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Non-interactive fish communities in the coastal streams of North-western France

THIERRY OBERDORFF*†, BERNARD HUGUENY‡, ARTHUR COMPIN† and DJAMILA BELKESSAM†

†Muséum National d'Histoire Naturelle, Laboratoire d'Ichtyologie Générale et Appliquée, 43 rue Cuvier, 75231 Paris Cedex 5, France; and ‡Antenne ORSTOM, Laboratoire d'Ecologie des Eaux Douces, Université Claude Bernard Lyon I, 43 Bld du 11 Novembre 1918, 69622 Villeurbanne Cedex, France

Summary

1. Spatial patterns of freshwater fish species at regional and local scales were investigated to explore the possible role of interspecific interactions in influencing distribution and abundance within communities occupying coastal streams of North-Western France.
2. Nine sites from nine streams situated in the same biogeographical region were sampled annually over the 6-year period from 1990 to 1995.
3. Similar habitats (sites) with richer regional colonization pools exhibited proportionally richer local communities in terms of number of species, total density and total biomass of individuals. Furthermore, no negative relationships were found between density and biomass of each of the most common species and local species richness.
4. Results of dynamic regression models (applied to the above-mentioned species) suggest an absence of strong competition between all pairs of species.
5. The evidence on lack of density compensation for species-poor communities and absence of perceptible interspecific competition between species suggest that the communities studied are non-interactive.
6. Two main explanations can be advanced. First, the local abundance of species in the communities studied could be determined through differential responses to unpredictable environmental changes, rather than through biological interactions. Second, as a result of historical events, the communities studied are reduced in congeneric species which can limit, in turn, the influence of interspecific competition in structuring these communities.
7. These results underline the strong influence of regional processes in shaping local riverine fish communities and minimize the possible influence of species interactions in governing these communities.

Key-words: density compensation, fish assemblages, interspecific interactions, local species richness, regional species richness.

Introduction

The assessment of the importance of interspecific interactions in shaping local communities is of particular interest to ecologists as well as conservationists and resource managers. Communities can be classified as interactive or non-interactive depending upon whether or not strong biotic interactions take place

among the residents of a local habitat (Cornell 1993). Evidence suggests that real communities lie on a continuum from interactive to non-interactive (Cornell & Lawton 1992). Nevertheless, direct assessment of the effects of interspecific interactions on communities is often difficult under natural field conditions and ecologists regularly use indirect methods to test for such interactions (Diamond 1986). Three types of approach are usually applied: laboratory experiments, field manipulations, and natural experiments. Natural experiments compare assemblages where competition

* To whom correspondence should be addressed.

is assumed to be low (species-poor assemblages) with assemblages where competition is assumed to be high (species-rich assemblages). In this study of local stream fish assemblages this last approach was used to address two questions: (i) is there community saturation? that is to say, do interspecific interactions fix a limit to the number of coexisting species in a local assemblage independently of the size of the regional pool?; and (ii) is there density compensation? in other words, do interspecific interactions fix a limit to the number of coexisting individuals in a local assemblage independently of the number of coexisting species?

Answering these questions can empirically indicate the presence or absence of interspecific interactions and help to assess their potential roles in determining community structure (Tonn 1985).

A simple test to check for local saturation (or unsaturation) with species is to examine the relationships between local species richness (LSR) and regional species richness (RSR) in standardized samples. Samples must be taken from comparable habitats within different geographical areas, and these areas must also contain different numbers of species acting as species pools for each local habitat (Cornell 1985a,b; Cornell & Lawton 1992; Cornell 1993). The insular nature of rivers (Sheldon 1988; Hugueny 1989; Oberdorff, Guégan & Hugueny 1995; Oberdorff, Hugueny & Guégan 1997) stipulates that the number of species able to colonize a given local habitat is the same as the number of species present in the whole drainage basin (regional species richness, RSR) (Hugueny & Paugy 1995; Belkessam, Oberdorff & Hugueny 1997). According to Cornell & Lawton (1992) two generalized results are possible: proportional sampling, which shows a linear relationship between LSR and RSR; and a ceiling in which LSR increases with RSR but rapidly reaches an asymptote. Proportional sampling indicates that the community is unsaturated with species. The ceiling hypothesis suggests that strong biotic interactions take place among the residents of a local habitat, ultimately limiting species richness.

Nevertheless, all that proportional sampling indicates is that, regardless of the nature of any local interactions that may be occurring, they are not sufficient to limit local diversity (Cornell 1993). Supporting evidence on lack of density compensation is required to confirm that the community is non-interactive (Cornell 1993). Density compensation is an ecological process by which summed population densities of individuals in species-poor assemblages equal summed population densities of individuals in species-rich assemblages. This phenomenon has often been associated with intense competition for resources (McArthur, Diamond & Karr 1972; Tonn 1985; Taylor 1996). In other words, the population density for each species should be greater in species-poor than in species-rich communities, the increased densities (fully or partially) compensating for the loss of some

populations from the species-rich communities. Conversely, if no density compensation occurs, the population density of a species is constant and independent of species richness. In this case, there is a linear relationship between summed densities and LSR.

Community saturation and density compensation are phenomena acting on the whole community. However, competition may affect only a limited number of species and thus may have no perceptible effect at the community level. Among the available methods usually applied to identify interacting species using field data, for this study the dynamic regression approach proposed by Pfister (1995) was chosen. The major assumption underlying this approach is that population change of a focal species between time t and time $t + 1$ is negatively linked to the density of some co-occurring species at time t .

