

Fish community variation along physical gradients in short streams of northern Spain and the disruptive effect of dams

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Abstract

Relationships between the fish community and selected habitat features were examined in a set of short temperate streams located at the northern end of the Iberian Peninsula. The fish fauna in these streams consists mostly of diadromous or estuarine species. Species richness and diversity increased with stream order, depth and width and decreased with elevation and distance from the sea. Stream order (positively) and elevation (negatively) were the two variables most highly correlated with species richness and diversity; higher order streams (order 3–4) showed greater values of species diversity than lower order ones (order 1) even when the elevation effect was removed. Addition of species in the downstream direction, but no replacement or loss was evidenced. We also compared the observed values of species diversity with those predicted from habitat features for a set of locations above unpassable dams. A great majority of the sites showed lower than predicted diversity values, which is an expected outcome for this mainly migratory fish fauna.

Introduction

Physical habitat features, such as depth, current velocity and substrate composition, have been widely recognized as major factors influencing species distribution and community organization of stream fishes (Gorman & Karr, 1978; Meffe & Sheldon, 1988; Angermeier & Schlosser, 1989). In turn, other studies have emphasized the role of biotic interactions, mainly competition and predation, in community regulation (Werner & Gilliam, 1984; Ross, 1986; Gilliam *et al.*, 1993). Recently, synthetic models have been developed that attempt to integrate the relative importance of both influential factors along upstream-downstream gradients (Zalewsky & Naiman, 1985; Schlosser, 1987). In general, it is believed that changes in species composition along the river course are more related to abiotic factors in upstream sections, whereas more complex biotic interactions, and generally increasing incidence of predator-prey interactions, occur when proceeding downstream. In contrast with this deterministic view of community organization, some studies have documented high temporal variability in the assemblage

structure of stream fishes and suggest that stochastic events, mainly related to unpredictability in the hydrologic regime, may largely determine fish assemblage composition. (Moyle & Li, 1979; Grossman *et al.*, 1982; Ross *et al.*, 1985). However, a number of studies have provided examples of rather stable assemblages, even when drastic flow fluctuations occurred (Matthews, 1986a; Meffe & Berra, 1988; Meador & Matthews, 1992).

Regardless of the processes implied in community regulation, an increase in species richness and diversity downstream the river course is often evidenced when considering large sections of a river system or a whole basin (e.g., Lotrich, 1973; Hawkes, 1975; Barila *et al.*, 1981). This pattern is generally attributed to increased habitat diversity and volume, and milder conditions in the lower reaches (Sheldon, 1968; Lotrich, 1973; Rahel & Hubert, 1991).

Human modifications of the stream channel may alter any of the fish-habitat relationships and thus may have substantial effects on the fish fauna (Swales, 1988). One frequent manipulation in our study area, interspersed dams for hydroelectric development or

water diversion, are likely to alter fish habitat in manifold ways (Burt & Mundie, 1986; Bain *et al.*, 1988), but blocking of migrants is usually the most evident consequence (Mills, 1989).

This paper has two main goals. First, to examine fish community-habitat relationships in a set of short temperate streams. Second, as fish communities in the study streams have a strong migratory component, to assess the effect of unpassable dams by comparing observed versus expected species diversity, as predicted by habitat characteristics, in sites located above dams.

Methods

Study area and sampling

The area studied (Fig. 1) lies between the Cantabrian Sea and a mountain range some 30–75 km from the coast (slightly northeast to southwest aligned). Streams rising from this range at over 1000 or 1500 m altitude generally flow no more than 100 km before entering the sea, and are high gradient and fast flowing over most of their course. There are also a number of small coastal streams that are typically low gradient and slow flowing.

We sampled 76 reaches (surfaces ranging from 106 to 720 m²) in first to fourth-order streams during the 1989–1993 period. All sampling was conducted with a backpack electroshocker between mid June and mid December. From the 76 study sites 42 were situated above unpassable dams and 34 were either below or in streams not having unpassable dams (see Fig. 1); from now these 34 locations will be simply referred as below dam. We searched for community and species-habitat relationships by analysing data from the 34 below dam locations, whereas data from upstream dam locations were only used to evaluate the effect of dams on species diversity.

