Hydrobiologia **259**: 157–167, 1993.

Patterns of fish species richness in the Seine River basin, France

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Received 29 April 1992; in revised form 13 October 1992; accepted 29 October 1992

Key words: assemblage organisation, trophic guilds, food availability, anthropogenic perturbations

Abstract

Variation in fish assemblage structure was examined in different rivers of the Seine Basin. Factor analysis was used to identify similarities among samples and species, and to show ichtyological changes along an upstream-downstream gradient. Fish species richness was correlated with catchment area, distance from the source and number of individuals. Relationships between species richness and number of individuals in a sample were largely an artifact of sampling.

Species richness increased with river size, reached a maximum in midsize rivers, then decreased in large rivers. This species richness pattern was consistent with the model of the River Continuum Concept. However, possible causes could include greater pollution effects in large rivers. Distribution of feeding guilds was related to river size. Species richness and proportion of omnivores and piscivores increased with river size, whereas species richness and proportion of invertivores declined downstream. These patterns suggest that trophic diversity of fish assemblages may be related to food availability.

Introduction

Fish community ecology must assess mechanisms and processes responsible for variation or similarity among fish assemblages (Angermeier & Karr, 1983). Very few studies of the structure and dynamics of fish assemblages are available for large rivers. Verneaux (1977), Balon *et al.* (1986), Lelek (1989), Boët *et al.* (1991), Penczak *et al.* (1991), Oberdorff & Hughes (1992), working on European rivers, found longitudinal changes of fish assemblages along an upstream-downstream gradient. Hughes & Gammon (1987) analysed species richness as a function of stream order in North American rivers. Paugy *et al.* (1988) noticed a positive relationship between species richness and distance from the source in a West African river, nevertheless, this was less pronounced than in temperate rivers (Merona, 1981). Hugueny (1989a) found that in West Africa, species richness of a river was related to the surface area of its catchment and its discharge. More has been done for streams. Huet (1959) first described biotic zones in European streams as a function of gradient, current velocity and temperature, and named them after dominant fish species. Schlosser (1982a), and Angermeier & Karr (1983) studied qualitative changes in the trophic structure of fish assemblages, respectively, in North American and tropical streams. Sheldon (1968), Whiteside & McNatt (1972), Beecher *et al.* (1988) analysed species richness as a function of stream order in North American streams. Horwitz (1978) examined the effect of temporal variation in discharge on species richness in North American streams. Eadie *et al.* (1986), Angermeier & Schlosser (1989) found species-area relationships in North American and central American streams. Despite all these studies and many others, there are few conceptual models of structure and dynamics of fish assemblages in rivers except one proposed by Schlosser (1987) who attempted to integrate the relative roles of abiotic and biotic processes in regulating fish assemblage structure along physical gradients in a North American warmwater stream. However, there is a model concerning invertebrate assemblages in temperate rivers, the River Continuum Concept (Vannote *et al.*, 1980). This model suggests a change in community structure and richness from upstream to downstream areas. Main reasons for this include flow regime, temperature, food availability and substrate conditions. Species richness increases with stream size, reaching a maximum in midorder streams, then decreases in large rivers. The low species richness in headwaters and its decline in large rivers is assumed to be due to the reduced environmental variability resulting from an interplay between riparian controls and water volume (Minshall *et al.*, 1985). Schlosser (1982b) applied this concept to fish assemblages in midwestern United States and related the recent shift in trophic structure of many large river fish assemblages to stream alteration in headwater areas.

In this paper we attempt: (1) to describe fish assemblage structure along an upstream-downstream gradient, (2) to describe how species richness and trophic structure change along this gradient, (3) to examine our results in light of the River Continuum Concept hypothesis, and (4) to discuss the results integrating anthropogenic perturbations in large rivers.

Materials & methods

Study area and sampling procedure

We examined fish species composition in 8 rivers of different length in the Seine Basin (Fig. 1). This basin is underlain by sedimentary deposits, in particular by permeable chalk, limestone, sandstone, sand, and gravel. Drained by five major systems (Seine, Marne, Oise, Yonne, and Aisne), it slopes from the southeast to the northwest, where it joins the English Channel. High quality water has become a rare and fragile resource for the Seine Basin. Demographic and economic growth, intensive agricultural and industrial production, and increasing urbanization (particularly near Paris) accentuate the problem of inadequate water resources in this region. Dams and channelizations used for navigation in the lower parts of the major river systems of the basin (Oise, Marne, Seine, Yonne) reduced flooding, habitat diversity, and hinder migrations of diadromous species. These human activities alter the pattern of autotrophy-heterotrophy (*i.e.* nutrient enrichment, organic pollution, channelization, alteration of riparian vegetation) and lead to changes in the river continuum.

