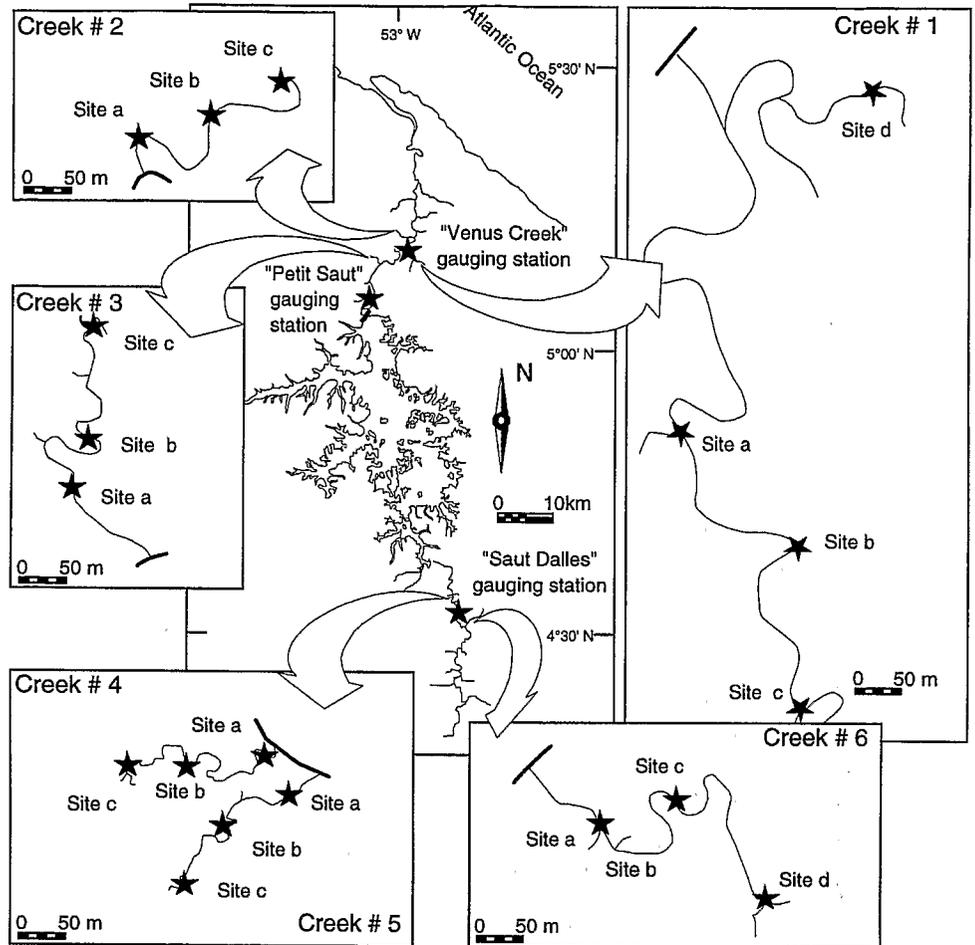
The Sinnamary River is the fifth largest river of French Guiana, with a length of approximately 260 km and a mean annual discharge of $230 \text{ m}^3 \text{ s}^{-1}$ (Fig. 1). Its drainage basin covers about 6565 km^2 and receives an annual average precipitation of 3000 mm. The upper Sinnamary River, upstream from the reservoir (hereafter called upstream section), crosses different forest types ranging from terra firme arborescent to flooded and permanent swamp forest. Downstream from the dam (downstream section), the river meanders through an old flat coastal plain (see Tito de Morais et al. 1995 for further details). Before the completion of Petit Saut dam in 1994, the hydrological regime in these two sections depended on the alternation of two (November–February and April–July) rainy seasons and a dry season (August–November) (Ponton and Copp 1997).

The creeks studied drain small catchments (Fig. 1) that are entirely covered by a natural floodplain forest. Therefore, the creeks are well-shaded, and aquatic macrophytes and planktonic algae are very rare. In addition, a large amount of woody debris cover the bottom of the creeks and mud, clay, and sand predominate the bottom substrate. These creeks have generally low current velocities. However, mean velocities can reach more than 1 m s^{-1} during floods (Ponton and Vauchel 1998).

Hydrology

A gauging station upstream from Saut Dalles rapids (Fig. 1) recorded upstream water levels of the Sinnamary in 1995 and 1996. Downstream water levels were recorded for the same period at a similar gauging station downstream from Petit Saut dam, and at a gauging station about 25 km downstream from the dam at the entrance of Venus Creek (Fig. 1). These gauging stations recorded water levels every hour. In addition, we set up 19 stream gauges in the six studied creeks where we regularly recorded the water levels for each of the 20 sampling sites under study (Fig. 1). We used these data to characterize temporal habitat variability in terms of flow disturbance (see Resh et al. 1988 for rationale) prior to each fish sample.

Fig. 1 Sampling sites in the six tributaries (creeks 1–6) of the Sinnamary River (French Guiana, South America) studied. Stars indicate the location of the different gauging stations in the Sinnamary River and the stream gauges at each of the 20 sampling sites (a,b,c,d). Only one gauge was used for sites a and b in creek 6



Fish sampling and spatial habitat characterisation

We regularly sampled six creeks of the Sinnamary River with rotenone from March 1995 to October 1996 (ten sampling campaigns; see Fig. 2 for the dates of sampling). We selected a mean area of about 50 m² at random (i.e., without knowing whether fish were present or not) in three (creeks 2–5) or four (creeks 1,6) sampling sites at each sampling campaign. Mérioux et al. (1998) give a complete description of the sampling method. In summary, we firstly measured temperature, pH, oxygen with a ICM 51000 multiparameter meter, and water turbidity with a LaMotte Model 2008 digital turbidity meter in undisturbed water. We also measured the current velocity at the water surface by observing the time required for a floating object to travel 1 m downstream, and assigned it to five categories (0–6, 7–9, 10–14, 15–25, and >25 cm s⁻¹). Preliminary measures showed that these variables varied little across the sampling volume, so we measured them only once. We then 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 (Predatox is a 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 water depth (cm), the presence/absence of organic litter (5 categories: leaves, wood diameter ≤5 and >5 cm, roots diameter ≤5 and >5 cm), vegetation (3 categories: aquatic, terrestrial herbaceous shrubs, trees), and substrate (6 categories: mud, clay, sand, gravel, stones, blocks) using point samples on a 1 × 1 m grid. We recorded bank slope (5 categories: smooth, medium, stiff, vertical, excavation) for the closest point samples to the bank. Finally, we determined total length, total bank length, mean width, volume,

and surface of each sampling area. In total, we obtained 200 samples, 100 from ten sites and ten campaigns in each of the studied sections of the Sinnamary River. We made no attempt to detoxify rotenone outside the sampling area with potassium permanganate because: (1) our sampling volume was always small compared to surrounding waters; (2) most fish species outside the sampling site detected and avoided rotenone; (3) clay, common at our sampling sites, is known to reduce rapidly the toxicity of rotenone (Gilderhus 1982); (4) above 23°C the half-life of rotenone is less than 1 day (Bettoli and Maceina 1996); and (5) we sampled each creek from down- to upstream.