Fish collected were identified to species and counted, and then Shannon-Wiener diversity was computed for each site. Densities of the most commonly occurring species (*Salmo trutta* L., *Anguilla anguilla* (L.) and *Phoxinus phoxinus* (L.)) were estimated by the Zippin's (1956) removal method. An estimate of catch per unit effort was recorded for each species in all sampled sections and then a regression of density (D , individuals 100 m⁻²) on catch per unit effort (CPUE, fish min⁻¹ in the first run) was calculated. This let us obtain a density estimate from a single catch in three

locations where a unique electrofishing run was carried out and in another five locations where large river size prevented the application of the removal method, by means of the equations:

$$D_s = 17.94 \text{ CPUE}_s + 3.33 \\ (r^2 = 0.65; N = 65; P < 0.0001),$$

$$D_a = 10.18 \text{ CPUE}_a + 1.05 \\ (r^2 = 0.90; N = 18; P < 0.0001),$$

$$D_p = 14.04 \text{ CPUE}_p + 23.66 \\ (r^2 = 0.58; N = 15; P < 0.001),$$

where the subindices s, a and p refer to *S. trutta*, *A. anguilla* and *P. phoxinus*, respectively.

Habitat variables were taken as follows. Depth of each fished section was measured at three or four points across the stream width along transects approximately every 10 m apart. Mean width and depth, and coefficient of variation of depth (CVP) were then calculated. Substrate was categorized according to particle size into 1, silt; 2, sand to cobble (< 20 cm); 3, boulder (20–50 cm); and 4, rock (> 50 cm). Percentage of each of the substrate categories in a section was visually estimated and Diversity (Shannon index) was computed. Elevation, distance from the sea and stream order were recorded from topographic maps.

Data analysis

We correlated species richness and species diversity with several habitat measurements using Spearman's rank or Pearson's correlation coefficients. Reach elevation and mean width were log-transformed to meet normality criteria. Differences in mean species diversity among stream orders were evaluated by analysis of covariance (elevation as covariate) and multiple *t*-tests, setting the table-wide significance level at $\alpha = 0.05$.

To explore patterns of species distribution in relation to the stream habitat and community characteristics, we performed a principal component analysis (PCA) on eleven community plus habitat variables. Proportion of sand to cobble was removed from the analysis as this variable was fully explained by the assembly of the other variables in the PCA. We extracted four factors with eigenvalues > 1 that were subsequently rotated by the varimax method to enhance the interpretability of the factors.

Habitat data from below dam locations were included in a stepwise multiple regression analysis to yield

