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Variabilité spatio-temporelle de l'environnement et structure des peuplements de juvéniles de poissons : cas d'un fleuve intertropical soumis à un aménagement hydroélectrique

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Résumé

Les hypothèses développées en milieux lotiques à partir de la théorie des perturbations intermédiaires prédisent que la richesse spécifique (Patch Dynamics Concept) et les combinaisons de traits biologiques des espèces (River Habitat Templet Concept) changent selon la variabilité temporelle et spatiale de l'environnement. J'ai testé ces hypothèses avec les communautés de jeunes poissons d'affluents du Sinnamary (Guyane Française) situés à l'amont du barrage de Petit Saut (conditions naturelles) et à l'aval du barrage (milieux soumis aux perturbations du barrage). J'ai réalisé 200 pêches d'une surface d'environ 50 m^2, par empoisonnement à la roténone, afin d'obtenir les caractéristiques des communautés de poissons de ces habitats. J'ai décrit la variabilité temporelle (c'est-à-dire la variabilité de l'hydrologie) et spatiale (par exemple la variabilité de la profondeur, des débris organiques et du substrat) de ces 200 échantillons. Pour chaque échantillon, j'ai également déterminé les conditions d'état (par exemple les conditions moyennes) à l'aide des variables de description de la variabilité du milieu et d'autres comme la concentration en oxygène dissous, la turbidité de l'eau ou la longueur du linéaire de berge de la station de pêche. Mon travail a permis d'inventorier les jeunes stades de 73 taxons (60% des espèces du Sinnamary) et confirme ainsi le rôle de nurserie des affluents de ce fleuve et de leurs zones d'inondation associées. A partir des traits d'histoire de vie obtenus dans la littérature, j'ai décrit pour les 57 taxons les plus abondants trois principales stratégies vitales qui correspondent aux stratégies d'équilibre, d'opportuniste et de périodique définies par Winemiller *(1989, Oecologia, 81: 225-241)*. De plus, j'ai montré que les jeunes poissons de la stratégie d'équilibre ont des corps plus profilés et un régime alimentaire plus spécialisé que les périodiques ou les opportunistes. Les prédictions du Patch Dynamics Concept ne sont pas validées par mon travail ; je n'ai pas observé une richesse maximale pour une variabilité temporelle intermédiaire et une variabilité spatiale maximale. Les prédictions de l'Habitat Templet Concept sont partiellement confirmées. Ainsi, la taille minimale à la première maturité, le diamètre moyen des oocytes et la hauteur relative du corps des jeunes stades, conférant une certaine résilience et/ou résistance aux organismes, diminuent avec une augmentation de la variabilité temporelle tandis que la taille minimale à la première maturité et le diamètre moyen des oocytes augmentent avec la variabilité spatiale. Mon travail démontre l'importance de la variabilité de l'habitat une fois prises en compte les conditions d'état et extrêmes de l'habitat, pour expliquer et/ou prédire la structure des communautés de jeunes poissons. Ainsi, j'ai pu prédire 37% et expliquer 47% de la variabilité de la richesse spécifique et 34% de la variabilité biologique dans les échantillons amont. Les paramètres d'état les plus structurants sont le niveau de l'eau, la concentration en oxygène dissous, la turbidité de l'eau et la longueur du linéaire de berge. L'approche sur les traits biologiques développée dans cette thèse ouvre des perspectives pour évaluer de manière fiable la diversité faunistique des communautés aquatiques. De plus, cette approche devrait permettre de s'affranchir du cadre taxonomique propre à la Guyane et donc de transposer les résultats obtenus à d'autres systèmes soumis à des perturbations naturelles ou anthropiques.

Mots clés: communautés aquatiques, richesse spécifique, traits biologiques, stratégies de vie, premiers stades de développement, variabilité hydrologique, diversité spatiale de l'habitat, Amérique du Sud.

Abstract

For running waters, concepts developed from the intermediate disturbance hypothesis predict that species richness (Patch Dynamics Concept) and combinations of biological traits of species forming a community (River Habitat Templet Concept) change across gradients of spatio-temporal variability. I tested these hypotheses with young fish communities in the floodplain creeks of the neotropical Sinnamary River (French Guiana) situated upstream (natural conditions) and downstream of the Petit Saut Dam (disturbed by the dam). I sampled fish with rotenone in 200 areas of about 50 m^2 to get data on fish community characteristics. For each sample, I described temporal (i.e. the hydrological) and spatial (e.g. depth, bottom substrate, litter type) variability of the fish habitat. In addition, I evaluated the state (e.g. mean conditions) of these habitats (re-using data describing habitat variability and other variables such as oxygen concentration and turbidity of the water). I surveyed the young fish of 73 taxa (60% of the Sinnamary species) and confirmed the hypothesis that the creeks and their associated floodplains play the role of a nursery. For 57 abundant species, I identified three main strategies of fairly homogeneous life history features that corresponded to the equilibrium, opportunistic and periodic strategies sensu Winemiller (*1989, Oecologia, 81: 225-241*). I demonstrated that young fish of species having the equilibrium strategy had more streamlined bodies and a more specialised diet than fish having the periodic and opportunistic strategy. The predictions of the Patch Dynamics Concept were not validated by my work; I did not observed a maximal species richness for intermediate temporal variability and maximal spatial variability. However, my results partially supported the predictions of the Habitat Templet Concept: the creek habitats significantly acted as a templet for species, and most of the relationships showed the predicted trends (e.g. traits conferring resiliency or resistance to the species such as minimal standard length at first maturity, mean diameter of mature oocytes, parental care and relative body height decreased with increasing temporal variability; minimal standard length at first maturity and mean diameter of mature oocytes increased with increasing spatial variability). I could predict and/or explain more of the variability in species richness and in the biological traits when I considered habitat variability together with habitat state variables. Thereby, I predicted 37% and explained 47% of the species richness variability and explained up to 34% of the trait variability. I demonstrated that the most important state variables were mean water level, water oxygen content, water turbidity and bank length. I agreed with previous publications that the Habitat Templet Concept is an important element in ecological theory that has also the potential to be applied in management. Its species trait approach offers broad insights for evaluating functional community diversity of freshwater organisms and for comparing, beyond the systematic details of the different taxa, biota of different systems affected by natural of human disturbances.

Key words: Aquatic communities, species richness, biological traits, life history strategies, young stages, hydrological variability, spatial habitat diversity, South America.

PREMIERE PARTIE : SYNTHESE

DEUXIEME PARTIE : ARTICLES

A1: Spatio-temporal distribution of young fish in tributaries of natural and flow regulated sections of a neotropical river in French Guiana, South America.

Mérigoux S. & Ponton D. *Freshwater Biology* (sous presse).

A2: Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks.

Mérigoux S., Hugueny B., Ponton D., Statzner B. & Vauchel P. *Oecologia* (sous presse).

A3: Body shape and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America.

Mérigoux S. & Ponton D. 1998. *Journal of Fish Biology* 52: 556-569.

A4: Species traits in relation to habitat variability and state : neotropical juvenile fish in floodplain creeks.

Mérigoux S., Dolédec S. & Statzner B. (à soumettre).

A5: Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America.

Mérigoux S., Ponton D. & Mérona B. 1998. *Environmental Biology of Fishes* 51: 25-39.

ANNEXES : articles réalisés en parallèle à la thèse

A6: Impact of dam in the neotropics: what can be learned from the assemblage structures of young fish in tributaries of the Sinnamary River (French Guiana, South America)?

Ponton D., Mérigoux S. & Copp G.H. *Aquatic Conservation* (Soumis en octobre 1998).

A7: The relationship between local and regional species richness: comparing biotas with different evolutionary histories.

Hugueny B., Tito de Morais L., Mérigoux S., Mérona B. & Ponton D. 1997.

Oikos 80: 583-587.

AVANT-PROPOS : ORGANISATION DE LA THESE

Cette thèse comporte une synthèse en français de cinq articles publiés ou en attente de publication (A1 à A5) sur les relations entre les facteurs abiotiques de l'environnement et la structure des communautés de jeunes poissons en zone intertropicale (Guyane Française). Les résumés de travaux réalisés parallèlement à ma thèse sont présentés en annexes (A6 et A7).

La synthèse se réfère largement aux articles qui la suivent (A1 à A5). Elle ne reprend ainsi que les résultats importants et ne donne pas de détails qui gêneraient une lecture et une compréhension rapide de l'ensemble du travail. Le "je" est utilisé dans le texte pour simplifier la rédaction. Il sous-entend bien sûr l'aide et les conseils de nombreuses personnes sur le terrain, mais aussi pour l'analyse des données et la rédaction (cf. co-signatures et remerciements des articles).

Les articles qui suivent sont écrits en anglais. Ils décrivent de manière précise le protocole d'échantillonnage des poissons et des mesures d'habitat. Ils donnent aussi les détails des méthodes d'analyses et des résultats. Les quatre premiers articles (A1 à A4) s'intéressent aux relations habitat-poissons des communautés de jeunes poissons d'affluents du Sinnamary. A1 décrit les variations de densité des espèces dans le temps et dans l'espace. A2 explique et prédit la richesse spécifique en fonction des facteurs abiotiques du milieu. A3 décrit le régime alimentaire et la morphologie des espèces de jeunes poissons. A4 étudie les relations entre traits biologiques et variables du milieu. J'ai choisi d'intégrer à cette étude sur les jeunes poissons du Sinnamary celle menée sur deux cours d'eau de la côte guyanaise (A5), pour différentes raisons: 1) cette étude traite aussi des relations entre les poissons et leur habitat, 2) ce travail a permis de mettre en place le protocole de pêche et de description des paramètres spatiaux de l'habitat utilisé dans le Sinnamary, 3) plus de 95% des espèces présentes dans la Malmanoury ou la Karouabo sont aussi rencontrées dans le Sinnamary et 4) environ 80% des individus capturés dans ces deux criques étaient des jeunes poissons.

Les annexes résument les travaux réalisés parallèlement à ma thèse sur des thèmes semblables. A6 démontre l'intérêt des jeunes stades de poissons comme descripteurs du milieu pour évaluer l'impact d'un barrage en zone intertropicale (Sinnamary, Guyane Française). Enfin, A7 traite des relations entre les richesses spécifiques locale et régionale de poissons de cours d'eau de Guyane Française et de Côte d'Ivoire.

1. Introduction

1.1 Cadre théorique

La compréhension de la nature et du rôle des facteurs de l'environnement qui structurent les communautés est un objectif majeur de la recherche en écologie (Begon *et al.*, 1996). La variabilité temporelle et spatiale du milieu joue par exemple un rôle primordial sur la distribution des organismes, leurs interactions et leur adaptation (Wiens, 1986). La part non prévisible de la variabilité temporelle d'un habitat est généralement exprimée en termes de perturbation (Connell, 1978). Sa variabilité spatiale exprime alors la quantité de refuges capable d'atténuer l'impact des perturbations sur les organismes (Townsend & Hildrew, 1994). Le rôle des perturbations dans la structure et la dynamique des communautés est désormais largement reconnu (Picket *et al.*, 1989). La conceptualisation théorique la plus connue, "l'hypothèse des perturbations intermédiaires" de Connell (1978), prédit une richesse maximale pour des fréquences et des intensités de perturbations intermédiaires (Figure 1).

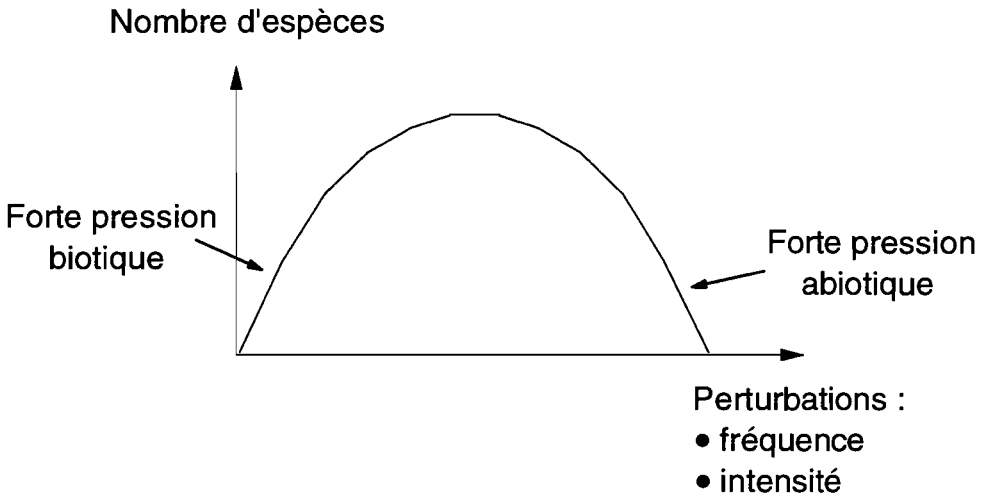


Figure 1 : "Hypothèse des perturbations intermédiaires" d'après Connell (1978) modifiée.

Dans des milieux non-perturbés, le nombre d'espèces est plus faible du fait d'une pression biotique trop forte (compétition par exemple). Dans des milieux très perturbés, les facteurs abiotiques provoquent une diminution du nombre d'espèces (Figure 1).

Les milieux lotiques sont typiquement caractérisés par une forte variabilité spatio-temporelle de l'environnement (Minshall, 1988 ; Pringle *et al.*, 1988 ; Resh *et al.*, 1988 ; Poff

PREMIERE PARTIE : SYNTHESE

& Ward, 1990). Dans ces systèmes, les perturbations sont généralement exprimées par la fréquence et l'intensité des crues (Poff & Ward, 1989) ou par la variabilité du régime hydrologique (Horwitz, 1978 ; Schlosser, 1990). L'hypothèse des perturbations intermédiaires de Connell (1978) a été adaptée aux milieux aquatiques par Ward & Stanford (1983). Les prédictions du "Patch Dynamics Concept" formulées par Townsend (1989) sont très similaires: une relation en dôme de la richesse spécifique en fonction de l'intensité des perturbations est aussi attendue. Par contre, dans le cadre de cette hypothèse, à intensités de perturbations identiques, la richesse spécifique est d'autant plus élevée que la variabilité spatiale est importante (Figure 2).

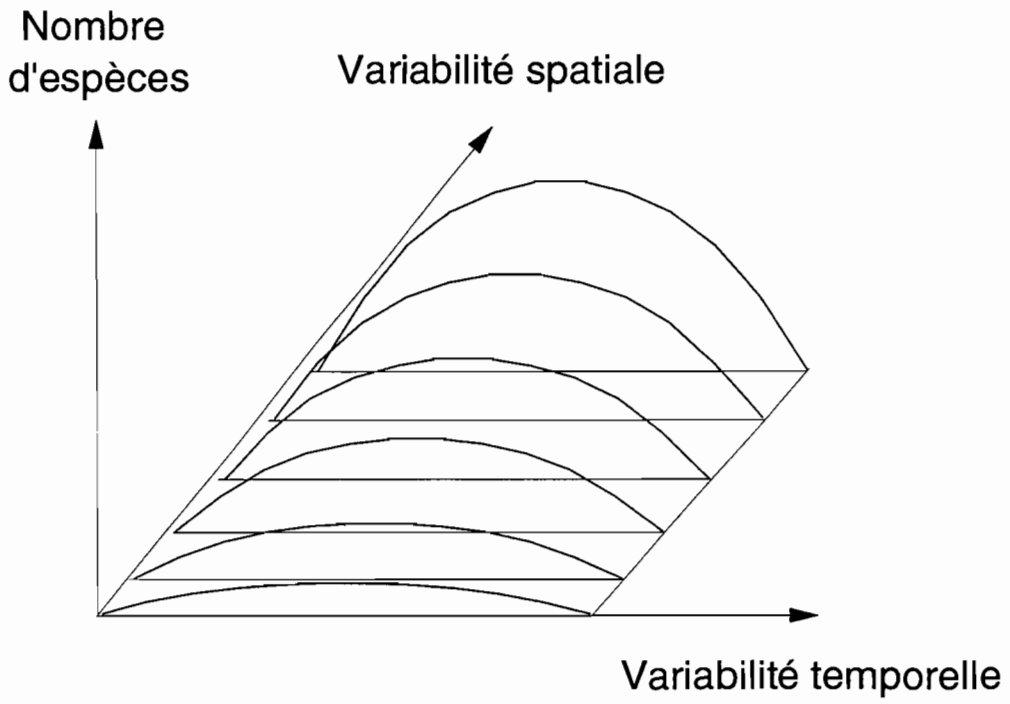


Figure 2 : Illustration simplifiée des hypothèses du "Patch Dynamics Concept" (Townsend, 1989).

Dans ce même cadre de variabilité temporelle et spatiale, le concept du "River Habitat Templet" (Townsend & Hildrew, 1994 ; Figure 3) repose sur la théorie de "l'Habitat Templet" de Southwood (1977 ; 1988) selon laquelle l'environnement sélectionnerait des stratégies d'histoire de vie (combinaisons de traits) adaptées à la survie des espèces. Dans ce cadre théorique, le concept du "River Habitat Templet" prédit le type de combinaisons de traits attendu suivant la variabilité temporelle et spatiale de l'habitat. Ainsi, Townsend & Hildrew (1994) prédisent que les organismes des milieux à forte variabilité temporelle et à faible

variabilité spatiale seraient plus résilients et/ou plus résistants (sensu Connell & Sousa, 1983) (par exemple : petite taille du corps, courte durée de vie ou forte fécondité) que les organismes vivant dans des milieux présentant des conditions temporelle et spatiale opposées (Figure 3).

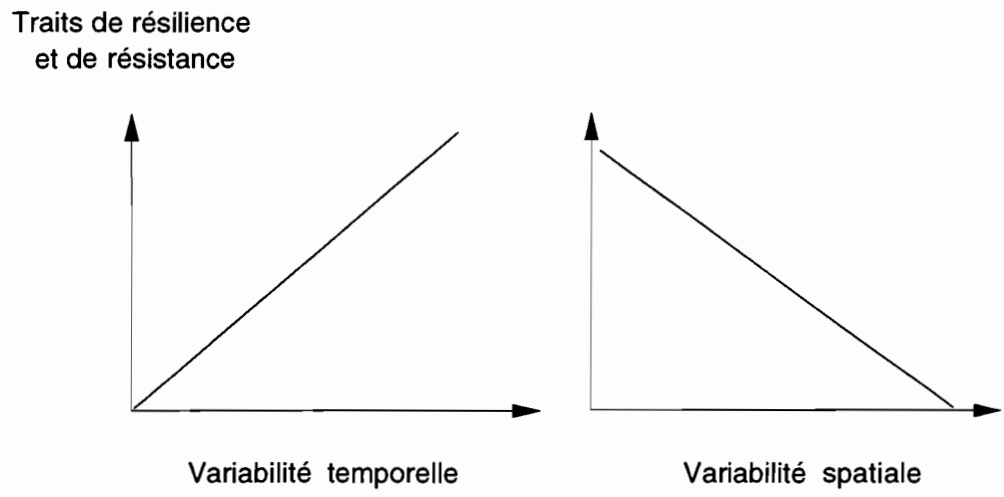


Figure 3 : Illustration simplifiée des hypothèses du "River Habitat Templet Concept" (Townsend & Hildrew, 1994)

En milieu lotique les hypothèses développées à partir de la théorie des perturbations intermédiaires de Connell (1978) ouvrent des perspectives théoriques et appliquées reconnues (Statzner *et al.*, 1997 ; Townsend *et al.*, 1997a). Cependant, dans ces milieux, les études testant les prévisions des concepts du "Patch Dynamics" et du "River Habitat Templet" ont montré des résultats décevants et/ou contradictoires et n'ont généralement pas permis une validation solide de ces concepts (Statzner *et al.*, 1994 ; Statzner *et al.*, 1997 ; Townsend *et al.*, 1997a ; 1997b). Par conséquent, Resh *et al.* (1994) ont suggéré de prendre en compte, en plus de la variabilité, les conditions d'état du milieu (par exemple conditions moyennes) dans les études reliant la richesse spécifique et les traits biologiques des espèces.

1.2 Les poissons

1.2.1 Un modèle adapté à ce cadre théorique

Les résultats de plusieurs études laissent penser que les poissons représentent un matériel biologique adapté pour tester les hypothèses liées à la théorie des perturbations intermédiaires. En effet, il a été observé 1) un nombre d'espèces réduit en milieu instable suite à une augmentation de débit (Horwitz, 1978 ; Schlosser, 1985), 2) un nombre d'espèces réduit en milieu stable dû à une forte pression biotique (Meffe, 1984), 3) un nombre d'espèces plus élevé dans des milieux spatialement diversifiés (Gorman & Karr, 1978 ; Hugueny, 1990) et 4) des espèces résilientes et/ou résistantes (petite taille maximale du corps, petite taille à la première maturité, courte durée de vie) en milieux à forte variabilité hydrologique (Schlosser, 1990). Cependant, le seul travail sur les poissons testant les concepts de Patch Dynamics et du River Habitat Templet n'a montré aucune des tendances attendues de richesse spécifique et de combinaison de traits biologiques dans un cadre de variabilité temporelle et spatiale de l'environnement (Persat *et al.*, 1994). Les auteurs discutent des problèmes de changements de niche ontogénétique qui pourraient être à l'origine de l'invalidation des prédictions. De plus, les poissons sont en général des organismes longévives; ils sont affectés par un spectre important de perturbations (journalières à décennales) et leur échelle temporelle d'étude doit donc être assez grande (Townsend & Hildrew, 1994). Cependant, l'effet d'une perturbation donnée sur les poissons dépend du stade de développement et les jeunes sont probablement plus sensibles à des événements de courte durée que les adultes.

1.2.2 Importance de l'étude des premiers stades de développement

Les premiers stades de développement des poissons déterminent la force des classes d'âge des adultes et par conséquent structurent les communautés de poissons adultes (Balon, 1984 ; Houde, 1987). En effet, la structure d'un peuplement de poissons adultes dépend d'une part du nombre d'œufs émis dans le milieu par les adultes, et d'autre part des facteurs de mortalité biotiques et abiotiques auxquels sont soumis les poissons au cours de leur vie.

L'importance des paramètres abiotiques varie en fonction de la taille et donc de l'âge des poissons (Schlosser, 1987) (Figure 4).

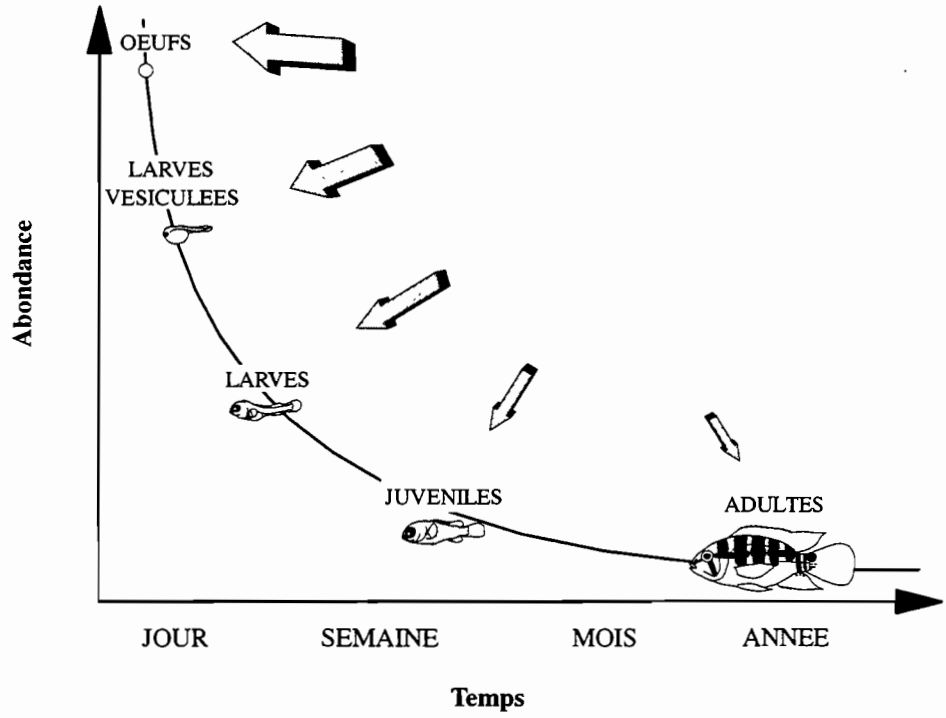


Figure 4: Variation de l'influence des facteurs abiotiques tels que la vitesse du courant, l'oxygène dissous ou la turbidité de l'eau, sur la survie des poissons en fonction de leur stade de développement. L'épaisseur des flèches est proportionnelle à cette influence.

Par exemple, les jeunes poissons sont plus sensibles à la variabilité du régime hydrologique (Schlosser, 1985) ou à la vitesse du courant (Harvey, 1987) que les plus âgés. Au cours de leur développement, les poissons acquièrent une meilleure faculté au déplacement qui leur permet de mieux résister à ces facteurs (Harvey, 1987 ; Schlosser, 1987) (Figure 4). Enfin, par leurs exigences écologiques très spécifiques, les jeunes poissons sont de bons descripteurs de la structure de l'habitat et de l'intégrité écologique des systèmes lotiques (Copp *et al.*, 1991 ; Schiemer *et al.*, 1991).

1.3 Cadre régional : l'Amérique du Sud et la Guyane Française

1.3.1 Caractéristiques hydrologiques et morphologiques des cours d'eau

Les cours d'eau du plateau des Guyanes sont sujets, en plus des variations hydrologiques saisonnières prévisibles, à de brutales variations imprévisibles dues aux précipitations locales (Covich, 1988 ; Westby, 1988 ; Ouboter & Mol, 1993). Cependant, même s'il existe un rythme hydrologique saisonnier dans ces cours d'eau, il n'est pas aussi marqué que dans les systèmes à vastes plaines d'inondations tels que l'Amazone ou l'Orénoque. L'amplitude et la durée des inondations sont donc plus réduites dans les cours d'eau guyanais que dans les grands fleuves d'Amérique du Sud. De plus, en Guyane Française, en raison du parcours relativement rectiligne et court des fleuves, la surface potentiellement inondable est réduite.

1.3.2 L'état des connaissances sur les poissons

1.3.2.1 Richesse spécifique et études sur les relations habitat-poissons

Les rivières d'Amérique du Sud présentent la faune piscicole la plus diversifiée de la planète (2400 espèces recensées, Winemiller, 1989). Paradoxalement, seulement trois ordres (Characiformes, Siluriformes et Perciformes) représentent 93% des espèces (Lowe-McConnell, 1987). La liste actualisée des poissons de Guyane Française comprend 430 espèces d'eau douce et saumâtre (Planquette *et al.*, 1996) dont 166 sont représentées dans le Sinnamary. Malgré la diversité piscicole très élevée dans les cours d'eau sud-américains, le nombre d'études sur les relations entre les poissons et leur environnement reste relativement faible. Selon Winemiller (1996) ceci n'est pas surprenant étant donné que "many fish biologists equate the state of ichthyological knowledge of the Neotropics with that of North America during the early nineteenth century". Les études les plus nombreuses à ce sujet s'intéressent aux adultes vivant dans les grands fleuves d'Amérique du Sud (Welcomme, 1979 Lowe-McConnel, 1987 ; Winemiller, 1989). Dans les cours d'eau à régimes hydrologiques plus instables du plateau des Guyanes, les études sur les relations habitat-poissons ont essentiellement porté sur les stades adultes dans les cours d'eau de Guyane Française. De plus, mis à part le travail de Boujard *et al.* (1990), ces travaux ont toujours traité de manière indépendante les dimensions temporelle et spatiale. Ainsi, Rojas-Beltran (1986) a décrit les variations saisonnières du peuplement, de la richesse spécifique et de la densité de poissons adultes dans un affluent du Kourou. Des études spatiales sur les adultes ont porté 1) sur la

distribution des poissons à une échelle biogéographique en relation avec les refuges glaciaires du quaternaire (Renno *et al.*, 1990 ; Boujard, 1992) ou avec les caractéristiques physico-chimiques de l'eau (Mol, 1994) et 2) sur la distribution longitudinale des taxons à l'échelle du bassin versant (Boujard & Rojas-Beltran, 1988 ; Tito de Morais & Lauzanne, 1994). Les premières études sur les jeunes poissons en relation avec leur habitat sont très récentes. Il s'agit du travail sur les poissons du Sinnamary 1) de Ponton & Copp (1997) qui décrit les exigences écologiques des espèces et celui 2) de Ponton & Vauchel (1998) qui teste le caractère significatif de la relation entre la distribution temporelle des poissons et les paramètres hydrologiques. Enfin, la variabilité spatio-temporelle n'a jamais été prise en compte pour expliquer la structure des communautés de poissons quel que soit le stade ontogénétique considéré.

1.3.2.2 Traits biologiques

Les premières synthèses des informations acquises sur les traits biologiques des poissons sud-américains sont les travaux de Winemiller (1989) sur les poissons de cours d'eau du Llanos Vénézuélien et ceux de Ponton & Tito de Morais (1994) et Ponton & Mérona (1998) sur les espèces du Sinnamary en Guyane Française. L'ensemble de ces études montre que les poissons sud-américains présentent une très grande diversité de modes de vie. Ainsi, Winemiller (1989) a déterminé pour les espèces de poissons du Llanos Vénézuélien, trois stratégies de vies extrêmes (équilibre, opportuniste et périodique) à partir de l'âge à la première maturité, la fécondité et la survie des juvéniles. La recherche bibliographique sur les traits d'histoire de vie des espèces présentes dans le Sinnamary de Ponton & Tito de Morais (1994) a révélé le manque d'informations disponibles dans la littérature à ce sujet. Ponton & Mérona (1998) ont donc par la suite décrit les traits d'histoire de vie de 87 des espèces du Sinnamary. Ainsi, dans ce système, de nombreuses guildes de reproduction (sensu Balon, 1975) sont représentées depuis les non-gardiens phytophiles (par exemple les espèces du genre *Chilodus*), jusqu'aux porteurs externes (les espèces du genre *Loricaria*), en passant par les gardiens que sont les Cichlidae (Ponton & Tito de Morais, 1994). Plus précisément, le nombre d'œufs produits par ponte peut varier de 3 individus (espèce vivipare) pour *Poecilia parae* (Poeciliidae) à plus de 160 000 pour *Leporinus frederici* (Anostomidae). De même, la taille des oocytes varie de 0.2 mm de diamètre pour *Anchovia surinamensis* (Engraulididae) à 4.8 mm pour *Hypostomus plecostomus* (Loricariidae) (Ponton & Mérona, 1998). Enfin,

aucune étude en zone intertropicale n'a porté sur les traits biologiques des espèces en fonction des paramètres du milieu.

1.3.2.3 Conclusion

Le manque d'information sur la nature et le rôle des facteurs abiotiques qui structurent naturellement les communautés de poissons en milieu intertropical pose un problème majeur pour mesurer de manière fiable l'impact des barrages récemment construits en Amérique du Sud (ex: barrage de Tucurui au Brésil ou de Petit Saut en Guyane Française). Les modifications de la fréquence et de l'amplitude ou de la durée des inondations sont susceptibles de changer les structures physiques et chimiques dans ces systèmes lotiques (Collier *et al.,* 1996). Même si les poissons sont en général bien adaptés aux variations physiques ou chimiques naturelles (Matthews, 1998), ces modifications anthropiques peuvent affecter les jeunes stades de poissons et donc avoir des conséquences non négligeables à long terme sur les communautés de poissons (Welcomme, 1995 ; Matthews, 1998).

1.4 Objectifs

En vue d'appliquer les concepts théoriques décrits précédemment aux jeunes poissons de la zone intertropicale, les quatre objectifs principaux fixés dans cette thèse sont :

- l'étude des relations poissons/milieu en déterminant les facteurs abiotiques:
  - qui contrôlent la distribution spatio-temporelle des espèces,
  - qui permettent d'expliquer et prédire la richesse spécifique,
- la réalisation d'une typologie des espèces à partir de leurs traits biologiques,
- l'étude des relations traits biologiques/milieu en déterminant l'influence des facteurs du milieu qui contrôlent les proportions d'espèces présentant différents traits biologiques.
- la comparaison de l'influence des paramètres de l'habitat sur les structures des communautés de jeunes poissons en milieux naturels ou soumis à la perturbation d'un barrage hydroélectrique.

2. Sites d'étude et méthodologie

2.1 Le fleuve Sinnamary

2.1.1 Caractéristiques hydrologiques et barrage de Petit Saut

Le fleuve Sinnamary, avec une longueur de 262 km et un débit moyen annuel de 230 $m^3.s^{-1}$ est le cinquième fleuve de la Guyane Française. Son bassin versant couvre 6565 km^2 et reçoit des précipitations moyennes annuelles de 3000 mm. A la fin des années 80, les travaux d'un barrage hydroélectrique EDF ont commencé au niveau des rapides de Petit Saut. Ce barrage d'une longueur totale de 750 m et d'une hauteur maximale de 44 m, produit au maximum 111 MW pour un débit turbiné de 430 $m^3.s^{-1}$. Depuis janvier 1994, le barrage divise le milieu en trois secteurs très différents du point de vue de leur hydrologie : l'amont et l'aval de la retenue et la retenue elle même. Comme la plupart des cours d'eaux naturels guyanais, dans le haut Sinnamary (en amont du barrage) de brutales variations hydrologiques journalières se superposent aux variations saisonnières (Figure 5). A l'aval du barrage, l'hydrologie du Sinnamary dépend du mode d'exploitation du barrage; les variations naturelles du niveau de l'eau sont donc perturbées. En outre, à l'aval, le niveau de l'eau dans le Sinnamary est soumis à l'influence de la marée.

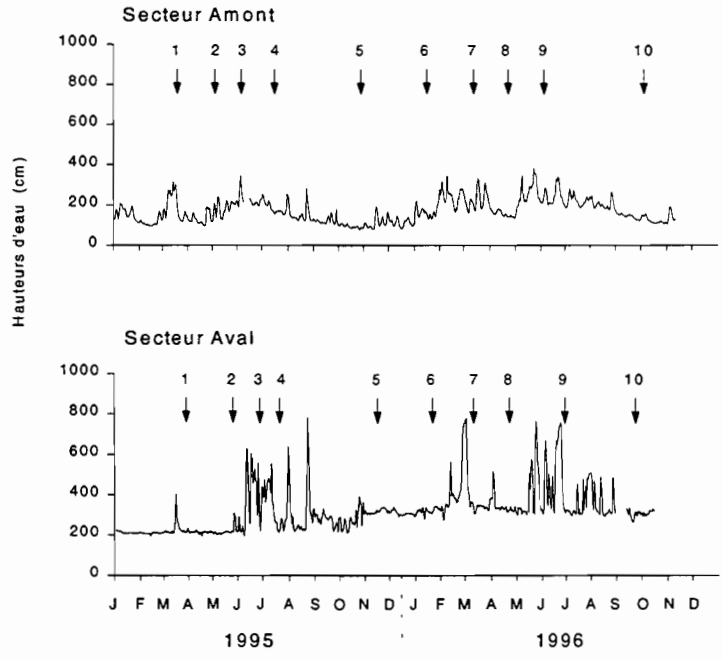


Figure 5: Hauteurs d'eau relevées à Saut Dalles (secteur amont) et à Petit Saut (secteur aval) au cours des années 1995 et 1996. Les campagnes d'échantillonnage sont indiquées par des flèches.

2.1.2 Les criques du Sinnamary

Les affluents du Sinnamary (appelés criques en Guyane) drainent généralement de petits bassins hydrographiques complètement recouverts de forêt primaire. Par conséquent, les criques sont très ombragées et la végétation aquatique ainsi que les algues planctoniques sont très rares. De plus, une quantité très importante de bois mort se trouve dans le lit des criques et le substrat est dominé par de la vase organique, de l'argile ou du sable.

Les criques et leurs zones d'inondation associées jouent le rôle de nurserie une grande partie de l'année (Ponton & Copp, 1997 ; Ponton & Vauchel, 1998). Enfin, le niveau de l'eau dans les criques est largement sous l'influence du Sinnamary (A2).

2.1.3 Des sites adaptés aux objectifs fixés

Les criques du Sinnamary représentent des sites idéals pour remplir les objectifs fixés dans le cadre de cette thèse : 1) le peuplement de poissons du Sinnamary offre une richesse spécifique et une diversité de traits biologiques importantes et donc idéales pour tester les prédictions des concepts du "Patch Dynamic" et du "River Habitat Templet"; 2) les criques choisies sont soumises à des conditions hydrologiques naturelles (amont du barrage de Petit Saut) ou perturbées (aval du barrage), elles offrent donc une grande variabilité temporelle naturelle et artificielle; 3) La morphologie des criques et de leurs zones d'inondation associées est naturelle, c'est-à-dire que l'homme n'a pas encore modifié la diversité spatiale des criques (ce qui n'est pas le cas de la plupart des cours d'eau de zones tempérées). Pour répondre à ces objectifs, j'ai considéré une échelle temporelle courte (semaines) et des échelle spatiales relativement petites (< 100 m^2 : échelle de la station de pêche, cf. A2 et A4 ; < 1000 m^2 : échelle de la zone, cf. A1). L'échelle temporelle considérée correspond à la courte durée de vie de la période juvénile de la plupart des poissons du Sinnamary (Ponton & Tito de Morais, 1994). L'échelle spatiale est bien adaptée à l'espace utilisé par les jeunes poissons (Schiemer *et al.*, 1991 ; Schiemer & Zalewski, 1992) et aux études intégrant de nombreuses espèces (Poizat & Pont, 1996). J'ai utilisé la variabilité du régime hydrologique comme mesure de perturbation pour les poissons et j'ai déterminé la variabilité spatiale à partir de la diversité de caractéristiques de l'habitat telles que la profondeur, les débris organiques, la végétation et le type de pente des berges.

2.2 Lieu et fréquence d'échantillonnage

Dans chacun des deux secteurs d'étude (amont et aval de la retenue du barrage de Petit Saut) dix stations, d'une surface inférieure à 100 m^2, ont été régulièrement échantillonnées. Les 20 stations de pêche choisies au hasard (c'est-à-dire sans a priori sur la présence ou l'absence de poissons) sont réparties dans trois ou quatre zones de pêche (notées a, b, c et d) de six criques (Figure 6). Dix campagnes ont été réalisées au cours des années 1995 et 1996 (Figure 5). Les campagnes ont été effectuées toutes les cinq semaines en saison des pluies et toutes les huit semaines en saison sèche. J'ai ainsi réalisé un total de 200 échantillons (dix campagnes x dix stations x deux secteurs).

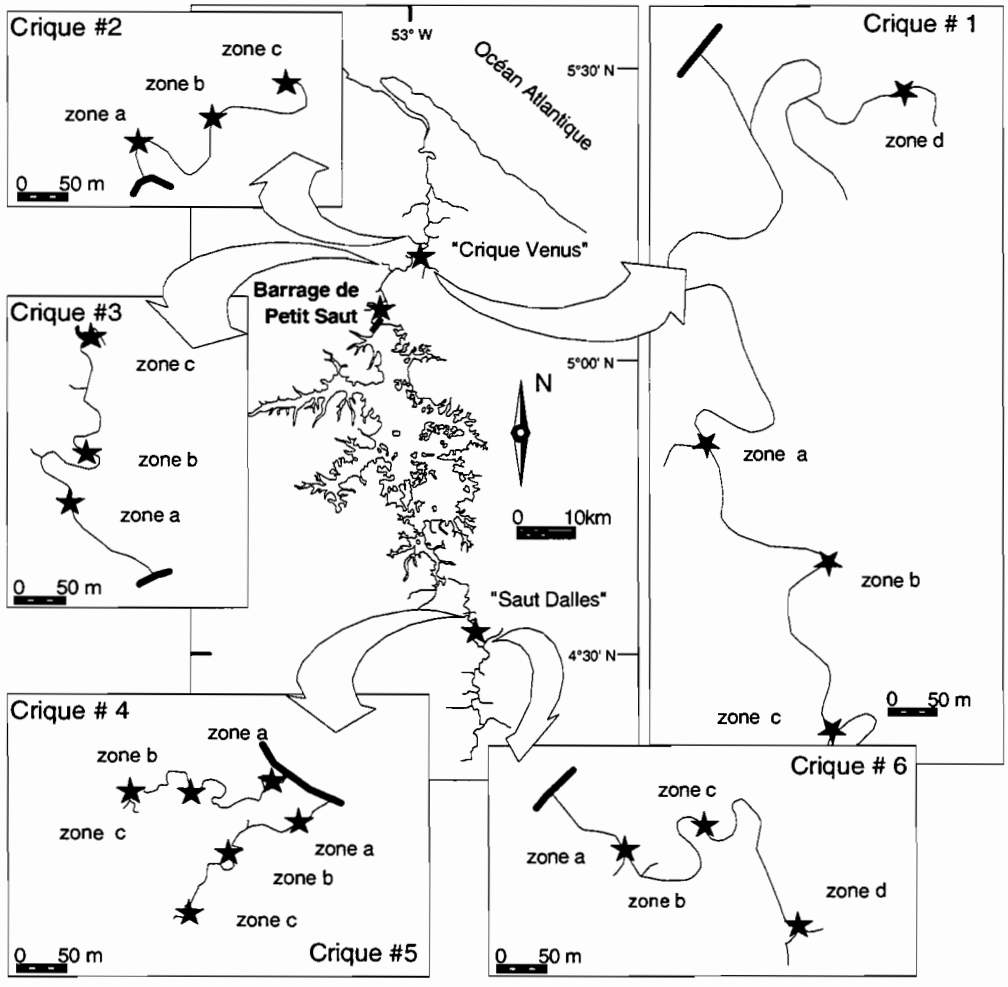


Figure 6: Situation sur le Sinnamary des six criques échantillonnées dans les secteurs amont et aval. Les stations hydrologiques du Sinnamary et les échelles hydrologiques de chaque zone de pêche sont indiquées par des étoiles.

2.3 Echantillonnage des poissons

2.3.1 Technique de pêche

Les engins de pêche électrique généralement utilisés en milieu tempéré pour capturer les jeunes poissons (Copp & Garner, 1995) sont inefficaces dans les cours d'eau guyanais à très faible conductivité électrique. Comme alternative, la méthode d'empoisonnement à la roténone a semblé la mieux adaptée à l'échantillonnage de jeunes poissons dans ces milieux (c'est-à-dire la moins sélective au niveau spécifique). L'efficacité de cette technique a en effet été vérifiée au préalable sur la crique de la Malmanoury (A5). Ainsi, pour chaque pêche, une portion du cours d'eau a été isolée par deux filets de vide de maille de 1 mm. Il fallait ensuite mélanger activement plusieurs doses successives de PREDATOX (solution de roténone extraite de Derris elliptica) dans le volume d'eau échantillonné. L'action du poison sur les juvéniles étant rapide, les poissons ont tout de suite été capturés à l'aide d'épuisettes et fixés dans de l'alcool à 75%.

2.3.2 Analyses des échantillons et problèmes d'identification

Au laboratoire, j'ai identifié et mesuré au mm près (longueur standard) tous les poissons collectés. Aucune clé de détermination sur les jeunes poissons n'étant disponible, le travail d'identification s'est basé sur celles d'adultes réalisées par Géry (1977), Rojas-Beltran (1984), Kullander & Nijssen (1989) et Planquette *et al.* (1996) et sur des séries de dessins de spécimens de taille variable de chaque espèce réalisées par D. Ponton. Les dessins ont été actualisés et complétés pendant toute la période d'échantillonnage. Des problèmes d'identification m'ont conduite à regrouper certaines espèces au niveau taxonomique supérieur (appelées taxons dans mon travail). J'ai séparé les jeunes poissons des stades adultes en fonction de la taille minimale à la première maturité observée pour chaque taxon dans le Sinnamary (A3, Ponton & Mérona, 1998). A partir de l'aspect morphologique et de la longueur standard, j'ai séparé les individus de chaque taxon en trois stades de développement, appelés : premier stade de développement, premier stade de juvénile et dernier stade de juvénile (A3).

2.3.3 Traits biologiques

Pour les taxons présents dans les affluents du Sinnamary, j'ai considéré un total de huit traits biologiques qui, selon Townsend & Hildrew (1994) devraient conférer aux espèces une

certaine résilience et/ou résistance (sensu Connell & Sousa, 1983) face aux perturbations hydrologiques. Les traits qui permettent une certaine résilience sont : (a) la diversité du régime alimentaire des jeunes poissons, (b) la longueur standard maximale du taxon, (c) la longueur standard minimale à la première maturité, (d) la longueur de la période de reproduction au cours d'une année, (e) le diamètre moyen des oocytes matures, (f) la fécondité moyenne et (g) les soins parentaux. Un régime alimentaire diversifié, une petite taille, une période de reproduction courte, de petits œufs et une forte fécondité sont des attributs qui devraient permettre à une population une croissance rapide après une perturbation du milieu (Townsend & Hildrew, 1994). J'ai aussi considéré un trait de résistance : (h) la hauteur relative du corps des jeunes poissons. Une faible valeur pour cette variable indique une forme bien profilée permettant aux animaux de résister aux fortes vitesses du courant (Sagnes et al., 1997). J'ai déterminé les traits (a) et (h) à partir de 10 à 30 individus de chaque taxon de jeunes poissons présents dans le Sinnamary (A3). Pour chaque taxon, j'ai calculé la diversité du régime alimentaire par un indice de Simpson sur les proportions moyennes des cinq classes alimentaires les mieux représentées : poissons, insectes terrestres, larves d'insectes, microcrustacés et débris organiques. L'information sur les traits relatifs à la reproduction (b), (c), (d), (e), (f) et (g) provient pour une grande partie du travail de Ponton & Mérona (1998).