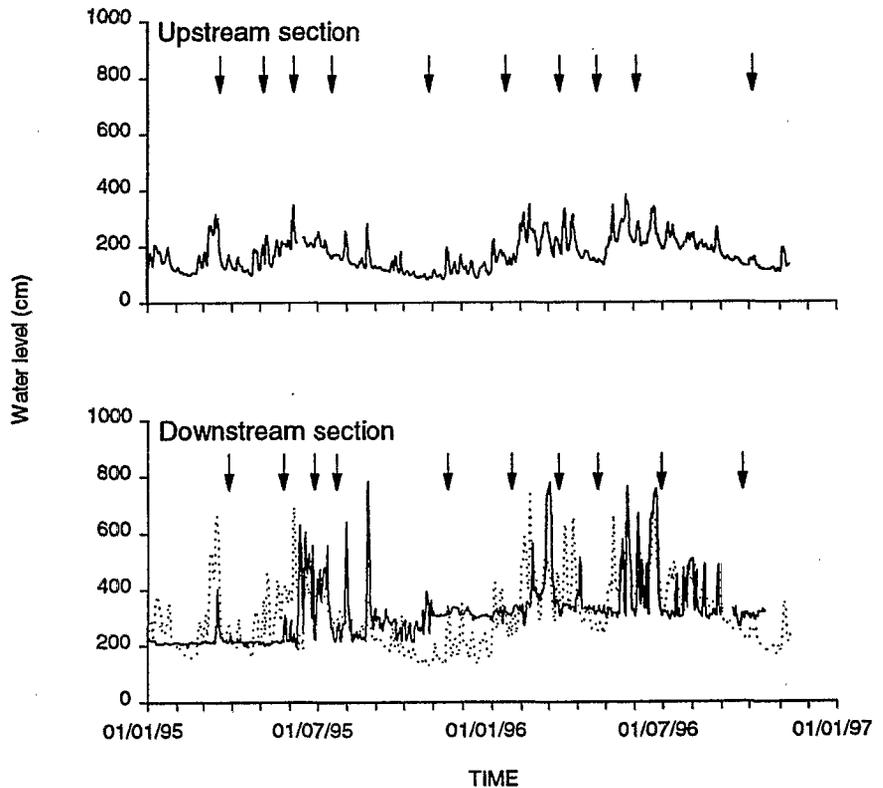
In the laboratory, we sorted and identified all specimens of the 200 samples using keys for adults by Géry (1977), Rojas-Beltran (1984), Kullander and Nijssen (1989), Planquette et al. (1996), and for juveniles by D. Ponton (unpublished work). Keys for juveniles were based on series of drawn specimens of variable size and on meristic parameters such as number of rays on the anal fin or position of fins. We had identification problems for a few species, which we usually grouped at the genus level. 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 (Mérioux and Ponton 1998; Ponton and Mérona 1998).

Data analysis

Temporal variables

We evaluated creek site water levels for the whole study period from water levels in the creeks and in the Sinnamary River. For

Fig. 2 Water levels recorded at Saut Dalles (upstream), and Petit Saut (downstream) gauging stations, from January 1995 to November 1996. Fish sampling campaigns are indicated by vertical arrows, and downstream values that would have been observed if the dam were not present by a dashed line, calculated using equations in Ponton and Vauchel (1998)



each site, we examined the relationship between the water levels recorded at its creek gauge and those obtained from the Saut Dalles (upstream section) and Venus Creek (downstream section) gauging stations of the Sinnamary. We used two types of models: linear (i.e., linear regressions) or linear in sections (i.e., piecewise regressions). The latter method allows the detection of a threshold below and beyond which relations between variables are linear, but slope and intercept are different for each piece (Wilkinson et al. 1996). Linear-in-sections models implied that the site water level depended on the river water level only beyond a given threshold of the Sinnamary water level. At other periods, it was only affected by local rains pouring over the creek catchment. For these periods, the regression line for the first section was described as:

$$Y = m_1 + \varepsilon \quad \text{if } WL \leq th$$

where Y is the water level at the creek site for $WL \leq th$, ε is the error term, WL is the Sinnamary water level, and th is the threshold beyond which the Sinnamary water level affects the creek. Beyond the threshold, water level in the creek depended on variations of the Sinnamary water level and the regression line for this second piece was described as:

$$Y = aWL + b + \varepsilon \quad \text{if } WL > th$$

We calculated the variance (temporal variability variable) and the mean of the water level (temporal state variable) observed 5, 10, 15, 20, and 30 days before sampling for each sampling area from each site stream gauge. We used the linear model for sites that had a linear relationship with the water level of the Sinnamary. For sites with linear-in-sections models, we decomposed the total variance into inter-variance (mean variance between the two sections of creek water levels delimited by the threshold for a given hydrological period before fishing), and intra-variance (mean variance of each piece, Sokal and Rohlf 1995) and estimated the variance for each sampling area as:

$$\text{Var} = p(m_2 - m)^2 + q(m_1 - m)^2 + pv_2 + qv_1$$

The two first terms define inter- and the two last the intra-variance of creek water level for a given period (days before fishing), Var is

the total variance of creek site water level, p is the frequency of hourly data for $WL > th$, m_2 is the predicted mean water level at the creek site for $WL > th$, m is the predicted overall mean water level at the creek site, as $m = pm_2 + qm_1$, q is the frequency of hourly data for $WL \leq th$, v_2 is the variance of water level at the creek site for $WL > th$ with water level predicted from the second part of the linear piecewise model, and v_1 is the observed variance of water levels at the creek site for $WL > th$, taken as residuals from the overall linear piecewise model.

Spatial variables

We calculated an index of spatial habitat variability from the replicated measures of litter, vegetation, bottom substrate, bank slope, and depth for each sampled area. The habitat variables differed in their characteristics, so we treated them accordingly. We first determined a local and a global index of variability for litter, vegetation, and substrate applying the methods used by Cellot et al. (1994). Each of these variables could be represented by several categories at the same point sample. Therefore, these variables were fuzzy coded (i.e., for each point sample we noted the proportions of the different categories of each variable; see Chevenet et al. 1994). We used the Simpson index on the proportions of the 14 categories of the three variables as a measure of within-sample point variability (the equivalent of species α -diversity, Lande 1996) to get local variability for each point sample. We obtained an index of local variability for each sampling area by calculating the average local diversity (i.e., the average of the point sample diversity). We obtained the global variability for each sampling area using the within-sample inertia calculated after a fuzzy correspondence analysis on the table containing, for each local point sample, the proportion of each category for litter, vegetation, and substrate (Cellot et al. 1994; Chevenet et al. 1994). Bank slope differed from the previous variables since only one category was possible at each point sample closest to the bank. Therefore, we obtained its global diversity by calculating the Simpson index on the proportion of each category in each sampling area (Cellot et al. 1994). Depth variance was used as an index of depth variability. We transformed

the four indices of habitat variability (local and global diversity of litter, vegetation, and substrate, Simpson index of bank slope and depth variance) for scale comparability over a range from 0 to 1 for the 200 sampled areas. We obtained the final index of spatial habitat variability of each sampling area as the first axis scores of a non-centred principal component analysis performed on the four individual spatial indices (Cellot et al. 1994). Most of the categories considered here represented potential refuges for young fish. Therefore, this index reflected not only the diversity of the habitat but also the potential refuge amount of each sampling area.

Fish

We classified individual fish based on their standard length into early life stages (about 4 to 15–20 mm SL, depending on species), young (about 15–20 to 30–50 mm SL), and older juveniles (about > 30–50 mm SL, see Méricoux and Ponton 1998 for the exact size limits for each taxon). For each sample, we determined global fish richness, richness in Characiformes and non-Characiformes (previous studies have demonstrated that young Characiformes are especially affected by dam operations: Ponton and Copp 1997; Ponton and Vauchel 1998), and richness in each of the three different ontogenetic stages.

Fish richness versus habitat variability

The patch dynamics concept predicts a bell-shaped relationship between fish richness and temporal variability and a positive monotonic relationship between fish richness and spatial variability. We checked for these tendencies by plotting overall taxa richness of the 200 samples against temporal and spatial variability. We repeated this procedure considering the upstream and downstream section of the Sinnamary, the taxonomic units (Characiformes and non-Characiformes), and each ontogenetic group separately.

Fish richness versus habitat variability and state

We used stepwise forward regression (Wilkinson et al. 1996) to identify significant variables describing habitat variability and state, which explained most of the variability in fish richness. For this purpose, we used the temporal variability variable and its log, square, and cubic transformations (as a bell-shaped relationship is

theoretically expected), the spatial variability variable and its log transformation, and all the habitat state variables and their log transformations.

We performed the stepwise analysis for all data (using hydrological pre-sampling periods of different duration), for the upstream and the downstream section, for taxa Characiformes and non-Characiformes, and for ontogenetic groups.

We tested the robustness of the models by Monte Carlo simulations (Manly 1991). We modeled fish richness as a function of the independent variables using half (selected at random) of the studied samples for each regression model. We used this new model to predict richness from the independent variables of the other half of the samples. Five to ten repetitions of this procedure led to a stable r^2 of the linear regression of observed versus predicted richness (Fig. 3). We tested whether the slope of the regression of observed versus predicted richness was equal to one and if its constant was equal to zero (i.e., $y = x$) using t -tests (Tomassone et al. 1983).

