

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	56	4	647–657	2008
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Regular research paper

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THE EFFECTS OF SMALL-SCALE IMPOUNDMENTS AND BANK REINFORCING ON FISH HABITAT AND COMPOSITION IN SEMI- NATURAL STREAMS

ABSTRACT: We studied the fish assemblages of thirty one, 2nd–4th order “least-impacted” streams with a varying degree of low-level management in central Portugal, using a standardised survey to document the river habitat. Channel, banks and riparian landuse, described separately according to principal component scores, were significantly related to altitude, slope and management intervention. Species diversity was low, represented by four endemic, four pan-European and one exotic species. TWINSPAN classification distinguished 3 community types, characterised by their dominant species: trout (*Salmo trutta* L.), chub (*Leuciscus carolitertii* Doadrio) and “roach” (*Squalius alburnoides* Steindachner and *Chondrostoma oligolepis* Robalo). Community types were associated with environmental differences with PC Channel scores higher at trout sites compared to other classification groups, whilst PC Bank-1 scores, temperature and conductivity were significantly different at trout compared to “roach” sites. Ecologically important habitat features were, in turn, related to landscape (map-derived) parameters and the extent of channel and bank management. The mis-classification of sites in discriminant analysis was related to management intervention, indicating the potential difficulty in the assignment river-community types for the biological monitoring of fish communities in these stream types.

KEY WORDS: streams, fish, community structure, river habitat, least-impacted, channel management.

1. INTRODUCTION

The EU Water Framework Directive requires member states to describe and subsequently monitor fish, and other community types, as defined by their quasi-pristine hydro-morphological and physicochemical quality elements (2000/60/EC). Due to the history of management intervention in European river systems defining river habitats that can be considered quasi-pristine (i.e. with nothing more than ‘very minor’ human disturbance) represents a critical process for implementation with inevitable compromise of desirable criteria (Nijboer *et al.* 2004, Furse *et al.* 2006). Ideally, such compromise should be ceded for habitat features that are considered to be of lesser ecological importance and typically relate to the wider river catchment (e.g. land use). However, in rural Mediterranean regions, with summer droughts and winter floods, historical management practices have often focused directly on the river habitat (Hamdy *et al.* 1995), manifest in a high frequency of small-scale impoundments and reinforced banks associated with subsistence farming practices.

The assignment of reference conditions in Portugal has been met by a systematic evaluation of candidate sites (Oliveira and Cortes 2006, Chaves *et al.* 2006). Despite its potential ecological importance, the widespread occurrence of damming and channelization in the river systems of central Portugal led Chaves *et al.* (2006) to conclude that these modified sites should be included in reference assignment. With an ecological interpretation based on invertebrate communities they were able to avoid sample collection from locations with modified physical habitats, however, the almost universal presence of management intervention in close proximity to sample sites led them to acknowledge their 'indirect' effects on ecological reference conditions. As fish communities are associated with larger areas, it is appropriate to collect biological samples over a larger spatial scale that may include modified channel and bank characteristics within the sampling reach. In the face of such pragmatism it is important to both describe the habitat change these modifications entail and to evaluate their ecological influence.

Previous studies of fish communities in Portuguese river systems have indicated the importance of catchment scale parameters as descriptors of community organisation (e.g. Godinho *et al.* 1998, Godinho *et al.* 2000, Pont *et al.* 2006). Because fish are affected by both large-scale and small-scale processes (Mesquita *et al.* 2006), there is a need to describe communities according to phenomena at both the reach and catchment scale (Oberdorff *et al.* 2001, Eros and Grossman 2005, Pont *et al.* 2005). Where

hierarchical relationship are evident between landscape and river habitat features (sensu. Frissell *et al.* 1986), it may be possible to describe ecological variation according to large-scale, map-derived variables (e.g. Pont *et al.* 2006). However, river regulation tends to alter the expected sequential changes associated with the hierarchical organisation of lotic habitats (Stanford and Ward 2001) and may reduce the relevance of large-scale, map derived variables for the modified river habitats that are predominant in central Portugal.