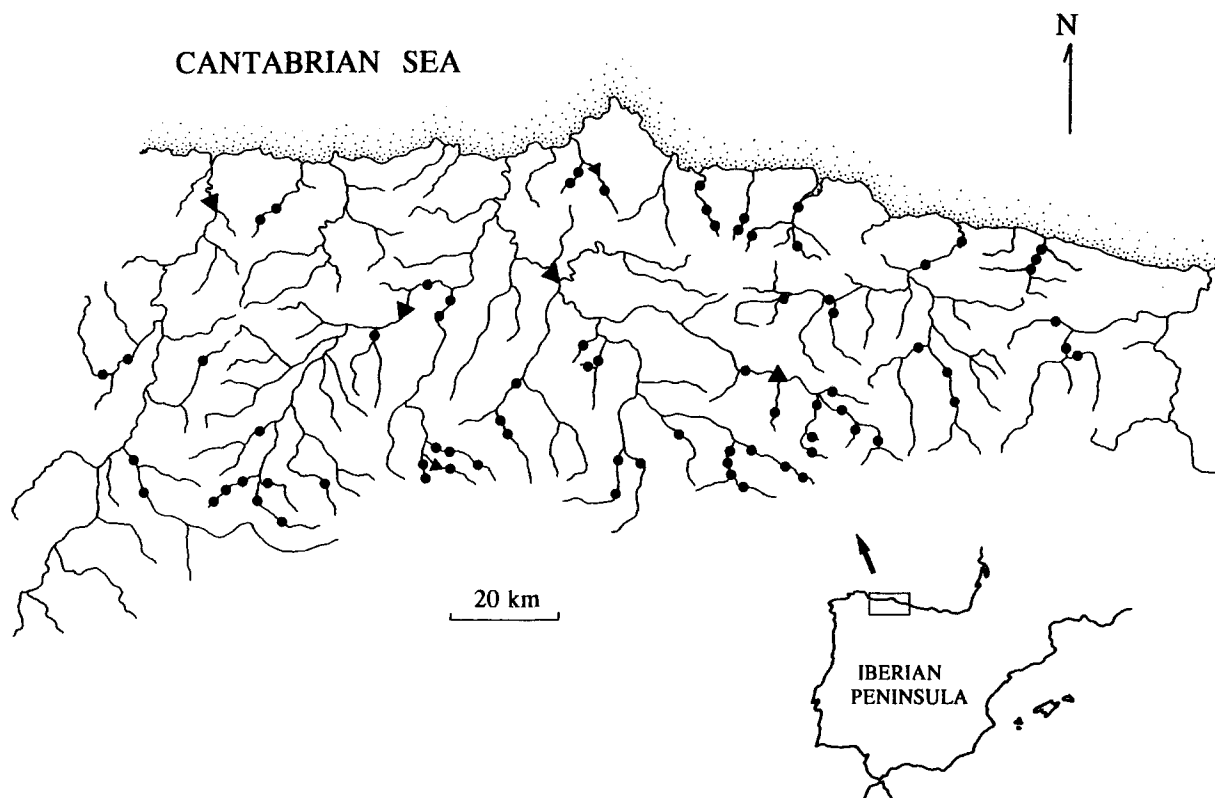


Fig. 1. Map of the study area indicating the location of sampling sites (circles) and the main impassable dams (triangles).

a predictive equation for species diversity. Relative frequencies of positive and negative residuals (observed minus predicted values) of species diversity at upstream sites were then compared by a binomial test with the 0.5 expected probability under the null hypothesis of no effect of dams on species diversity.

Results

The fish fauna in most of the streams was dominated by *S. trutta*, whose variation throughout essentially the same sites has been described elsewhere (Reyes-Gavilán *et al.*, 1994). Only six additional species were collected, two of which occurred both above and below dams: *A. anguilla* and *P. phoxinus*, perhaps an introduced species (Lozano, 1964), and four exclusively below dams: *Salmo salar* L. juveniles, *Petromyzon marinus* L. ammocoetes, *Platichthys flesus* (L.) and *Chelon labrosus* (Risso). Of the species captured, *S. trutta*, *S. salar* and *P. marinus* are anadromous, although migratory populations of *S. trutta* were com-

mon only in lower stream sections (Toledo *et al.*, 1993; this study); *A. anguilla* and presumably *P. flesus* (Dando, 1984) are catadromous; *C. labrosus* is a marine species that frequents estuaries, whereas *P. phoxinus* is the only typical freshwater fish. Thus the fish communities in these streams consisted mostly of diadromous or estuarine species.

The number of fish species showed a strong negative correlation with reach elevation (Fig. 2). Only one species, always brown trout, was collected at sites above 500 m altitude (order 1 reaches in all cases). The number of species also was negatively related to distance from the sea ($r_s = -0.48$, $P < 0.01$) and positively to mean depth and width ($r_s = 0.49$, $P < 0.01$ and $r_s = 0.51$, $P < 0.01$, respectively). Correlation with stream order was somewhat stronger than with the preceding variables (Fig. 2), and this relationship held within the same altitude range (Fig. 3), although all the four orders were represented only at elevations below 200 m.

Species diversity was likewise most highly correlated negatively with elevation and positively with