2.4 Echantillonnage des paramètres du milieu

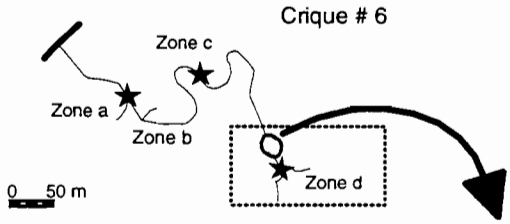
2.4.1 Paramètres temporels

Les niveaux d'eau dans le Sinnamary ont été enregistrés en 1995 et 1996 par trois stations installées par l'équipe d'hydrologie du centre ORSTOM de Cayenne, à Saut Dalles (amont de la retenue), à Petit Saut (aval immédiat du barrage) et à l'entrée de la crique Venus (environ à 25 km à l'aval du barrage). De plus, j'ai régulièrement relevé les hauteurs d'eau au niveau d'échelles hydrologiques installées dans les 20 zones d'échantillonnage (Figure 6).

2.4.2 Paramètres spatiaux

Au niveau de chaque station de pêche, et avant toute perturbation du milieu due à l'activité de pêche, j'ai effectué une mesure de la vitesse du courant de surface, de la turbidité, de la température, du pH, de la concentration en oxygène dissous et de la conductivité. Après la pêche, j'ai réalisé une description fine de l'habitat à l'aide des paramètres suivants : la profondeur, les débris organiques, la végétation, le substrat et le type de pente de la berge.

La méthode a consisté à effectuer des mesures ponctuelles régulières (points d'observation) des paramètres dans la station de pêche échantillonnée (Figure 7). A chaque point d'observation d'une grille composée de carrés de 1 x 1m, j'ai mesuré la profondeur et j'ai relevé l'occurrence des différentes catégories (présence/absence) de débris organiques (cinq catégories : feuilles, bois avec un diamètre ≤ 5 et >5 cm, racines avec un diamètre ≤5 et >5 cm), de végétation (trois catégories : végétation aquatique, végétation terrestre immergée herbacée et végétation terrestre immergée arbustive) et de substrat (six catégories : vase organique, argile, sable, graviers, pierres et blocs). Pour les points les plus proches de la rive, j'ai déterminé le type de la pente (cinq catégories : pente verticale, forte, moyenne, douce et excavation) (Figure 7).



Une station de pêche :

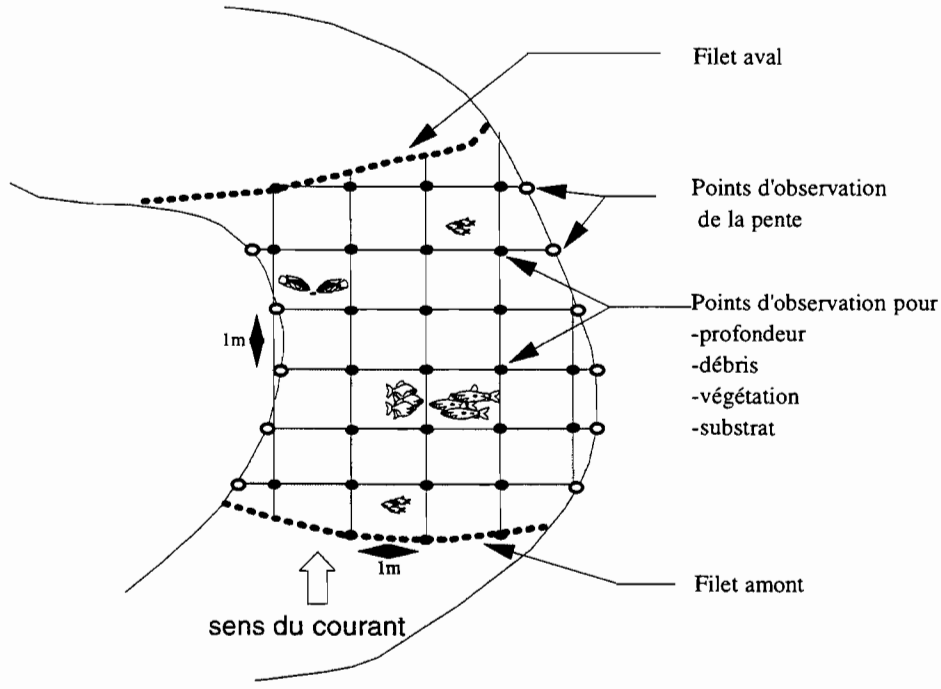


Figure 7: Représentation schématique du protocole utilisé pour chaque pêche, pour décrire les paramètres du milieu. La surface échantillonnée est délimitée par deux filets de vide de maille de 1 mm.

Pour chaque pêche, j'ai également mesuré la distance de la station de pêche au Sinnamary, le linéaire de berge, la longueur totale, la largeur moyenne, la surface et le volume échantillonnés. Finalement, à partir de mesures de la largeur du lit, de la profondeur du lit et de la hauteur d'eau, j'ai déterminé un indice de potentialité d'inondation pour chaque zone de pêche. Cet indice correspond au nombre de jours, au cours des deux années d'échantillonnage, pendant lesquels au moins une partie de la zone est inondée (A1).

2.4.3 Variabilité et conditions d'état de l'habitat

Les variables utilisées pour exprimer la variabilité et les conditions d'état de l'habitat sont décrites dans le Tableau 1. Pour les deux échelles spatiales d'observation (pêche, cf. A2 et A4 et zone, cf. A1) j'ai calculé les variables temporelles à partir des données de hauteur d'eau des 5, 10, 20 et/ou 30 jours précédant chaque pêche. La variabilité spatiale était exprimée par un indice de diversité regroupant les données de profondeur, de substrat, de débris, de végétation et/ou de type de pente.

Tableau 1: Description des variables utilisées pour exprimer la variabilité et les conditions d'état de l'habitat. NJ: nombre de jours.

Echelle	Variables temporelles (hydrologie)		Variables Spatiales	
	Variabilité	Etat	Variabilité	Etat
Pêche A2 et A4	Variance	Moyenne	Profondeur Débris Végétation Substrat Pente	Turbidité Linéaire de berge Longueur totale Largeur moyenne Distance au Sinnamary Volume Surface
Zone A1	Variance	Moyenne Minimum Maximum NJ>cote donnée	Débris Végétation Substrat	Idem ci dessus + Indice de potentialité d'inondation

3. Résultats

3.1 Structure des peuplements de jeunes poissons du Sinnamary (A1 et A2)

Au total, 34790 jeunes individus représentant 73 taxons (69 espèces distinctes), 25 familles et six ordres ont été capturés dans les 200 échantillons (A1). Parmi ces taxons, beaucoup sont peu représentés (Figure 8). Ainsi, dans plus de 80% des échantillons, 20% des individus capturés contribuent à la moitié de la richesse spécifique (A2).

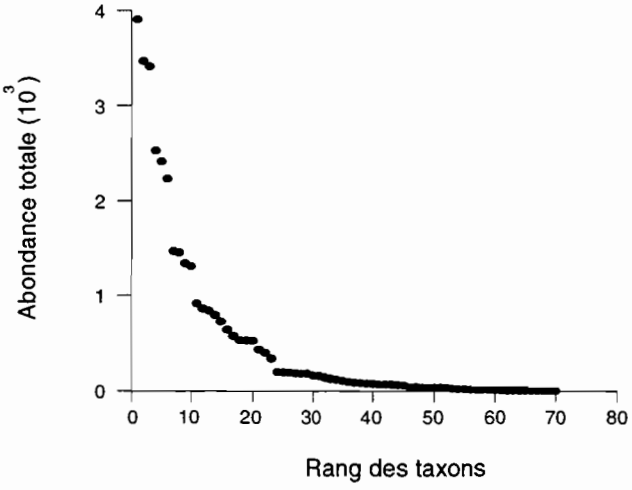


Figure 8: Diagramme rang-fréquence des 73 taxons capturés dans les 200 échantillons amont et aval.

Les Characiformes et les Perciformes sont les deux ordres les mieux représentés avec respectivement 66% et 26% des individus. Les proportions dans les deux secteurs étudiés ne sont cependant pas identiques. Les Characiformes représentent en effet 82% des individus capturés à l'amont alors qu'à l'aval ils ne comptent que pour 49%. Les proportions sont inversées pour les Perciformes qui sont beaucoup plus nombreux à l'aval qu'à l'amont (43% et 11% respectivement).

Dans le secteur amont, les taxons les plus fréquemment rencontrés sont Curimatidae spp., *Moenkhausia oligolepis*, *Hoplias* spp., *Moenkhausia collettii*, *Krobia guianensis* et *Pseudopristella simulata.* Dans le secteur aval, les taxons les plus abondants sont *Eleotris amblyopsis*, *Krobia guianensis*, *Moenkhausia hemigrammoides*, *Crenicichla saxatilis*, *Hoplias* spp. et *Moenkhausia chrysargyrea.*

Malgré des surfaces et des volumes totaux échantillonnés plus importants dans le secteur aval, plus d'individus ont été collectés dans le secteur amont (A2) (Tableau 1). Cependant, le

nombre moyen d'individus par pêche n'est pas significativement différent entre les deux secteurs (test t, $p = 0.599$). De plus, le nombre de taxons rencontrés dans les deux secteurs est sensiblement identique (59 à l'amont et 60 à l'aval) mais le nombre moyen de taxons par pêche est significativement supérieur dans le secteur amont (test t, $p = 0.016$) (A2).

Tableau 2: Composition faunistique des 200 pêches des secteurs amont et aval. Avec N: nombre et Moy: moyenne.

	Amont	Aval	Total
N pêches	100	100	200
Volume échantillonné (m^3)	1622	2914	4536
Surface échantillonnée (m^2)	4649	5865	10514
N ordres	6	6	6
N familles	19	22	24
N individus	18234	16556	34790
N taxons	59	60	73
Moy N taxons par pêche	16	14	15
Moy N individus par pêche	182	166	174

3.2 Traits biologiques (A3 et A4)

Pour les 57 taxons les mieux représentés dans les échantillons, il existe une variabilité importante de traits biologiques entre les différents taxons étudiés pour 1) la longueur standard maximale (de 21 mm pour *Poecilia parae* à 830 mm pour *Hoplias aimara*) ; 2) la longueur standard minimale à la première maturité (de 12 mm pour *Poecilia parae* à 400 mm pour *Hoplias aimara*) ; 3) le diamètre moyen des oocytes matures (de 0.2 mm pour *Eleotris amblyopsis* à 3.4 mm pour *Synbranchus marmoratus*) et 4) la fécondité (de 3 individus par ponte pour *Poecilia parae* à plus de 80000 œufs par ponte pour *Leporinus* spp.). Par contre, les autres traits présentent des variations interspécifiques moins prononcées: 1) les jeunes de plus de 50% des taxons ont une alimentation diversifiée (Indice de Simpson ≥ 0.50) ; 2) la plupart des poissons ont des silhouettes intermédiaires avec notamment une hauteur relative comprise entre 0.20 et 0.40 (Figure 9) ; 3) plus de 80% des taxons se reproduisent pendant la moitié de l'année ou plus, et 4) 57% des taxons ne dispensent pas de soins parentaux après la ponte, 93% d'entre eux étant des Characiformes.

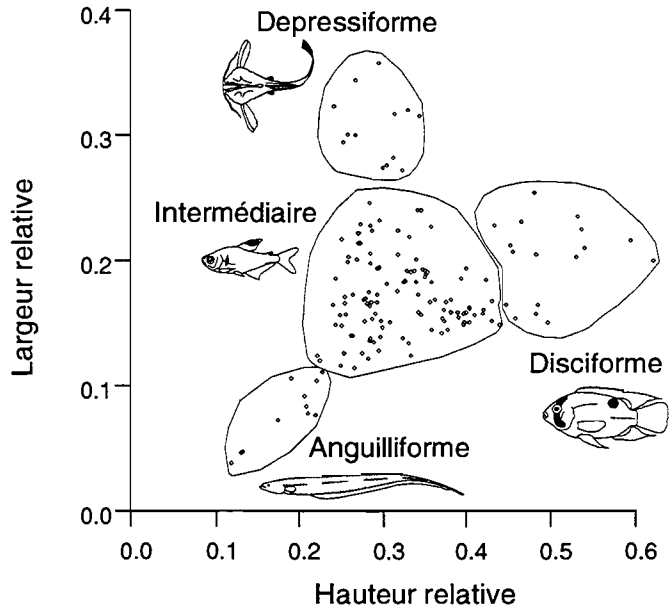


Figure 9: Largeur relative du corps en fonction de sa hauteur relative pour les taxons de jeunes poissons du Sinnamary. Les quatre groupes ont été déterminés par une analyse complète de cluster (pour plus de détails et pour la composition faunistique des différents groupes cf A3).

A partir des traits liés à la reproduction des 57 taxons étudiés, j'ai déterminé trois stratégies extrêmes correspondant aux stratégies "équilibre, opportuniste et périodique" définies par Winemiller (1989) au Venezuela (Figure 10) (A4). Les poissons qui présentent les caractéristiques de la stratégie d'équilibre sont des taxons dont la taille maximale potentielle et celle à la première maturité sont grandes et qui présentent un investissement important en soins parentaux sur de gros œufs peu ou moyennement abondants (par exemple *Gymnotus* spp., *Synbranchus marmoratus*, *Krobia guianensis*). Les poissons de la stratégie des opportunistes sont des taxons dont la taille maximale et à la première maturité sont petites et qui pondent de nombreux œufs de petite taille sur lesquels ils ne dispensent aucun soin parental. De plus, 75% des taxons appartenant à ce groupe pondent en continu au cours de l'année (par exemple *Gasteropelecus sternicla*, *Pseudopristella simulata*, *Hemigrammus ocellifer*) (A1). La stratégie des périodiques regroupe les taxons dont la taille maximale et à la première maturité sont grandes, qui pondent de petits œufs en très grand nombre et qui dispensent des soins parentaux limités. De plus, 50% de ces taxons se reproduisent effectivement après des périodes de hautes eaux saisonnières (par exemple *Leporinus* spp., *Acestrorhynchus* sp., *Astyanax bimaculatus* ou *Moenkhausia oligolepis*) (A1).

Outre les trois stratégies extrêmes d'équilibre, d'opportuniste et de périodique, j'ai aussi identifié des taxons qui présentent des stratégies intermédiaires. Ainsi, *Hemiodopsis*

quadrimaculatus, *Hoplias* spp. et *Rhamdia quelen* ont une fécondité trop élevée pour appartenir à la stratégie d'équilibre et font donc partie d'une stratégie "équilibre-périodique" (Figure 10). De même, *Moenkhausia chrysargyrea* présente des caractéristiques intermédiaires aux stratégies opportuniste et périodique.

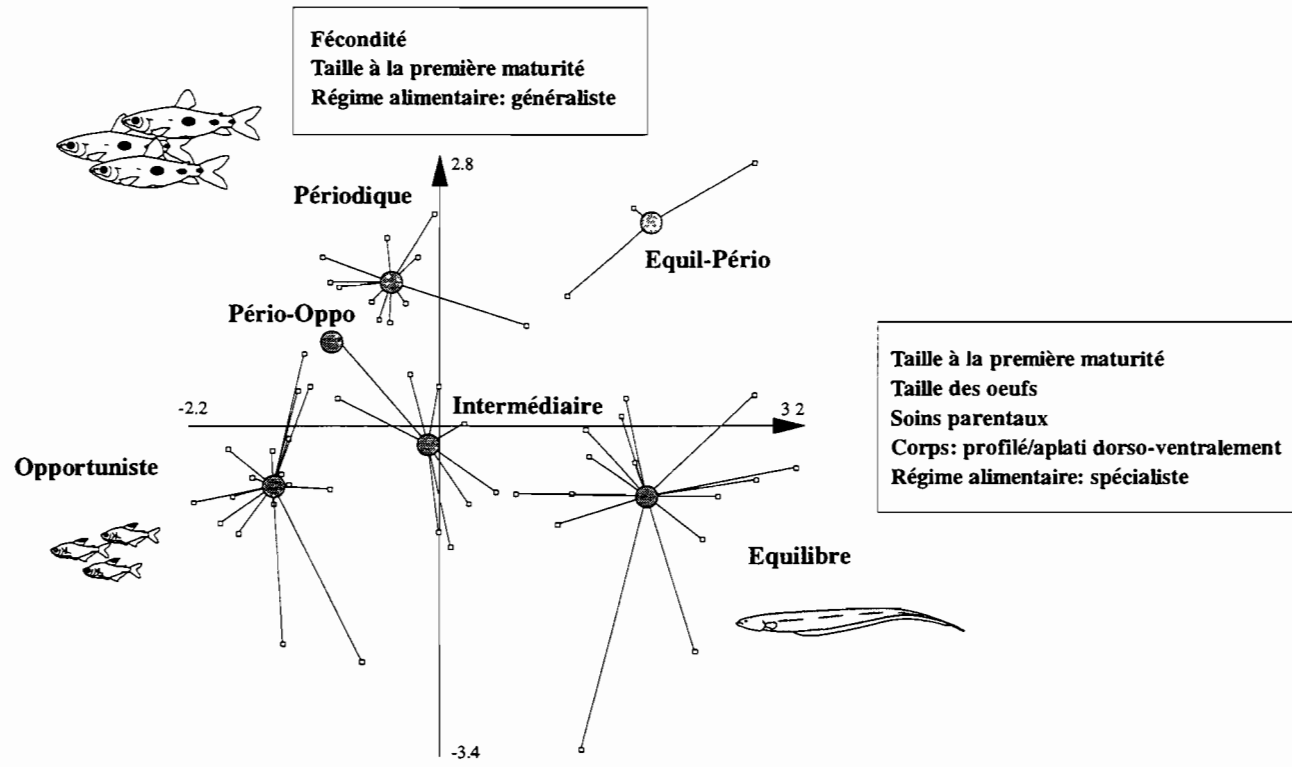


Figure 10: Coordonnées des taxons sur le premier plan de l'ACP réalisée à partir des traits d'histoire de vie. Les étoiles représentent chacune une combinaison de traits (c'est-à-dire une stratégie). Pour chaque stratégie, chaque taxon est relié au centre de l'étoile qui est à la moyenne des coordonnées des taxons appartenant à cette stratégie. Le régime alimentaire et la forme du corps des différentes stratégies sont aussi indiqués (A4).

J'ai aussi montré que les jeunes poissons de taxons de la stratégie des équilibres (sauf *Krobia guianensis* et *Cleithracara maronii*) ont des corps plus profilés et une alimentation plus spécialisée que les périodiques ou les opportunistes (A4).

L'approche par les traits biologiques a par ailleurs permis de mettre en évidence des différences entre les secteurs situés à l'amont et à l'aval du barrage. Par exemple les taxons de petites tailles qui pondent de petits œufs peu nombreux mais qui dispensent des soins parentaux sur leur progéniture sont mieux représentés à l'aval du barrage qu'a l'amont (Tableau 3).

Tableau 3: Comparaison par Tests t (dl = 99) entre les secteurs amont et aval des moyennes des traits concernant la diversité du régime alimentaire (ALIM, carré), la hauteur relative du corps (HCR), la longueur standard minimale à la première maturité (LS1M, log), la longueur de la période reproduction (LPR, carré), le diamètre moyen des oocytes matures (DMO, racine carrée), la fécondité moyenne (FM, log) et les soins parentaux (SP).

Traits	Moyenne			
	Amont	Aval	t	p
ALIM	0.289	0.292	0.513	0.609
HCR	0.259	0.257	-0.525	0.601
LS1M	1.801	1.754	-2.886	0.005
LPR	86.075	93.387	5.016	0.000
DMO	0.991	0.960	-2.056	0.042
FM	3.245	3.124	-3.314	0.001
SP	0.421	0.581	6.148	0.000

Enfin, les stratégies les mieux représentées à l'amont sont celles des périodiques et des opportunistes avec 42 et 30% des individus totaux respectivement, alors qu'à l'aval, les équilibres, les intermédiaires et les opportunistes sont les plus abondants avec 27, 26 et 24% des individus respectivement.

3.3 Relation habitat-poissons

3.3.1 Variation des densités de jeunes poissons en fonction du temps et de l'espace (A1)

Plus des deux tiers des taxons rencontrés dans ce travail présentent des variations de leur densité avec le temps et/ou l'espace et répondent de manière différente à ces deux dimensions, suivant qu'ils se trouvent en amont ou en aval du barrage. Ainsi dans le secteur amont, 52% des premiers stades de développement et 79% des juvéniles montrent des variations significatives de leurs densités avec le temps et/ou l'espace alors que dans le secteur aval ces pourcentages sont de 70 et 61% respectivement. Les premiers stades de développement et les juvéniles montrant des variations de densités avec le temps sont principalement des Characiformes dans les deux secteurs d'étude. Les variables hydrologiques et les variables telles que l'oxygène dissous, la turbidité et la structure de l'habitat (linéaire de berge, quantité

d'excavations et richesse en débris, végétation et substrat) ont permis d'expliquer les variations de densités dans le temps et dans l'espace de la plupart des taxons (cf. A1 et §3.3.3.2, 3.3.3.3 et 3.3.3.4).

3.3.2 Structure des communautés et variabilité de l'habitat

3.3.2.1 Richesse spécifique en fonction de la variabilité spatio-temporelle (A2)

Les données obtenues sur la richesse spécifique et la variabilité du milieu ne permettent pas de valider les prédictions du Patch Dynamics Concept. Quels que soient l'échelle de variabilité temporelle, le jeu de données considéré (amont ou aval de la retenue), l'unité taxonomique (Characiformes ou non-Characiformes) ou le stade de développement considérés (premiers stades de développement, premiers stades de juvéniles et derniers stades de juvéniles), la richesse spécifique ne montre pas de relation en dôme en fonction de la variabilité temporelle et la richesse expliquée par la variabilité spatiale est faible (cf Figure 11 pour un exemple).

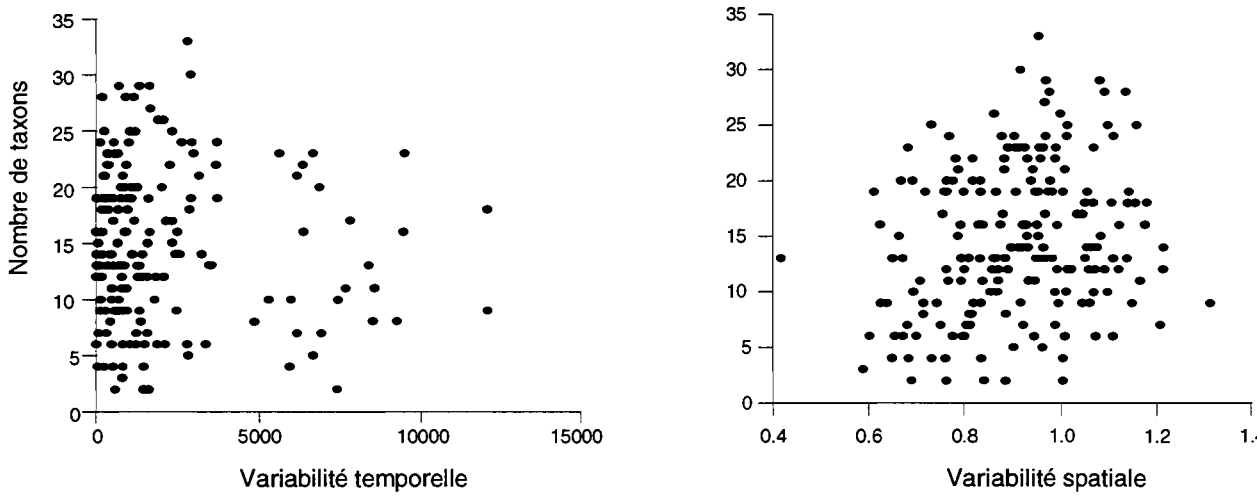


Figure 11: Un exemple typique de la représentation de la richesse spécifique en fonction de la variabilité de l'habitat considérant les 200 pêches et pour la période hydrologique de 30 jours avant la pêche (les mêmes tendances sont observées avec les jeux de données considérant séparément les deux secteurs, les Characiformes et les non-Characiformes et les trois groupes ontogénétiques). Dans cet exemple, la richesse en taxons n'est pas significativement corrélée à la variabilité temporelle et la variabilité de la richesse spécifique expliquée par la variabilité spatiale est faible: $r^2 = 0.044$ et $p = 0.003$.

3.3.2.2 Traits biologiques en fonction de la variabilité spatio-temporelle (A4)

Dans l'étude testant les hypothèses du River Habitat Templet Concept sur le jeu de données total (n=200), deux traits montrent la relation négative prédite avec la variabilité temporelle : la longueur standard minimale à la première maturité et le diamètre moyen des oocytes matures (Tableau 4). La longueur standard minimale à la première maturité montre aussi la relation positive attendue avec la variabilité spatiale. Au contraire, la longueur de la période de reproduction contredit la relation négative prédite avec la variabilité spatiale.

Tableau 4: Coefficients de corrélation de Pearson et probabilités associées entre chaque trait biologique et la variabilité temporelle et spatiale. Avec Tot: 200 échantillons, Am: 100 échantillons amont et Av: 100 échantillons aval. Cf Tableau 3 pour le code et les transformations des traits biologiques.

	Variabilité temporelle						Variabilité spatiale					
	Tot	p	Am	p	Av	p	Tot	p	Am	p	Av	p
ALIM	0.005	ns	0.080	ns	-0.063	ns	0.132	ns	0.291	0.004	0.009	ns
HCR	-0.029	ns	0.198	ns	-0.210	0.036	0.051	ns	0.093	ns	0.014	ns
LS1M	-0.157	0.028	-0.203	0.046	-0.028	ns	0.248	0.000	0.213	0.036	0.289	0.004
LPR	0.114	ns	-0.033	ns	0.082	ns	0.163	0.022	0.293	0.003	0.070	ns
DMO	-0.171	0.016	-0.331	0.001	-0.065	ns	0.135	ns	-0.216	0.033	0.314	0.001
FM	0.009	ns	0.103	ns	0.055	ns	0.085	ns	0.374	0.000	-0.227	0.023
SP	0.131	ns	-0.313	0.002	0.201	0.045	-0.025	ns	-0.109	ns	0.012	ns

Les résultats des analyses considérant séparément le jeu de données amont et aval montrent des tendances différentes. Seuls les échantillons de l'amont confirment les relations décrites ci-dessus avec le jeu de données total. De plus, à l'amont, le trait "soins parentaux" confirme la relation négative attendue avec la variabilité temporelle. Au contraire, avec la variabilité spatiale, la diversité du régime alimentaire, le diamètre moyen des oocytes matures et la fécondité moyenne montrent des tendances opposées aux prédictions. Dans les échantillons de l'aval, la relation entre les soins parentaux et la variabilité temporelle est inverse à la tendance attendue alors que la relation entre la hauteur relative du corps et la variabilité temporelle confirme les prédictions. De plus, et contrairement aux échantillons de l'amont, le diamètre moyen des oocytes matures est positivement corrélé et la fécondité moyenne négativement corrélée à la variabilité spatiale (Tableau 4).

3.3.3 Structure des communautés et conditions d'état de l'habitat

3.3.3.1 Importance relative de la variabilité et des conditions d'état de l'habitat (A2 et A4)

Les résultats de mes travaux soulignent l'importance de la variabilité spatio-temporelle en association avec les variables d'état pour expliquer et prédire la richesse spécifique et pour expliquer la distribution des traits biologiques des taxons rencontrés dans les échantillons. Ainsi, les modèles que j'ai développés permettent d'expliquer 36% de la variabilité de la richesse spécifique des 200 pêches et jusqu'à 47% des 100 pêches du secteur amont (toutes unités taxonomiques confondues) (Tableau 5). Dans ces conditions, j'ai montré une relation positive entre la richesse spécifique et la variabilité temporelle et spatiale dans les échantillons amont (Tableau 5).

	Amont		Aval	
r^2	0.473		0.237	
p	<0.001		<0.001	
	signe	p	signe	p
Constante		ns	+	0.000
Turbidité de l'eau (log)		ns	-	0.005
Linéaire de berge	+	0.000	+	0.000
Largeur moy (log)	+	0.037		ns
Hauteur d'eau moy	+	0.001		ns
Variabilité spatiale (log)	+	0.001		ns
Variabilité temporelle (log)	+	0.007		ns

Tableau 5: Régression multiple pas à pas de la richesse spécifique dans les criques amont et aval en fonction des variables exprimant la variabilité et l'état de l'habitat pour des périodes hydrologiques de 30 jours avant échantillonnage. r^2: coefficient de détermination, F: valeur du ratio F et p: la probabilité associée aux modèles entiers et à chaque terme des modèles. (log) indique si la variable a été transformée en logarithme (A2).

Des tests de Monte Carlo m'ont permis de tester la robustesse de ces modèles. J'ai pu ainsi prédire 31% (200 pêches) et jusqu'à 37% (secteur amont toutes unités taxonomiques confondues) de la variabilité de la richesse spécifique (Figure 12).

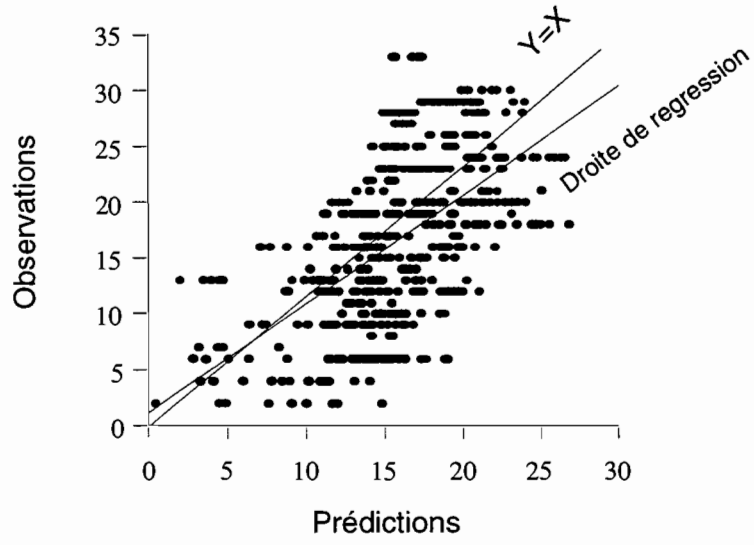


Figure 12: Observations versus prédictions de la richesse spécifique après test de Monte Carlo (modèle réalisé sur la moitié du jeu de données et le test sur l'autre moitié) sur le modèle prenant en compte la variabilité de l'habitat et les paramètres d'état pour les échantillons amont avec: $y = 0.963(\pm 0.112)x$, $r^2 = 0.370$ et $p < 0.001$, (l'intervalle de confiance de 95% est donné entre parenthèses).

De même, en considérant la variabilité avec les conditions d'état de l'habitat, j'ai expliqué une plus grande part de la variabilité des traits biologiques (14 à 34% contre au maximum 13% avec uniquement la variabilité de l'habitat) dans le secteur amont (Tableau 6).

Tableau 6: Régressions multiples pas à pas des traits biologiques dans les échantillons amont en fonction de la variabilité et de l'état de l'habitat. r^2: coefficient de détermination, F: valeur du ratio F et p: la probabilité associée aux modèles entiers. Pour chaque variable de l'habitat, j'ai indiqué le signe de la relation et sa probabilité associée (ns: p > 0.05). (Cf. Tableau 3 pour les codes et les transformations des traits).

Statistiques	Traits biologiques						
et variables d'habitat	ALIM	HCR	LS1M	LPR	DMO	FM	SP
r^2	0.215	0.327	0.138	0.158	0.338	0.255	0.288
P	<0.001	<0.001	0.008	<0.001	<0.001	<0.001	<0.001
Variabilité temporelle	ns	ns	- 0.045	ns	- 0.001	+ 0.004	- 0.003
Variabilité spatiale	ns	+ 0.015	ns	+ 0.006	- 0.013	ns	ns
Niveau d'eau moyen	ns	+ 0.005	ns	ns	ns	ns	ns
Oxygène de l'eau	ns	- 0.004	+ 0.027	ns	+ 0.000	ns	+ 0.002
Turbidité de l'eau	ns	ns	- 0.044	ns	- 0.001	ns	- 0.000
Linéaire de berge	ns	- 0.005	ns	- 0.006	ns	ns	ns
Largeur moyenne	+ 0.000	ns	+ 0.005	ns	ns	+ 0.000	ns
Profondeur moyenne	ns	- 0.000	ns	ns	ns	ns	ns

3.3.3.2 Hydrologie

Les niveaux d'eau avant chaque campagne de pêches se sont révélés être très important pour expliquer les variations temporelles des densités des jeunes poissons et pour décrire et prédire la richesse spécifique. J'ai ainsi démontré 1) à l'amont, pour des périodes de 10, 20 ou 30 jours avant la campagne d'échantillonnage, une relation positive entre la densité des premiers stades de développement et la hauteur d'eau moyenne et le nombre de jours pendant lesquels la cote 200 cm était dépassée, et entre la densité des juvéniles et le minimum et la moyenne des hauteurs d'eau (A1), 2) à l'aval une relation positive entre la densité des premiers stades de développement et le nombre de jours pendant lesquels les cotes 500, 600, 700 et/ou 800 cm étaient dépassées (A1) et 3) une relation positive entre le nombre de taxons présents dans les échantillons amont et la hauteur d'eau moyenne 5, 10, 20 et 30 jours avant la pêche (A2).

3.3.3.3 Qualité de l'eau

J'ai montré l'importance de paramètres tels que la concentration en oxygène dissous ou la turbidité de l'eau sur la structure des communautés de jeunes poissons. Ainsi, à l'aval du barrage, de nombreux Characiformes sont inféodés à des eaux claires et bien oxygénées (A1) et la richesse en taxons diminue avec une augmentation de la turbidité de l'eau (A2). A l'amont du barrage, les taxons présentant les caractéristiques biologiques correspondant à la stratégie des opportunistes se trouvent dans des milieux plus turbides et moins oxygénés que les taxons correspondant à la stratégie d'équilibre (A4).

3.3.3.4 Linéaire de berge

Dans la crique côtière de la Malmanoury, j'ai montré que de nombreux taxons sont inféodés à des habitats présentant un linéaire de berge important (A5). De même, la distribution spatiale de la densité d'un grand nombre de non-Characiformes dans les échantillons situés à l'amont de la retenue de Petit Saut est déterminée en partie par la présence d'un linéaire de berge important (A1). Enfin, dans le Sinnamary, j'ai démontré qu'il existe une relation positive entre la diversité spécifique et la longueur du linéaire de berge quels que soient l'échelle de variabilité temporelle, le jeu de données considéré (amont ou aval de la retenue) et l'unité taxonomique (Characiformes ou non-Characiformes) (A2).

4. Discussion

4.1 Caractéristiques des peuplements de poissons du Sinnamary

La très grande richesse spécifique et biologique des poissons du Sinnamary est sans commune mesure à celle observée en zones tempérées (Mahon, 1984 ; Wootton, 1984 ; Tito de Morais & Lauzanne, 1994 ; mon travail). Avec 73 taxons inventoriés, mon travail confirme le rôle de nurseries des criques pour plus de 60% des espèces du Sinnamary. Comme dans la plupart des cours d'eau d'Amérique du Sud, les Characiformes et les Perciformes dominent les communautés du Sinnamary. A l'amont de la retenue de Petit Saut, les proportions de Characiformes et de Perciformes (80 et 10% respectivement) sont très similaires à celles observées en 1994 par Ponton & Copp (1997). Par contre, j'ai observé plus de Characiformes à l'aval de Petit Saut qu'en 1994, c'est-à-dire juste après la mise en eaux du barrage (cf Ponton & Copp, 1997). Ce résultat soutient l'hypothèse de Ponton *et al.* (en préparation) selon laquelle le succès de la reproduction des Characiformes aurait augmenté rapidement après une forte diminution de celui-ci causée par la fermeture du barrage.

Mon travail a permis de décrire trois grandes stratégies vitales pour les espèces de poissons des affluents du Sinnamary. Ces trois groupes de combinaisons de traits biologiques correspondent aux stratégies d'équilibre, d'opportuniste et de périodique définies par Winemiller (1989) pour les poissons du Llanos vénézuélien. Dans le Sinnamary, les Siluriformes, les Gymnotiformes et les Perciformes Cichlidae sont les principaux représentants de la stratégie d'équilibre alors que les Characiformes sont en majorité opportunistes ou périodiques. Dans le Llanos vénézuélien, les périodiques sont en proportion beaucoup plus nombreux et les opportunistes beaucoup moins nombreux que dans le Sinnamary. Ceci est à mettre en relation avec les variations hydrologiques saisonnières plus marquées dans le Llanos (Ponton & Mérona, 1998). En accord avec les hypothèses de Winemiller & Rose (1992), les communautés de poissons à l'amont du barrage (conditions plus ou moins prévisibles) sont dominées par les périodiques. Par contre, les opportunistes ne sont pas les plus abondants à l'aval du barrage (conditions imprévisibles) comme on aurait pu l'attendre. Deux années d'études seulement après la mise en eaux du barrage ne sont probablement pas suffisantes pour détecter une dominance des opportunistes.

4.2 Application du cadre théorique aux jeunes poissons du Sinnamary

Les prédictions du Patch Dynamics Concept ne sont pas validées par mon travail mais celles de l'Habitat Templet Concept sont partiellement confirmées. Ainsi, je n'ai pas observé une richesse maximale pour une variabilité temporelle intermédiaire et une variabilité spatiale maximale. Cette étude est le onzième test sur treize qui rejette les prédictions du Patch Dynamics Concept en système lotique (cf Statzner *et al.*, 1997). Une hypothèse pour expliquer ce rejet est que, dans ces milieux, les paramètres physiques induisent une telle instabilité que les interactions biotiques ne seraient que marginales. L'hypothèse du Patch Dynamics Concept qui prévoit une réduction du nombre d'espèces en milieu stable ne serait donc pas adaptée aux systèmes lotiques. De plus, le nombre important d'espèces rares dans les communautés d'animaux lotiques (Statzner & Resh, 1993 ; ce travail) réduit la fiabilité des modèles visant à prédire la diversité des espèces.

La moitié des relations entre traits biologiques et variabilité de l'habitat des criques amont et aval sont significatives, mais plus d'un tiers contredisent les prévisions du Habitat Templet Concept. Ainsi, en accord avec les prédictions, la taille minimale à la première maturité, le diamètre moyen des oocytes et la hauteur relative du corps des jeunes stades diminuent avec une augmentation de la variabilité temporelle et la taille minimale à la première maturité et le diamètre moyen des oocytes augmente avec la variabilité spatiale. Certains traits ne montrent aucune tendance avec la variabilité du milieu. Ceci n'est pas surprenant et a déjà été souligné par d'autres travaux (Statzner *et al.*, 1997 ; Townsend *et al.*, 1997a). Les prévisions de Townsend & Hildrew (1994) ont été développées pour un nombre important d'organismes aquatiques. Or, les combinaisons de traits biologiques peuvent être très diverses selon les groupes et même selon les espèces (Resh *et al.*, 1994). En effet, ces combinaisons sont contraintes par le génome qui varie d'une espèce à l'autre (Southwood, 1988). De plus, chaque espèce n'est pas supposée posséder toutes les caractéristiques biologiques qui confèrent à ses populations des capacités de résilience ou de résistances face aux perturbations. Ainsi, à partir du moment où un trait assure le succès d'une espèce dans un milieu instable, les autres traits ne sont plus forcément nécessaires. Enfin, la contrainte de la taille sur d'autres traits et les compromis entre certains traits que j'ai détectés dans ce travail sont sûrement à l'origine de combinaisons inattendues (A4).

4.3 Structure des communautés et variabilité plus conditions d'état du milieu

Même si les prédictions du Patch Dynamics Concept ne sont pas validées et si celles du Habitat Templet Concept ne sont que partiellement confirmées, mon travail souligne l'importance de la variabilité de l'habitat une fois les paramètres d'état pris en compte, pour expliquer et/ou prédire la variabilité de la structure des communautés de jeunes poissons. Ainsi, j'ai pu prédire dans les échantillons amont, 37% et expliquer 47% de la variabilité de la richesse spécifique et jusqu'à 34% de la variabilité biologique (A2 et A4).

Dans ces conditions, j'ai montré que la richesse en taxons augmente avec la variabilité temporelle à l'amont du barrage. Contrairement à ce résultat, d'autres études ont montré un effet négatif des variations du régime hydrologique sur la richesse spécifique de poissons (Horwitz, 1978) et notamment sur les premiers stades de développement (Schlosser, 1985 ; Finger & Stewart, 1987). Cependant, ces études n'ont pas considéré simultanément les variations hydrologiques et d'autres paramètres du milieu qui peuvent potentiellement atténuer l'impact des fortes variations hydrologiques sur la richesse en poissons. Par exemple, dans mes échantillons, la richesse spécifique augmente avec la variabilité spatiale du milieu. Un milieu diversifié présente potentiellement des refuges qui permettent aux organismes de résister aux perturbations (Townsend & Hildrew, 1994). L'importance de ces abris en période de crue a été démontrée pour les poissons dans des hydrosystèmes Nord Américains (Fausch & Bramblett, 1991 ; Pearson *et al.*, 1992). L'influence positive de la diversité spatiale du milieu sur la richesse en poissons a été confirmée par les travaux de Gorman & Karr (1978) et d'Angermeier & Schlosser (1989) dans les rivières du Panama, d'Hugueny (1990) dans le fleuve Niger et par mon travail dans les deux criques côtières de Guyane Française (A5). Parallèlement, j'ai montré que la distribution de nombreux taxons de jeunes poissons du Sinnamary dépend de la richesse du milieu en débris, végétation et substrat (A1).

4.4 Structure des communautés et conditions d'état du milieu

A plusieurs reprises dans cette étude, j'ai mis en évidence l'importance de paramètres d'état de l'habitat tels que le niveau de l'eau, la concentration en oxygène dissous, la turbidité de l'eau et/ou la longueur du linéaire de berge, pour expliquer la distribution spatio-temporelle des taxons et décrire en association avec la variabilité de l'habitat, la richesse spécifique et la distribution des traits biologiques des jeunes poissons rencontrés dans le Sinnamary. Ainsi, la relation positive entre le niveau des eaux et d'une part, la densité de nombreuses espèces de

jeunes poissons et d'autre part, leur richesse spécifique, confirme l'importance des zones d'inondation pour de nombreuses espèces de poissons. En effet, ces zones sont actuellement reconnues comme étant une composante essentielle des systèmes fluviaux (Lowe-McConnel, 1979 ; 1987 ; Welcomme, 1979 ; 1985 ; Finger & Stewart, 1987 ; Junk *et al.*, 1989 ; Ward, 1989 ; Bayley, 1991 ; Bayley & Li, 1992 ; Amoros & Petts, 1993). Ces zones procurent de nouveaux habitats potentiels dans lesquels les organismes aquatiques trouvent de la nourriture, des abris et des sites favorables à la reproduction (Finger & Stewart, 1987 ; Bonetto *et al.*, 1989 ; Bayley & Li, 1992 ; Junk & Da Silva, 1995). Mes résultats confirment aussi la forte influence du niveau de l'eau du chenal principal d'une rivière neotropicale sur la structure des communautés de jeunes poissons dans les zones adjacentes. En effet, la surface d'inondation dans les zones annexes des criques est largement sous la dépendance du niveau de l'eau du Sinnamary (A2). Ainsi, la montée du niveau de l'eau dans le Sinnamary peut entraîner la migration des adultes qui viendraient se reproduire dans les criques ou dans les zones d'inondation associées comme cela a été démontré dans d'autres systèmes (Welcomme, 1979 ; 1985 ; Lowe-McConnel, 1987 ; Bayley, 1988 ; Munro, 1990 ; Boujard, 1992 ; Schwassmann, 1978 ; 1992 ; Val & Almeida-Val, 1995). Par exemple, les Characiformes sont connus pour se reproduire pendant la saison des pluies en relation avec la montée du niveau des eaux (Lowe-McConnel, 1987 ; Munro, 1990) et en effet, 90% des espèces appartenant à la stratégie des périodiques sont des Characiformes dans le Sinnamary (A4).

L'importance de l'oxygène dissous et de la turbidité de l'eau sur la structure des communautés de jeunes poissons du Sinnamary est soulignée à plusieurs reprises dans mon travail. Il est bien connu qu'une faible concentration en oxygène et une forte turbidité de l'eau peuvent causer des comportements de stress et limiter la distribution et l'activité des poissons (Matthews, 1998). En milieu intertropical, de nombreux poissons répondent à une diminution de l'oxygène par une migration rapide (Lowe-McConnel, 1987). D'autres sont capables de développer des adaptations telles que des protubérances dermiques de la lèvre inférieure (Casciotta, 1993) ou une respiration aérienne (Kramer & McClure, 1982). En eaux turbides, une diminution de la capacité visuelle peut provoquer un entraînement passif des jeunes poissons par les forces du courant (Olivier, 1992) et/ou une diminution de l'activité alimentaire d'espèces qui chassent à vue (par exemple les Characiformes, Goulding, 1980). Dans le Sinnamary, la présence de certains taxons dans des milieux peu oxygénés et/ou turbides pourrait être le résultat soit d'un compromis entre le stress lié à la vie dans ces

milieux et par exemple les risques de prédation plus importants en milieu oxygéné et clair, soit d'une combinaison de traits biologiques correspondant à la stratégie des opportunistes capables de survivre dans de tels milieux. Enfin, l'influence positive du linéaire de berge souligne l'importance des zones riveraines qui procureraient des abris et de la nourriture aux poissons (cf. Schiemer *et al.*, 1991 ; Schiemer & Zalewski, 1992 ; Araujo-Lima *et al.*, 1995 ; Tito de Morais *et al.,* 1995) et pourraient aussi atténuer l'impact des perturbations sur les jeunes poissons.