This study is based on a broad-scale survey of the fish assemblages in small (2–4th order) semi-natural hill streams in central Portugal. We applied a standardised habitat survey to detail features of the physical habitat and investigate the relationship between management intervention, the river habitat and fish community structure. This general aim was defined by the particular objectives of: 1) classifying biological variation in terms of respective community types 2) identifying key habitat characteristics associated with ecological variation and assessing the role of channel and bank management as determinants of habitat structure, 3) investigating the potential hierarchical relationship between reach-scale (survey-derived) and catchment scale (map-derived) descriptors.

2. STUDY AREA

The study was conducted in the Vouga and Mondego river basins draining an area of 3,635 km² and 6,645 km², respectively, before discharging into the Atlantic (Fig. 1).

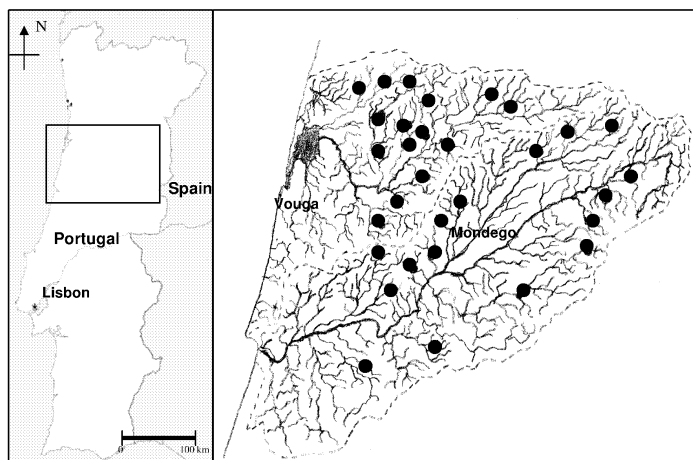


Fig. 1. Location of the study area showing the distribution of sample sites in the river catchments of the Vouga and Mondego, Central Portugal.

These adjacent catchments are characterised by siliceous bedrock in their upper and middle reaches with calcareous geology in their lower reaches. The Mediterranean climate is strongly influenced by the Atlantic with wet winters and dry summers. Annual precipitation varies with altitude and is highest in mountainous areas (average: 2800 mm year⁻¹) and lower in costal areas (average: 1200 mm year⁻¹), almost three-quarters of the annual precipitation falls between October and March presenting an annual discharge regime that is strongly seasonal. Commercial agricultural production is mainly located in the lowland regions with major urban development concentrated in costal areas. Extensive eucalyptus plantation and to a lesser extent pine forest dominate land use in upland areas giving way to moor and scrub at higher altitudes with agricultural production in upland areas limited to small-scale subsistence production (Abelho and Graca 1996, Ferreira *et al.* 2006).

3. MATERIALS AND METHODS

Fish surveys were conducted at 31 sites. Site selection targeted relatively small, discrete catchments to provide statistically independent streams and simplify interpretation at the catchment scale. Further discrimination was provided by “least-impacted” criteria. Initial selection was based on the inspection of 1:50,000 topographical maps, excluding streams close to urban development. The presence of potential impacts was assessed prior to fish surveys by conducting a visual survey and a preliminary bank side analysis of macroinvertebrate indicator taxa collected from riffle habitats, based on the Iberian modified Biological Monitoring Working Party (BMWP) system (Alba-Tercedor and Sanchez-Ortega 1988), rejecting streams with an average score per taxa ≤ 7 .

Survey sites ranged from 2nd to 4th order (Strahler 1952). Despite the criteria of “least-impacted”, evidence of channel and bank management were common with 38% demonstrating channel modification (damming) and 80% with evidence of bank modification. These management alterations were generally built with alluvial material, typi-

cally represented by a wall of large boulders across the channel and/or reinforcing the banks. Channel weirs tended to be low, less than 1m high, whilst the walled banks were variable in height and location, constructed either adjacent to or set back from the wetted stream channel.

Surveys were conducted in August 2004 during the summer low-flow period to coincide with low waters and environmental conditions that were naturally stressful for the fish community. Fish samples were collected from a delineated reach, not less than 40 m, that was representative of the site, i.e. inclusive of respective habitat diversity. Survey reaches were isolated to restrict fish movement using stop-nets and/or exploiting discontinuities (natural/artificial) associated with existing channel features. At dammed sites surveys were conducted in the more natural channel habitat below dams, however, in some cases (associated with extreme dewatering) the only viable fish habitat was the still waters retained behind dams, in such instances the upstream section was fished. Fish were sampled using portable 300w AC electrofishing equipment. Electrofishing was conducted in an upstream direction with multiple passes ($\times 3$) to permit estimates of fish density. Fish were processed on the bank side with identification based on Pereira (1994), Maitland (2000) and Coelho *et al.* (1998) before being returned to the stream.