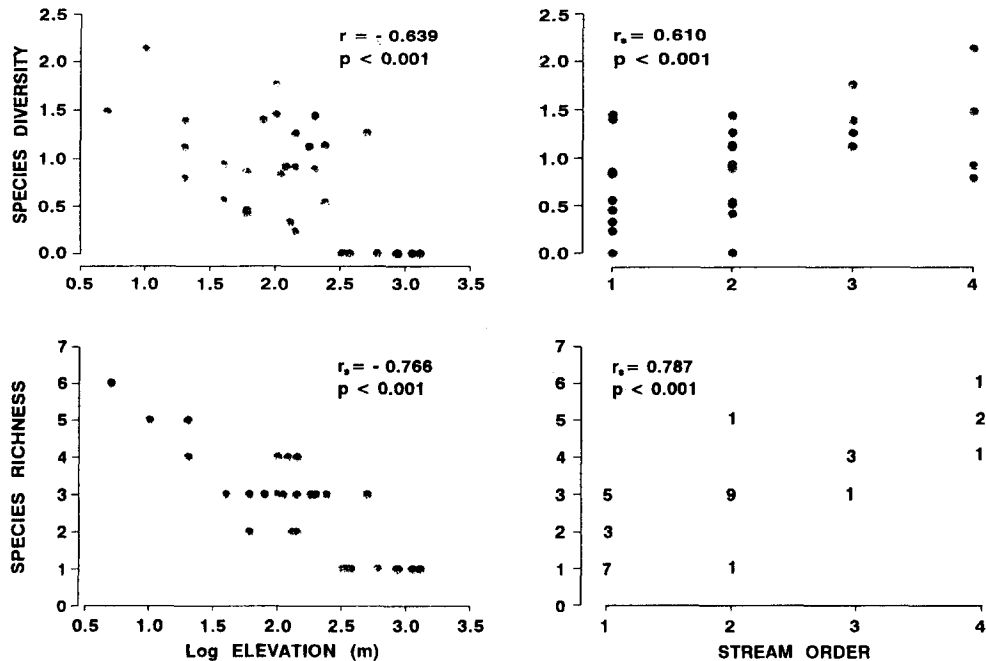


Fig. 2. Relationships between species richness and diversity and their two main correlates, elevation and stream order. Correlation coefficients (r , Pearson or r_s , Spearman) and probability value are given ($N = 34$ in all cases). The numbers in plot D indicate the number of locations with the same species richness and stream order.

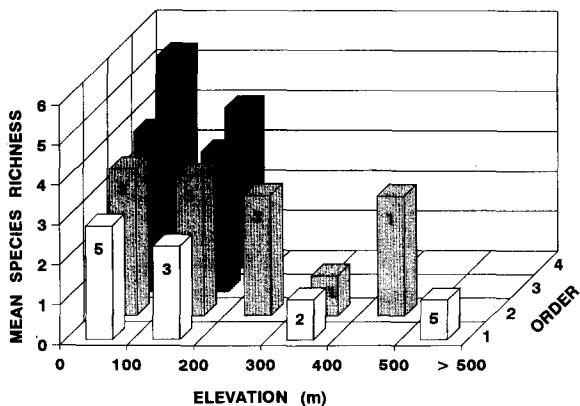


Fig. 3. Mean number of species by stream order and elevation classes. Number of cases in each category is indicated on the bars.

stream order (Fig. 2). Moreover, differences in mean species diversity were detected in relation to stream order even when elevation was employed as the covariate (ANCOVA, $F_{(2,30)} = 4.56$, $P < 0.05$). A more diverse fish fauna was present in large streams (orders 3 and 4, grouped due to low numbers of sites in each category) than in those of order 1 (multiple t -test, $P < 0.05$). Species diversity was also positively correlated with mean depth ($r = 0.52$, $P < 0.01$) and width

($r = 0.35$, $P < 0.05$), and negatively with distance from the sea ($r = -0.37$, $P < 0.05$).

We did not find significant correlations between species richness or diversity and the two measures of structural complexity we considered (coefficient of variation of depth and substrate diversity). There also was no significant longitudinal pattern of variation in the two measures of structural complexity and elevation, distance from the sea or stream order. Mean depth and width both increased with stream order ($r_s = 0.70$ and $r_s = 0.74$ respectively; $P < 0.001$) and the former was also negatively correlated with elevation ($r = -0.46$, $P < 0.01$).

The four main factors extracted by the PCA accounted for 76% of the total variance. The first factor was strongly related to river size, elevation and community complexity (Table 1) and was primarily a longitudinal axis highly correlated with stream order ($r_s = 0.85$, $P < 0.001$); the second reflected substrate composition and distance from the sea, but was not correlated with stream order. Proportion of rocks was the most important variable loading on third axis and coefficient of variation of depth on the fourth. Plots showing fish density (for *S. trutta*, *A. anguilla* and *P. phoxinus*) or only presence (for *S. salar*, *P. mari-*

Table 1. Loadings of the variables on the first four factors extracted by a principal component analysis, and percentage of variance accounted for by each factor. Bold type: loadings greater than 0.5.