4.5 Milieux soumis aux perturbations du barrage de Petit Saut

Mon travail souligne à plusieurs reprises des résultats différents ou même contradictoires entre les échantillons amont et aval. Ainsi, les taxons communs aux deux secteurs présentent une distribution spatio-temporelle différente selon le secteur d'étude (A1). De même, à l'aval, je n'ai expliqué qu'une part très faible de la variabilité de la richesse spécifique à partir des variables du milieu (A2) et les relations entre certains traits biologiques et la variabilité de l'habitat contredisent les tendances observées en milieu naturel (c'est-à-dire à l'amont de la retenue) (A4). Dans les échantillons aval, le nombre de taxons rencontrés est moins important en moyenne par pêche et les taxons présentant de petites tailles (maximale et à la première maturité), de petits œufs en nombre réduit et des soins parentaux sont mieux représentés qu'à l'amont du barrage. Ces résultats sont probablement les conséquences du mode d'exploitation du barrage de Petit Saut. Le régime hydrologique a en effet été sérieusement perturbé dans les criques aval : pendant la saison des pluies, le niveau d'eau moyen est plus bas qu'en conditions naturelles alors que pendant la saison sèche, des lâchers d'eau brutaux produisent de grandes crues artificielles de courte durée. Les différences de la richesse spécifique et de traits biologiques entre les deux secteurs confirment les résultats d'autres travaux : 1) Horwitz (1978) et Schlosser (1985) ont observé une diminution du nombre d'espèces avec une augmentation de l'instabilité du milieu et 2) Schlosser (1987 ; 1990) et Heins (1991) ont observé des traits biologiques particuliers qui permettent une meilleure survie des espèces dans un milieu instable.

5. Conclusions et perspectives

Les résultats des tests des prédictions du Patch Dynamics Concept et du River Habitat Templet Concept obtenus dans mon travail ouvrent de nombreuses perspectives. Le rejet des prédictions du Patch Dynamics Concept souligne le besoin de nouvelles méthodes pour prédire la diversité faunistique en milieu lotique. Dans ces milieux, ces prédictions sont difficiles car la richesse des communautés est le plus souvent déterminée par les espèces rares (Modukhai-Boltovskoi, 1978 ; Edwards & Brooker, 1982 ; Statzner & Resh, 1993 ; mon travail). Le problème des espèces rares ne concerne pas uniquement les communautés de poissons mais celles des eaux douces en général (Statzner & Resh, 1993) et aussi celles de milieux terrestres et marins (Gaston, 1994). Or, évaluer et maintenir la biodiversité à l'échelle mondiale est au centre des débats en écologie (Heywood & Watson, 1995). Aussi, il est urgent de développer des outils fiables de mesure de la biodiversité.

Mes tests des hypothèses du River Habitat Templet Concept et d'autres travaux récents (Sagnes, 1997 ; Statzner *et al.,* 1994 ; Townsend *et al.*, 1997a) ont montré que certains traits biologiques des espèces (liés à la reproduction, au régime alimentaire et à la forme du corps des jeunes stades ou aux capacités hydrodynamiques) étaient significativement liés aux caractéristiques du milieu. Ces traits biologiques offrent donc des perspectives prometteuses pour évaluer de manière fiable la diversité fonctionnelle des communautés de poissons. De plus, mes résultats concordent avec ceux d'autres études pour dire que le River Habitat Templet Concept est un élément important en écologie d'un point de vue théorique mais aussi appliqué (Charvet *et al.*, 1998).

L'approche par les traits biologiques ouvre aussi d'autres perspectives. Ainsi, les trois stratégies de vie de Winemiller (1989) rencontrées dans le Sinnamary permettront de vérifier sur le long terme, les hypothèses selon lesquelles les milieux instables (par exemple les criques à l'aval du barrage) contiendraient essentiellement des espèces opportunistes (Winemiller & Rose, 1992 ; Poff & Allan, 1995), les milieux plus ou moins prévisibles (par exemple les criques à l'amont de la retenue) contiendraient essentiellement des espèces périodiques, et les milieux stables (par exemple la retenue) des espèces de la stratégie d'équilibre (Winemiller & Rose, 1992) (Figure 13). Cette approche sur les traits biologiques et leurs combinaisons permettra de s'affranchir du cadre taxonomique propre à la Guyane. Les résultats obtenus seront ainsi transposables à d'autres systèmes soumis à des perturbations naturelles et anthropiques.

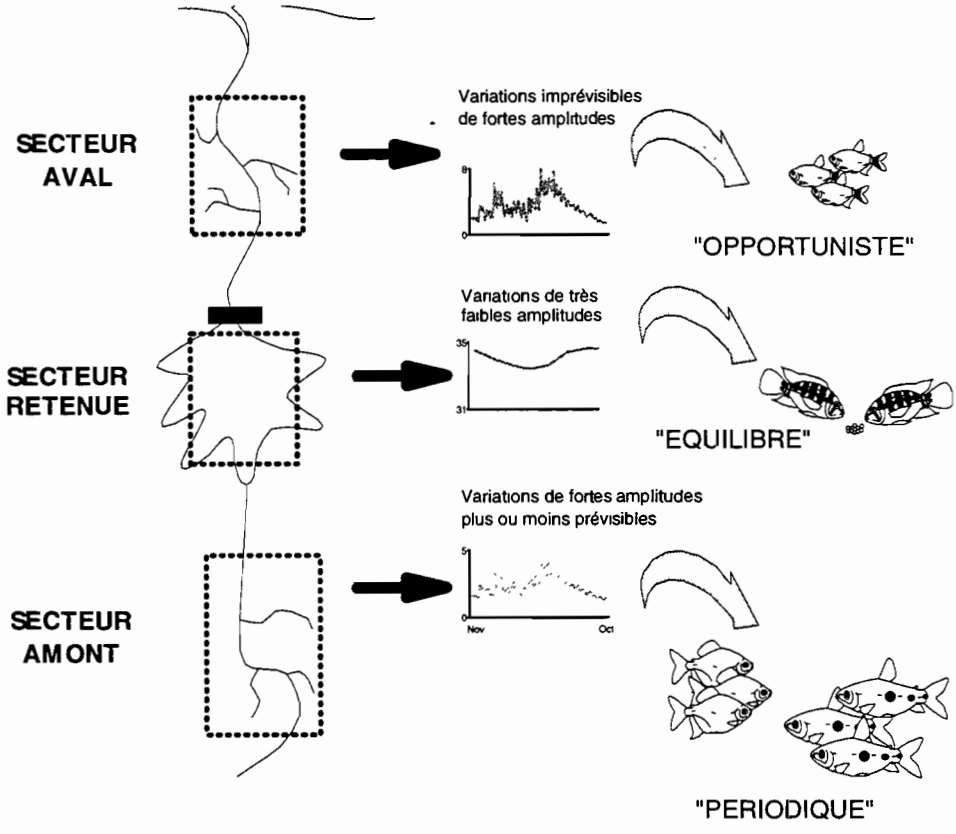
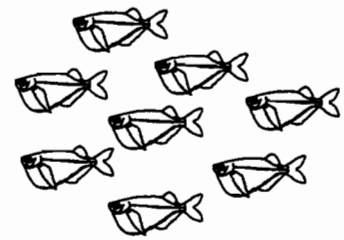


Figure 13: Distribution hypothétique des stratégies de vie suivant les conditions hydrologiques des trois secteurs amont, retenue et aval du barrage de Petit Saut.

Les connaissances acquises ces dernières années sur la faune piscicole du Sinnamary sont considérables et uniques en milieu tropical. Ces travaux sur les communautés d'adultes (Tito de Morais & Lauzanne, 1994 ; Tito de Morais *et al.*, 1995), sur leur stratégie de reproduction (Ponton & Tito de Morais, 1994 ; Ponton & Mérona, 1998) et sur les premiers stades de développement (Ponton & Copp, 1997 ; Ponton & Vauchel, 1998, mes travaux) constituent une base solide pour étudier les impacts du barrage de Petit Saut sur la faune piscicole. Mon travail a permis de confirmer des différences de structure des communautés de jeunes poissons entre le secteur d'étude en milieu naturel et celui soumis aux perturbations du barrage. Cependant, des études complémentaires sur le long terme sont nécessaires dans ces deux secteurs. Ces études permettront d'établir les variations naturelles de la structure des communautés de jeunes et ainsi de distinguer les effets des perturbations naturelles de ceux induits par le barrage. Il est par exemple urgent dans ces milieux d'évaluer l'impact de la régulation des débits sur les zones d'inondation. La dégradation de ces zones de nurseries, primordiales pour la survie des jeunes poissons (Hyslop, 1988 ; Jurajda, 1995), a été démontrée dans des cours d'eau régulés d'Alabama Central (Scheidegger & Bain, 1995). Dans

le Sinnamary, le mode d'exploitation du barrage conduit à une diminution du niveau d'eau moyen en saison des pluies et réduit donc l'amplitude, la fréquence et la durée des inondations dans les criques situées à l'aval. Dans les années futures, ce phénomène pourrait s'accentuer si le lit des criques se creuse comme Ponton & Vauchel (1998) en ont fait l'hypothèse. Les modifications du rythme des crues naturelles ont de fortes répercussions sur les organismes aquatiques (Bain *et al.*, 1988 ; Bonetto *et al.*, 1989) et représentent des menaces directes pour plus de la moitié des espèces de poissons du Sinnamary dont les jeunes sont inféodés aux zones de nurserie.



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A1

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

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(Freshwater Biology, sous presse)

Abstract

1. In this paper, we determine which environmental parameters control in space and time the variations of densities of early life and juvenile stages of fish in tributaries of a natural and a flow regulated section of the Sinnamary River, French Guiana.
2. We show that densities of the progeny of a large majority of taxa vary significantly with space and/or time. However, most of the non- Perciformes taxa respond differently to space and/or time effects depending on the section.
3. We demonstrate the importance of oxygen, turbidity and habitat structure (bank length, occurrence of undercut bank, richness in litter, vegetation and substrate) in both section, and the importance of the position of the sampling sites relatively to the main channel in the downstream tributaries, for explaining the spatial density variations of young fish. We suggest that both habitat complexity and distance from the main channel protect young fish against unpredictable flow releases downstream from Petit Saut dam.
4. Our findings substantiate that hydrological events play an important role in the temporal variations of densities of many fish taxa. Densities of most early life and many juvenile stages (mostly Characiformes) are positively related to hydrological events.
5. We also confirm that some fish taxa present reproductive habits relatively independent from abiotic factors such as flow variability and whose progeny show no significant variations of their densities with time.
6. Globally, our study demonstrates the need to consider separately early life and juvenile stages as well as areas with different environmental conditions for a better understanding of the effects of space and time on young fish assemblages. It also confirms that flow regulation and the associated degradation of the nurseries of more than 60% of the fish species inhabiting the Sinnamary River are potential threats to the conservation of natural and diverse riverine fish fauna.

Key words: Juvenile fish, density variation, local habitat, hydrology, dam

Introduction

Many recent studies emphasised that a complete understanding of the structure of any animal community is possible only in the context of spatial and temporal variations (e.g. Wiens, 1986; Southwood, 1988; Morris, 1990). However, how environmental conditions and biotic processes determine the abundance and distribution of species in space and time remains a central problem in ecology (Brown, 1984). The importance of these spatial and temporal dimensions is especially true for stream communities (e.g. Frissel *et al.*, 1986; Minshall, 1988; Matthews, 1990; Townsend & Hildrew, 1994; Poff & Allan, 1995). In these lotic systems and within ecological time, habitat features such as depth, current and substrate (e.g. Schlosser, 1982; Bain, Finn & Booke, 1988), water quality (e.g. Matthews, 1998), presence of shelter or habitat diversity (e.g. Gorman & Karr, 1978; Mérigoux, Ponton & Mérona, 1998) may play a major role in shaping fish communities in space. Flow (e.g. Horwitz, 1978; Resh *et al.*, 1988) and water temperature (e.g. Baltz *et al.*, 1987; Matthews, 1998) are the main physical parameters structuring fish assemblages in time. These physical parameters together with biotic interactions such as competition for food and avoidance of predation (Angermeier, 1987; Govoni, Hoss & Colby, 1989) have strong effects on individual fish, consisting in high fluctuations in the relative abundance of species and thus in the composition of fish communities in space and time.

In this context, determining how young fish depend on particular combinations of habitat conditions in space and time is of major importance for predicting the structure of adult fish assemblages. Indeed, survival rates of larvae and juvenile fish determine the year-class strength of most fish species (e.g. Balon, 1984; Houde, 1987). Moreover,

due to their narrow and specific requirements, young fish are good indicators of habitat structure and the ecological integrity of river systems (Schiemer *et al.*, 1991; Copp *et al.*, 1991).

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

This lack of information of the spatial and temporal parameters that affect the densities of neotropical young fish, and thus shape the assemblages of adults, is an essential problem for the Sinnamary River in French Guiana because of the completion

of the Petit Saut hydroelectric dam in 1994 (Fig. 1). Indeed, fish are generally well adapted to deal with natural physical and chemical variations (Matthews, 1998) and to select habitat in a way to maximise their lifetime reproductive success (Morris, 1990). However, anthropogenic induced disturbances such as alterations of the timing, frequency, magnitude or duration of flood patterns strongly impact aquatic biota (Bain, Finn & Booke, 1988; Bonetto, Wais & Castello, 1989; Richter et al., 1996; Poff *et al.*, 1997). These disturbances may also change river and stream physical and chemical structures (Collier, Webb & Schmidt, 1996). All these modifications are likely to impact young stages of fish and thus have serious long-term consequences for fish assemblages (Welcomme, 1995; Matthews, 1998).

In this context, our objectives were to 1) determine the young fish taxa of the Sinnamary River which density vary with space and time, by considering a small spatial scale (i.e. reach, sensu Frissel *et al.*, 1986) and a short temporal scale (weeks) which are well adapted to study young fish-habitat relationships (Poizat & Pont, 1996), 2) examine which local habitat characteristics determine the spatial variations of young fish taxa densities, 3) test how hydrological events relate to the temporal density variations, and 4) compare these patterns in a natural and in a flow regulated section of the Sinnamary River.

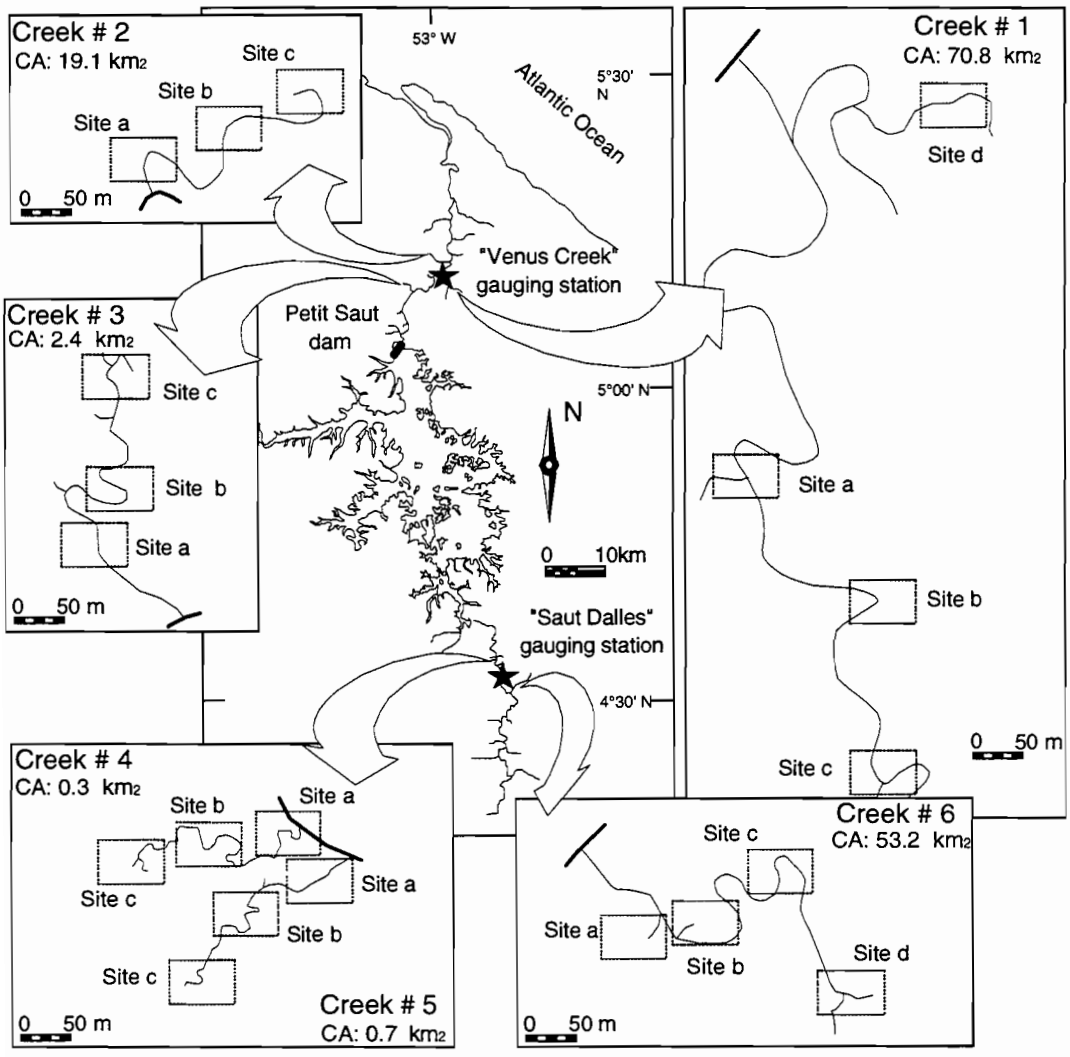

Fig. 1. Studied sites (dashed rectangles, n=20) of ca. 1000m² in the six tributaries under survey in the Sinnamary River (French Guiana, South America). Stars indicate the location of the different gauging stations in the river. During each of the ten campaigns performed in 1995 and 1996, we sampled one area of ca. 50m² at random within each site.

Materials and Methods

Study area

The Sinnamary River (Fig. 1) is the fifth largest river of French Guiana, with a length of approximately 260 km and a mean annual discharge of 230 m^3s^{-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 (for a description of the entire river system, see Boujard, 1992; Tito de Morais, Lointier & Hoff, 1995). Before the completion of Petit Saut dam in 1994, the hydrological regime in these two sections was both dependent of the alternation of the short, November to February, and long, April to July, rainy seasons and the dry season from August to November, accompanied by unpredictable short-term events imposed by sudden heavy rains (Ponton & Copp, 1997).

Fish sampling and spatial habitat characterisation

From March 1995 to October 1996, we sampled fish in three tributaries (or creeks) and their associated floodplains of the upstream section and three others of the downstream section of the Sinnamary River with Rotenone (Fig. 1). At each sampling campaign (Fig. 2), we selected an area of about 50 m^2 at random, i.e. without knowing whether fish were present or not, within each of the three (creek #2, 3, 4 and 5, Fig. 1) or four (creek #1 and 6) 1000 m^2 studied sites per tributary. In total, we sampled each of the ten downstream and ten upstream sites ten times and thus obtained 200 samples.

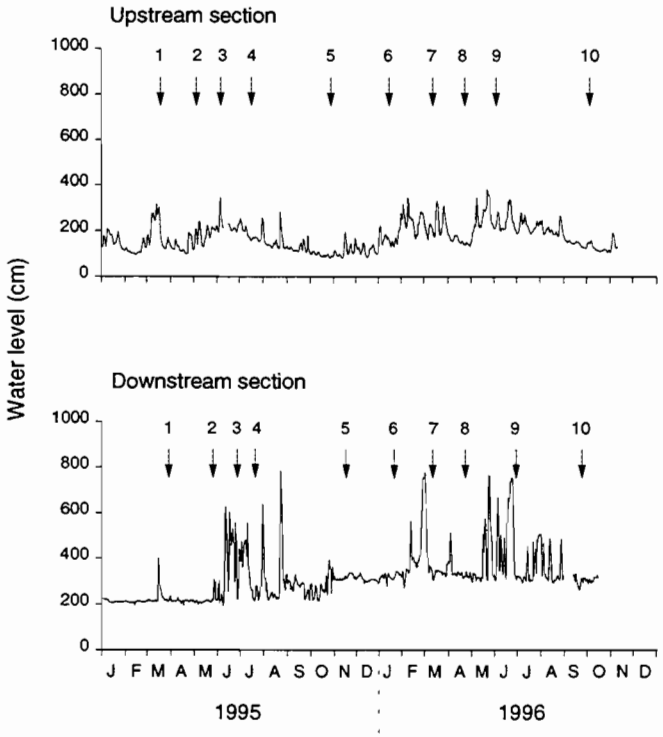

Fig. 2. Water levels recorded at Saut Dalles (upstream) and Petit Saut (downstream) gauging stations, from January 1995 to November 1996. Vertical arrows indicate the 10 fish sampling campaigns.

Mérigoux, Ponton & Mérona (1998) give a complete description of the sampling method. In summary, we first measured temperature, pH and oxygen with a ICM 51000 multiparameter and water turbidity with a LaMotte Model 2008 digital turbidity meter in the undisturbed water. We also measured the current velocity at the water surface by observing the time required for a floating object to traverse one meter downstream and assigned it to five categories (1: 0 to 6, 2: 7 to 9, 3: 10 to 14, 4: 15 to 25 and 5: > 25 cm s^{-1}). Preliminary measures showed that these variables varied little across the sampling volume, so we measured them only once. Then, we enclosed the sampling area with two or three stop nets (1 mm mesh) and applied at least two subsequent doses of PREDATOX well mixed with water (6.6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France). We collected fish with dip nets (1mm mesh) and immediately preserved them in 90% alcohol. After fish sampling, we recorded at each point sample of a 1x1 m grid the depth (in cm) and 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 or trees) and substrate (6 categories: mud, clay, sand, gravel [4-16 mm diameter[, stones [16-256 mm[, blocs > 256 mm). We recorded bank slope (3 categories: smooth to medium ≤ 60°, stiff to vertical > 60°, undercut sensu Gordon, McMahon & Finlayson, 1992) for the point samples closest to the bank. We also measured the distance of the sampling area to the main channel and determined the total bank length, mean width, and surface for each sampling area. Finally, we surveyed four to ten cross sections per sampling site for which we measured bankfull width with an horizontal tape, bankfull depth and water surface depth every meter along the horizontal tape (Gordon, McMahon & Finlayson, 1992).

In the laboratory, we sorted and identified all specimens of the 200 samples using keys for adults by Géry (1977), Rojas-Beltran (1984), Kullander & Nijssen (1989), Planquette, Keith & LeBail (1996) and for juveniles by Ponton (unpublished). 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 faced identification problems for a dozen of species, which we grouped in the genus they belong to. We referred to species and species groups as taxa.

Hydrology

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

Data analysis

Fish

We measured the standard length of each specimen to the nearest 1 mm. We separated juveniles from adults according to the minimal size at first maturity observed for each species in the Sinnamary River (Mérigoux & Ponton, 1998; Ponton & Mérona, 1998). We classified individual fish based on their standard length into early life stages (about 4 to 15-20 mm SL, depending on species) and juveniles (about > 15-20 mm SL, see Mérigoux & Ponton, 1998 for the exact size limits for each taxon). We determined the density of each ontogenetic stage for each sampling area, each sampling site and

each sampling campaign by dividing the number of individuals by the corresponding sampled area. Ontogenetic stages of taxa with low densities (sum in the 100 up- or 100 downstream samples < 0.4 individuals per m^2) were excluded from further analyses.

Spatial habitat parameters

For each site under study, we calculated the mean distances to the Sinnamary River (D_Sin in m) of the ten areas sampled (from the ten sampling campaigns), the mean of their bank lengths (Ba_Le in m), widths (M_Wi in m), depths (M_De in m), turbidities (TURB in NTU) and oxygen concentrations (OXY in mg l^{-1}). Water temperature (mean = 24.1 and 24.7°C, respectively in up- and downstream sites and SD = 0.3 for both sections) and pH (mean = 4.8 and 4.6, SD = 0.1 and 0.2, respectively in up- and downstream sites) varied little and were excluded from further analyses. We also omitted water current velocity as 83% of the samples had a velocity ≤ 6 cm s^{-1}. We determined the percentages of the three categories of bank slope (≤ 60°, > 60°, and undercut in %) at each studied site. For each point sample of the 1x1 m grid, we merged the occurrences of the categories of litter, vegetation and type of substrate coded 0 (absence) or 1 (presence) (see above for the different categories). We assigned each point sample to one type of habitat that corresponded to a given chain of 0 and 1. Then, we counted the different types of chains observed in the ten sampling areas of each site, in order to get an index of the richness of litter, vegetation and substrate (LVS).

We related bankfull depth of each of the four to ten surveyed cross sections to the corresponding water level in the Sinnamary River using the hydrological models defined by Mérigoux *et al.* (in press). This way, for each cross section, we were able to

assess the water level of the Sinnamary River above which flows would overtop the banks. Finally, we counted the number of days during which at least a part of each sampling site was flooded during our study period by using the smallest values of the four to ten water heights per creek site. Thereby, could estimate an "index of inundation potentiality" (IP) for each sampling site.

Temporal parameters

Parallel studies (Mérigoux *et al.*, in press) highlighted the strong influence of the water levels of the Sinnamary River on those of the tributaries and their associated floodplains. Therefore, we calculated the minimum, maximum, mean and variance of water levels 10, 20, and 30 days before each sampling campaign (DBS) from the Sinnamary water levels recorded from the upstream and downstream section gauging stations. In the upstream section, we also determined the number of days with water levels exceeding 100, 200 and 300 cm observed for the same values of DBS and made the same enumeration for water levels exceeding 500, 600, 700 and 800 cm downstream from the dam.

Densities vs space and time

For each section of the Sinnamary River, we determined how space (i.e. site effect, $n = 10$) and time (i.e. campaign effect, $n = 10$) contributed to the variations of densities of the two ontogenetic stages of each taxon with a two way ANOVA (Sokal & Rohlf, 1995).

Fish density vs spatial habitat parameters

We examined the habitat parameters that influenced the densities of taxa in space (i.e. taxa sensible to the site effect detected by the two way ANOVA). Therefore, we arranged fish densities and sampling site habitat characteristics in two data matrices: Sites-by-Fish Taxa and Sites-by-Environmental Variables (both rows-by-columns) separately for the upstream and the downstream data sets. The Samples-by-Fish Taxa matrix contained $\log(x + 1)$ transformed densities of the fish taxa. We retained 11 environmental variables in the upstream and downstream creeks Sites-by-Environmental Variables matrices (Table 1).

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

Table 1. Habitat characteristics for each studied site in the upstream and the downstream sections. With D_Sin: mean distance to the Sinnamary River; Ba_Le: mean bank length; M_Wi: mean width; M_De: mean depth; TURB: mean water turbidity; OXY: mean water oxygen content; ≤60°: percentage of smooth to medium bank slopes; >60°: percentage of stiff to vertical bank slopes; UND: percentage of undercuts; LVS: richness of litter, vegetation and substrate; IP: index of inundation potentiality. With *p*: exact probability of the one sided Wilcoxon rank-sum test (Mehta & Patel, 1995, p218) with Ho="one distribution is not shifted relative to the other".

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

In preparation for co-inertia analysis, we first submitted the Sites-by-Fish Taxa matrix to correspondence analysis and the Sites-by-Environmental Variables to principal components analysis. These ordination techniques respectively elucidate the relationships among taxa and provide the best combinations of environmental variables according to their correlation between each others (Escofier & Pagès, 1990). We then subjected the results from these two analyses to co-inertia analysis to assess the relationship (i.e. the co-structure) between taxa and environmental variables. Finally, we tested the significance of the resulting correlation by a Monte-Carlo method with 10000 random permutations of the rows of the environmental data set.

Fish density vs temporal parameters

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

We performed all these analyses separately for the up- and the downstream data set with Systat® 6.01 for Windows (Wilkinson, Blank & Gruber, 1996), ADE 4 software (Thioulouse *et al.*, 1997) and StatXact®, a statistic software for exact distribution-free inference that uses the algorithms developed by Mehta and Patel for performing permutation tests (Mehta & Patel, 1995). Permutation tests, also known as randomisation tests, are exact under few demanding conditions and provide protection

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

order family species	authority	code	Upstream ELS	 J	Downstream ELS	 J
Characiformes						
Hemiodontidae						
Hemiodopsis quadrimaculatus	(Pellegrin 1908)	HQUA	388	16		
Parodon guyanensis	Géry 1959	PGUI	186			
Curimatidae						
Chilodus zunevei	Puyo 1945	CZUN	11	4		
Curimatidae spp.		CUSP	2995	786	62	65
Anostomidae						
Anostomus brevior	Géry 1960	ABRE		1		
Leporinus despaxi	Puyo 1943	LDES		35		
Leporinus spp.		LESP	38	63	6	4
Erythrinidae						
Erythrinus erythrinus	(Schneider 1801)	EERY	53	24	5	
Hoplerythrinus unitaeniatus	(Spix 1829)	HOUN				20
Hoplias spp.		HOPL	1127	307	880	104
Lebiasinidae						
Copella carsevennensis	(Regan 1912)	CCAR	24	74	18	86
Nannostomus beckfordi	Günther, 1872	NBEC				79
Pyrrhulina filamentosa	Val. in Cuv. 1846	PFIL	64	216	9	507
Gasteropelecidae						
Gasteropelecus sternicla	(Linnaeus 1758)	GSTE			160	27
Characidae						
Acestrorhynchus sp.		ACSP	29	69	32	31
Astyanax bimaculatus	(Linnaeus 1758)	ABIM	32	476	6	17
Astyanax cf *keithi*	Géry, Planquette & LeBail 1996	AKEI	15	318	145	252
Astyanax meunieri	Géry, Planquette & LeBail 1996	AMEU			3	
Bryconops spp.		BRSP	14	92	116	122
Characidium fasciadorsale	Fowler 1914	CFAS	68	108	5	2
Charax pauciradiatus	Günther 1864	CPAU			35	
Hemigrammus ocellifer	(Steindachner 1882)	HOCE	58	300	34	473
Hemigrammus unilineatus	(Gill 1858)	HUNI	5	10	35	145
Hyphessobrycon aff. *sovichtys*	Schultz 1944	HSOV			12	28
Melanocharacidium sp.		MESP	62	2		
Microcharacidium eleotrioides	(Géry 1960)	MELE	52	48	34	33
Moenkhausia chrysargyrea	(Günther 1864)	MCHR	146	234	376	551
Moenkhausia collettii	(Steindachner 1882)	MCOL	248	1091	594	301
Moenkhausia georgiae	Géry 1966	MGEO	14			
Moenkhausia hemigrammoides	Géry 1966	MHEM	1	1	37	1300
Moenkhausia oligolepis	(Günther 1864)	MOLI	423	1759	33	315
Moenkhausia sp.		MOSP		3		
Moenkhausia surinamensis	Géry 1966	MSUR		69	1	
Phenacogaster aff. *megalostictus*	Eigenmann1909	PMEG	214	625	2	2
Piabucus dentatus	(Köhlreuter 1761)	PDEN			25	14
Poptella brevispina	(Reis 1989)	PBRE	38	6	461	74
Pristella maxillaris	(Ulrey 1894)	PMAX	138	502	30	250
Pseudopristella simulata	Géry 1960	PSIM	161	1049	55	185
Siluriformes						
Doradidae						
Doras carinatus	(Linnaeus 1766)	DCAR	1			
Auchenipteridae						
Parauchenipterus galeatus	(Linnaeus 1766)	PGAL			5	1
Tatia intermedia	(Steindachner 1876)	TINT	22	15	181	220

Table 2. Continued

order family species	authority	Code	Upstream ELS	 J	Downstream ELS	 J
Siluriformes (continued)						
Pimelodidae						
Pimelodella sp.		PISP	6	79	8	13
Pseudopimelodus raninus	(Valenciennes 1840)	PRAN	25	24	42	41
Rhamdia quelen	(Quoy & Gaimard 1824)	RQUE		2	1	9
Helogenidae						
Helogenes marmoratus	(Günther 1863)	HMAR		14		2
Cetopsidae						
Paracetopsis sp.		PASP		2		
Aspredinidae						
Bunocephalus coracoideus	Cope 1874	BCOR			5	37
Trichomycteridae						
Trichomycterus guianense	(Eigenmann 1909)	TGUI	29	49	17	4
Callichthyidae						
Callichthys callichthys	Linnaeus 1758	CCAL	5	11	2	3
Hoplosternum thoracatum	(Val. in Cuv. & Val. 1840)	HTHO	4		9	20
Loricariidae						
Ancistrus aff. *hoplogenys*	(Günther 1864)	AHOP		6	9	9
Farlowella reticulata	Boeseman 1971	FRET	1			
Gymnotiformes						
Sternopygidae						
Eigenmannia virescens	(Valenciennes 1847)	EVIR		1		
Sternopygus macrurus	(Bloch & Schneider 1801)	SMAC	12	5	31	11
Hypopomidae						
Brachyhypopomus beebei	(Schultz 1944)	BBEE	4	62	3	78
Hypopomus artedi	(Kaup 1856)	HART	26	36	12	15
Gymnotidae						
Gymnotus spp.		GYSP	126	287	35	197
Cyprinodontiformes						
Aplocheilidae						
Rivulus agilae	Hoedeman 1954	RAGI	1	51	1	35
Rivulus igneus	Huber 1991	RIGN		2		
Rivulus xiphidius	Huber 1979	RXIP	197	282	23	26
Poeciliidae						
Poecilia parae	(Eigenmann 1894)	PPAR			45	
Tomeurus gracilis	Eigenmann 1909	TGRA				1
Synbranchiformes						
Synbranchidae						
Synbranchus marmoratus	Bloch 1795	SMAR	7	15	25	22
Perciformes						
Nandidae						
Polycentrus schomburgkii	Müller & Troschel 1848	PSCH				72
Cichlidae						
Cleithracara maronii	(Steindachner 1882)	CMAR	33	74	1	15
Crenicichla saxatilis	(Linnaeus 1758)	CSAX	146	131	737	451
Krobia guianensis	(Regan 1905)	KGUI	676	553	1353	888
Nannacara anomala	Regan 1905	NANO	91	228	11	205
Eleotridae						
Dormitator macrophtalmus	Puyo 1944	DMAC			6	9
Eleotris amblyopsis	(Cope 1870)	EAMB			966	2446
Total number of orders			6		6	
Total number of families			19		22	
Total number of taxa			56		57	
Total number of individuals			18234		16556	
Total Sampled Volume (m^3)			1622		2914	
Total Sampled Area (m^2)			4649		5865	

against deviations from parametric assumptions. Moreover, permutation tests are particularly indicated in studies based on small samples as they remain as powerful as the corresponding unbiased parametric test (Good, 1993). They can even become more powerful with data from non-standard distributions (Manly, 1997).

Results

Fish

We collected 34790 young individuals representing 70 taxa from 25 families and 6 orders (Table 2). Characiformes and Perciformes were numerically dominant with 66% and 26% respectively of the total individuals. However, Characiformes accounted for 82% and Perciformes for 11% of the total individuals in the upstream section, whereas they accounted for 49% and 43% respectively, in downstream tributaries. Curimatidae spp., *Moenkhausia oligolepis* (Günther 1864) and *Hoplias* spp. were the most abundant taxa in the upstream creeks and *Eleotris amblyopsis* (Cope 1870), *Krobia guianensis* (Regan 1905), and *Moenkhausia hemigrammoides* Géry 1966, dominated in the downstream ones. We caught more individuals in upstream creeks and nearly the same number of taxa despite that the total sampled area and volume were more important in downstream creeks (Table 2). The early life stages were less abundant than the juveniles with 44% and 41% of the total number of collected fish in the up- and downstream section respectively.

Density variations among sites and/or campaigns

In the upstream section, 52% of early life stages and 79% of juveniles had significant variation of their densities among sites and/or campaigns (Table 3). In the downstream

Table 3. Significance of sites (space) and campaigns (time) for explaining the variations of taxa densities of early life stages (ELS) and juvenile (J) in up- and downstream sections by two way ANOVA. With ns: not significant, * $0.01<p\leq0.05$, ** $0.001<p\leq0.01$, and *** $p\leq0.001$. F is indicated only if $p\leq0.05$. We omitted taxa with low density (sum of densities in the 100 up- or 100 downstream samples < 0.4 individuals per m^2). See Table 2 for taxa codes.

		Upstream								Downstream							
		ELS				J				ELS				J			
Order	CODE	space		time		space		time		space		time		space		time	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Characiformes																	
	HQUA		ns		ns		-		-		-		-		-		-
	PGUI		ns		ns		-		-		-		-		-		-
	CUSP	4.54	***		ns	3.43	***	2.01	*		ns		ns		ns		ns
	LDES		-		-		ns		ns		-		-		-		-
	LESP		ns	2.85	**	2.00	*		ns		-		-		-		-
	EERY	4.70	***	2.36	*	4.21	***		ns		-		-		-		-
	HOUN		-		-		-		-		-		-		-		-
	HOPL		ns		ns	2.74	**	5.79	***	2.52	*	3.06	**	2.06	*		ns
	CCAR		ns		ns		ns		ns		-		-	2.32	*	3.32	**
	NBEC		-		-		-		-		-		-		ns	4.63	***
	PFIL		ns	2.16	*		ns	5.13	***		-		-		ns	2.31	*
	GSTE		-		-		-		-		ns	2.56	*	2.19	*		ns
	ACSP	2.11	*	3.15	**	2.1	*	5.73	***		ns	3.75	***		ns		ns
	ABIM		ns	4.51	***		ns	2.89	**		-		-		-		-
	AKEI		-		-	2.37	*		ns		ns		ns		ns	2.79	**
	BRSP		-		-		ns		ns		5.81	***	ns		ns		ns
	CFAS	3.27	**	2.93	**	2.59	*	2.87	**		-		-		-		-
	CPAU		-		-		-		-		2.08	*	ns		-		-
	HOCE		ns		ns		ns	2.37	*		ns		ns		ns	2.75	**
	HUNI		-		-		-		-		ns		ns		ns	2.18	*
	HSOV		-		-		-		-		-		-		ns		ns
	MESP		ns	2.83	**		-		-		-		-		-		-
	MELE		2.19	*	ns		ns		ns	2.30	*	4.01	***	4.18	***		ns
	MCHR		ns	6.09	***		ns	13.97	***		ns		ns		2.18	*	ns
	MCOL		ns		ns	3.53	***	3.81	***		ns	2.19	*		ns		ns
	MHEM		-		-		-		-	2.11	*	2.20	*		ns	2.46	*
	MOLI		ns	4.08	***	2.23	*	3.21	**		ns	3.42	***		ns		ns
	MSUR		-		-	2.61	*		ns		-		-		-		-
	PMEG		ns		ns		ns	2.06	*		-		-		-		-
	PBRE		ns	2.93	**		-		-	2.04	*	8.32	***		ns		ns
	PMAX		ns		ns		ns	2.04	*		ns		ns		ns		ns
	PSIM		ns		ns		ns	2.98	**		ns	2.05	*		ns	3.49	***
Siluriformes																	
	TINT		ns		ns		-		-	2.76	**	2.49	*		2.25	*	ns
	PISP		-		-	2.09	*	3.20	**		-		-		-		-
	PRAN	3.16	**		ns	4.39	***		ns	2.24	*		ns		ns	4.54	***
	BCOR		-		-		-		-		-		-	2.18	*		ns
	TGUI		ns		ns	3.83	***		ns		-		-		-		-
Gymnotiformes																	
	SMAC		-		-		-		-	8.99	***		ns		-		-
	BBEE		-		-		ns		ns		-		-		ns		ns
	HART	2.61	*		ns		6.51	***	ns		-		-		-		-
	GYSP		ns	5.03	***	4.30	***	3.14	**		ns	2.69	**		ns		ns
Cyprinodontiformes																	
	RAGI		-		-	2.47	*	5.72	***		-		-		ns		ns
	RXIP	3.31	**	2.07	*		ns	5.19	***	3.44	***		ns		2.71	**	ns
	PPAR		-		-		-		-	2.67	**		ns		-		-
Synbranchiformes																	
	SMAR		-		-		-		-	2.75	**		ns	7.56	***	2.13	*
Perciformes																	
	PSCH		-		-		-		-		-		-	3.05	**	2.18	*
	CMAR		ns		ns	2.64	*		ns		-		-		-		-
	CSAX		ns		ns		ns		ns		ns		ns		ns		ns
	KGUI		ns		ns		ns		ns		ns		ns		ns		ns
	NANO		ns		ns	2.1	*	2.02	*		-		-	6.66	***	2.26	*
	EAMB		-		-		-		-		ns	27.84	***		ns	8.54	***

creeks these percentages were 70 and 61% respectively. The early life stages and juveniles having variable densities among campaigns were mostly Characiformes whatever the section considered. Remarkably, most of the early life stages and of the juveniles of a given taxon present in the two sections responded differently to sites and/or campaigns effects depending on the section, the noticeable exception being found among the Perciformes (Table 3).

Spatial variations of densities

Sites in the upstream section were less shallow (lower depths and amounts of stiff bank slope and an higher index of inundation potentiality), more narrow and were less turbid than those downstream from the dam (Table 1). The two matrices, Samples-by-Fish Taxa and Samples-by-Environmental Variables were significantly related ($p < 0.001$, Monte-Carlo method with 10000 permutations) for both upstream and downstream data sets.

In the upstream section, the first two axes of the co-inertia analysis explained 85% of the total co-inertia (Figure 3a) with the first axis being particularly important. According to the quality of the representation of each taxon and each habitat variable on the first two axes, (i.e. the relative contribution which corresponds to the percentage of the inertia extracted by, in our case, a taxa or by a habitat variable, Lebart, Morineau & Piron, 1995), we distinguished four groups of life stage taxa (hereafter referred to as "taxa") associated with four types of habitats (Figures 3b & 3c and Tables 4 & 5). Group 1 (46% of the taxa, Figure 3c) comprised taxa associated with shallow and narrow sites characterised by long bank length, few smooth to medium bank slopes but a lot of

undercuts, clear waters with high oxygen concentrations and low index of inundation potentiality. Taxa of the group 2 belonged all to the Characiformes order. We collected them in habitats with characteristics opposite to those favourable to group 1 (Figure 3b and 3c). Group 3 consisted of taxa mainly found in habitats presenting a high diversity of litter, vegetation and substrate and situated far from the Sinnamary River confluence. Juveniles of *Leporinus* spp. (LESP) were the only taxa represented in group 4 and were found in sampling sites with low diversity of litter, vegetation and substrate near the confluence. Finally, juveniles of *Pimelodella* sp. (PISP) were found in habitat characteristics of groups 1 and 4. The six taxa for which we had enough individuals for both early life and juveniles stages (CUSP, EERY, ACSP, CFAS, PRAN and HART) presented no ontogenetic shifts between the four types of habitat.