Details of the physical habitat relevant to fish production were recorded using a modified version of the salmonid habitat survey, HABSCORE (based on details of channel dimensions, flow character, in-stream and out of stream cover; Wyatt *et al.* 1995), whilst general details of the banks, riparian zone and catchment land-use were documented according to the River Habitat Survey (RHS, Environment Agency, 1997) modified for use in Portugal. Surveys were based on a series of transect observations made at spot checks 10 m apart recording habitat features of the channel (e.g. substratum, flow regime), bank (e.g. bank material, character) and riparian zone (vegetation structure) according to both measured (width, depth, etc.) and descriptively defined categories (substrate size, flow patterns, etc.). Additional catchment-scale

attributes such as slope, altitude and stream link magnitude (representing the sum of all 1st order streams above the sampling site; Shreve 1966) were derived from 1:50,000 topographical maps (Instituto Português de Cartografia e Cadastro).

Parameters of water quality were recorded on site using portable meters (pH, temperature, conductivity). Water samples were collected at the same time as fish surveys, frozen and later analysed in the laboratory for nutrients: nitrogen (nitrate and nitrite) and phosphorus (phosphate).

Structural characteristics recorded by habitat surveys were reduced to key variates to describe major habitat trends between sites. Recorded characteristics were generalised by calculating mean values for spot check features. Categorical variables were coded as dummy variables with fuzzy coding used to describe variation in classifications (Lepš and Šmilauer 2003). Index values were calculated from key structural features to describe heterogeneity associated with longitudinal variation between spot-checks. Major changes in habitat characteristics across sites were described in terms of principal components (PC's) following ordination by Principal component analysis (PCA). By excluding slope, altitude and the extent of management intervention from ordination analysis the resultant PC's were limited to expressions of habitat characteristics. Habitat characteristics were separated into features describing the channel, banks, or riparian and catchment land-use to evaluate their respective importance and compare the mutual relationship between these components. The relationship between major PCA axes and potential deterministic parameters were investigated by Pearson's product-moment correlation.

Fish densities were estimated by the iterative calculation formula of Carle and Strub (1978). Community data were subsequently classified using TWo-way INDicator Species Analysis (TWINSPAN, Hill 1979), a hierarchical divisive cluster analysis, grouping sites on the basis of global similarities (Jongman *et al.* 1995). Classification was based on the estimated relative abundance of taxa so that stream types identified by TWINSPAN reflected structural differences according to relative dominance.

Ecological differences distinguished by TWINSPAN were investigated in relation to environmental variation by one-way analysis of variance applying the Tukey-Kramer range test ($\alpha=0.05$) for pair-wise comparison of group means. Multiple discriminant analysis was used to assess the scope for habitat parameters to predict sites to their respective TWINSPAN groups, comparing the success rate of key environmental variables measured at the local (habitat PC's, water quality, etc.) and catchment (slope, altitude, distance from source) scale.

4. RESULTS

Sites ranged in altitude from 90 m to 1,040 m above sea level with slope ranging from 2.9° to 36.9° (Table 1). In general ionic content of streams waters were low with conductivity ranging from 36.6 to 230.0 μSm^{-1} with only four streams registering above 100.00 μSm^{-1} . Nutrients concentrations were low with nitrate ranging from 0.120–1.94 mg l^{-1} , nitrite from 0.02–0.031 mg l^{-1} and orthophosphate from 0.0–0.25 mg l^{-1} . Two sites, both tributaries of the Mondego river, were fishless and excluded from all subsequent analysis.