Methods

STUDY AREA AND FISH ASSEMBLAGES

Nine sites having quite similar habitat characteristics were selected (based on information from a preliminary review of available data) within nine different stream basins situated in the same biogeographical unit (the Basse Normandie region) and containing different numbers of species acting as species pools for each site. The sites were sampled annually over the 6-year period from 1990 to 1995 (Fig. 1 and Table 1). All sampled streams shared a common fish fauna (Belkessam *et al.* 1997). Seven abiotic environmental variables were measured at each site. The environmental variables retained (e.g. distance from the ocean, gradient, elevation, stream width, specific discharge, distance from sources, surface area of the drainage basin) can be considered as synthetic variables reflecting other physical factors influencing species richness (temperature, depth, current velocity, substrate, channel form) (Huet 1959; Rahel & Hubert 1991).

Species lists (estuarine species were omitted) from entire drainage basins of these streams were extracted from the database held by the Conseil Supérieur de la Pêche (Banque Hydrobiologique et Piscicole) and covering 10 years of survey. Consequently, these values can be considered as reliable. Nevertheless, all the fish species present in a stream basin do not have a general distribution throughout the entire basin. In other words, all the fish species in a given stream basin cannot arrive at and survive in a given site. In fact, species composition in stream fish assemblages changes longitudinally with an increase in stream size through the addition and replacement of species, resulting in distinct biotic zones (Huet 1959; Verneaux 1981). This implies that the regional pool can be overestimated if it includes species specialized to habitats other than the ones of interest, so that the species included in it can never reach or colonize the local

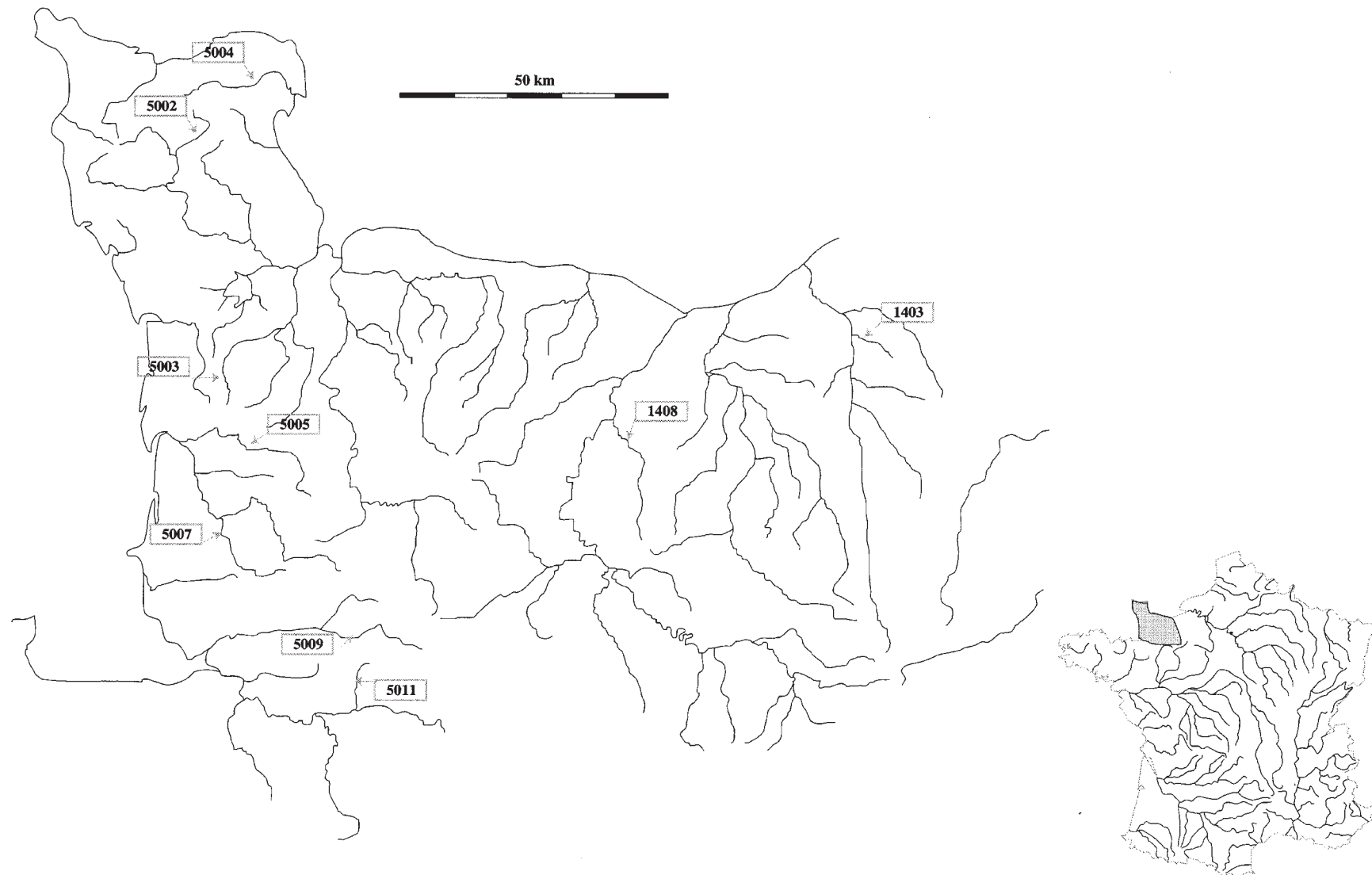


Fig. 1. Location of the nine sampled sites from nine coastal streams of North-Western France.