In the downstream section, the first two axes of the co-inertia analysis explained 80% of the total variability (Figure 3d). According to the quality of the representation of each taxon and each habitat variable on the first two axes, we distinguished four groups of taxa associated with four types of habitat. Taxa of group 1 were associated with large habitat with high concentrations of oxygen, high diversity of litter, vegetation and substrate, low turbidity, short distance to the Sinnamary River and low index of inundation potentiality (Figure 3e and f). Most taxa of the group 2 were non Characiformes except juveniles of *Moenkhausia chrysargyrea* (Günther 1864) (MCHR) and were collected in sites presenting characteristics opposite to those favourable to group 1. Early life stages of *Poecilia parae* (Eigenmann 1894) (PPAR) were the only representative of the group 3. They preferred shallow habitats with short bank length, a high percentage of smooth to medium bank slopes and few undercuts. We found taxa of

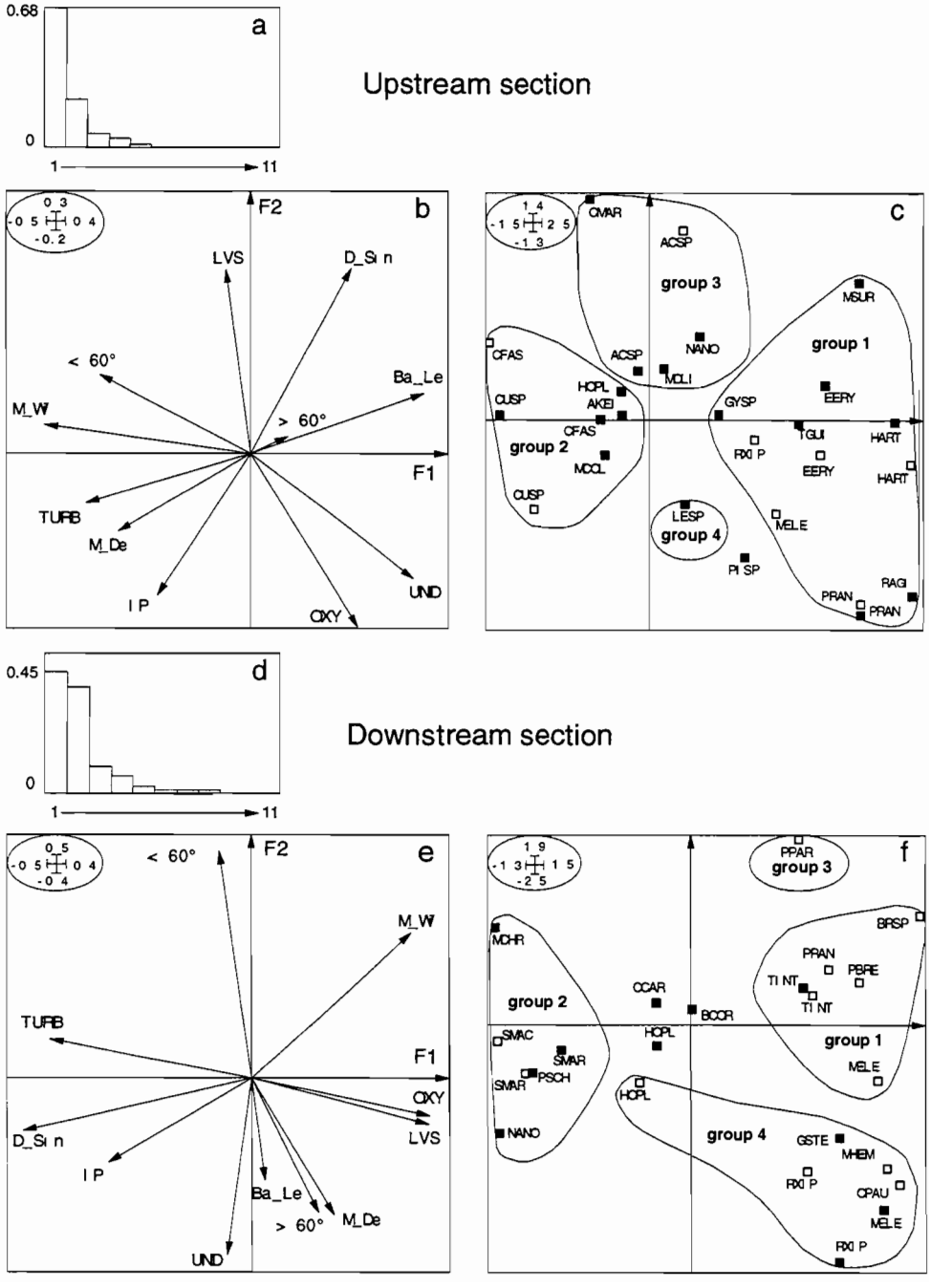
a
0.68
0
1
11
Upstream section
b
F2
F1
LVS
D_Si n
< 60°
> 60°
Ba_Le
M_W
TURB
M_De
I P
OXY
UND
c
group 3
group 1
group 2
group 4
OMAR
ACSP
MSUR
NANO
CFAS
MCLI
HOPL
AKEI
CUSP
GYSP
EERY
TGLI
HART
RXO P
MCOL
LESP
MELE
PI SP
RAGI
PRAN
d
0.45
0
1
11
Downstream section
e
F2
F1
< 60°
> 60°
M_W
TURB
OXY
LVS
D_Si n
I P
Ba_Le
M_De
UND
f
PPAR
group 3
group 2
group 1
group 4
MCHR
BRSP
PRAN
PBRE
TI NT
OCAR
BCOR
SMAC
HOPL
SMAR
PSCH
MELE
NANO
GSTE
MHEM
RXO P
CPAU

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

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

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

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

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

group 4 in habitats with features opposite to those favourable for *Poecilia parae* early life stages. Among the five taxa represented by early life and juvenile stages (HOPL, MELE, TINT, RXIP and SMAR), only *Microcharacidium eleotrioides* (Géry 1960) (MELE) showed a clear ontogenetic shift between the habitat characteristics favourable to group 4 to group 1 (Fig. 3f). *Hoplias* spp. (HOPL), *Copella carsevennensis* (Regan 1912) (CCAR) and *Bunocephalus coracoideus* Cope 1874 (BCOR) did not show any preference among the studied local habitat parameters.

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

Temporal variations of densities

Hydrological events explained the temporal density variation of all early life stages and of 72% of juveniles in the upstream section (Table 6). Densities of early life stages were always positively related to hydrological events among which, mean water level and number of days exceeding 200 cm were the most influential. Densities of a large part of juveniles were also positively influenced by the mean of the water level and number of days exceeding 200 cm. However, densities of *Hemigrammus ocellifer* (Steindachner 1882) (HOCE), *Phenacogaster* aff. *megalostictus* Eigenmann 1909 (PMEG), *Pristella maxillaris* (Ulreys 1894) (PMAX), *Pseudopristella simulata* Géry 1960 (PSIM), *Rivulus agilae* (RAGI), *R. xiphidus* (RXIP) and *Nannacara anomala* (NANO) juveniles decreased with increasing variance of water levels 10, 20 and/or 30 DBS.

In the downstream section, hydrological events explained the temporal density variation of 58% of early life stages and of only 23% of juveniles (Table 7). Density variation of early life stages of *Microcharacidium eleotrioides* (MELE) was mainly linked to the mean water levels, whereas densities of early life stages of *Gasteropelecus sternicla* (Linnaeus 1758) (GSTE) and *Moenkhausia hemigrammoides* (MHEM) were more sensible to the variance of water level and densities of early life stages of *Moenkhausia collettii* (Steindachner 1882) (MCOL) and *Poptella brevispina* (Reis 1989) (PBRE) were mainly linked to the number of days water levels in the Sinnamary River exceeded 500, 600, 700 and/or 800 cm before sampling (see Table 7 for some of these results). Density variation of *Pseudopristella simulata* (PSIM) early life stages was equally linked to the mean- and variance of water levels. *Eleotris amblyopsis* (EAMB)

Table 6. Exact significance of Spearman's coefficient of rank-order correlation (Mehta & Patel, 1995, p 643) between hydrological variables and densities of each taxon sensitive to the time effect at the early life (ELS) and juvenile (J) stages in the upstream section (see Table 3). With o: non significant, + or -: $0.01<p\leq0.05$, + + or - -: $0.001<p\leq0.01$, + + + or - - -: $p\leq0.001$, n=10, signs indicate positive or negative relationship. Results are given only for mean- and variance of water levels as well as the number of days during which water levels exceeded 200 cm (ND>200) 10, 20, and 30 days before sampling (DBS) as the analysis with closely related variables such as minimum and maximum or ND>100 and ND>300 gave similar results. See Table 2 for taxa codes.

		Mean			Variance			ND>200		
		DBS	10	20	30	10	20	30	10	20	30
Code	Stage										
Characiformes											
CUSP	J		o	o	o	o	o	o	o	o	o
LESP	ELS		+	+	++	o	o	o	++	++	++
EERY	ELS		o	o	o	o	o	o	o	o	+
HOPL	J		o	o	+	o	o	o	o	o	o
PFIL	ELS		++	++	++	+	+	o	++	++	+
PFIL	J		o	o	o	o	o	o	o	o	o
ACSP	ELS		+	+	++	o	o	o	++	+	+
ACSP	J		+	+	++	o	o	o	+	+	+
ABIM	ELS		+	+	+	++	+	+	+	o	o
ABIM	J		++	++	++	o	o	o	++	+	++
CFAS	ELS		+	++	++	o	o	o	+	+	++
CFAS	J		o	o	o	+	o	o	o	o	o
HOCE	J		+	o	o	- - -	-	-	o	o	o
MESP	ELS		o	+	+	o	o	o	+	+	+
MCHR	ELS		+	+	++	o	o	o	o	o	+
MCHR	J		o	o	o	o	o	o	o	o	o
MCOL	J		-	o	o	o	o	o	o	o	o
MOLI	ELS		++	+++	+++	+	+	+	++	+	++
MOLI	J		o	o	+	o	o	o	o	o	o
PMEG	J		o	o	o	-	o	o	o	o	o
PBRE	ELS		+++	+++	++	+	+	+	+++	+++	+++
PMAX	J		-	-	o	o	-	- - -	o	o	-
PSIM	J		- -	-	o	-	- -	-	-	-	-
Siluriformes											
PISP	J		o	o	o	o	o	o	o	o	o
Gymnotiformes											
GYSP	ELS		o	o	o	o	o	+	o	o	o
GYSP	J		o	o	o	o	o	o	o	o	o
Cyprinodontiformes											
RAGI	J		-	o	o	-	-	o	-	-	o
RXIP	ELS		o	o	+	o	o	o	o	o	o
RXIP	J		o	o	o	-	-	o	o	o	o
Perciformes											
NANO	J		-	o	o	- -	- -	-	o	o	o

Table 7. Exact significance of Spearman's coefficient of rank-order correlation (Mehta & Patel, 1995, p 643) between hydrological variables and densities of each taxon sensitive to the time effect at the early life (ELS) and juvenile (J) stages in the downstream section (see Table 3). With o: non significant, + or -: $0.01<p\leq0.05$, + + or - -: $0.001<p\leq0.01$, + + + or - - -: $p\leq0.001$, n=10, signs indicate positive or negative relationship. Results are given only for mean- and variance of water levels as well as the number of days during which water levels exceeded 500 cm (ND>500) 10, 20, and 30 days before sampling (DBS) as the analysis with closely related variables such as minimum and maximum or ND>600, ND>700 and ND>800 gave similar results. See Table 2 for taxa codes.

			Mean			Variance			ND>500		
		DBS	10	20	30	10	20	30	10	20	30
Code	Stage										
Characiformes											
HOPL	ELS		o	o	o	o	o	o	o	o	o
CCAR	J		o	o	o	o	o	o	o	o	o
NBEC	J		o	o	o	o	o	o	o	o	o
PFIL	J		o	o	o	o	o	o	o	o	o
GSTE	ELS		o	+	+	o	+ +	+ +	o	o	+
ACSP	ELS		o	o	o	o	o	o	o	o	o
AKEI	J		o	o	o	o	o	o	o	o	o
HOCE	J		o	o	o	o	o	o	o	o	o
HUNI	J		o	o	o	o	o	o	o	o	o
MELE	ELS		+	+ +	+ + +	o	+	o	o	+ +	+ +
MCOL	ELS		o	+	+	o	+	+	o	+	+ +
MHEM	ELS		o	o	+	o	+ +	+ +	o	o	+
MHEM	J		o	o	o	o	o	o	o	o	o
MOLI	ELS		o	o	o	o	o	o	o	o	o
PBRE	ELS		+ +	+	o	+	o	o	+	+	+ +
PSIM	ELS		o	+	+	o	+	+	o	o	o
PSIM	J		o	o	o	o	o	o	o	o	o
Siluriformes											
TINT	ELS		o	o	o	o	o	o	o	o	o
PRAN	J		+ +	+	+	o	o	o	+	+ +	o
Gymnotiformes											
GYSP	ELS		o	o	o	o	o	o	o	o	o
Synbranchiformes											
SMAR	J		o	o	o	o	o	o	o	o	o
Perciformes											
PSCH	J		o	o	o	o	o	o	o	o	o
NANO	J		o	o	+	o	o	o	o	o	o
EAMB	ELS		o	- -	- -	o	o	o	o	- -	- -
EAMB	J		- -	- -	- -	-	o	o	-	- -	-

was the only taxon whose early life stage and juveniles densities were strongly negatively influenced by hydrological events. Early life stage taxa with temporal density variations were not or very little influenced by hydrological events 10 DBS.

Discussion

The list of young fish taxa we collected in the tributaries of the Sinnamary River compares well with those established in the same area with the same sampling method by Ponton & Copp (1997) and by Ponton, Mérigoux & Copp (unpublished data). Our list shares respectively 58 and 64 taxa with these previous works. Our work confirmed that tributaries play the role of nurseries for more than 60% of the fish species inhabiting the Sinnamary River. In the upstream section, we observed a relative abundance of Characiformes and Perciformes very similar to those found by Ponton & Copp (1997) in unperturbated areas. Downstream from the dam, we found a higher relative abundance of young Characiformes than those observed in 1994 by these authors, i.e. just after dam's gates were closed. Therefore, our results support the hypothesis expressed by Ponton, Mérigoux & Copp (unpublished data) that Characiformes reproduction recovered rapidly from the failures induced by dam closure.

Our work emphasised that water oxygen content and/or turbidity were important parameters in determining the spatial variations of young fish density in both sections. Downstream from the dam, early life and juvenile stages of many taxa had highest densities in well oxygenated clear waters. It is well known that low oxygen concentrations cause a wide array of stress-related responses and limits distribution and activities of fish (Matthew, 1998). In the neotropics many fish species respond to

decreasing O_2 levels by active migration (Lowe-McConnel, 1987). Others display adaptations such as dermal lip protuberance (Casciotta, 1993) or aerial respiration (Kramer & McClure, 1982) to cope with this limiting factor. Young neotropical fish (i.e. taxa belonging to group 2, Fig. 3c and f) may choose to stay in poor oxygenated tributaries as a result of a trade off between the cost of such adaptations and lack of sufficient food, or higher risk of predation or entrainment in the more oxygenated waters of the main channel. Not surprisingly, more than half of the most abundant taxa in clear waters of the downstream tributaries were Characiformes. These taxa are known to be diurnal and to rely on vision for food intake (Goulding, 1980) and they are usually abundant in clear waters (Rodriguez & Lewis, 1997). However, in the upstream section some young Characiformes (those belonging to group 2, Fig. 3f) were clearly more abundant in deep and turbid habitats. Again, these habitat preferences may reflect some trade-offs between impeded vision and for instance predation risks. Indeed, identically to adults for which depth (Power, 1984; Schlosser, 1987; Lonzarich & Quinn, 1995) and turbidity (Cambray & Bruton, 1994; Rodriguez & Lewis, 1997) provide refuges from predators, some young stages of neotropical Characiformes may have found some advantages in these environments.

We also demonstrated the importance of the spatial structure of the habitats for explaining the variations of the densities of young fish in space. In the upstream section, we observed that the longer the bank length, the higher were the densities of many young fish taxa. This observation confirms the importance of the riparian zones for the progeny of neotropical fish (Mérigoux, Ponton & Mérona, 1998). In these zones they may find shelter against predation or flow variability and diversified food (Schiemer &

Zalewski, 1992; Tito de Morais, Lointier & Hoff, 1995). The positive relationship between the density of some young fish taxa and the percentage of bank undercut supports this hypothesis. Moreover densities of early life stages of *Acestrorhynchus* sp. (ACSP) and juveniles of *Cleithracara maronii* (Steindachner 1882) (CMAR) in the upstream section as well as those of numerous taxa downstream from the dam increased with increasing richness in litter, vegetation and substrate (LVS, Fig. 3). Habitat diversity is known to enhance fish species diversity in temperate- (e.g. Gorman & Karr, 1978) and tropical rivers (Mérigoux, Ponton & Mérona, 1998). One possible explanation is that diverse habitats provide numerous refuges against environmental fluctuations (Pearson, Li & Lamberti, 1992). The highest number of taxa associated with high values of LVS in the downstream section supports the hypothesis of Lonzarich & Quinn (1995) that habitat complexity is especially important to stream fish exposed to anthropogenic disturbances. Indeed, dam operations modified strongly the seasonal pattern of the Sinnamary River flow in the downstream reaches in 1995 and 1996 (Fig. 2). Water levels fluctuations in the main channel is the main factor driving those observed in the tributaries (Mérigoux *et al.*, in press) and Ponton & Vauchel (1998) emphasised how artificial low water levels in the main channel during the rainy season may increase the water speed in the tributaries. Thus, we can hypothesise that vegetation, roots, wood, litter or blocs might be more crucial in providing refuges for young fish inhabiting unpredictable downstream environments.

Interestingly, the position of the sampling sites relatively to the main channel (D_Sin, Fig. 3) was a more discriminating variable in the downstream section than in the upstream one. In downstream tributaries, the influence of dam operations and of the tide

that regularly pushes up the freshwater (Ponton & Copp, 1997) induce a variability of the water level that is maximal at the confluence of the creeks with the main channel and that decrease with the distance from the river (Mérigoux *et al.*, in press). *Sternopygus macrurus* (Bloch & Schneider 1801) (SMAC), *Synbranchus marmoratus* Bloch 1795 (SMAR), *Polycentrus schomburcki* Müller & Troschel 1848 (PSCH) or *Nannacara anomala* (NANO) occurred at sites distant from the main channel. These species have parental care for relatively few large offsprings (Winemiller, 1989; Ponton & Tito de Morais, 1994; Ponton & Mérona, 1998). Their reproductive habits correspond well to the definition of the equilibrium strategy (Winemiller, 1989) i.e. to the use of stable environments. Thus, the restriction of the progeny of these species to sites distant from the river may have been a consequence of their reproductive strategy.

Our findings confirmed that hydrological events play an important role for explaining the temporal density variations of most young Characiformes. In temperate rivers, peak densities of eggs and larval fish are often related to temperature and river discharge (Holland, 1986) or to photoperiod (Billard & Gillet, 1984). In the neotropics, where temperature and photoperiod remain stable along the year, raising waters at the beginning of the rainy season is the main cue for the reproduction of many fish species, especially among the Characiformes (Lowe-McConnel, 1987; Menezes & Vazzoler, 1992). With increasing water level, medium to large species of this order usually colonise the adjacent floodplains where they are supposed to find suitable spawning sites and where their progeny will find food and shelter (Bayley, 1988; Junk, Bayley & Sparks, 1989). Among the taxa that have such a seasonal strategy (Winemiller, 1989), and accordingly with our results, at least in upstream creeks, *Acestrorhynchus* sp.

(ACSP), *Astyanax bimaculatus* (Linnaeus 1758) (ABIM), *Moenkhausia chrysargyrea* (MCHR), *Moenkhausia oligolepis* (MOLI) and *Poptella brevispina* (PBRE) are the best representatives in the Sinnamary River (Ponton & Mérona, 1998). However, the high densities of juveniles we observed during periods of high water may also result from their foraging habits. Juveniles of *Hoplias* spp. (HOPL), *Acestrorhynchus* sp. (ACSP) or *Pseudopimelodus raninus* (PRAN) may concentrate in the inundated areas in order to find the small fish they prey upon (Mérigoux & Ponton, 1998). Comparably, juveniles of *Moenkhausia oligolepis* (MOLI) (which occurred at high densities after periods of high waters) feed on terrestrial insects (Mérigoux & Ponton, 1998) that they may find in great quantities in flooded areas (Welcomme, 1979).

Eleotris amblyopsis (EAMB) was the only taxa for which density was negatively related to water levels of the Sinnamary at early life stages. This species is known to reproduce at the end of the rainy season (Ponton & Copp, 1997) and densities of their early life stages would therefore be greater after periods of low water levels.

Early life stages of some taxa were present the all year round in the tributaries of the Sinnamary River without significant variations of their densities with time. These findings confirm that some fish taxa have reproductive habits being relatively independent from abiotic factors such as flow variations. Early life stages of the erythrinids *Hoplias malabaricus* (Bloch 1794) (grouped at the genus level with *H. aimara* (Valenciennes 1840) in this study) and those of all the cichlids did not vary with time in upstream tributaries. These species are known to be nest spawners (Breder & Rosen, 1966; Ponton & Tito de Morais, 1994) and thus among the representatives of the equilibrium strategy (Winemiller, 1989). On the other hand, in upstream creeks

Hemigrammus ocellifer (HOCE), *Microcharacidium eleotrioides* (MELE), *Moenkhausia collettii* (MCOL), *Phenacogaster* aff. *Megalostictus* (PMEG), *Pristella maxillaris* (PMAX) and *Pseudopristella simulata* (PSIM) had also stable densities of their early stages over time. But in contrast to erythrinids and cichlids, these small-sized characids present all the characteristics associated with the opportunistic strategy: short generation time, small eggs, low fecundity and multiple bouts of reproduction (Winemiller, 1989; Ponton & Mérona, 1998). Thus, different reproductive strategies may result in the same stability in the offspring abundance's in time. Interestingly, density of early life stages of *Microcharacidium eleotrioides* (MELE), *Moenkhausia colletti* (MCOL), *Pseudopristella simulata* (PSIM) and *Hoplias* spp (HOPL) were not time influenced in the upstream creeks but varied significantly with time in the downstream creeks. It remains to be tested whether these variations in the downstream creeks originated from a cyclic reproduction induced by the unstable conditions prevailing in this section or by cyclic variations of mortality rates superimposed on constant reproduction.

Conclusions

In this study we detected space and/or time variations of densities for the progeny of a large majority of taxa and we highlighted the necessity of considering these two dimensions when studying young fish species assemblages. We demonstrated the need to consider separately early life and juvenile stages as well as areas with different environmental conditions for a better understanding of the effects of space and time on young fishes.

Globally, our results support those of Scheidegger & Bain (1995) in Central Alabama that showed differences in composition, distribution and microhabitat use of young fish in natural and flow regulated rivers. These authors stressed the fact that flow regulation and the associated degradation of nursery habitat are potential threats to the conservation of natural and diverse riverine fish fauna. Indeed, the availability of suitable nurseries is a major factor that affects the survival of young fish (e.g. Hyslop, 1988). Ponton & Vauchel (1998) hypothesised that downstream tributaries of the Sinnamary River will present in the future deeper channels that will require higher discharge in the river to overspill their banks and inundate their floodplains. Thus, if their hypothesis reveals truth, dam operations will lead to shorter periods of favourable conditions for young fish along the year.

The relationships between hydrological events and density of many young fish in the Sinnamary confirmed that human impact should be monitored more closely through surveys of young fish rather than adult fish (see also Copp *et al.,* 1991; Ponton, Mérigoux & Copp, unpublished data). Moreover, our results show that most young Characiformes were dependent on hydrological events in the Sinnamary so that we confirmed the hypothesis of Ponton & Vauchel (1998) that monitoring the relative abundance of young Characiformes may be the most practical approach for documenting damming effects on fish communities in neotropical rivers.

During the last years a great amount of knowledge has been gained on the adult fish assemblages of the Sinnamary River (Tito de Morais & Lauzanne, 1994; Tito de Morais, Lointier & Hoff, 1995), on their reproductive strategies (Ponton & Tito de Morais, 1994; Ponton & Mérona, 1998), and on the ecology of their young stages (Ponton &

Copp, 1997; Mérigoux & Ponton, 1998; Ponton & Vauchel, 1998; this present study). These different works constitute a unique framework in the neotropics for investigating the long term consequences of damming on young stages of freshwater fish species and thereby on adults communities.

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

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(Oecologia, sous presse)

Abstract

The species richness of communities should largely depend on habitat variability and/or on habitat state. We evaluated the power 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 not including habitat state variables), 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, we explained 36% of the variability in species richness for all data and at best 47% for all taxonomic units at upstream sites with 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 variability in species richness from these model types. This limited precision should be primarily related to the fact that rare species produced most of the richness patterns in our creeks. The prediction of these rare species is generally difficult for various reasons and a problem relevant 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 for 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 variability, species richness should depend on habitat state (i.e. the mean conditions) (Resh et al. 1994). Therefore, evaluating the power of habitat variability and habitat state to predict the diversity of communities is an important exercise. This paper assesses that power using 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). Disturbance frequency 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, current stream ecology considers abiotic factors in terms of temporal and spatial habitat heterogeneity to be of major importance (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; Schlosser 1985)

and 2) reduction of diversity through biotic interactions at stable discharge pattern (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, 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 on fish suggests that the Patch Dynamics Concept can be applied for mobile organisms (see Frid and Townsend 1989; Downes 1990 for a debate of this point).

However, the only study testing the Patch Dynamics Concept for lotic fish did not support the concept (Persat et al. 1994). Therefore, the authors suggested separate studies of juveniles and adults as ontogenetic niche shifts could explain why the Patch Dynamics Concept predictions were not supported. In addition, long-living 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 to include variables describing the state of habitats in studies relating species richness to habitat variability.

A study of lotic young fish in diverse neotropical communities considering a short temporal scale (weeks) and a small spatial scale (< 100 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 studied creeks (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 well adapted to study multi-species patterns (Poizat and Pont 1996). In addition, the studied creeks of the neotropical Sinnamary River (French Guiana) play the role of 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 variations (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, depending on 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 to study the impact of the variability and the state of abiotic factors on young fish species richness.

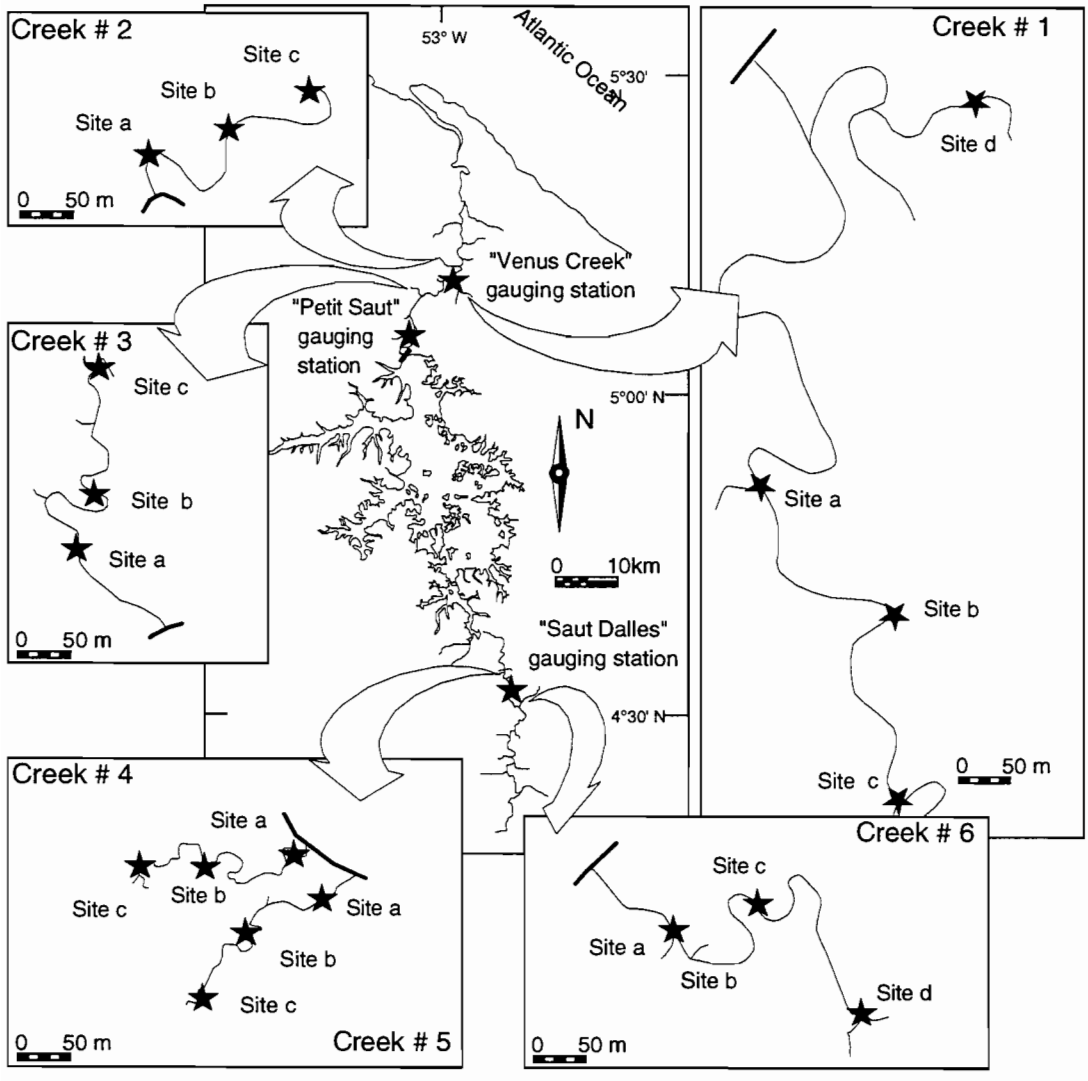

Fig. 1. Sampling sites in the six studied tributaries of the Sinnamary River (French Guiana, South America). Stars indicate the location of the different gauging stations in the Sinnamary River and the stream gauges of each of the 20 sampling sites (labelled a,b,c and/or d). Only one gauge was used for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

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. highest species richness 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.

Study area

The Sinnamary River is the fifth largest river of French Guiana, having a length of approximately 260 km and a mean annual discharge of 230 $m^3 s^{-1}$ (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 was dependent of the alternation of two (November to February) and (April to July) rainy seasons and a dry season (August to November) (Ponton and Copp 1997).

The studied creeks drain small catchments (Fig. 1) that are entirely covered by a natural floodplain forest. Therefore, the creeks are well-shaded and aquatic macrophytes

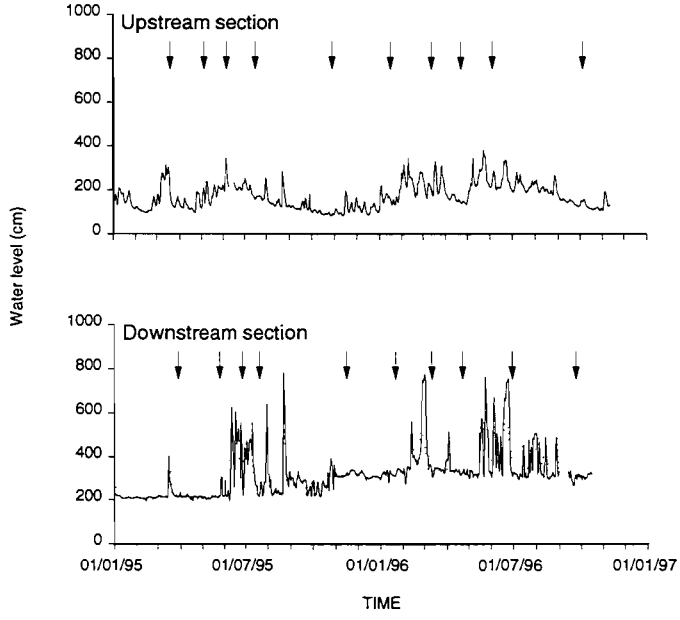

Fig. 2. Water levels recorded at Saut Dalles (upstream) and Petit Saut (downstream) gauging stations, from January 1995 to November 1996. We indicated fish sampling campaigns by vertical arrows and downstream values that would have been observed without the dam by a dashed line. We calculated these latter values using equations in Ponton and Vauchel (1998).

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 1m s^{-1} during floods (Ponton and Vauchel 1998).

Material and Methods

Hydrology

A gauging station upstream from Saut Dalles rapids (Fig. 1) recorded upstream section water levels of the Sinnamary in 1995 and 1996. Downstream section water levels were recorded for the same period with a similar gauging station downstream from Petit Saut dam and with a gauging station about 25 km downstream from the dam at the entrance of Venus Creek (Fig. 1). These Sinnamary gauging stations recorded water levels every hour. In addition, we set up 19 stream gauges in 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 characterise temporal habitat variability in terms of flow disturbance (see Resh et al. 1988 for rationale) prior to each fish sample (see below).

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 m^2 at random (i.e. without knowing whether fish were present or not) in three (creek #2, 3, 4 and 5) or four (creek #1 and 6) sampling sites at each sampling campaign. Mérigoux et al. (1998) give a complete description of

the sampling method. In summary, we firstly measured temperature, pH, oxygen with a ICM 51000 multiparameter and water turbidity with a LaMotte Model 2008 digital turbidity meter in the undisturbed water. We also measured the current velocity at the water surface by observing the time required for a floating object to traverse one meter downstream and assigned it to five categories (in cm s^{-1}: 0 to 6, 7 to 9, 10 to 14, 15 to 25 and > 25). Preliminary measures showed that these variables varied little across the sampling volume, so we measured them only once. Then, we enclosed the sampling area with two or three stop nets (1mm 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 (1mm mesh) and immediately preserved them in 90% alcohol. After fish sampling, we recorded at each point sample of a 1 x 1 m grid the water depth (in cm) and 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, blocs). 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 of the sampling site detected and avoided rotenone; 3) clay, largely represented in our sampling sites, is known to reduce rapidly the toxicity of rotenone (Gilderhus 1982); 4)

above 23 °C the half life of this toxicant 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 Ponton (unpublished). 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 faced identification problems for few species, which we usually grouped at the genus level. We measured the standard length of each specimen to the nearest mm. We separated juveniles from adults according to the minimal size at first maturity observed for each species in the Sinnamary River (Mérigoux and Ponton 1998; Ponton and Mérona 1998).

Data analysis

Temporal variables

We had to evaluate creek site water levels for the whole study period from water levels in the creeks and in the Sinnamary River. For each site, we examined the relationship between the water levels recorded at its creek gauge and those obtained from "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 pieces (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 pieces models implied that the site water level depended on the river water level only

beyond a given threshold of the Sinnamary water level. In other periods, it was only under the influence of local rains pouring over the creek catchment. For these periods, the regression line for the first piece was described as:

$Y = m_1 + \varepsilon$ if $WL \leq th$

Y : water level in the creek site

m_1 : observed mean water level at the creek site for $WL \leq th$

ε : error term.

WL : Sinnamary water level

th : 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:

$Y = aWL + b + \varepsilon$ 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 having a linear relationship with the water level of the Sinnamary. For sites having linear in pieces models, we decomposed the total variance into inter-variance (mean variance between the two pieces 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:

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

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

Var : total variance of creek site water level

p : frequency of hourly data for $WL > th$

m_2 : predicted mean water level at the creek site for $WL > th$

m : predicted overall mean water level at the creek site, as $m = pm_2 + qm_1$

q : frequency of hourly data for $WL \leq th$

v_2 : variance of water level at the creek site for $WL > th$ with water level predicted from the second part of the linear piecewise model

v_1 : observed variance of water levels at the creek site for $WL \leq th$ 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 (see above for the different categories) 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 for each sampling area an index of local variability 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 Mérigoux 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 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 vs 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 separately the upstream and downstream section of the Sinnamary, the taxonomic units (Characiformes and non-Characiformes) and each ontogenetic group.

Fish richness vs 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 shape relationship is theoretically expected),

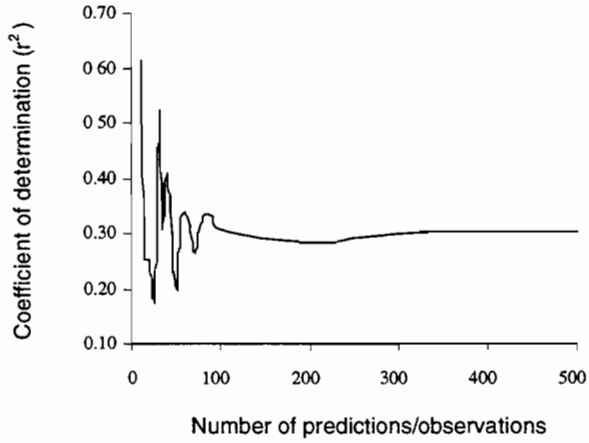

Fig. 3. Coefficient of determination in the regressions of observed versus predicted fish taxa richness versus the number of predictions/observations included (included samples were drawn at random for all taxa and all samples, cf. Fig. 9).

the spatial variability variable and its log transformation and all the habitat state variables and their log transformation.

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

We tested the robustness of the models by Monte Carlo simulations (Manly 1991). We modelled 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 if 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 (1995a, b, and 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 alternance

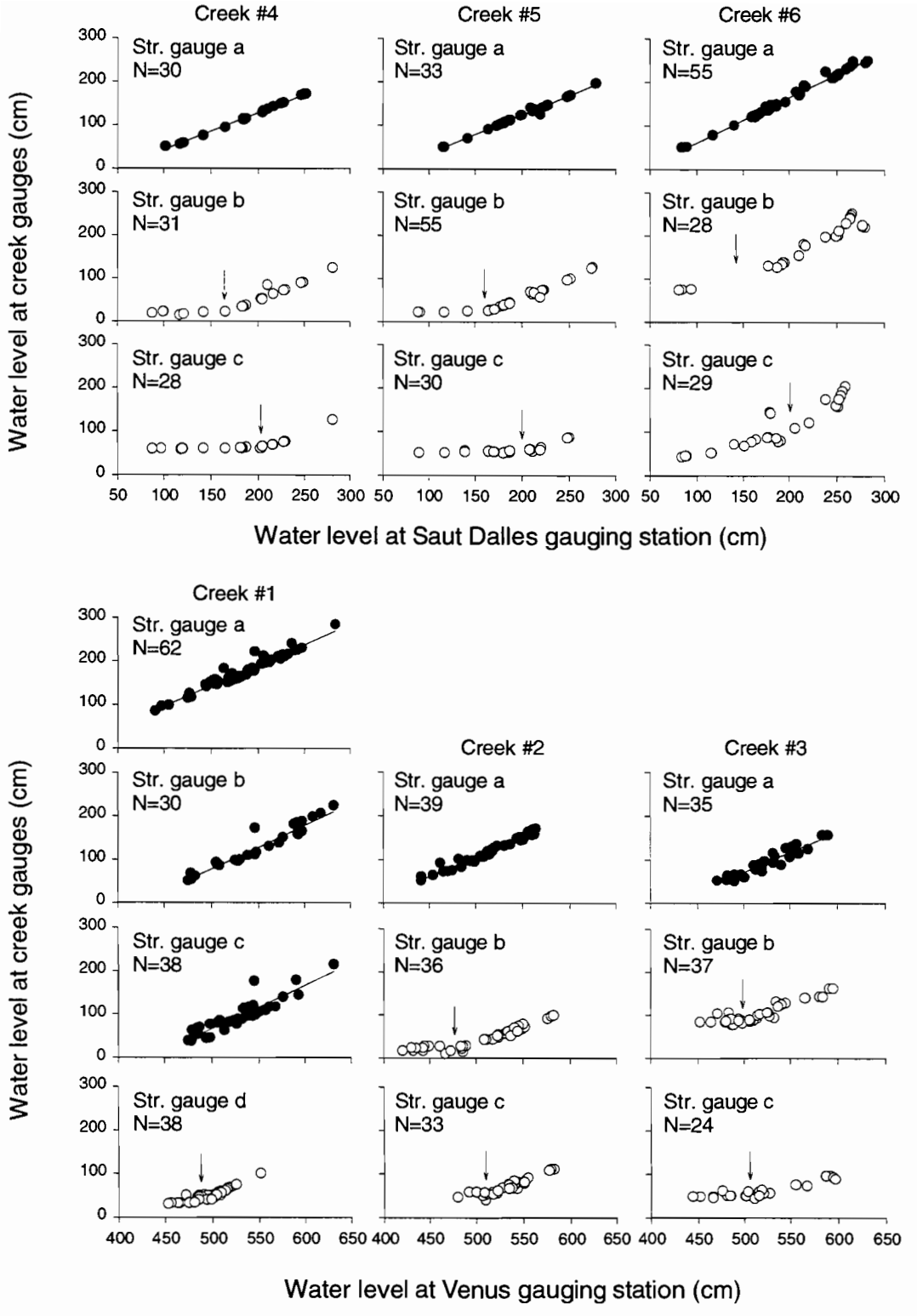

Fig. 4. Relationships between the water level recorded at each creek site and the main river, respectively in its upstream (Saut Dalles gauging station) and downstream section (Venus Creek gauging station). We indicated linear relationships by black dots and linear in pieces relationships by white dots (vertical arrows: inflection points; N: number of records). Note, that we used stream gauge "a" in creek #6 for two close-by sampling sites.

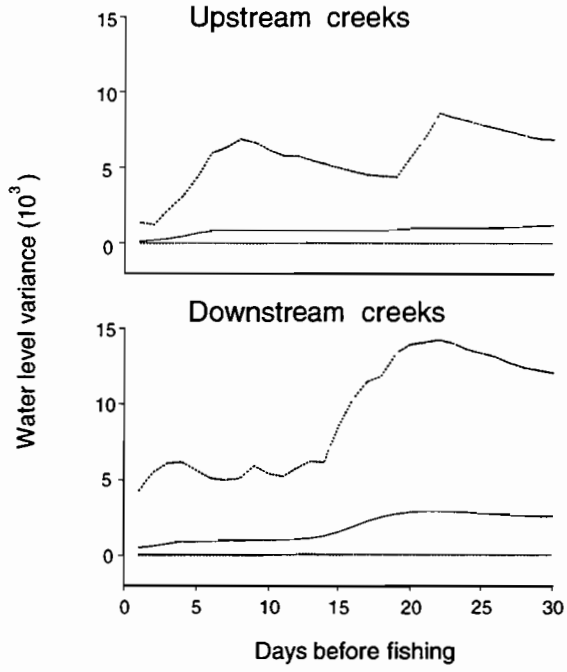

Fig. 5. Mean (solid lines), minimum and maximum (dashed lines) of water level variance for time considered (as days before fishing) in each, 100 samples from upstream and downstream creeks.

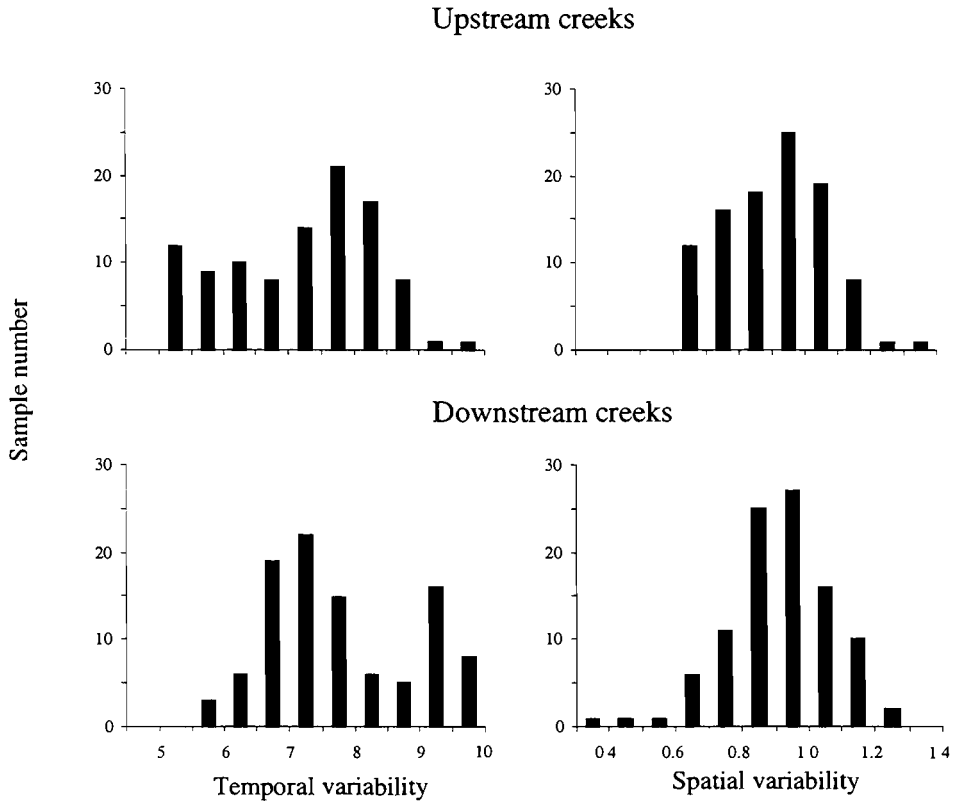

Fig. 6. Frequency of the temporal (log) and the spatial variability habitat scores in each, 100 samples from upstream and downstream creeks.

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). A seasonal pattern was not detectable 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 depended permanently on that of the Sinnamary River (Fig. 4). Most of these sites were located 30 to 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 type 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 differed as well 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 1.4 (Fig. 6). The test of the Patch Dynamics 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 to 8% of the point samples of 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 to 25 % of the point samples) and/or 3) a wide range of depth values (e.g. a depth ranging from 6 to 135 cm).

Concerning habitat state, water temperature (°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 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 (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 34790 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 to half of the species richness in more than 80% of the samples. Globally, the Characiformes and the 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 significantly differ 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-test with t = 2.462, df = 99 and p = 0.016).

Richness vs habitat variability

Temporal and spatial habitat variability investigated were poor descriptors of fish taxa richness in the framework of the Patch Dynamics Concept, whatever 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

Table 1. Sample characteristics and fish composition in the upstream and downstream creeks and in the total samples. N: number.

	Upstream	Downstream	Total
N samples	100	100	200
Sampled volume (m^3)	1622	2914	4536
Sampled area (m^2)	4649	5865	10514
N orders	6	6	6
N families	20	22	25
N individuals	18234	16556	34790
N taxa	59	60	73
N Characiformes taxa	32	31	39
N non-Characiformes taxa	27	29	34
N ELS[1] taxa	46	52	57
N YJ[2] taxa	50	54	60
N OJ[3] taxa	44	38	53
Mean N taxa per sample	15.7	13.7	14.7
Mean N individuals per sample	182.3	165.6	174.0
Mean N Characiformes ELS taxa per sample	4.6	3.2	3.9
Mean N Characiformes YJ taxa per sample	6.0	4.6	5.3
Mean N Characiformes OJ taxa per sample	3.6	2.7	3.2

[1]ELS: early life stages, [2]YJ: young juveniles, [3]OJ: old juveniles.