4.1. The river habitat

Table 2 summarises the major transitions in habitat features across sites in terms of the river channel, riverbanks, and riparian and catchment land-use. The proportion of overall variation explained by the primary axes varied depending on the habitat component. The first PC axes described the majority of the variation for both channel structure and land use, accounting for 62% and 96% of their respective variability across sites. Whilst the first axis captured over half the variation in bank structure, the second incorporated a further 23% and was therefore considered a useful parameter of environmental change across sites (Table 2). The relationship between the principal axes and key environmental parameters are described in Table 3 in terms of their coefficients of Pearson product-moment correlation.

Significant differences were associated with the sub-set of 11 sites where chan-

Table 1. Summary of key environmental parameters (mean value and range) for the 29 tributary streams of the River Mondego and River Vouga supporting fish communities.

Key parameters	Streams size (number of streams)		
	2nd order (3)	3rd order (13)	4th order (13)
Altitude (m)	226.0 (100–323)	306.1 (120–1040)	349.1 (90–600)
Slope (°)	15.6 (14.6–17.2)	18.05 (5.7–36.9)	13.4 (2.9–31.0)
Width (m)	1.92 (1.44–2.82)	2.01 (0.72–2.59)	2.75 (1–5)
Conductivity ($\mu\text{S m}^{-1}$)	50.0 (43.4–60.97)	100.4 (37.7–189.5)	71.3 (20.3–106.2)
Temperature (°C)	16.2 (15.4–17.25)	18.3 (15.9–24.7)	18.8 (16.2–25.2)
Phosphate (mg l^{-1})	0.006 (0.00–0.010)	0.054 (0.00–0.54)	0.009 (0.00–0.070)
Nitrate (mg l^{-1})	0.23 (0.18–0.31)	0.65 (0.21–1.94)	0.68 (0.12–1.53)

Table 2. Summary of the major transitions in habitat features for the channel, banks and land use described according to Principal Component Analysis. Percentages heading columns describe the variation explained by respective axes, values in parentheses are the axes weighting of the respective selected variables.

Channel-1 62%	Banks-1 56%	Banks-2 23%	Land-1 96%
Bedrock (0.99)	Bank top width (0.85)	Vegetation with high structural diversity (0.76)	Moorland heath (0.92)
Boulder cobble cover (0.88)	Bank height (0.67)	Eroding cliff (0.54)	Fertilized grassland (0.72)
Depth (0.63)	Vegetated side bars (0.49)	Composite structure (0.40)	Unfertilized grassland (0.51)
Flow diversity (0.55)	Height variation (0.20)	Undercut (0.34)	Tilled land (0.33)
Emergent vegetation (-0.28)	Profile variation (-0.26)	Stable cliff (-0.19)	Eucalyptus plantation (-0.39)
Floating leafed vegetation (-0.41)	Gentle banks (-0.44)	Vertical banks (-0.48)	Broadleaf woodland (-0.57)
Gravel+pebble (-0.67)	Diverse material (-0.64)	Vertical + toe (-0.58)	Vegetation with high struc- tural diversity (-0.66)
Embeddedness (-0.84)	Side bars (-0.79)	Large bank material (-0.73)	Overhanging branches (-0.81)

nel damming was present with Channel PC scores significantly higher for surveys conducted below dams compared to those conducted above dams ($F_{1,9}=7.50$, $P=0.023$). Primary variation in bank characteristics was significantly correlated with altitude, whilst

secondary variation was negatively correlated with slope and positively correlated with stream size expressed as stream order. A significant relationship was also evident for sites including dammed channels with Bank-1 scores significantly higher for sur-

veys conducted below dams compared to surveys conducted above dams ($F_{1,9} = 5.83$, $P = 0.039$). Features of the terrestrial environment described by Riparian/Land-1 were strongly correlated with altitude (Table 3). Characteristics of channel, banks and land-use described by PCA were significantly correlated (Table 4).

4.2. Fish community

Species richness was low, varying from 1 to 6 across sites with a total of nine species recorded. In general ecological differences across sites were characterised by variation in the five widespread species *Anguilla anguilla* (L.), *Squalius alburnoides* (Steindachner 1866), *Chondrostoma oligolepis* (Robalo 2005), *Leuciscus carolitertii* (Doadrio 1988) and *Salmo trutta* (L.) with no apparent differences in geographic distribution between river basins (Vouga River versus Mondego River). Of the remaining, rare species, *Gobio gobio* (L.) and *Lampetra planeri* (Bloch 1784) were recorded from a single site in the Mondego basin as was *Cobitis taenia* (Linnaeus 1758), whilst *Chondrostoma polylepis* (Stein-

dachner 1864) was restricted to single site in the Vouga basin.

