

Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness

G. Grenouillet, D. Pont, and C. Hérissé

Abstract: Local species richness (LSR) in stream fish assemblages is related to both local habitat conditions and stream spatial position. In this study, we examined the within-basin distribution of LSR in the Upper Saône River (France). We describe the longitudinal patterns in LSR and assess the relative effects of both local habitat and spatial (upstream and downstream) influences on species richness. We showed that among the different local habitat variables, only stream width and gradient significantly influenced LSR. Spatial factors also influenced the within-basin distribution of LSR and resulted in spatial autocorrelation, highlighting contagious biotic processes in structuring stream fish assemblages. However, we did not confirm other published predictions that headwater streams entering large rivers directly should have greater species richness. The spatial autocorrelation was only significant downstream (from 4th- to 7th-order streams), suggesting that the relative importance of local habitat and biotic processes may depend on the position along the longitudinal gradient.

Résumé : Dans les systèmes lotiques, la richesse spécifique locale (LSR) des assemblages piscicoles dépend à la fois de conditions locales d'habitat et du positionnement spatial du cours d'eau. Dans cette étude, nous avons étudié la distribution de LSR dans le bassin de la Haute-Saône (France). Nous avons abordé les effets relatifs de facteurs locaux d'habitat et de facteurs spatiaux (amont et aval) sur la richesse spécifique. Parmi les variables locales d'habitat, seules la largeur et la pente du cours d'eau influencent significativement LSR. Des facteurs spatiaux interviennent également dans la distribution de LSR et induisent une autocorrélation spatiale, révélant ainsi des processus biotiques contagieux qui structurent les communautés piscicoles. Cependant, nous n'avons pas pu vérifier les prédictions selon lesquelles des cours d'eaux de tête de bassin se jettant directement dans de grands cours d'eaux devraient avoir des richesses spécifiques plus élevées. L'autocorrélation spatiale ne concernait que les cours d'eau aval (ordre 4 à 7), suggérant ainsi que l'importance relative de l'habitat local et des processus biotiques pourrait dépendre de la position le long du gradient longitudinal.

Introduction

Most natural ecological phenomena display geographical patchiness (e.g., Legendre 1993), and a central idea in community ecology is that the spatial heterogeneity in community structure is the result of the combined effects of environmental and biotic processes. These spatial patterns (i.e., spatial autocorrelation) come either from environmental influences or from community processes. Studies on the spatial structuring of communities have clearly underlined the importance of integrating space in the study of structure in species distribution (Borcard et al. 1992; Legendre 1993; Cooper et al. 1997). However, very few studies dealing with spatially distributed data have taken the spatial structure of their observations into account. Consequently, the relative

importance of physical vs. biotic regulation of locally occurring species remains poorly investigated.

In lotic systems, space can be described as a complex hierarchical network of individual reaches. From the perspective of fishes, both of the views of streams as large continua or as patchy mosaics seem important (Matthews 1998). Taking the drainage into account, the drainage structure is thus critical to understanding fish distribution. In this context, two spatial features have been shown to influence stream fish assemblages: (i) the position along the upstream–downstream gradient, and (ii) the spatial position of the stream within the drainage network.

The upstream–downstream gradient is probably the most well-known, large-scale pattern in stream fish assemblages. Longitudinal changes along physical and chemical gradients generally reflect an increase in fish species richness with increasing stream size (reviewed in Matthews 1986). This typical longitudinal pattern has been well discussed, with different explanations being advanced such as habitat diversity (Gorman and Karr 1978), differential rates of immigration and extinction (Power et al. 1988), or sampling phenomenon (Angermeier and Schlosser 1989). Much of the debate on the mechanisms responsible for such a pattern has focused on the concepts of “addition” versus “replacement”

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of species from headwaters to lower mainstems (see Matthews 1998). Whereas some authors reported an asymptote or a decrease in fish species richness in the lower part of some rivers (e.g., Oberdorff et al. 1993), most available studies have provided evidence in support of addition as a prevailing pattern, at least in rivers lacking geographical discontinuities (e.g., Welcomme 1985).

What is the influence of stream spatial position in a drainage network on the structure of fish assemblages is a poorly addressed question. This question was raised by Fausch et al. (1984), who observed higher species richness in collections near mouths of tributaries entering large rivers. Gorman (1986) first considered the effects of discontinuity on tributary streams for river fish assemblages and suggested that small streams directly joining large rivers should have different assemblages than small streams that increase gradually in size downstream. Osborne and Wiley (1992) first devoted a paper entirely to this question and examined the relationships between fish species richness and four measures of stream size (drainage area, stream order, and two measures of linkage of stream reaches). They revealed that the link magnitude of the stream below the next downstream confluence explained most of the variance in local species richness. Thus they verified the hypothesis that for streams of similar size's order, fish assemblages should have greater species richness in tributaries to the main channel than in streams located in the headwaters of a basin. This hypothesis is based on displacement of individuals within the drainage network and suggests that large river species can potentially migrate into the lower parts of tributaries. Larger streams could thus serve as a colonizing source and may provide a pool of immigrants for subsequent recolonization following a disturbance. The immigration-extinction hypothesis (MacArthur and Wilson 1967) therefore appears to be an important mechanism influencing fish assemblage structure at the drainage network scale.

To date, the study of Osborne and Wiley (1992) remains one of the key papers highlighting the influence of stream spatial position on fish assemblage structure. Although Osborne and Wiley (1992) emphasized the necessity of considering stream spatial position to better predict local fish assemblages, the theoretical and applied implications of such an approach have received little attention. More curiously, local habitat conditions and stream spatial position have rarely been examined together. Consequently, addressing the question of the relative influence of local habitat and stream spatial position on local species richness remains of crucial interest and should be helpful in the debate on the relative importance of physical vs. biotic regulation of stream fish assemblages.

This study investigates river fish assemblages in the Upper Saône River (France) in relation to both local habitat conditions and stream spatial position. Our data set covered a wide range of stream habitats in which both fish assemblages and local habitat conditions were described. We examined local species richness with the objectives of (i) describing the within-basin distribution of local fish species richness, (ii) examining the effects of local habitat on species richness, (iii) assessing the evidence for upstream and downstream influences on local species richness, and

(iv) determining the relative importance of both habitat and spatial factors.

Materials and methods

Site selection

As part of the "Fisheries Orientation Schemes" (Souchon and Trocherie 1990), the French river network has been subjected to systematic investigations using a standardized method since 1982. Depending on their geomorphologic, physical, and chemical characteristics, rivers have been divided into ecologically homogeneous sections in which both habitats and fish assemblages have been described (Changeux and Pont 1995).