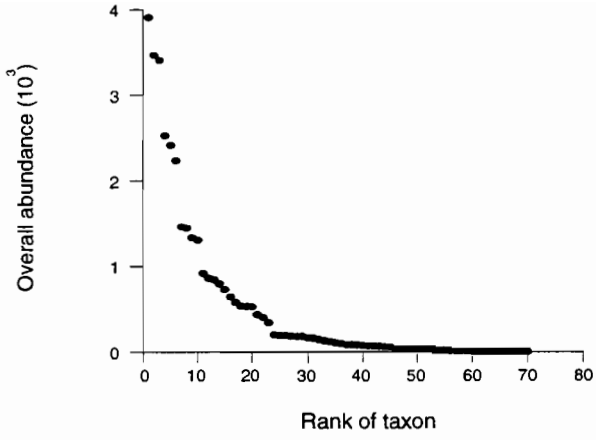

Fig. 7. Rank frequency diagram of the 73 taxa collected in the 200 samples.

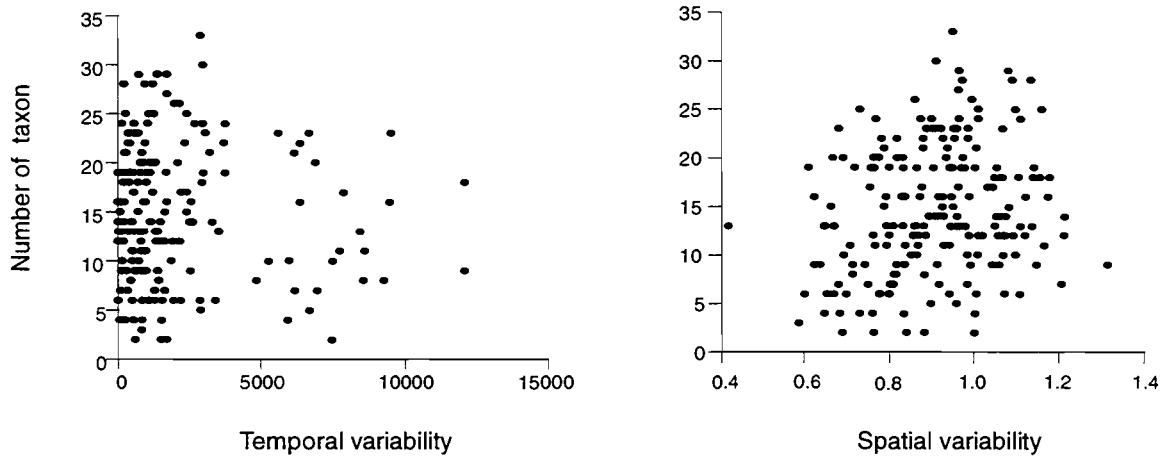

Fig. 8. A typical example of fish taxa richness versus habitat variability, showing all 200 samples for a hydrological period of 30 days before fishing (using other hydrological periods or separating sections, taxonomic units and ontogenetic stages did not produce clearer patterns). Richness was positively related to spatial variability by $y = 6.486(\pm 2.767) + 9.051x(\pm 2.998)$ (95% confidence limits in brackets), $r^2 = 0.044$, and $p = 0.003$.

spatial variability, but the variability of the richness explained by this habitat parameter was very low (e.g. 4% in the complete data set, cf. Fig. 8).

Richness vs habitat variability and state

Depending on the hydrological pre-sampling period included, we explained 32 to 36% of the overall fish richness variability if considering habitat variability and state 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 theses periods species richness slightly increased along with low values of temporal variability and decreased at higher temporal variability. Using the significant variables of the model considering 30 days before fishing in Monte Carlo simulations produced predictions that scattered considerably around observations (Fig. 9). The model predicted 31% of the observed variability in species richness in an accurate way (its constant did not significantly differ from zero and its slope did not significantly differ from one, 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 considering 30 days before fishing were the most significant in most of these separate analyses. Therefore, we only presented results considering this period in further analyses.

Table 2: Stepwise multiple regressions of taxa 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 and p: associated probability for the entire model. For each variable and DBF, we indicated in brackets if a variable was log transformed, its sign, and its associated probability (ns: $p > 0.05$)

Statistical traits and variables sign		DBF 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

Table 3: Robustness of richness predictions (N = 500) from different types of models on richness versus habitat variables. We regressed observations versus predictions (see Fig. 10 for one example) to obtain r^2: coefficient of determination, p: associated probability, Const: constant if significantly ($p < 0.05$) different from 0, S: slope and 95% confidence limits in brackets, t: t value for testing if S = 1, with S = 1 if $t \leq 1.965$.

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[1] Characiformes	0.104	< 0.001	ns	0.873 (±0.256)	0.992
Upstream YJ[2] Characiformes	0.227	< 0.001	1.203	0.851 (±0.140)	2.129
Upstream OJ[3] Characiformes	0.238	< 0.001	0.592	0.864 (±0.138)	1.971

[1]ELS: early life stages, [2]YJ: young juveniles, [3]OJ: old juveniles.

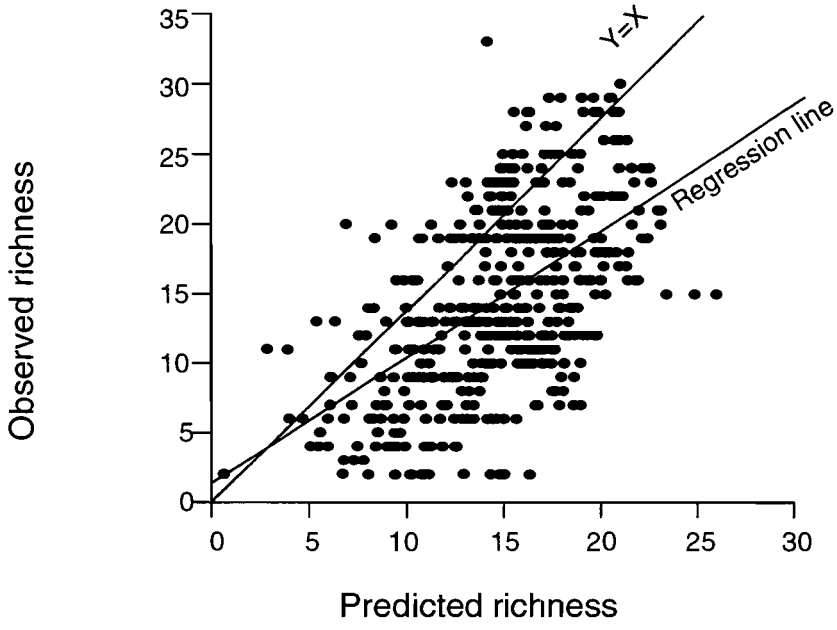

Fig. 9. Observed fish taxa richness versus "blind" predictions of taxa richness (from Monte Carlo simulations, for $n = 500$), using the variables for $DBF = 30$ from Table 2 and the whole data set, $y = 0.894(\pm 0.120)x$ (95% confidence limits in brackets) $r^2 = 0.305$, and $p < 0.001$.

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

Statistical traits	Upstream		Downstream	
and variables	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 taxa richness of Characiformes and non-Characiformes in upstream creeks, versus habitat variability and state variables for 30 days before fishing. See Tables 2 and 4 for further details.

Statistical traits and variables	Characiformes Sign	Statistics	non-Characiformes Sign	Statistics
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

Total fish richness of the upstream creeks was more significantly explained by habitat variability and state than 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 taxa richness.

We obtained similar results to those in the previous upstream example if separating Characiformes and non-Characiformes taxa in the upstream creeks (Table 3 and 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 to 24% of the observed variability in taxa richness (Table 3). In addition, these models were very unstable and often not accurately predicting as the constant differed significantly from zero and the slope differed significantly from one twice (Table 3).

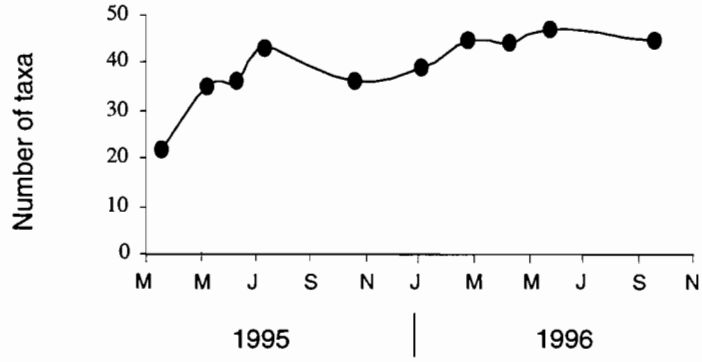

Fig. 10. Total number of taxa observed in the upstream creeks for each sampling campaign (indicated by black dots) in 1995 and 1996.

Discussion

Richness vs habitat variability

Predictions of the Patch Dynamics Concept were not supported by our data although the study design was well adapted 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). Despite these well adapted conditions, we were unable to demonstrate any pattern of richness in relation to temporal variability (if not including habitat state variables), regardless of the temporal period before fishing, 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 in support of the Patch Dynamics Concept was related to patterns of species richness produced by interfering biological phenomena that were not disturbance controlled. 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 of the Characiformes taxa are known to reproduce during the rainy season at increasing water levels (Munro 1990; Lowe-McConnel 1987). This 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 (Fig. 2 and 10).

Thus, seasonal reproduction did not affect the potential number of young fish taxa in our creeks.

Only two 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. 1997), 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 for lotic animals according to this weight of evidence. An underlying assumption of the Patch Dynamics Concept producing the 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 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 in species richness of lotic animals (e.g. Statzner and Resh 1993). In our case, about 20% of the collected individuals contributed half to 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 vs 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. Thereby, we

could accurately predict 31% of the observed variability in species richness for all data. Species richness slightly increased along 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 a more elevated temporal variability (than upstream samples) and a reduced diversity 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. Taxa richness increased with temporal variability (including habitat state 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 not simultaneously other environmental parameters that may potentially act as a buffer against temporal variability. For example, in upstream creeks, species richness increased with higher spatial heterogeneity. Correspondingly, a positive relationship was found 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 was 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) providing fish shelter and diversified food. This importance was demonstrated for temperate (Schiemer and Zalewski 1992) and tropical (Tito de Morais 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 with the raising waters of the Sinnamary River. It is well known that floodplains are essential components of large rivers (Lowe-McConnel 1987). Flood pulses are the driving force for river-floodplain systems (Junk et al. 1989) and provide diverse habitats where fish find food, shelter and spawning sites (Bonetto et al. 1989; Junk and Da Silva 1995).

In the upstream creeks, Characiformes richness had relations with habitat variables similar to those of all taxa. Differently, 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 Morais 1994). We did not detect any 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 taxa 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 detect 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 impact aquatic biota (Bain et al. 1988; Bonetto et al. 1989). Thus, brutal water releases at the dam like the one that rose the water level for 5 m over two days in August 1995 could have reduced fish diversity.

Conclusion and perspectives

We demonstrated the need to consider separately studied 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 play the role of nurseries for early life stages and the discharge in the main channel largely 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 on ontogenetical habitat changes.

Although we demonstrated that abiotic factors influence species richness of young fish, biotic factors probably had effects on 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 (see above for the discussion of

this pattern). Predation upon young fish should 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 are feeding on the same food items (small crustaceans, larvae and adults of insects, Mérigoux and Ponton 1998). However, it is difficult to speculate that 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 variability in fish richness. In terms of predictive power, the models "blindly" predicted at maximum 37% of the observed variability in species richness. This limited precision should be primarily related to the fact that 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 ecology has to face the fact that it will be difficult to predict animal species richness on a spatial scale in focus of 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 to predict 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 being 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. 1997). Therefore, such traits could serve to create metrics of functional community diversity. Consequently, our next task will be to exploit our data from the Sinnamary testing the hypothesis that fluctuating environments such as 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.

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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.

	UPSTREAM																				
	Depth (cm)	Litter (%)					Vegetation (%)			Substrate (%)						Bank slope (%)				
		1	2	3	4	5	1	2	3	1	2	3	4	5	6	1	2	3	4	5
Min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Max	126	100	57	47	100	12	0	76	27	82	100	100	0	6	45	100	88	100	50	50
Median	35	42	19	11	34	0	0	11	0	9	38	57	0	0	0	19	25	14	10	11
Mean	40	46	22	14	39	1	0	17	2	17	41	49	0	0	1	28	26	17	14	14
SD	23	23	12	11	24	2	0	18	6	21	23	30	0	1	6	28	17	16	13	15
	DOWNSTREAM																				
	Depth (cm)	Litter (%)					Vegetation (%)			Substrate (%)						Bank slope (%)				
		1	2	3	4	5	1	2	3	1	2	3	4	5	6	1	2	3	4	5
Min	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Max	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

A3

Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America

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Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America

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A total of 1468 young fish representing 66 taxa from the Sinnamary River, French Guiana was classified by complete cluster analysis of mean relative body width and mean relative body height into four groups. These had anguilliform, disciform, flat or intermediate body shapes and belonged chiefly to Gymnotiformes, Perciformes, Siluriformes and Characiformes, respectively. Several of the taxa shifted from one to another body shape during ontogenesis. Seven diet groups were defined by complete cluster analysis. Among these, six groups were represented by carnivorous fish. The three most frequent groups had diets of (1) mainly insect larvae and small crustaceans, (2) insect larvae, and (3) predominantly terrestrial insects. The majority of the fish taxa showed ontogenetic diet shifts. Carnivorous fish usually switched from small-size prey, such as small crustaceans, to intermediate-size prey, such as insect larvae and/or to large-size prey, such as insects and/or fish. However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. Taxa of different body shapes had significantly different diets. Disciform fish fed mainly on aquatic insect larvae and terrestrial insects but also, in small amounts, on small curstaceans. Most anguilliform taxa ate insect larvae. Individuals belonging to the depressiform or intermediate morphotype had varied diets ranging from plant debris and substratum to fish.

Key words: neotropical fish; young stages; morphology; food regime; ontogenetic diet shifts; French Guiana.

INTRODUCTION

Studying the early life stages of fish is of major importance for understanding the structure of fish communities, as events that occur during this crucial period determine year-class strength (Snyder, 1983; Balon, 1984; Houde, 1987; Grosberg & Levitan, 1992). Among the different factors influencing survival of young fish, the availability of suitable prey (Hartmann, 1983), feeding efficiency (locating and catching prey) and capabilities of avoiding predators (Webb & Weihs, 1986) are of central importance. These factors are linked strongly to body shape and morphological features that constrain swimming capabilities (Webb, 1984), and thus resource use (Gatz, 1979), or predator avoidance (Keast, 1978; Webb & Weihs, 1986; Bone *et al.*, 1996).

Tropical freshwater fish species exhibit a great diversity of biological and ecological attributes (Lowe-McConnell, 1987). In South America, only Winemiller (1991) has studied freshwater fish morphology while most studies on

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fish diets focus only on the adult stages (Knöppel, 1970; Zaret & Rand, 1971; Lowe-McConnell, 1979; Goulding, 1980; Power, 1983, 1984; Carvalho, 1984; Flecker, 1992). Thus, very few detailed studies are available on the food habits of young tropical fish (piscivores: Winemiller, 1989; armoured catfish: Mol, 1995). Consequently, while ontogenetic diet shifts have been studied well in temperate freshwater fish (Keast, 1978, 1980; Hartmann, 1983; Ponton & Müller, 1988; Copp & Mann, 1993; Garner, 1996), few studies exist on ontogenetic diet shifts in neotropical freshwater fish (Angermeier & Karr, 1983; Winemiller, 1989; Mol, 1995). For French Guiana, the area of our study, the few data that have been published on fish diet focused only on a limited number of adult taxa (Boujard *et al.*, 1988, 1990; Rojas-Beltran, 1989; Horeau *et al.*, 1996).

Therefore, from young fish caught regularly in six tributaries of the Sinnamary River, the objectives of this paper were: (1) to identify groups homogeneous by their body form and to document changes in their shape during ontogeny; (2) to describe their food regimes and to detect ontogenetic diet shifts; and (3) to evaluate the relationships between body form and diet. Thereby, the present study is the first step of a larger project aiming to understand the relationships between habitat and life-history strategies of neotropical fish species during their early life. Beyond this fundamental aspect, the present investigations have an applied aspect concerning river regulation in the neotropics, as the Sinnamary River has been subjected to strong hydrological disturbance (Ponton & Copp, 1997) since the construction of the Petit Saut hydroelectric dam in 1994.

MATERIALS AND METHODS

SAMPLING

From January 1995 to October 1996, six tributaries of the Sinnamary River (Fig. 1) were sampled regularly with rotenone (for a complete description of the sampling method see Mérigoux *et al.*, 1998). For each of the 200 samples, all fish were preserved in 90% alcohol in the field and then transferred to 75% alcohol in the laboratory where they were processed later. All specimens were sorted and identified using keys for adults by Géry (1977); Rojas-Beltran (1984); Kullander & Nijssen (1989); Planquette *et al.* (1996), and keys for juveniles by Ponton (unpublished) and measured for standard length (L_s) to the nearest 1 mm. Keys for juveniles are 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. Juveniles were retained for analysis by separating them from adults according to the minimal size at first maturity observed for each species in the Sinnamary River (Ponton & Mérona, 1998). Depending on the number of individuals available, up to three size classes were separated for each taxon. Size limits were chosen in order to separate roughly early life stages (about 4 to 15–20 mm, depending on species) from young (about 15–20 to 30–50 mm) and older juveniles (about >30–50 mm). Within each of these size classes, three to 10 specimens (depending on their availability) were chosen randomly for analysis without any consideration of the time and place of sampling (Table I).

BODY SHAPE AND DIET

For the description of body shape, three variables were measured on each individual: standard length, maximum height and maximum width. For smaller individuals measurements were taken on fish outlines drawn with the help of a camera lucida set up on a dissecting microscope. Calipers were used for larger individuals. With both techniques measurements were made to the nearest 0·1 mm.

Stomach contents (or contents of the anterior part of the digestive tract for stomachless species) were removed carefully under a dissecting microscope. Fish with an empty

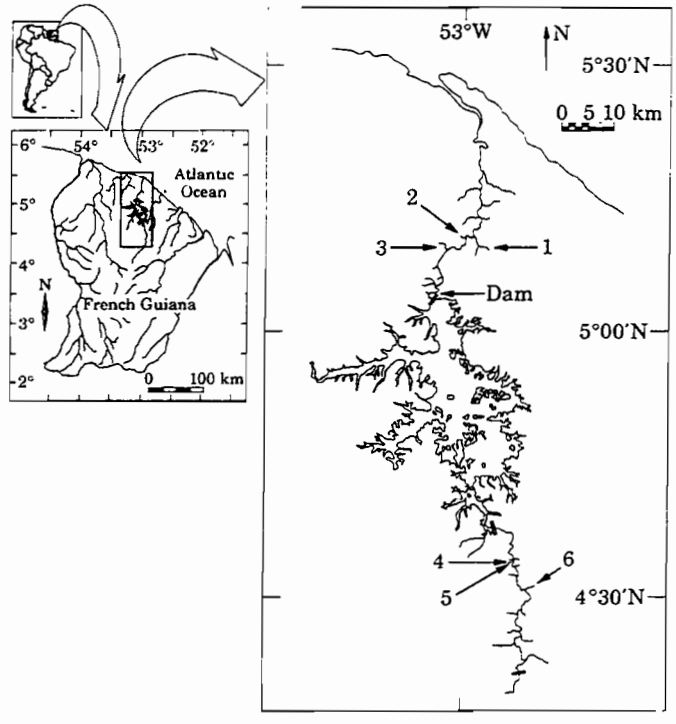

FIG. 1. Map of the Sinnamary River (French Guiana, South America) with the six tributaries sampled.

stomach were replaced randomly by other individuals, if sufficient material was available. Diet items were identified under a dissecting microscope (up to 50 × magnification) or a microscope (100–400 × magnification) and assigned to 10 categories: fish (Fi), molluscs (snails) (Mo), large crustaceans (shrimps) (Cr), small crustaceans (Copepoda, Cladocera and Ostracoda) (sCr), terrestrial insects (TeIn), insect larvae (InLa), water mites (WaMi), rotifers (Ro), vegetative debris (VeDe), and substratum (Su). The relative volumes of each category were estimated following the method of Sheldon & Meffe (1993). For each fish, the most abundant food category was assigned rank 1, the second most abundant rank 2, and so on.

DATA ANALYSIS

Mean relative body width (ratio of maximum width to standard length) and mean relative body height of each size class were calculated. These ratios were treated with cluster analysis by the complete linkage method (Legendre & Legendre, 1979) using Euclidean distances.

For each individual, ranks of food categories were first converted into percentages by a modified version of the MacArthur broken stick model (Magurran, 1988). This model gives the expected percentage N_r of each food category when eaten randomly and simultaneously by a fish by:

$$N_r = \frac{100}{S} \sum_{n=r}^{S} \frac{1}{n}$$

with S=total number of food categories, and r=rank number of food category [$r \varepsilon (1, \ldots S)$].

Thus, a fish feeding on two food categories would have 100/2(1/1 + 1/2)=75 assigned to category ranked 1 and 100/2(1/2)=25 to category ranked 2. Identically, an individual

TABLE I. Body shape and diet of fish taxa for different ontogenetical stages, with species authority and occurrences of switches between morphological or diet groups

Species	Authority	Early life stages				Young juveniles				Old juveniles				Body shape switch	Diet switch
		n	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet		
Characiformes															
Hemiodontidae															
Hemiodopsis quadrimaculatus	(Pellegrin, 1908)	10	9–14	Ang	sCr-InLa	10	15–24	Int	InLa					—	—
Parodon guyanensis	Géry, 1959	10	7–16	Int	sCr-InLa									—	—
Curimatidae															
Chilodus zunevei	Puyo, 1945	10	9–13	Int	InLa-sCr	10	14–30	Int	InLa-sCr	7	31–65	Int	InLa-sCr	No	No
Unidentified young Curimatidae		10	5–14	Int	InLa-sCr	10	15–30	Int	VeDe-Su	10	31–75	Int	VeDe-Su	No	Yes
Anostomidae															
Leporinus despaxi	Puyo, 1943									10	30–90	Int	VeDe-Su	—	—
Unidentified young Leporinus		10	8–13	Int	sCr-InLa	10	14–45	Int	InLa-sCr	10	48–115	Int	VeDe-Su	No	Yes
Erythrinidae															
Erythrinus erythrinus	(Schneider, 1801)	10	7–16	Int	InLa-sCr	10	17–50	Int	InLa-sCr					—	—
Unidentified young *Hoplias*		10	4–20	Int	InLa-sCr									—	—
Hoplias aimara	(Valenciennes, 1840)					10	21–50	Int	InLa-Fi					—	—
Hoplias malabaricus	(Bloch, 1794)					10	21–50	Int	InLa-Fi	10	51–160	Int	InLa-Fi	No	Yes
Lebiasinidae															
Copella carsevennensis	(Regan, 1912)	10	6–12	Int	sCr-InLa	10	13–19	Int	InLa-sCr	10	20–24	Int	InLa	No	Yes
Nannostomus beckfordi	Günther, 1872					10	13–20	Int	InLa	10	21–25	Int	InLa	—	—
Pyrrhulina filamentosa	Val. in. Cuv., 1846	10	6–14	Int	InLa-sCr	10	15–30	Int	InLa-sCr	10	31–49	Int	TeIn	No	Yes
Gasteropelecidae															
Gasteropelecus sternicla	(Linnaeus, 1758)	10	6–11	Int	TeIn	10	12–15	Int	TeIn					—	—
Characidae															
Astyanax bimaculatus	(Linnaeus, 1758)	10	9–14	Int	InLa-sCr	10	15–30	Int	InLa-sCr					—	—
Astyanax cf *keithi*	Géry, Planquette & LeBail, 1996	10	6–11	Int	sCr-InLa	10	12–25	Int	InLa-sCr	10	26–55	Disc	TeIn	Yes	No

TABLE I. *Continued*

Species	Authority	Early life stages				Young juveniles				Old juveniles				Body shape switch	Diet switch
		n	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet		
Characidae (cont'd)															
Bryconops spp		10	8–15	Int	InLa	10	16–35	Int	TeIn	10	36–80	Int	TeIn	No	Yes
Characidium fasciadorsale	Fowler, 1914	10	7–14	Int	InLa-sCr	10	15–30	Int	InLa	10	31–45	Int	InLa	No	Yes
Charax pauciradiatus	Günther, 1864	10	6–13	Int	sCr-InLa									—	—
Hemigrammus ocellifer	(Steindachner, 1882)	10	7–12	Int	sCr-InLa	10	15–19	Int	InLa-sCr	10	20–25	Int	TeIn	No	Yes
Hemigrammus unilineatus	(Gill, 1858)	10	9–12	Int	sCr-InLa	10	13–19	Int	InLa-sCr	10	20–29	Int	TeIn	No	Yes
Hyphessobrycon aff. *sovichthys*	Schultz, 1944	7	7–10	Int	InLa-sCr	10	11–15	Int	InLa-sCr	10	16–20	Int	InLa-sCr	No	No
Melanocharacidium sp.		10	5–13	Int	InLa-sCr									—	—
Microharacidium eleotrioides	(Géry, 1960)	10	5–9	Int	InLa-sCr	10	10–14	Int	InLa					—	—
Moenkhausia chrysargyrea	(Günther, 1864)	10	7–14	Int	InLa-sCr	10	15–30	Int	TeIn	10	31–45	Disc	TeIn	Yes	Yes
Moenkhausia collettii	(Steindachner, 1882)	10	5–12	Int	sCr-InLa	10	13–25	Int	InLa-sCr	10	26–35	Int	TeIn	No	Yes
Moenkhausia georgiae	Géry, 1966	10	7–13	Int	sCr-InLa									—	—
Moenkhausia hemigrammoides	Géry, 1966	10	7–13	Int	InLa-sCr	10	14–25	Int	TeIn	10	26–35	Disc	TeIn	Yes	Yes
Moenkhausia oligolepis	(Günther, 1864)	8	6–13	Int	InLa-sCr	10	14–30	Disc	TeIn	10	31–65	Disc	TeIn	Yes	Yes
Moenkhausia surinamensis	Géry, 1966					10	14–30	Int	TeIn	10	31–60	Disc	TeIn	—	—
Phenacogaster aff. *megalostictus*	Eigenmann, 1909	10	5–12	Int	InLa-sCr	10	13–19	Int	InLa	10	20–29	Int	InLa	No	Yes
Piabucus dentatus	(Köhlreuter, 1761)	10	9–14	Int	InLa-sCr	10	15–40	Int	TeIn					—	—
Poptella brevispina	(Reis, 1989)	10	5–13	Int	InLa-sCr	10	14–30	Disc	TeIn					—	—
Pristella maxillaris	(Ulrey, 1894)	10	7–10	Int	sCr-InLa	10	11–15	Int	InLa-sCr	10	16–19	Int	InLa-sCr	No	Yes
Pseudopristella simulata	Géry, 1960	10	6–11	Int	sCr-InLa	10	12–17	Int	InLa-sCr	9	18–22	Int	sCr-InLa	No	?
Unidentif. young *Acestrorhynchus*		10	9–15	Int	InLa-sCr	10	16–40	Int	InLa-Fi	10	41–120	Int	Fi	No	Yes
Siluriformes															
Auchenipteridae															
Tatia intermedia	(Steindachner, 1876)	10	7–14	Int	TeIn	10	14–25	Int	TeIn	7	26–60	Int	TeIn	No	No

TABLE I. *Continued*

Species	Authority	Early life stages				Young juveniles				Old juveniles				Body shape switch	Diet switch
		n	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet		
Siluriformes (cont'd)															
Pimelodidae															
Unidentified young *Pimelodella*		10	8–20	Int	InLa-sCr									—	—
Pimelodella cristata	(Müller & Troschel, 1848)					10	21–40	Int	InLa-sCr	10	41–95	Int	InLa-Fi	No	Yes
Pimelodella gracilis	(Val. in Cuv. & Val., 1840)					10	21–40	Int	InLa	3	41–100	Int	InLa-sCr	No	?
Pseudopimelodus raninus	(Valenciennes, 1840)	10	8–13	Dep	InLa-sCr	10	14–30	Dep	InLa	10	31–65	Dep	InLa-Fi	No	Yes
Rhamdia quelen	(Quoy & Gaimard, 1824)					9	18–50	Int	InLa-Fi					—	—
Helogenidae															
Helogenes marmoratus	(Günther, 1863)					5	14–30	Int	TeIn	10	31–60	Int	TeIn	—	—
Aspredinidae															
Bunocephalus coracoideus	Cope, 1874	4	7–14	Dep	InLa	10	15–39	Dep	InLa-Fi	10	40–70	Dep	TeIn	No	Yes
Trichomycteridae															
Trichomycterus guianense	(Eigenmann, 1909)	10	8–14	Int	InLa	10	15–29	Int	InLa	10	30–50	Int	InLa	No	No
Callichthyidae															
Callichthys callichthys	Linnaeus, 1758	7	6–13	Dep	sCr-InLa	10	14–50	Dep	InLa-sCr					-	- -
Hoplosternum thoracatum	(Val. in Cuv. & Val., 1840)	8	6–13	Dep	sCr-InLa	10	14–50	Dep	sCr-InLa					—	— —
Loricariidae															
Ancistrus aff. *hoplogenys*	(Günther, 1864)	9	11–13	Dep	VeDe-Su	10	14–30	Dep	VeDe-Su	5	31–65	Dep	VeDe-Su	No	No
Gymnotiformes															
Sternopygidae															
Sternopygus macrurus	(Bloch & Schneider, 1801)	10	7–20	Int	InLa-sCr	10	21–60	Int	InLa	8	61–145	Ang	InLa	Yes	Yes
Hypopomidae															
Brachyhypopomus beebei	(Schultz, 1944)	7	8–20	Int	InLa-sCr	10	21–50	Aug	InLa	10	51–100	Ang	InLa	Yes	Yes
Hypopomus artedi	(Kaup, 1856)	10	7–20	Int	InLa-sCr	10	21–50	Ang	InLa	10	51–130	Ang	InLa	Yes	Yes

TABLE I. *Continued*

Species	Authority	Early life stages				Young juveniles				Old juveniles				Body shape switch	Diet switch
		n	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet	*n*	L_S (mm)	Body shape	Diet		
Gymnotiformes (cont'd)															
Gymnotidae															
Unidentified young *Gymnotus*		10	9–19	Int	InLa									—	—
Gymnotus anguillaris	Hoedeman, 1962					10	20–50	Ang	InLa	10	51–185	Ang	InLa	Yes	No
Gymnotus carapo	Linnaeus, 1758					10	20–50	Ang	InLa	10	51–185	Ang	InLa-sCr	Yes	No
Cyprinodontiformes															
Aplocheilidae															
Rivulus agilae	Hoedeman, 1954					10	11–15	Int	InLa-sCr					—	—
Rivulus xiphidius	Huber, 1979	10	5–10	Int	sCr-InLa	10	11–15	Int	InLa					—	—
Poeciliidae															
Poecilia parae	(Eigenmann, 1894)	10	6–12	Int	InLa-sCr									—	—
Synbranchiformes															
Synbranchidae															
Synbranchus marmoratus	Bloch, 1795	9	32–59	Ang	sCr-InLa	7	60–100	Ang	InLa	9	101–200	Ang	InLa	No	Yes
Perciformes															
Nandidae															
Polycentrus schomburgkii	Müller & Troschel, 1848					10	14–19	Disc	InLa-sCr	10	20–30	Disc	InLa-sCr	—	—
Cichlidae															
Cichlasoma bimaculatum	(Linnaeus, 1758)									10	30–70	Disc	InLa-sCr	—	—
Cleithracara maronii	(Steindachner, 1882)	10	10–13	Disc	InLa-sCr	10	14–34	Disc	InLa	10	35–52	Disc	InLa-sCr	No	?
Crenicichla saxatilis	(Linnaeus, 1758)	10	8–20	Int	InLa-sCr	10	21–50	Int	InLa-sCr	10	51–140	Int	InLa-Fi	No	Yes
Krobia guianensis	(Regan, 1905)	10	4–13	Disc	InLa-sCr	10	14–29	Disc	InLa	10	30–75	Disc	InLa-sCr	No	?
Nannacara anomala	Regan, 1905	10	6–12	Disc	InLa	10	13–19	Disc	InLa	10	20–29	Disc	InLa	No	No
Satanoperca aff. *leucosticta*	(Müller & Troschel, 1848)					10	14–30	Int	sCr-InLa	10	31–70	Int	sCr-InLa	—	—
Eleotridae															
Eleotris amblyopsis	(Cope, 1870)	10	10–15	Int	sCr-InLa	10	16–20	Int	InLa	10	21–25	Int	sCr-InLa	No	?

n, Number of individuals; L_S, range of standard length; Disc, disciform body; Ang, anguilliform; Dep, depressiform; Int, intermediate body; Fi, fish; TeIn; terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, vegetative debris; Su, substratum. Body shape and diet shifts are presented only for species with data for the three stages.

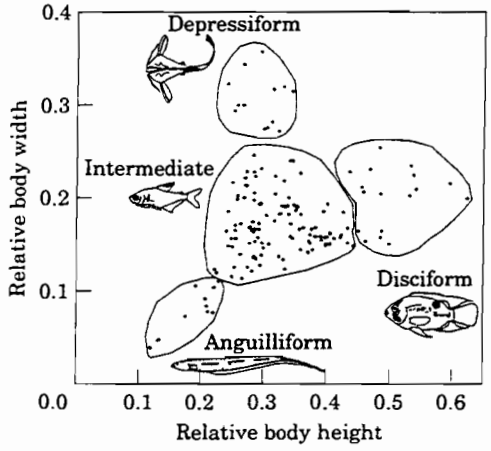

FIG. 2. Relative body width v. relative body height, indicating the four groups of body shapes resulting from complete cluster analysis of the 152 size classes of 66 taxa captured in the Sinnamary River (see Table I for the faunistic composition of the different groups).

feeding on three different categories would have 1100/18, 500/18, and 200/18 assigned for categories ranked 1, 2, and 3 respectively. Mean N_r values calculated for all the individuals of each size class were also treated with cluster analysis by the complete linkage method (Legendre & Legendre, 1979) using Euclidean distances. In order to provide a simpler index of prey use, the resulting diet groups were described by the prey items averaging >70% within the individuals of the group. Differences in diet among groups of fish with different body shapes were then tested by R^*C test of independence using G-test (Sokal & Rohlf, 1995).

RESULTS

MORPHOMETRY

The total of 1468 fish from 66 taxa grouped in 152 size classes (Table I) was separated by complete cluster analysis on mean relative body width and mean relative body height into four groups of different body shapes (Fig. 2). Disciform fish (*sensu* Holčik *et al.*, 1989) were characterized by high relative body height and medium relative body width values. This group included all stages of the Perciformes *Cleithracara maronii* (Steindachner), *Krobia guianensis* (Regan) and *Nannacara anomala* Regan, and juveniles of the Perciformes *Polycentrus schomburgki* Müller & Troschel and *Cichlasoma bimaculatum* L., and juveniles of the Characidae *Astyanax* cf. *keithi* Géry, Planquette & le Bail, *Moenkhausia chrysargyrea* (Günther), *M. hemigrammoides* Géry, *M. oligolepis* (Günther), *M. surinamensis* Géry and *Poptella brevispina* (Reis) (Table I). Anguilliform fish (*sensu* Holčik *et al.*, 1989) presented low relative body height and low relative body width values and included early life stages of *Hemiodopsis quadrimaculatus* (Pellegrin), juveniles of all Gymnotiformes, and all stages of *Synbranchus marmoratus* Bloch. Depressiform taxa (*sensu* Holčik *et al.*, 1989) were characterized by high relative body width and intermediate relative body height values. All stages of the Siluriformes *Pseudopimelodus raninus* (Valenciennes), *Bunocephalus coracoideus* Cope, *Callichthys callichthys* L.,

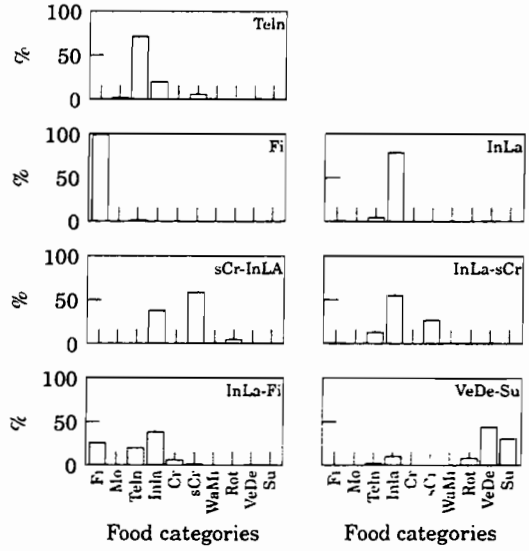

FIG. 3. Food spectra of each of the seven diet groups resulting from complete cluster analysis of Euclidean distances computed from percentages of food categories of the 152 size classes of 66 taxa captured in the Sinnamary River. Diet groups were defined by the categories representing ≥ 70% of the food items: Fi, fish; TeIn, terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, plant debris; Su, substratum (see Table I for faunistic composition of diet groups).

Hoplosternum thoracatum (Valenciennes) and *Ancistrus* aff. *hoplogenys* (Günther) belonged to this group. The remaining taxa, mainly Characiformes, presented intermediate body shapes.

Only 11 taxa presented a body shape that switched from one group to another during their ontogeny (Table I). Most of these shifts were from an intermediate body shape during early life to an anguilliform shape (*Sternopygus macrurus* (Bloch & Schneider), *Brachyhypopomus beebei* (Schultz), *Hypopomus artedi* (Kaup), *Gymnotus anguillaris* Hoedeman and *G. carapo* L., or a disciform shape (*A.* cf. *keithi*, *M. chrysargyrea*, *M. hemigrammoides* and *M. surinamensis*) during the juvenile period.

DIET

Among the 1468 full fish stomachs analysed (Table I), seven groups of diet were obtained by complete cluster analysis (Fig. 3). All these groups were defined by one or two main sources of food: terrestrial insects (TeIn, 16·5% of the groups; Table I, Fig. 3), fish (Fi, 0·7% of the groups), mostly small crustaceans and also insect larvae (sCr-InLa, 12·5%), mostly insect larvae and also fishes (InLa-Fi, 5·9%), insect larvae only (InLa, 23·0%), and mostly insect larvae and also small crustaceans (InLa-sCr, 36·8%) for the carnivorous fish and mostly plant debris and also substratum (VeDe-Su, 4·6%) for the other fish.

Most taxa showed ontogenetic diet shifts (Table I). Carnivorous fish switched usually from small-size prey such as small crustaceans to intermediate-size prey such as insect larvae and/or to large-size prey such as insects and/or fish (Table I). However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. Some fish even started feeding directly on

TABLE II. Relative dietary abundance (in %) for the different fish body shapes

Body shape	*n*	Diet groups						
		VeDe-Su	sCr-InLa	InLa-sCr	InLa	TeIn	InLa-Fi	Fi
Disciform	19	0·0	0·0	36·8	26·4	36·8	0·0	0·0
Aguilliform	13	0·0	7·7	15·4	76·9	0·0	0·0	0·0
Depressiform	13	23·1	15·4	7·6	15·4	23·1	15·4	0·0
Intermediate	107	3·7	14·0	42·1	16·8	15·9	6·6	0·9

n, Number of size groups of the 66 species; Fi, fish; TeIn, terrestrial insects; InLa, insect larvae; sCr, small crustacean; VeDe, vegetative debris; Su, substratum.

insect larvae and switched to insects and/or fish (Table I). Only seven taxa belonged to the same diet groups from early life stages to older juveniles: *Chilodus zunevei* Puyo and *Hyphessobrycon* sp. aff. *sovichthys* Schultz fed mainly on insect larvae and also on small crustaceans, *Tatia intermedia* (Steindachner) fed mainly on terrestrial insects, *Ancistrus* aff. *hoplogenys* on plant debris and substratum, *Trichomycterus guianense* (Eigenmann), *G. anguillaris* and *N. anomala* on insect larvae.

RELATIONSHIPS BETWEEN BODY SHAPE AND DIET

Taxa of different body shapes had significantly different diets (Table II; G-value=46·131, d.f.=18, $P<0·001$). Disciform fish fed mainly on aquatic insect larvae and terrestrial insects but also, in small amounts, on small crustaceans. Most anguilliform taxa specialized on insect larvae. Individuals belonging to the depressiform of intermediate morphotype presented varied diets ranging from plant debris and substratum, to fish.

DISCUSSION

In a study based on 17 temperate fish species, Douglas & Matthews (1992) argued that interrelationships between body shape, diet, and taxonomic status are predictable. They demonstrated that often studies on eco-morphology reflect only taxonomic or phylogenetic aspects. Phylogenetic systematics is increasingly used to interpret morphological and ecological data in an evolutionary context (Westneat, 1995). Unfortunately, the systematic relationships between neotropical fish species of entire families are still largely unknown (see Montoya-Burgos *et al.*, 1997, for an example in Loricariidae). However, the importance of the systematic position of a fish species for the determination of its body shape is suggested in our study: 69·2% of taxa with an anguilliform body belonged to Gymnotiformes, 63·2% of the taxa with a disciform body were Perciformes, all flat fishes were Siluriformes and 71% of the taxa with an intermediate body shape belonged to Characiformes.

Independent of their systematic position, most of the young fish inhabiting the tributaries of the Sinnamary River feed mainly on small crustaceans, insect larvae, and terrestrial insects. For most fish taxa, the importance of small crustaceans in the diet decreased with increasing age and size and small

crustaceans were replaced progressively by terrestrial insects. These results correspond well to those of Horeau *et al.* (1996), who highlighted the importance of allochtonous inputs in the diets of several adult fish of the Sinnamary River. In rivers, flooding cycles modify on a regular basis food resource availability and thus feeding specializations of fish tend to appear poorly (Winemiller, 1990). However, two types of specialization were detected for early stages in Guianese fish: piscivory and use of plant debris and substratum (Table I). Indeed, several young taxa presented piscivorous feeding habits at a very small size: young of *Acestrorhynchus* spp. were able to ingest fish occasionally, and juveniles of *Hoplias aimara* (Valenciennes) and *H. malabaricus* (Bloch) preyed upon fish as soon as they had reached >20 mm (Table I). Thus, the young stages of these species have diet spectra identical to those of the adults (Planquette *et al.*, 1996). Piscivorous tendency during early life stages was also noted for other species known to eat fish later in their lives: *Pimelodella cristata* (Müller & Troschel) and *P. gracilis* (Valenciennes) (Planquette *et al.*, 1996), *Rhamdia* sp. and *Crenicichla saxatilis* (L.) (Knöppel, 1970; Angermeier & Karr, 1983; Winemiller, 1989), and *Synbranchus marmoratus* (Winemiller, 1989). The young of Curimatidae, *Leporinus despaxi* Puyo, *L.* spp. and *Ancistrus* aff. *hoplogenys* ate mainly plant debris and substratum. The adults of several species of Curimatidae such as *Cyphocharax spilurus*, *C. helleri*, *Curimata cyprinoides* (Planquette *et al.*, 1996, *C. pristigaster* (Carvalho, 1984) are known to be detritivores and Angermeier & Karr (1983) found that adults of species of *Ancistrus* fed exclusively on algae in Panamanian streams. Similar to what has been demonstrated for the adults (Power, 1983, 1984), young *A.* aff. *hoplogenys* might have ingested large amounts of substratum in order to ingest the algae it contains.

Wainwright & Richard (1995) argued that all fish species change prey use during ontogeny. In our study, the majority of the fish taxa showed ontogenetic diet shifts and young fish were usually able to feed on larger prey at a larger size (Table I). However, taxa differed in their capacities to switch from small prey to intermediate and/or to large prey. So far, evidence for diet changes with age for neotropical freshwater fishes are scarce in the scientific literature. Mol (1995) observed for the two armoured catfish *Callichthys callichthys* and *Hoplosternum thoracatum*, a diet shift from small crustaceans and rotifers to a mixed diet dominated by insect larvae when individuals reached 8·4 mm, a pattern that agrees well with our results. Identically to Winemiller's (1989) results in the Venezuelan Llanos, Guianese *G. carapo* of <50 mm preyed mainly upon insect larvae and switched later to a food regime composed of insect larvae and terrestrial insects. Dietary shifts are induced usually by changes with growth of morphological features correlated to body size (Wainwright & Richard, 1995). The enlargement of the mouth gape (Keast, 1978, 1985; Hartman, 1983; Dabrowski & Bardega, 1984), the development of fins, muscles and swimbladder (Bone *et al.*, 1996) and body shape (Keast, 1978) influence prey selection and catch efficiency.

With data for 66 of the 126 freshwater and 18 euryhaline fish taxa recorded in the Sinnamary River (Lauzanne *et al.*, 1995), our work forms the largest database ever gathered and published for body shape and diet of young neotropical Guianese fish. The large percentage of young fish with intermediate body shapes stresses the need for complementary morphological variables as

indicators of ecological fish groups. As the most useful morphological variables are those that affect behavioural performances (Wainwright, 1996), further investigations should relate size and position of fins, mouth gape, development of dentition, development of the digestive system, among other variables, to feeding habits during ontogeny. Moreover, future studies should also define if young fish exhibit seasonal variability in their diets as shown for adult fish in other freshwater tropical systems (Lowe-McConnell, 1979; Zaret & Rand, 1971; Goulding, 1980; Boujard *et al.*, 1990). Comparisons of seasonal variability of diets between sites situated downstream of the dam and upstream of the reservoir would allow evaluation of the impacts of flow disturbances on food resource use by fish during their early life. Beyond these topics, body shape and diet described in this work will be used together with other biological traits related to reproduction to define aspects of life history strategies of fishes in the Sinnamary River. The understanding of the relationships between these life history strategies and environmental parameters will enable us in future to link general community characteristics to the environment (Statzner *et al.*, 1994) beyond the systematic details of the different fish taxa. This approach should provide insights into the fundamental factors structuring fish communities as well as the broader applications of the impacts of hydroelectric dams on neotropical fish assemblages.

