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Environmental Factors Influencing Local Fish Species Richness and Differences between Hydroregions in South-Western France

key words: fish, Garonne basin, general linear modelling, hydroregions, species richness

Abstract

The aim of this study was to investigate the influence of 5 typological variables on the spatial distribution patterns of fish species richness in south-western France, and, subsequently, to analyse differences in the number of species occurring in 6 major hydroregions located within the overall study area. The data were collected at 329 sampling sites. General Linear Modelling was used to assess the influence of each typological variable on local fish species richness, and to determine the differences in local fish species richness between the 6 hydroregions. Local species richness was significantly influenced by altitude, slope and catchment area, whereas distance from the source and stream width showed no significant relations with local richness. The Côteaux de Gascogne hydroregion had a significantly lower species richness, whereas no significant differences occurred among other neighbouring hydroregions. These results were congruent with the spatial distribution patterns of freshwater invertebrate species richness in the area, which were analysed in previous studies. At such a regional scale, we suggest that congruent patterns between fish and invertebrate species richness are almost certainly a result of similar responses by different taxa to environmental conditions, rather than to biotic interactions.

1. Introduction

Both scientific studies and regional surveys of stream ecosystems have provided large volumes of site-specific data (e.g., WHITTIER et al., 1988; CAYROU et al., 2000), from which local and regional spatial patterns of biological communities can be derived (HAWKINS and NORRIS, 2000; DETHIER and CASTELLA, 2002). Several authors have thus emphasized the importance of geographic differences in biotic and abiotic characteristics of streams (CULP and DAVIES, 1982; ORENDT, 2003), so that classification has become an integral part of efforts to study, monitor and manage ecosystems at a regional scale (WARREN, 1979; OMER-NIK, 1987; TATE and HEINY, 1995; SANDIN and JOHNSON, 2000). The identification of areas containing rivers with similar biological and environmental characteristics may help in selecting reference rivers for impact assessments, or in selecting monitoring sites from which results may be extrapolated regionally (RHOM et al., 1987). By knowing what the ecosystem should be like in a given geographic zone, ecologists can thus determine the degree to which human activity has altered it (HAWKINS et al., 2000). Such approaches to river bioassessment were recently developed in Europe (e.g., River Invertebrate Prediction and Classification System), Australia (Australian River Assessment System), and Canada (Benthic Assessment of Sediment) (reviewed in WRIGHT et al., 2000).

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The partitioning of a large area into relatively homogeneous regions also provides spatial order for assessing complex patterns of ecosystem variation (HUANG and FERNG, 1990). Concordances between the distribution of organisms or communities and such geographic regions test our understanding of how organisms respond to combinations of biotic and abiotic factors (OSWOOD et al., 2000). Catchments are commonly adopted when defining boundaries and partitioning variance among aquatic communities (e.g. JOHNSON, 2000). Among aquatic organisms, stream fish communities offer excellent opportunities to examine the relative influence of local and regional factors on species richness. Understanding the patterns of geographic variation in the structure of fish assemblages is therefore of crucial importance to develop a comprehensive assessment of stream conditions. The number of fish species occurring in a given area is related to numerous local factors (OBERDORFF et al., 1993; HOLCÍK, 2003; KRUK and PENCZAK, 2003), and species richness patterns are important biodiversity indicators (GASTON, 1996). Specifically, in the River Garonne drainage basin (S. W. France), MASTRORILLO et al. (1996) observed that there were natural differences in the spatial distribution of fish species richness, but did not assess the influence of environmental factors on the observed patterns.

Fish distribution patterns might not correspond exactly to those suggested by hydroregions (VAN SICKLE and HUGHES, 2000). However, LARSEN *et al.* (1986) found that the correspondence is encouraging. Therefore, the objectives of this study were to investigate the influence of five environmental variables on local fish species richness in south-western France, and, to analyse differences in the number of species occurring in 6 neighbouring hydroregions within the overall study area. We thus attempted to assess the potential of fish species richness to differentiate hydroregions. The results were analysed with reference to geographic differences in environmental conditions, and to previous studies in the same river basin (CEREGHINO *et al.*, 2001, 2003) which yielded regionalisations of stream invertebrates communities in the stream system.

