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Composition of endemic fish assemblages in relation to exotic species and river regulation in a temperate stream

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Abstract

Spatial variation in the fish community of the regulated Raia stream (Portugal) was examined during the summer of 1995. Variation in the native fish community (abundance of species–size combinations) was explicitly related to both the abundance of exotic species and habitat variables. The fish community changed in space from assemblages characterised by the high relative abundance of *Leuciscus pyrenaicus*, *Leuciscus alburnoides* and the smaller size classes of *Barbus bocagei* (all Iberian endemics with total length, TL, < 100 mm) to assemblages characterised by the high relative abundance of *Chondrostoma polylepis* (Iberian endemic) and *B. bocagei* with TL > 200 mm and of exotics *Micropterus salmoides* and *Lepomis gibbosus* (> 100 mm TL). The former assemblages used shallow sites far from downstream dams with some current whereas the latter assemblages used deeper sites closer to downstream dams without current velocity and with abundant floating macrophytes. Both exotic species and habitat variables were significant correlates of endemic assemblage composition in the Raia stream and the abundance of *M. salmoides* > 150 mm in TL was the best biotic predictor of endemic assemblage composition. The total variation in the community of endemic fish was partitioned into four components: (i) associated uniquely with exotic species – 12.6%, (ii) associated uniquely with habitat variables – 27.6%, (iii) associated both with exotic species and habitat variables – 14.5%, and (iv) that unexplained – 45.3%. A significant association of exotic species with the endemic fish community remained after accounting for the selected environmental variables and a strong (habitat) × (exotic species) interaction was indicated.

Introduction

The decline of riverine native fish communities is a global problem (e.g. Williams et al. 1989; Elvira 1990; Moyle and Williams 1990; Arthington and Welcomme 1995; Moyle 1995; Penczak and Kruk 2000). Among major disruptive factors are widespread human-induced habitat alterations, such as pollution, hydraulic engineering and changes in land use, and the introduction of exotic species (Marsh and Minckley 1984; Crivelli 1995; Elvira 1995; Kubecka and Vostradovsky 1995; Moyle and Light 1996; Ross 1997; Lucas and Marmulla 2000). River regulation by dams is the greatest source of anthropogenic habitat alteration, with 77% of the total water discharge of the 139 largest river systems in North America and Europe European being at present affected (Cowx and Welcomme 1998). Concomitantly, several exotic species have been introduced worldwide, frequently into reservoirs, and many have quickly become established over large areas revealing invasive characteristics (Elvira 1995; Ross 1997).

Mediterranean type streams in the Iberian Peninsula are a good example of the strong human induced influences potentially affecting native fish communities. Reservoirs have been constructed in almost every Iberian river basin altering the typical seasonal events of flooding and drying over an annual cycle (Moyle 1995; Gasith and Resh 1999). In addition, several exotic species have been introduced, often predatory game species such as the pike, *Esox lucius* and the largemouth bass, *Micropterus salmoides* (Elvira 1995). Concurrently with these changes many of the species composing the interesting Iberian native fish fauna, depauperate in species and highly endemic, are declining in range and abundance (Almaça 1983; Doadrio et al. 1991; Elvira et al. 1998; Cowx and Collares-Pereira 2000). Seventy-three percent of the native species are classified in a particular IUCN threatened category in the Portuguese vertebrate red data book (SNPRCN 1991).

Although it is well known that both environmental and biotic factors influence river fish communities (Meffe 1984; Harvey 1991), most survey studies have focused on only a group of explanatory variables (biotic or environmental), or even on a single factor, thus presuming all other factors to have a neutral effect (Moyle and Vondracek 1985; Meffe and Sheldon 1988; Osborne and Wiley 1992; Poff and Allan 1995). This latter approach has been used to evaluate the effect of exotic species on native fish communities (Lemnly 1985; Rincon et al. 1990; Scoppettone 1993). However, such an approach may not only bias the results but it also provides no information on the relative contribution of each factor for the observed patterns. When such interactions are not considered one may overemphasise or misinterpret the effect of one or more factors, especially when these factors are interrelated (Rodriguez and Magnan 1995). This aspect may be critical in the evaluation of exotic species influence upon native communities since the establishment of exotic species can be facilitated by the alteration of riverine habitats (Meffe 1984; Moyle and Light 1996). Few studies have explicitly related native communities both to exotic species and habitat variables (Godinho and Ferreira 1998).

In this study we examine the spatial variation in an Iberian fish community, including both native and exotic species, from a small stream which is regulated by three shallow reservoirs. In addition to a global analysis, the variation in endemic fish community was separately related to biotic (abundance of exotic fish) and habitat factors by means of multivariate direct gradient analysis (ter Braak 1986). By using an appropriate statistical framework we partitioned the total variation in native community composition into independent components and evaluated whether exotic species had a detectable association with native community variation after accounting for the influence of habitat variables (Rodriguez and Magnan 1995; ter Braak and Verdonschot 1995; Godinho and Ferreira 1998).

