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Nested patterns of spatial diversity revealed for fish assemblages in a west European river

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Abstract – The longitudinal distribution of fish assemblages across a large west European river basin, the Garonne river (south-west France) were investigated using a self-organising map. This nonlinear statistical method was employed to classify sampling sites according to their species composition. We found three main nested patterns in an aggregated hierarchy: a replacement and succession of species along a gradient without defined boundaries, four main zones of fish assemblages and an upstream-downstream shift of fish communities. We suggest that fish assemblages are too complex to be identified with a single species as in the zonation model, and that the diversity patterns found might be part of the same ecological process influencing fish assemblages on different spatial scales. Thus, discrepancies in the analysis of longitudinal patterns of fish communities in streams may have been basically a matter of local conditions and of conceptual perception.

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Key words: fish zonation; longitudinal distribution; Garonne basin; self-organising map

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Riverine fish communities are highly structured and follow nonrandom patterns along a longitudinal profile (Jackson et al. 2001). Two well-defined communities located at both ends of a river (one upstream and another downstream) were first described for headwater streams (Schlosser 1982, 1987) and later confirmed for larger rivers (Oberdorff et al. 1993; Lyons 1996). Upstream communities inhabit headwaters, present low species richness and their structure is largely defined by abiotic factors. In contrast, downstream communities are richer in species, dwell in more stable conditions and biotic interactions have a more prominent role in conforming their structure (Matthews 1998; Vila-Gispert et al. 2002). Between both communities there is an addition and replacement of species which has been described as a continuum without defined boundaries (Vannote et al. 1980). However, it has been observed that, along this longitudinal continuum, several discontinuities or faunal breaks represent boundaries or transitions between ecological patches or zones (Matthews 1986; Naiman et al. 1988; Rahel & Hubert 1991) corresponding presumably to different fish communities. For example, in places where there is an abrupt change in altitude, fish assemblages seem to occur along a longitudinal zonation (Matthews 1998). This is the case of west European rivers for which Huet (1959) described four zones according to their most representative species: brown trout, *Salmo trutta fario* L., grayling, *Thymallus thymallus* (L.), barbel, *Barbus barbus* (L.) and bream, *Abramis brama* (L.). However, the consideration of only one species as representative of a zone may not be sufficient to provide a relevant characterization of fish assemblages. We therefore tested: (i) whether fish assemblages fit Huet's zonation on a large scale (i.e., the whole Garonne basin, one of the largest European rivers) and (ii) whether a more comprehensive description of the fish fauna is needed to identify characteristic assemblages.

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Materials and methods

Area of study

The Garonne basin is one of the largest basins in Europe comprising 56,536 km^2 of catchment area in the south-west of France (Fig. 1). The main channel runs over 580 km from the Pyrenees to the Gironde estuary in the Atlantic coast. Its main tributaries have their sources in the Massif Central plateau and the Pyrenees range. Due to biogeographical reasons, fish fauna in the Garonne basin is poorer than in adjacent basins, including the absence of grayling (Persat & Keith 1997). Although the Garonne basin is considered as one of the least impacted by flow regulation in Europe and one of the least polluted (Etchanchu & Probst 1988), it has suffered from intensive damming during the second half of the 20th century (Steiger et al. 1998) and the quantity of applied fertiliser has dramatically increased in the past few years (Semhi et al. 2000), leading to several concerns on fish conservation, most notably on diadromous and native species (Keith 2000).

Data

Data were obtained from the fish database of the Aquatic Environment Team, School of Agronomy at Toulouse (ENSAT) and from the French Fisheries Council (CSP) obtained during collection campaigns between 1986 and 1996, although not sampled at regular intervals. From this database a subset for