The rivers were sampled during 1989 and 1990 by the Conseil Supérieur de la Pêche by electrofishing during low-flow periods (September through October) to evaluate fish assemblages throughout the basin (Fig. 1). Although sites were not selected to analyse effects of point sources pollution, stations located in the lower parts of the basin (compared to headwater stations) were obviously more subjected to anthropogenic impact. Depending on river width and depth, two different sampling methods were used. When is was possible (small rivers) each site was sampled by wading in an upstream direction. The equipment comprised a control box delivering a pulsed direct current (400–600V) via three hand held anodes and a braided wire cathode. In large rivers, the same gear was used but sampling was undertaken by Zodiac boat only on nearshore areas. Although this last approach may not have yielded a complete invertory of all species, we combined these data with the ones obtained for small rivers supposing that the largest part of the species in channelized large rivers was concentrated in nearshore areas. This hypothesis was corroborated by a recent study using sonar technics to evaluate fish assemblages in the main

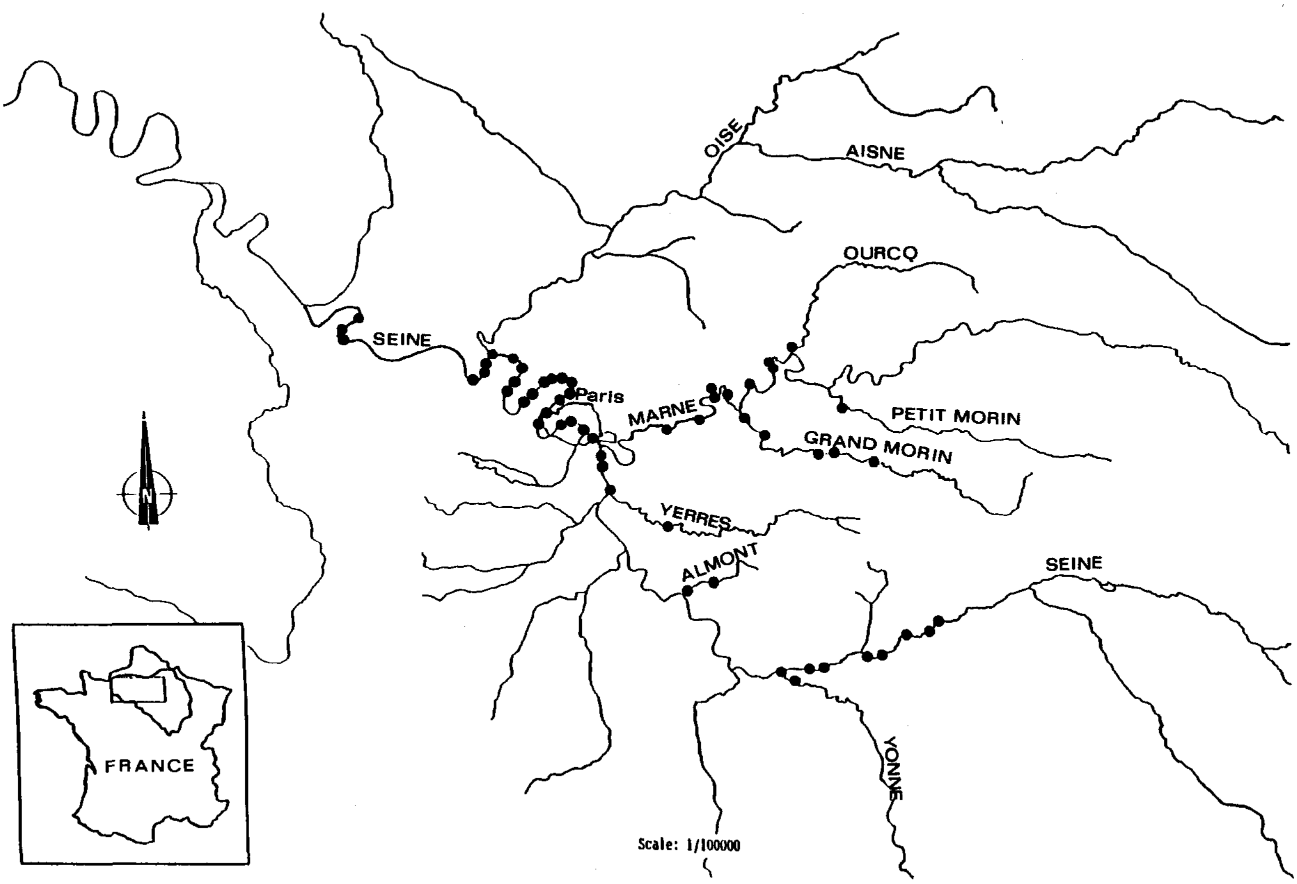

Fig. 1. Partial map of the Seine Basin showing locations of sample sites during 1989 and 1990.

channel of channelized Seine River (CEMAGREF, unpublished data). Sampling effort for all sites (small and large rivers) was measured as the time that power was applied to the electrodes, and was kept constant (30–35 mn) to permit comparison between stations. At this point (chosen after several pilot surveys), only a few new species were encountered and the length of the sample was long enough to include the home range (*i.e.* major habitat types) of the dominant fish species. Fish were identified by species, measured to the nearest millimeter (fork length), weighed in the field, and then released.