Materials and methods

Study area

The Raia stream is a tributary of the River Sorraia, the largest Portuguese tributary of the Tagus, the second largest Iberian river (Ferreira and Moreira 1995). The stream flows for 70 km with a low gradient through an alluvial plain having a mean altitude of 200 m. The study area encompassed a stream reach regulated by three small irrigation reservoirs (inundated area $<$ 30 ha) (Figure 1). This area has Mediterranean features: 80% of the annual rainfall (600–800 mm) occurs in a period of three winter months, mild winters, an annual average temperature of 16–18 °C, and summer drought during an average of four months per year. About 60% of the basin is used for forestry of cork oak *Quercus suber*, maritime pine, *Pinus pinaster*, and eucalyptus, *Eucalyptus globulus*. Most of the remaining area is utilised for intensive agriculture (the irrigated crops rice and maize), which has resulted in high nutrient run-off (Ferreira and Moreira 1995). Sand (mainly in riverine sites) and silt (mainly in reservoir sites) dominate the substratum. In the stream lotic sections emergent and submerged macrophytes are widespread and sometimes develop abundant instream cover. Dominating species are *Myriophillum spicatum* and *Potamogeton* spp., that appear to have been stimulated by the nutrient load resulting from agricultural development (Ferreira and Moreira 1995). The high level of nutrients are also considered the cause for the extensive development of floating macrophytes (dominated by *Azolla caroliniana*) in the reservoirs but the high annual water level variation ($>$ 2 m) curtails the establishment of emergent and submerged macrophytes. Riparian vegetation presents continuous bank cover over large stream segments in the lotic sections and is composed primarily of willows, *Salix* sp.

The reservoirs store water during the autumn and winter that is distributed by pumping to the systems

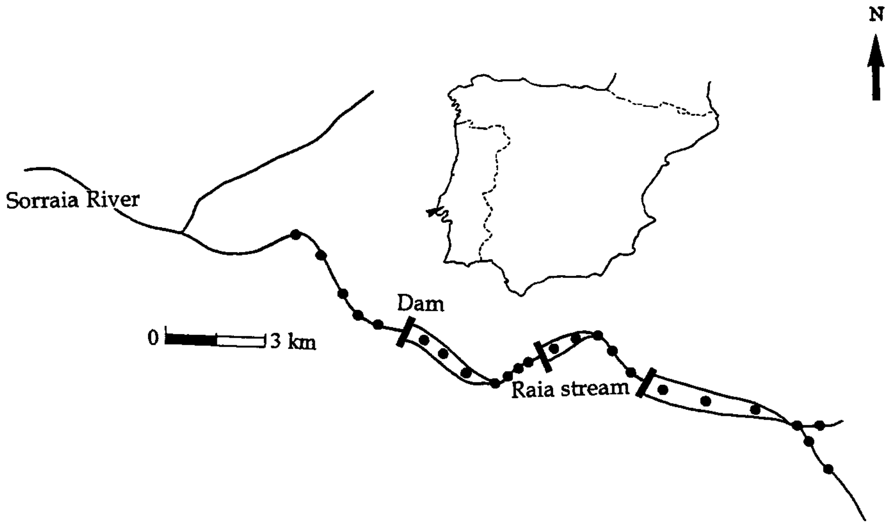

Figure 1. Map of the Raia stream showing study sites.

of irrigation canals that cross the Sorraia valley during the irrigation period (late spring and summer). Consequently, during summer lacustrine conditions prevail in the reservoirs while in lotic sections the intermittent characteristic of this Mediterranean stream is exacerbated due to the water volume abstracted for irrigation. Nevertheless during summer some of the water stored is irregularly discharged through the dams to prevent the complete drying of extensive stream segments. During sampling the stream was 4–70 m wide and velocity was low (0–10 $\mathrm{cm\,s^{-1}}$); water temperature ranged from 18.6 to 25.8 °C, dissolved oxygen ranged from 6.1 to 10.5 $\mathrm{mg\,l^{-1}}$ and conductivity ranged from 377 to 603 $\mu\mathrm{S\,cm^{-1}}$. As is typical in Iberia the native fish community of the Sorraia catchment is species-poor. All the native species are Iberian endemics, however, and three are listed as threatened in the Portuguese and Spanish vertebrate red data books, the portuguese nase, *Chondrostoma lusitanicum* (Cyprinidae), and long snouted barbel, *Barbus comiza* (Cyprinidae) and the lamprey, *Lampetra fluviatilis* (Petromyzontidae), (SNPRCN 1991; Blanco and Gonzâlez 1992). There is also a lack of specialised piscivorous fish species although some endemics do occasionally prey upon fish (Magalhães 1993; Coelho et al. 1997). Besides two long-standing fish introductions, common carp, *Cyprinus carpio* (Cyprinidae), and goldfish, *Carassius auratus* (Cyprinidae, four species have been introduced successfully into the study area since 1930 onwards (Almaça 1983): – the mosquitofish, *Gambusia holbrooki* (Poecilidae), the gugdeon, *Gobio gobio* (Cyprinidae), and the largemouth bass, *Micropterus salmoides* (Centrarchidae), and pumpkinseed, *Lepomis gibbosus* (Centrarchidae).

Field procedures

Twenty-four sites were sampled during July 1995 (Figure 1). Survey site lengths varied between 30 and 40 m to ensure that the range of macrohabitats available at each site was surveyed (Hankin and Reeves 1988). Each site was electrofished thoroughly with D.C. at 400–500 V, 4–5 A, as recommended by Reynolds (1983) for efficient collection. Sampling was conducted once in an upstream, usually zigzag direction, during daylight by wading (in areas < 1 m) or from a boat (in areas > 1 m) (Godinho et al. 1997a). The duration of sampling ranged from 20 to 40 min per site and the same electrofishing gear (Hans Grassl EL62, two hand-held anodes with 300 mm diameter rings) was used in all sites. Though electrofishing is considered the least biased method of sampling stream fishes, it only works in shallow water conditions, up to ~2 m (Cowx 1989; Zalewski and Cowx 1990). Consequently, deeper sites (i.e. deeper areas in the reservoirs) could have been sampled with relatively low efficacy (but see Miranda and Schramm 2000; Vaux et al. 2000).