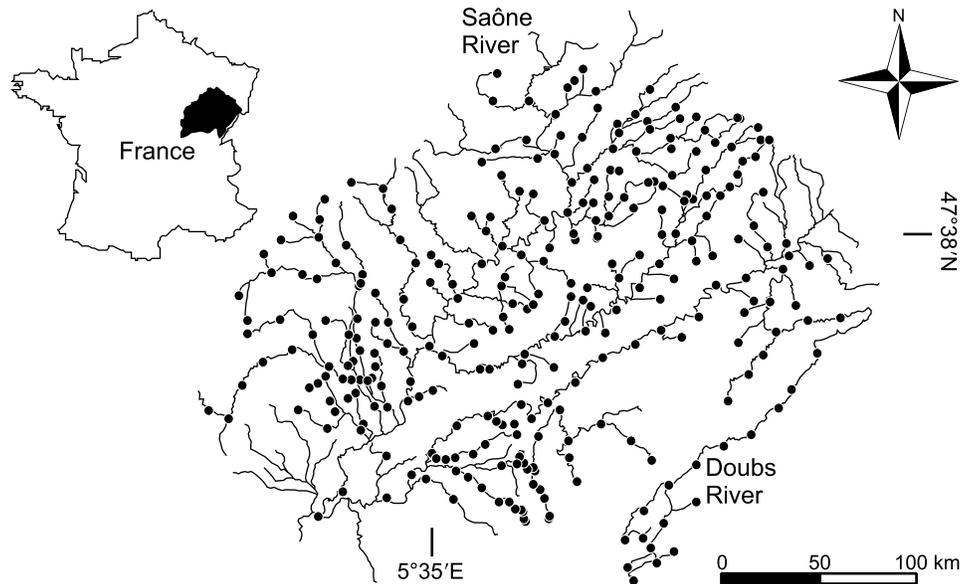
The study area (Upper Saône River in northeastern France) covers approximately 19 600 km² and consists of two major subbasins: the Saône River (12 300 km²) and the Doubs River (7300 km²). The whole river network contains 113 streams with a total length of about 3028 km (2115 km and 913 km for the Saône River and the Doubs River, respectively). Within these 113 streams, the investigation method defined 295 adjacent sections, hereafter called sample sites (Fig. 1). These sites encompassed a wide range of stream habitats: stream order (sensu Strahler 1957) varied between 1 and 7, and stream altitude ranged from about 930 m (the sources of the Doubs River) to 173 m at the confluence between the Doubs and Saône rivers. Despite some hydraulic modifications, the sample sites were characterized by the absence of impassable barriers (e.g., dams) to fish. Therefore, fish have had the opportunity to colonize all of the tributary streams in the basin, and from a biogeographical viewpoint, this river network was thus of primary interest.

Fish and habitat sampling

At each site, fish distribution data were collected by the Conseil Supérieur de la Pêche. Standardized electrofishing methods were used during low flow periods (from August to October), and depending on river width and depth, two different sampling methods were used. When it was possible (small rivers), each site was sampled by wading. In large rivers, sampling was undertaken by boat in nearshore areas (see Oberdorff et al. (2001) for more details). Fish assemblages were described in presence and absence terms. Lists of fish species were compiled from this database, and the number of fish species occurring in a site defined the local species richness (LSR). Most of the sites were sampled once. For sites sampled many times, observations were pooled so that interannual variability could not be addressed in this study.

At each site, geomorphologic, chemical, and climatic variables were used to describe local environmental conditions. The geomorphologic variables used were gradient (GRA, ‰) and stream width (WID, m). Water quality (QUA) was coded semiquantitatively from 1 (absence of pollution) to 5 (highly polluted) as defined by the Water Quality Index developed by the French Water Agency. Climatic variables were not available for each site. To describe local climatic conditions, data were thus interpolated according to the geographical coordinates of upstream and downstream positions

Fig. 1. Map of the Upper Saône River drainage in northeastern France. Solid circles (●) indicate the upstream locations of the 295 sample sites.



derived from IGN (Institut Géographique National) topographic maps (1:25 000 scale) and using mean monthly values supplied by the French Meteorological Office. Therefore, two climatic variables were generated for each site: July mean air temperature (T_{July}) and January mean air temperature (T_{January}). We then defined two climatic variables related to temperature requirements of fish species: mean annual temperature (T_{mean}) and annual thermal amplitude (T_{amp}):

$$T_{\text{mean}} = (T_{\text{July}} + T_{\text{January}})/2$$

$$T_{\text{amp}} = (T_{\text{July}} - T_{\text{January}})/2$$

These two variables, which are potential explanations for fish spatial distribution patterns (Oberdorff et al. 2001), are therefore potential correlates of local fish species richness.

Stream spatial position

Among the geomorphic variables traditionally used to describe lotic systems, drainage area, stream order (Strahler 1957), and link magnitude (Scheidegger 1965) reflect stream size and describe upstream characteristics relative to the entire subcatchment upstream of a given site (Osborne and Wiley 1992). Although stream order incrementally increases only below the confluence of two streams of the same order, link magnitude accounts for the addition of tributaries of order $x - n$ ($n \geq 1$) to a section of order x . As a result, the junction of two streams of unequal order does not affect stream order, whereas link magnitude increases below each confluence and finally represents the number of 1st-order segments upstream of a given site (see Osborne and Wiley (1992) for more details). Catchment area (AREA) was extracted with the geographic information system (GIS) program ArcView 3.2.2 from thematic maps produced by Rogers et al. (2001). Stream order (ORDER) and link magnitude (LINK) were derived from IGN topographic maps (1:25 000 scale).

According to Osborne and Wiley (1992), we defined downstream characteristics for each site using geomorphic

metrics of the next downstream site. For each site, we defined the stream order and the link magnitude of the next downstream site (downstream order (D-ORDER) and downstream link (D-LINK), respectively). These two variables were used as indices of the spatial location of a stream within the drainage network. Because biological processes (e.g., colonization dynamics) have been proposed to explain downstream influences, we used local species richness of the next downstream site (downstream LSR (D-LSR)) as a downstream characteristic potentially influencing local fish assemblages.