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A4

Species traits in relation to habitat variability and state: neotropical juvenile fish in floodplain creeks

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(A soumettre)

Abstract

The River Habitat Templet Concept predicts that combinations of biological traits of species forming a community change across spatio-temporal variability gradients. We tested this hypothesis with young fish communities in the floodplain creeks of the neotropical Sinnamary River (French Guiana). For 200 samples, we collected data on fish community characteristics and temporal (i.e. the hydrological) and spatial (e.g. depth, bottom substrate, litter type) variability of the fish habitat. In addition, we evaluated the state (i.e. mean conditions) of these habitats (re-using data describing habitat variability and other variables such as oxygen concentration and turbidity of the water). We obtained the information on the biological traits of the species from the literature. We used correlation and multivariate analyses (e.g. Principal Component Analyses and multiple regressions) to determine relations among biological traits as well as relations between traits and habitat characteristics. For the 57 studied species, we identified three main strategies of fairly homogeneous life history features that corresponded to the equilibrium, opportunistic and periodic strategies sensu Winemiller (*1989, Oecologia, 81: 225-241*). We demonstrated that young fish of species having the equilibrium strategy had more streamlined bodies and a more specialised diet than fish having the periodic and opportunistic strategy. We discovered 13 significant relationships between species traits and habitat variability. Thus, our results partially supported the predictions of the Habitat Templet Concept: the creek habitats significantly acted as a templet for species, and most of the relationships showed the predicted trends (e.g. minimal standard length at first maturity, mean diameter of mature oocytes, parental care and relative body height decreased with increasing temporal variability; minimal standard length at first maturity and mean diameter of mature oocytes increased with increasing spatial variability). However, these relationships explained little of the variability in biological traits because our trait patterns were rather complicated and differed between the two studied sections (up- and downstream from the Petit Saut dam). We explained more of the variability in the biological traits when we considered habitat variability together with habitat state variables in the upstream creeks (14 to 34% of the trait variability explained). There, we demonstrated that water oxygen content and turbidity explained much of the trends in life history traits such as

minimal standard length at first maturity, mean diameter of mature oocytes or parental care. In upstream creeks, we observed a higher number of fish specimens from species having a large size, many big eggs and no parental care compared to the downstream samples, which was probably due to the dam. We agreed with previous publications that the Habitat Templet Concept is an important element in ecological theory that has also the potential to be applied in management. However, the richness of response patterns so far published demonstrates that we are far from understanding the mechanisms producing particular trait combinations in a given habitat.

Key words: Habitat Templet Concept, life history strategies, spatial habitat diversity, hydrological variability, young fish, French Guiana.

Introduction

Environmental variability in time and space is known to shape the distribution of organisms, their interactions and their adaptations (Wiens 1986). Such spatio-temporal variability is a basic characteristic of running water systems (Minshall 1988; Poff and Ward 1990). Thus, freshwater ecologists recently began to relate various biological responses to habitat heterogeneity (e.g. Hildrew and Townsend 1987; Schlosser 1987; Townsend 1989; Poff and Allan 1995). In this context, a few studies (Statzner et al. 1994; 1997; Townsend et al. 1997) focused on species traits in the framework of habitat templet theory (Southwood 1977; 1988). According to this theory, temporal and spatial variations of the habitat are assumed to filter characteristic life history strategies (combinations of traits) of the species that enable survival in a given environment. Townsend and Hildrew (1994) developed a theoretical framework (River Habitat Templet Concept) that predicts such combinations of traits across spatio-temporal variability gradients. The authors predicted that lotic organisms in habitats with high temporal and low spatial variability would be more resilient and/or more resistant (e.g. small body size, short life span or high fecundity) than organisms in habitat with opposite temporal and spatial conditions. In this framework, temporal variability refers to the frequency of disturbances for the organisms whereas spatial variability refers to the abundance of refugia buffering the effect of disturbances (Townsend and Hildrew 1994; Townsend et al. 1997).

Several studies showed statistically significant relationships between species traits and lotic habitat use (e.g. Schlosser 1990; Scrasbrook and Townsend 1993; Statzner et al. 1994; 1997; Poff and Allan 1995; Townsend et al. 1997) supporting the view of

Southwood (1977) that the habitat acts as a templet for species traits. However, studies that tested the predictions of Townsend and Hildrew (1994) often rejected details of the predictions (except Townsend et al. 1997). Therefore, Resh et al. (1994) suggested to include variables describing the state of habitats (i.e. mean conditions) in studies relating species traits to habitat variability.

The only habitat templet study dealing with lotic fish showed that the observed species traits did not correspond to the predictions of the River Habitat Templet Concept (Persat et al. 1994). Therefore, the authors suggested to focus the study either on juveniles or on adults, as ontogenetic niche shifts might explain why predictions were not supported. In addition, long-living organisms such as fish are supposed to be disturbed by only a small fraction of temporal variability events (Townsend and Hildrew 1994). However, juveniles and adults should respond differently to a given event and young fish should be more affected by short term events than adults.

Neotropical freshwater fish are known to have a high diversity of reproductive patterns (Lowe-McConnell 1987). However, only two studies systematically described the life history traits of neotropical freshwater lotic fish. Winemiller (1989) determined three main life history strategies (equilibrium, opportunistic and seasonal) based on age at first maturity, fecundity and juvenile survival in streams of the Llanos region (Venezuela). Ponton and Mérona (1998) described the life history traits of 87 taxa in the Sinnamary River (French Guiana).

A study relating neotropical communities of lotic young fish of species having a wide range of life history traits (Ponton and Mérona 1998) to habitat variability considering

short temporal (weeks) and small spatial (< 100 m^2) scales (well adapted to young fish, see Poizat and Pont 1996) was appropriate for evaluating the power of habitat variability in species trait predictions. For this study, we selected habitats in creeks of the neotropical Sinnamary River because these creeks play the role of nurseries for fish larvae and juveniles throughout most of the year (Ponton and Copp 1997; Ponton and Vauchel 1998; Mérigoux and Ponton unpublished data). In contrast to most running waters in temperate regions, the morphology of the Sinnamary creeks and the surrounding floodplain forest have not yet been impacted by human activities. The habitats in the Sinnamary creeks covered a large range of temporal variability due to unpredictable natural hydrological variations typical of the majority of the Guianese watercourses but also because of the completion of the Petit Saut Dam in 1994, which strongly changes the natural hydrology (Ponton and Vauchel 1998). Hydrological instability was often used to describe disturbance for lotic fishes (Horwitz 1978; Schlosser 1990), so we used it to characterise disturbance frequency. We also determined spatial variability using the diversity of some habitat characteristics (depth, litter, vegetation, substrate and bank type).

In this paper, we used neotropical fish species to 1) determine the relationships among species traits and to determine their main life history strategies; 2) describe relationships between these life history strategies and additional biological traits such as diet and body shape of young fish; 3) test the Habitat Templet Concept predictions using young fish and the hydrological instability as temporal and habitat diversity as spatial variability axes; 4) evaluate the relative importance of habitat variability and state variables (i.e. mean conditions) for predictions of young fish species traits and 5) detect

differences for the two last aims between a natural and a flow regulated section of the Sinnamary River. To achieve these objectives, we re-used data on fish communities and habitat characteristics that were previously exploited in a different context (Mérigoux et al. 1998).

Study area

A detailed description of the study area is given in Mérigoux et al. (1998). In summary, the Sinnamary River is the fifth largest river of French Guiana. It has a length of approximately 260 km and a mean annual discharge of 230 m^3s^{-1} (see Fig. 1 in Mérigoux et al. 1998). Its drainage basin covers about 6565 km^2 and receives an annual average precipitation of 3000 mm. The Upper Sinnamary River, i.e. 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 was dependent of the alternation of two (November to February) and (April to July) rainy periods and a dry period (August to November) (Ponton and Copp 1997).

The creeks that we studied drained small catchments (see Fig. 1 in Mérigoux et al. 1998) that were entirely covered by a natural floodplain forest. Therefore, the creeks were well-shaded and aquatic macrophytes and planktonic algae hardly colonised them. In addition, a large amount of woody debris generally covered the bottom of the creeks and mud, clay and sand predominate the bottom substrate.

Material and Methods

Most of the material and methods we used are described in Mérigoux et al. (1998) and summarised below.

Hydrology

A gauging station upstream from Saut Dalles rapids and another one about 25 km downstream from the dam at the entrance of Venus Creek (see Fig. 1 in Mérigoux et al. 1998) recorded hourly water levels in up- and downstream section of the Sinnamary from 1995 to 1996. In addition, we set up 19 stream gauges in the studied creeks to record the water levels at each of our 20 sampling sites (see Fig. 1 in Mérigoux et al. 1998).

Habitat sampling

We regularly sampled six creeks of the Sinnamary River from March 1995 to October 1996. We selected a mean area of about 50 m^2 at random in three or four sampling sites per creek at each sampling campaign. Before fishing, we measured the current velocity, the temperature, the pH, the oxygen and the turbidity in the undisturbed water. After fish sampling, we recorded at each point sample of a 1 x 1 m grid the water depth (in cm) and the presence/absence of organic litter (5 categories: leaves, wood diameter $\leq$ 5 and >5 cm, roots diameter $\leq$ 5 and >5 cm), vegetation (3 categories: aquatic, terrestrial herbaceous shrubs, trees) and substrate (6 categories: mud, clay, sand, gravel, stones, blocs). We also recorded bank slope (5 categories: smooth, medium, stiff, vertical, excavation) for the closest point samples to the bank. Finally, we determined the total length, the total bank length, the mean width, the volume and the surface of

each sampling area. Our sampling procedure yielded a total of 200 samples (10 sampling sites x 10 campaigns x 2 sections).

Fish sampling

We enclosed each sampling area with stop nets (1mm mesh) and we applied at least two subsequent doses of PREDATOX (emulsifiable solution of rotenone) well mixed with water. We collected fish with dip nets (1mm mesh) and immediately preserved them in alcohol. In the laboratory, we sorted and identified all specimens of the 200 samples using keys cited in Mérigoux et al. (1998). We measured the standard length of each specimen to the nearest mm. For each species, we separated juveniles from adults according to their minimal size at first maturity (Mérigoux and Ponton 1998; Ponton and Mérona 1998). Overall, we collected a total of 73 fish taxa. Here, we considered 57 of these taxa that were present at least in four sampling areas and that accounted for more than 16 individuals.

Species traits

We could accumulate data for eight biological traits for the 57 selected taxa (Table 1) that could serve to test predictions of resilience or resistance to disturbance (Townsend and Hildrew 1994). The following traits described the potential resilience of the fish: (a) food regime diversity (DIET, see below), (b) maximal standard length of the taxon (MSL, in cm), (c) minimal standard length at first maturity (SL1M, in cm), (d) length of the reproductive period within a year (LRP, in months), (e) mean diameter of mature oocytes (MDO, in mm), (f) mean fecundity (MF, as eggs number) and (g) parental care (PC, present or absent). Diversified diet, small size, long reproductive period, small

eggs, high fecundity and no parental care would enable rapid population growth after disturbance (Townsend and Hildrew 1994).

We could include one resistance trait: (h) relative body height (RBH). This variable is used in hydrodynamics to minimise the drag of a body (by modifying the height to length ratio) and many fish have an ideally streamlined body form with a $RBH \approx 0.17$ (Sagnes et al. 1997). Decreasing values of this variable indicated better streamlining and a lower risk of dislodgement during floods.

Traits (a) and (h) were determined using 10 to 30 individuals of young fish per taxon (Mérigoux and Ponton 1998). Here, we used the five most important food items (fish, terrestrial insects, insect larvae, small crustaceans, and debris) and calculated for each taxon the Simpson's index to determine its diet diversity. Information on the six remaining traits (all life history traits) came mostly from Ponton and Mérona (1998) but also from Ponton and Tito de Morais (1994). In rare cases, we used educated guesses or data of very close species from the literature to complete Table 1. All traits were quantitative variables except parental care that was coded 0 (presence) or 1 (absence).

Data analysis

Temporal and spatial parameters

Mérigoux et al. (1998) showed that hydrological variations over 30 days prior to fish sampling were the most appropriate periods to predict community characteristics of the juvenile fish. Therefore, we re-used their variance of the water level for a period of 30 days before fishing as the temporal axis of our habitat templet. In contrast to the previous analysis (Mérigoux et al. 1998), who used a log (x+1) transformation, we

transformed the water level variance into log (x+100) to achieve a better normality. We also re-used the mean water level 30 days before fishing at each sampling area from Mérigoux et al. (1998). This variable was the temporal state variable.

Comparably, we re-used the index of spatial habitat variability from Mérigoux et al. (1998). This index synthesised the overall spatial variability from the depth, litter, vegetation, substrate and bank slope characteristics of each sampling area. Most of the categories considered by these spatial variables 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. Finally, concerning spatial habitat state variables, we included water current velocity, water temperature, pH, water oxygen concentration, water turbidity, total length, bank length, mean width, mean depth, volume and surface of the sampling area (see Mérigoux et al. 1998 for details).

Relationships among biological traits

We first square- (DIET and LRP), log- (MSL, SL1M and MF) and square root- (MDO) transformed the biological variables to achieve normality. RBH and PC did not required a transformation. We calculated Pearson's coefficient of correlation and associated Bonferonni probability for each possible pair of variables to check for redundancy among biological traits.

To investigate the typology of taxa according to their traits, we performed two normalised Principal Component Analyses (PCA) on the two different taxa-by-traits matrices: 1) on the traits similar to those used by Winemiller (1989) to separate taxa into

different life history strategies sensu Winemiller and 2) on all traits to determine the relation among these life history strategies and diet and body shape of young fish.

Relationships between habitat characteristics and biological traits

We first log (x+1) transformed the sample-by-fish taxa matrix (200 samples and 57 taxa). We then calculated the proportion of individuals of each taxon for each sample. We combined the latter matrix and the fish taxa-by-traits matrix (57 taxa and 8 traits) to get a sample-by-trait matrix (200 samples and 8 traits). This matrix contained the average of each quantitative trait per sample. For parental care, the matrix contained the proportion of individuals that presented parental care.

We used t-test to check for differences in biological attributes between the up- and downstream samples.

To check if our observations corresponded significantly to the predictions made by Townsend and Hildrew (1994), we calculated Pearson's coefficient of correlation and associated Bonferonni probability between each trait and the temporal and spatial axis. We performed these analyses for the whole data set, and separately for the up- and downstream samples.

Finally, we used stepwise forward regression (Wilkinson et al. 1996) to determine if state variables together with habitat variability improved the description of trait variability. We performed this stepwise analysis separately for the up- and downstream samples.

We used Systat® 6.01 for Windows (Wilkinson et al. 1996) and ADE 4 software (Thioulouse et al. 1997) for data analyses.

Results

Temporal and spatial parameters

The mean temporal variability of the water level 30 days before fishing differed significantly between the up- and downstream samples (t-test with $t = 4.895$, $df = 99$ and $p < 0.001$). In upstream samples most temporal scores ranged from 5 to 8.5, whereas in downstream samples most scores ranged between 6.5 to 8 and 9 to 10 (see Fig. 6 in Mérigoux et al. 1998). The 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 most scores ranged from 0.7 to 1.2 (see Fig. 6 in Mérigoux et al. 1998). Concerning habitat state, water temperature (°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 ≤ 6 cm s^{-1}. Homogeneity of water velocity at the time we were fishing did not imply homogeneity of water level (i.e. flow) variance during 30 days before fishing (i.e. our measure of disturbance). The remaining state variables included in the analyses were oxygen concentration of the water (mg l^{-1}, mean = 5.2, SD = 1.2), water turbidity (NTU, mean = 5.4, SD = 6.4), left plus right 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).

Biological traits

We observed large interspecific variation in maximal standard length, minimal standard length at first maturity, mean diameter of mature oocytes and mean fecundity (Table 1). For example, mean fecundity ranged from three progenies laid per reproduction event in *Poecilia parae* to 83219 eggs in *Leporinus* spp. (Table 1). Interspecific variations were less important for the remaining traits as 1) more than 50% of the young fish taxa had a diversified food (Simpson's index ≥ 0.50); 2) most young fish species had values of relative body height ranging from 0.20 to 0.40; 3) more than 80% of the taxa were reproducing at least during half of the year and 4) a total of 57% of the taxa showed no parental care for the offsprings, 93% being Characiformes.

Relationships among biological traits

Maximal standard length of the 57 taxa was highly and positively correlated with minimal standard length at first maturity (Table 2). Consequently, we excluded the variable "maximal standard length" to avoid redundancy in further analyses. Other significant coefficients showed that the larger the fish at maximum or at first maturity, the bigger the diameter of their mature oocytes, the higher the mean fecundity and the more intense the parental care. At the same time and independently of the fish size, correlations showed that the bigger the eggs, the lower the mean fecundity and the higher the parental care. Other significant correlations demonstrated a positive relation between diet diversity and mean fecundity and a negative relation between the relative body height and the mean diameter of mature oocytes.

Table 1. Species traits of fifty-seven fish taxa. DIET: Simpson index of food regime diversity, RBH: relative body height, MSL, maximal standard length (cm), SL1M: minimal standard length at first maturity (cm), LRP, length of the reproductive period (months), MDO: mean diameter of mature oocytes (mm), MF: mean fecundity (eggs number per reproductive event), PC: parental care (presence/absence).

Order Family Species	CODE	authority	DIET	RBH	MSL	SL1M	LRP	MDO	MF	PC
Characiformes										
Hemiodontidae										
Hemiodopsis quadrimaculatus	HQUA	(Pellegrin 1908)	0.50	0.17	200	90	12	0.8	8748	No
Parodon guyanensis	PGUI	Géry 1959	0.49	0.17	90	60	12	0.4*	?	No*
Curimatidae										
Chilodus zunevei	CZUN	Puyo 1945	0.44	0.27	96	65	10	1.3	1560	No
Curimatidae spp.	CUSP		0.43	0.31	249	75	8	0.6	32273	No
Anostomidae										
Leporinus spp.	LESP		0.69	0.26	405	90	7	1.1	83219	No
Erythrinidae										
Erythrinus erythrinus	EERY	(Schneider 1801)	0.60	0.20	170	150	12	1.2*	43748*	Yes
Hoplias spp.	HOPL		0.64	0.20	830	400	12	1.7	34478	Yes
Lebiasinidae										
Copella carsevennensis	CCAR	(Regan 1912)	0.51	0.20	53	24	10	0.6	335	No
Nannostomus beckfordi	NBEC	Günther, 1872	0.35	0.21	35	25	2	0.5	425	No
Pyrrhulina filamentosa	PFIL	Val. in Cuv. 1846	0.65	0.21	95	49	8	0.7	2207	Yes*
Gasteropelecidae										
Gasteropelecus sternicla	GSTE	(Linnaeus 1758)	0.57	0.25	44	20	5	0.4*	700*	No
Characidae										
Characidium fasciadorsale	CFAS	Fowler 1914	0.34	0.21	60	45	6	0.7	3986	No
Melanocharacidium sp.	MESP		0.47	0.24	22	30	8	0.5*	209*	No*
Microcharacidium eleotrioides	MELE	(Géry 1960)	0.44	0.21	23	14	10	0.5	209	No*
Acestrorhynchus sp.	ACSP		0.60	0.17	285	120	12	0.8	16459	No
Charax pauciradiatus	CPAU	Günther 1864	0.42	0.25	140	80	10	0.7	3605	No
Pristella maxillaris	PMAX	(Ulrey 1894)	0.54	0.29	32	19	10	0.7	785	No
Pseudopristella simulata	PSIM	Géry 1960	0.51	0.30	39	22	6	0.7	1476	No*
Poptella brevispina	PBRE	(Reis, 1989)	0.53	0.36	126	65	12	0.7	2507	No
Astyanax bimaculatus	ABIM	(Linnaeus 1758)	0.64	0.29	130	80	6	0.7	25398	No
Astyanax cf *keithi*	AKEI	Géry, Planquette & LeBail 1996	0.65	0.34	108	55	12	0.7	5845	No
Bryconops spp.	BRSP		0.50	0.24	161	80	12	0.7	2858	No
Hemigrammus ocellifer	HOCE	(Steindachner 1882)	0.67	0.30	63	25	6	0.5	1930	No
Hemigrammus unilineatus	HUNI	(Gill 1858)	0.66	0.30	42	29	6	0.7	883	No
Hyphessobrycon aff. *sovichtys*	HSOV	Schultz 1944	0.62	0.27	42	20	6	0.6	882	No
Moenkhausia collettii	MCOL	(Steindachner 1882)	0.68	0.27	86	35	8	0.6	1031	No*
Moenkhausia chrysargyrea	MCHR	(Günther 1864)	0.57	0.33	103	45	10	0.7	5785	No*
Moenkhausia georgiae	MGEO	Géry 1966	0.49	0.25	113	60	4	0.7	3440	No*
Moenkhausia hemigrammoides	MHEM	Géry 1966	0.65	0.31	50	35	6	0.6	1130	No*
Moenkhausia oligolepis	MOLI	(Günther 1864)	0.60	0.35	100	65	10	0.6	11130	No*
Moenkhausia surinamensis	MSUR	Géry 1966	0.28	0.34	116	60	4	0.7	8412	No
Phenacogaster aff. *megalostictus*	PMEG	Eigenmann1909	0.40	0.27	55	29	6	0.6	857	?
Piabucus dentatus	PDEN	(Köhlreuter 1761)	0.55	0.19	153	110	6	1.0	1614	No

Table 1 (continued)

Order Family Species	CODE	authority	DIET	RBH	MSL	SL1M	LRP	MDO	MF	PC
Siluriformes										
Auchenipteridae										
Tatia intermedia	TINT	(Steindachner 1876)	0.02	0.25	76	60	12	2.6	264	Yes*
Pimelodidae										
Pseudopimelodus raninus	PRAN	(Valenciennes 1840)	0.39	0.25	225	65	2	1.7	770	?
Rhamdia quelen	RQUE	(Quoy & Gaimard 1824)	0.70	0.19	180	100	?	1.2*	25000*	Yes*
Pimelodella sp.	PISP		0.62	0.18	161	95	10	0.7	5323	Yes
Helogenidae										
Helogenes marmoratus	HMAR	(Günther 1863)	0.27	0.21	66	60	4	1.0	146	?
Aspredinidae										
Bunocephalus coracoideus	BCOR	Cope 1874	0.61	0.18	93	70	3	3.0*	30*	Yes
Trichomycteridae										
Trichomycterus guianense	TGUI	(Eigenmann 1909)	0.24	0.16	77	50	6	1.6	452	Yes
Callichthyidae										
Callichthys callichthys	CCAL	Linnaeus 1758	0.49	0.22	145	90	8	1.3	519	Yes*
Hoplosternum thoracatum	HTHO	(Val. in Cuv. & Val. 1840)	0.49	0.24	130	75	8	1.5	1753	Yes
Loricariidae										
Ancistrus aff. *hoplogenys*	AHOP	(Günther 1864)	0.06	0.18	110	65	12	2.2	58	Yes
Gymnotiformes										
Sternopygidae										
Sternopygus macrurus	SMAC	(Bloch & Schneider 1801)	0.40	0.17	330	145	12	2.3	697	Yes*
Hypopomidae										
Brachyhypopomus beebei	BBEE	(Schultz 1944)	0.37	0.15	335	100	8	1.0	125	Yes
Hypopomus artedi	HART	(Kaup 1856)	0.43	0.14	320	130	10	1.2	681	Yes*
Gymnotidae										
Gymnotus spp.	GYSP		0.37	0.13	380	185	7	2.7	232	Yes
Cyprinodontiformes										
Aplocheilidae										
Rivulus agilae	RAGI	Hoedeman 1954	0.46	0.18	50	15	4	1.1	65	No
Rivulus xiphidius	RXIP	Huber 1979	0.50	0.20	45	15	10	1.3	13	No
Poeciliidae										
Poecilia parae	PPAR	(Eigenmann 1894)	0.41	0.21	21	12	12	2.0	3	Yes
Synbranchiformes										
Synbranchidae										
Synbranchus marmoratus	SMAR	Bloch 1795	0.36	0.05	500	200	6	3.4	500*	Yes
Perciformes										
Nandidae										
Polycentrus schomburgkii	PSCH	Müller & Troschel 1848	0.56	0.45	70	30	10	0.6	104	Yes
Cichlidae										
Krobia guianensis	KGUI	(Regan 1905)	0.51	0.38	125	75	12	1.4	206	Yes
Cleithracara maronii	CMAR	(Steindachner 1882)	0.51	0.50	90	52	8	1.0	413	Yes
Crenicichla saxatilis	CSAX	(Linnaeus 1758)	0.69	0.22	222	140	8	1.3	676	Yes
Nannacara anomala	NANO	Regan 1905	0.32	0.39	66	29	10	0.8	416	Yes
Eleotridae										
Eleotris amblyopsis	EAMB	(Cope 1870)	0.52	0.19	80	25	10	0.2	4217	Yes

* Educated guess or data from very closed species

? data not available

Table 2: Pearson's correlation matrix and associated Bonferonni probabilities (ns: not significant) of the eight biological traits (see method section for variable transformations). See Table 1 for trait abbreviations.

	DIET	p	RBH	p	MSL	p	SL1M	p	LRP	p	MDO	p	MF	p
DIET														
RBH	0.23	ns												
MSL	0.06	ns	-0.30	0.027										
SL1M	0.03	ns	-0.30	0.022	0.92	0.000								
LRP	0.00	ns	0.05	ns	0.19	ns	0.21	ns						
MDO	-0.34	0.019	-0.40	0.003	0.42	0.001	0.48	0.000	0.10	ns				
MF	0.40	0.001	0.14	ns	0.46	0.000	0.45	0.000	0.08	ns	-0.37	0.000		
PC	-0.18	ns	-0.20	ns	0.35	0.007	0.40	0.002	0.18	ns	0.60	0.000	-0.26	0.047

The first two axes of the PCA on the five life history traits similar to those used by Winemiller (1989), explained 71% of the total data variability (Figure 1a). According to the quality of the representation of each taxon and each life history variable on the first two axes, we distinguished three main groups of taxa associated with three types of traits (Figure 1b and 1c). Group 1 comprised large fish at first maturity, having parental care for low to medium numbers of big eggs. Most of these fish were Siluriformes, Gymmnotiformes, Synbranchiformes and Perciformes (Figure 1d). Fish in group 2 were all Characiformes being small fish at first maturity and having no parental care for low to medium numbers of small eggs. Group 3 contained large fish at first maturity, having no parental care for numerous eggs of small to medium size. All taxa of group 3 except *Pimelodella* sp. (PISP) were Characiformes. Some taxa were well represented on the two axes and could not clearly be assigned to one of these three groups. For example, *Hemiodopsis quadrimaculatus* (HQUA), *Hoplias* spp. (HOPL), *Rhamdia quelen* (RQUE) were intermediates between group 1 and 3 and *Moenkhausia chrysargyrea* (MCHR) was intermediate between group 2 and 3. *Rivulus agilae* (RAGI) and *Rivulus xiphidus* (RXIP) had many characteristics of group 2 but had such a low fecundity that they ordinated on the negative side of axis 2. *Poecilia parae* (PPAR) had many attributes being close to those of group 1 but was so small that it was distinct in its F2 scores. A few remaining taxa could not be assigned to these groups. However, based on the quality of the representation of some of these taxa on the third axis, we could determine a fourth group of taxa (underlined taxa, Figure 1c). This third axis was mainly determined by the length of the reproductive period within a year (which accounted for 78% of its variability). *Parodon guyanensis* (PGUI), *Polycentrus schomburcki* (PSCH) and *Nannacara anomala* (NANO) had a very long reproductive period within a year

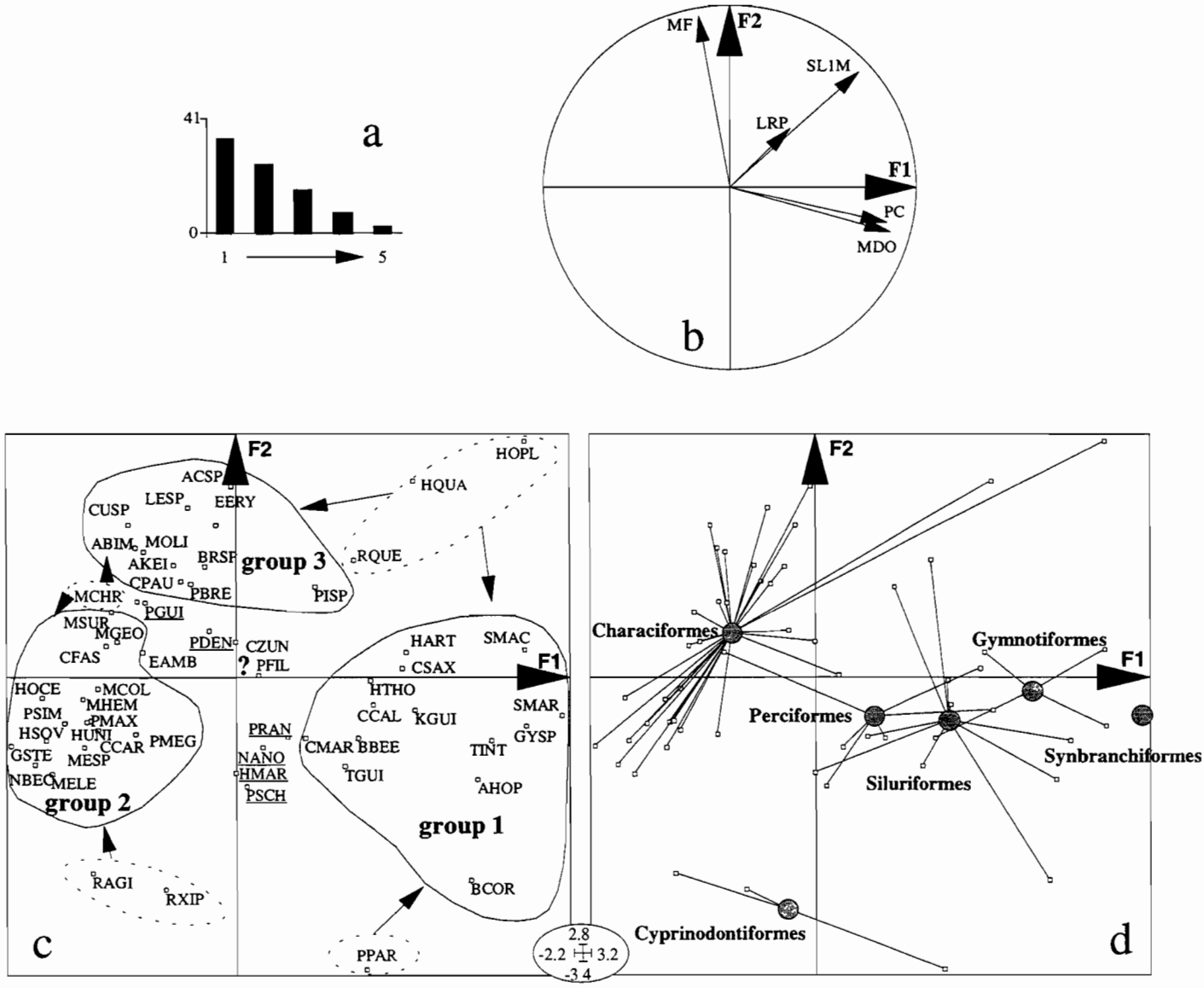
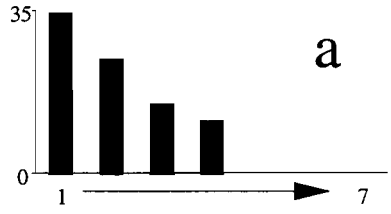
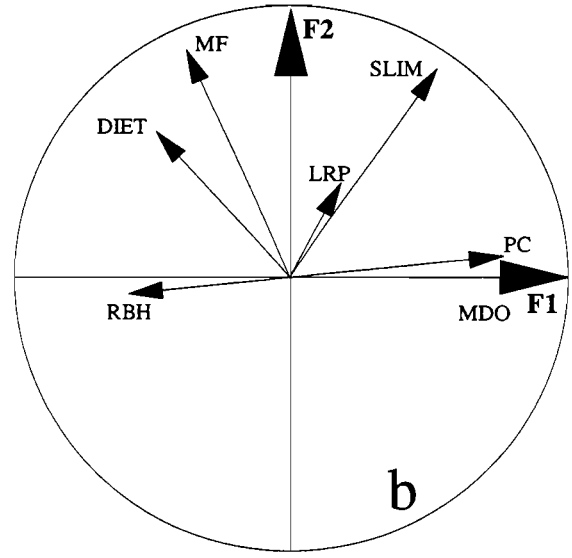


Fig. 1. Results of the normalised Principal Component Analysis (PCA) on the five life history traits. (a) Variability explained (%) by each axis. (b) Correlation circle on the first factorial plane of traits similar to those used by Winemiller (1989) to define life history of neotropical lotic fish (see Table 1 and methods for abbreviations and transformations). (c) Fish taxa coordinates on the first factorial plane (see Table 1 for taxa codes). We determined the taxa groups (shaded) according to the quality of the representation of each taxon on the first two axes (i.e. based on its relative contribution to the axes, Lebart, Morineau & Piron 1995). We considered a taxon as well represented by an axis if its relative contribution to it was above 23%. Taxa with doubtful assignments are indicated by broken ellipses and "?". Underlined taxa formed a fourth group on axis F3. (d) Fish taxa coordinates on the first factorial plane related to fish orders. Each taxon is related to its order position, which is at the mean of the coordinates of the taxa of each order.





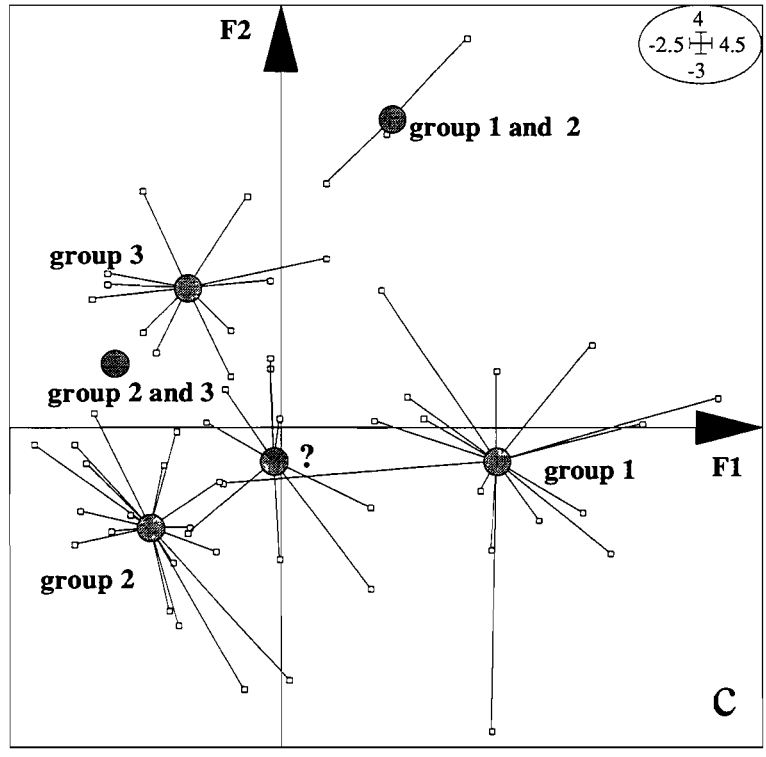


Fig. 2. Results of the normalised PCA on the biological traits of Fig. 1 plus the food diversity index and the relative body height. See Fig. 1 for further details and note that group in (c) correspond to those in Fig. 3 (taxa labelled by "?" could not be assigned to one of these three groups.

(≥10 months), whereas *Piabucus dentatus* (PDEN), *Pseudopimelodus raninus* (PRAN) and *Helogenes marmoratus* (HMAR) had a shorter reproductive period (≤ 6 months). Finally, *Chilodus zunevei* (CZUN), *Pyrrhulina filamentosa* (PFIL) and *Eleotris amblyopsis* (EAMB) were species having average values for the five life history traits analysed in Fig. 1.

The first two axes of the PCA on all traits (except the redundant maximal standard length) explained 58% of the total data variability (Figure 2a). For the three main groups defined above we found that young fish of group 1 had a low relative body height (RBH<0.23 except *Krobia guianensis* (KGUI) and *Cleithracara maronii* (CMAR)) and that some young fish taxa of this group had a specialised diet (e.g. *Tatia intermedia* (TINT), *Trichomycterus guianense* (TGUI) or *Ancistrus hoplogenys* (AHOP)). In contrast, most young fish taxa of group 2 and group 3 had higher relative body heights and fed on a wide range of food items (Figure 2b and c).

Relationships between habitat characteristics and biological traits

A comparison between up- and downstream samples showed that species with large size at first maturity (hence, with large maximal size, see above), having short reproduction periods, large and many eggs and few parental care were significantly more abundant in upstream samples than in downstream samples (Table 3).

Two traits had a significant negative relationships with temporal variability in the whole data set (i.e. all 200 samples). These were minimal standard length at first maturity and mean diameter of mature oocytes (Table 4). Concerning spatial variability, minimal standard length at first maturity and the length of the reproductive period

Table 3: Means t-test and probabilities for each biological trait in up- and downstream samples (df = 99). See Table 1 for biological variable codes and method section for variable transformations.

Biological traits	Mean		t	p
	Upstream	Downstream		
DIET	0.289	0.292	0.513	0.609
RBH	0.259	0.257	-0.525	0.601
SL1M	1.801	1.754	-2.886	0.005
LRP	86.075	93.387	5.016	0.000
MDO	0.991	0.960	-2.056	0.042
MF	3.245	3.124	-3.314	0.001
PC	0.421	0.581	6.148	0.000

Table 4. Pearson's correlations and associated Bonferonni probabilities for each biological trait and temporal and spatial variability in the total data set (i.e. 200 samples). See Table 2 for further details.

	Temporal variability		Spatial variability	
	r	p	r	p
DIET	0.005	ns	0.132	ns
RBH	-0.029	ns	0.051	ns
SL1M	-0.157	0.028	0.248	0.000
LRP	0.114	ns	0.163	0.022
MDO	-0.171	0.016	0.135	ns
MF	0.009	ns	0.085	ns
PC	0.131	ns	-0.025	ns

Table 5. Pearson's correlations and associated Bonferonni probabilities for each biological trait and temporal and spatial variability, for upstream (up) and downstream (Do) samples. See Table 2 for further details.

	Temporal variability				Spatial variability			
	Up	p	Do	p	Up	p	Do	p
DIET	0.080	ns	-0.063	ns	0.291	0.004	0.009	ns
RBH	0.198	ns	-0.210	0.036	0.093	ns	0.014	ns
SL1M	-0.203	0.046	-0.028	ns	0.213	0.036	0.289	0.004
LRP	-0.033	ns	0.082	ns	0.293	0.003	0.070	ns
MDO	-0.331	0.001	-0.065	ns	-0.216	0.033	0.314	0.001
MF	0.103	ns	0.055	ns	0.374	0.000	-0.227	0.023
PC	-0.313	0.002	0.201	0.045	-0.109	ns	0.012	ns

within a year had a positive significant relationship in the whole data set (Table 4). The analyses separately considering up- and downstream data sets demonstrated different trends. Significant temporal and spatial relationships observed in the whole data set (SL1M, MDO and LRP) were again significant and had the same sign in the upstream samples (Table 5). In addition, in these samples parental care had a significant negative relationship with temporal variability. Concerning spatial variability and upstream samples, diet diversity and mean fecundity had a positive relationship and mean diameter of mature oocytes had a negative one (Table 5). In the downstream samples, relative body height had a negative and parental care a positive relationship with temporal variability. In contrast to upstream samples, mean diameter of mature oocytes was positively and mean fecundity was negatively related to spatial variability of the downstream samples (Table 5). Although all these relationships were significant ($p<0.005$), the data had considerable scatter (Fig. 3 and 4).

When we added habitat state to habitat variability we explained more of the biological variability in the upstream samples only (compare Tables 5, 6 and 7). There, we explained between 14 to 34% of the trait variability if including habitat state (Table 6), whereas we explained at best 14% of this variability ($r = 0.374$, mean fecundity vs spatial variability, Table 5) using only habitat variability.

In the downstream samples we barely explained more of the biological variability through addition of the habitat state variables. In these samples, most of the significant relationships with variability (Table 5) became insignificant as state variables replaced temporal and spatial variability in the models (Table 7).

Table 6: Stepwise multiple regression on biological traits in upstream samples using habitat variability and state (note that we omitted habitat variables that were never significant with one of the traits from this table). r^2: coefficient of determination, F: value of the F ratio and p: associated probability for the entire model. For each habitat variable, we indicated its sign and its associated probability (ns: $p > 0.05$).

Statistics and habitat variables	Biological traits						
	DIET	RBH	SL1M	LRP	MDO	MF	PC
r^2	0.215	0.327	0.138	0.158	0.338	0.255	0.288
F	26.073	8.830	3.673	8.848	11.746	16.095	12.518
p	<0.001	<0.001	0.008	<0.001	<0.001	<0.001	<0.001
Temporal variability	ns	ns	- 0.045	ns	- 0.001	+ 0.004	- 0.003
Spatial variability	ns	+ 0.015	ns	+ 0.006	- 0.013	ns	ns
Mean water level	ns	+ 0.005	ns	ns	ns	ns	ns
Water oxygen	ns	- 0.004	+ 0.027	ns	+ 0.000	ns	+ 0.002
Water turbidity	ns	ns	- 0.044	ns	- 0.001	ns	- 0.000
Bank length	ns	- 0.005	ns	- 0.006	ns	ns	ns
Mean width	+ 0.000	ns	+ 0.005	ns	ns	+ 0.000	ns
Mean depth	ns	- 0.000	ns	ns	ns	ns	ns

Table 7: Stepwise multiple regression on biological traits in downstream samples using habitat variability and state (note that we omitted habitat variables that were never significant with one of the traits from this table). r^2: coefficient of determination, F: value of the F ratio and p: associated probability for the entire model. For each habitat variable, we indicated its sign and its associated probability (ns: $p > 0.05$).

Statistics and habitat variables	Biological traits DIET	RBH	SL1M	LRP	MDO	MF	PC
r^2	0.050	0.048	0.100	0.050	0.162	0.074	0.040
F	5.155	4.942	10.850	5.193	9.349	7.857	4.135
p	0.025	0.029	0.001	0.025	<0.001	0.006	0.045
Temporal variability	ns	ns	ns	ns	ns	ns	+ 0.045
Mean water level	ns	ns	ns	ns	- 0.004	+ 0.006	ns
Water turbidity	ns	ns	ns	+ 0.025	ns	ns	ns
Mean depth	- 0.025	- 0.029	+ 0.001	ns	+ 0.015	ns	ns

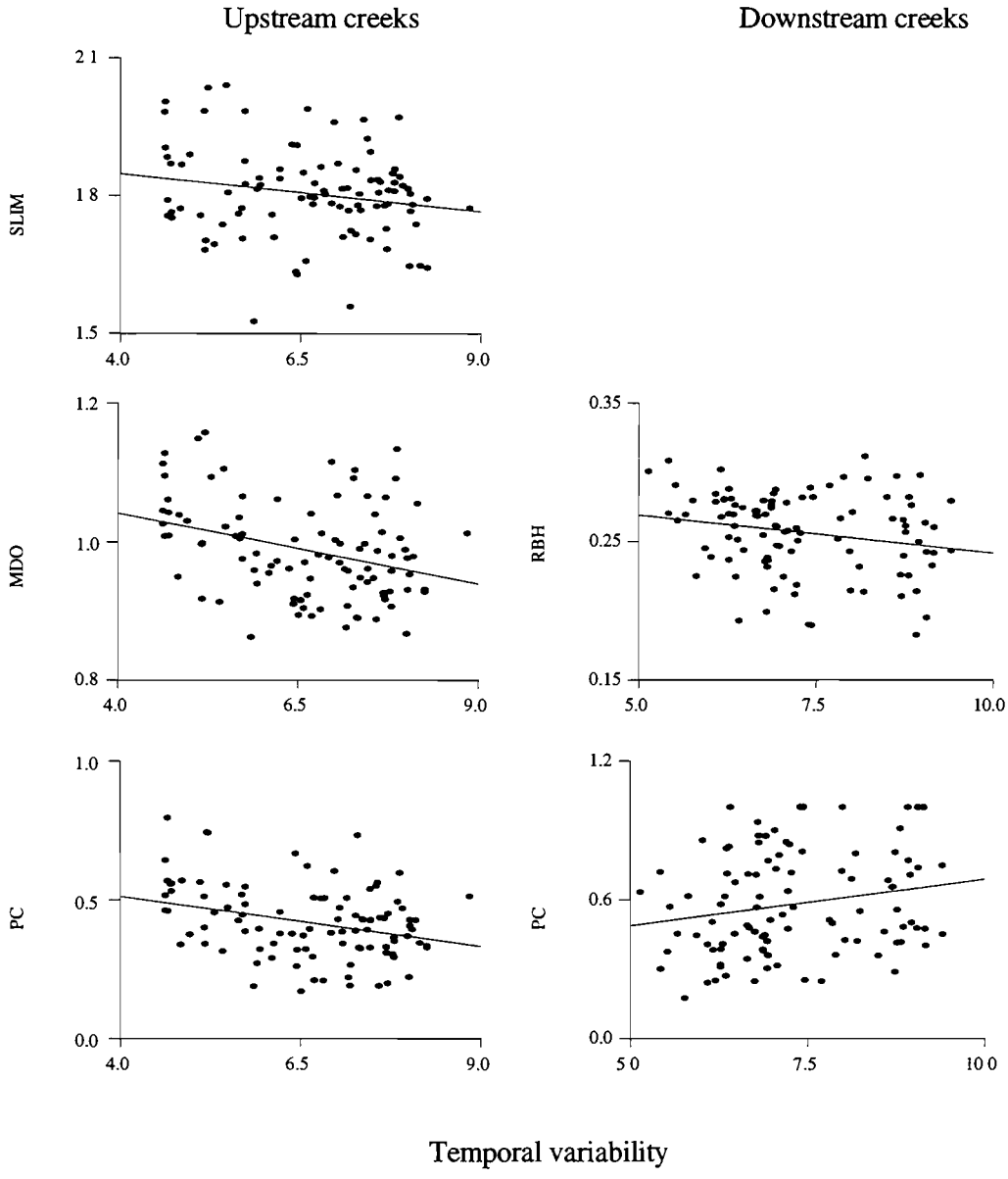


Fig. 3. Mean of each trait per sample in relation to temporal variability in up- and downstream creeks. We indicated only significant relationships (see Table 5). Note that some of the variables were transformed (see Table 1 and 2 for details about the variables).