The catchment area for each site was measured with a digital planimeter on a 1:1 000 000-scale map of the Seine Basin.

Considering the variability of electrofishing selectivity (function of species behaviour and fish length), we excluded, for comparison between sites, species representing less than 5% (in number) of the total number of fish in the sample. To homogenize variances and minimize effects of non-normality on relative abundance data we used a log (x + 1) transformation. The final transformed Stations-by-Fauna matrix, which contained the relative abundance of the 28 species in each of the 55 sites, was then analysed using a factor analysis, the factorial analysis of correspondences (Benzecri, 1973; Greenacre, 1984; Thioulouse, 1989). This analysis, developed to show correspondences among samples, is based on Chi^2 distance, thus ordination is performed on a dissimilarity matrix. This ordination technique is similar to the detrended correspondence analysis (DCA), and is especially useful for non-linear variables, such as species data. Columns and rows are simultaneously analysed and play symmetric roles. These characteristics allow presentation of species and site data on a same graph, where all scales are standardized.

Two measures of river position were used: distance from the source and the catchment area; the latter is believed to give a more reliable measure of water body size than does stream order (Hughes & Omernik, 1981, 1983).

Relationships among total species richness, total number of individuals, number of invertivore species, number of omnivore species, number of piscivore species, proportion of total biomass as invertivores, omnivores, and piscivores, proportion of total individuals as invertivores, omnivores, and piscivores, distance from the source, and catchment area were examined using correlations and simple linear regressions. The relations between total species richness and catchment area and between species richness and distance from source were regressed using a polynomial function. A multiple regression model was used to assess predictive capability of total number of individuals and catchment area on species richness. Distance from source, catchment area, and number of individuals were log transformed in analysis in order to minimize effects of non-normality. When it was appropriated, because distributions of the data variables were commonly non-normal, we used Kendall's non-parametric correlation coefficient.

Analysis of feeding groups

Assignment of fish species to feeding groups was difficult because of seasonal changes in diets, opportunism and lack of knowledge of some species. Only adult fishes were considered. We assigned each of them to one of the 3 following trophic groups on the basis of its principal adult food as indicated by the literature (Spillmann, 1961; Muus & Dahlström, 1968; Grandmottet, 1983; Gregoire, 1983; Philippart & Vranken, 1983): Piscivores (P); Invertivores (I); Omnivores (O) (Table 1). We omitted the trophic group Herbivores (H) because it was represented by only

Table 1. Trophic guilds for common freshwater fishes of the Seine Basin found during this study, including invertivore (I), piscivore (P), omnivore (O), herbivore (H).

Family species	Trophic guild	Species code
Anguillidae		
Anguilla anguilla	I/P	ANA
Salmonidae		
Salmo trutta fario	I/P	SAT
Esocidae		
Esox lucius	P	ESL
Cyprinidae		
Phoxinus phoxinus	I	PHP
Gobio gobio	I	GOG
Leuciscus leuciscus	I	LEL
Leuciscus cephalus	O	LEC
Chondrostoma nasus	O	CHN
Barbus barbus	I	BAB
Cyprinus carpio	O	CYC
Carassius carassius	O	CAC
Tinca tinca	I	TIT
Abramis brama	I	ABB
Blicca bjoerkna	I	BLB
Rutilus rutilus	O	RUR
Scardinius erythrophtalmus	O	SCE
Rhodeus sericeus	H	RHS
Alburnoides bipunctatus	I	ALB
Alburnus alburnus	I	ALA
Nemacheilinae		
Barbatula barbatula	I	BBB
Ictaluridae		
Ictalurus melas	I	ICM
Lotidae		
Lota lota	P	LOL
Gasterosteidae		
Gasterosteus aculeatus	I	GAA
Pungitius pungitius	I	PUP
Centrarchidae		
Lepomis gibbosus	I	LEG
Micropterus salmoides	P	MIS
Percidae		
Perca fluviatilis	I/P	PEF
Stizostedion lucioperca	P	STL
Gymnocephalus cernua	I	GYC
Cottidae		
Cottus gobio	I	COG

one species (*Rhodeus sericeus*), which appeared in only five stations and in low abundance ($<5\%$ of the total number of fish in the sample) during this study. Piscivores are fishes that eat primarily fish and crayfish and a smaller amount of aquatic and terrestrial insects. Invertivores include generalized insectivores, surface and water column insectivores and benthic insectivores. We prefered the more general term of invertivores because these fishes typically eat crustaceans, oligochaetes, and mollusks, as well as aquatic or terrestrial insects. Omnivores consume a wide range of plants, detritus, and animal material, with at least 25% plants and 25% animals (Schlosser, 1982b; Karr *et al.*, 1986)