Table 1. Designation, localization and description of the nine sampled sites

Site	Basin	River	Distance from ocean (km)	Elevation (m)	Discharge ($l\ s^{-1}\ km^{-2}$)	Surface area of the drainage basin (km^2)	Distance from the sources (km)	Stream width (m)	Gradient (‰)
1403	Touques	Chaussey	22.0	40	5.00	30.0	6.5	4.6	6.1
1408	Orne	Laize	30.0	20	1.50	144.0	22.5	5.5	4.2
5002	Douve	Gloire	53.0	50	2.50	29.0	9.0	4.0	5.0
5003	Taute	Taute	33.0	35	0.75	25.0	7.5	3.2	5.0
5004	Saire	Saire	15.0	40	2.50	50.0	11.5	5.8	10.0
5005	Soulles	Soulles	16.5	45	1.50	85.5	22.0	6.3	5.0
5007	Sienne	Airou	24.5	45	2.50	89.0	17.0	7.8	5.0
5009	See	See	32.0	80	3.50	86.0	16.0	5.7	12.5
5011	Selune	Cance	92.0	120	3.50	36.8	11.0	6.3	20.0

communities under study. Consequently, a regional but ecologically based species richness would include only those species from true regional richness that are able to maintain populations within the sites studied. Thus, RSR was defined as species suitably adapted to the specific biotic zone in which each site was found, as defined by Verneaux (1981). Data for local freshwater fish species richness (LSR) were collected between 1990 and 1995. Two species (*Gasterosteus aculeatus* L. and *Scardinius erythrophthalmus* L.) were excluded because of their rarity in samples (<three occurrences). The richness of the fish communities between sites varied from four to ten species, all of which (*Anguilla anguilla* L., *Salmo trutta* L., *S. salar* L., *Cottus gobio* L., *Barbatula barbatula* L., *Gobio gobio* L., *Phoxinus phoxinus* L., *Leuciscus leuciscus* L., *L. cephalus* L., *Rutilus rutilus* L.) feed primarily on insect larvae and more precisely chironomid, ephemeropteran and trichopteran larvae (except *Rutilus rutilus*, which is a more generalist feeder) (Michel & Oberdorff 1995). Hartley (1948) analysed food and feeding relationships in a comparable community of freshwater fishes (eight species common to both studies) on the upper reaches of the River Cam (UK) and concluded that, although the feeding habits of each species were not identical, there was potential competition between all the fish in the community for certain staple foods. Furthermore, habitat partitioning, assumed to result from interactions between some of these species has been noticed by several authors (Welton, Mills & Pygott 1991; Mastroiello, Dauba & Belaud 1996). The species captured during the present study, even if they do not constitute a guild in the true sense of the word, can thus be considered as potentially competitive, both in terms of food and space.

Sites were sampled each year with standardized electro-fishing methods conducted during low flow periods (from August to the end of September). The size of sampling area (> 100 m) was sufficient to include the home range (i.e. major habitat types) of the dominant fish species as defined by Stott (1967),

Kennedy & Pitcher (1975), Nicolas, Pont & Lambrechts (1994), Minns (1995), and encompassed complete sets of the characteristic stream form (e.g. pools, riffles, runs). Two passes were made through each of the sites. Fish were identified to species, weighed in the field, and then released. Populations of each species were estimated using the maximum-likelihood estimates of Carle & Strub (1978). This method estimates fish assemblages from repeated sampling using identical fishing effort. Furthermore, it takes into account, compared to other related catch-effort methods, differential catchability (the probability of capturing one fish) of fishes. This method allows comparison between sites.

Because the species differ so much in body size both total density and total biomass estimates of individuals were used to check for density compensation. The total size of the fish community at each site, for each census year, was determined by summing both density and biomass estimates of individuals per species. Sites were compared over several years to account for temporal variations in community structure, thereby enhancing the reliability of the models (Table 2).

STATISTICAL ANALYSES

To account for possible effects of habitat characteristics on fish assemblages in subsequent analyses, an environmental data matrix was compiled for the nine sites (Table 1). All environmental factors were \log_{10} transformed in order to minimize effects of non-normality. The final matrix was analysed by a principal components analysis (Gauch 1982). Principal components analysis (PCA) was used to reduce dimensionality and eliminate collinearity in the environmental variables (James & McCulloch 1990). Three principal components (PC1, PC2, PC3) were retained as (synthetic) independent environmental variables for further analyses; all had eigenvalues greater than 1.

To test for unsaturation in species richness LSR

Table 2. Designation, sampling year, total density estimates, total biomass estimates, local species richness (LSR) and regional species richness (RSR) of the nine sites studied. Missing entries indicate absence of sampling due to harsh hydrological conditions. *See text for explanation