We used Systat 6.01 for Windows (Wilkinson et al. 1996), S-PLUS 3.2. for Windows (Statistical Sciences 1995a,b,c), and ADE 4 software (Thioulouse et al. 1997) for data analyses.

Results

Temporal habitat variability

Patterns of water level variations in the Sinnamary differed strongly between the two sections (Fig. 2). In the upstream section, the natural flow pattern had two types of fluctuations: (1) predictable long-term variations of the water level due to the alternation of rainy and dry seasons, and (2) unpredictable short-term events caused by sudden heavy rains. Downstream from the reservoir, dam operations significantly changed water levels from those that would have been observed without the dam (Wilcoxon signed-ranks test, $n = 649$, $Z = -3.666$, $P < 0.001$, Fig. 2). No seasonal pattern was detected in this section, and unpredictable flow events of huge amplitude were prevailing. The creek water level of four sites in the upstream and five sites in the downstream section always depended on that of the Sinnamary River (Fig. 4). Most of these sites were located 30–200 m upstream from the confluence of the creeks with the main river (Fig. 1). The water level of all the other creek sites varied linearly with those of the Sinnamary River only beyond a threshold (Fig. 4, piecewise models).

Maximum temporal variability in the creeks was higher in the downstream than in the upstream section (Fig. 5). Mean temporal variability was significantly higher in the downstream than in the upstream section (t -test with: $t = 7.692$, $P < 0.001$ and $df = 29$, Fig. 5). Therefore, the frequency distributions of the temporal variability in the 30 days preceding each fish sample also differed among the sections (Fig. 6).

Spatial habitat variability and habitat state

Mean spatial variability did not significantly differ between the up- and downstream samples (t -test with $t = 0.115$, $df = 99$ and $P = 0.908$), and scores ranged from 0.4 to 1.5 (Fig. 6). The test of the patch dynamics

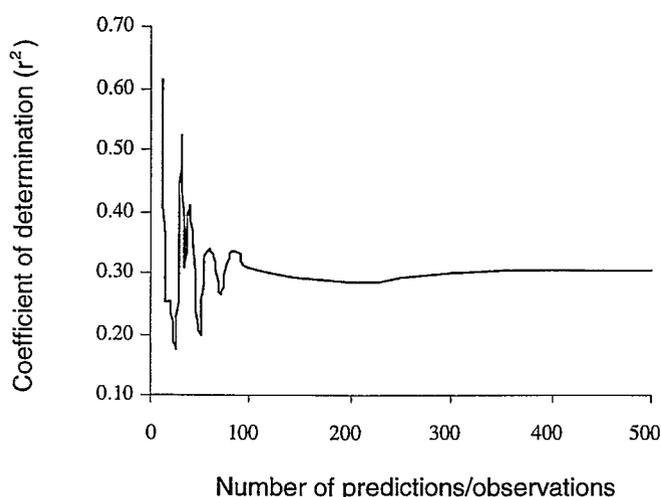
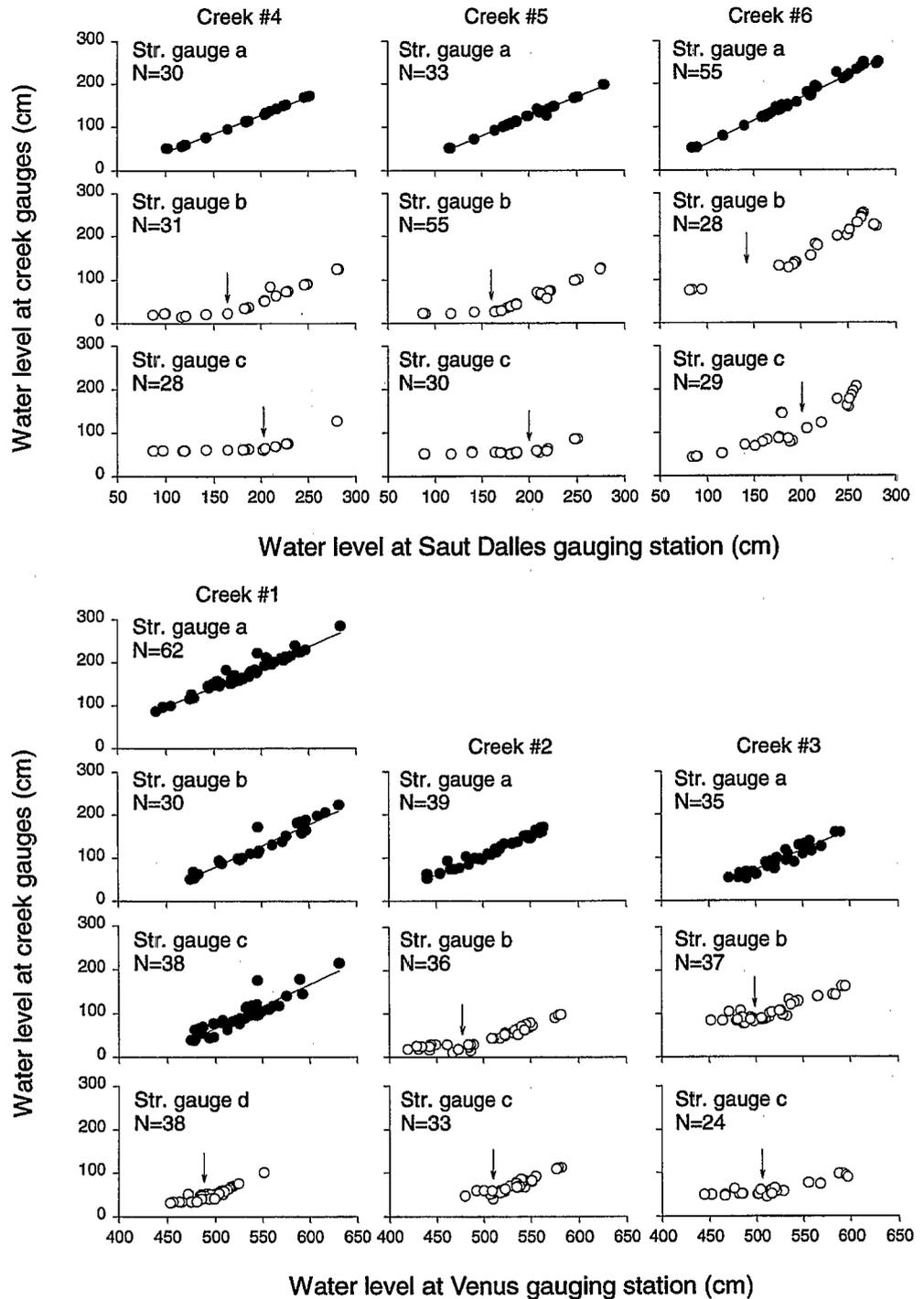


Fig. 3 Coefficient of determination for the regressions of observed versus predicted fish taxon richness versus the number of predictions/observations included (included samples were drawn at random for all taxa and all samples, cf. Fig. 9)

Fig. 4 Relationships between the water level recorded at each creek site and the main river, in its upstream (Saut Dalles gauging station) and downstream (Venus Creek gauging station) sections, respectively. Linear relationships are indicated by *solid dots* and linear-in-sections relationships by *open dots* (vertical arrows inflection points, *N* number of records). Note that we used stream gauge *a* in creek 6 for two nearby sampling sites



concept required the synthesis of the overall variability and abundance of refugia, so these scores were appropriate for our following tests. However, scores did not demonstrate how variable the habitat were from the perspective of a fish. Details on the frequency distributions of the values for these variables (Appendix 1) demonstrated that the range of habitat conditions encountered in the study was large. For instance, low spatial variability was either due to (1) homogeneous litter, vegetation, and substrate characteristics (e.g., 70% of the bottom substrate points of a sampled area had

only sand or clay and neither litter nor vegetation) and/or (2) homogeneous bank slope (e.g., 90% of the bank slope sampling points were medium), and/or (3) homogeneous depth point samples (e.g., depth was between 20 and 46 cm). In contrast, high spatial variability corresponded to (1) many combinations of litter, vegetation, and substrate categories that were equally represented in a sampled area (e.g., 39 combinations, each of them found at 1–8% of the point samples for an area), and/or (2) several bank slope categories that were equally represented (e.g., five bank slope categories, each of them

found at 15–25 % of the point samples), and/or (3) a wide range of depth values (e.g., a depth ranging from 6 to 135 cm).