Results

Longitudinal changes of the fish assemblages

Thirty species (Table 1) and 10154 individuals representing 11 families were captured at the 55 stations. The family Cyprinidae accounted for 53% of the species and 90% of individuals. In this family, *Rutilus rutilus* was the most numerous and widely distributed, and accounted for 53% of the individuals collected.

The first 2 axes of the factorial analysis of correspondence accounted for 36.24% of the dispersion. Major contributors (Table 2) to the axis 1-by-axis 2 ordination from the correspondence analysis (Fig. 2a, b) were *Phoxinus phoxinus*, *Barbatula barbatula*, *Cottus gobio*, *Gasterosteus aculeatus* and *Gobio gobio* for headwater tributary streams (Grand Morin, Petit Morin), *Alburnoides bipunctatus*, *Barbus barbus*, *Tinca tinca*, and *Gymnocephalus cernua* for midsized rivers (Marne, Ourq), and *Rutilus rutilus* for large rivers (Seine River). Dispersion of the samples for the two axes was significantly correlated with catchment area as shown in Fig. 3 (a, b) (axis 1, $\tau = 0.198$, $p < 0.05$; axis 2, $\tau = 0.471$, $p < 0.001$). Axis 1 separated small headwater tributary streams from all other systems and reflected the greater influence of stream's position (in the drainage basin) on fish assemblages rather than a gradual longitudinal change of these assemblages. Changes in fish assemblage along the longitudinal gradient were further described by axis 2 as illustrated by the high positive relationship between this axis and the variable catchment area.

Table 2. Inertia analysis for axes one and two of the correspondance analysis of the sites-by species data matrix from the Seine Basin in 1989–1990, presenting the absolute and relative contribution of species to the ordination. Major contributors are underlined.

Species	Axis 1 species		Axis 2 species	
	Absolute	Relative	Absolute	Relative
A. anguilla	57	459	180	1007
S. trutta	1	4	1	3
E. lucius	8	62	85	437
A. brama	26	145	131	502
C. carassius	30	1274	16	482
L. cephalus	78	464	3	11
G. gobio	410	2277	93	361
P. phoxinus	5284	8143	279	300
B. bjoerkna	95	347	1	1
P. fluviatilis	76	671	9	59
S. erythrophtalmus	56	418	330	1710
A. alburnus	40	288	16	80
B. barbus	483	1389	2169	4356
L. leuciscus	1	39	2	87
C. nasus	10	554	4	148
R. rutilus	490	1945	1753	4857
C. carpio	5	65	2	20
R. seriseus	2	101	16	563
G. cernua	166	694	1240	3618
L. gibbosus	3	338	31	2853
T. tinca	61	905	360	3751
A. bipunctatus	275	728	3027	5596
B. barbatula	1797	5509	15	33
L. Iota	12	126	25	179
P. pungitius	29	237	1	5
G. aculeatus	188	2853	13	139
S. lucioperca	6	43	170	840
C. gobio	311	3321	28	210

Relationships between species richness, distance from the source, catchment area and number of individuals

We examined relationships between species richness and site characteristics (catchment area, distance from the source, and number of individu-