Site	Year	Total density estimates (individuals per 100 m ²)	Total biomass estimates (g per 100 m ²)	LSR	RSR*
1403	1990	56.5	2459.0	4	9
	1991	36.8	1277.5	3	9
	1992	34.8	1313.5	3	9
	1993	28.1	1422.4	3	9
	1994	28.9	1521.0	3	9
	1995	11.7	991.0	3	9
1408	1990	55.1	4127.0	6	15
	1991	50.7	2671.7	7	15
	1992	82.0	2712.0	6	15
	1993	55.9	2035.0	6	15
	1994	41.0	1464.1	7	15
	1995	87.5	1898.5	7	15
5002	1990	58.2	3074.7	5	13
	1991	43.4	1672.3	5	13
	1993	24.6	1637.4	5	13
	1994	20.3	1132.0	5	13
	1995	33.1	799.2	4	13
5003	1991	69.1	3090.0	5	10
	1993	32.0	2004.7	5	10
	1994	43.1	2004.8	5	10
	1995	22.8	1076.6	5	10
5004	1991	57.0	2990.0	5	10
	1992	47.2	2178.0	5	10
	1993	40.7	2568.0	5	10
	1994	34.6	1802.0	5	10
	1995	39.0	2927.0	7	10
5005	1990	227.0	4835.0	9	12
	1991	109.1	3591.0	9	12
	1993	51.1	2204.0	9	12
	1994	42.0	1302.0	7	12
	1995	52.7	1785.0	6	12
5007	1990	40.0	1396.0	7	14
	1991	183.8	2595.0	9	14
	1993	97.5	1679.0	9	14
5009	1990	69.2	1948.0	6	11
	1991	100.0	2415.0	6	11
	1993	63.6	2662.0	7	11
	1994	80.7	1805.0	7	11
	1995	92.0	2880.0	8	11
5011	1990	55.4	885.0	6	12
	1993	27.0	1109.0	5	12
	1994	38.0	762.0	5	12
	1995	29.0	1052.0	6	12

was analysed as a function of RSR and RSR^2 without the constant (absence of the constant in the model allows the regression line to pass through the origin) because when regional diversity (RSR) is zero, so too is local diversity (LSR). Relationships between RSR and LSR were examined for curvilinearity by comparing linear and curvilinear (second-order poly-

nomial) regressions. The linear model is nested within the second-order polynomial model. Therefore, the relative fits of the two models were compared by testing for a significant contribution of the quadratic term to the linear regression. Effects of habitat characteristics on the relationship between LSR and RSR were accounted for by introducing in the model the

following interaction terms: (PC1 \times RSR); (PC2 \times RSR); (PC3 \times RSR). Introduction of straight habitat terms instead of interaction terms would have generated an intercept in the model, preventing the regression from crossing the origin. The underlying hypothesis is that habitat may have a systematic effect on the proportion of the regional pool present at the local scale. Cornell & Lawton (1992) argued that detection of a curvilinear relation between local and regional richness does not necessarily provide an unambiguous test for saturation. They noted that sampling bias could make linear local–regional relations appear curvilinear. This bias, called ‘pseudosaturation’, refers to an increasing overestimation of the true size of the regional pool caused by the inclusion of species unable to colonize the local communities under study. In the present study, the regional pool was limited to species potentially able to colonize the sites studied, so that ‘pseudosaturation’ could not affect the data set obtained. Then, the hypothesis of community saturation is accepted if RSR² has a statistically significant contribution to the multiple regression model.

To test for density compensation, the contribution of LSR and LSR² to the among-site variation in total density was first analysed. If complete density compensation occurred, then absence of relationship between total density and LSR would be expected. If partial density compensation occurs, then it would be expected that total density would not increase proportionally with LSR. Consequently, the hypothesis of partial density compensation is accepted if LSR² has a significant negative contribution to the regression model. The possible effects of habitat characteristics on the relationship between total density and LSR were accounted for by introducing into the model the following interaction terms: (PC1 \times LSR); (PC2 \times LSR); (PC3 \times LSR). The same procedure was repeated with total biomass instead of total density. Interaction terms were used instead of habitat characteristics to prevent the relationships from crossing the origin.

In a second step, the contribution of LSR and synthetic environmental variables (e.g. PC1, PC2, PC3, PC1², PC2², PC3²) in explaining density and biomass estimates for each species at different sites was analysed. PC1², PC2² and PC3² were used to account for possible curvilinear relationships between density or biomass estimates and environmental variables. For this last analysis only species present in at least half of the surveyed sites were retained (the most common species).

In a third step, using this restricted set of species, and with the aim of identifying strongly interacting pairs of species, dynamic regression models expressing population change through time of a focal species were used as a function of densities of co-occurring species (Pfister 1995). The dynamic regression approach is based on a difference equation model

for competition between two species which can be linearized as:

$$\ln[N1(t+1)/N1(t)] = r - rN1(t)/K1 - r\alpha_{12}N2(t)/K1$$

where $N1(t)$ is the density of the focal species at time t , $N2(t)$ the density of the competing species at time t , r is the intrinsic rate of increase of the focal species, $K1$ is the carrying capacity of the focal species, and α_{12} is the competition coefficient of the species 2 over species 1. The extension to more than two competing species is straightforward. The \ln of the ratio of the focal species density at year $t+1$ over density at year t is regressed against densities of co-occurring species at year t including density of the focal species itself at year t (to integrate density dependence). Density ratios have been computed for each species within each locality and pooled in the same analysis leading to sample sizes ranging from 22 to 28 depending on the species. Regression coefficients, assumed to be proportional to intraspecific or interspecific competition coefficients, can be estimated by least squares. However, confidence intervals cannot be assessed in the usual way because of the autoregressive structure of the model (Dennis & Taper 1994). The jackknife procedure described by Lele (1991) was used to deal with temporally dependent data. The same procedure was repeated using biomasses instead of densities.

All statistical analyses were performed using ADE Software (Chessel & Doledec 1992) and Systat 5 version 5.2.1. for the Macintosh (Wilkinson 1990), except dynamic regression analyses for which a specific program was written.