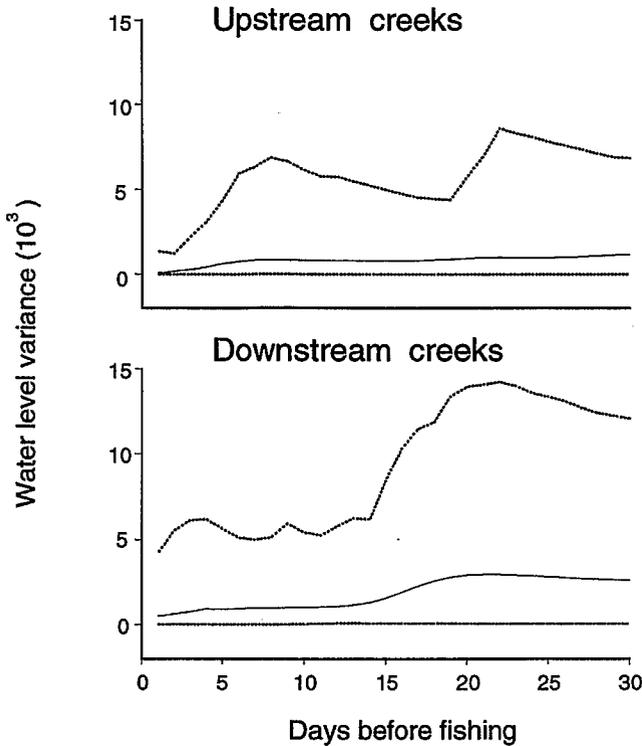
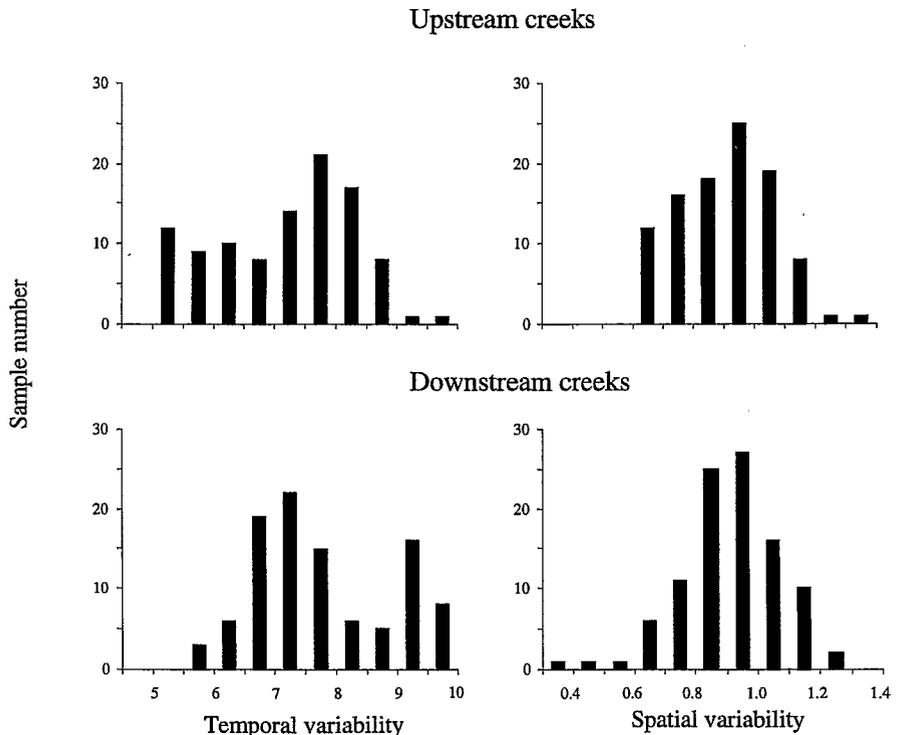


Fig. 5 Mean (solid lines), minimum, and maximum (dashed lines) of water level variance for time considered (as days before fishing, DBF) in 100 samples each from upstream and downstream creeks

Fig. 6 Frequency of the temporal (log) and the spatial variability habitat scores in 100 samples each from upstream and downstream creeks



For habitat state, water temperature ($^{\circ}\text{C}$, mean = 24.4, SD = 0.7), and pH (mean = 4.7, SD = 0.4) varied little and were excluded from further analyses. We also omitted water current velocity, as 83% of the samples had a velocity $\leq 6 \text{ cm s}^{-1}$. Homogeneity for that variable among samples was due to the generally low velocity encountered in the creeks, and to sampling constraints (fishing with rotenone requires limited current velocities to achieve maximum efficiency). However, homogeneity for water velocity at the time we fished did not imply homogeneity of flow or water level variance in the days before fishing (i.e., our measure of disturbance). The remaining state variables included in the analyses were mean water level (cm, mean = 67.1, SD = 60.7), oxygen concentration of the water (mg l^{-1} , mean = 5.2, SD = 1.2), water turbidity Nephelometric turbidity units (NTU), mean = 5.4, SD = 6.4), bank length (m, mean = 25.4, SD = 9.4), mean width (m, mean = 4.4, SD = 1.7), mean depth (cm, mean = 46.2, SD = 17.3), total length (m, mean = 12.0, SD = 4.4), sampled volume (m^3 , mean = 22.7, SD = 13.8), and surface (m^2 , mean = 52.6, SD = 19.2).

Fish community characteristics

We collected 34,790 young individuals representing 73 taxa (69 distinct species) from 25 families and 6 orders (Table 1). Among these 73 taxa many were rare on the scale of all 200 samples (Fig. 7). Considering the scale of each sample, about 20% of the collected individuals contributed half of the species richness in more than 80% of the samples. Globally, the Characiformes and the

Table 1 Sample characteristics and fish composition in the upstream and downstream creeks, and in the total samples (*ELS* early life stages, *YJ* young juveniles, *OJ* old juveniles)

	Up stream	Down stream	Total
No. samples	100	100	200
Sampled volume (m ³)	1622	2914	4536
Sampled area (m ²)	4649	5865	10514
No. orders	6	6	6
No. families	20	22	25
No. individuals	18234	16556	34790
No. taxa	59	60	73
No. Characiformes taxa	32	31	39
No. non-Characiformes taxa	27	29	34
No. ELS taxa	46	52	57
No. YJ taxa	50	54	60
No. OJ taxa	44	38	53
Mean no. taxa per sample	15.7	13.7	14.7
Mean no. individuals per sample	182.3	165.6	174.0
Mean no. Characiformes ELS taxa per sample	4.6	3.2	3.9
Mean no. Characiformes YJ taxa per sample	6.0	4.6	5.3
Mean no. Characiformes OJ taxa per sample	3.6	2.7	3.2

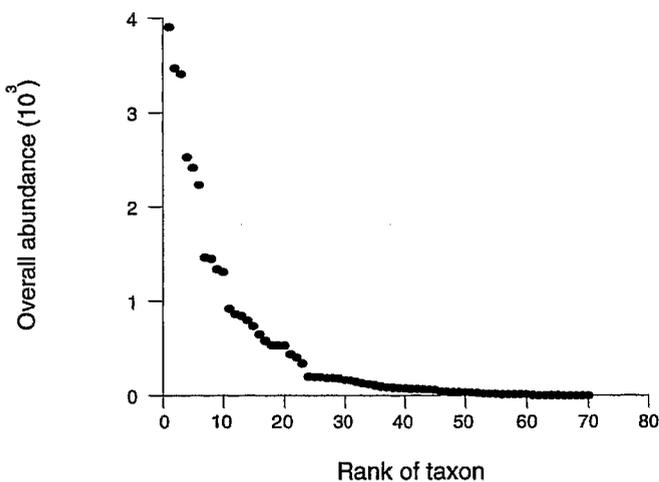


Fig. 7 Rank frequency diagram of the 73 taxa collected in the 200 samples

Perciformes accounted for about 66% and 26% of the total individuals, respectively. However, Characiformes accounted for 82% and Perciformes for 11% of the total individuals in upstream creeks, whereas they accounted for 49% and 43% in downstream creeks. The mean number of individuals per sample did not differ significantly between upstream and downstream sites (*t*-test with *t*=0.528, *df*=99 and *P*=0.599). However, mean number of fish taxa per sample was significantly higher in the upstream section (*t*=2.462, *df*=99 and *P*=0.016).