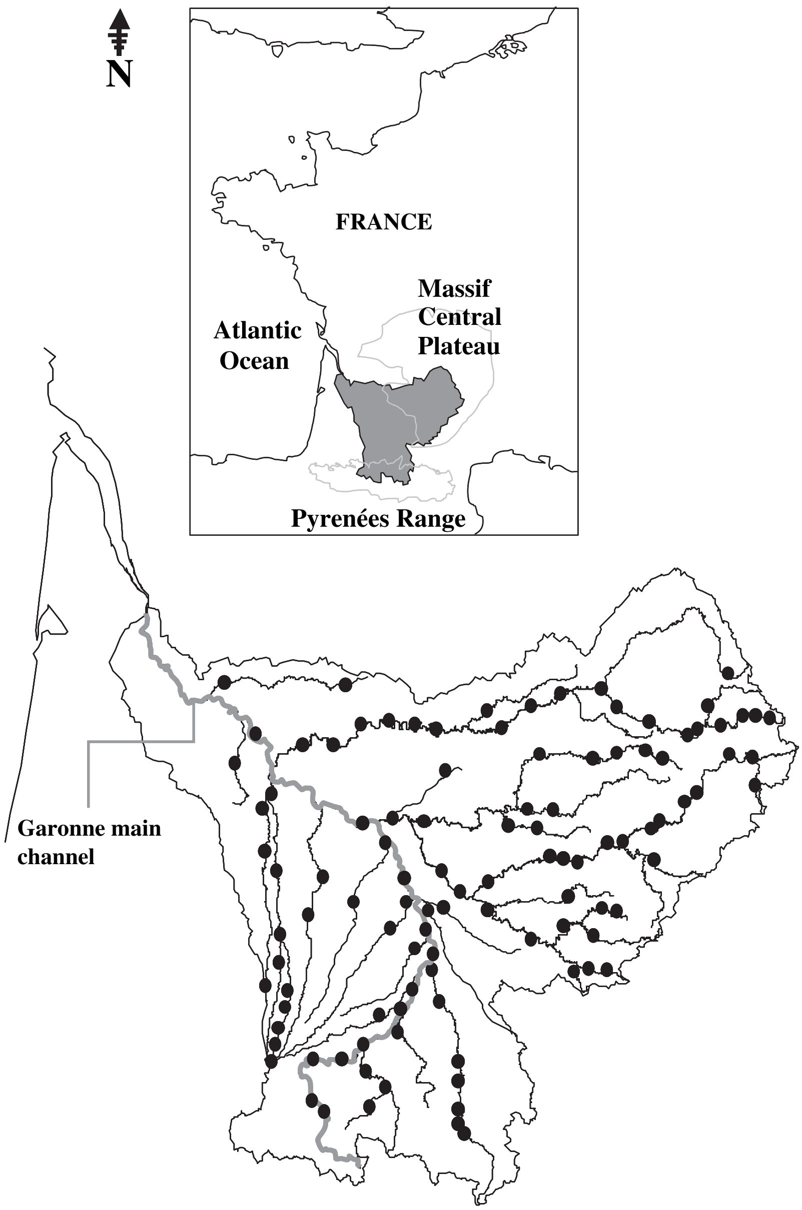

Fig. 1. Location of the Garonne basin, showing the sampling sites as dots.

which collection of species richness was the objective of the sampling was chosen. Electrofishing surveys were made either by wading in shallow areas or by boat in the deeper reaches during low-flow periods (i.e., late summer). In the case of wider and deeper rivers, gill-netting was used in still waters and both gill- and drift-netting for running waters. This combination of methods allows an effective assessment of fish diversity in rivers (Seegert 2000), however, as abundance measures reflect collection intensity (Angermeier & Smogor 1995), only presence–absence data were considered in order to remove sampling bias as recommended by Hughes & Gammon (1987). Fish samplings were not made on a year-to-year basis as it implied a high financial cost. Indeed, many studies assuming large spatial and temporal scales use species presence–absence as the level of data resolution because of the difficulties in obtaining reliable estimates of relative rank abundance (Jackson et al. 2001). For the analyses, it was assumed therefore, a large spatio-temporal scale: a 10-year span as the time unit, and the whole Garonne basin as the spatial unit. Thus, the time dimension had to be taken aside, pooling all observations together in a similar way as described by Sipponen & Muotka (1996). Moreover, local repeated surveys on some sampling sites showed that both environmental features and fish assemblages did not dramatically vary along the 10-year sampling period (Bengen et al. 1992; Mastrorillo 1997; Hutagalung 1998; Cattanéo et al. 1999; Reyjol 2002; Aguilar Ibarra 2004; P. Lim, unpublished data). We reckoned this database, nevertheless, as a reliable representation of fish fauna in this area, according to our field experience and with the information of fish atlases (Bruslé & Quignard 2001; Keith & Allardi 2001). The resulting data set contained 109 sampling sites spread over the whole Garonne basin (Fig. 1), with 40 species belonging to 13 orders and 16 families. Cyprinidae was the better represented with 17 species, followed by Salmonidae (four) and Percidae (three). Data were arranged in a 109×40 presence–absence matrix, i.e., sampling sites in rows and species in columns.