Results

Together, the first three principal components of the PCA performed on the sites-by-environmental variables matrix (Table 1) explained 90% of the overall variability among the nine sites and could be readily interpreted as general habitat gradients. PC1 reflected the longitudinal gradient with high positive loadings for surface area of the drainage basin, and distance from sources. PC2 separated sites by stream widths. PC3 correlated positively with distance from the ocean, but negatively with specific discharge. The remaining axes did not provide useful information (Table 3).

LOCAL SPECIES RICHNESS

Analysing the relationship between local (within sites) and regional (within basins) species richness, the best fit is obtained with a linear model (Table 4 and Fig. 2). Thus, similar sites with richer regional colonization pools (greater RSR) exhibit proportionally richer local assemblages (richer LSR). Integrating habitat characteristics does not alter the proportional relationships between LSR and RSR. Nevertheless, the slope of the relationships between LSR and RSR is

Table 3. Principal component loading for seven habitat variables measured from the nine sites studied. Principal components analysis was used to reduce dimensionality and collinearity in the environmental variables. Three principal components (PC1, PC2, PC3), accounting for 90% of the variability displayed by the seven environmental variables, were retained. Loadings greater than 0.50 in bold

Environmental variables	PC1	PC2	PC3
Distance from ocean	−0.66	0.10	0.64
Elevation	−0.75	0.56	0.15
Specific discharge	−0.54	0.48	−0.58
Surface area of the drainage basin	0.77	0.59	0.10
Distance from sources	0.73	0.60	0.29
Stream width	0.29	0.90	−0.14
Gradient	−0.68	0.60	0.05

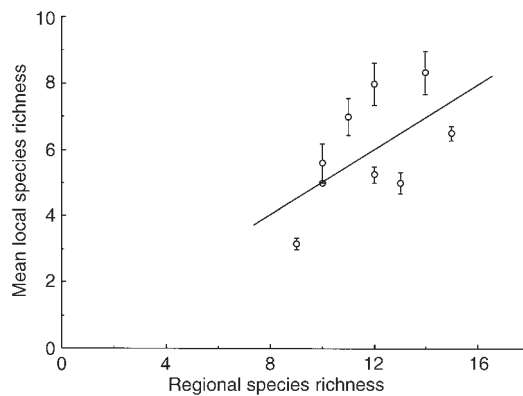


Fig. 2. Relationship between mean local species richness per site and regional species richness for the nine sites studied. Mean local species richness over 6 years (circles) and standard deviation (bars) are figured for each site. Absence of the constant in the model allows the regression line to cross the origin because when regional diversity is zero, so too is local diversity. Fitted using the entire data set ($n = 43$). See Table 4 legend for further explanations.

higher in upstream sections than downstream sections and increases with river width.

DENSITY COMPENSATION

Total density and total biomass increase linearly with an increase in LSR (Table 5 and Fig. 3). The slope of the relationships between total density or total biomass and LSR is not affected by habitat characteristics. This suggests that the species present in species-poor assemblages do not compensate for the loss of some populations from the species-rich communities. To corroborate this result, density and biomass estimates of each of the five species retained (e.g. *Anguilla anguilla* L., *Salmo trutta* L., *Cottus gobio* L., *Barbatula barbatula* L., *Phoxinus phoxinus* L.) were regressed against LSR and synthetic environmental variables (to control for potential environmental effects). If interspecific interaction occurred, then one would expect a significant negative influence of LSR on (a given) species density and biomass estimates. No negative correlation was found between density and biomass estimates of each species and LSR (Table 6). Densities and biomass per species are not less in species-rich sites than in species-poor sites.

DYNAMIC REGRESSIONS

The use of dynamic regression models does not lead to the identification of competing pairs of species, as none of the interspecific estimated competition coefficients were significant either as a function of density or biomass (Table 7). Moreover the analyses do not reveal any significant intraspecific density dependence. There is no evidence that interannual population dynamics are strongly affected by densities or biomasses of co-occurring species.

Discussion

The positive, linear correlation between LSR and RSR demonstrates that riverine fish assemblages are locally unsaturated with species. Other studies dealing

Table 4. Results of the multiple regression of local species richness (LSR) against regional species richness (RSR), RSR^2 , and three interaction terms ($RSR \times PC1$), ($RSR \times PC2$), ($RSR \times PC3$) involving RSR and principal components axes (see text for explanations). The model contains no constant to allow regression to be through the origin. Also given are slope, standard coefficients and P values

Variables	Slope coefficient	Standard coefficient	P
Regional species richness (RSR)	0.747	1.465	0.0001***
(Regional species richness) ²	−0.021	−0.519	0.1110
(RSR \times PC1)	0.029	0.108	0.0210*
(RSR \times PC2)	0.034	0.089	0.0090**
(RSR \times PC3)	−0.015	−0.026	0.5140

* $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Table 5. Results of the multiple regression of total density estimates (model A) and total biomass estimates (model B) against LSR, LSR^2 , and three interaction terms ($LSR \times PC1$), ($LSR \times PC2$), ($LSR \times PC3$) involving local species richness (LSR) and principal components analysis (PCA) axes (see text for explanations). The models contain no constant to allow regressions to be through the origin. Also given are slope, standard coefficients and P values

