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CHARACTERIZATION OF SPANISH PYRENEAN STREAM HABITAT: RELATIONSHIPS BETWEEN FISH COMMUNITIES AND THEIR HABITAT

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ABSTRACT

Spanish Pyrenean streams are characterized by extreme summer drought and torrential flows during spring snowmelt and their fish communities are dominated by trout at high altitudes and by barbel in the lower reaches. The Instream Flow Incremental Methodology (IFIM) was adapted to analyse the fisheries habitat of Spanish streams. Parameters were developed that measure the particular characteristics of these streams, taking into account the habitat needs of the main developmental stages (adults, juveniles, fry and spawning) in different seasons. For this analysis 'potential habitat' was defined as that determined by hydraulics and geomorphological features. 'Real habitat used' was defined by the fish population characteristics (densities, biomass, age-structure and population dynamics). Habitat complexity was calculated as the diversity of habitats of different developmental stages and different species. Habitat conditions during summer-drought were analysed by the simulation of low flow conditions as measured by gauging stations. Habitat parameters were measured in several stream reaches and compared with the characteristics of the fish populations they supported by multivariate analysis. The results show that fish abundance increases downstream along the river continuum, indicating that the habitat carrying capacity increases downstream. The depth and rock surfaces are the main factors limiting the capacity of the stream to provide refuges. Trout populations are also influenced by submerged macrophytes. This IFIM evaluation of stream habitat was not correlated with fisheries features because factors other than hydraulics appear to limit trout population in the Pyrenean study streams. Hydraulic factors may limit the fish populations during brief periods, but population recovery from these disturbances may take longer than the time available between disturbances events.

KEY WORDS: habitat structure; fish communities; habitat classification

INTRODUCTION

Fluvial ecosystems contain a great diversity of habitats characterized by dynamic and enduring features to which freshwater fish have adapted (Hynes, 1970). From a fisheries point of view stream habitat is seen as the place where fish develop. The habitat needs of a fish population vary with life stage. Therefore habitat can be subdivided into areas for refuge, spawning and egg incubation, fry development areas and food supply. Each species has its own life cycle with distinctive habitat requirements. Consequently, knowledge of the ecological requirements of fish is basic to habitat management; much has been published about the habitat needs of salmonids (Wesche, 1985; Raleigh *et al.*, 1986; García de Jalón, 1992).

One of the most important questions facing the fisheries manager concerns the stability of habitat for fish populations. At the heart of this question is the degree to which habitat structure can be correlated with fish population size and structure. Physical habitat factors are generally more predictable and more easily measured than biological factors and are thus preferable descriptors of streams. The factors that are good

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predictors of fish abundance often limit populations and therefore knowledge of habitat influences on fish populations is essential for fisheries management.

North America has been a focal point for the development and testing of habitat models for predicting salmonid standing stocks. Binns and Eiserman (1979) and Wesche (1980) proposed predictive models for trout biomass. Wesche's model was built around a composite index of cover called the trout cover rating that includes three structural features of streams: (1) instream cover from boulders, rubble and aquatic vegetation; (2) overhead bank cover, including riparian vegetation; and (3) deep water. Several research teams have tested this model or similar models and have found very good to excellent correspondence between cover variables and the biomass of trout (Wesche *et al.*, 1987a; 1987b; Kozel and Hubert, 1989; Platts and Nelson, 1989).

Thus cover has proved to be remarkably successful in predicting the standing stocks of trout in a large number of streams. Most of this model development and testing, however, has focused on a single geographical region: the intermountain west of the USA. Few studies have been conducted in other areas with different hydrological regimes or fishing pressures. An extensive analysis of the relationship of trout biomass to habitat in streams in southern Ontario also identified significant correlations between pools and overhead cover and with trout biomass (Bowlby and Roff, 1986). Nielsen (1986) also found that cover, including undercut banks, riparian vegetation and depth were the best predictors of trout population density in Danish streams. In addition, Bagliniere and Arribe-Moutounet (1985) found that the brown trout of a French river mainly use deeper habitats near overhanging banks.