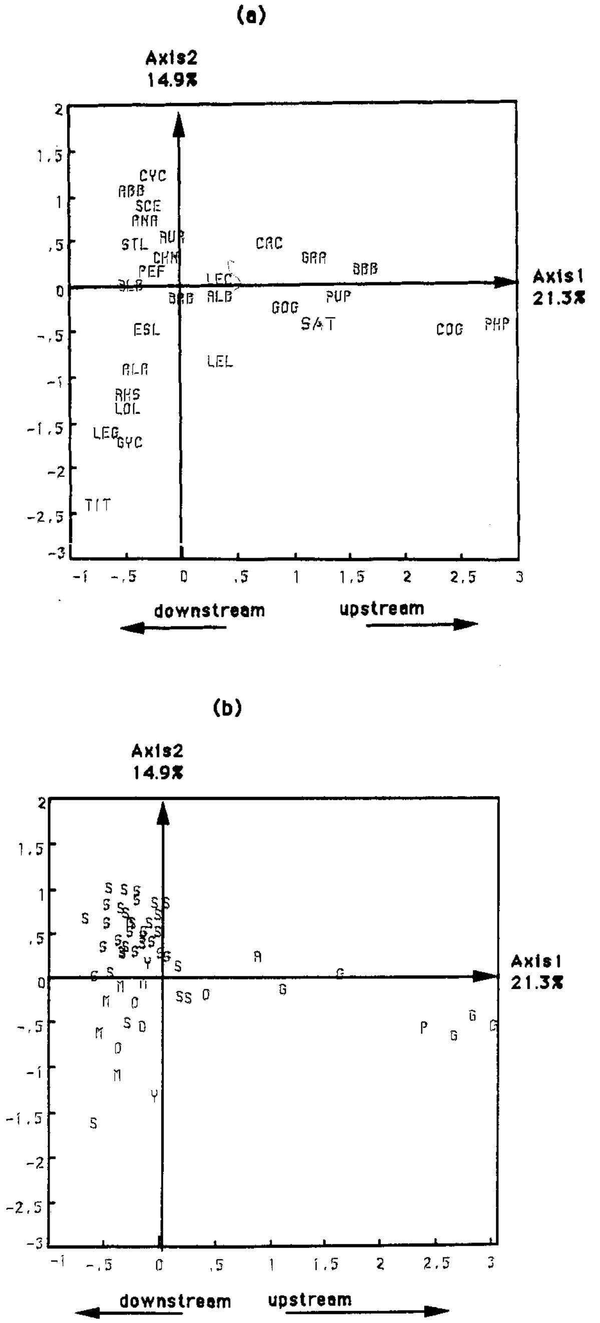

Fig. 2. Trends in Seine Basin fish assemblages as revealed by correspondence analysis. Plots of (a) fish species (see Table 1 for abbreviations), and (b) rivers on the two first factor axes. Seine River = S; Marne River = M; Yonne River = Y; Ourq River = O; Yerres River = Ye; Almont River = A; Grand Morin River = G; Petit Morin River = P.

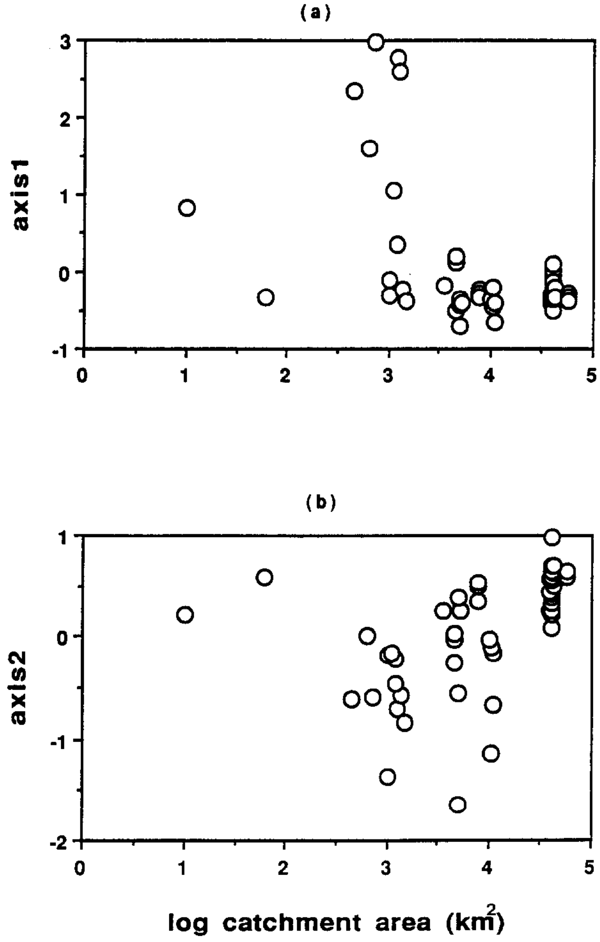

Fig. 3. Relationships between catchment area and the two first axes of the factorial analysis: (a) first axis; (b) second axis.