The three community types classified at the second division of TWINSpan classification are summarised in Fig. 2. The principal dichotomy distinguished sites characterised by either cyprinids (group 1) or salmonids (trout, group 2). Further classification separated cyprinid communities into those dominated by either “roach” (*Squalius/Chondrostoma*, group 3) or chub (*Leuciscus*, group 4). These biological classifications were associated with environmental differences between groups. Temperature and conductivity were significantly lower in group 2 compared to group 3 ($F_{2,26} = 3.99$, $P = 0.031$ and $F_{2,26} = 3.65$, $P = 0.04$ respectively). Channel-1 scores were significantly higher for group 2 sites compared to groups 3 and 4 ($F_{2,26} = 7.60$, $P = 0.003$, Fig. 3a). Similarly Bank-1, was significantly higher for group 2 sites compared to group 3 ($F_{3,95} = 3.95$, $P = 0.032$, Fig. 3b). Of the map derived variables slope, measured over 10 km, was higher for group 2 compared to group 3 ($F_{2,28} = 4.09$, $P = 0.029$).

Discriminant analysis based on the key site-survey details (Channel-1, Banks-1,

Table 3. Pearson's product-moment correlation between map-derived parameters and the extent of bank management recording during on-site surveys, see text for details. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Habitat parameters	Altitude	Slope (1km)	Distance from source	Stream order	Bank management
Channel-1	0.657***	0.558**	-0.055	0.092	-0.474**
Banks-1	0.434*	0.333	0.064	0.287	-0.149
Banks-2	-0.036	-0.448**	0.276	0.541**	-0.154
Riparian/Land-1	0.637***	0.267	-0.097	0.168	-0.169

Table 4. Pearson's product-moment correlation describing the mutual relationship between habitat parameters described according to principal component analysis. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Habitat parameters	Channel-1	Banks-1	Banks-2
Banks-1	0.448**		
Banks-2	-0.210	0.000	
Riparian/Land-1	0.429*	0.350	-0.246

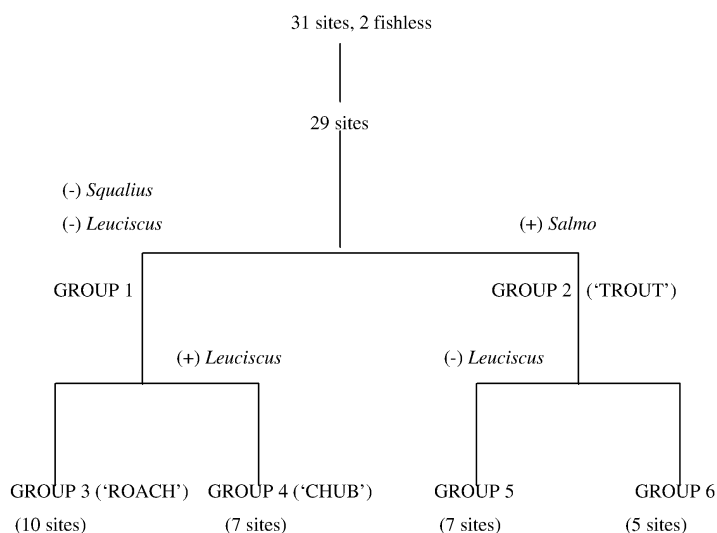
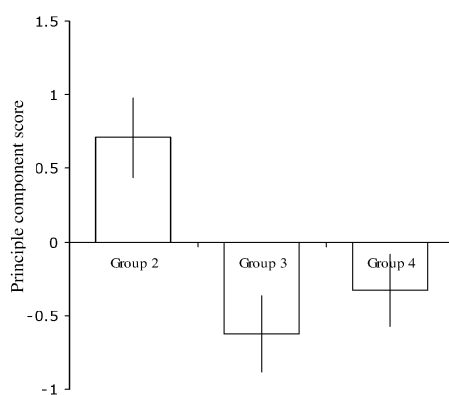


Fig. 2. Dendrogram of site classifications according to TWINSpan, fish community types used in comparative analysis are characterised by their dominant taxa.