However, all three reservoirs are shallow (average depth < 1.5 m) and narrow (average width < 30 m), which could have ensured a high electrofishing success.

Table 1. Species codes, size-classes, frequency of occurrence (FO = number of sampling sites with presence) and abundance ranking (based on average CPUE, including absences) of fishes collected in the Raia stream.

Species	Common name	Code	Size-classes (mm)[a]			FO	Abundance ranking
			1	2	3		
Endemic species							
Cyprinidae							
Barbus bocagei Steindachner	Iberian barbel	Bb	47–100	100–200	200–375	22	2
Chondrostoma polylepis Steindachner	Iberian nase	Cp	50–100	100–200	200–270	16	4
Chondrostoma lusitanicum Collares-Pereira[b]	Portuguese nase	Cl	60–110			1	6
Leuciscus pyrenaicus Günther	Iberian chub	Lp	52–70	70–100	100–193	8	3
Leuciscus alburnoides (Steindachner)	Iberian roach	La	35–50	50–100	100–126	12	1
Cobitidae							
Cobitis paludica Pellegrin[b]	Iberian loach	Cpa	70–84			2	5
Exotic species							
Cyprinidae							
Cyprinus carpio Linnaeus	Common carp	Cc	39–100	100–200	200–317	7	4
Carassius auratus (Linnaeus)	Goldfish	Ca	149–227			5	5
Gobio gobio (Linnaeus)[b]	Gugdeon	Gg	60–75			1	6
Poecilidae							
Gambusia holbrooki (Girard)	Mosquitofish	Gh	18–50			6	1
Centrarchidae							
Lepomis gibbosus (Linnaeus)	Pumpkinseed sunfish	Lg	67–100	100–160		15	2
Micropterus salmoides (Lacepède)	Largemouth bass	Ms	87–150	150–355		13	3

[a] Species codes and size-class codes are combined to indicate a species–size class, e.g. Bb1 = *B. bocagei* 47–100 mm.
[b] Species not included in CCA analysis due to their rarity.

Fishing success (numbers collected per unit of effort) was not significantly related to either depth or width ($r = 0.23$ and 0.15, respectively both $P > 0.10$, $n = 24$, F. Godinho, unpublished data). In addition, other environmental factors that may affect electrofishing performance, such as temperature and conductivity, appear to have favoured efficient capture in the study reach (Reynolds 1983). Nevertheless, sources of habitat related bias in the collection method could remain in relation to particular species and will be addressed in the discussion. The fishes collected were identified, individually measured for total length (TL) to the nearest mm, and allocated to size classes created based on major breaks on size–frequency histograms for each species (Table 1). Although electrofishing may be biased against small fish (Cowx 1989), many small specimens were collected and no lower cut-off was evident in the distribution of species TL (Table 1). The numerical abundance of the species–size combinations in each site was expressed as a catch-per-unit-effort, CPUE = catch per 20 min (Reynolds 1983; Godinho et al. 1997a).

After collection of the fish, the following habitat variables were evaluated in each site: temperature, dissolved oxygen, pH, conductivity, velocity, depth, wetted width, abundance of emergent, submerged and floating macrophytes, and substrate composition. Depth was measured at a number of random points within each site using a graduated dip-net pole, and then converted to the following classes (< 0.2, 0.2–0.3, 0.3–0.5, 0.5–1.0, > 1.0 m). The dominant substrate class (mud/silt < 0.05, sand 0.05–2, gravel 2–16, pebble 16–64, cobble 64–256, bedrock/boulder > 256 mm) was visually estimated within a 0.5 m radius circle of these same points (Godinho et al. 1997a). Two variables were derived from the substrate observations, the dominant (most frequent) substrate class (coarseness) and the number of different substrate classes (heterogeneity). The maximum wetted width was measured and then converted to classes (< 5, 5–10, 10–20, 20–30, > 30 m). The macrophytic cover was estimated visually (absent, 1–19, 20–49, $\geqslant$ 50% cover) separately for emergent, submerged and floating forms. Subsurface water velocity (cm s^{-1}) was measured with a current meter along transects that were positioned, perpendicular to the direction of flow, every two meters along the total length of each site. In these same points temperature (°C), dissolved oxygen (mg l^{-1}), conductivity

(μS cm^{-1}) and pH were measured *in situ* with portable probes. Riparian bank cover (bushes or trees) was assessed visually (absent, 1–19, 20–49, $\geqslant$50% bank cover). The downstream and upstream distances to the nearest dam (DDND and UDND, respectively) were obtained for each site from topographical maps. The placement of a sampling site in a reservoir was also noted.