Statistical analysis

We applied a Kohonen self-organising map (SOM) which is a nonlinear clustering technique capable of displaying patterns from complex data sets (Kohonen 2001). We chose this method because it has proved effective in characterising distribution patterns in ecological analysis with the advantage of representing nonlinear relationships (Lek et al. 2000). Other conventional methods cannot handle outliers and species with low frequency of occurrence (i.e., rare species) contained in many ecological data sets (Brosse et al. 2001; Giraudel & Lek 2001). In fact, we reckon rare species as important to accurately describe beta diversity, playing an important role in the fish assemblage structure (Przybylski 1993), and in the determination of their biological integrity (Cao et al. 1998).

The SOM consisted of two layers of nodes, with the input layer directly connected by weight vectors to a two-dimensional output layer (Fig. 2). Modelling was carried out using the SOM Toolbox© (Alhoniemi et al. 2000) for Matlab© (The Mathworks Inc., Natick, MA, USA) in a PC platform, and required five steps. First, the input layer, which may be interpreted as a surrogate of the gamma diversity of the basin (i.e., regional species pool) was fed with the presence–absence matrix. Second, the SOM calculated the connection intensities (i.e., weights) between input and output layers using an unsupervised competitive learning procedure (Kohonen 2001) which iteratively looks for clusters in the data, based on their species composition. The connection intensity of the SOM can be considered as the probability of occurrence of a species at a group of sites, and can be displayed on the SOM as shades of grey, where the darker the colour,

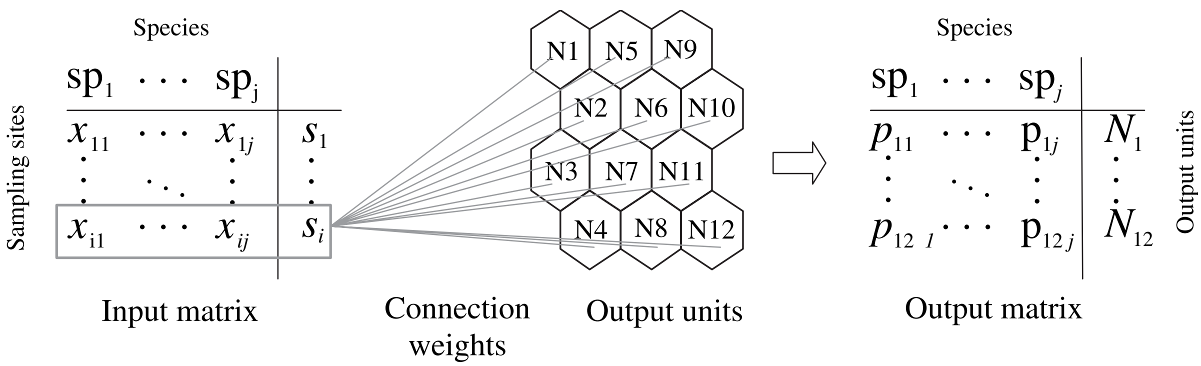

Fig. 2. Simplified representation of the SOM modelling. The input matrix constitutes the input layer and contains the presence–absence data (i.e., x_{ij}). These data are used to train the SOM by changing the connection weights until a low training error is obtained. An output matrix is then produced with the final connection weights (i.e., p_{ij}) of each node (i.e., output unit).

the higher the probability (e.g., black means species occurred in >90% of samples) (Lek et al. 2000). Third, these sites were clustered in each node according to their similarities in species composition (i.e., pooled alpha diversity), resulting in an output matrix, with output nodes in rows and species in columns (Fig. 2). The differences between nodes thus represent the beta diversity of the basin. We chose a 12-node SOM following the results of Park et al. (2003a) and Gevrey et al. (2004), because it was easier to interpret and because it presented a low training error. In fact, the SOM was trained with different number of nodes to find the optimum map size based on the minimum values of both quantisation and topographic errors which are used to assess classification quality (Park et al. 2003b; Gevrey et al. 2004). Fourth, we looked whether there was a significant zonation of fish assemblages by performing (i) a cluster analysis (Ward's Method with Chebychev distance metric) with the new matrix (12×40, nodes $\times$ species) estimated by the SOM, and (ii) a Duncan's multiple comparison test for species richness in each assemblage, producing boxplots. Fifth, the clustered groups were displayed in geographical maps to view the spatial distribution of fish assemblages. Both the input and the output matrices are available upon request from the authors.