Data analysis

Within-basin distribution of local species richness

We described within-basin distribution of LSR by examining (i) spatial covariance (i.e., autocorrelation) in LSR and (ii) the relationship between LSR and stream order. According to Cliff and Ord (1973), spatial covariance for the vector X is defined by the product

$$X^t \frac{1}{2m} MX$$

where X^t is the transpose of X , m is the total number of pairs of neighbors, and M is the neighborhood matrix, so that only neighbor pairs of sites are used to calculate the spatial covariance of X . We used randomization tests for spatial autocorrelation in LSR. In comparison with more standard statistical methods, the main advantage of these tests is that it is relatively easy to take into account the peculiarities of the situation of interest and no particular assumption is made on the distribution of the test statistic (Manly 1994). We took into account the spatial structure of the river network by means of a neighboring relationship in which only successive sample sites along the river network were neighbors. Monte Carlo permutations were used to test if the observed covariance in neighbor LSR values differed from those ex-

pected under the null hypothesis (i.e., LSR is randomly distributed within the river network). To do this, we permuted the LSR observed among the sampling sites and calculated the resulting covariance between neighbors. We evaluated the significance of the observed covariance by comparing it with the distribution of 1000 random permutation values obtained under the null hypothesis (Manly 1994). If less than 5% of the permutation values were higher than the observed one, we concluded that LSR was not randomly distributed but correlated with the neighborhood. Spatial autocorrelation tests were performed using (i) the whole data set (295 sampling sites) and (ii) separate subsets for each stream order.

Local habitat determinants of LSR

We tested the hypothesis that fish assemblages were regulated by local habitat conditions by using the multiple linear regression model (model 1):

$$(1) \quad \text{LSR} = a + b(\text{GRA}) + c(\text{WID}) + d(\text{QUA}) \\ + e(T_{\text{mean}}) + f(T_{\text{amp}}) + \varepsilon$$

Before the analyses, a log transformation was applied to GRA, WID, T_{mean} , and T_{amp} to minimize effects of extreme values. After transformation, only GRA was normally distributed (Lilliefors test; $P = 0.330$), but all variables showed bell-shaped, unimodal distribution and low colinearity.

We used stepwise forward regression (Sokal and Rohlf 1995) to identify significant variables, which explained most of the variance in LSR. At each step, a new variable was added to the model if it significantly ($P < 0.05$) reduced the unexplained variance using the Akaike criterion.

Upstream and downstream influences on LSR

We tested the hypothesis that stream spatial location influenced fish assemblages by comparing the least-squares fits for spatial location characteristics and fish assemblage descriptors. Variables compared included upstream (ORDER, LINK, and AREA) and downstream (D-ORDER, D-LINK, and D-LSR) characteristics. Following Osborne and Wiley (1992), these variables were tested against LSR. Then we also tested these variables against the residuals from model 1 after having removed the effects of local habitat conditions.

Relative importance of both habitat and spatial factors

Because only D-LSR appeared to influence LSR after having removed local habitat effects, we used D-LSR as a spatial descriptor potentially influencing LSR. Total LSR variation was partitioned into four independent components: (i) a local habitat effect; (ii) a D-LSR effect; (iii) a combined effect extracted by both habitat factors and D-LSR; and (iv) a residual (see Whittaker 1984). Finally, we examined whether the influence of D-LSR on LSR differed between stream orders.

Results

Environmental characteristics

Local habitat conditions and stream spatial position were described at the 295 sampling points (Table 1). For local habitat variables, the two surrogates of stream size (GRA and WID) ranged from 0.1‰ to 126.0‰ and from 0.8 m to

175.0 m, respectively. T_{mean} and T_{amp} ranged from 8.0 °C to 10.5 °C and from 16.0 °C to 18.5 °C, respectively. GRA, WID, and T_{mean} differed significantly ($P < 0.05$) between stream orders, whereas there was no significant difference for T_{amp} and QUA (Table 1).

LINK ranged from 1 to 398 and AREA ranged from 1 km² to 19 263 km² (Table 1). These two variables showed a similar exponential increase with stream order. Pairwise correlations between the five local habitat variables, when significant, were not high (Table 2). The highest correlation observed involved GRA and WID ($R^2 = 40.3\%$, $P < 0.0001$). For the five descriptors of stream spatial position, correlation ranged from $R^2 = 36.8\%$ (D-ORDER and AREA) to 91.4% (LINK and ORDER), and these variables were all significantly and positively correlated (Table 2).

Correlations between local habitat and stream spatial position descriptors showed that GRA, WID, and T_{mean} were significantly correlated with the five spatial position descriptors, with the highest correlation between WID and AREA ($R^2 = 71.9\%$, $P < 0.0001$), negative correlations between GRA and spatial descriptors, and positive correlations between T_{mean} and spatial descriptors.

Within-basin distribution of LSR

A total of 36 fish species were collected, with 35 and 36 species from the Doubs and the Saône basins, respectively. Twenty-nine species were considered as being native to the studied area (Changeux and Pont 1995). LSR did not significantly differ between the two basins (one-way analysis of variance (ANOVA) test, $P > 0.05$), and LSR ranged from 0 to 29 species (mean 9.63 ± 6.75) (Fig. 2). LSR increased along the upstream–downstream gradient, but this typical longitudinal pattern did not fit in with a linear relationship. The mean number of fish species increased from five in 1st-order streams to 25 in 7th-order sites, but although LSR regularly increased from 1st- to 5th-order sites, an abrupt increase was apparent from 5th- to 6th-order sites (Fig. 3).

According to geographical coordinates of sample sites, LSR was clearly not randomly distributed but exhibited high spatial autocorrelation at the basin scale, illustrating the well-known increase in fish species richness with increasing stream size (Fig. 2). Results from randomization tests based on the neighboring relationship between sites revealed high spatial covariance in LSR (Table 3). None of the random permutations generated covariance values higher than the observed one, so we concluded that LSR was significantly ($P < 0.001$) correlated to the neighborhood space. However, when examining spatial covariance for each stream order, permutation tests then indicated that LSR was not spatially autocorrelated among sites from 1st- to 3rd-order streams. For 4th- to 7th-order streams, observed spatial covariance in LSR was significantly higher than that obtained from random permutations (Table 3).

Local habitat determinants of LSR

Results from the multiple regression model of LSR versus local habitat variables (model 1) indicated that LSR was only influenced by two surrogates of stream size, stream width and gradient, with residuals normally distributed (Lilliefors test; $P = 0.180$). LSR was positively correlated

Table 1. Characteristics of local habitat, spatial position, and fish variables of the Upper Saône River in northeastern France.