Analytical procedures

Two matrices were initially created from the data: a matrix of species–size combinations (in CPUE) × sampling sites (response variable) and a matrix of habitat variables × sampling sites (explanatory variables). As recommended in survey type studies all putative explanatory factors were initially considered for analysis (Rodriguez and Magnan 1995). The data matrices were submitted to canonical correspondence analysis (CCA) using CANOCO (ter Braak 1986, 1987) which is an eigenvalue ordination specifically developed to directly relate multivariate ecological data matrices. The advantages of CCA for ecological studies of communities were reviewed by Palmer (1993). This direct gradient analysis is particularly suited for biological data sets with many zeros (i.e. frequent absences), is sensitive to the relative abundance of taxa but not to absolute abundance values (more prone to sampling error) and has found widespread use in aquatic sciences since its initial description in 1986 (e.g. ter Braak 1986; Snoeijs and Prentice 1989; Bakker et al. 1990; Kautsky and Maarel 1990; Copp 1992; Cortes 1992; Jones et al. 1993; Rodriguez and Magnan 1993; Godinho and Ferreira 1994; Magnan et al. 1994; Frenzel and Swanson 1996; Godinho et al. 1997a,b; Rodriguez and Lewis 1997; Marshall and Elliott 1998; Tejerina-Garro et al. 1998; Pires et al. 1999; Godinho et al. 2000). In contrast to indirect gradient analysis (e.g. principal component analysis, correspondence analysis or multidimensional scaling) in CCA the ordination (canonical) axis extracted has a known environmental basis, allowing also the powerful use of covariables. A partial CCA amounts to a normal CCA, but with the extra requirement that each synthetic gradient must be uncorrelated with covariables (ter Braak and Verdonschot 1995). With covariables CANOCO will give a direct ordination of the residual variation in the species data that remain after fitting the effects of covariables (ter Braak 1987).

CCA generates a diagram (biplot) that displays approximate values of the weighted averages of species (represented by points) with respect to the supplied explanatory variables (represented by arrows that roughly point in the factor direction of maximum variation) (ter Braak 1986; ter Braak and Verdonschot 1995). Before analysis the CPUE data were transformed $[y' = \ln(y + 1)]$ to reduce the influence of very abundant species–size combinations (ter Braak 1987). Species–size combinations rarely collected (i.e. present in fewer than three sampling sites) were removed to prevent analysis distortion (Table 1). From all the explanatory variables considered, the best predictors (those retained for analysis) within the habitat data table were selected by a forward selection procedure available in version 3.1 of CANOCO, a multivariate extension of the stepwise regression method. As in Magnan et al. (1994) a significance cut-off point of 0.10 was used.

After this first analysis two matrices were further developed: CPUE of endemic species–size combinations by sampling sites (response variable) and CPUE of exotic species–size combinations by sampling sites (explanatory variables). The endemic species matrix was separately related to the exotic species matrix and to the habitat matrix with CCA (Godinho and Ferreira 1998). Again, from all the explanatory variables considered, the best predictors (those retained for analysis) within the biotic and habitat data tables were selected by the CANOCO forward selection procedure. Next, the total variation in endemic assemblage composition was partitioned into four components (Borcard et al. 1992; Magnan et al. 1994; Rodriguez and Magnan 1995). In brief, the following figures were generated: (1) variation accounted for by the selected habitat variables (obtained from a CCA relating endemic species with the habitat variables), (2) variation accounted for by the selected biotic variables (obtained from the CCA relating endemic with the exotic species), (3) variation accounted for by the habitat variables after partialling out the influence of biotic variables with partial CCA (obtained from a partial CCA relating endemic species with the habitat variables after using the exotic species as covariables), and (4) variation accounted for by the biotic variables after partialling out the influence of habitat variables with partial CCA (obtained from a partial CCA relating endemic species with the exotic species after using the habitat variables as covariables). Each component of variation was obtained by dividing the canonical eigenvalues of a particular CCA (or partial CCA) by the total inertia, i.e. the sum of all eigenvalues of a correspondence analysis of the endemic species matrix. The 'pure' habitat variation was given by step 3, whereas the 'pure' biotic variation was given by step 4. The total explained variation was obtained with the sum of 1 and 4 or 2 and 3, whereas the variation shared by both habitat and biotic variables was obtained subtracting 3 from 1 or 4 from 2. For each CCA and partial CCA performed, a Monte Carlo simulation test of both the first axis eigenvalue and trace (i.e. the sum of all canonical eigenvalues) was used to evaluate the statistical significance of the associations under analysis (ter Braak 1990; ter Braak and Verdonschot 1995).

Results

Altogether, 780 fishes were collected belonging to six endemic species (Table 1). Of all the species referenced for the Sorraia basin the lamprey, eel, *Anguilla anguilla* and long snout barbel were not encountered though some doubts exist as to the occurrence of this barbel in the Raia stream. Iberian barbel, *Barbus bocagei*, occurred most frequently whereas Iberian roach *Leuciscus alburnoides* was the most abundant in sampling sites (Table 1). Among the exotic species collected (720 fishes), largemouth bass and pumpkinseed occurred most frequently but mosquitofish was the most abundant.

In the global CCA four explanatory variables were selected from the 16 considered; these explained 45% of the total variation in fish assemblage composition (Table 2, Figure 2). The fish community changed in space from assemblages characterised by the high relative abundance of Iberian chub, *Leuciscus pyrenaicus* (specimens < 100 mm TL), Iberian roach (specimens < 100 mm TL), and the smaller size classes of Iberian barbel and Iberian nase, *Chondrostoma polylepis* (specimens < 100 mm TL) to assemblages characterised by the high relative abundance of largemouth bass, pumpkinseed (> 100 mm TL) and barbel above 200 mm in TL. The former assemblages used shallow sites far from downstream dams with some current whereas the latter assemblages used deeper sites closer to downstream dams without current velocity and with abundant floating macrophytes. Assemblages with intermediate sized barbel and nase (100–200 mm TL), the larger size classes of roach and chub (100–193 mm TL), common carp and mosquitofish were associated with sites presenting transitional environmental characteristics. Assemblage composition was significantly associated with the selected environmental variables, $P < 0.01$ for both the first axis eigenvalue and trace (Monte Carlo simulation with 100 permutations).