	PC1	PC2	PC3	PC4
Species richness	0.921	-0.184	-0.177	-0.006
Species diversity	0.805	-0.176	-0.027	0.181
Elevation	-0.726	0.485	0.371	-0.124
Distance from sea	-0.348	0.583	0.469	-0.260
Mean width	0.737	0.235	0.142	-0.412
Mean depth	0.754	-0.018	0.214	0.123
C.V. of depth	0.127	0.085	0.061	0.878
Substrate diversity	0.041	0.788	-0.146	0.317
% silt	0.319	-0.559	-0.240	-0.307
% boulder	-0.054	0.846	0.009	-0.172
% rock	0.091	-0.023	0.899	0.084
% Variance explained	30.8	21.4	12.2	11.8

nus, *C. labrosus* and *P. flesus*) of each fish species at locations on the two first axes space (52% of variance explained) have been drawn to illustrate patterns of species distribution in relation to habitat and community characteristics (Fig. 4). Differences in distribution among species occurred mainly along the first axis. *S. trutta* occurred alone in the upper, small sized reaches, at most of which the highest density levels for this species were recorded, but was present in all except two sites. *A. anguilla* and *P. phoxinus* were widespread from middle reaches to the lowermost ones. *S. salar* juveniles were caught in a few sites that had positive scores on the first axis, corresponding to low sections of medium or large sized rivers. The three remaining species (*P. flesus*, *C. labrosus* and *P. marinus*) occurred at sites located in the lower right quadrant, that is, low stretches, in cases brackish, at the downstream end of rivers. Table 2 further details the distribution of each species in relation to several habitat variables.

Habitat variables entering a multiple linear regression model for species diversity (SH) were altitude (log ALT) and distance from the sea (DS), that explained 48% of the variance ($F_{(2,31)} = 14.30$, $P < 0.001$). The following predictive equation resulted:

$$\text{SH} = -1.053 \log \text{ALT} + 0.012 \text{DS} + 2.651.$$

A great majority of above-dam sites (40 out of 42) showed values of species diversity lower than expected from their position in the basin according to the above equation (binomial test, $Z = 5.86$, $P < 0.0001$; Fig.

5). When we excluded from analysis sections located above 500 m altitude (where only *S. trutta* was present and consequently the species diversity value was zero) most sites (17 out of 19) again showed lower than predicted diversity values (binomial test, $Z = 3.44$, $P < 0.001$).

Discussion

Species richness and diversity increased following downstream physical gradients of depth, width, distance from sea, elevation and stream order. Elevation and stream order were the variables most highly correlated with species richness and diversity and, although each was correlated to the other, their effects on community composition were partially independent: species richness increased with elevation and stream order when considering sections of the same stream order and discrete elevation categories respectively. Also, species diversity was found to be greater in higher order streams even when the elevation effect was removed. While several authors have reported increased number of species in lower reaches as related to increased habitat diversity (Gorman & Karr, 1978; Schlosser, 1982), we found neither greater habitat diversity downstream, as measured by the coefficient of variation of depth and substrate diversity, nor significant correlations between these two variables and species richness or diversity. Therefore, in the studied streams habitat complexity does not appear to significantly contribute to the increase in the number of species in the lower sections, although it is possible that other aspects of habitat complexity (such as current velocity, cover, etc.) could be influencing community characteristics. Rahel & Hubert (1991) found a similar pattern in a Rocky Mountain stream which showed a transition between a coldwater upstream zone to a lower warmwater one. In the absence of a downstream increase in habitat diversity they suggested that the greater stream living space and moderating environmental conditions were the important factors contributing to the increase in species richness downstream. In our study area increasing stream size, proximity to the marine environment and decreasing elevation seem to be the most important implied factors. However, the influence of elevation in these streams should not mainly result from changes in thermal conditions (despite the wide altitudinal gradient considered), as all the species captured in this study can be found in quite higher latitudes in Europe, but possibly from