Variables		Stream order							<i>P</i>
		1 (<i>N</i> = 55)	2 (<i>N</i> = 50)	3 (<i>N</i> = 48)	4 (<i>N</i> = 60)	5 (<i>N</i> = 39)	6 (<i>N</i> = 31)	7 (<i>N</i> = 12)	
Local habitat	GRA	14.89a (19.85)	6.93b (11.74)	4.24b (7.26)	2.44b (1.90)	1.76b (1.70)	0.66b (0.37)	0.21b (0.15)	<0.0001
	WID	4.01a (2.75)	5.75a (5.82)	8.09a (7.01)	12.25a (6.30)	29.05b (15.06)	62.29c (36.45)	94.58d (44.01)	<0.0001
	<i>T</i> _{mean}	9.52a (0.69)	9.86a (0.69)	9.79a (0.75)	9.87a (0.64)	9.56a (0.87)	10.26b (0.32)	10.36b (0.21)	<0.0001
	<i>T</i> _{amp}	17.58a (0.39)	17.55a (0.59)	17.51a (0.54)	17.54a (0.48)	17.38a (0.45)	17.71a (0.42)	17.71a (0.43)	ns
	QUA	2.36a (1.02)	2.70a (0.92)	2.63a (0.73)	2.77a (0.97)	2.77a (1.16)	3.00a (0.80)	2.58a (0.49)	ns
Spatial position	LINK	1.00a (0.00)	2.02a (0.32)	3.73a (1.04)	7.42a (1.69)	23.36b (8.47)	60.68c (28.83)	138.50d (111.87)	<0.0001
	AREA	6.53a (29.31)	24.84a (53.15)	64.33a (78.87)	183.48a (128.87)	927.77b (512.51)	2939.03c (1994.70)	6761.17d (4669.69)	<0.0001
Fish	LSR	5.15a (3.35)	5.42a (2.42)	7.42a (3.43)	9.42b (4.22)	11.08b (5.08)	20.26c (5.61)	25.58d (2.06)	<0.0001

Note: *N*, number of sampling sites. For each stream order, the given characteristics are mean values with standard deviation below in parentheses. For each variable, values among stream order with a common letter are not significantly different at *P* = 0.05 (Tukey–Kramer test). Probabilities (*P*) (ns, not significant) are given for testing the effect of stream order on each variable (analysis of variance and χ^2 tests for continuous and categorical variables, respectively). Variables: GRA, gradient; WID, stream width; *T*_{mean}, mean annual temperature; *T*_{amp}, annual thermal amplitude; QUA, water quality; LINK, link magnitude; AREA, catchment area; LSR, local species richness.

Table 2. Matrix of pairwise correlation between environmental variables.

Variables	GRA ^a	WID ^a	<i>T</i> _{mean}	<i>T</i> _{amp}	QUA	LINK ^a	D-LINK ^a	ORDER	D-ORDER	AREA ^a
Local habitat	GRA ^a		<0.0001	<0.0001	0.002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	WID ^a	-0.635		ns	ns	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	<i>T</i> _{mean}	-0.441	0.040		<0.0001	0.012	0.024	<0.0001	0.008	<0.0001
	<i>T</i> _{amp}	-0.291	-0.020	0.444		0.012	ns	0.029	ns	ns
	QUA	-0.239	0.108	0.212	0.211		ns	0.004	ns	<0.0001
Spatial position	LINK ^a	-0.695	0.845	0.201	0.057	0.148		<0.0001	<0.0001	<0.0001
	D-LINK ^a	-0.638	0.603	0.309	0.198	0.227	0.726		<0.0001	<0.0001
	ORDER	-0.726	0.813	0.216	0.016	0.144	0.956	0.681		<0.0001
	D-ORDER	-0.625	0.529	0.312	0.129	0.255	0.621	0.906	0.648	
	AREA ^a	-0.737	0.848	0.196	0.026	0.152	0.923	0.658	0.942	0.607

Note: Variables: GRA, gradient; WID, stream width; *T*_{mean}, mean annual temperature; *T*_{amp}, annual thermal amplitude; QUA, water quality; LINK, link magnitude; D-LINK, downstream link; ORDER, stream order; D-ORDER, downstream order; AREA, catchment area. Above the diagonal, *P* (Bonferroni probabilities) values (ns, not significant); below the diagonal, Pearson's correlation coefficients.

^aVariables expressed in logarithmic values.

with stream width and negatively correlated with gradient. Both variables were of similar relative importance in the model, which accounted for 63.9% of the variation in local species richness (Table 4).

Upstream and downstream influences on LSR

Among the different variables describing upstream characteristics, stream order consistently provided the best relationship with fish species richness and accounted for 53.5% of the variation in LSR (Table 5). For downstream characteristics, the best relationship was between LSR and D-LSR, whereas D-ORDER provided the weakest relationship and accounted for only 34.1% of the variation. After having removed the effects of local habitat conditions, no relationship was found between the residuals from model 1 and the geomorphologic parameters used (Table 5). Only D-LSR

significantly (*P* < 0.001) influenced fish species richness, explaining 9.9% of the remaining variance in LSR.

Relative importance of both habitat and spatial factors

The five local habitat variables combined explained 65.6% of the variation in local species richness. Although D-LSR explained 40.8% of the variation in LSR, 70.3% of the variation in LSR was explained by both habitat variables and D-LSR combined. Thus, the effects of D-LSR and those of local habitat conditions were largely confounded, and the total variation in LSR could be partitioned as follows: local habitat (29.5%), local habitat + D-LSR (36.1%), D-LSR (4.7%), and undetermined (29.7%) (Fig. 4). Finally, when plotting the residuals of the local habitat model (model 1) versus D-LSR, it then appeared that (i) D-LSR had no significant effect on LSR in sites from low-order (≤ 4) streams, and

Fig. 2. Local fish species richness (LSR) within the river network. The diameters of the circles are proportional to the values represented.