als). Species richness was significantly correlated with number of individuals ($\tau = 0.445$, $p < 0.001$), catchment area (curvilinear relationship, $r = 0.437$, $p < 0.01$) and distance from the source (curvilinear relationship, $r = 0.349$, $p < 0.05$) (Fig. 4). The multiple regression analysis of species richness (SPP) versus number of individuals (IND), catchment area (CA), and CA^2 (CA^2 was used to linearize the relationship between CA and SPP) gave the following results:

$$\log SPP = -1.241 + 0.265 \log IND + 0.927 \log CA - 0.129 \log CA^2$$

$$(R^2 = 0.542)$$

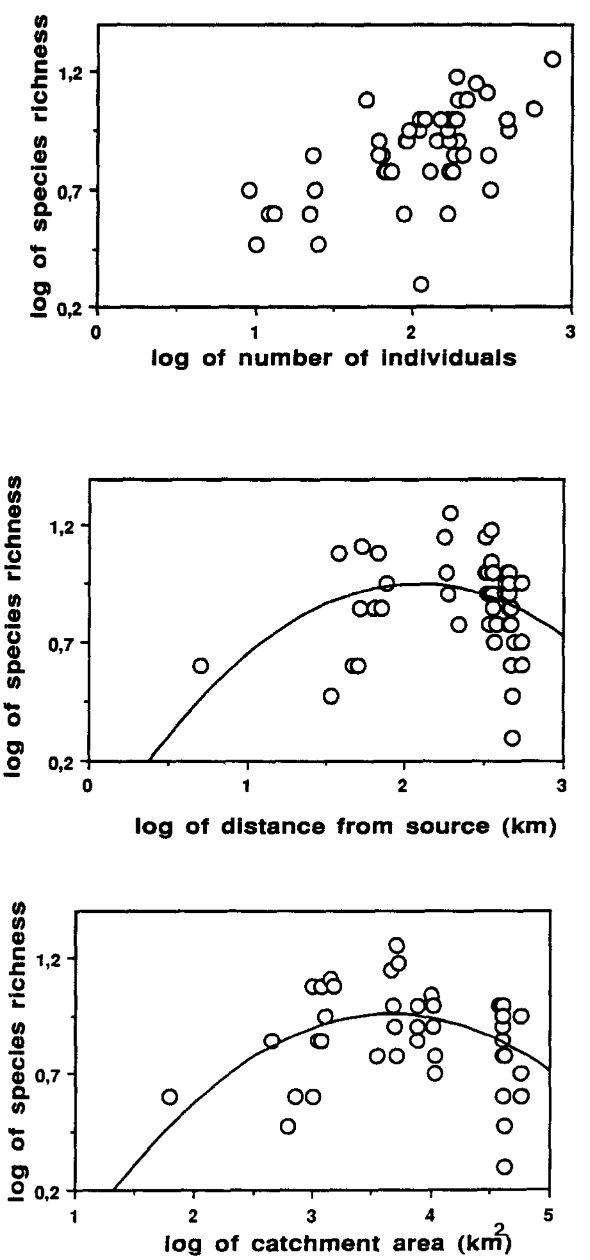

Fig. 4. Relationships between (a) species richness and number of individuals, (b) species richness and distance from source, and (c) species richness and catchment area.

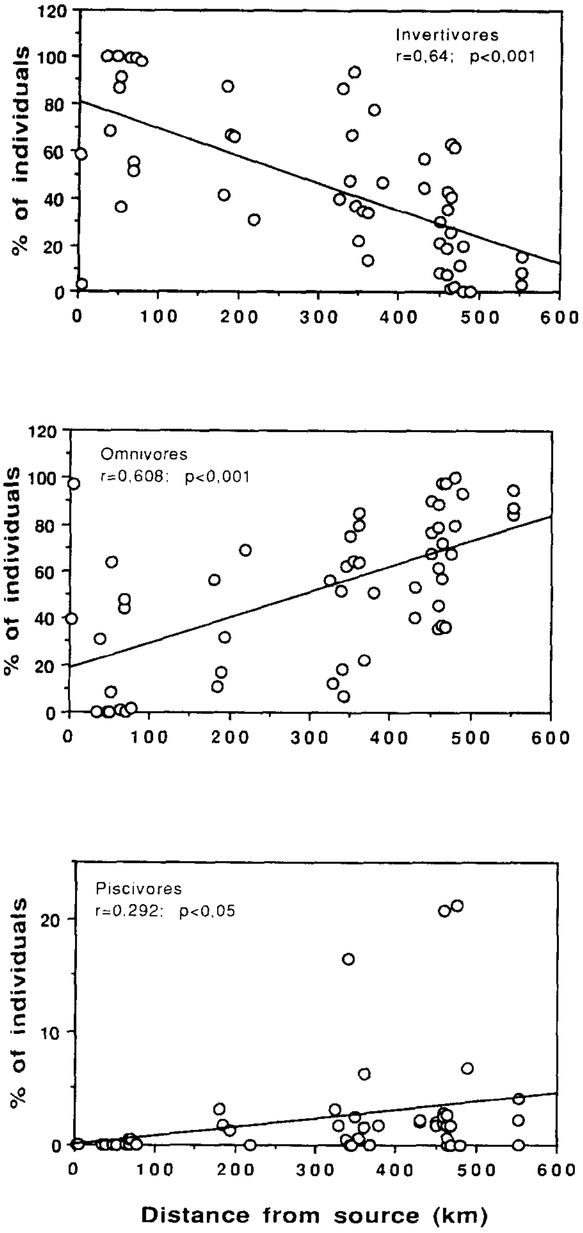

Fig. 5. Relationships between species richness patterns of fish feeding guilds and distance from the source. Species numbers were computed over all samples.

p values for logIND, logCA, and $\log CA^2$ were <0.001, 0.002, and 0.002 respectively.