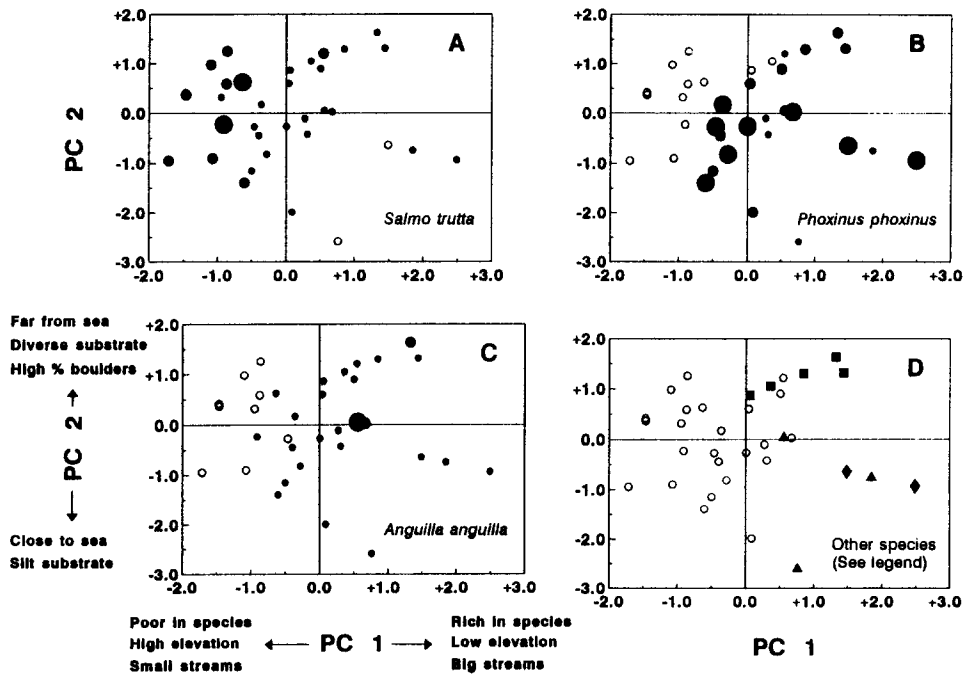


Fig. 4. Species distribution on the two first factors space of a principal component analysis. For plots A–C, size of dots represents three increasing levels of fish density (indiv./100 m²): < 20, 20–50, and > 50. For plot D, symbols represent only presence: square, *Salmo salar*; triangle, *Platicthys flesus* and *Chelon labrosus*; diamond, *S. salar*, *P. flesus* and *Petromyzon marinus*. Empty circles indicate in all cases locations where the respective species were absent.

the increasing occurrence of natural obstacles and the steepening of the channel in upstream reaches.

No substitution, nor loss of species was evident in the upstream-downstream direction in our study area, but the increase in species richness resulted from a longitudinal downstream addition of species. Actually, because of the marine origin of most species, the observed pattern reflects an upstream loss of species. Lotrich (1973) suggested that addition of species along the river course could in most cases follow changes in stream order. This would be the case if major environmental changes along the river course accompanied changes in stream order. However, Matthews (1986b) and Edds (1993) did not find changes in the fish community to occur more commonly with changes in stream order. As Rahel & Hubert (1991) pointed out, the sharpness of community transitions should mainly reflect the sharpness of environmental discontinuities. An abrupt loss of species in our study area could be associated with the breaking of slope toward the middle reaches and possibly with the gradient of salinity operating near the river mouth. Gradual transitions, in turn, would more probably occur in intermediate sections subjected to milder environmental conditions, in

association with changes in local microhabitat characteristics (Matthews, 1986b). For instance, the presence of *P. marinus* ammocoetes and *P. flesus* could be linked with the availability of a silt or sand substrate in which to bury, and decrease of these species upstream could be partly associated with decreasing abundance of suitable substrates. On the contrary, the abundance of optimal gravel and pebble substrates for the spawning of salmonids probably favours their dominance in upstream reaches.