Table 2. Summary statistics for the canonical correspondence analysis relating fish species–size combinations to environmental variables in the Raia stream.

	Canonical coefficients		Correlation with canonical axes	
	Axis 1	Axis 2	Axis 1	Axis 2
Environmental variables				
Downstream distance to the nearest dam	0.68*	0.57*	0.59*	0.09
Depth	0.31*	0.70*	−0.38*	0.45*
Current velocity	0.38*	0.01	0.43*	−0.13
Floating macrophytes	−0.51*	0.08	−0.39*	0.08

$^{*}P < 0.05$.

Eigenvalues were 0.54 for the first canonical axis and 0.18 for the second.

In the CCA relating endemic species with habitat factors, from the 16 variables considered for inclusion four were retained by the forward selection procedure and accounted for 42.1% of the variation in endemic assemblage composition (Table 3, Figure 3). Three of the four environmental variables selected in the global CCA were again selected in the ordination of endemic assemblages. The first two axes explained 24.8% of the total variation. As depicted in the biplot, assemblages characterised by the larger size-classes of barbel, Iberian nase and roach were related to sites near downstream dams, with abundant floating macrophytes and low or no flow. In contrast, assemblages dominated by the smaller size classes of these Cyprinidae and Iberian chub were associated with sites far from downstream dams, with some flow. They were also, particularly roach < 50 mm in TL, related to abundant emergent macrophytes. Chub < 100 mm in TL were associated with the highest current velocities available. The association between habitat variables and endemic assemblage composition was significant (Monte Carlo simulation test with 100 permutations).

From the nine variables initially considered in the biotic CCA two were retained for analysis: the abundance of largemouth bass > 150 mm in TL and pumpkinseed < 100 mm in TL. This CCA accounted for 27.2% of the total variation in endemic assemblage composition (Figure 4, Table 3). The first axis (19.8% of the total variation) primarily separated species and size-classes along a gradient that mostly reflected the

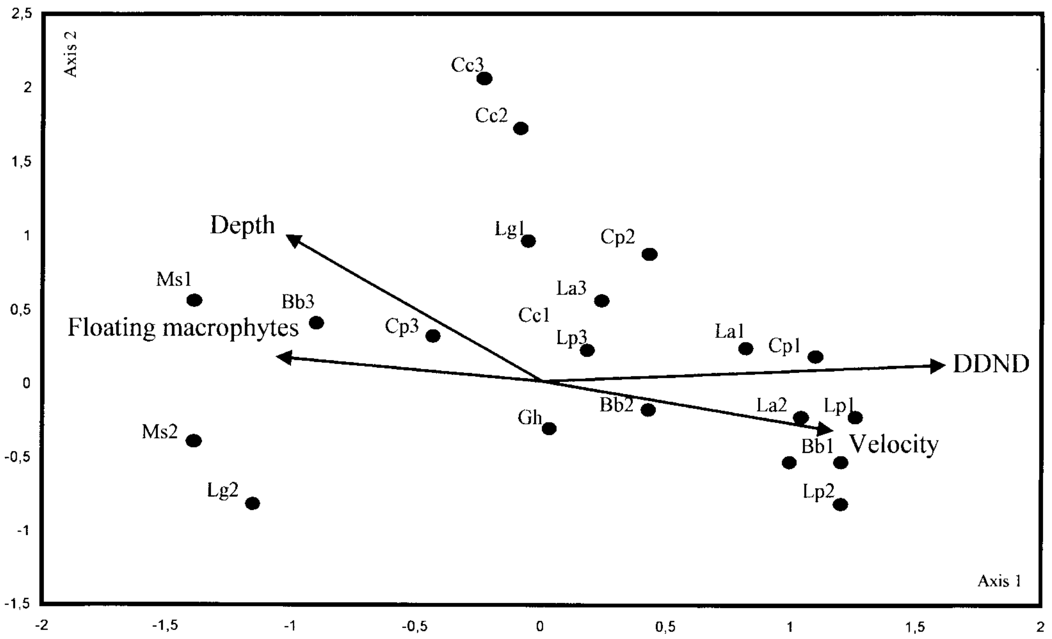

Figure 2. Axis one and two of the canonical correspondence analysis biplot for the fish species–size combinations and environmental variables. DDND is the downstream distance to the nearest dam. The length of an arrow is relative to the importance of that environmental variable in assemblage ordination. The species position on the biplot is a composite of all species–species and species–explanatory variables interactions. The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular explanatory variable. Species codes are given in Table 1.

Table 3. Summary statistics for the canonical correspondence analysis relating endemic species–size combinations to environmental variables and exotic species.

	Canonical coefficients		Correlation with canonical axes	
	Axis 1	Axis 2	Axis 1	Axis 2
Environmental variables				
Downstream distance to the nearest dam	−0.68*	0.28*	−0.69*	0.15
Current velocity	−0.04*	0.43*	−0.27	0.43*
Floating macrophytes	0.43*	0.16	0.30	0.23
Emergent macrophytes	−0.04*	−0.65*	−0.40*	−0.52*
Biotic variables				
M. salmoides > 150 mm (Ms2)	0.70*	0.13	0.78*	0.22
L. gibbosus < 100 mm (Lg1)	−0.20	0.55*	−0.19	−0.74*

*$P < 0.05$.

Eigenvalues were 0.29 for the first axis and 0.17 for the second in the environment CCA, and 0.27 for the first axis and 0.11 for the second in the biotic CCA.

abundance of larger largemouth bass. The second axis was much less informative, explaining 7.4% of the total variation in endemic species abundance. The abundance of exotic species and endemic assemblage composition were significantly related ($P < 0.01$, Monte Carlo test for both the first axis eigenvalue and trace).