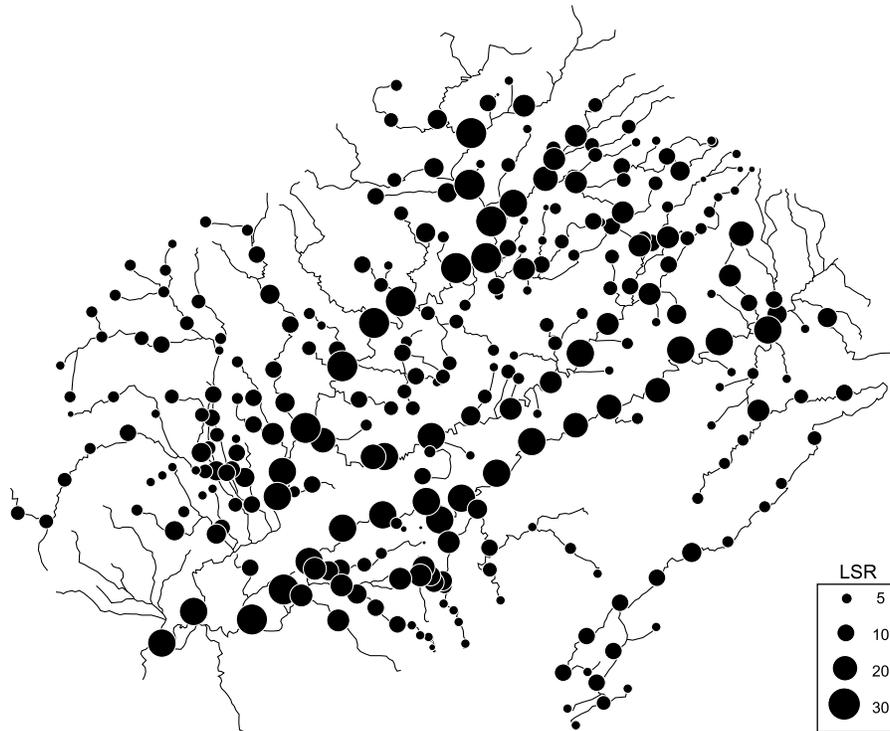
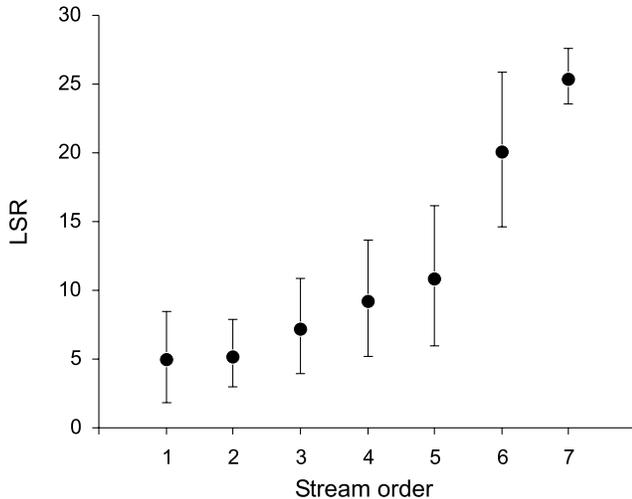


Fig. 3. Local species richness (LSR; mean \pm standard deviation) by stream order.



(ii) the relative importance of D-LSR in explaining LSR continually increased from the headwaters to large streams (Fig. 5).

Discussion

Although fish assemblages are likely to exhibit temporal (i.e., interannual) variability, we did not address temporal variability in this study because of the lack of available data for the whole data set. Here we focused on spatial fish distribution and the aim of this study was to examine the within-basin distribution of fish species richness and to test the relative importance of local habitat and spatial factors on fish as-

Table 3. Results of Monte Carlo tests for spatial autocorrelation in local species richness.

Stream order	Spatial covariance	<i>P</i>
1 (<i>N</i> = 55)	0.212	ns
2 (<i>N</i> = 50)	0.476	ns
3 (<i>N</i> = 48)	0.134	ns
4 (<i>N</i> = 60)	4.784	0.002
5 (<i>N</i> = 39)	4.576	0.018
6 (<i>N</i> = 31)	11.931	<0.001
7 (<i>N</i> = 12)	1.450	0.005
All (<i>N</i> = 295)	17.015	<0.001

Note: Given are spatial covariance and estimated probabilities *P* (number of random permutations: 1000). *N*, number of sampling sites; ns, not significant.

Table 4. Stepwise multiple-regression model (model 1) of local species richness (LSR) vs. local habitat variables (gradient (GRA) and stream width (WID)).

Independent variables	Coefficients	<i>t</i> value	<i>P</i>	Multiple <i>R</i> ²
GRA ^a	-5.137 (0.556)	-9.245	<0.0001	0.639
WID ^a	6.108 (0.613)	9.970	<0.0001	

Note: Given are regression coefficients (with standard error in parentheses), *t* values, probabilities (*P*), and multiple *R*².

^aVariables expressed in logarithmic values.

semblage structure in the Upper Saône River. The most significant way in which our study differed from most others was that the whole river network was sampled as a succession of contiguous stream segments. Moreover, the study site was characterized by the absence of large obstacles (i.e.,

Table 5. Comparison of least-squares fits for upstream (ORDER, LINK, and AREA) and downstream (D-ORDER, D-LINK, and D-LSR) variables and local species richness (LSR) and residuals from model 1.

	Parameter	F ratio	P	R ²
LSR	ORDER	337.324	<0.0001	0.535
	LINK ^a	320.584	<0.0001	0.522
	AREA ^a	272.219	<0.0001	0.482
	D-ORDER	150.857	<0.0001	0.341
	D-LINK ^a	158.708	<0.0001	0.352
	D-LSR	201.380	<0.0001	0.408
	Residuals from model 1			
	ORDER	1.923	1	0.007
	LINK ^a	1.081	1	0.004
	AREA ^a	0.074	1	0.001
	D-ORDER	5.082	0.150	0.017
	D-LINK ^a	1.979	0.966	0.007
	D-LSR	32.010	<0.0001	0.099

Note: Given are F ratio, Bonferroni probabilities (P), and R².
^aVariables expressed in logarithmic values.

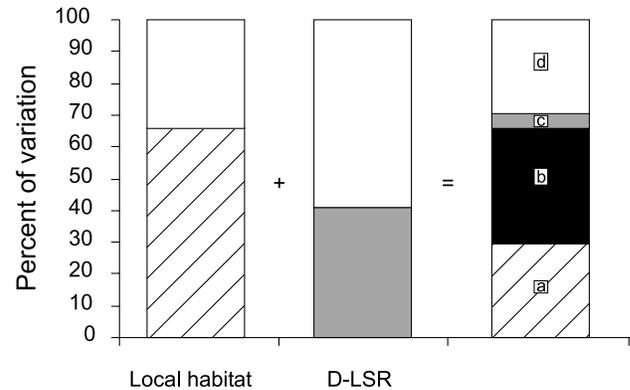
dams) to fish movements and was never covered by glaciers during the Quaternary glaciations (Changeux and Pont 1995). Therefore, the Upper Saône basin is homogeneous from a biogeographical viewpoint: fish species remained almost free to move throughout the river network, and historical factors are unlikely to explain current patterns of fish species richness at this spatial scale.