2. Methods

2.1. Study Area

The River Garonne has its source in the Maladetta Glacier (Spain), and it slopes from the southeast to the north-west, where it reaches the Atlantic ocean through the Gironde estuary. The River Garonne drains an area of about 57000 km² and its total length is 525 km. The mean annual discharge amounts to about 545 m³ s⁻¹. Compared with other French rivers (e.g. the Seine river and the Rhône river), the Garonne river is less disturbed by industrial pollution. However, its natural flow has been modified by the presence of several dams, resulting in animal and vegetal community fragmentation within the river channel and the alluvial floodplain (DÉCAMPS *et al.*, 1988). The climate of the region is influenced by oceanic processes, but this lessens to the southeast where it undergoes the Mediterranean influence with dry winds and weaker pluviometry.

2.2. Data Collection

To build the model, we used data from 329 fish sampling sites evenly distributed throughout the piedmont zone of the Garonne river basin, which corresponds to the grayling zone (*Thymallus thymallus*) and the common barbel zone (*Barbus barbus*) according to Huet's zonation (1949). We focused on the piedmont zone in order to prevent differences due to natural longitudinal gradients in fish species richness (MASTRORILLO, 1997). Data for local fish species richness were collected between 1980 and 2000. All sites were sampled once by electro fishing, during low-flow periods, using standardized methods (two-pass removal sampling, DE LURY 1947; SEBER and LE CREN 1967).

Each site was characterised with six environmental variables and one biological variable. The environmental variables were chosen to relate the location of sampling sites within the overall stream system: altitude (a.s.l. m), distance from the source (km), catchment area (km²) and hydroregion data were obtained from a Geographic Information System, whereas slope (per thousand) and stream width (m) where measured on the field. The biological variable was the local fish species richness.

2.2.1. Defining Hydroregions

Understanding the role of regional influences in community organization requires careful definition of regional boundaries. The classification into hydroregions consisted of six sub-drainage basins: CGA (Côteaux de Gascogne, number of sampling sites: n = 45), GAR (Garonne river, n = 58), ARI (Ariège river, n = 42), TAR (Tarn river, n = 56), AVE (Aveyron river, n = 70) and LOT (Lot river, n = 58). Hydroregions (Fig. 1) were defined as the whole drainage basin area of the 6 largest rivers in the area (indexed by the French Water Agency: http://www.eau-adour-garonne.fr/, see also SOULARD, 2000).

2.2.2. Data Analyses

The dependent variable used in our study (species richness) corresponds to count data. The analysis of this type of data is often problematic with usual ANOVA and standard regression methods due to the violation of the assumption of normally distributed errors of the dependent variable. However, General Linear Modelling (GLM) allows a more versatile analysis of correlation than standard regression methods, because the error distribution of the dependent variable and the function linking predictors to it can be adjusted to the characteristics of the data. For analysing species richness (CRAWLEY, 1993) we fitted models using a Poisson distribution and a log link function. River was included as a random factor in the model to control pseudoreplication due to the inclusion of more than one point from each river. Data were analysed with the GLIMMIX macro for SAS 8.2 (SAS INSTITUTE 2000), fitting a mixed effects General Linear Model (river as a random variable and environmental variables as fixed variables). Main effects were fitted using type III tests and a stepwise backwards removal procedure was used to obtain a final model containing only significant factors.

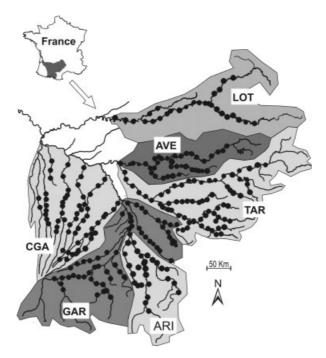


Figure 1. Map of river basin including the six hydroregions and sampling sites on the main rivers, 3-letter codes indicate hydroregion (see text).

3. Results

The model explained 87.2% of the total variance in species richness (cf. Table 1), as estimated by the deviation of the final model (F = 200.28) and that of the null model (F = 1561.27). Four variables significantly influenced local species richness (Table 2 and 3): altitude (p < 0.0001), slope (p < 0.0001), catchments area (p < 0.008), and, to a lesser degree, hydroregion (p = 0.05). Conversely, stream width and distance from the source did not influence the local species richness. When hydroregions were compared, Côteaux de Gascogne had significantly lower cumulative species richness than Garonne (p < 0.003) and Tarn (p < 0.004) hydroregions. Other pairwise contrasts were not significant (Fig. 2). Thus, local species richness was higher at sites with low altitude and weak slopes and in larger catchments. Nevertheless, if in the case of Côteaux de Gascogne, the hydroregion seemed to significantly influence local species richness, other hydroregions showed a weak influence on species richness.