Richness versus habitat variability

The aspects of temporal and spatial habitat variability investigated here were poor descriptors of fish taxon

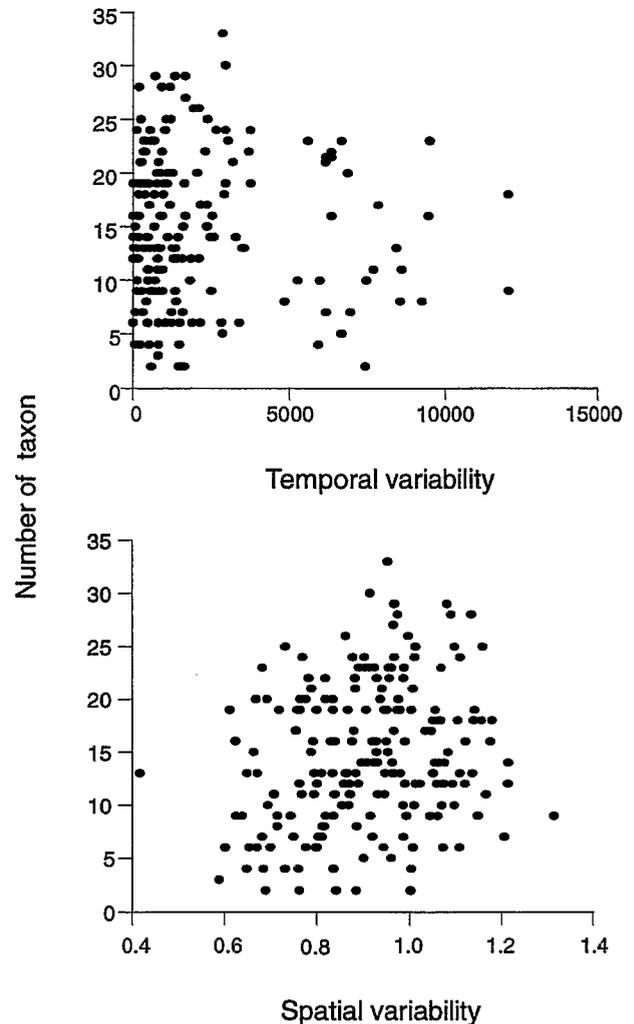


Fig. 8 A typical example of fish taxon richness versus habitat variability, showing all 200 samples for a hydrological period of 30 days before fishing (using other hydrological periods or separating sections, taxonomic units, and ontogenetic stages did not produce clearer patterns). Richness was positively related to spatial variability: $y = 6.486(\pm 2.767) + 9.051x(\pm 2.998)$ (95% confidence limits in parentheses), $r^2 = 0.044$, and $P = 0.0003$

richness in the framework of the patch dynamics concept, whichever data set was considered (five different hydrological periods, all data, different sections, taxonomic units, or ontogenetic groups). We never observed a peak of fish richness at intermediate levels of temporal variability (see Fig. 8 for one example). Fish richness increased with spatial variability, but the proportion of the variance in richness explained by this habitat parameter was very low (e.g., 4% in the complete data set, cf. Fig. 8).

Richness versus habitat variability and state

Depending on the hydrological pre-sampling period included, 32–36% of the overall variance in fish taxon richness was explained when habitat variability and state

were considered together (Table 2). Overall fish richness was positively related to bank length, mean width, mean water level, and spatial variability, and negatively related to water turbidity, whatever the duration of the hydrological period before fishing included. Temporal variability significantly explained fish richness only if we described it for periods of 20 or 30 days before fishing. For these periods species richness increased slightly with low values of temporal variability and decreased with higher temporal variability. Using the significant variables of the model, including data for 30 days before fishing in Monte Carlo simulations produced predictions with considerable scatter around the observations (Fig. 9). The model predicted 31% of the observed variability in species richness accurately (its constant did not significantly differ from zero, and its slope did not significantly differ from 1, Table 3).

Separate analyses of up- and downstream data, Characiformes and non-Characiformes, and/or the different ontogenetic stages showed the same tendencies whatever the hydrological period considered. Results including data for 30 days before fishing were the most significant in most of these separate analyses. Therefore, we only present results that take into account this period in further analyses.

Total fish richness in upstream creeks was better explained by habitat variability and state than that in downstream creeks (Table 4). Total fish richness in downstream creeks was less easy to model (Table 4) and thus was not presented further in detail. In upstream creeks, fish richness was positively related to bank length, mean width, mean water level, and temporal and spatial variability (Table 4). The accuracy of the model was high, as the regression of observations on predictions corresponded closely to $y = x$ (Table 3). The model predicted 37% of the observed variability in taxon richness.

We obtained similar results to those in the previous upstream example if Characiformes and non-Characiformes in the upstream creeks were separated

(Tables 3,5). However, non-Characiformes richness was only positively related to bank length, mean water level, and spatial variability. Separating Characiformes and non-Characiformes in downstream creeks yielded clearly less powerful models compared to upstream creeks. Upstream creek models for the three ontogenetic stages predicted only 10–24% of the observed variability in taxon richness (Table 3). In addition, these models were very unstable, and often did not give accurate predictions, as in two cases the constant differed significantly from 0 and the slope differed significantly from 1 (Table 3).

Discussion

Richness versus habitat variability

The predictions of the patch dynamics concept were not supported by our data even though the study was appropriately designed to test it. The young-fish fauna of the creeks was very diverse. The samples were well distributed over a wide range of temporal and spatial habitat variability. Moreover, the scales included were appropriate for young fish (Poizat and Pont 1996). In spite of this, we were unable to demonstrate any pattern of richness in relation to temporal variability (if habitat state variables were not included), regardless of the period before fishing, or the grouping of sites, taxonomic units or life stages considered. In addition, species richness was only weakly related to spatial habitat variability.

We could argue that this failure to support the patch dynamics concept was related to patterns of species richness produced by interfering biological phenomena that were not controlled by disturbance. For example, water level variability in a creek during a period of rising discharge of the Sinnamary could have caused adults to migrate into the creek to reproduce there or in the associated floodplain. Most Characiformes are known to reproduce during the rainy season as water levels increase (Munro 1990; Lowe-McConnell 1987). This type

Table 2 Stepwise multiple regressions of taxon richness in all 200 samples versus habitat variability and state variables for five hydrological periods (5, 10, 15, 20 and 30 days before fishing, DBF) (r^2 coefficient of determination, F value of the F ratio, P associated

probability for the entire model). For each variable and DBF value, whether a variable was log transformed is indicated in parentheses, and its sign and associated probability are given

Statistical values and variables	Sign	DBF (days)				
		5	10	15	20	30
r^2		0.317	0.321	0.316	0.351	0.355
F		18.015	18.378	17.951	14.838	15.107
p		<0.001	<0.001	<0.001	<0.001	<0.001
Constant	–	NS	NS	NS	NS	NS
Water turbidity (log)	–	0.000	0.000	0.000	0.000	0.000
Bank length	+	0.000	0.000	0.000	0.000	0.000
Mean width (log)	+	0.000	0.000	0.001	0.000	0.001
Mean water level	+	0.000	0.000	0.000	0.001	0.000
Spatial variability (log)	+	0.000	0.000	0.000	0.000	0.000
Temporal variability	–	NS	NS	NS	0.000	0.000
Temporal variability (log)	+	NS	NS	NS	0.006	0.002

NS $P > 0.05$

of reproduction could have affected patterns of young-fish species richness observed by us. However, the total number of taxa observed in the upstream creeks (i.e., in natural seasonal hydrological conditions) appeared to be independent of hydrological events in 1995 and quite stable in 1996 (Figs. 2,10). Thus, seasonal reproduction did not affect the potential number of young fish taxa in our creeks.