Fausch *et al.* (1988) reviewed 99 models predicting the standing crop of stream fish from habitat variables and concluded that relatively precise models often lacked generality due to differences in habitats and management practices. Other workers have not found habitat variables predicting the abundance of whole populations, but have been successful at predicting the densities of early stages. The length of stream edge and the area of lateral habitat have been used to predict the abundance of young of the year cutthroat trout (Moore and Gregory, 1988); pools influence the distributions of juvenile coho salmon (Nickelson *et al.*, 1979) and the availability of fry habitat during the emerging period for their respective year class strengths in salmonid populations (Bovee, 1982).

Usually some habitat features predict fish abundance whereas others do not. When habitat features have predictive power, it seems reasonable to hypothesize that 'habitat' is acting as a limiting factor and that fish production is constrained by particular habitat factors. Special attention should be given to identifying those physical factors limiting populations. Examples of habitat 'bottlenecks' in the life history of salmonids are provided by Mason (1976) and by Murphy and Meehan (1991).

In this study, our purpose was to analyse the structure of fisheries habitat in Spanish Pyrenean streams and to test the hypothesis that habitat components may limit stream fish production and biomass. Our objective was to produce a robust, predictive model based on habitat that could be used in the management of the fisheries of these streams.

STUDY AREA

Spanish Pyrenean streams are fluvial ecosystems greatly influenced by torrential flow regimes and show marked fluctuations in water temperature. Both of these factors determine the structure and function of these fluvial ecosystems and the composition of the biota adapted to them. Each fish population in these streams may have developed a particular pattern of distribution across the fluvial habitat. If so, this pattern of occupancy would have two potential dimensions: a spatial dimension, shown by the distribution of fish along the river continuum; and a temporal dimensions, represented by migrations upstream and downstream.

The present study was carried out in three Spanish Pyrenean rivers: Aragón-Subordán, Veral and Osia. The reaches studied in each river start near their sources at 1300 m altitude and end at their confluence with the Aragón River at 615–620 m, a distance of approximately 45 km. The three rivers flow approximately north to south. Their catchments are elongated with areas ranging from 76 km^2 in the Osia River to 358 km^2 in the Aragón-Subordán River.