We know of no study explicitly testing fish species richness against both local habitat and spatial factors at a similar spatial scale. Nevertheless, our results confirm earlier findings that LSR increases with stream size, but it also appears that this relationship is not linear. Among the different local habitat variables, stream width and gradient significantly influenced LSR, but spatial factors also influenced the within-basin distribution of LSR and resulted in spatial autocorrelation among sites from 4th- to 7th-order streams. This suggests that the relative importance of local habitat and spatial factors may depend on the position along the longitudinal gradient.

Longitudinal pattern in local species richness

Our results show that fish assemblages of the Upper Saône basin follow the general pattern of river fish distribution in that local species richness increases with stream order. The stream order system, traditionally used to classify lotic systems as estimator of stream size (Strahler 1957), was introduced to fish ecology by Kuehne (1962) and has since been frequently used as a framework for variation in fish assemblages along the upstream–downstream gradient (Matthews 1998). Thus, the relationship between fish species richness and stream order has been widely assessed and largely discussed (e.g., Matthews 1986), and different patterns have been revealed. As suggested by the river continuum concept (Vannote et al. 1980), fish species richness may peak and then decline with increasing stream size. Such a decline has been observed in highly regulated large European rivers and could be due to anthropogenic disturbances affecting habitat diversity (i.e., the loss of natural lotic habitats in the lowermost reaches of the Seine River; Oberdorff et al. 1993). However, Pont et al. (1985) suggested that this

Fig. 4. Percentages of variation of local species richness (LSR) explained by local habitat conditions and by downstream local species richness (D-LSR). Separate analyses (two left-hand columns) and total variation partitioning (right-hand column) are shown. (a) Local habitat; (b) local habitat + D-LSR; (c) D-LSR; (d) undetermined.



decline was no more apparent when highly modified sites are excluded from the analyses. Thus, the bell-shaped pattern is not a general rule for European systems, and many studies have documented a continuous longitudinal increase in fish species richness. Some authors have described linear increases in fish species richness with stream order (e.g., Naiman et al. 1987), whereas others have noted that changes in stream order do not necessarily result in abrupt changes in fish assemblage structure (Matthews 1986).

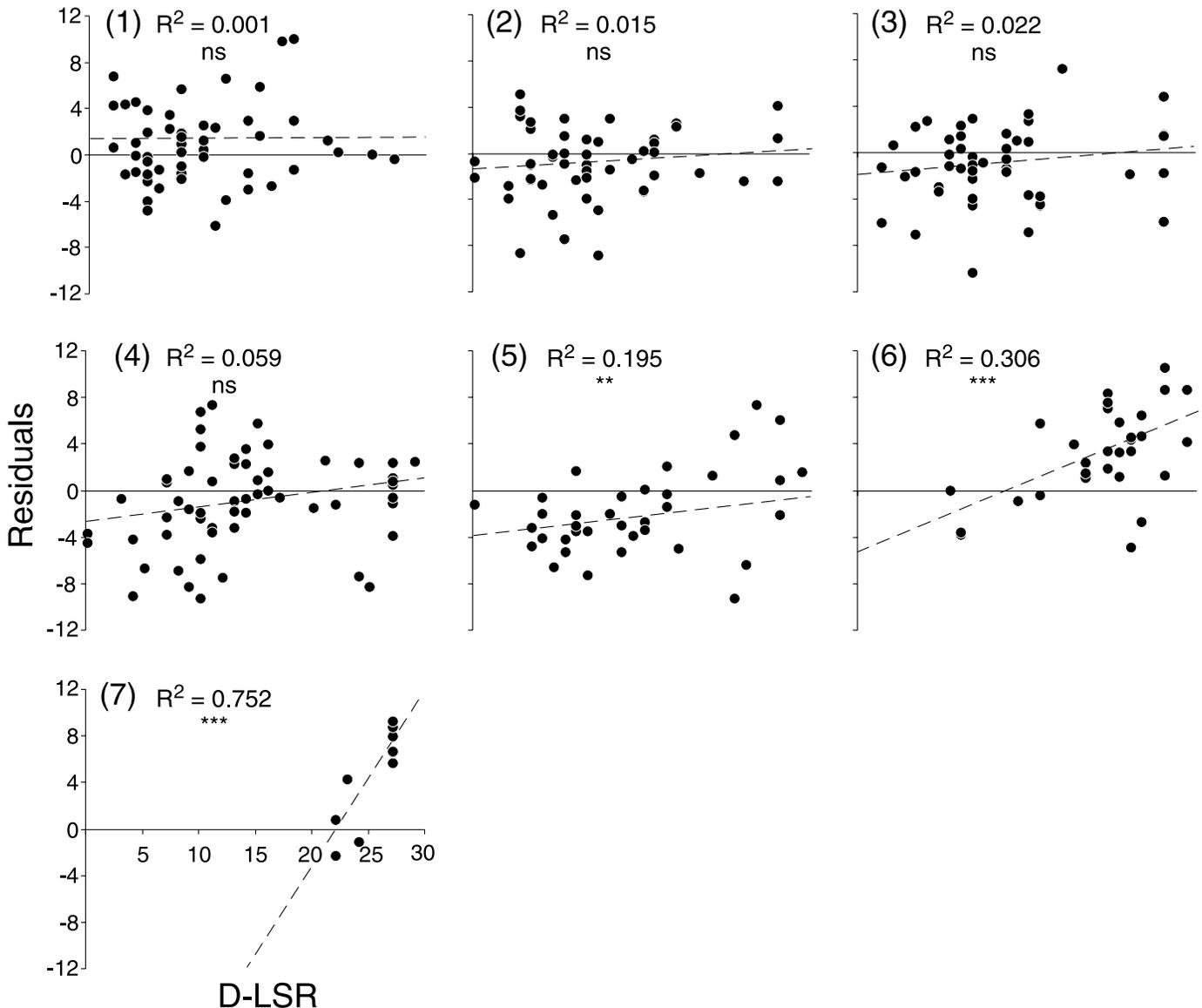
In this study, fish species richness exhibited a nonlinear relationship with stream order, clearly partitioning the river network into two parts: tributaries (1st- to 5th-order streams) and main channels (6th- and 7th-order streams). This result is consistent with the results of other studies showing that (i) species assemblages could differ as much within as between stream orders (e.g., Stewart et al. 1992) and (ii) fish species obviously respond to local habitat features, not to stream classification schemes of humans (Matthews 1998). Some authors have therefore called into question the utility of stream order and recommended the use of more measurable variables (e.g., Hughes and Omernick 1983).