A. Channel-1



B. Bank-1

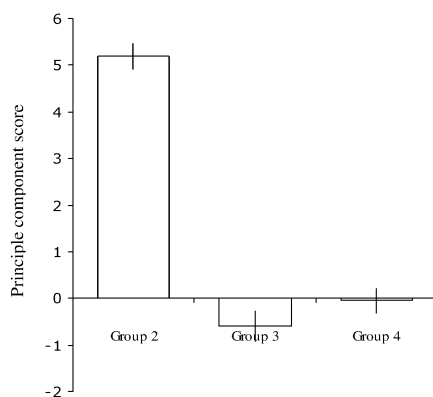


Fig. 3. Mean value for descriptors of the physical habitat summarised according to principal component scores: A. channel features, B. bank features for sites grouped according to TWINSpan classification. Error bars represent 1S.E.

conductivity and temperature) produced an overall success rate of 79%, with 83% of trout sites, 71% of chub sites and 80% of “roach” sites allocated to their correct TWINSPAN group. Basing the discriminant model on the most important map-derived variables (slope, altitude, distance from source) achieved an overall success rate of 59%, with the classification of chub sites falling to 29%, with 67% and 70% of trout and “roach” sites correctly classified. Including bank modifications (as a continuous variable representing the frequency of walled sections in spot checks) and dams (as a nominal variable: present-upstream, present-downstream or absent), increased the overall classification rate of map-derived variables to 72% with respective community types at 75%, 71% and 70% for trout, chub and “roach” respectively. Examining site mis-classifications revealed that 17% of the mis-classified sites based on survey-derived data included a dammed channel. However, 42% of mis-classifications were dammed sites when the model was based on map-derived variables. The improvement in classification success achieved by including parameters of management intervention alongside map-derived variables was associated with a change in the percentage of mis-classified dammed sites, falling to 25%.

5. DISCUSSION

In this first documented broad-scale survey of the fish assemblages of central Portugal almost half the species encountered were endemics (Calandino roach, *S. alburnoides*, Portuguese roach *C. oligolepis*, Iberian nase, *C. polylepis*, northern Iberian chub, *L. carolitertii*), with the remaining proportion represented by four pan-European species and one exotic. The low taxonomic diversity both within and between sites conforms to a general pattern observed in previous broad-scale surveys in both northern and southern regions of Portugal (e.g. Godinho and Ferreira 1998, Cortes *et al.* 1999, Magalhães *et al.* 2002a) reflecting the relatively impoverished species pool of the Iberian peninsula composed of relatively few native species and a high proportion of endemics (Elvira 1995, Godinho *et al.* 1997).

In general species diversity is highest in the Mediterranean river systems of the south where exotic taxa constitute a considerable portion of the species pool (e.g. Collares-Pereira *et al.* 2000). Whilst published information is limited, it is suggestive of a geographic pattern described by a declining incidence of exotics in river systems towards the north (Cortes *et al.* 1999, Penczak and Formigo 2000, Santos *et al.* 2004). A total of 12 exotic taxa have been recognised as naturalised in Portuguese freshwaters (Almaça 1995) with previous studies demonstrating that their success is improved by river regulation (Elvira 1995, Godinho *et al.* 1998, Cortes *et al.* 1999, Penczak and Formigo 2000, Santos *et al.* 2004). The distribution and abundance of exotics in Portuguese rivers varies with spatial scale: at the catchment scale alien taxa tend to be more common in the principal river channel and at the reach scale in pool habitats, whilst native species typically dominate the smaller, unregulated tributaries at the catchment scale and run-glide habitats at the reach scale (Godinho and Ferreira 1998, Pires *et al.* 1999, Magalhães *et al.* 2002b). Fish surveys in this study were based on a stratified sampling strategy inclusive of all habitat types, with site selection restricted to small tributaries feeding the Vouga and Mondego river systems with limited, small-scale management intervention. The low incidence of exotic taxa (one species, at one site) suggest that these streams conform to the generalised pattern of native-exotic taxa at the catchment scale and indicates that despite the widespread occurrence of physically altered habitats these impacted streams were not biologically degraded in terms of introduced fish species.