4. Discussion

Our models did show that a few pertinent variables could explain spatial variations in local fish richness, and that, subsequently, the use of simple variables in a successful final model could reduce the effort and cost of data collection for basic investigations and/or water management applications. Even though our study sites were located within a given biogeographic area (i.e., the piedmont – or transition – zone), altitude remained a major ecological factor. For example, MORIN and NAIMAN (1990) showed that the number of fish species in streams of northern Quebec was negatively correlated with stream altitude, which fits with our results. The literature supports the idea that altitude influences local fish species richness through water temperature (e.g. HUET, 1949). It is indeed commonly recognized that

Family	Scientific names	Common names Brook lamprey	
Petromyzonidae	Lampetra planeri		
Anguillidae	Anguilla anguilla	European eel	
Salmonidae	Salmo trutta fario	Brown trout	
	Salmo salar	Atlantic salmon	
Esocidae	Esox lucius	Pike	
Cyprinidae	Alburnus alburnus	Bleak	
	Barbus barbus	Barbell	
	Barbus meridionalis	Mediterranean barbel	
	Abramis brama	Common bream	
	Carassius carassius	Crucian carp	
	Leuciscus cephalus	Chub	
	Rutilus rutilus	Roach	
	Gobio gobio	Gudgeon	
	Scardinius erythrophthalmus	Rudd	
	Chondrostoma toxostoma	Southwest european nase	
	Phoxinus phoxinus	European minnow	
	Leuciscus leuciscus	Dace	
Balitoridae	Barbatula barbatula	Stone loach	
Ictularidae	Ictalurus melas	Black bullhead	
Percidae	Perca fluviatilis	European perch	
Cottidae	Cottus gobio	Bullhead	

Table 1. List of fish species collected.

Table 2. Descriptive statistics mean \pm S.E. (range), for each environmental variable and species richness for each hydroregions, 3-letter codes indicate hydroregions (see text).

Hydroregion	Altitude	Catchment area	D from the source	Slope	Width	Species richness
CGA	152.8 ± 9.9 (34-285)	350.8 ± 106.4 (2-2810)	41.3 ± 5.9 (2.12-135)	2.67 ± 0.22 (0.50-6.25)	10.1 ± 1.5 (1.4-40.0)	8.6 ± 0.5 (4-17)
GAR	251.2 ± 23.0 (8-715)	7481.1 ± 1511.0 (2-54051)	132.2 ± 14.3 (2.4-446.4)	1.99 ± 0.24 (0.50-7.14)	47.2 ± 6.5 (0.9-200.0)	15.6 ± 1.3 (2-32)
ARI	291.6 ± 16.7 (120-545)	1052.0 ± 142.1 (6-4050)	57.0 ± 5.8 (6.0-156.7)	2.13 ± 0.31 (0.50-6.66)	29.7 ± 3.0 (1.7-75.0)	9.8 ± 0.8 (2-17)
TAR	402.5 ± 31.8 (72-810)	1158.1 ± 216.4 (8-5155)	89.3 ± 11.5 (2-292)	2.79 ± 0.30 (0.50-7.14)	$18.9 \pm 2.1 \ (1-75)$	13.6 ± 0.9 (1-26)
AVE	284.2 ± 23.9 (60-836)	2327.8 ± 359.9 (3-15400)	117.7 ± 11.5 (3-364)	2.31 ± 0.23 (0.50-6.66)	$44.2 \pm 4.8 (1-200)$	13.5 ± 1.0 (1-26)
LOT	209.2 ± 25.9 (13-1000)	$5023.1 \pm 468.1 \ (60{-}10712)$	$205.6 \pm 17.1 \ (20{-}480)$	$1.43 \pm 0.19 (0.38 {-} 7.00)$	56.9 ± 4.8 (2.25-125.00)	$18.1\pm0.8~(2{-}25)$

Table 3. Cumulative species richness of fish testing hydroregions. Backwards model. Only variables with p < 0.05 are interpreted as statistically significant. For variables not included in the model no parameter estimate is presented and the F and p values correspond to the values when added to the final model.