Only 2 of the more rigorous tests of the patch dynamics concept or related concepts supported its species richness hypotheses for lotic animals (Richoux 1994; Townsend et al. 1997b), while 11 tests rejected these hypotheses (ours, and 10 others summarised in Statzner et al. 1997). Thus, we suggest that the species richness hypotheses of the patch dynamics concept are only rarely relevant to lotic animals according to this weight of evidence. An underlying assumption of the patch dynamics concept that produces the predicted patterns in species richness is that interspecific competition increases from intermediate to low levels of temporal, and, for lower temporal variability, from high to low levels of spatial variability (Townsend 1989). In many

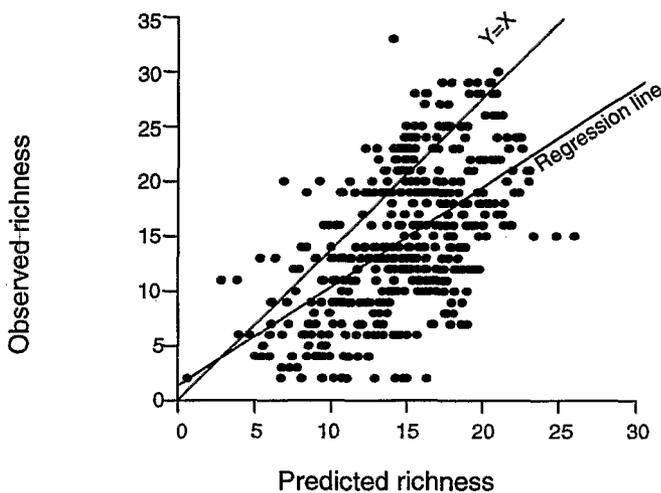


Fig. 9 Observed fish taxon richness versus "blind" predictions of taxon richness (from Monte Carlo simulations, for $n=500$), using the variables for $DBF=30$ from Table 2, and the whole data set: $y=0.894(\pm 0.120)x$ (95% confidence limits in parentheses), $r^2=0.305$, and $P<0.001$

Table 3 Robustness of richness predictions ($n=500$) from different types of models on richness versus habitat variables. We regressed observations on predictions (see Fig. 10 for one example) to obtain r^2 (coefficient of determination), P (associated prob-

Grouping	r^2	P	Const	S	t
Total taxa	0.305	<0.001	NS	0.894 (± 0.120)	1.767
Upstream taxa	0.370	<0.001	NS	0.963 (± 0.112)	0.661
Upstream Characiformes	0.314	<0.001	NS	0.930 (± 0.138)	1.014
Upstream non-Characiformes	0.343	<0.001	NS	0.927 (± 0.114)	1.043
Upstream ELS Characiformes	0.104	<0.001	NS	0.873 (± 0.256)	0.992
Upstream YJ Characiformes	0.227	<0.001	1.203	0.851 (± 0.140)	2.129
Upstream OJ Characiformes	0.238	<0.001	0.592	0.864 (± 0.138)	1.971

streams, however, the physical conditions are permanently or periodically so harsh that biotic interactions among animals are often unimportant (e.g., Ferminella and Resh 1990; Peckarsky et al. 1990). In addition, rare species usually dominate patterns of species richness of lotic animals (e.g., Statzner and Resh 1993). In our case, about 20% of the individuals collected contributed half of the species richness in the majority of the samples. In our view, it is quite improbable that biotic interactions produce the richness patterns of these rare species, and thus the overall species richness as predicted by the patch dynamics concept.

Richness versus habitat variability and state

Our results demonstrated the need to consider the habitat variability and state together to explain and to predict young-fish richness in our study area. Taking them together, we accurately predicted 31% of the observed variance in species richness for all data. Species richness increased slightly with low values of temporal variability and decreased at higher temporal variability. This pattern was caused by a positive relationship between diversity and temporal variability in upstream creeks (see Table 4), and greater temporal variability and lower diversity (than upstream samples) in the downstream creek samples.

We explained and predicted more of the fish richness for the natural upstream creeks than for the downstream ones that were disturbed by the dam operations at Petit Saut. Therefore, we focused our discussion on patterns found in the upstream creeks. Taxon richness increased with temporal variability (when habitat state was included in the model). This result differed from others showing that elevated temporal variability of discharge has negative effects on fish diversity (Horwitz 1978), and especially on early life stages (Schlosser 1985; Finger and Stewart 1987). However, all these studies only considered discharge variability, and did not simultaneously consider other environmental parameters that may potentially act as buffers against temporal variability. For example, in upstream creeks, species richness increased with higher spatial heterogeneity. Correspondingly, a positive relationship was found

ability), Const (constant if significantly different from 0 at $P < 0.05$), S (slope), and 95% confidence limits (in parentheses), and t value for testing if $S = 1$, with $S = 1$ if $t \leq 1.965$

Table 4 Stepwise multiple regressions of taxon richness in the upstream and downstream creeks versus habitat variability and state variables (for temporal variability and mean water level, 30 DBF). See Table 2 for further details

Statistical values and variables	Up stream		Down stream	
	Sign	Statistics	Sign	Statistics
r^2		0.473		0.237
F		16.864		15.097
P		<0.001		<0.001
Constant		NS	+	0.000
Water turbidity (log)		NS	-	0.005
Bank length	+	0.000	+	0.000
Mean width (log)	+	0.037		NS
Mean water level	+	0.001		NS
Spatial variability (log)	+	0.001		NS
Temporal variability (log)	+	0.007		NS

Table 5 Stepwise multiple regressions of taxon richness of Characiformes and non-Characiformes in upstream creeks, versus habitat variability and state variables for 30 DBF. See Tables 2 and 4 for further details

Statistical values and variables	Characiformes		Non-Characiformes	
	Sign	Statistics	Sign	Statistic
r^2		0.415		0.442
F		13.320		25.307
P		<0.001		<0.001
Constant	-	0.026	-	0.031
Water turbidity (log)		NS		NS
Bank length	+	0.000	+	0.000
Mean width (log)	+	0.002		NS
Mean water level	+	0.021	+	0.000
Spatial variability (log)	+	0.004	+	0.006
Temporal variability (log)	+	0.005		NS

between fish species richness and habitat diversity in Panamanian streams (Gorman and Karr 1978), in the Niger River (Hugueny 1990), and in two Guianese coastal streams (Mérigoux et al. 1998). Indeed, patchy habitats should provide refuges and decrease the impact of discharge disturbances on fish (Townsend and Hildrew 1994). This point has been demonstrated in North American river systems where complex habitats provided refuges for fish during flood events (Pearsons et al. 1992). Moreover, the positive relation of fish richness with bank length reflected the relative importance of the riparian zones (relative to the aquatic habitat) in providing fish with shelter and diversified food. This importance has been demonstrated for temperate (Schiemer and Zalewski 1992) and tropical (Tito de Moraes et al. 1995) rivers. We also observed higher species richness at higher mean water level. It is obvious that the surface of flooded areas adjacent to our creeks increased as the waters of the Sinnamary River rose. It is well known that floodplains are essential components of large rivers (Lowe-McConnell 1987). Flood pulses are the driving force for river-floodplain systems (Junk et al. 1989), which provide diverse habitats where fish find

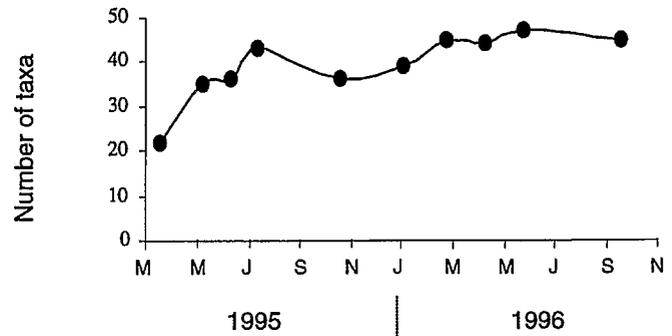


Fig. 10 Total number of taxa observed in the upstream creeks for each sampling campaign (solid dots) in 1995 and 1996

food, shelter, and spawning sites (Bonetto et al. 1989; Junk and Da Silva 1995).