Determinants of LSR

Both instream habitat characteristics and allogenic processes influence stream communities, and previous studies emphasized the role of geomorphology and riparian vegetation on the functional structure of stream communities. For example, Maridet et al. (1998) examined the relative importance of these two control factors on trophic structure of stream fish assemblages. These authors showed that riparian vegetation could be of first importance when anthropogenic alteration of riparian vegetation was severe, whereas stream fish assemblages were mainly structured by geomorphological control under natural conditions.

Here our study focused on instream processes, and geomorphological, physical, and chemical variables were used to explain fish spatial distribution. We showed that among local habitat factors, only stream width and gradient significantly influenced LSR and that no effect of stream order was apparent after having removed the effects of these two surro-

Fig. 5. Relationship between residuals from model 1 and downstream local species richness (D-LSR) for each stream order (stream order in parentheses). Broken lines represent the regression line for the stream order, with R^2 and probability P (ns, not significant; **, $P < 0.01$; ***, $P < 0.001$).



gates of stream size. This result is consistent with the results of many studies concluding that stream size was the most important factor influencing fish species composition (e.g., Matthews and Robison 1988). Note, however, that we selected significant variables using a forward-selection procedure in which variables enter the analysis by decreasing additional explanatory power. In this way, variables that could be significantly related in isolation to LSR could consequently appear nonsignificant once correlated variables were incorporated in the model. In our study, water quality, mean temperature, and thermal amplitude were all significantly and negatively correlated with stream gradient. Therefore, this could explain why neither water quality nor temperature significantly influenced LSR.

Concerning upstream and downstream influences on LSR, our results can be discussed in the light of those of Osborne and Wiley (1992), who first assessed spatial factors likely to

influence fish species richness. In their study, Osborne and Wiley (1992) showed that the link magnitude of the next downstream confluence (D-LINK) accounted for the greatest proportion of variance in species richness among stations. They stressed that downstream processes could significantly influence the structure of stream fish assemblages and that the extinction-immigration hypothesis appeared to be the most plausible mechanism for the observed pattern in fish assemblage structure within a catchment.

In our study, and after removing the effect of local habitat, only local species richness of the next downstream site (D-LSR) significantly influenced LSR. This result confirms the findings of Osborne and Wiley (1992) that downstream processes can significantly influence the structure of stream fish assemblages. However, our study did not confirm Osborne and Wiley's (1992) predictions that headwater streams entering large rivers directly should have greater species richness.

In our study, downstream influence was not apparent for smaller streams, only for larger ones. Consequently, our study not only clearly highlights spatially contagious processes in structuring stream fish assemblages, but also reveals that these processes only become significant downstream.

Biotic processes may explain variations in fish assemblage structure not explained by environmental differences among sites, and spatial autocorrelation may be interpreted as a reflection of the relative importance of biotic processes in structuring lotic communities (Wilkinson and Edds 2001). In assessing spatial autocorrelation of the Spring River basin fish assemblage, Wilkinson and Edds (2001) suggested that contagious biotic processes were important in structuring the fish assemblage. Our study reveals that the relative importance of both local habitat and spatial factors varies with the location within the river network. This is consistent with the classical view on biotic versus abiotic controls in lotic systems (e.g., Power et al. 1988) that abiotic factors are predominant upstream, whereas biotic factors are more likely to occur downstream.

Potential mechanisms responsible observed patterns

Although it was not the aim of our study to test the different mechanisms potentially responsible for the within-basin patterns in fish species richness, we can examine the different mechanisms currently invoked. Among these potential mechanisms, the importance of immigration and extinction dynamics in structuring stream fish assemblages has been underlined in a number of studies (e.g., Angermeier and Schlosser 1989; Gotelli and Taylor 1999b; Taylor and Warren 2001).

The fact that our results emphasize the importance of stream size in structuring stream fish assemblages can be interpreted in the light of these dynamics of immigration and extinction. Stream size has been considered as an estimator of habitat complexity (Gorman and Karr 1978) and stability (Schlosser 1987), which both have been shown to be crucial in structuring stream fish assemblages (e.g., Horwitz 1978; Angermeier and Schlosser 1989). Taylor and Warren (2001) revealed that stream size was positively correlated with immigration rates and negatively correlated with extinction rates, and they successfully attempted to relate the variability of the flow regime to the dynamics of immigration and extinction. They suggested that larger streams, characterized by larger habitats and therefore higher species richness, have a greater number of potential colonists than upstream areas. Therefore, immigration and extinction rates vary predictably along the stream gradient, and the stream-fish distribution can reflect spatial gradients in colonization and extinction probabilities (Gotelli and Taylor 1999a; Taylor and Warren 2001). To date, separating the relative effects of habitat heterogeneity and solely biotic processes remains challenging because very few studies have addressed how immigration and extinction rates vary along environmental gradients. Further investigations are now needed to generalize these first results to a variety of systems.

Implications

Because the location of a stream in a river network can significantly affect the number of local fish species, Osborne and Wiley (1992) recommended that managers take into ac-

count spatial influences when evaluating species richness and assemblage structure measurements. This has already been emphasized by Fausch et al. (1984), who proposed that samples from tributaries close to their confluence with larger rivers of higher stream order should be excluded from analyses when calculating index of biotic integrity (IBI) scores. However, to date, a quantitative rule for exclusion of such samples remains to be established.

Since Fausch et al. (1984), other studies have stressed the necessity of taking into account spatial influences. For example, Hinch et al. (1994) revealed that fish-habitat relationships were dramatically modified after spatial autocorrelation of sites was considered, suggesting that spatial autocorrelation may strongly affect inferences about large-scale distributional patterns. It appears from our study that spatial autocorrelation can be of major importance in the determination of local species richness. Such results are a warning for managers against neglecting spatial autocorrelation when assessing the sustainability and biological integrity of stream systems.

To provide a more comprehensive view of fish distribution patterns, some authors have attempted to use ecological attributes (or species traits) to explain within-drainage fish assemblage structure. This has been done with reproductive or trophic guilds (Oberdorff et al. 1993; Belliard et al. 1997) and revealed that the longitudinal trends in functional fish feeding groups followed the predictions of the river continuum concept (i.e., a transition from insectivorous to omnivorous and piscivorous species from headwaters to large rivers). It now seems necessary to take into account other ecological attributes of fish species, especially biological traits associated with fish colonization abilities. Indeed, differences among species in their potential to use or move among habitat patches may be critical (Matthews 1998), and some authors have recently stressed the necessity to consider variables related to dispersal success, which can dramatically affect interpretations of spatially explicit population models (e.g., Dunham and Rieman 1999).