Effect	Estimate \pm standard error	DF	F	Р
Intercept	2.8211 ± 0.1722			
Hydroregions	-0.3242 ± 0.2093	5.68	2.36	0.05
Altitude	-0.0020 ± 0.0001	1.252	258.45	< 0.0001
Catchments area	0.0000 ± 0.0000	1.252	7.08	0.008
D from the source		1.251	0.25	0.62
Slope	-0.0510 ± 0.0121	1.252	17.83	< 0.0001
Width		1.251	0.17	0.68

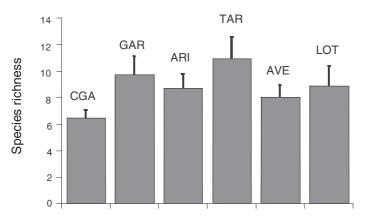


Figure 2. Summary of GLM model for predicting species richness using hydroregion and environmental variables. Means are corrected for the effects of fixed and random variables included in the final backwards model. Variance bars indicate standard errors (S.E.).

temperature may influence local fish species richness by governing population dynamics through growth and fecundity (GILLET *et al.*, 1995), i.e. by acting as a physicochemical habitat filter (*sensu* POFF, 1997) with respect to species traits such as metabolism and energetic demands. Slope is also a key variable in stream ecosystems, as it strongly contributes to the erosive force acting on substrate and causing bed scour in a given area (COBB and FLANNA-GAN, 1990; COBB *et al.*, 1992), and subsequently impacts stream animals. According to REYJOL *et al.* (2003), weaker slopes within the piedmont zone in our study area are associated to higher habitat heterogeneity, thus favouring higher species richness (e.g., coexistence of both salmonid and cyprinid fish).

Nevertheless, our results tend to demonstrate that fish species richness does not have the potential to differentiate hydroregions. Indeed, although two communities from different hydroregions could differ in terms of species composition, they could have similar number of fish species. Although the principle that a catchment's features control aquatic life in streams is usually well accepted (Ross, 1963; HYNES, 1975), the literature often provides contradictory results, probably depending on both the fauna and the environmental features of the study area. For example, HUGUENY (1989) found that fish species richness of a river was related to the surface area of its catchment in West Africa, while HUGUES et al. (1987) suggested that fish assemblages reflect catchments and physiographic provinces. In our study area, two recent works used macroinvertebrates to produce stream classifications. These classifications were based on assemblage compositions (Céréghino et al., 2001) or species richness (Céréghino et al., 2003), and provided two different biogeographic models which may help to highlight our own results. CÉRÉGHINO et al. (2001) clearly segregated three geological areas on the basis of assemblage compositions (Pyrenees Mountains in the southern part of the system, Massif Central Mountains in the eastern part, and alluvial plain in north western areas) that encompasses the six hydroregions we considered. Specifically, Côteaux de Gascogne (which showed the lowest fish species richness) is located within the alluvial plain, i.e., where macroinvertebrate species richness was among the lowest. CÉRÉGHINO et al. (2003) then showed that elevation and stream order contributed most to the model in the Garonne stream system, whereas water temperature and distance from the source had a weaker contribution, i.e., local invertebrate species richness was the lowest when sites combined low elevation (<500 m) with low stream order (1 and 2). Concordant spatial patterns in species richness among different taxa may result from : 1) random mechanisms, 2) biotic interactions among different taxa, 3) common environmental determinants, or 4) spatial covariance in different environmental factors that independently account for diversity variation in different taxa (GASTON, 1996). If local systems are compared, it is likely that a high degree of concordance could be generated through biotic factors (PASZKOWSKI and TONN, 2000). However, at broader spatial scales such as hydroregions within the Garonne stream system, congruent patterns between fish and invertebrate species richness are almost certainly a result of similar responses by different taxa to environmental conditions rather than to biotic interactions (HEINO, 2002). This indicates streams characterized by low order and low elevation, such as those in the Côteaux de Gascogne hydroregion, are likely to support lower biodiversity.

During the last decades, there have been many attempts to produce stream classifications based on aquatic community features (e.g., ILLIES and BOTOSENEANU, 1963; GIBON and STATZNER, 1985; OMERNIK, 1987; WHITTIER *et al.*, 1988; TATE and HEINY, 1995). Nevertheless, few typological systems have had more than local acceptance (PENNAK, 1971). In this context, our results (i.e., altitude and slope were the most significant variables when explaining local fish species richness) support the idea that the most universal classification systems basically remain those which are based on stream size and location within a stream system. Two reference works fundamentally highlighted this approach, i.e., the study by ILLIES (1961), which recognized eight zones within a single drainage system, ranging from zone I (springs or "eucrenon") to zone VIII (brackish zone or "hypopotamon"), and the River

Continuum Concept (VANNOTE *et al.*, 1980), which had a key influence on stream ecology during the last 20 years (RESH and KOBZINA, 2003). Despite geographic differences in species assemblages, such models have the broadest capability of describing spatial patterns of community diversity in the River Garonne basin.

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