The partition performed showed that 54.7% of the total variation in endemic assemblage composition was accounted for by the habitat plus the biotic variables, leaving 45.3% unexplained. The largest portion of the explained variation was pure habitat (27.6% of total variation, significant at $P < 0.01$, Monte Carlo simulation test of both the first axis eigenvalue and trace). The pure biotic component of variation (12.6% of total variation), though smaller than the habitat component, was also significant ($P < 0.03$

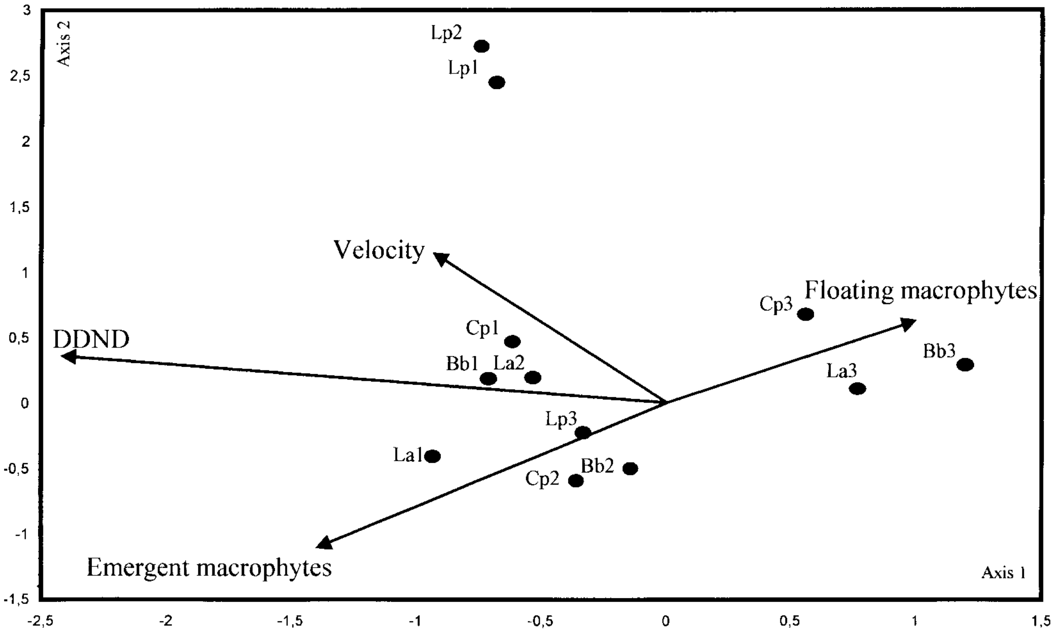

Figure 3. Axis one and two of the canonical correspondence analysis biplot for the endemic species–size combinations and environmental variables.

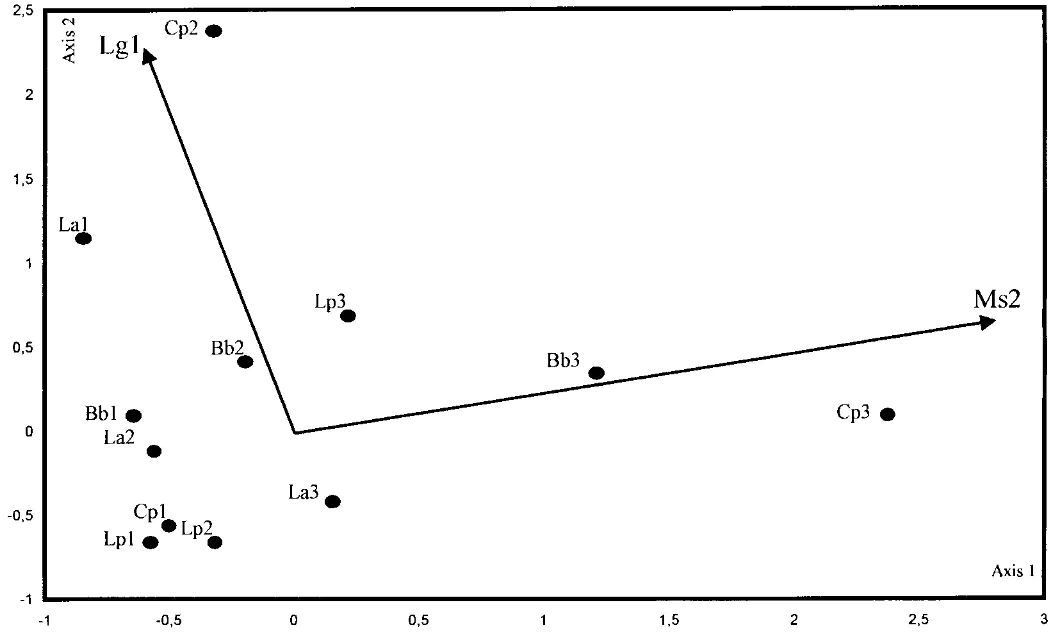

Figure 4. Axis one and two of the canonical correspondence analysis biplot for the endemic species–size combinations and biotic variables.

for both the first axis eigenvalue and the trace). The variation shared by both the habitat and biotic variables accounted for the remaining 14.5% of total variation.