Ecological differences distinguishing community types were based on species turnover of the 5 dominant taxa with an apparent restricted distribution for trout and, to a lesser extent the Caladino and Portuguese roach. The ecological differences between trout and cyprinid type communities were associated with significant differences in a number of environmental factors. Whilst it is therefore difficult to attribute causal factors evidence from previous research indicates that temperature was probably a decisive factor with trout growth limited to

4–19.5°C and egg development 0–15°C (Elliott 1982, Crisp 1989). Thus, the “roach” sites (Group 3) would have precluded trout growth. In addition, the significantly higher channel-1 scores at trout sites describe aerated waters, coarse benthic substrate and an absence of channel vegetation, corresponding to the autecological requirements of trout in relation to spawning habitat and dissolved oxygen (Elliott 1994). Whilst geographically restricted to the rivers above 39°N (Coelho *et al.* 1998) the northern Iberian chub, *L. carolitertii* D., inhabits sites of contrasting lotic character (Cortes *et al.* 1999, Santos *et al.* 2004). Similarly the endemic “roach” *C. oligolepis* R. and *S. alburnoides* S., have been documented from a wide range of environmental conditions throughout their geographic range (Collares-Pereira 1989, Martins *et al.* 1998, Cortes *et al.* 1999, Pires *et al.* 1999, Santos *et al.* 2004). Trout, in contrast, tend to be most frequently encountered in the smaller tributaries of the northern river systems (Cortes *et al.* 1999, Santos *et al.* 2004).

Acknowledging that the functional relationship between river organisms and the river habitat incorporates a range of spatial scales the HABSCORE model, in common with predictive models for other lotic communities, employs environmental descriptors at both the reach and catchment scale (Milner *et al.* 1998, Wright *et al.* 2000, Tison *et al.* 2005). The strong correlation between habitat characteristics with altitude and slope in these Portuguese rivers lends support to the hierarchical deterministic model of Frissell *et al.* (1986) and parallels the findings from more comprehensive studies of lotic habitat structure in other European countries (Fox *et al.* 1998). The goal of describing ecological communities from catchment-scale, map-derived variables not only reduces costs associated with assessment but, moreover, provides a safe-guard against incorporating degraded habitat conditions, that might be implicit within reach-scale surveys, in the derivation of ecological expectations (Raven *et al.* 2002).

Whilst the frequency of dammed sites amongst mis-classifications indicates that the predictive capacity of map-derived variables would be improved for a dataset based exclu-

sively on non-modified rivers, the improvement achieved by including management intervention as a predictor variable indicates that channel damming disrupts the hierarchical relationship between catchment and reach-scale variables, and their associated ecological communities, in a consistent and predictable manner (Standford and Ward 2001). The lack of correlation between bank management (expressed by the frequency of artificially walled banks) and Bank PC scores indicated that overall bank management was relatively uncommon at spot-checks and that its presence appeared have a minimal effect on adjacent, unmodified banks. The extent of bank modification and its strong correlation with channel characteristics have important relevance to the criteria used to define reference conditions. Whilst management intervention alters the form and often the material of river-banks, bank management and the multivariate descriptors of bank character were not correlated. Under the dynamic forces of lotic geomorphology river channels, banks and riparian zones are mutually determined (Robert 2003), as indicated by their significant correlation in these streams. Thus respective habitat components, such as river banks or riparian landuse, may exercise an indirect effect on the fish community mediated through their influence on channel morphology and discharge. Despite the relatively minor extent of bank management within the surveyed reaches, its statistical association with channel habitat is suggestive of a proportionately magnifying effect on the overall river habitat. Given the strategic motivation for selective bank management it is not, perhaps, surprising that this type of small-scale intervention should be focused on particular sensitive areas with high stream energy. However, the potentially ramifying effects of such small-scale modifications present complex caveats for accepting minor modifications in the designation of rivers as semi-natural (e.g. Raven *et al.* 1998).

ACKNOWLEDGMENTS: We thank Abel Ferreira for technical help with field and lab equipment, Victor Vingada for assistance with fish taxonomy and António José Nogueira for help and advice on statistical analysis and software packages. This research was supported by the

Fundação para a Ciência e Tecnologia, Ministério da Ciência e do Ensino Superior.

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Received after revising July 2008