Results

Sampling sites were classified by the SOM according to their species composition in the 12 output nodes, so that each node included sites with similar fish fauna. Hence, each species has a probability of occurrence in

Table 1. List in alphabetical order of fish species with a mean probability of occurrence >0.50 in at least a SOM node.

Scientific name	Common name	U		D	
		I	II	III	IV
Abramis brama (Linnaeus, 1758)	Common bream				*
Alburnus alburnus (Linnaeus, 1758)	Bleak			*	*
Alosa alosa (Linnaeus, 1758)	Allis shad				
Alosa fallax (Lacèpède, 1803)	Twaite shad				
Anguilla anguilla (Linnaeus, 1758)	Eel			*	*
Barbatula barbatula (Linnaeus, 1758)	Stone loach	*	*	*	
Barbus barbus (Linnaeus, 1758)	Barbel	*	*	*	*
Blennius fluviatilis Asso, 1801	Freshwater blenny				
Blicca bjoerkna (Linnaeus, 1758)	White bream				
Carassius sp.	Silver carp				
Chondrostoma toxostoma (Vallot, 1837)	Toxostome			*	
Cottus gobio Linnaeus, 1758	Bullhead sculpin				
Cyprinus carpio Linnaeus, 1758	Common carp				*
Esox lucius Linnaeus, 1758	Pike			*	*
Gambusia affinis (Baird & Girard, 1853)	Mosquito fish				
Gasterosteus aculeatus Linnaeus, 1758	Three-spined stickelback				
Gobio gobio (Linnaeus, 1758)	Gudgeon	*	*	*	*
Gymnocephalus cernua (Linnaeus, 1758)	Ruffe				
Ictalurus melas (Rafinesque, 1820)	Black bullhead				*
Lampetra planeri (Bloch, 1784)	Brook lamprey				
Lepomis gibbosus (Linnaeus, 1758)	Pumpkinseed			*	*
Leuciscus cephalus (Linnaeus, 1758)	Chub	*	*	*	*
Leuciscus leuciscus (Linnaeus, 1758)	Dace		*	*	*
Micropterus salmoides (Lacépède, 1802)	Black bass				
Mugil cephalus Linnaeus, 1758	Lisa				
Oncorhynchus mykiss (Walbaum, 1792)	Rainbow trout				
Pachychilon pictum (Heckel & Kner, 1858)	Albanian roach				
Perca fluviatilis (Linnaeus, 1758)	Perch			*	*
Petromyzon marinus Linnaeus, 1758	Sea lamprey				
Phoxinus phoxinus (Linnaeus, 1758)	Minnow	*	*	*	*
Platichthys flesus (Linnaeus, 1758)	European flounder				
Pseudorasbora parva (Temminck & Schlegel, 1842)	Top mouth gudgeon				
Rhodeus sericeus (Pallas, 1776)	Bitterling				
Rutilus rutilus (Linnaeus, 1758)	Roach		*	*	*
Salmo salar Linnaeus, 1758	Atlantic salmon				
Salmo trutta fario Linnaeus, 1758	Brown trout	*	*	*	
Salmo trutta trutta Linnaeus, 1758	Sea trout				
Scardinius erythrophthalmus (Linnaeus, 1758)	Rudd				*
Stizostedion lucioperca (Linnaeus, 1758)	Pikeperch				*
Tinca tinca (Linnaeus, 1758)	Tench				*

Roman numerals indicate the four Huet's zones. U, upstream; D, downstream.

each node, even when it was not found in sampling surveys (Table 1). The assumption behind is that local assemblages are unsaturated and might be colonised by potential species which have the same ecophysiological features as those present in local assemblages. This similarity brought about a counter-clockwise arrangement of nodes within the SOM showing a longitudinal gradient, which becomes evident when looking at the SOM and its geographical correspondence. As an example, we show some of the most common species in the basin, bleak, *Alburnus alburnus* (L.), chub, *Leuciscus cephalus* (L.), minnow, *Phoxinus phoxinus* (L.), brown trout, and of two 'rare' species – bullhead sculpin, *Cottus gobio* L. and allis shad, *Alosa alosa* (L.) (Fig. 3).