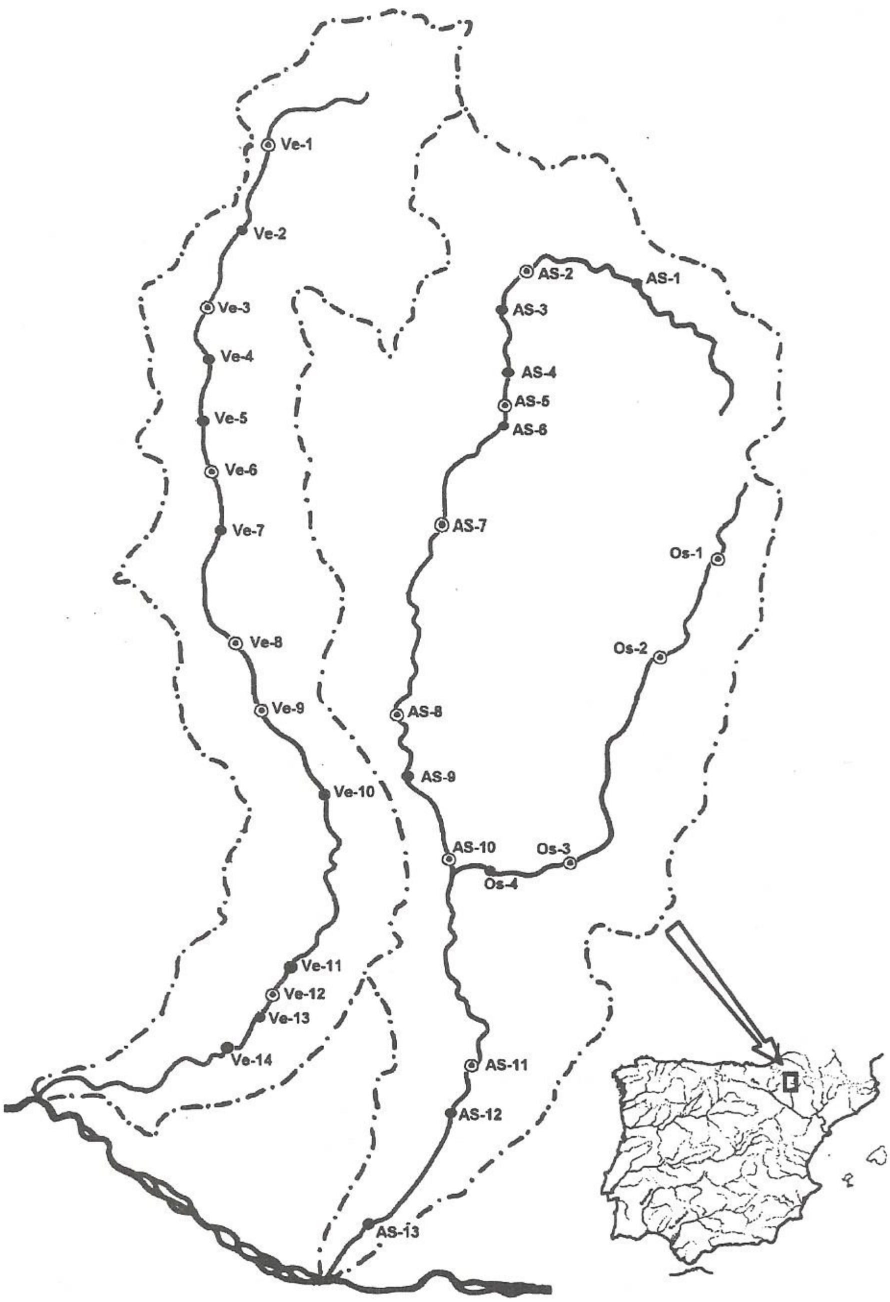

Figure 1. Location of sampling stations for habitat characterization along rivers Veral, Aragón-Subordan and Osia. Fish community quantitative samplings were also carried out at stations with a double circle

Habitat characteristics were measured at 31 sampling sites distributed along the rivers: 13 on Aragón-Subordan, 14 on Veral and four on Osia (Figure 1). Each sampling site included a stream reach 200–400 m long.

METHODOLOGY

The habitat of stream fish can be described in terms of several components. We evaluated habitat through

Table I. Scores of the refuge coefficients

Scores:		0	1	2	3	4	5
Csh	(%)	0	< 0	10–25	25–50	50–75	75–100
Cbk		No	Aereal undercut	Submerged undercut	Deep submerged undercut	Riparian roots	Deep undercut and roots
Cst		Rock surface	Fines	Sand	Gravels	Cobbles	Boulder
Csv	(%)	0	+	1–5	5–15	15–30	> 30
Cde	(cm)	< 15	15–50	50–80	80–100	100–150	> 150

Csh, shadow; Cbk, bank shelter; Cst, substrate type dominance; Csv, submerged vegetation cover and; Cde water depth

the major physical components: substrate, channel morphology and water quality. We also measured special habitat features of potential importance to the fish population, including refuge capacity, food resources and the availability of habitat for each developmental stage of fish.

Physical characteristics

Stream substrate was characterized by its size composition and was determinated by visual estimation as described by Platts *et al.* (1983). We considered the following size classes: fines, $x < 2$ mm; gravel, $2 < x < 200$ mm; cobbles, $200 < x < 100$ mm; boulders, $x > 1000$ mm; and rocky surfaces, $> 4\,m^2$.

The characteristics of channel morphology measured were: mean width, mean depth, slope and pool to riffle ratio. The mean width and depth determine the dimensions of the water column and predominant stream velocities. Stream depth is important in providing fish cover. The channel slope was measured with a topographic level. The pool–riffle ratio measured by the length of a series of riffles divided by the length of their contiguous pools. This ratio indicates the capacity of a stream to provide resting and feeding pools for fish and riffles to produce food and support spawning.

The studied streams were relatively unpolluted and have a similar catchment geology. Therefore we measured only two water quality parameters, water temperature and conductivity, both of which reflect the longitudinal zonation in physical conditions in streams.

Refuge capacity

From a fisheries perspective, the habitat must provide fish with refuge from extreme physical conditions and from predators. We assessed the refuge capacity with a 'refuge index' (RI) that includes several aspects of the stream habitat: shade, bank and substrate refuges, cover of submerged vegetation and water depth. These aspects have been quantified through five coefficients (Csh, Cbk, Cst, Csv and Cde), each ranging from 0 to 5 (Table I). The RI was quantified as a weighted mean of these five coefficients on each site.