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References

- Angermeier, P.L., and Schlosser, I.J. 1989. Species-area relationships for stream fishes. *Ecology*, **70**: 1450–1462.
- Belliard, J., Boët, P., and Tales, E. 1997. Regional and longitudinal patterns of fish community structure in the Seine River basin, France. *Environ. Biol. Fishes*, **50**: 133–147.
- Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, **73**: 1045–1055.
- Changeux, T., and Pont, D. 1995. Ichthyogeographic regions and watershed size in the French river Rhône network. *Hydrobiologia*, **300/301**: 355–363.
- Cliff, A.D., and Ord, J.K. 1973. *Spatial autocorrelation*. Pion, London.

- Cooper, S.D., Barmuta, L., Sarnelle, O., Kratz, K., and Diehl, S. 1997. Quantifying spatial heterogeneity in streams. *J. North Am. Benthol. Soc.* **16**: 174–188.
- Dunham, J.B., and Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecol. Appl.* **9**: 642–655.
- Fausch, K.D., Karr, J.R., and Yant, P.R. 1984. Regional application of an index of biotic integrity based on stream fish communities. *Trans. Am. Fish. Soc.* **113**: 39–55.
- Gorman, O.T. 1986. Assemblage organization of stream fishes: the effects of rivers on adventitious streams. *Am. Nat.* **128**: 611–616.
- Gorman, O.T., and Karr, J.R. 1978. Habitat structure and stream fish communities. *Ecology*, **59**: 507–515.
- Gotelli, N.J., and Taylor, C.M. 1999a. Testing metapopulation models with stream fish assemblages. *Evol. Ecol. Res.* **1**: 835–845.
- Gotelli, N.J., and Taylor, C.M. 1999b. Testing macroecology models with stream fish assemblages. *Evol. Ecol. Res.* **1**: 847–858.
- Hinch, S.G., Somers, K.M., and Collins, N.C. 1994. Spatial autocorrelation and assessment of habitat–abundance relationships in littoral zone fish. *Can. J. Fish. Aquat. Sci.* **51**: 701–712.
- Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecol. Monogr.* **48**: 307–321.
- Hughes, R.M., and Omernick, J.M. 1983. An alternative for characterizing stream size. *In* Dynamics of lotic ecosystems. *Edited by* T.D. Fontaine III and S.M. Bartel. Ann Arbor Science Publishers, Ann Arbor, Mich. pp. 87–101.
- Kuehne, R.A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. *Ecology*, **43**: 604–614.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**: 1659–1673.
- MacArthur, R.H., and Wilson, E.O. 1967. The theory of island biogeography. Monograph in population biology. Princeton University Press, Princeton, N.J.
- Manly, B.F.J. 1994. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.
- Maridet, L., Wasson, J.B., Philippe, M., Amoros, C., and Naiman, R.J. 1998. Trophic structure of three streams with contrasting riparian vegetation and geomorphology. *Arch. Hydrobiol.* **144**: 61–85.
- Matthews, W.J. 1986. Fish faunal “breaks” and stream order in the eastern and central United States. *Environ. Biol. Fishes*, **17**: 81–92.
- Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.
- Matthews, W.J., and Robison, H.W. 1988. The distribution of the fishes of Arkansas: a multivariate analysis. *Copeia*, 1988: 358–374.
- Naiman, R.J., Melillo, J.M., Lock, M.A., Ford, T.E., and Reice, S.E. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology*, **68**: 1139–1156.
- Oberdorff, T., Guilbert, E., and Lucchetta, J.C. 1993. Patterns of fish species richness in the Seine River basin, France. *Hydrobiologia*, **259**: 157–167.
- Oberdorff, T., Pont, D., Hugué, B., and Chessel, D. 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. *Freshw. Biol.* **46**: 399–415.
- Osborne, L.L., and Wiley, M.J. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. *Can. J. Fish. Aquat. Sci.* **49**: 671–681.
- Pont, D., Belliard, J., Boet, P., Changeux, T., Oberdorff, T., and Ombredane, D. 1985. Analyse de la richesse piscicole de quatre ensembles hydrographiques français. *Bull. Fr. Pêche Piscic.* **337–339**: 75–81.
- Power, M.E., Stout, R.J., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Stutzner, B., and Wais De Badgen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *J. North Am. Benthol. Soc.* **7**: 456–479.
- Rogers, C.F., Dolédec, S., Pont, D., and Etlicher, B. 2001. Approches multi-échelles d’indicateurs d’interactions entre biodiversité fluviale et modifications anthropiques des hydrosystèmes. Rapport final. Programme interdisciplinaire de recherche “Environnement, Vie et Société”, Systèmes écologiques et développement durable. Université de Saint-Etienne, Saint-Etienne, France.
- Scheidegger, A.E. 1965. The algebra of stream-order numbers. Prof. Pap. No. 525B, U.S. Geological Survey, Washington, D.C.
- Schlösser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. *In* Evolutionary ecology of North American stream fishes. *Edited by* W.J. Matthews and D.C. Heins. Oklahoma University Press, Norman. pp. 17–26.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman & Co., New York.
- Souchon, Y., and Trocherie, F. 1990. Technical aspects of French legislation dealing with the freshwater fishery (June 1984): “Fisheries orientations schemes” and “Fishery resources management plans”. *In* Management of freshwater fisheries. *Edited by* W.L.T. Van Densen, B. Steinmetz, and R.H. Hughes. Pudoc, Wageningen, The Netherlands. pp. 190–214.
- Stewart, B.G., Knight, J.G., and Cashner, R.C. 1992. Longitudinal distribution and assemblages of fishes of Byrd’s Mill Creek, a southern Oklahoma Arbuckle Mountain stream. *Southwest. Nat.* **37**: 138–147.
- Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *Trans. Am. Geophys. Union*, **38**: 913–920.
- Taylor, C.M., and Warren, M.L. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology*, **82**: 2320–2330.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Welcomme, R.L. 1985. River fisheries. *FAO Fish. Tech. Pap.* **262**: 1–330.
- Whittaker, J. 1984. Model interpretation from the additive elements of the likelihood function. *Appl. Stat.* **33**: 52–64.
- Wilkinson, C.D., and Edds, D.R. 2001. Spatial patterns and environmental correlates of a midwestern stream fish community: including spatial autocorrelation as a factor in community analyses. *Am. Midl. Nat.* **146**: 271–289.