Nodes at the top-right of the map included sites belonging to high mountain areas, both the top and bottom left cells incorporated sites of the piedmont, and finally, at the bottom-right were gathered sites from larger and wider rivers, typical of the plains. In

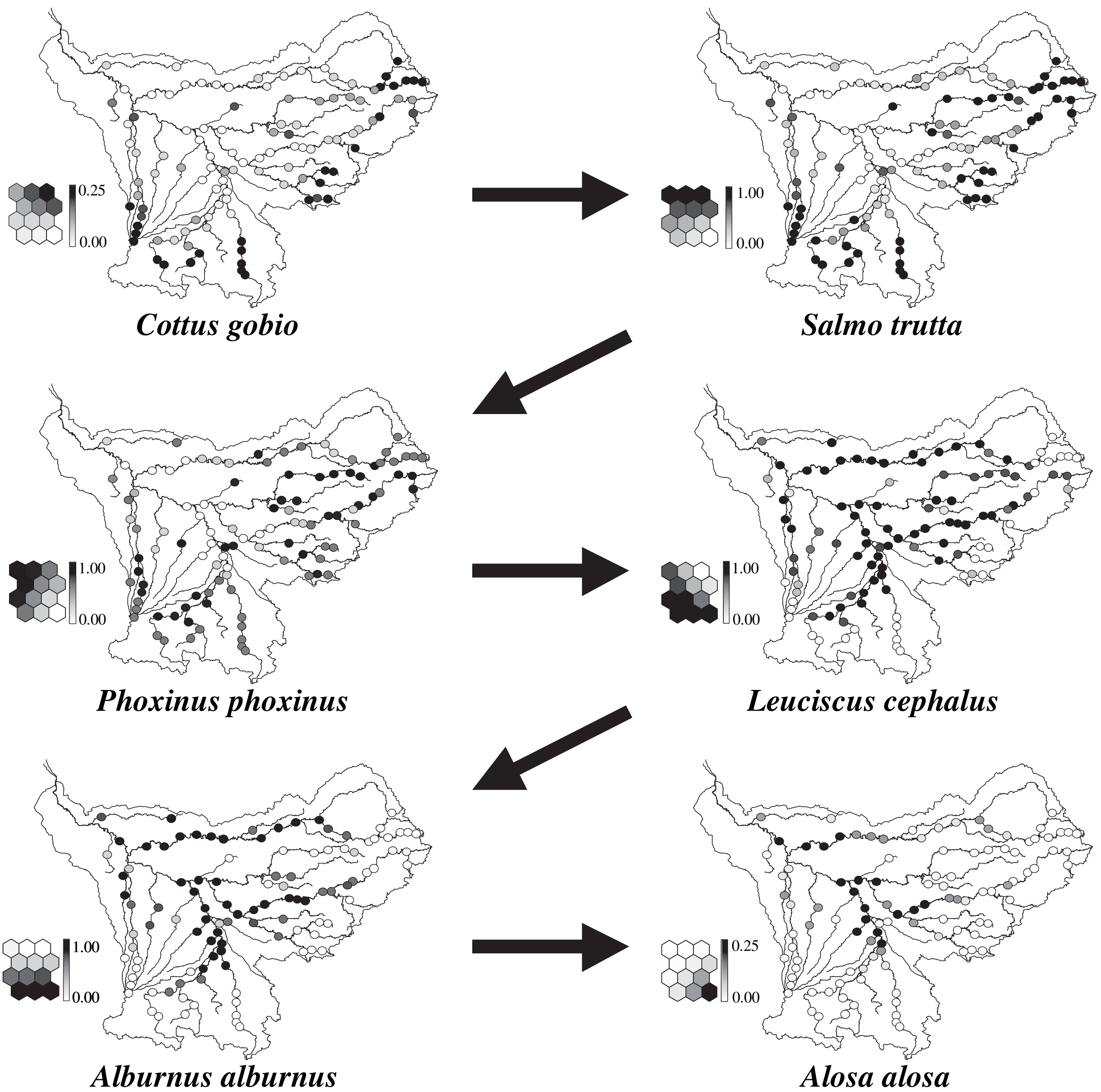

Fig. 3. SOM and geographical maps of the species with the highest probability of occurrence, depicted in the SOM as shades of grey (i.e., the darker the colour, the higher the probability). For example, black means species occurred in >90% of samples. *Cottus gobio* and *Alosa alosa* were species with low-occurrence but were included for explanative purposes (see text). The longitudinal succession of species is noted counter-clockwise from the top-right map to the bottom-right map.