In the upstream creeks, Characiformes richness was related to habitat variables in a similar way to taxa. In contrast, non-Characiformes richness was independent of temporal habitat variability. Most Siluriformes, Gymnotiformes, and Perciformes have reproductive habits that are relatively independent of habitat variations. For instance, all the Cichlids present in the Sinnamary River are nest spawners (Breder and Rosen 1966; Ponton and Tito de Moraes 1994). We found no ontogenetic habitat shifts in the Characiformes of the upstream creeks that could improve the species richness predictions for different age classes. This point probably reflected the low taxon number found per ontogenetic group in each sample (Table 1). However, such ontogenetic changes should have existed in our creeks, as they exist in temperate streams (e.g., Schiemer et al. 1991; Sagnes et al. 1997), and as fish sensitivity to abiotic factors decreases with increasing size and mobility (Harvey 1987; Schlosser 1987).

We did not find clear fish richness patterns in the creeks downstream from the dam. There, a lower mean number of taxa per sample occurred compared to the upstream creeks, probably because of the dam. Dam operations strongly modified the flow pattern in the downstream creeks, especially by keeping the mean water level low during the rainy seasons (Fig. 2). Moreover, they produced short periods of artificial extreme high water during the dry season. Such alterations of the timing, frequency, magnitude or duration of flood patterns strongly affect aquatic biota (Bain et al. 1988; Bonetto et al. 1989). Thus, abrupt water releases at the dam like the one that raised the water level 5 m over 2 days in August 1995 could have reduced fish diversity.

Conclusion and perspectives

We have demonstrated the need to consider separately areas with very different environmental conditions, and taxonomic units with different biology, for a better understanding of fish richness patterns. In the Sinnamary

Basin, the creeks in the floodplain act as nurseries for early life stages, and the discharge in the main channel strongly influenced their water level (at least during floods). However, further studies on the relative importance of flow regimes in the main river and the creeks are needed to understand the relative importance of direct (on fish displacement) and indirect (on fish reproduction) hydrological effects. Moreover, future investigations should focus on the most abundant species to improve knowledge of ontogenetic habitat changes.

Although we have demonstrated that abiotic factors affect species richness of young fish, biotic factors probably also affected the assemblages. For example, the reduction of species richness with decreasing temporal variability in the upstream creeks (Table 4) could have been the result of such biotic interactions. Predation upon young fish would have occurred during the dry season, when fish densities in the creeks increased with decreasing water levels. Piscivores are known to modify the young fish assemblage structure by culling the most vulnerable prey species during low water in floodplain lakes of the Orinoco river (Rodriguez and Lewis 1997). In the Sinnamary Basin, some fish species are specialised in preying upon fish at very early stages (Mérigoux and Ponton 1998). In addition, young fish of many species in the Sinnamary creeks feed on the same food items (small crustaceans, larvae, and adults of insects, Mérigoux and Ponton 1998). However, it is difficult to speculate whether competition for food was high in our young fish communities.

Evidently, potential biotic interactions among fish of the Sinnamary creeks were not strong enough to produce species richness patterns as predicted by the patch dynamics concept. Habitat variability alone, as measured in this study, did not explain fish richness, and had to be combined with habitat state variables for this purpose. Even then, the models explained at best 47% of the observed variance in fish richness. In terms of predictive power, the models "blindly" predicted at most

37% of the observed variance in species richness. This limited precision is probably because rare species produced most of the richness patterns in our creeks. It will be generally difficult to predict species richness of lotic animal communities on the scale of habitats or stream reaches (cf. Minshall 1988), as rare species typically produce most of the richness in lotic animal communities (e.g., Modukhai-Boltovskoi 1978; Edwards and Brooker 1982; Statzner and Resh 1993). Habitat or stream reach is the spatial scale primarily examined by stream ecologists (Minshall 1988; Statzner et al. 1997) and primarily considered in stream management (Gore 1985; Statzner and Sperling 1993). Consequently, stream ecologists have to face the fact that it will be difficult to predict animal species richness on a spatial scale appropriate to both theoretical and applied considerations. Solution of this general problem is urgent in the context of the current global efforts to assess and maintain biodiversity (Heywood and Watson 1995). Rare species also often dominate species richness in other ecosystem types (e.g., Gaston 1994), so the problems of predicting biodiversity are not limited to running waters. Thus, what we need are metrics of biodiversity that are easier to predict than species richness, or diversity indices that are closely related to species richness (Washington 1984).

There is growing evidence that species traits such as longevity, mobility, and reproduction are significantly related to habitat characteristics (Statzner et al. 1997; Townsend et al. 1997a). Therefore, such traits could serve to create metrics of functional community diversity. Consequently, our next task will be to use our data from the Sinnamary to test the hypothesis that fluctuating environments, such as those in the downstream creeks, should contain weakly interactive opportunists with generalised strategies (Poff and Ward 1990; Poff and Allan 1995). The results of this test should enable us to develop metrics for the functional diversity of the fish communities in the Sinnamary Basin that are easier to predict than species richness.

Appendix 1 Spatial habitat characteristics expressed as synthesis of all point samples (depth) or proportions of variable categories found in all of the 100 sampled areas in the up- and downstream

creeks (litter, vegetation, substrate, and bank slope). See text for the variable categories

	Depth (cm)	Litter (%)					Vegetation (%)				Substrate (%)					Bank slope (%)				
Upstream																				
Minimum	0	1	2	3	4	5	1	2	3	1	2	3	4	5	6	1	2	3	4	5
Maximum	126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Median	35	100	57	47	100	12	0	76	27	82	100	100	0	6	45	100	88	100	50	50
Mean	40	42	19	11	34	0	0	11	0	9	38	57	0	0	0	19	25	14	10	11
SD	23	46	22	14	39	1	0	17	2	17	41	49	0	0	1	28	26	17	14	14
		23	12	11	24	2	0	18	6	21	23	30	0	1	6	28	17	16	13	15
Downstream																				
Minimum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maximum	150	88	65	62	100	11	96	48	21	100	100	86	15	1	42	80	87	75	75	61
Median	51	31	24	24	17	0	0	0	0	21	38	3	0	0	0	11	25	23	21	0
Mean	54	35	28	25	22	0	1	3	1	29	41	22	1	0	1	16	27	26	22	9
SD	27	17	16	12	20	2	10	8	4	27	23	27	3	0	7	17	15	16	16	16

Acknowledgements 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 for providing some hydrological data, D. Chessel and S. Dolédec for help in data analyses and statistics, Nigel Bras Mort for linguistic advice, and two anonymous referees for their helpful comments on a previous version of the manuscript. Electricité De France (Contracts GP 7572 and 7585) and the ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération) funded this study.