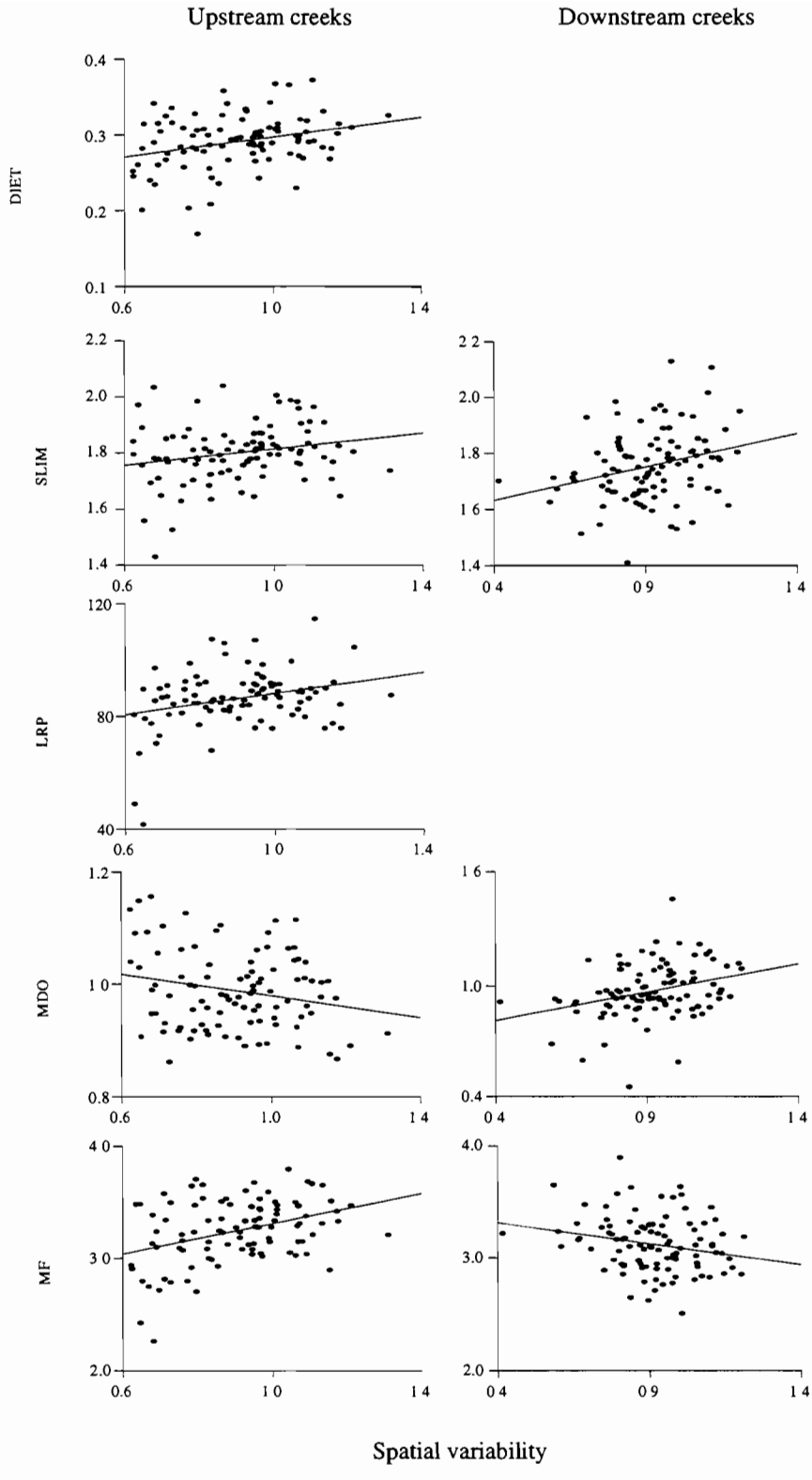


Fig. 4. Mean of each traits per sample in relation to spatial variability in up- and downstream creeks. We indicated only significant relationships (see Table 5). Note that some of the variables were transformed (see Table 1 and 2 for details about the variables).

We found positive upstream relationships between water oxygen concentration and minimal standard length at first maturity, mean diameter of mature oocytes and parental care. Water oxygen concentration was also negatively related to relative body height. Water turbidity was negatively related to minimal standard length at first maturity, mean diameter of mature oocytes and parental care. Bank length was negatively related to relative body height and length of the reproductive period within a year. Mean width was positively linked with diet diversity, minimal standard length at first maturity and mean fecundity. Finally, relative body height was negatively related to mean depth and positively related to mean water level 30 days before fishing in the upstream samples

In the downstream samples, water depth was the state variable most frequently related to the biological traits (positively with minimal standard length at first maturity and with mean diameter of mature oocytes; negatively with diet diversity and with relative body height). Mean water level 30 days before fishing was twice (positively with mean fecundity; negatively with mean diameter of mature oocytes) and water turbidity once (positively with length of the reproductive period within a year) significantly related with a biological trait.

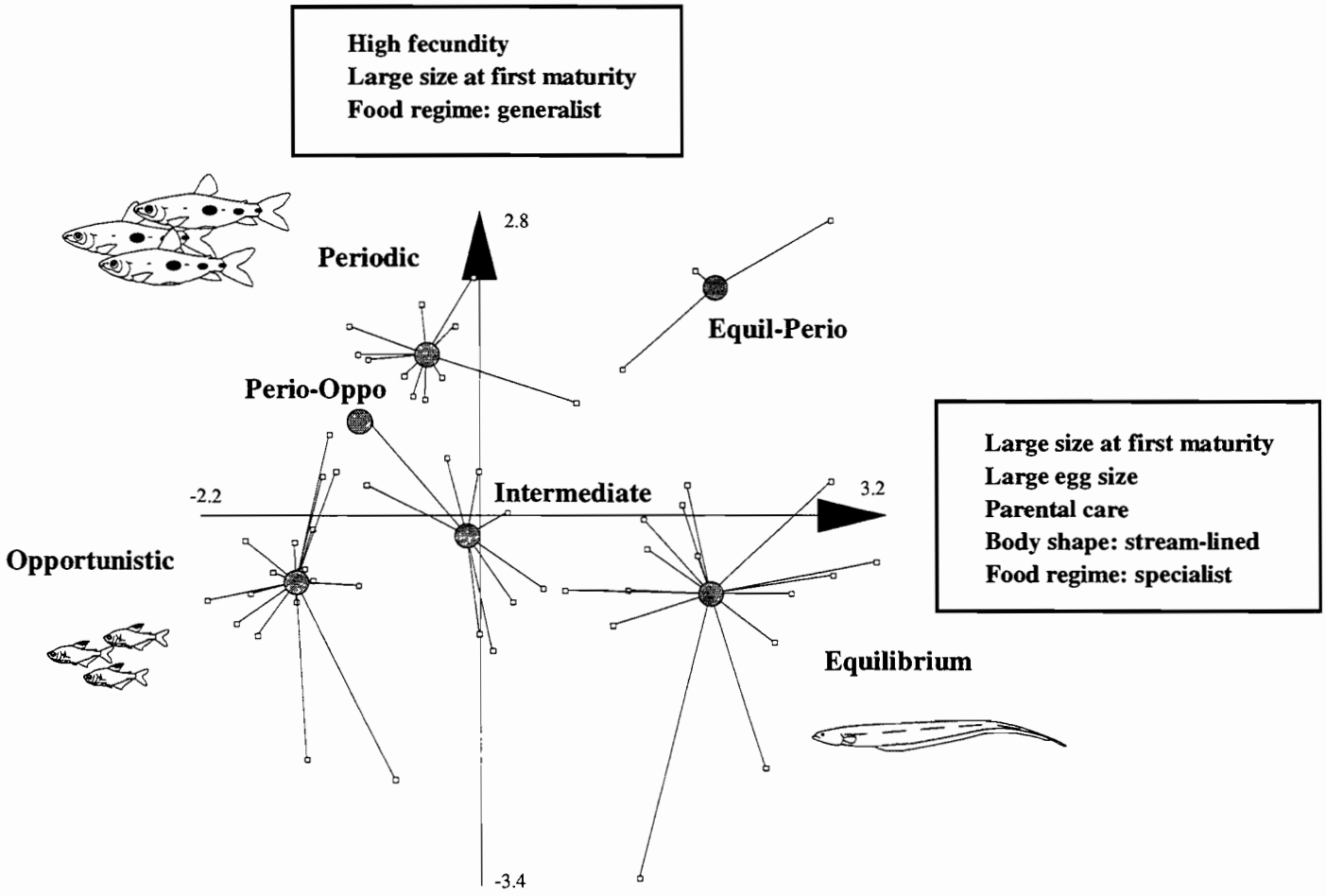


Fig. 5. Fish taxa coordinates on the first plane of the PCA made on life history traits of Fig. 1, rearranged in groups that corresponded closest to the different life history. We indicated the life history traits describing each strategy and also the diet and body shape characteristics (not used here to calculate fish taxa coordinates) of each strategy.

Discussion

Compared with fish community in temperate zones (Mahon 1984; Wootton 1984) the fish of the Sinnamary had an extremely large range of life history attributes. The positive correlations between maximal standard length of the taxa and 1) minimal standard length at first maturity; 2) mean diameter of mature oocytes and 3) mean fecundity implied that size represents a truly physical constraint for these three traits (Wootton 1992). The negative correlations between 1) mean diameter of mature oocytes and mean fecundity and 2) mean fecundity and parental care implied potential life history trade-offs that should have resulted from fundamental physiological constraints (Mahon 1984; Wootton 1984; Cambray and Bruton 1994). Reproductive output (egg size x number) of teleost fish is determined by body size (Elgar 1990; Wootton 1992). Therefore, for a given body size, an increase in egg numbers results in a decrease of egg size (Duarte and Alcaraz 1989). The production of larger eggs requires a higher metabolic cost and therefore leads to a reduction in the number of eggs that can be produced. However, larger eggs have compensatory advantages for the larger hatched fish such as a better survival through a better ability 1) to escape predators; 2) to exploit a favourable environment or 3) to consume a broader array of foods (Coleman and Galvani 1998). Finally, the positive relationship between egg size and parental care confirmed the expectation that these two traits have co-evolved (e.g. Sargent et al. 1987).

We identified three main strategies of fairly homogeneous life history features. A first strategy was to be a large fish, that invested in parental care for low to medium numbers of large eggs (e.g. *Gymnotus* spp. (GYSP), *Synbranchus marmoratus* (SMAR)

or *Krobia guianensis* (KGUI)). This association of life history traits was similar to the "equilibrium strategy" defined by Winemiller (1989) (Fig. 5). This strategy leads to higher juvenile survival as parents invest more into each offspring. It is favoured by relatively stable habitats (Winemiller and Rose 1992). A second strategy was to be a small fish having no parental care for low to medium numbers of small eggs. In addition, 75% of the taxa of this group (e.g. *Gasteropelecus sternicla* (GSTE), *Pseudopristella simulata* (PSIM), *Hemigrammus ocellifer* (HOCE)) spawn continuously (Mérigoux and Ponton unpublished data). Therefore, this group corresponded to the "opportunistic strategy" (Winemiller 1989) which is a strategy adapted to recolonize habitats after disturbance. The third strategy was to be a large fish having no or little parental care and many small eggs. This group corresponded to the "seasonal strategy" (Winemiller 1989) or the "periodic strategy" (Winemiller and Rose 1992). Fifty % of these taxa reproduced after a period of high seasonal water level in the Sinnamary River (e.g. *Leporinus* spp. (LESP), *Acestrorhynchus* sp. (ACSP), *Astyanax bimaculatus* (ABIM) or *Moenkhausia oligolepis* (MOLI)) (Mérigoux and Ponton unpublished data). These three strategies defined by Winemiller (1989) were fairly distinct but in accordance with Winemiller's results, we also found intermediate strategies at the boundaries of these three strategies. For instance, *Hemiodopsis quadrimaculatus* (HQUA), *Hoplias* spp. (HOPL) and *Rhamdia quelen* (RQUE) had much higher fecundity than fishes exhibiting the "true" equilibrium strategy. Comparably, *Poecilia parae* (PPAR) was much smaller than the other taxa having the equilibrium strategy. *Rivulus agilae* (RAGI) and *Rivulus xiphidus* (RXIP), being small and having very low fecundity corresponded to the opportunistic strategy but had larger eggs than most other taxa having this strategy.

In our creeks, fish (members of taxa) having the equilibrium strategy were mainly Siluriformes, Gymnotiformes, Synbranchiformes and Perciformes of the family Cichlidae. This result was similar to that of Winemiller (1989) in streams of the Venezuelian Llanos region (except for the Gymnotiformes). Characiformes were dominating the opportunistic and the periodic group in our study. In contrast, in the Llanos, Characiformes and Cyprinodontiformes were both equally represented in the opportunistic group, whereas Characiformes, Siluriformes and Gymnotiformes were the dominating taxa of the periodic group. Finally, periodic strategists were more and opportunists were less dominant in the Llanos than in the Sinnamary River. This should be related to the more contrasted hydrological seasonal pattern in the Llanos compared to the Sinnamary River (Ponton and Mérona 1998).

Young fish of species having the equilibrium strategy (except *Krobia guianensis* (KGUI) and *Cleithracara maronii* (CMAR)) had more streamlined bodies than fish having the periodic and opportunistic strategy. This feature contradicts the predictions of the Habitat Templet Concept (Townsend and Hildrew 1994) as well as the hypothesis of Winemiller and Rose (1992) that equilibrium strategists would primarily live in temporally stable environments. In contrast, the young fish diet of the equilibrium strategists was more specialised than that of the periodic and opportunistic strategists, corresponding to the predictions of the River Habitat Templet Concept.

The downstream creeks were hydrologically more unstable than the upstream creeks, due to the dam. In addition, the dam changed the clear seasonal hydrological pattern of the downstream creeks compared to patterns found in upstream creeks. Winemiller (1989) and the River Habitat Concept (Townsend and Hildrew 1994) predict that

equilibrium and/or periodic strategists should predominate in the upstream creeks, whereas the downstream creeks should be dominated by opportunists. Our data only partly confirmed these predictions as the upstream/downstream creeks dominance (%) for all captured specimens was 13/27 for equilibrium strategists, 42/11 for periodic strategists and 30/24 for opportunists. The remaining percentages were caused by fish groups for which no clear predictions are available.

Comparably, the 13 significant relationships found in the up- and the downstream creeks between traits and habitat variability either supported or contradicted predictions of the Habitat Templet Concept. As predicted minimal standard length at first maturity (upstream), mean diameter of mature oocytes (upstream), parental care (upstream) and relative body height (downstream) decreased with increasing temporal variability. Also as predicted, minimal standard length at first maturity (up- and downstream) and mean diameter of mature oocytes (downstream) increased and mean fecundity (downstream) decreased with increasing spatial variability. In contradiction to the predictions, parental care increased (downstream) with increasing temporal variability and food specialisation (upstream), length of the reproductive period within a year (upstream) and mean fecundity (upstream) increased and mean diameter of mature oocytes decreased (upstream) with increasing spatial variability. Thus, in contrast to European fish communities that are relatively poor in species number and traits because of glaciations (Persat et al. 1994), we found significant relationships between species traits and habitat variability for neotropical fish communities being rich in species and traits.

However, our trait patterns were rather complicated and differed between up- and downstream creeks. In addition, the data scatter was important and we needed a high

number of samples to demonstrate these trends. In the downstream creeks, parental care was positively related to temporal variability. However, we found more individuals of species reproducing at a small size, laying few and small eggs and having parental care in downstream than in upstream creeks. We speculated that reproducing at a smaller size and laying a small amount of small eggs could represent an effective gain of metabolic costs (see above). As a result, fish could spend more energy in taking care of their progeny after spawning. This trait would be crucial in habitats with unpredictable water level variations induced by the dam since 1994 (Ponton and Copp 1997; Ponton and Vauchel 1998). In upstream creeks, diet of species was more diversified in spatially more diverse habitats and we did not detect any pattern between diet diversity and temporal variability. Again, we speculated that in the absence of strong disturbances, generalist species found a wide range of food in spatially diverse habitats. Trends in the length of the reproductive period within a year contradicted the Habitat Templet Concept predictions because a long reproductive period may be due to two different causes: reproduction may be either independent of the environmental conditions (equilibrium strategy) or high temporal variability may lead to continuous spawning over the entire year (opportunistic strategy). Finally, the contrasting trends of mean diameter of mature oocytes and mean fecundity across spatial variability in up- and downstream creeks may be attributed to different overall proportion of periodic strategists (large fish, high fecundity and small to medium eggs) in the up- (42%) and downstream (11%) creeks. Therefore, we observed in upstream creeks larger fish in spatially more diverse habitats (as predicted by the Habitat Templet Concept) associated with a higher number of smaller eggs (contrasting the predictions). In the upstream

creeks, the number of eggs and their size seemed to be determined by fish species size instead of the habitat conditions.

Like in previous major tests of the River Habitat Templet (e.g. Statzner et al. 1994; 1997; Townsend et al. 1997) some of the traits we studied did not show significant relationships with either temporal or spatial variability. Townsend and Hildrew (1994) made predictions for a wide range of aquatic organisms; given that the relationships among biological traits are very diverse (Resh et al. 1994), it is clear that one should not expect that a given habitat acts as a templet in a uniform way for all traits of all its species (Stearns 1992; Townsend and Hildrew 1994).

We explained more of the variability in the biological traits when we considered habitat variability together with habitat state variables in the upstream creeks but not in the downstream creeks. We demonstrated for the upstream creeks that water oxygen content and turbidity were important for trends of life history traits such as minimal standard length at first maturity, mean diameter of mature oocytes or parental care. In clear, well oxygenated water, we found more individuals of species having large size at first maturity, bigg eggs and parental care. These biological attributes corresponded to the equilibrium strategy (see above). In contrast, in turbid, poorly oxygenated water we found more individuals of species having life history characteristics of the opportunistic strategy. Low oxygen concentrations generally cause a wide array of stress-related responses and limit distribution and activities of fish (Matthew 1998). High turbidity would also impede visual performances required for foraging (Matthew 1998). Thus, opportunistic strategists can more easily invade stressful habitats than equilibrium ones (Winemiller and Rose 1992)

Our study also demonstrated the need to separately consider studied areas with very different environmental conditions to match biological traits to habitat conditions. First, we obtained quite contradicting patterns between up- and downstream samples. Second, we improved relationships of biological traits with habitat conditions in the up- but not in the downstream creeks when considering habitat variability together with habitat state. Downstream, we observed a higher number of individuals of species having small size, few small eggs and more parental care compared to the upstream samples, which was probably due to the dam. Dam operations strongly modified the flow pattern in the downstream creeks, as the average water level remained low during the rainy season whereas short periods of extreme artificial floods occur during the dry season (Ponton and Vauchel 1998; Mérigoux et al. unpublished data).

Conclusion and perspectives

Our results only partially supported the predictions of the Habitat Templet Concept, although our study design was adapted to test the concept because 1) the species of the young fish fauna had a wide range of biological traits; 2) the samples were well distributed over a wide range of temporal and spatial habitat variability and 3) the habitat scales of the study was appropriate for young fish (Poizat and Pont 1996). Concerning the habitat scales, the period describing temporal variability (30 days before fishing) corresponded to a large part of the young fish life span in the creeks (Ponton and Tito de Morais 1994). Comparably, the small sample area (<100 m^2) corresponded to the space used as habitat by young fish (Schiemer et al. 1991; Schiemer and Zalewski 1992). However, future fish studies on the subject could improve the description of the

disturbance axis, should better consider the implication of trade-offs among traits and should be long term studies.

For example, to improve the description of the disturbance axis of the Sinnamary creeks, it would be better to evaluate the relative influence of flow regimes of the main river and of the creeks on the water level in the creeks. Even if flow in the creeks was most of the time feeble and was largely under the influence of the main channel discharge (Mérigoux et al. 1998), it was also rarely subjected to sudden variations due to local rains (Mérigoux pers. obs.). Such rain events should barely affect the fish if water level in the Sinnamary is high enough to slow the flooded creeks. In contrast, if the water level in the Sinnamary is very low, these rare heavy rains cause sudden creeks floods that can have strong disturbance effects for young fish by flushing them away (Ponton and Vauchel 1998). However, in the over 600 samples on creek water level at sampling sites during the ten sampling campaigns no observation indicated such an event (Mérigoux et al. 1998). Thus, we suppose that these events are very rare.

In further studies, we would also consider constraints and trade-offs among species traits which is a major concern in current concepts on the evolution of life histories (Roff 1992; Stearns 1992). When one or more traits are constrained in some way, unpredictable combinations may occur (Stearns 1980). For example, we showed that maximal fish size imposed a minimal standard length at first maturity, a mean diameter of mature oocytes and a mean fecundity. Furthermore, we demonstrated trade-offs between the mean diameter of mature oocytes and the mean fecundity as well as between the mean fecundity and the parental care. These constraints or trade-offs led to unexpected combinations that made it difficult to match traits and habitat conditions

(see also Resh et al. 1994; Statzner et al. 1997). Moreover, some constraints on trait combinations are determined by the potential of the genome that varies from taxon to taxon (Southwood 1988). Each species can not have all the biological characteristics that enable population resilience or resistance to disturbance. Once a particular trait has ensured success of the species in a temporally variable habitat, further traits might not be necessary (Townsend and Hildrew 1994). Thus, predictions considering several taxa may be globally rejected by observations although each taxon (or groups of taxa) may confirm the templet predictions at least for a particular trait.

We demonstrated differences in the trait patterns between the up- and the downstream samples. Life history traits of fish may show considerable phenotypic plasticity within a generation (Wootton 1990) and variations of traits that enhance survival in a variable environment have been observed for fish (Schlosser 1987; 1990; Heins 1991). Thus, to clarify the potential impact of the Petit Saut dam on the variation of life history traits, future studies should focus on intraspecific variations in life history traits (Jones and Ballinger 1987; Stearns 1992). This would require long term monitoring of the fish to discover the natural range of temporal variation in life history patterns and to discriminate the effect of the dam from natural disturbance with greater reliability. Given that the dam was closed only one year before we started this study, the downstream fish communities probably did not have enough time to change so that their traits corresponded to the habitat conditions we measured. This is another question to be solved by long term observations.

A previous paper on fish of the Sinnamary demonstrated difficulties to predict species richness from habitat conditions in our creeks (Mérigoux et al. 1998). It

concluded that functional community characteristics such as biological traits are potentially easier to predict that species richness. The results of our study demonstrated that the predictions of biological traits are certainly not so easy. As all previous major studies relating traits to habitats we found significant relationships between biological traits and habitat conditions. Thus, we agree with previous publications that the Habitat Templet Concept is an important element in ecological theory that has also the potential to be applied in management (Charvet et al. 1998). However, the richness of response patterns so far published demonstrates that we are far from understanding the mechanisms producing particular trait combinations in a given habitat.

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Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America

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Fish richness and species-habitat relationships in two coastal streams of French Guiana, South America

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Synopsis

We examined the factors controlling fish species richness and taxa-habitat relationships in the Malmanoury and Karouabo coastal streams in French Guiana between the short and long rainy seasons. The aims were to evaluate the environmental factors that describe species richness on different scales and to define the ecological requirements of fish taxa in the two streams at that period of the year. We sampled ten regularly spaced freshwater sites in each stream with rotenone. We caught a total of 7725 individuals representing 52 taxa from 21 families and 6 orders. More taxa were caught in the Malmanoury (n = 46) than in the Karouabo stream (n = 37). These values augmented by the number of fish taxa caught only by gill nets in a parallel survey fitted very well to a log-log model of fish richness versus catchment area in Guianese rivers. Most of the fish taxa encountered in the Malmanoury and Karouabo streams were of freshwater origin and nearly all the fish species caught in these two small coastal streams were also found in the nearby Sinnamary River with the exceptions of the cichlid *Heros severus* and the characid *Crenuchus spirulus*. Moreover, no significant relationship was found between a size-independent estimate of fish richness and distance from the Ocean. Thus, despite their coastal position, the Malmanoury and Karouabo streams contained fish assemblages with strong continental affinities. At a local scale, independently of site size, those with relatively more habitat types harbored a relatively greater number of fish taxa. Canopy cover, water conductivity and bank length were the most important environmental variables for fish assemblage composition at that period of the year. Oxygen and vegetation participated also in defining fish habitat requirements but to a lesser extent.

Introduction

One approach in evaluating the impacts of human disturbances on streams and rivers is to understand the relationship between their organisms and the environment. As the complexity of lotic systems implies different functional scales, such studies must be carried out on different levels of observation that depend on the questions to be answered (Wiens et al. 1986, Minshall 1988, Bayley & Li 1992, Hildrew & Giller 1994).

On very large scales, such as zoogeographical areas (sensu Bayley & Li 1992), fish species richness is usually considered to be mainly determined by climatic and/or geological events (Mahon 1984, Moyle & Herbold 1987, Hugueny & Lévêque 1994). The

number of fish species in a specific drainage basin is generally mainly explained by catchment area (Livingstone et al. 1982, Hugueny 1989, Welcomme 1990) and river discharge (Oberdorff et al. 1995). On more local scales such as pool/riffle sections or reaches (sensu Frissel et al. 1986), the physical factors useful to predict the number of species are usually: (i) habitat size or volume (Angermeier & Schlosser 1989, Hugueny 1990), (ii) habitat diversity expressed by an index that incorporates either depth, current velocity and substrate (Gorman & Karr 1978; Angermeier & Schlosser 1989), (iii) diversity of current velocities (Hugueny 1990), and (iv) distance from the ocean and/or channel width and depth (Angermeier & Karr 1983, Hugueny 1990, Lyons & Schneider 1990).

Fish species-habitat associations are generally established by studying ecological preferences of the taxa. Such studies are usually undertaken on small spatial scales such as microhabitats, pool/riffle sections and reaches (sensu Frissel et al. 1986). On these scales, current velocity, water depth and substrate proved to be good predictors of fish assemblage characteristics (e.g. Pouilly 1993), fish densities (e.g. Bain et al. 1988), and fish richness and diversity (e.g. Schlosser 1982). However, fish species can also be associated with other environmental parameters such as vegetation (Lobb & Orth 1991, Copp 1991), low oxygen conditions prevailing in leaf litter (Henderson & Walker 1990), water conductivity (Taylor et al. 1993) or temperature (Baltz et al. 1987).

In general, most of the knowledge concerning the relationships between lotic fishes and their environment relates to temperate climates and very little is known of factors structuring fish species richness and taxa-habitat relationships in neotropical rivers. In French Guiana, South America, such studies are even scarcer. Those performed on a biogeographical scale have addressed only certain taxonomic groups (see Boujard 1992 for cichlids) and the only study on the scale of a drainage basin considered longitudinal distributions of fish taxa in the Sinnamary River (Boujard & Rojas-Beltran 1988). On a more local scale such as reaches, Rojas-Beltran (1986) described the temporal variations of a fish assemblage in a small tributary of the Kourou River. In addition, Boujard et al. (1990a, b, c) studied the association between fish species and different types of habitats in the Arataye River but the use of gill nets limited the study to large species. All these studies were undertaken in large rivers or in their tributaries and no data have yet been published on fish-habitat relationships in the numerous small streams that drain the French Guiana Atlantic coast.

In this context, the aim of our study on fish assemblages in the Malmanoury and Karouabo coastal streams was to evaluate the environmental factors that describe species richness on different scales and to define the ecological requirements of the different fish taxa encountered in the two streams. This information is of particular concern with respect to these two streams as they border the European Space Center from where the toxic product emitting Ariane 5 rocket will be launched.

Study sites

The Malmanoury and Karouabo streams drain the Atlantic coastal plain of French Guiana to the north-east (Figure 1). These streams are 21 and 26 km long and drain areas of approximately 93 km^2 and 98 km^2, respectively. The mean annual discharge of the Karouabo Stream has been estimated at ca. 5.0 $m^3 s^{-1}$ with maximal instantaneous values > 60 $m^3 s^{-1}$ (Lointier unpublished). Its flow regime depends on the alternation of the short-, November to February, and long-, April to July, rainy season, with May and June being the wettest months, and the dry season (August to November), which is typical of the Guianese climate. Almost nothing is known about the flow characteristics of the Malmanoury Stream. Given its slightly larger drainage area, its mean annual discharge can be estimated to be somewhat above 5.0 $m^3 s^{-1}$, and its flow regime should be comparable to the Karouabo.

The upstream parts of both streams drain a dense forest dominated by *Parinari campestris* (Granville 1992). In its intermediate part the Karouabo Stream flows through a savannah and then loses its way in swamps with herbaceous plants such as *Eleocharis interstincta* alternated with subcoastal remnants of

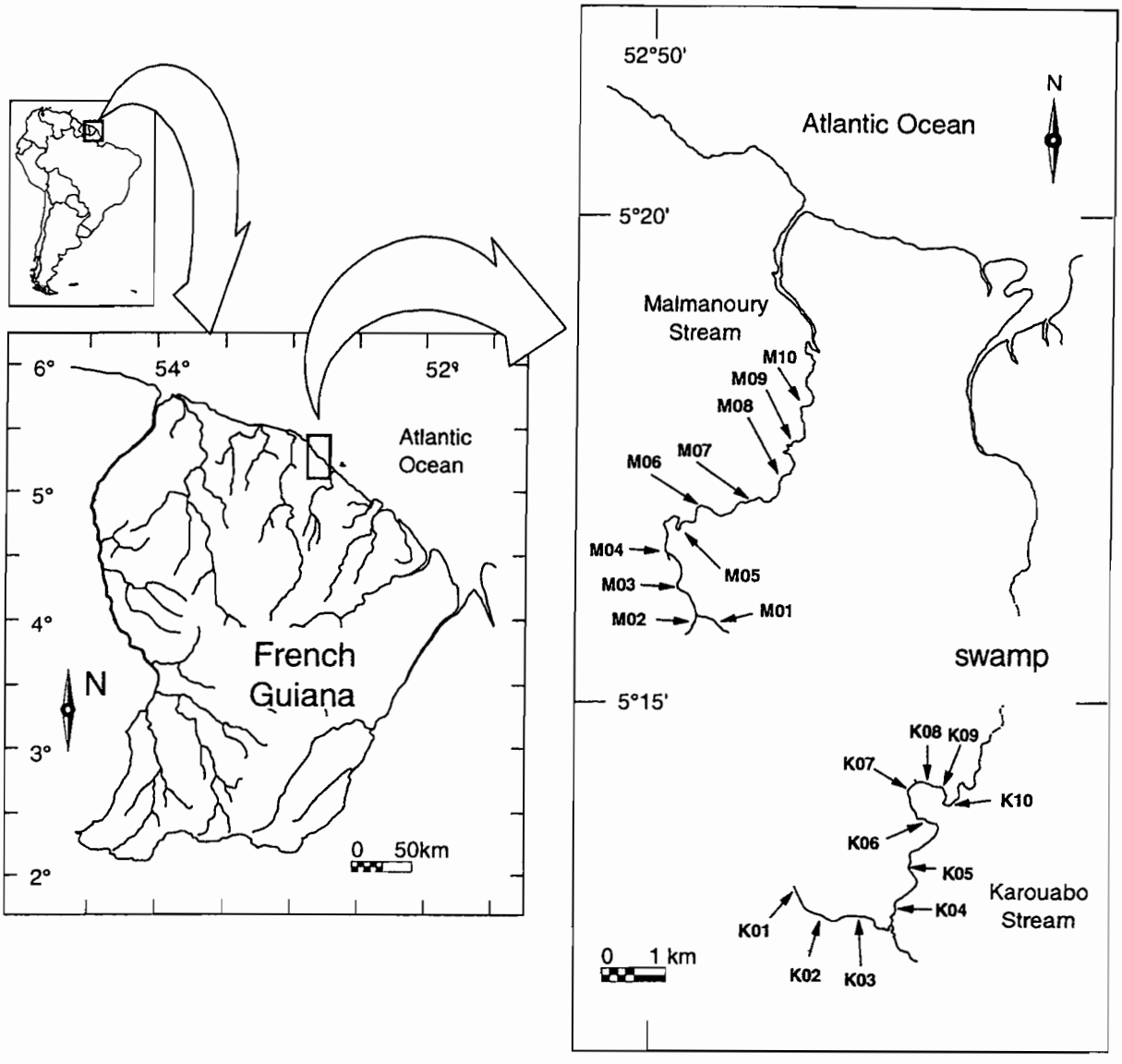

Figure 1. Map of the Malmanoury and Karouabo streams (French Guiana, South America) showing sampling sites (M01 to M10: Malmanoury Stream and K01 to K10: Karouabo Stream).

sandy shorelines where *Hymenaea courbaril* dominates (Loubry unpublished). The lower reaches of the Malmanoury stream meander through an hydromorphic forest of *Pterocarpus officinalis* and *Rhizophora racemosa*, the later being increasingly dominant near the estuary. Large herbaceous swamp areas occur on each bank of the main channel.

Material and methods

Fish sampling and habitat descriptions

We sampled ten regularly spaced sites (Figure 1) at random, i.e. without knowing whether fish were present or not, between the short and long rainy seasons (Malmanoury: 30 January – 3 February, 1995; Karouabo: 6 – 9 April 1995). At each site we measured water temperature, pH, oxygen and con-

ductivity with a ICM 51000 multiparameter before we enclosed an area (varying from 20 to 131 m^2 among sites) with two or three 1 mm mesh stop nets. Per enclosed area we applied at least two successive doses of PREDATOX (6.6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France) well mixed with water (for a complete description of the sampling method see Ponton & Copp 1997). We collected fish with 1 mm mesh dip nets and immediately preserved them in 95% alcohol. All individuals were identified later in the laboratory using keys for adults by Géry (1977), Le Bail et al. (1983, 1984), Rojas-Beltran (1984), Planquette et al. (1996), Lauzanne (unpublished) and keys for juveniles by Ponton (unpublished).

At the end of fish sampling, we recorded habitat characteristics following a method modified from Gorman & Karr (1978). At each point sample of a 1 × 1 m grid we measured depth with a graduated stick and then recorded the occurrences of different categories of organic litter, vegetation and substrate (see Table 1). Then we measured water current velocity at 0.2 and 0.8 water depth and at 1-m intervals along three transects with a C2 OTT flowmeter. Finally, we visually estimated percentage canopy cover and measured total bank length and total area.

In a parallel survey gill nets (2.5 x 25 m, mesh size 10, 15, 20, 25, 30, 35, 40, 50 mm knot to knot) were also set in four sampling sites of the Malmanoury Stream and three other in the Karouabo Stream between 17:00 and 8:00 h.

Data analysis

Habitat and fish taxa richness of each site. – At each point sample, we first merged the occurrences of the categories of depth, type of substrate, organic litter and vegetation coded 0 = absence or 1 = presence (see Table 1 for the different categories). Thus each point sample could be assigned to one of the different types of habitat each corresponding to a given chain of 0 and 1. In order to obtain size-independent estimates of habitat richness of each site, we then used the residuals of the regression of the total number of habitat types against the total number of point samples per site. Similarly, we regressed the total number of fish taxa caught per site against the total number of fish caught at that site in order to obtain size-independent (i.e. residuals) estimates of fish richness at each site.

Fish–habitat relationships and ecological requirements of taxa. – We first arranged habitat characteristics and fish densities in two data matrices: 'sites-by-environmental variables' and 'sites-by-fish taxa' (both rows-by-columns). Only the eight environmental variables in Table 1 were retained in the 'sites-by-environmental variables' matrix. Water temperature (mean = 26.3, SD = 1.24) and pH (mean = 4.8, SD = 0.25) varied little and were excluded. We also rejected water velocity as only three sites presented detectable current. Then we grouped data of canopy cover, conductivity, oxygen, bank length and depth in categories of equal

Table 1. Categories and codes of the environmental variables used to describe the habitat of each sampling site.

Variables	Categories	Codes
Disjunctive variables (1 category per site)		
Canopy cover (%)	< 75	1
	≥75	2
Conductivity (µs cm^{-1})	0–29	1
	30–36	2
	37–130	3
Oxygen (mg l^{-1})	1.2–2.9	1
	3–3.9	2
	4–6.8	3
Bank length (m)	0–10	1
	11–100	2
Fuzzy coded variable (> 1 category per site)		
Depth (cm)	0–27	1
	28–55	2
	56–82	3
	83–138	4
Litter	leaves	1
	wood diameter > 5 cm	2
	wood diameter < 5 cm	3
	roots diameter > 5 cm	4
	roots diameter < 5 cm	5
Vegetation	aquatic	1
	terrestrial herbaceous	2
	terrestrial shrubs or trees	3
Substrate	mud	1
	clay	2
	sand, gravels, stones, blocs	3

frequencies. The first four variables were disjunctive; i.e. they were represented by only one category per site (Table 1). Their codes were thus directly included in the 'sites-by-environmental variables' matrix. Water depth, litter, vegetation and substrate were described by using several categories per site (Table 1). We first submitted the frequencies of these different categories to fuzzy coding (Van Rijckevorsel 1987) in order to obtain only one positive score at each site (see Chevenet et al. 1994). These scores, or fuzzy-coded values, were then included in the 'sites-by-environmental variables' matrix. The 'samples-by-fish taxa' matrix contained $\log(x+1)$ transformed densities of the different fish taxa, except those occurring at only one site that have been excluded.

We submitted each matrix to correspondence analysis. This ordination technique first elucidated separately the typology of environmental variables and the relationships among taxa (Escofier & Pagès 1990, Chevenet et al. 1994). We then subjected the results from these two correspondence analyses to co-inertia analysis, a way to examine species-environment relationships when many species and several environmental variables are sampled in few sites (Dolédec & Chessel 1994). This technique is used to demonstrate whether a co-structure exists between environmental and faunistic data sets. The co-structure is determined by the maximization of the square-rooted projected inertia (which defines the structure of each table separately) and of the correlation between the two new sets of projected coordinates (Dolédec & Chessel 1994). We tested the significance of the resulting correlation by a Monte-Carlo method with 1000 random permutations of the rows of the environmental and faunistic data sets. All analyses and graphics were performed with ADE software (Thioulouse et al. 1995).

Results

A total of 7725 individuals representing 52 taxa from 21 families and 6 orders were collected at the 20 sampling sites (Table 2). More taxa were caught in the Malmanoury ($n = 46$) than in the Karouabo Stream ($n = 37$). Including additional taxa caught only by gill nets in a parallel survey ($n = 6$ and $n = 4$ respectively, Table 3), fish species richness in both streams fitted very well to a log-log model of fish richness versus catchment area in Guianese rivers (Figure 2).

In both Malmanoury and Karouabo streams, the Characiformes and the Perciformes accounted for 57% and 36% of the total individuals, respectively. The Siluriformes were poorly represented in the Karouabo Stream where only three taxa out of the ten encountered were found (Table 2). A total of 13 taxa collected in the Malmanoury Stream were not found in the Karouabo Stream and only five taxa encountered in the Karouabo Stream were not caught in the Malmanoury Stream (Table 2).

A total of 495 and 293 point samples allowed us to differentiate 164 and 134 different types of habitat in the Malmanoury and the Karouabo streams, respectively (Table 4). The mean relative number of habitat types per square meter was significantly higher in the Karouabo than in Malmanoury Stream. Identically, the mean relative richness of fish taxa was significantly greater in the Karouabo than in Malmanoury (Table 4).

A significant linear relationship was found between the number of habitat types and the total number of point samples per site (Figure 3a). In addition, the relationship between the number of fish taxa and the total number of fish individuals caught per site could also be expressed by a linear relationship (Figure 3b). Finally, a significant linear relationship was found between the residuals of these two regressions, i.e. between size-independent estimates of fish richness and habitat richness (Figure 3c). Thus, independently of site size, the higher the relative richness of habitat, the higher was the relative richness of fish.

The two matrices, Samples-by-Fish Taxa and Samples-by-Environmental Variables were significantly linked ($p < 0.001$, Monte-Carlo method with 1000 permutations). The first two axes of the analysis explained together 78% of the total co-inertia (Figure 4a). When examining the correlation ratios (Table 5), these axes separated taxa and sampling sites mainly according to canopy cover, conductivity and bank length, and to a lesser extend to oxygen contents and vegetation (Figure 4c). Co-inertia

Table 2. List of fish taxa, authority, abbreviated species code, number of fish (N) and range of standard length (SL in mm) in ten sampling sites of the Malmanoury Stream and ten other in the Karouabo Stream.

Order family sub-family species	Authority	CODE	Malmanoury		Karouabo	
			N	SL min-max	N	SL min-max
Characiformes						
Curimatidae						
Cyphocharax spilurus	Günther, 1864	CYSP	1	34–34	93	14–45
Curimatidae unidentified juveniles		CUSP	-	-	53	7–22
Anostomidae						
Leporinus gossei	Géry, Planquette & LeBail, 1991	LGOS	–	–	1	66–66
Erythrinidae						
Erythrinus erythrinus	(Schneider, 1801)	EERY	2	70–85	1	58–58
Hoplerythrinus unitaeniatus	(Spix, 1829)	HOUN	4	170–200	–	–
Hoplias aimara	(Valenciennes, 1840)	HAIM	–	–	1	20–20
Hoplias malabaricus	(Bloch, 1794)	HMAL	33	15–220	7	17–231
Hoplias unidentified juveniles		HOPL	1	9–9	–	–
Lebiasinidae						
Pyrrhulininae						
Copella carsevennensis	(Regan, 1912)	CCAR	90	10–38	230	7–38
Nannostomus beckfordi	Günther, 1872	NBEC	84	10–30	105	11–30
Pyrrhulina filamentosa	Val. in Cuv. & Val., 1846	PFIL	536	9–75	45	8–65
Gasteropelecidae						
Gasteropelecus sternicla	(Linnaeus, 1758)	GSTE	391	10–42	12	9–13
Characidae						
Characidiinae						
Microcharacidium eleotrioides	(Géry, 1960)	MELE	31	7–21	4	17–19
Characinae						
Acestrorhynchus falcatus	(Bloch, 1794)	AFAL	17	31–155	–	–
Acestrorhynchus unidentified juveniles		ACSP	5	20–30	–	–
Cheirodontinae						
Pristella maxillaris	(Ulrey, 1894)	PMAX	71	6–26	11	18–28
Pseudopristella simulata	Géry, 1960	PSIM	501	8–30	298	14–30
Crenuchinae						
Crenuchus spirulus	Günther, 1863	CRES	2	35–35	–	–
Serrasalminae						
Metynnis cf. *lippincottianus*	(Cope, 1870)	MLIP	–	–	1	33–33
Tetragonopterinae						
Astyanax bimaculatus	(Linnaeus, 1758)	ABIM	7	22–86	1	93–93
Astyanax cf. *keithi*	(Géry et al., 1996)	AKEI	1	39–39	2	6–14
Hemigrammus boesemani	(Géry, 1959)	HBOE	1	28–28	–	–
Hemigrammus ocellifer	(Steindachner, 1882)	HOCE	389	10–36	33	11–32
Hemigrammus unilineatus	(Gill, 1858)	HUNI	30	12–37	–	–
Hyphessobrycon aff. *sovichtys*	Schultz, 1944	HSOV	21	18–25	29	14–30
Moenkhausia chrysargyrea	(Günther, 1864)	MCHR	151	11–66	18	21–92
Moenkhausia collettii	(Steindachner, 1882)	MCOL	891	9–53	20	20–45
Moenkhausia hemigrammoides	Géry, 1966	MHEM	182	12–37	–	–
Moenkhausia oligolepis	(Günther, 1864)	MOLI	–	–	6	8–10
Characidae unidentified juveniles		CHSP	25	9–18	–	–
Siluriformes						
Auchenipteridae						
Tatia intermedia	(Steindachner, 1876)	TINT	10	46–65	–	–
Auchenipteridae unidentified juveniles		AUCH	2	8–10	–	–
Pimelodidae						
Pimelodella cristata	(Müller & Troschel, 1848)	PCRI	5	58–112	–	–
Pseudopimelodus raninus	(Valenciennes, 1840)	PRAN	34	14–73	–	–
Rhamdia quelen	(Quoy & Gaimard, 1824)	RQUE	8	38–293	–	–
Pimelodidae unidentified juveniles		PIME	1	17–17	–	–

Table 2. Continued.