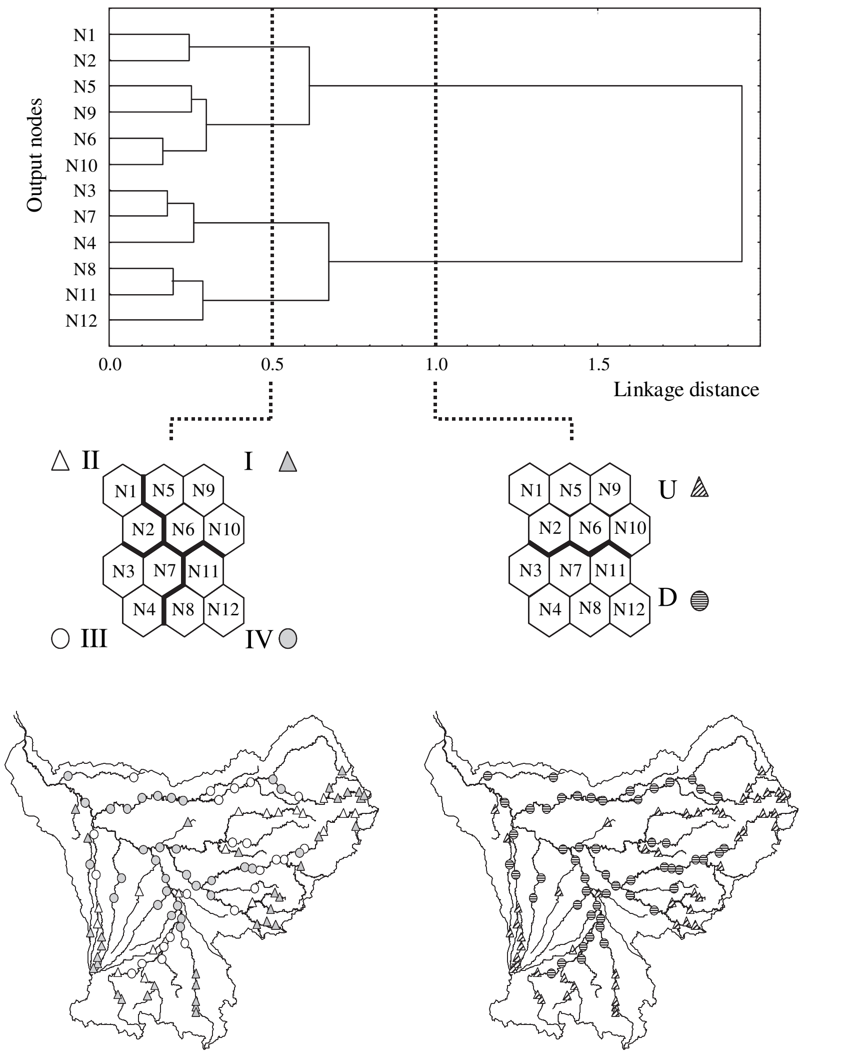

Fig. 4. Dendrogram obtained with the output matrix. A cut-off represented with the dotted lines may serve just as a graphical aid for relating the clustered groups. Hence, we observe a two-group SOM (right) and a four-group SOM (left) with their respective geographical correspondence.

this example, *C. gobio* was present in sites clustered at the top-right of the SOM, indicating that its populations dwell in oxygen-rich waters in the highlands. *Salmo trutta* has a wider distribution: from mountain streams, where it shares its habitat with *C. gobio*, down to upper piedmont rivers where it is mostly associated to *P. phoxinus*. In contrast, *L. cephalus* and *A. alburnus*, are more frequent and widespread, being distributed in warmer waters of the lower piedmont and the plains. Finally, *A. alosa*, a marine species, remained in large rivers and estuary-influenced sites, clustered by the SOM into node N12.