This model demonstrated that both catchment area and number of individuals had predictive capabilities on species richness. However, we believe that the relationship found during this study between number of species and number of individuals was a sampling problem. As sample size increased (total number of individuals), so did the number of species encountered (species richness).

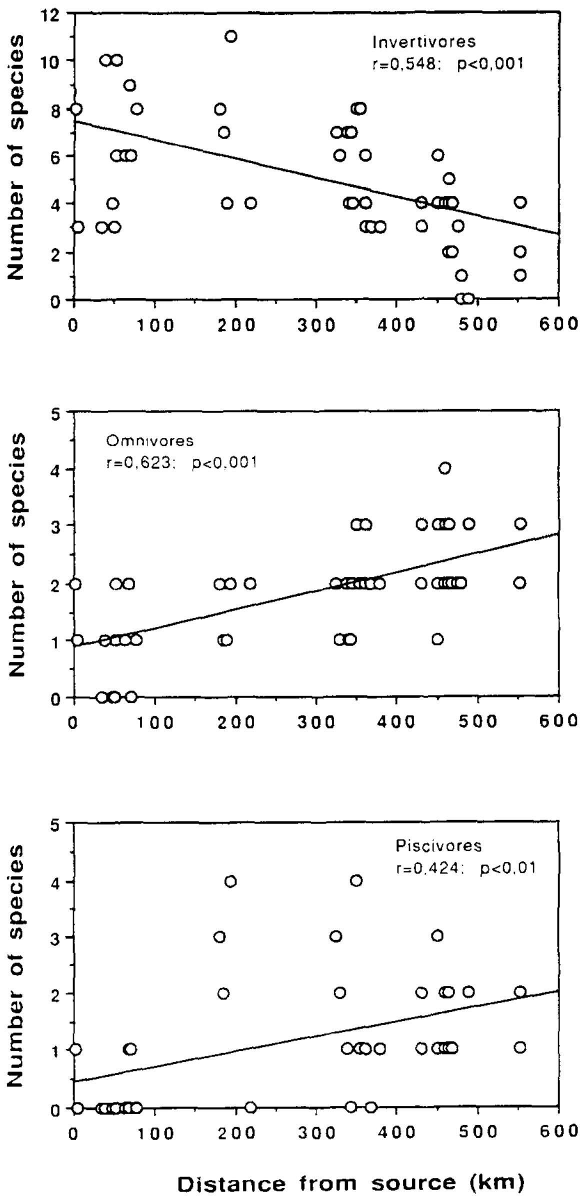

Fig. 6. Effects of river size (distance from source) on % of individuals for each feeding guilds.

Nevertheless, as shown by the model described above, even if the relation between species richness and number of individuals was taken into account, the curvilinear relationship between species richness and catchment area remained true.

There was a pattern of low species richness in headwaters followed by an increase in midsize rivers and then a drop in richness in large rivers (Fig. 4b, c). Thus, it appeared that species distribution followed a pattern of longitudinal changes, and that, for the Seine Basin, these changes were partially related to river size.

Trophic structure upstream versus downstream

Effects of river size were observed for species richness patterns of feeding guilds. Species richness of omnivores, percentage of individuals as omnivores, species richness of piscivores, and percentage of individuals as piscivores increased significantly with distance from the source (Fig. 5, 6). Species richness of invertivores, and percentage of individuals as invertivores declined significantly from upriver to downriver (Fig. 5, 6).

Discussion

Longitudinal changes of fish assemblages

Our results confirm longitudinal changes of the fish assemblage along an upriver-downriver gradient. Previous studies in European rivers have shown the same results (Verneaux, 1977; Mahon, 1984; Balon *et al.*, 1986; Penczak & Mann, 1990; Boët *et al.*, 1991, Oberdorff & Hughes, 1992). Although correlations between species richness and catchment area or distance from the source were significant during this study, number of individuals predicted species richness better than catchment area or distance from the source did. A similar relationship has been reported for North American and West African streams (Meffe & Berra, 1988; Angermeier & Schlosser, 1989) and is largely viewed as a sampling problem. This could be related to the Passive Sampling Hypothesis (Connor & McCoy, 1980) which postulates that as the number of individuals caught increases, the probability of catching rare species increases. In this study, these differences in the number of fish per sample represented differences in stock densities rather than differences in sampling effort, as most of the species were captured within a single site.