Order family sub-family species	Authority	CODE	Malmanoury		Karouabo	
			N	SL min-max	N	SL min-max
Siluriformes						
Helogenidae						
Helogenes marmoratus	(Günther, 1863)	HMAR	1	53–53	–	–
Aspredinidae						
Bunocephalinae						
Bunocephalus sp.		BUNO	16	50–84	–	–
Trichomycteridae						
Trichomycterus guianense	(Eigenmann, 1909)	TGUI	22	17–70	1	40–40
Callichthyidae						
Hoplosternum thoracatum	(Val. in Cuv. & Val., 1840)	HTHO	11	17–135	4	14–26
Loricariidae						
Ancistrus aff. *hoplogenys*	(Günther, 1864)	AHOP	23	17–106	3	40–83
Rhineloricaria stewarti	(Eigenmann, 1909)	RSTE	1	31–31	–	–
Gymnotiformes						
Sternopygidae						
Eigenmannia virescens	(Valenciennes, 1847)	EVIR	8	83–110	1	90–90
Hypopomidae						
Brachyhypopomus beebei	(Schultz, 1944)	BBEE	18	15–165	14	22–85
Gymnotidae						
Gymnotus anguillaris	Hoedeman, 1962	GANG	8	76–268	5	82–138
Gymnotus carapo	Linnaeus, 1758	GCAR	13	20–57	16	55–180
Gymnotus unidentified juveniles		GYSP	7	13–21	–	–
Electrophoridae						
Electrophorus electricus	Gill, 1864	ELEL	1	709–709	–	–
Cyprinodontiformes						
Aplocheilidae						
Rivulus agilae	Hoedeman, 1954	RAGI	136	8–30	76	12–30
Rivulus igneus	Huber, 1991	RIGN	–	–	1	22–22
Rivulus xiphidius	Huber, 1979	RXIP	–	–	13	9–24
Synbranchiformes						
Synbranchidae						
Synbranchus marmoratus	Bloch, 1795	SMAR	40	30–140	12	40–130
Perciformes						
Nandidae						
Nandinae						
Polycentrus schomburgkii	Müller & Troschel, 1848	PSCH	7	23–43	134	7–57
Cichlidae						
Cleithracara maroni	(Steindachner, 1882)	CMAR	73	13–75	41	9–70
Crenicichla saxatilis	(Linnaeus, 1758)	CSAX	141	8–185	18	25–152
Heros severus	Heckel, 1840	HSEV	86	7–65	29	9–70
Krobia guianensis	(Regan, 1905)	KGUI	1671	7–132	67	13–125
Nannacara anomala	Regan, 1905	NANO	119	8–50	168	7–50
Cichlidae						
unidentified juveniles		CICH	2	11–13	–	–
Eleotrididae						
Eleotris amblyopsis	(Cope, 1870)	EAMB	214	7–50	–	–
Others						
Unidentified		INDE	3	7–11	3	7–10
Total number of orders			6		6	
Total number of families			21		16	
Total number of taxa*			46		37	
Total number of individuals			6148		1577	

* Number calculated without taxa corresponding to the codes HOPL, CHSP, AUCH, PIME, GYSP, CICH, INDE and with pooling CYSP-CUSP and ACSP-AFAL.

analysis allowed us to distinguish five groups of fish (Figure 4d) that correspond to four groups of stations (Figure 4b). These taxa were characterized by specific habitat requirements (Figure 4c). Sites with low bank length (0-10m) and < 75% canopy cover harbored characteristic taxa like Curimatidae, *Rivulus xiphidus*, and *Polycentrus schomburcki* when conductivity was medium (30 to 36 µs cm^{-1}) or *Hyphessobrycon* aff. *sovichtys* and *Heros severus* when aquatic vegetation was abundant (Figures 4, 5). *Nannostomus beckfordi* was typical of sites where both aquatic vegetation and medium conductivity were encountered. Sites with > 75% canopy cover and banks from 10 to 100 meters long presented fish assemblages whose composition depended on water characteristics. In these sites *Hoplerythrinus unitaeniatus* and *Hemigrammus unilineatus* were typical of waters with high conductivity

Table 3. List of fish taxa, authority, number of fish (N) in four sampling sites of the Malmanoury Stream and three other in the Karouabo Stream sampled with gill nets (mesh size 10, 15, 20, 25, 30, 35, 40, 50 mm knot to knot) during one night in a parallel survey. * = taxa caught only by gill nets.

order family sub-family species	Authority	Malmanoury N	Karouabo N
Elopiformes			
Megalopidae			
Megalops atlanticus	Valenciennes, 1846	4 *	2 *
Characiformes			
Anostomidae			
Leporinus friderici	(Bloch, 1794)	–	8*
Leporinus gosseti	Géry, Planquette & LeBail, 1991	15*	1
Erythrinidae			
Hoplerythrinus unitaeniatus	(Schneider, 1801)	4	2
Hoplias malabaricus	(Bloch, 1794)	38	8
Characinae			
Acestrorhynchus falcatus	(Bloch, 1794)	242	63
Tetragonopterinae			
Astyanax bimaculatus	(Linnaeus, 1758)	15	6
Moenkhausia chrysargyrea	(Günther, 1864)	3	1
Piabucus dentatus	(Köhlreuter, 1761)	2 *	–
Siluriformes			
Auchenipteridae			
Parauchenipterus galeatus	(Linnaeus, 1766)	82*	76*
Pseudauchenipterus nodosus	(Bloch, 1794)	7*	–
Tatia intermedia	(Steindachner, 1876)	1	–
Callichthyidae			
Hoplosternum thoracatum	(Valenciennes in Cuvier & Valenciennes, 1840)	7	2
Loricariidae			
Ancistrus aff. *hoplogenys*	(Günther, 1864)	6	–
Hypostomus ventromaculatus	Boeseman, 1968	1*	–
Rhineloricaria stewarti	(Eigenmann, 1909)	1	–
Gymnotiformes			
Sternopygidae			
Eigenmannia virescens	(Valenciennes, 1847)	1	–
Cichlidae			
Crenicichla saxatilis	(Linnaeus, 1758)	7	–
Heros severus	Heckel, 1840	11	2
Number of taxa caught only by gill nets		6	4

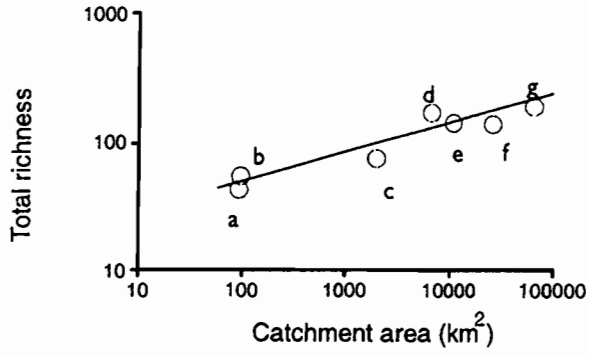

Figure 2. Relationship between total fish richness and catchment area for different Guianese rivers (log fish richness = 0.2154*log catchment area + 1.2471, F = 42.2009, df = 6, p = 0.0013). With a and b – Malmanoury and Karouabo streams respectively (this study), c – Kourou River (Planquette, INRA, Kourou unpublished data), d – Sinnamary River (Lauzanne & Tito de Morais, ORSTOM Cayenne unpublished data), e – Approuague River (Boujard et al. 1990 a, b), f – Oyapock River (Boujard et al. 1990 a, b), and g – Maroni River (Planquette, INRA, Kourou unpublished data). Data of catchment areas for c, d, e, f, and g are from Hiez & Dubreuil (1964).

(> 36µs cm^{-1}) and low oxygen concentrations (< 3 mg l^{-1}). *Pimelodella cristata* and *Bunocephalus* sp. were more often caught when water conductivity was less than 30 µs cm^{-1}. *Pseudopimelodus raninus*, *Trichomycterus guianense*, and *Eleotris amblyopsis* were indifferent to water quality (Figures 4, 5). More than 50% of the fish taxa were classified as habitat generalists (Figure 4d). Among them *Nannacara anomala*, *Hoplosternum thoracatum*, *Cleithracara maroni*, *Pyrrhulina filamentosa*, and *Copella carsevennensis* were the most typical (Figures 4, 5).

Discussion

Fish richness in the Malmanoury and Karouabo streams

With total richness of 52 and 41 taxa respectively, the Malmanoury and Karouabo streams fit well to a log-log model linking fish richness to catchment area for different Guianese rivers (Figure 2). Our data confirm that catchment size is one of the main factors determining fish species richness in French Guiana as elsewhere (Livingstone et al. 1982, Hugueny 1989, Welcomme 1990, Oberdorff et al. 1995). Nearly all fish species caught in these two small coastal streams were also found in the nearby Sinnamary River (Boujard & Rojas-Beltran 1988, Lauzanne & Tito de Morais unpublished data). The only exceptions are the cichlid *Heros severus*, which was probably introduced accidentally into coastal

Table 4. Characteristics of sampling sites, point samples, habitat types and fish taxa in the Malmanoury and Karouabo streams. With SE = standard error, t = value of Student's t statistic when testing Ho = 'there is no difference between mean values observed in each stream', p = associated probability. Only probabilities for significant differences are given. Habitat types were obtained by merging the presence/absence data of each category of the four variables: depth, litter, vegetation, and substrate at each point sample (see explanation in text).

	Malmanoury	Karouabo	t	p
Sampling sites				
total number	10	10		
total sampling area (m²)	638.9	278.2		
mean area (SE)	63.88 (2.92)	27.82 (3.24)	3.677	0.001
Point samples				
total number	495	293		
mean number per m² (SE)	0.88 (0.01)	1.09 (0.01)	1.812	–
Habitat types				
total number	164	134		
mean number per m² (SE)	0.358 (0.008)	0.619 (0.016)	3.753	0.001
Fish taxa				
total number	46	37		
mean number per m2 (SE)	0.386 (0.022)	0.659 (0.031)	3.520	0.001

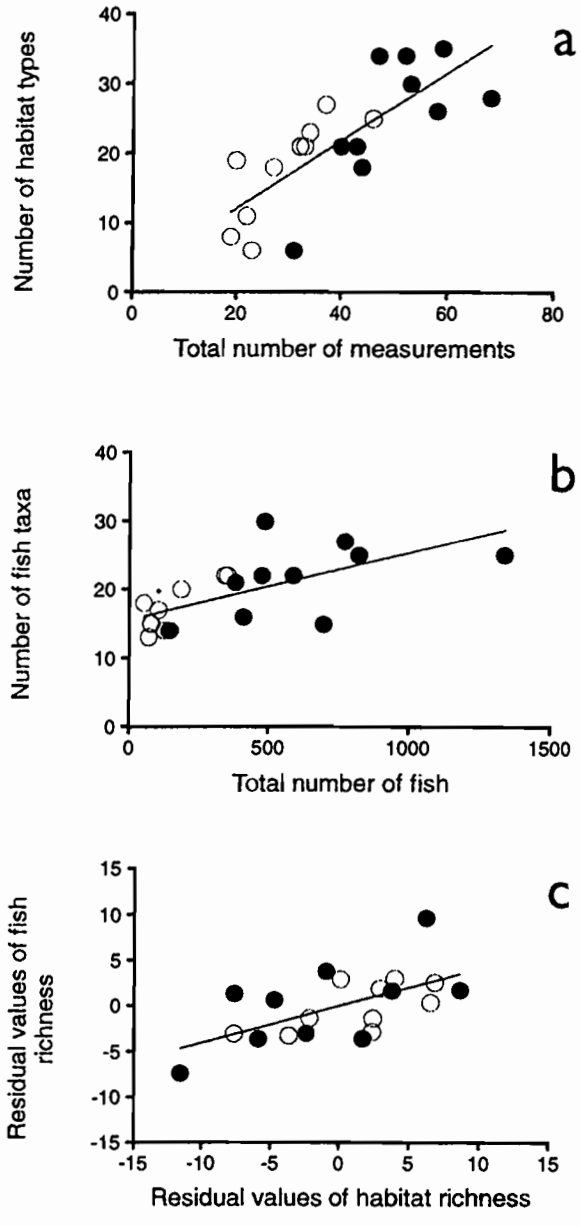

Figure 3. Relationships between (a) number of habitat types and total number of habitat measurements per site (number of habitat types = 0.488* number of point samples +2.386, F = 27.290, df = 19, p 0.001), (b) number of fish taxa and total number of fish caught per site (number of fish taxa = 0.010* number of individuals +15.534, F = 13.724, df = 19, p = 0.002), and (c) residuals of regression a and residuals of regression b (residuals regression figure 3b = 0.408* residuals regression figure 3a, F = 10.453, df = 19, p = 0.005). Closed circles = data from Malmanoury Stream and open circles = data from Karouabo Stream.

streams in the seventies,[1] and the characid *Crenuchus spirulus*, which is characteristic of coastal marshes in French Guiana (Planquette et al. 1996). The similarity of their fish fauna indicates that temporary connections between these three closely located river basins must have existed in the past (Sinnamary River) or must exist at present during periods of very high water levels (Malmanoury and Karouabo streams).

In contrast to Central American streams and rivers flowing into the Pacific where most fish species have marine affinities (Lyons & Schneider 1990), a large majority of the taxa caught in the Malmanoury and Karouabo streams are primary freshwater fish. Most of them belong to the Characiformes, as in larger Guianese rivers (Boujard et al. 1990a, Tito et al. 1995) and in Central Amazon rivers (Goulding 1980, Lowe-McConnell 1987). Nevertheless, some differences between the two streams could be explained by the free connection of the Malmanoury to the Ocean while the studied portion of the Karouabo is isolated from marine waters by a large swamp. Indeed, taxa supposed to have marine affinities like *Bunocephalus* sp. (Siluriformes, Aspredinidae) and *Eleotris amblyopsis* (Perciformes, Eleotrididae) were only found in the Malmanoury.

[1] Our late colleague Dr Paul Planquette, INRA Kourou, French Guiana, personnal communication 1996d.

Table 5 Correlation ratios of the habitat variables on the first two axes F1 and F2 of the co-inertia analysis. These ratios represent proportions of the total variance explained by each axis to depict the separation among modalities of a variable.

Variables	Correlation ratios	
	F1	F2
Canopy cover	0.857	0.007
Conductivity	0.762	0.827
Oxygen	0.370	0.486
Bank length	0.637	0.026
Depth	0.219	0.033
Litter	0.028	0.008
Vegetation	0.218	0.181
Substrate	0.204	0.076

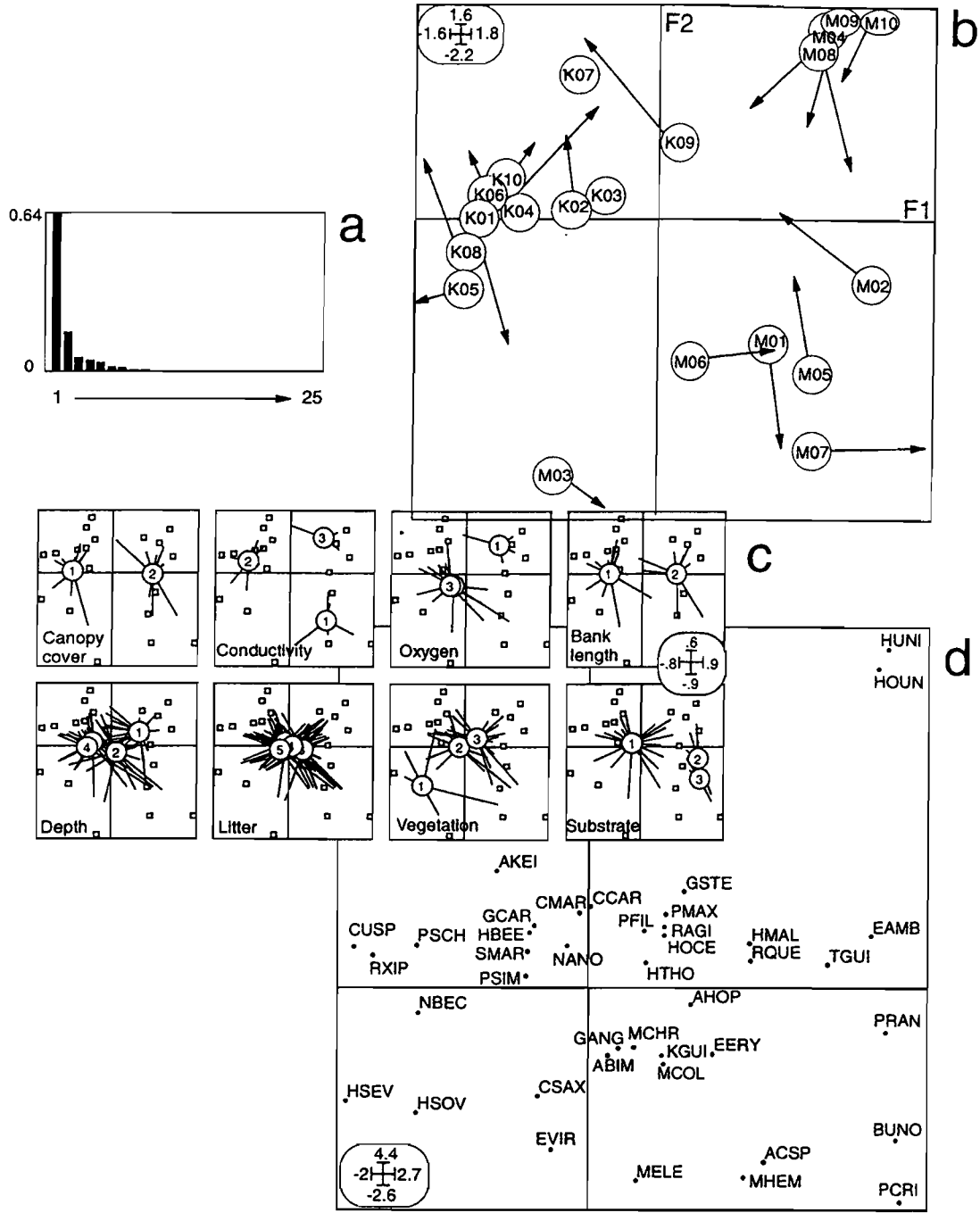

Figure 4. Results of co-inertia analysis expressing the relationships between fish taxa and habitat: a – histogram of the relative inertia of each axis, b – sampling site coordinates on the F1 × F2 plane of the co-inertia analysis. The arrows link the positions of sites obtained from habitat ordination to those given by faunistic ordination. c – Ordinations of the different modalities of habitat variables resulting from co-inertia analysis (see Table 5 for correlation ratios of each variable). Squares correspond to the positions of sampling sites determined by the faunistic table coordinates. Variable categories (codes in circles, see Table 1) are located at the weighted average of the coordinates of the sampling sites presenting that modality. Lines link sampling sites to their modalities but are only 60% of their total length for readability. They are omitted when a species contributed less than 1% to the modality distribution. d – Fish taxa coordinates on the F1 x F2 plane of the co-inertia analysis. See Table 2 for taxa codes.

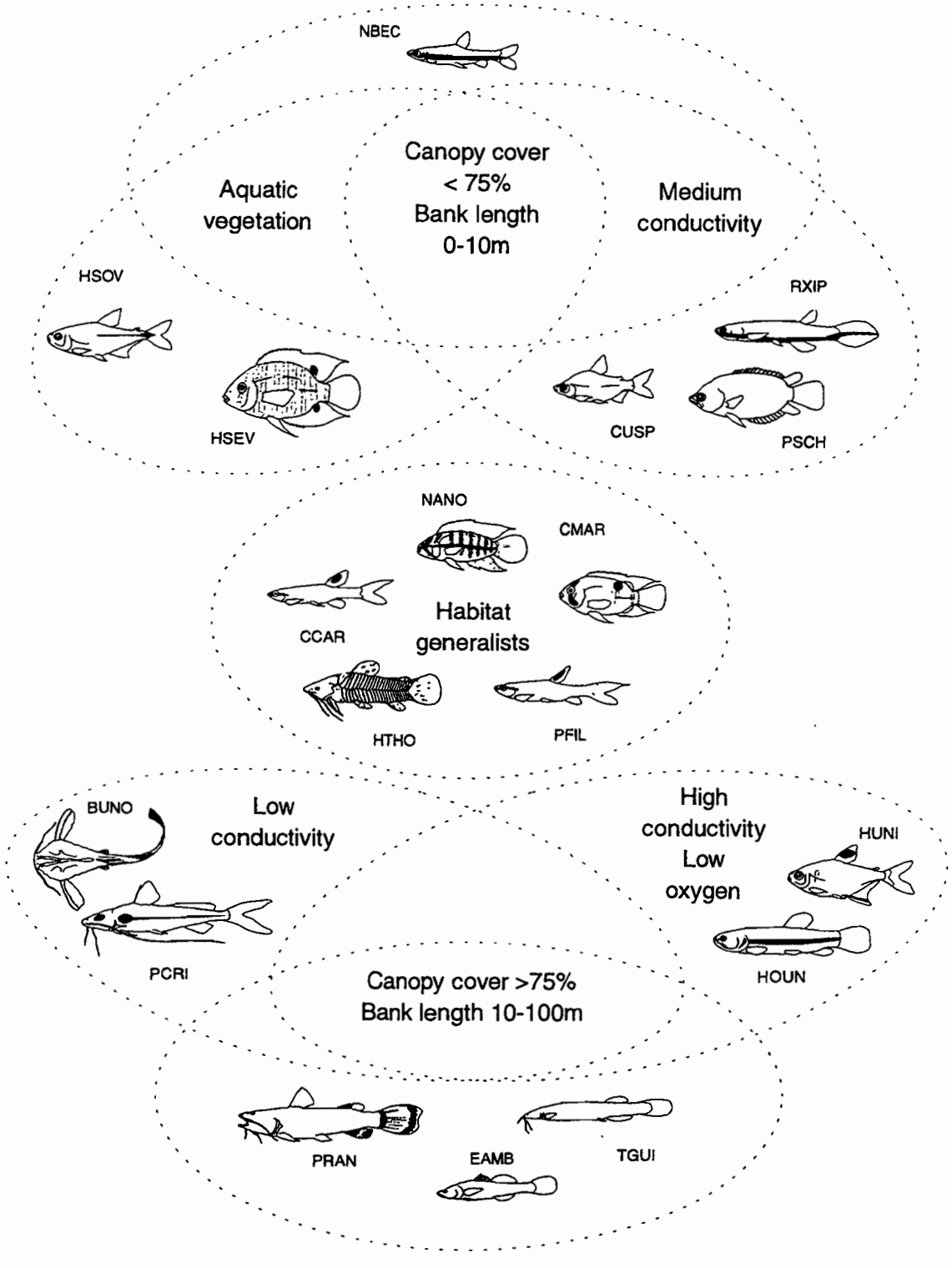

Figure 5. Schematic representation of fish assemblages that are most likely to be found in four types of habitat in the Malmanoury and Karouabo streams. Fish taxa considered as habitat generalists are also presented. Fish drawings, not to scale, after Lauzanne (unpublished) modified. See Table 2 for taxa codes.

Fish taxa richness at a local scale

At a local scale, the higher the relative richness of habitat, the higher was the relative richness of fishes (Figure 3c). This relationship agrees well with the hypothesis that interspecific competition and predation decrease in complex and/or highly diverse habitats (Hugueny 1990). It also confirms the positive relationship between fish species richness and habitat found in Panamanian streams by Gorman & Karr (1978) and Angermeier & Schlosser (1989). Contrary to Lyons & Schneider (1990) we found no significant relationship between size-independent estimates of fish richness and distance from the Ocean either in the Malmanoury ($F = 0.756$, $df = 9$, $p = 0.400$) or in the Karouabo Stream ($F = 1.452$, $df = 9$, $p = 0.263$). However, while fish assemblages in our streams were dominated by taxa of freshwater origin, those studied by Lyons & Schneider had predominantly marine affinities and thus taxa were colonizing the stream from the ocean.

Fish taxa and their habitat

The main environmental variables that define habitats of fish assemblages in the Malmanoury and Karouabo streams between the short and long rainy seasons were canopy cover, water conductivity and bank length. Oxygen and vegetation were also influential but to a lesser extent. Our results can be compared to those of Taylor et al. (1993) who found that conductivity was the strongest descriptor of site-specific assemblage structure in the upper Red River system, southwestern Oklahoma, U.S.A. However, type of substrate, depth and current velocity are usually stated as being the best environmental variables predicting fish assemblage composition at small scales (see for example Gorman & Karr 1978, Schlosser 1982, Hugueny 1990). These discrepancies may be due to the homogeneous bottom of most of our sampling sites consisting mainly of mud. Thus, we principally collected fish taxa either preferring muddy substrates or being neutral with respect to substrate. Moreover, for maximum efficiency, sampling with rotenone requires limited depths and current velocities reducing variability among the sites.

The habitat requirements of some fish taxa may be explained by their feeding and/or reproductive habits. For example *Hoplerythrinus unitaeniatus*, *Hemigrammus unilineatus*, *Pimelodella cristata*, *Pseudopimelodus raninus*, *Bunocephalus* sp., *Trichomycterus guianense* and *Eleotris amblyopsis* were more frequently caught in sites with significant bank length in dense forests (Figure 5). These taxa may have selected these riparian ecotones as they provide a diversified food source in Guianese rivers (Tito et al. 1995). Conversely, in open water sites with dense aquatic vegetation, fish species depend more on autochthonous food than on prey of terrestrial origin. Indeed, food items of *Heros severus* include large quantities of aquatic vegetation, at least in captivity (Ponton unpublished), while *Nannostomus beckfordi*, which is characteristic of coastal swamps in French Guiana (Planquette et al. 1996), may feed on microcrustaceans and insect larvae in aquatic vegetation. Moreover, some fish taxa may have used specific habitats because of their reproductive habits. For example, small-sized Characiformes of the genus *Hyphessobrycon* and *Nannostomus* are known to lay their adhesive eggs on plants during the rainy season (Breder & Rosen 1966, Burt et al. 1988).

Although descriptive, our work is a first step towards understanding fish richness and species-habitat relationships in Guianese coastal streams at different spatial scales. At a large scale, our results indicate that the total number of fish species in these streams is strongly dependent on their catchment area. At a local scale, we found that (1) the relative number of fish in a given site increases with its relative complexity, and (2) the composition of fish assemblages at each site depends to a large part on the type of habitats present. These last two patterns are based on observations made between the short and long rainy seasons and future investigations should include temporal variability. Indeed, Karr et al. (1983) pointed out that relationships between fish richness and habitat may vary seasonally due to migrations induced by changing flow conditions, food availability and the search for suitable spawning and nursery areas. Similarly, microhabitat use by

fish species depends on environmental conditions, species interactions, food availability and threat of predation (Bain 1995). Finally, future studies will attempt to detail relationships between environmental parameters and the life styles (mainly feeding and reproductive ones) of the different fish taxa. Outgoing the systematic position of the different fish taxa, will give broad applicable insights on human impacts in neotropical areas and specifically on the effects of toxic products emitted during launchings of the Ariane 5 European rocket.

Acknowledgements

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A6

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

Ponton D., Mérigoux S. & Copp G.H.

(Soumis à Aquatic Conservation)

Abstract

1. In this paper, we assess the usefulness of surveying young fish assemblages in tributaries of the Sinnamary River (French Guiana, South America) as a means of monitoring environmental changes in a neotropical river subjected to hydrodam operations.
2. We confirm that the tributaries of the Sinnamary River are nurseries for more than half the fish species present in the river.
3. We show 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 favored in the impacted sections.
4. Our 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 scale for detecting the immediate effects of flow disturbances on fish communities.
5. Our findings suggest that it is more informative and less time-consuming to consider only the abundance of juveniles, and to group them at the order level instead of calculating diversity indices.
6. We conclude that use of the relative abundance of Characiformes juveniles at the end of the rainy season can be a cost-efficient way to assess ecosystem function in neotropical rivers subjected to hydrological impact.

A7

The relationship between local and regional species richness: comparing biotas with different evolutionary histories

Hugueny B., Tito de Morais L., Mérigoux S., Mérona B. & Ponton D.

(Oikos, 1997, 80: 583-587)

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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

The relationship between local and regional species richness: comparing biotas with different evolutionary histories

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The fact that the local richness of communities is not strictly dependent on local conditions but is also affected by regional richness was recently stressed (Cornell and Lawton 1992, Cornell 1993, Schluter and Ricklefs 1993). According to Cornell and Lawton (1992) local species richness (LSR) and regional species richness (RSR) are interrelated in various ways. Graphically, two endpoints along a continuum can be distinguished: proportional sampling (linear relationship between the two variables, Type I curve) and ceiling (local species richness increases with regional species richness but reaches an asymptote, Type II curve). Proportional sampling reveals unsaturated communities in which species interactions are not sufficient to limit local species richness. Cornell and Lawton (1992) considered how the relationship between LSR and RSR could be affected if species' characteristics of the regional pool change over evolutionary time. For instance they argued that the LSR/RSR ratio increases if species added, by immigration or speciation, to the regional pool are better dispersers and decreases if they are superior competitors. The same arguments hold if regional pools from areas which have undergone different evolutionary histories are compared. The major aim of this note will be to illustrate the effect that the mixing of biotas with different evolutionary histories has on the assessment of the relationship between LSR and RSR. Hypothetical as well as real examples are included, and methodological and conceptual issues will be briefly addressed.

History may obscure the LSR-RSR relationship

Up to now, community saturation studies have only integrated two spatial scales: local and regional. A region is delimited in such a way that propagules of all species are available to all of its localities over ecological time scales. Within the region, localities are the areas where ecological processes (species interaction, disturbance) predominate. Province, as defined by Rosenzweig (1995: 264), is hereby introduced as a third spatial scale. By definition, two different provinces have very few or no species in common and they are assumed to harbor independently evolved biotas. This "three spatial scale" framework taken into consideration, two categories of community saturation studies can now be distinguished. The first category includes works in which regions are drawn from the same province and species similarity between regions is high. An example is provided by the work of Ricklefs (1987) on bird communities in West Indian islands. The second category includes works in which regions are drawn from different provinces. Lawton et al. (1993), for example, compared insect herbivore species richness on bracken between UK, USA, South Africa and New Guinea. These two kinds of studies are generally considered as equivalent with regard to community saturation testing. It is thus implicitly assumed that there is no historical effect on the LSR-RSR relationship; or in other words the LSR-RSR relationship does not differ between provinces. However, we emphasize that the mixing of regions which are highly dissimilar in species composition may introduce substantial noise in the data by increasing the likelihood that biological features affecting the LSR-RSR relationship (such as dispersal ability) are not distributed equally between regional biotas. As for a hypothetical example of how not taking into account the historical factor may obscure the results, let us consider the relationship between LSR and RSR assessed with regions belonging to three different provinces (Fig. 1). If we assume that there is no historical effect then there is only one LSR-RSR relationship.

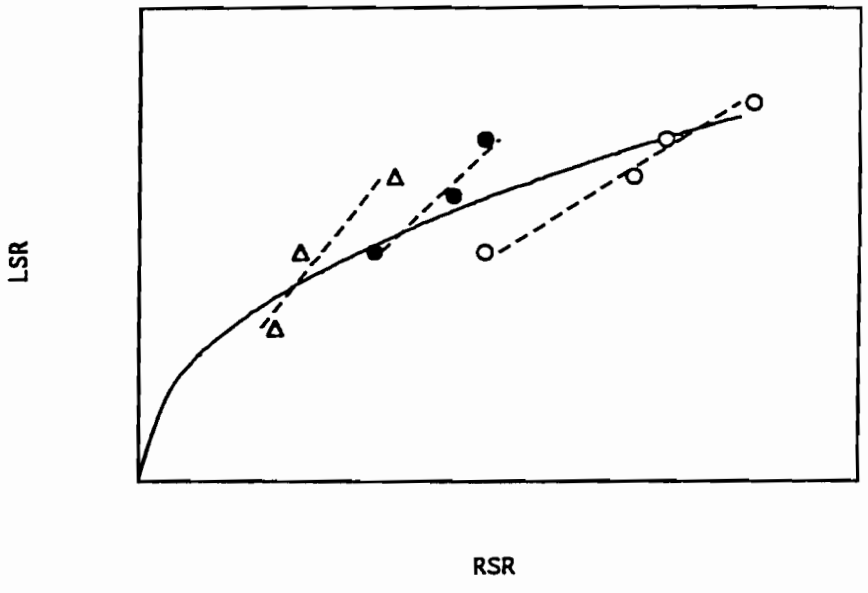

Fig. 1. Relationship between local species richness (LSR) and regional species richness (RSR) for three provincial biotas. Two models are fitted to these data. The first assumes that there is no historical effect: one curve describes the relationship between LSR and RSR (a Type II curve in this case; solid line). The second model considers that there is a historical effect: three different curves (Type I curves in this case; broken lines) are fitted, one for each province.

In our hypothetical example the best fit is provided by a curvilinear relationship. Conversely if we assume that there is a historical effect then three different LSR-RSR curves must be fitted, one per province. In this case, the best fit is provided by three Type I curves. Accepting the existence of a historical effect leads to the conclusion that the communities are unsaturated whereas rejecting this existence leads to the opposite conclusion. Deciding if there is a statistically significant historical effect becomes, therefore, crucial and is the aim of the next section.

Testing for a historical effect

We will assume that curves displaying non-proportional sampling are roughly fitted by a second order polynomial. For convenience these curves are called Type II curves even if an asymptote is not reached. Another valid approach is to use a log-log transformation of the data so that non-proportional sampling appears with a slope significantly less than unity (see, for instance, Griffiths 1997). However, we will only focus on the polynomial approach because it allows us to test simultaneously for saturation and historical effect in an easier way than by a log-log transformation. To test for a historical effect we used a regression procedure which included one predicted variable: LSR (local species richness); two explanatory variables: RSR (regional species richness), RSR^2; and two interaction terms: PROV × RSR and PROV × RSR^2; where PROV is a dummy variable coding the province. Since the curves were constrained to pass through the origin, the constant term is excluded from the model. For the same reason, PROV is not considered as an explanatory variable. We then applied a stepwise selection. This method permitted us to distinguish between four cases according to the variables included in the regression model (Table 1): 1) the same Type I curve is fitted within each province; 2) the same Type II curve is fitted within each province; 3) different Type I curves are fitted within each province; 4) different Type II curves are fitted within each province or there is a mixing of Type I and Type II curves. Obviously if there are not enough data to assess the LSR-RSR relationship independently within each province, there can be no way of testing for historical effect and thereby no reliable conclusion can be made about the occurrence of saturation in the communities studied.

An example of a historical effect

We will now further illustrate these points with a concrete case. The LSR-RSR relationship has been assessed for river fish communities of two intertropical areas: Côte d'Ivoire in West Africa (Sahelo-Soudanian region), and French Guiana in South America (Guianan-Amazonian region). A complete separation of the two continents was achieved between 106 and 84 million years ago (Goldblatt 1993) and they have no freshwater fish species in common. Experimental fishing was carried out using sets of gill nets 15 to 25 m long and 2 or 2.5 m deep with various mesh sizes (from 10 to 40 mm in Africa, 10 to 70 mm in Guiana). Sampling took place in pools more than 1 m deep, 15 m wide, and 500 m long, with low current velocity (lower than

Table 1. Intraprovincial LSR-RSR relationships implied by various regression models.

RSR	RSR^2	RSR × PROV	RSR^2 × PROV	Conclusions
Yes	No	No	No	NH, all Type I
Yes/No	Yes	No	No	NH, all Type II
Yes/No	No	Yes	No	H, all Type I
Yes/No	Yes/No	Yes/No	Yes	H, all Type II
Yes/No	Yes	Yes	Yes/No	or Type I + Type II

Note: The explained variable is LSR (local species richness) and a stepwise selection of variables is used (RSR: regional species richness, PROV: dummy variable coding the province). "Yes" means that the presence (absence if a "No" occurs) of the variable in the regression model is a necessary condition to validate the corresponding conclusion. "Yes/No" means that the absence or presence of the variable has no effect on the conclusion. "NH" means that there is no historical effect, "H" means that there is an historical effect. Type I and Type II refer to the shape of the intraprovincial LSR-RSR relationships.

0.2 m/s). Regional species richness (RSR) is the number of species known to occur in a river and local species richness (LSR) is the number of species sampled by locality within this river. Data from 47 localities distributed among 10 West African rivers come from Hugueny and Paugy (1995). Data for four Guianan rivers (Karouabo, Malmanoury, Sinnamary and Approuague) and 22 localities were provided by Boujard et al. (1990), Tito de Morais et al. (1995) and B. de Mérona, D. Ponton and S. Mérigoux (unpubl.). In the Approuague river, Boujard et al. (1990) computed species richness in each locality per mesh size but not for the entire gang of nets. Consequently, we estimated the local species richness by the midpoint between possible maximum value (the sum of the species richness observed per mesh size) and possible minimum value (the highest species richness observed per mesh size). The resulting value conforms with the value of the Sinnamary river which has an RSR similar to the Approuague river.

Without distinction between the two provinces it is tempting to claim that community saturation has been demonstrated because a Type II curve, described by a second order polynomial, gives a good and significant fit (the second order term has a significant contribution, $p < 0.00001$). When the above stepwise regression procedure is applied, only RSR and PROV × RSR are included in the model ($p < 0.00001$ in both cases). According to Table 1, the LSR-RSR relationship differs between provinces, i.e. each province displayed its own Type I curve (Fig. 2). As previously demonstrated (Hugueny and Paugy 1995), Ivoirian rivers are clearly unsaturated. Guianan rivers are probably unsaturated too, but data are less reliable due to a lower number of rivers studied. If we accept that a Type I curve is a good model for Guianan rivers, its slope is smaller (0.18) than the slope obtained with Ivoirian rivers (0.27). A comparative study (Tito de Morais and Hugueny unpubl.) carried out on small stream fish communities of the Sinnamary river (Guiana) and those of an Upper Niger tributary (West Africa) suggests that the low LSR/RSR ratio may be a general feature of the Guianan ichthyofauna compared to the West African one. This study was based on rotenone samples effected in habitats covering similar environmental gradients between the two rivers. The LSR/RSR ratio was found higher in the Niger river than in the Sinnamary river after removing the effect of local habitat structure. As a whole, the data analyzed in this note suggest that the different evolutionary histories undergone by the two ichthyofaunas compared lead to different LSR-RSR relationships. However, the effect of some confounding factors, such as sampling bias or habitats imperfectly matched between provinces, cannot be completely ruled out and our data must be considered merely as a possible case of historical effect waiting for other supporting evidence. One major process that can produce such a historical effect is that some biological features affecting the LSR-RSR relationship are not distributed equally between the West African and the Guianan ichthyofaunas. Body size distributions are different between the two ichtyofaunas: small species (less than 20 cm in body length) constitute a higher proportion ($\chi^2 = 9.24$, 1 df, $p < 0.005$) of the fauna in the Synnamary river than in Côte d'Ivoire (75%, $n = 126$, versus 58%, $n = 154$). In freshwater fishes, body length is related to characteristics that probably enhance dispersal ability, for instance optimum swimming speed increases with body size (Videler 1993), and large fishes migrate more than small fishes (Roff 1988). Our results seem to be consistent with the suggestion made by Cornell and Lawton (1992) that the LSR/RSR ratio increases with average dispersal ability of species. Whatever the underlying processes, our example provides the first evidence of a provincial effect on the LSR-RSR relationship.

Conclusion

The LSR-RSR relationship can differ between provinces, as illustrated by river fish communities of Côte d'Ivoire and Guiana. As a result, sampling local richness in different provinces without simultaneously sampling regions within provinces can lead to incorrect interpretation of the LSR-RSR relationship. Mixing different provincial biotas increases the likelihood that biological features affecting the LSR-RSR relationship

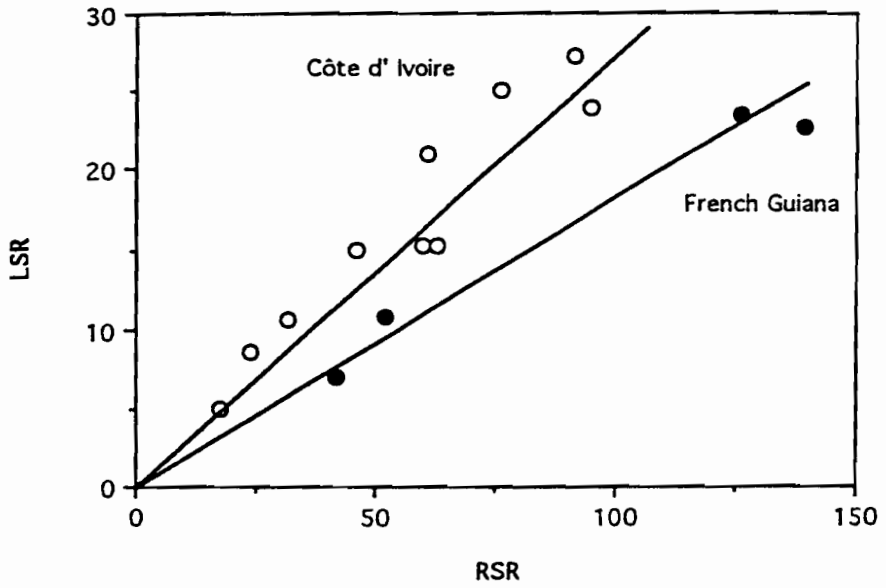

Fig. 2. Relationship between local species richness (LSR) and the number of fish species in the catchment area (RSR). Mean local species richness is plotted for each river. Regression lines are constrained to pass through the origin and fitted separately for Ivoirian and Guianan rivers using the 69 local species richness estimates.

will not be distributed equally between the different biotas, due to different evolutionary histories. Theoretically the same problem could be encountered when comparing regions within provinces. However, the high species similarity expected between regions located in the same province (as defined in this note) impairs this possibility.

Within the 17 community saturation studies reviewed by Cornell and Karlson (in press) we identified at least four studies (Hawkins and Compton 1992, Lawton et al. 1993, Caley and Schluter 1997, Griffiths 1997) that have employed data drawn from regions located on different continents or within the same continent but along a large latitudinal gradient. It is very likely that, in these studies, biotas with different evolutionary histories have been mixed. Other studies may be influenced by history, such as those based on host-parasite systems in which a host species is assimilated to a region (Cornell 1985, Aho 1990, Hawkins and Compton 1992, Aho and Bush 1993, Dawah et al. 1995, Kennedy and Guégan 1995). Parasite species frequently display a high host specificity leading to parasite species pools that overlap slightly among host species. In this case, according to our definition, host species are different provinces with regard to parasite biotas. Unfortunately, except for Caley and Schluter's (1997) study, none of the above-mentioned investigations provided the data necessary for assessing the importance of history in shaping the LSR-RSR relationship. Using data from 8 taxa and 2 continents (Australia and North America), Caley and Schluter (1997) showed that the slope of the curve relating local to regional species richness was the same for the two continents. This result suggests that the effect of history can be neglected. In contrast, a re-analysis of Caley and Schluter's data (Hugueny unpubl.) reveals that the slope of the LSR-RSR relationship decreases with latitude, a result that may be explained in part by a historical effect. Empirical evidence supporting the view that the LSR-RSR relationship is partly shaped by history is therefore still scarce but we believe that this reflects more the paucity of suitable data than the low occurrence of historical effects.

The exploration of the relationship between local and regional species richness is probably not the most effective way of testing community saturation if biotas with different evolutionary histories are mixed. Nevertheless these studies may reveal interesting macroecological patterns and processes. As a concluding footnote, we want to comment briefly on this point in terms of speculative guidelines only because of the present paucity of empirical data. We agree with Ricklefs (1987) who suggested that rate of speciation may have a profound impact on the structure of local communities as well as on regional pattern of diversities. We hypothesize that between-province differences in speciation rate may affect intraprovincial LSR-RSR relationships if at least two processes are coupled: patch occupancy dynamics and selective speciation. Theoretical models of patch occupancy dynamics have shown that the LSR-RSR relationship is affected by intrinsic features of the species composing the regional pool (Caswell and Cohen 1993). Selective speciation is the process by which some properties of species increase the likelihood of a speciation event (Fowler and MacMahon 1982). If we assume that there is a biological feature affecting both patch occupancy dynamics and speciation rate then it follows that the LSR-RSR relationship is affected by speciation rate. As an example, dispersal ability is assumed to increase the LSR/RSR ratio (Cornell and Lawton 1992, Caswell and Cohen

1993) and to decrease speciation rate (Jackson 1974, Hansen 1978, Reaka 1980). Given this framework, it is expected that speciation-prone provincial biotas are composed of species with low dipersal ability and, ceteris paribus, that they display a lower LSR/RSR ratio than provincial biotas which have undergone a lower number of speciation events. Undoubtedly, more inter-provincial comparisons of the interplay between local and regional controls on richness are needed for assessing the validity of these speculations. A multi-scale understanding of community structure may greatly benefit from these comparisons.

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