The cluster analysis applied to the output matrix with the connection weights of each species resulted in the dendrogram of Fig. 4. The number of groups of clusters in a dendrogram is commonly left to the analyst in order to look at the largest linkage distances (Everitt & Dunn 1991). At a linkage distance of *c*. 0.5, four groups become evident: one comprised the sites at the highest altitudes (N5, N6, N9, N10), the second included those broadly corresponding to the upper piedmont (N1, N2), the third the lower piedmont (N3, N4, N7) and the fourth the plains (N8, N11, N12). At a linkage distance of *c*. 1.0, these clusters merge forming two groups, one corresponding to sites located upstream (i.e., the top half of the SOM), and another downstream (i.e., the bottom half of the

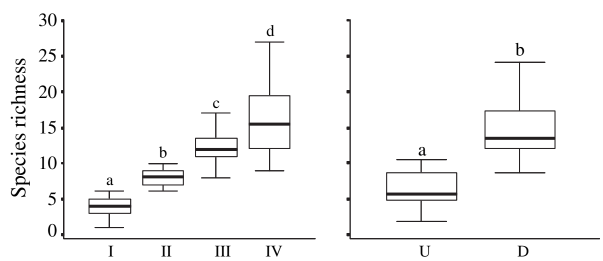

Fig. 5. Box plots showing fish species richness for the fish assemblages found with the cluster analysis (see Fig. 4). Different characters indicate significant difference between groups ($P < 0.05$, Duncan's multiple comparison test). Bold lines within boxes represent the median.

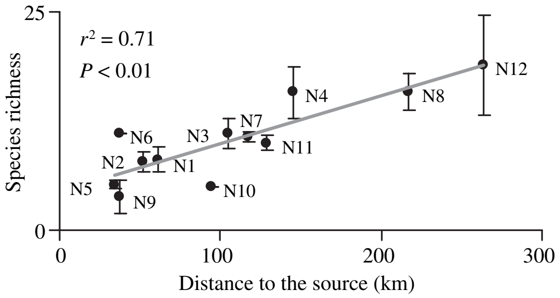

Fig. 6. Plot of mean distance to the source and mean species richness in every output node, showing a positive and highly significant ($r^2 = 0.71$, $P < 0.01$) relationship. Vertical bars denote standard deviations.

SOM). All assemblages were statistically different ($P < 0.05$, Duncan's multiple comparison test) in species richness composition (Fig. 5). Both distance to the source and species richness showed a positive relationship and a gradual increment along the river profile (Fig. 6), consistent with the counter-clockwise arrangement of the SOM. Combining, on the one hand, information on the species assemblages provided by the 40 SOM maps representing probability of occurence of the 40 species in each map cell (as exemplified for six species in Fig. 3), and on the other hand, results on the different clusters displayed on the SOM map of the sites (Fig. 4), we obtained a general view of the upstream–downstream organisation of fish assemblages, as synthesised in Table 1.

Discussion

The spatial distribution of the sampling sites followed an upstream–downstream pattern and fish assemblages broadly matched the physiography of the landscape. However, there were few exceptions or 'atypical' sites in our analysis which did not correspond to the classical longitudinal profile. For example, some rare sites (three sites) were identified as downstream sites by their species assemblage, but were geographically located upstream (Fig. 4). This may be the result of human disturbances, such as agriculture, increasing nutrient load (Rahel & Hubert 1991; Harding et al. 1998), or urbanisation and flow regulation inducing higher water temperatures and creating lotic–lentic environments along a river (Ward & Stanford 1983). Both the temporal variability of fish assemblages (Oberdorff et al. 2001) and the location of sampling sites in the basin (Osborne et al. 1992; Osborne & Wiley 1992) are other sources of community change that may explain atypical sites clustering. However, these sites were scarce and hardly influenced our analyses. In the same way, as the sampling occurred at different times in different sites, time might be covarying with space in our data set (Oberdorff et al. 2001; Ostrand & Wilde 2002). However, no drastic changes in fish composition have been recorded in the Garonne river basin, at least since the 1980s (Bengen et al. 1992; Hutagalung 1998). Therefore, the combination of samples gathered during several years would not bias our analysis. Nevertheless, some local anthropic disturbances may have modified the relative abundance of some species in some sites. Hence, samples collected by different sampling teams and during different seasons, can provide varied abundance patterns for each species. However, the species composition did not vary, as testified by the results obtained in sites where repeated sampling was performed (Bengen et al. 1992; Mastrorillo 1997; Hutagalung 1998; Cattanéo et al. 1999; Reyjol 2002; Aguilar Ibarra 2004; P. Lim, unpublished data). In this way, the use of presence–absence data, although implying a substantial loss of information compared with abundance data, ensures a relevant consideration of all the sampling sites, whatever their sampling date.