Discussion

Fish assemblage composition varied along the Raia stream according to environmental variables, a widespread feature of stream fish communities (e.g. Angermeier and Karr 1984; Aadland 1991; Lobb and Orth 1991; Pusey et al. 1995; Frenzel and Swanson 1996; Marsh-Matthews and Matthews 2000). Overall, the fish community changed from assemblages dominated by endemic species (Cyprinidae of small average size and the smaller size classes of bigger sized Cyprinidae) to assemblages characterised by the exotic largemouth and pumpkinseed, and the larger size classes of bigger sized Cyprinidae. Native Cyprinidae of intermediate size classes (100–200 mm TL) as well as common carp and mosquitofish characterised assemblages that were somewhat intermediate between these two extreme assemblages. Although studies on the environmental organisation of freshwater fish communities in Iberia are still limited, some of the trends revealed by our analysis were described in other systems (Collares-Pereira et al. 1995; Godinho et al. 1997a). Seemingly, some of the patterns noticed are also consistent with the spatial patterns described in other geographic areas (e.g. Aadland 1990; Lobb and Orth 1991).

The main habitat factor associated with variation both in the global assemblage and only in endemic assemblage composition was the downstream distance to the nearest dam, a possible measure of 'lentic' characteristics. Besides separating riverine from reservoir sites, this variable likely accounted for the longitudinal environmental gradient that can develop in reservoirs from a lacustrine zone, near the dam, to a riverine zone, far from the dam (Thornton et al. 1990). Hence, downstream distance to the nearest dam probably represented a powerful synthetical explanatory variable and its inclusion in the CCA clearly indicates the important influence of reservoirs upon the studied fish community.

For most endemic species there was an inverse relationship between fish size and both downstream distance to the nearest dam and site depth (note that depth was correlated with downstream distance to the nearest dam, $r = -0.74$, $P < 0.01$, and therefore DDND could have acted as a partial surrogate for depth in the CCA of endemic species × habitat variables). This size-segregation could suggest that riverine shallow sites are being used as spawning and nursery grounds by adults that return to the lacustrine deeper environment after spring spawning. In fact, at least barbel and nase are reported to make upstream spring migrations to spawn in other Iberian streams (Rodriguez-Ruiz and Granado-Lorencio 1992). In addition, the lacustrine sites could have been the only habitats providing safe abiotic (e.g. nocturnal oxygen levels) and biotic (e.g. refuge from terrestrial non-gape limited predators) conditions during summer for bigger sized fishes, in particular the large barbel (Schlosser 1987).

Besides separating size-classes within species these factors also segregated species, specifically the largemouth bass and pumpkinseed > 100 mm TL, that were restricted in their occurrence to lacustrine sites and increased their relative abundance towards the dams. Largemouth bass and pumpkinseed are limnophylic species that have been introduced successfully to warmwater reservoirs where they usually establish populations (Heidinger 1976; Zapata and Granado-Lorencio 1993; Moyle and Light 1996; Godinho et al. 1998; Rodriguez-Ruiz 1998). However, these Centrarchidae, in particular bass, apparently have difficulties colonising intermittent streams (Moyle and Cech 1996, Rodriguez-Ruiz 1998). Limitations in (i) available spawning and nursery habitat (e.g. spawning nests are made in protected areas without current velocity, Heidinger 1976; Harvey 1987) and (ii) adult habitat (e.g. adults need sheltered wintering habitats, Carlson 1992; Raibley et al. 1997) may have limited largemouth bass and pumpkinseed distribution within the Raia to the available lacustrine environments.

Assemblage composition was also related to current velocity and the abundance of macrophytes, variables found to be associated with fish communities in other stream studies (Aadland 1991; Collares-Perereira et al. 1995; Godinho et al. 1997a). Plants may be important as food, may increase invertebrate production (particularly submerged and emergent species), may be used as spawning and nursery habitat, and may increase structural habitat complexity (Moyle and Cech 1996; Ross 1997). Both large barbel and nase eat large quantities of macrophytes during summer (Magalhães 1992; Collares-Pereira et al. 1996) and Iberian roach is a phytophil spawner, sensu Balon (1984). On the other hand largemouth bass is frequently associated to areas with abundant macrophytes (Annett et al. 1996). Current velocity could be important for drift feeding fish, such as chub and roach, as well as for the progeny of reophilic spawners, such as barbel and nase (Balon 1984; Magalhães 1993; Coelho et al. 1997).

The abundance of larger largemouth bass was clearly the strongest biotic correlate of endemic assemblage composition and the results of the biotic-CCA suggested a gradient driven by predation. It has also been demonstrated in North-American streams that large *Micropterus* spp. (i.e piscivorous sizes) constrain the spatial use and abundance of vulnerable fish species–size combinations, with prey responses corresponding to the relative vulnerability of prey (e.g. Schlosser 1987; Harvey 1991). With a gape-limited predator such as largemouth bass, prey size is a major determinant of prey vulnerability; smaller Cyprinidae (roach and chub) and smaller size classes of bigger nase and barbel should be more vulnerable than larger size classes of barbel and nase (Hoyle and Keast 1987). On the other hand, water-column dwellers such as roach and chub should be more vulnerable than benthic dwellers, such as *Chondrostoma* and *Barbus*, for a visual predator (Grossman et al. 1987; Schlosser 1987; Harvey 1991). These predictions are consistent with our results. As displayed in the biotic-CCA, the group of endemic species–size combinations farthest from large largemouth bass included small sizes ($<$ 50 mm TL) of all species and intermediate sizes ($<$ 100 mm TL) of water column dwellers. Large sizes ($>$ 200 mm TL) of the two benthic dwellers were the only species–size combinations associated with abundant large largemouth bass, whereas the remaining species–size combinations were positioned between these two groups. Furthermore, the endemic species could be especially vulnerable to predation because they have not experienced any specialist piscivore fish in their recent evolutionary history (Brown and Moyle 1991).