With respect to biotic interactions, the intensity of inter-specific competition in these streams is likely reduced by the high degree of morphological dissimilarity among species (Gatz, 1979) and, as reported in this paper, the noticeable spatial segregation along the longitudinal axis in the basin. According to general information (Thomas, 1962; Kennedy & Strange, 1986; Mann & Blackburn, 1991) and to particular research in our study area (Suárez *et al.*, 1988), only juvenile *S. salar* and *S. trutta* are likely to be potential competitors, as they overlap substantially in resource use. However, evidence of habitat segregation (Suárez *et al.*, 1988) and the low densities found in most sites where the two species co-occurred suggest that com-

Table 2. Distribution of the seven species in relation to habitat variables for the 34 below-dam locations. Total ranges available equal those for *Salmo trutta*

	Elevation (m)	Distance from sea (km)	Mean width (m)	Mean depth (cm)	Stream order	<i>n</i>
<i>Salmo trutta</i>	5–1280	2–78	2.9–45.0	18–52	1–4	32
<i>Anguilla anguilla</i>	5–500	2–66	3.1–45.0	18–52	1–4	25
<i>Phoxinus phoxinus</i>	5–500	2–66	3.1–45.0	18–52	1–4	22
<i>Salmo salar</i>	5–240	4–40	10.6–45.0	25–52	2–4	7
<i>Platichthys flesus</i>	5–20	2–12	5.6–40.0	25–52	2–4	5
<i>Chelon labrosus</i>	10–20	2–7	5.6–10.1	25–52	2–4	3
<i>Petromyzon marinus</i>	5–20	4–12	30.0–40.0	42–52	4	2

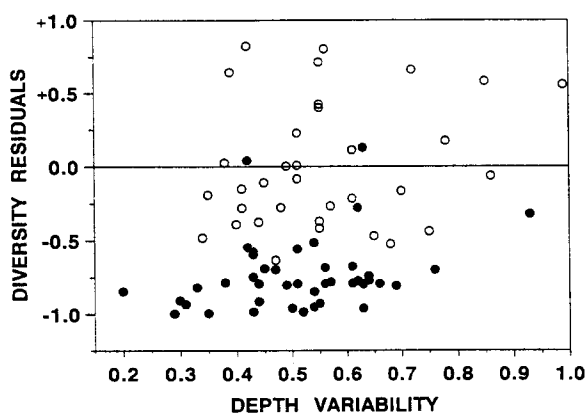


Fig. 5. Residuals of species diversity (observed species diversity minus predicted from elevation and distance from sea measurements) against coefficient of variation of depth, for sites located below (empty circles) and above (filled circles) unpassable dams.

petition should not be too intense. In turn, predation is not expected to play a major role in community organization. *A. anguilla* and large *S. trutta* are the only piscivorous fishes, and percentage of fish in the diet of both species is small (Suárez *et al.*, 1988; Toledo *et al.*, 1993; M. J. Lara, pers. com.). On the other hand, the strength of species interactions in these streams is expected to vary considerably in a temporal scale, partly because of the occurrence of several diadromous species whose abundance in a certain river section may greatly fluctuate on an annual or seasonal basis, and partly due to extensive ontogenetic and seasonal longitudinal movements of resident species (Baglinière *et al.*, 1989; Zalewsky *et al.*, 1990).

Fish diversity was low in sites located above dams. These sites lacked anadromous species and therefore

sustained simple fish communities, composed of three species at most. From patterns of species distribution shown above it is apparent that the impact of dams on fish fauna will greatly depend on their location along the river length and the climbing abilities of the species present at that location. Many species appear to be limited naturally to low elevations. For example, *S. salar*, *P. marinus* and anadromous *S. trutta* did not occur at elevations above 250 m. Also, *P. flesus* and *C. labrosus* appear to be unable to circumvent even minor natural obstacles. Taking a conservative upper limit for these species of 500 m altitude, the presence of barriers above this limit would not restrict their upper distribution and might only block *A. anguilla* in this area. Given the capacity of this last species to overcome barriers, providing dams even with coarse passage facilities would be probably enough to ensure that it remains upstream. Besides stopping upstream migration of diadromous fishes, unpassable obstructions can also limit both seasonal instream migrations and ontogenetic movements that have been reported to be widespread among stream fishes (Solomon & Templeton, 1976; Northcote, 1978; Schlosser, 1991). In addition, blocking precludes recolonization from downstream areas and could eventually lead to genetic differentiation (Northcote & Hartman, 1988; Hinder *et al.*, 1991; Cross *et al.*, 1992).

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