We can therefore interpret the dendrogram of Fig. 4 as a general conceptual framework of nested patterns of diversity of riverine fish within a large basin. Hence, two main assemblages were distinguished at a linkage distance of *c.* 1.0: an upstream community and a downstream community. This upstream–downstream pattern has been observed elsewhere, although on smaller scales (Schlosser 1982, 1987; Zalewski et al. 1990; Oberdorff et al. 1993; Lyons 1996; Matthews 1998; Ostrand & Wilde 2002). The upstream community would be exposed to higher environmental variability and would present lower species richness than the downstream community (Schlosser 1987; Jackson et al. 2001). Indeed, fish species richness increased along with distance to the source (Fig. 6). We observed in our data that upstream communities were characterised by trout populations and trout-associated species (e.g., minnow, stone loach), whereas in downstream areas, these populations had a low probability of occurrence, giving place instead to warm water fish like cyprinids (e.g., bleak, common bream), several piscivores (e.g., perch, pike), and some estuarine species (e.g., shads) (Table 1). Fish assemblages from both ends seem to be dissimilar in species composition but assemblages located in between might represent an ecological boundary or a gradual transition of species (Naiman et al. 1988), suggesting an overlapping of communities in the form of a two-step transition zone. Indeed, as defined by Paller (1994) a transitional zone results from an overlapping of upstream and downstream species. Such longitudinal transition of species fits the upstream–midstream–downstream framework of Schlosser (1987) proposed for small headwater streams in Illinois. It also parallels Lyons (1989, 1996) results, mentioning a transitional effect in Wisconsin where groups of species were segregated along a fish-environment gradient, from cold-water to warm-water streams. The four assemblages found in this study may also be coupled to the zones of Huet (1959), as Rahel & Hubert (1991) suggested that both the grayling and barbel zones would represent a transition between the trout and the bream zones. Although grayling is not a native species in the Garonne basin, fish often associated to it like brown trout, stone loach, gudgeon, and minnow (Mastrorillo et al. 1998; Reyjol et al. 2001) do correspond to our assemblage II (Table 1). This may indicate that fish assemblages are too complex to be identified with a single species. Indeed, as demonstrated by Marsh-Matthews & Matthews (2000), a numerically dominant species does not always control fish assemblage structure.

These results imply that fish zonation in large basins, with a diversity of habitats ranging from mountains to coastal plains, is part of a series of nested patterns of diversity, aggregated hierarchically. We suggest, therefore, that gradual changes in species, fish zonation and an upstream–downstream shift in communities might be part of the same ecological process influencing fish assemblages on different spatial scales (Naiman et al. 1988; Tonn 1990; Rahel & Hubert 1991; Jackson et al. 2001). In that way, the discrepancies in the analysis of longitudinal patterns of fish communities in streams have been basically a matter of local conditions (Balon & Steward 1983; Matthews 1998) and of conceptual perception. Moreover, fish assemblages are too complex to be identified with a single species, as commonly used in the Huet (1959) classification.

Finally, in this paper we have only dealt with general long-term aspects of fish species distribution and assemblages composition in the upstream–downstream longitudinal profile. This evidence of nested patterns was probably facilitated by a simple fish fauna in this region, and by the basin-scale approach we used. Instructive results would be obtained by analysing time-series of density and biomass estimates, and incorporating ecological traits or guilds of species in further analyses.

Resumen

1. Investigamos la distribución longitudinal de grupos de peces a través una gran cuenca de Europa occidental, el Río Garona, al sudoeste de Francia, utilizando un mapa auto-organizativo. Este método estadístico no linear fue utilizado para clasificar estaciones de muestreo según su composición específica.

2. Identificamos una jerarquía conceptual de patrones a tres niveles: una sucesión gradual de especies sin límites definidos, cuatro zonas y un cambio de comunidades de peces entre río arriba y río abajo.

3. Proponemos que los conjuntos de peces son demasiado complejos para identificarlos con una sola especie y que los patrones de diversidad encontrados forman parte de un mismo sistema ecológico que influencia a los ríos a diferentes escalas espaciales.

4. Por consiguiente, las discrepancias en el análisis de los patrones longitudinales de peces pueden deberse básicamente a condiciones locales y a la percepción conceptual.

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