Variables	Slope coefficient	Standard coefficient	P
Model A			
Local species richness (LSR)	8.293	0.711	0.0060**
(Local species richness) ² (LSR^2)	0.246	0.158	0.5500
(LSR \times PC1)	0.671	0.101	0.2020
(LSR \times PC2)	-0.031	-0.003	0.9620
(LSR \times PC3)	-1.547	-0.108	0.1280
Model B			
Local species richness (LSR)	338.647	0.917	0.0001***
(Local species richness) ² (LSR^2)	1.301	0.026	0.9060
(LSR \times PC1)	1.380	0.007	0.9210
(LSR \times PC2)	-22468.000	-0.077	0.2080
(LSR \times PC3)	-29.071	-0.064	0.2800

*** $P < 0.001$; ** $P < 0.01$.

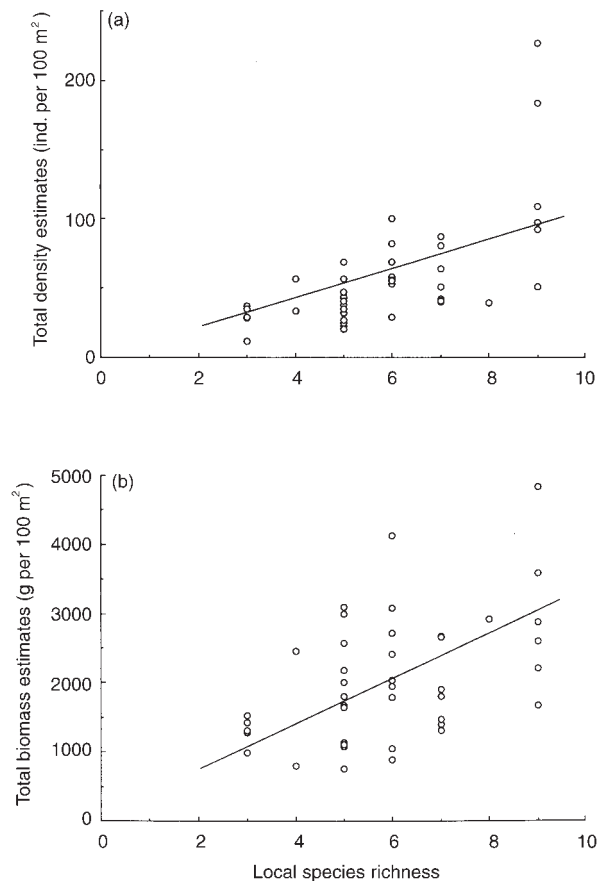


Fig. 3. Relationships among (a) total density of individuals and local species richness, and (b) total biomass of individuals and local species richness. Absence of the constant in the model allows the regression line to cross the origin because when local diversity is zero, so too is total density or total biomass of individuals. See Table 5 legend for further explanations.

with riverine fish species richness at the local scale (Hugueny & Paugy 1995; Belkessam *et al.* 1997) corroborate this result. While there is a strong regional

effect on LSR, local effects of habitat cannot be discarded, as shown by the statistical analyses presented above. These local effects of habitat are due to the

Table 6. Results of the multiple regression (standard coefficients) of (a) total density and (b) total biomass of each of the five species retained against local species richness (LSR), PC1, PC2, PC3, PC1², PC2², PC3²

(a) Species	Density estimates vs.		PC3	(PC1) ²	(PC2) ²	(PC3) ³	LSR
	PC1	PC2					
<i>Anguilla anguilla</i> L.	0.969***	0.414	2.131*	−1.171	−0.573	1.598	0.169
<i>Cottus gobio</i> L.	−0.103	0.098	0.282	−0.327	0.077	0.839	1.075***
<i>Barbatula barbatula</i> L.	−0.115	−0.551	−2.108	1.316	0.500	−1.869	0.081
<i>Salmo trutta</i> L.	−0.254	0.522*	1.740*	−1.140*	−0.821*	2.019**	0.117
<i>Phoxinus phoxinus</i> L.	0.041	−0.239	−1.043	0.558	0.356	−1.181	0.051

(b) Species	Biomass estimates vs.		PC3	(PC1) ²	(PC2) ²	(PC3) ²	LSR
	PC1	PC2					
<i>Anguilla anguilla</i> L.	0.565*	−0.200	0.211	−0.273	−0.024	−0.156	0.002
<i>Cottus gobio</i> L.	0.139	0.789	2.808	−1.702	−0.676	2.983*	0.998**
<i>Barbatula barbatula</i> L.	−0.105	−0.346	−1.860	1.302	0.604	−1.615	0.124
<i>Salmo trutta</i> L.	−0.053	0.864**	3.438**	−2.02**	−1.582***	3.157***	0.059
<i>Phoxinus phoxinus</i> L.	−0.162	−0.358	−0.333	0.191	−0.040	−0.709	0.126

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 7. Results of dynamic regression models relating change in (a) density (N) and (b) biomass (M) of focal species between year t and $t + 1$ to density and biomass of co-occurring species at year t . Numbers in bold represent the Student's t -test values. Sample size of each species is put in brackets. None of the regression coefficients is statistically significant

(a)	N_t <i>Anguilla anguilla</i> L. (26)	N_t <i>Cottus gobio</i> L. (28)	N_t <i>Salmo trutta</i> L. (28)	N_t <i>Phoxinus phoxinus</i> L. (22)	N_t <i>Barbatula barbatula</i> L. (23)
$\ln(N_{t+1}/N_t)$					
<i>Anguilla anguilla</i> L.	−0.00545 −0.27728	−0.00606 −0.12984	−0.01463 −0.39898	−0.00017 −0.00431	−0.00681 −0.37047
<i>Cottus gobio</i> L.	0.0123 0.548	−0.02394 −0.37838	−0.00016 −0.00348	−0.00114 −0.04105	−0.00579 −0.18623
<i>Salmo trutta</i> L.	−0.01148 −0.48664	−0.00036 −0.00835	−0.01827 0.35239	−0.00363 −0.09728	−0.00301 −0.0789
<i>Phoxinus phoxinus</i> L.	0.00394 0.06335	−0.00468 −0.05718	0.01157 0.05631	−0.01885 −0.1297	−0.0114 −0.17802
<i>Barbatula barbatula</i> L.	0.00142 0.05575	−0.06625 −0.3652	−0.0506 −0.35542	−0.02676 −0.40278	−0.01342 −0.44877