References

- Bain MB, Finn JT, Booke HE (1988) Streamflow regulation and fish community structure. *Ecology* 69:182–192
- Bettoli PW, Maceina MJ (1996) Sampling with toxicants. In: Murphy BR, Willis DW (eds) *Fisheries techniques*. American Fisheries Society, Bethesda, pp 303–333
- Bonetto AA, Wais JR, Castello HP (1989) The increasing damming of the Parana Basin and its effects on the lower reaches. *Reg Riv Res Manage* 4:333–346
- Breder MC, Rosen DE (1966) *Modes of reproduction in fishes*. TFH, Jersey City
- Cellot B, Dole-Olivier MJ, Bornette G, Pautou G (1994) Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biol* 31:311–325
- Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biol* 31:295–309
- Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310
- Downes BJ (1990) Patch dynamics and mobility of fauna in streams and other habitats. *Oikos* 59:411–413
- Edwards RW, Brooker MP (1982) *The ecology of the Wye*. Junk, The Hague
- Ferminella JW, Resh VH (1990) Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. *Ecology* 71:2083–2094
- Finger TG, Stewart EM (1987) Response of fishes to flooding regime in lowland hardwood wetlands. In: Matthews WJ, Heins DC (eds) *Community and evolutionary ecology of North American stream fishes*. Oklahoma University Press, Norman, pp 86–92
- Frid CLJ, Townsend CR (1989) An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. *Oikos* 56:137–141
- Gaston KJ (1994) *Rarity*. Chapman Hall, London
- Géry J (1977) *Characoids of the world*. TFH, Neptune City
- Gilderhus PA (1972) Exposure times necessary for Antimycin and rotenone to eliminate certain freshwater fish. *J Fish Res Bd Can* 29:199–202
- Gore JA (1985) *The restoration of rivers and streams*. Butterworth, Boston
- Gorman OT, Karr JR (1978) Habitat structure and stream fish communities. *Ecology* 59:507–515
- Grossman GD, Moyle PB, Whitaker JO (1982) Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *Am Nat* 120:423–454
- Harvey BC (1987) Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Trans Am Fish Soc* 116:851–855
- Heywood VH, Watson RT (eds) (1995) *Global biodiversity assessment*. Cambridge University Press, Cambridge
- Hildrew AG, Townsend CR (1987) Organization in freshwater benthic communities. In: Gee JHR, Giller PS (eds) *Organization of communities past and present*. Blackwell, Oxford, pp 347–372
- Horwitz RJ (1978) Temporal variability patterns and the distributional patterns of stream fishes. *Ecol Monogr* 48:307–321
- Huguény B (1990) Richesse des peuplements de poissons dans le Niandan (Haut Niger, Afrique) en fonction de la taille de la rivière et de la diversité du milieu. *Rev Hydrobiol Trop* 23:351–364
- Junk WJ, Da Silva CJ (1995) Neotropical floodplains: a comparison between the Pantanal of Mato Grosso and the large Amazonian river floodplains. In: Tundisi JG, Biardo CEM, Tundisi TM (eds) *Limnology in Brazil*. Brazilian Academy of Sciences, Rio de Janeiro, pp 195–217
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) *Proceedings of the international large river symposium*. *Can Spec Publ Fish Aquat Sci* 106:110–127
- Kullander SO, Nijssen H (1989) *The cichlids of Surinam*. EJ Brill
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Lowe-McConnell RH (1987) *Ecological studies in tropical communities*. Cambridge University Press, Cambridge
- Manly BJB (1991) *Randomization and Monte Carlo methods in biology*. Chapman Hall, London
- Meffe GK (1984) Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65:1525–1534
- Mérigoux S, Ponton D (1998) Body shape and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America. *J Fish Biol* 52:556–569
- Mérigoux S, Ponton D, Mérona B de (1998) Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America. *Environ Biol Fish* 51:25–39
- Minshall GW (1988) Stream ecosystem theory: a global perspective. *J N Am Benthol Soc* 7:263–288
- Mordukhai-Boltovskoi PD (1978) *The river Volga and its life*. Junk, The Hague
- Munro AD (1990) Tropical freshwater fish. In: Munro AD, Scott AP, Lam TJ (eds) *Reproductive seasonality in teleosts: environmental influences*. CRC, Boca Raton, pp 145–239
- Palmer MA, Poff NL (1997) Heterogeneity in streams. The influence of environmental heterogeneity on patterns and processes in streams. *J N Am Benthol Soc* 16:169–173
- Pearsons TN, Li HW, Lamberti GA (1992) Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Trans Am Fish Soc* 121:427–436
- Peckarsky BL, Horn SC, Statzner B (1990) Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshwater Biol* 24:181–191
- Persat H, Olivier JM, Pont D (1994) Theoretical habitat templates, species traits, and species richness: fish in the Upper Rhône River and its floodplain. *Freshwater Biol* 31:439–454
- Planquette P, Keith P, LeBail PY (1996) *Atlas des poissons d'eau douce de Guyane*, vol 1. Collection du Patrimoine Naturel, vol 22. IEGB, MNHN, INRA, CSP Ministère de l'Environnement, Paris
- Poff NL, Allan JD (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627
- Poff NL, Ward JV (1990) Physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environ Manage* 14:629–645
- Poizat G, Pont D (1996) Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshwater Biol* 36:611–622
- Ponton D, Copp GH (1997) Early dry-season community structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after hydrodam operation. *Environ Biol Fish* 50:235–256
- Ponton D, 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. *Pol Arch Hydrobiol* (in press)
- Ponton D, Tito de Moraes L (1994) Les stratégies de reproduction et les premiers stades de vie des poissons du fleuve Sinnamary (Guyane Française): une revue bibliographique. *Rev Hydrobiol Trop* 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 Guiana, South America). *Reg Riv Res Manage* 14:227–243

- Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourn MJ (1988) Patch dynamics in lotic systems: the stream as a mosaic. *J N Am Benthol Soc* 7:503-524
- Resh VH, Brown AV, Covich AP, Gurtz ME, Li HL, Minshall GW, Reice SR, Shelton AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. *J N Am Benthol Soc* 7:433-455
- Resh VH, Hildrew AG, Statzner B, Townsend CR (1994) Theoretical habitat templates, species traits, and species richness: a synthesis of long-term ecological research on the upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biol* 31:539-554
- Richoux P (1994) Theoretical habitat templates, species traits, and species richness: aquatic Coleoptera in the upper Rhône River and its floodplain. *Freshwater Biol* 31:377-396
- Rodriguez MA, Lewis WM (1997) Structure of fish assemblages along environmental gradients in floodplain lakes of the Oronico River. *Ecol Monogr* 67:109-128
- Rojas-Beltran R (1984) Clé de détermination des poissons continentaux et côtiers de Guyane (Bulletin de Liaison du Groupe de Recherche de Guyane 7). INRA, Kourou
- Sagnes P, Gaudin P, Statzner B (1997) Shifts in morphometrics and their relation to hydrodynamic potential and habitat use during grayling ontogenesis. *J Fish Biol* 50:846-858
- Schiemer F, Zalewski M (1992) The importance of riparian ecotones for diversity and productivity of riverine fish communities. *Neth J Zool* 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. *Verh Int Ver Limnol* 24:2497-2500
- Schlosser IJ (1985) Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484-1490
- Schlosser IJ (1987) The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68:651-659
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Statistical Sciences (1995a) S-PLUS user's manual, version 3.3 for Windows. MathSoft, Seattle
- Statistical Sciences (1995b) S-PLUS programmer's manual, version 3.2. MathSoft, Seattle
- Statistical Sciences (1995c) S-PLUS guide to statistical and mathematical analysis, version 3.3. MathSoft, Seattle
- Statzner B, Resh VH (1993) Multiple-site and -year analyses of stream insect emergence: a test of ecological theory. *Oecologia* 96:65-79
- Statzner B, Sperling F (1993) Potential contribution of system specific knowledge (SSK) to stream-management decisions: ecological and economic aspects. *Freshwater Biol* 29:313-342
- Statzner B, Gore JA, Resh VH (1988) Hydraulic stream ecology: observed patterns and potential applications. *J N Am Benthol Soc* 7:307-360
- Statzner B, Hoppenhaus K, Arens MF, Richoux P (1997) Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biol* 37:463-472
- Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. *Stat Comput* 7:75-83
- Tito de Morais L, Lointier M, Hoff M (1995) Extent and role for fish populations of riverine ecotones along the Sinnamary river (French Guiana). *Hydrobiologia* 303:163-179
- Tomassone R, Lesquoy E, Miller C (1983) *La régression*, Masson, Paris
- Townsend CR (1989) The patch dynamics concept of stream community ecology. *J N Am Benthol Soc* 8:36-50
- Townsend CR, Hildrew AG (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biol* 31:265-275
- Townsend CR, Dolédec S, Scarsbrook MR (1997a) Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biol* 37:367-387
- Townsend CR, Scarsbrook MR, Dolédec S (1997b) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnol Oceanogr* 42:938-949
- Washington HG (1984) Diversity, biotic and similarity indices - a review with special relevance to aquatic ecosystems. *Water Res* 18:653-694
- Westby GWM (1988) The ecology, discharge diversity and predatory behaviour of Gymnotiformes electric fish in the coastal streams of French Guiana. *Behav Ecol Sociobiol* 22:341-354
- Wilkinson L, Blank G, Gruber C (1996) *Desktop data analysis with Systat*. Prentice Hall, Upper Saddle River