Although this biotic pattern may have been influenced by habitat related sampling biases we suggest that it reflected primarily the influence of largemouth bass. Despite a possible low electrofishing efficiency for small benthic species in deeper reservoir sites (though most areas sampled within reservoirs were $<$ 2 m deep) the predation gradient involved not only nase and barbel but also water column fishes (i.e. chub and roach), which if present in the reservoirs would have been collectable. Moreover, small sized barbel and nase often co-occur with chub and roach in Portuguese streams, suggesting similar habitat requirements (Collares-Pereira et al. 1995; Godinho et al. 1997a, Pires et al. 1999). Sampling conducted with different collection methods (passive nets, counts after complete dry-outs and creel surveys) in other reservoirs in central and southern Portugal has also revealed reservoir assemblages with the absence or extreme low abundance of chub, roach and of the small size classes of barbel and nase (Braband and Saltveit 1989; Godinho and Ferreira 1996; Godinho et al. 1998).

Both exotic species and habitat variables were significant correlates of endemic assemblage composition in the Raia stream. However, habitat variables, rather than exotic species, were the primary factors associated with endemic assemblage composition. The high structuring potential of dams might have favoured the higher relative contribution of habitat variables to endemic assemblage ordination in the study reach. Unregulated southern Iberian streams are highly fluctuating fluvial systems having both occasional winter floods and extended summer drought. The endemic fish fauna has evolved accordingly with life history adaptation such as early maturity, multiple spawning and short life span (Herrera et al. 1988; Herrera and Fernandez-Delgado 1992; Fernandez-Delgado and Herrera 1995). During summer flow frequently ceases and streams become a succession of harsh desiccating sites. Dams have largely disrupted this natural flow variability by blocking longitudinal movement and creating lacustrine habitats upstream dams, and by altering river flow downstream dams. Migratory species are usually the first affected by the loss of longitudinal connectivity (Granado-Lorencio 1991). Sea lamprey, *Petromyzon marinus*, and eel occurring in the Sorraia basin were not collected in the Raia stream (Magalhães 1993). Downstream dams having strong impacts upon fish communities have been described in other areas (e.g. Brittain and L'Abée-Lund 1995) but according to the analysis performed, dam impact upon assemblage composition in the Raia stream operated mainly by the lacustrine environments created in reservoirs. Though very likely different from the pre-damming situation (unfortunately not known), asemblages below the dams of the three small reservoirs were characterised by endemic species during summer, whereas in the reservoirs exotic Centrarchidae predominate. This pattern appears to be similar to that in other southern Iberian streams where assemblages in reservoirs are dominated by exotic species, particularly Centrarchidae, but downstream from dams native assemblages are able to persist (Godinho et al. 1997a, 1998; Rodriguez-Ruiz 1998; J. Oliveira unpublished data). Also supporting this pattern is the clear dominance of fish assemblages by native species along the Sorraia main river, that despite strong habitat alterations (banks and river bed linearization, riparian vegetation control and nutrient run-off) is not directly impacted by reservoirs (Collares-Pereira et al. 1995).

Nevertheless, although considerably smaller, the pure influence of exotic species on the endemic community was significant, i.e. exotic species were related to the endemic community after accounting (statistically) for the effects of major habitat variables. In addition, more than half of the variation in endemic assemblage composition accounted for by the abundance of exotic species was simultaneously accounted for by the habitat variables, i.e. both CCA were partially redundant (Borcard et al. 1992). This shared variation might have come about due to the effects of habitat mediated biotic interactions (chiefly predation by large largemouth bass) on the endemic assemblages, but also to some other spurious effect of an extraneous variable, not included in the analysis (Borcard et al. 1992). Environmentally mediated biotic interactions may occur when a predator restricts its prey to a particular habitat (Harvey 1991) or when a particular type of site is associated with the absence of a particular exotic species and the presence of an endemic species or assemblage (Meffe 1984). Clearly, in the Raia stream the intermittent conditions provided by riverine sites should have prevented bass presence (and thus its influence upon endemic species) in riverine sites far from downstream dams during summer. Elsewhere, the limitations placed by the environment upon introduced fish are apparently crucial for their relative influence upon native communities (Meffe 1984; Moyle and Light 1996).

Exotic species and habitat variables together accounted for 54.7% of the total variation, but left a fairly high portion unexplained. However, the analytical methods used herein cannot discriminate between potentially explainable variation and true stochastic variation, presumably high in such a variable system (Borcard et al. 1992). Moreover, factors that can be important structuring stream fish assemblages, such as invertebrate food abundance and the presence of terrestrial predators were not measured, and they could have accounted for some of the unexplained variation. Nevertheless, the total variation explained in this study exceeds many values reported in other direct gradient multivariate studies relating various ecological descriptors to explanatory variables (Borcard et al. 1992; Magnan et al. 1994; ter Braak and Verdonschot 1995; Poizat and Pont 1996; Godinho et al. 1997a,b, 1998, 2000)

Although the present results appear to have ecological significance they should be viewed with caution. This study is observational (sensu Rodriguez and Magnan 1995) and variables were selected by a forward selection procedure on the basis of variation explained and statistical significance (ter Braak and Verdonschot 1995). Accordingly, interpretation of the results should be regarded only as tentative requiring subsequent verification and if possible experimentation (Magnan et al. 1994; Rodriguez and Magnan 1995).

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