(b)	M_t <i>Anguilla anguilla</i> L.	M_t <i>Cottus gobio</i> L.	M_t <i>Salmo trutta</i> L.	M_t <i>Phoxinus phoxinus</i> L.	M_t <i>Barbatula barbatula</i> L.
$\ln(M_{t+1}/M_t)$					
<i>Anguilla anguilla</i> L.	−0.00011 −0.1176	−0.00251 −0.27768	−0.00023 −0.23245	0.00181 0.20087	−0.00159 −0.13983
<i>Cottus gobio</i> L.	0.00016 0.34795	−0.00646 −0.45804	0.00022 0.26689	0.00041 0.0286	−0.00382 −0.40374
<i>Salmo trutta</i> L.	−0.00006 −0.35172	0.00068 0.07105	−0.0002 −1.42505	0.00148 0.1349	−0.00009 −0.03019
<i>Phoxinus phoxinus</i> L.	−0.00011 −0.19032	−0.00072 −0.37652	−0.00042 −0.30047	−0.00794 −0.35526	−0.00401 −0.51966
<i>Barbatula barbatula</i> L.	0.00004 0.06562	−0.00604 −0.15622	0.00019 0.11376	−0.00998 −0.48315	−0.00182 −0.11325

well known upriver–downriver positive gradient of species richness (Kuehne 1962; Sheldon 1968; Horwitz 1978; Beecher, Dott & Fernau 1988).

Results of the present study demonstrate a positive

linear relationship between total density (and total biomass) and LSR. Furthermore, no negative relationships were found between density and biomass of each of the most common species and LSR.

If the results of density compensation studies are to be analysed with respect to competition theory, the species studied must compete for resources, especially food (Case, Gilpin & Diamond 1979). In the present study all the species analysed have quite similar diets and, thus, can potentially compete for food (Hartley 1948; Michel & Oberdorff 1995).

Density compensation studies are usually questionable due to some methodological weaknesses (Wright 1980). First, studies based on the comparison of only two communities during a single season or year are not reliable because they do not account for temporal or spatial variability in density unrelated to species richness. Thus, Tonn (1985) suggests a multi-year comparison of total population density among a series of ecologically similar sites which differ in species number, as was attempted in the present study. However, making a perfect match between localities with regard to habitat is an unattainable goal and the possibility cannot be overlooked that some confounding environmental factors affected results of this study through habitat productivity or habitat appropriateness. This is unlikely because the potential effects of habitat characteristics on fish assemblages were controlled for as far as possible. Furthermore, in this attempt to account for habitat appropriateness, it was not possible to demonstrate a negative effect of LSR on population density. Second, several authors (Case 1975; Case *et al.* 1979; Wright 1980; Faeth 1984) emphasize that the conclusions of density studies frequently involve a comparison between island habitats (species-poor communities) and mainland habitats (species-rich communities), a comparison which introduces potential bias due to reduced predation, moderate climate and reduced dispersal frequently observed in islands. While rivers are biogeographical islands (Sheldon 1988; Hugueny 1989), these biases probably do not affect the results obtained here because: (i) the localities are within a climatically homogeneous region; (ii) a fence effect is unlikely to have occurred because localities are open habitats where individuals can disperse freely; and (iii) predation pressure on the communities studied is probably low because ichthyophagous fishes were absent from the localities surveyed. These arguments lead to the belief that the relationship observed between LSR and total density is real.

As emphasized by Wright (1980) and Faeth (1984), niche and competition theory actually predicts that complete density compensation cannot occur unless species have strictly the same ecological niche. Within species-rich communities, each species restricts its niche to that portion of the resource spectrum which it can most efficiently use. Species which expand their niche in species-poor communities to exploit vacant resources, will be less efficient in the novel niche space than the species which they replace. Thus, according to the theory, partial density compensation is the likely outcome: total density decreases from species-

rich to species-poor communities, but average density per species increases along this gradient. As it is probably more difficult to detect partial density compensation than complete density compensation, powerful tests are required and thus large sample sizes. Despite the quite high sample size used in the present study (43) no evidence of partial density compensation has been found in the communities studied.