Food availability and longitudinal changes

The River Continuum Concept (Vannote *et al.*, 1980) attempts to relate the gradient in physical factors that occurs along fluvial systems, to changes in lotic assemblage structure and function. According to this hypothesis, available food resources should change along this gradient and thus should be reflected by the trophic composition of the communities. Headwaters are influenced primarily by riparian vegetation, which reduces autotrophic production by shading and contributes large amounts of allochthonous organic matter. Thus, headwater fish assemblages include a high proportion of insectivorous species (Lowe-McConnell, 1975; Rahel & Hubert, 1991). As river size increases, autochthonous primary production, and the quantity of fine particulate organic matter increase. Therefore, the proportion of omnivores and herbivores should increase in midsized and large rivers (Lowe-McConnell, 1975; Rahel & Hubert, 1991). Piscivores, which depend on fish prey availability and on deep areas for hunting (Hugueny, 1989b) should be most common in large rivers.

Headwater rivers were dominated (both species richness and number) by invertivore species; but, as river size increased, this trophic group decreased significantly. Species with more generalized diets (omnivores) increased significantly with river size. Fishes with more specialized diets (piscivores) comprised a minor component of the headwater fish assemblage, but became more abundant in large rivers. These patterns conformed to the River Continuum Concept and suggested that trophic diversity of fish assemblage in the Seine Basin may be related in part to food resources availability. The great proportion of invertivore species compared to omnivore and piscivore species observed during this study conformed to previous studies in West Africa (Bowen, 1988; Hugueny, 1989b; Paugy & Bénech, 1989).

The decline in species richness of the fish assemblage in large rivers mainly represented in this study by the Seine River is not a general rule for European systems. Mahon (1984), Balon *et al.* (1986), and Penczak & Mann (1990) also examined longitudinal patterns of river fish distribution but did not find such a decline in species richness. This one could be due to man-induced disturbances (Oberdorff & Hughes, 1992). The lower Seine is characterized by an extreme uniformity in environmental conditions especially due to channelization used for reduction of flow extremes and navigation. These regulations lead to the disappearance of lotic zones and generate a decrease of rheophilous cyprinids like *Barbus barbus*, *Alburnoides bipunctatus*, and *Leuciscus leuciscus*. Furthermore, channelization and alteration of riparian vegetation have induced heavy siltation which leads (1) to degradation of spawning grounds and could explain the decrease of lithophilous species like *Lota lota* or *Gymnocephalus cernua* and the predominance of ubiquitous species like *Rutilus rutilus* in the lower Seine, and (2) to reduction of food diversity (especially reduction of insect density and diversity) (Berkman & Rabeni, 1987) which could be responsible for the shift of the lower Seine fish assemblages from predominance of invertivores (*Tinca tinca*, *Alburnus alburnus*, *Gymnocephalus cernua*) to predominance of omnivores (*Rutilus rutilus*, *Cyprinus carpio*, *Scardinius erythrophtalmus*).

Conclusions

Almost all large river systems in Europe have been subjected to anthropogenic disturbances, thus, there is a need for a theoretical basis to efficiently study and manage the recovery of these perturbed ecosystems. The development of some kind of classification to serve as a guide for understanding relationships among sections of a river, among rivers, and between rivers and land they drain would be useful. In this study, the longitudinal trends in functional fish feeding groups followed the predictions of the River Continuum Concept (relationship between productivity and trophic composition of stream communities) and indicate a transition from invertivorous dominance in headwater streams to omnivorous and piscivorous appearance in large rivers. Nevertheless, if we consider that the gradual decline in fish species richness noticed for the lower Seine is a consequence of the loss of natural lotic habitats, trophic structure trends of fish assemblages found in this study could be peculiar to the Seine Basin. It would be interesting to generate comparative studies with none regulated European large rivers (like the Loire River in France) to evaluate how fish assemblage structure differs in less impacted lotic systems.

Acknowledgements

This work was supported by the Centre National de la Recherche Scientifique (ENVIRONNEMENT program), the Ministère de l'Environnement (SRETIE-Actions Internationales), the Ministère de la Recherche et de la Technologie (Agriculture Demain program), and by Sepia International/ANRT who provided a fellowship. We are grateful to the Conseil Supérieur de la Pêche who kindly provided data. We thank D. Paugy, B. Hugueny, B. de Merona, R. Billard, C. Lévêque, P. Angermeier, and R. M. Hughes for their helpful comments on earlier drafts of this paper.

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