Community saturation or density compensation are mainly expected if there is diffuse competition (i.e. total competitive effect of the remainder of the community on a particular population) (Pianka 1983). However, competition may affect only a limited number of species and thus may have no perceptible effect at the community level. Nevertheless, results of dynamic regressions failed to reveal estimated competition coefficients significantly different from zero. Thus none of the species pairs under study are involved in strong interspecific competition. If individuals are competing for limiting resources, intraspecific competition must be higher (in order for coexistence to occur) than interspecific competition, unless species are identical with regard to resource use. None of the intraspecific competition coefficients estimated by dynamic regression are significant, suggesting that resources are not depleted by conspecifics and, *a fortiori*, by heterospecifics. The estimation of competition coefficients from census data has been the subject of some criticisms (see Fox & Luo 1996 for a recent review). However, most of them deal with the static approach in which censuses of population sizes among species at one point in time over many sites are used to estimate interspecific coefficients. The main difficulty raised by this approach is how to integrate spatial variability in the species carrying capacities. Pfister (1995) pointed out that, assuming populations are at equilibrium, carrying capacities that covary positively can result in positive estimated coefficients (whereas negative coefficients are expected) in a static model even when competition occurs. Dynamic models do not assume equilibrium conditions and are not as affected by spatially covarying species carrying capacities if time series from different localities are pooled in the same analysis. Dynamic models allow for delayed numerical responses of populations to resource depletion induced by intra- and interspecific competition and are thus more realistic than static models which assume that populations quickly reach their equilibrium. The drawback of the dynamic approach is that it does not take into account environmental factors acting on mortality, recruitment and exchanges of individuals between localities that are likely to be involved in riverine fish population dynamics. Thus dynamic models can only reveal competitive signals strong enough to emerge from environmental noise.

The absence of community saturation and the absence of density compensation in the present study show that species interactions have no perceptible

effect on community composition or on total density. Moreover, interannual changes in populations are not strongly affected by densities of co-occurring species. Consequently, these communities can be considered as non-interactive. Nevertheless, the possibility cannot be overlooked that interspecific interactions could be too weak to be revealed by the analyses used in the present study. In any event, it is clear that some factors other than those related to interspecific competition structure these communities. One possible explanation could be that streams are highly variable environments and are periodically subjected to extreme and often unpredictable fluctuations in their physical and chemical characteristics. These disturbances can lead to local population extinctions and individual immigration and emigration in response to current conditions. Furthermore, climatic and hydrological variability may have a profound impact on population dynamics through recruitment success (Freeman *et al.* 1988; Carrel & Rivier 1996). These factors have been identified as major determinants of fish community stochasticity (Matthews & Styron 1981; Grossman, Moyle & Whitaker 1982; Grossman, Dowd & Crawford 1990) together with factors that promote community openness and regional dependence of local community structure (Detenbeck *et al.* 1992; Osborne & Wiley 1992). Studies dealing with the persistence of stream fish communities within the Basse Normandie region show that, within the empirical scheme proposed by Grossman *et al.* (1990), communities are considered to be highly fluctuating (a 7-year period, mean value for the CV (coefficient of variation) of population abundance for community members > 75: T. Oberdorff, unpublished data). This suggests that the local abundance of species in such communities could be determined through differential responses to unpredictable environmental changes, rather than through biological interactions (Grossman *et al.* 1982). The importance of interdrainage immigration in shaping community structure, particularly the relationship between distance from colonization source and local species richness, has been emphasized in recent studies on riverine fish assemblages (Detenbeck *et al.* 1992; Osborne & Wiley 1992). Local community saturation through species exclusion by competition is thus prevented by the ability of these species to recolonize from neighbouring sites.

Another possible explanation is based on historical events. It is generally accepted that the West European fish fauna is reduced in richness due to historical processes (Mahon 1984; Oberdorff *et al.* 1997). As a result, few congeneric species coexist in such communities. If it is assumed that congeneric species have similar ecological niches (closely related species), then they should be strong competitors and competitive exclusion or density adjustments should occur more often among congeneric species than in more distantly related ones. This may explain why the results

obtained by the present study differ from the only other study focusing on density compensation in riverine fish communities and which concerns a guild of North American benthic stream fishes (Taylor 1996). Taylor reports density overcompensation, but the communities he studied included numerous species belonging to the same genus. Of course, more studies are needed to quantify this historical effect and its possible impact on community structure.

Density compensation and community saturation studies provide conflicting results with regard to the occurrence of competition in freshwater fish communities. Tonn (1985), analysing fish communities of five North American lakes, noticed complete density compensation for species poor communities. Nevertheless, a recent study of local/regional richness patterns in lacustrine fish in North America supports the idea of unsaturation with species (Griffiths 1997). Concerning streams, both density compensation (Taylor 1996) and absence of density compensation (as in the present study) as well as community unsaturation (Hugueny & Paugy 1995; Belkessam *et al.* 1997) have been reported. Nevertheless, these different results appear contradictory only if it is assumed that density compensation and community saturation are studied in communities having the same level of competitive intensity. Actually, it is likely that numerical responses, such as density compensation, occur at a lower level of competitive intensity than species exclusion which is the extreme outcome of competition. Given this framework, communities can be classified as several types with regard to their position along the interactive–non-interactive continuum:

1. Non-interactive communities where species are not numerically affected by co-occurring species and, *a fortiori*, where neither density compensation nor community saturation occur;
2. Partially interactive communities where only a small fraction of the species are interacting but where neither summed densities nor LSR are affected in a perceptible way;
3. Lowly interactive communities where most of the species are interacting, leading to partial or total density compensation but not to species exclusion;
4. Highly interactive communities where most of the species are strongly interacting such that both density compensation and community saturation occur.

The communities in the present study clearly belong to the first category while, for instance, fish communities in North American lakes probably belong to the third one. Obviously, more studies, testing unsaturated patterns in fish species richness and density compensation jointly, are needed to validate this classification scheme.

The data and analyses presented in this paper lead to the conclusion that the local riverine fish communities studied here are unsaturated with species and with individuals and support the idea that these

communities are non-interactive. If this is truly the case, then the determinants of local richness cannot be discovered by studying local species assemblages in isolation, and the principal direction of control for species richness is from regional to local (Cornell & Lawton 1992).

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