Habitat complexity

We used a modification of the Instream Flow Incremental Methodology or IFIM (Bovee, 1982) to measure the capacity of the habitat to meet the needs of different fish developmental stages. The IFIM has been developed to evaluate fisheries physical habitat at different flow intensities and takes into account the habitat needs of the different life stages of fishes. The IFIM has become accepted in USA as a 'standard' method an, even though it has been criticized for reflecting potential habitat only, it remains an effective tool as it incorporates biological and hydrological and geomorphological aspects (see Mathur *et al.*, 1985; Scott and Shirvell, 1987; Orth, 1987).

Our modified IFIM, which is conceptually similar to the original, has been presented elsewhere (García de Jalón *et al.*, 1993; Mayo *et al.*, 1993). The hydraulic simulation model used is based on the determination of water surfaces elevations by Manning's equation for each cross-section. The model is calibrated by adjusting the roughness parameter using two sets of water surface elevations. Suitability curves for depth, velocity, substrate and cover were modified according to indigenous populations. The main differences consist of our using weighted and potential width (WPW) instead of the weighted useful area (WUA) and not using the software PHABSIM (Milhous *et al.*, 1989). We used brown trout, *Salmo trutta*, which inhabits all our sampling sites, as an indicator species and implemented its suitability curves according to the IFIM.

In each sampling reach 10 cross-sections were measured and each section was representative of a certain length of stream. Weighted potential width on each reach was calculated by the weighted mean of the WPW of its cross-sections. In doing so, we obtained the curves that link the potential habitat (WPW) for each developmental stages (adult, juvenile, fry and spawning) with instream flows. The potential habitats at the flow levels at the summertime sampling were recorded for each sampling reach and for each developmental stage (WPWad, WPWjuv, WPWfry and WPWspaw). These measurements were used to characterize the habitat.

A major assumption of the IFIM methodology is that the value of a stream habitat should be greater if is capable of providing for the needs of all the developmental stages of a fish population rather than for just one or two. With this assumption in mind, we evaluated habitat complexity using a habitat diversity index (HDI) using the Shanon–Weaver diversity index

$$\mathrm{HDI} = -\sum ni \times \log_2(ni)$$

where ni is the ratio $\mathrm{WPW}i'/\sum(\mathrm{WPWi}')$ where $\mathrm{WPW}i'$ are the potential habitats of different development fish stages expressed in WPW adults units (WPWad) through a conversion rate similar to that proposed by Bovee (1982)

$$\mathrm{WPW}'\ \mathrm{adult} = 1{\cdot}5 \times \mathrm{WPW\ juvenile}$$

$$\mathrm{WPW}'\ \mathrm{adult} = 4{\cdot}5 \times \mathrm{WPW\ fry}$$

$$\mathrm{WPW}'\ \mathrm{adult} = 9{\cdot}0 \times \mathrm{WPW\ spawning}$$

Stream communities

Benthic macroinvertebrate and fish communities were analysed to evaluate the biological response to habitat features. Biological communities were sampled on 15 stations: Ve1, Ve3, Ve6, Ve8, Ve9, Ve12, AS2, AS5, AS7, AS8, AS10, AS11, Os1, Os2 and Os3.

Benthic macroinvertebrates were sampled in lotic reaches as they are relatively homogenous habitats (which enables better comparisons between streams) and are assumed to be more productive in benthos. A sampling cylinder of $0{\cdot}1\ \mathrm{m}^2$ base area and 0·25 mm mesh net was used. Each quantitative sample consisted of four replicas. Invertebrates were preserved in 4% formalin until sorting and counting. Benthic macroinvertebrates samples were oven-dried at 60°C for 15 hours and densities and biomass (dry weight) were determined for each population.

Fish populations were sampled by electrofishing with direct current using settings of 440 V and 0·2–0·3 A. Two quantitative surveys were made in December 1991 and July 1992. Fish population sizes were estimated during low flow conditions by successive captures at a constant effort in reaches blocked off with nets. Each sampling reach had an area of $500\text{–}1400\ \mathrm{m}^2$ and was fished three times. Fish densities were estimated using the weighted maximum likelihood method of Carle and Strub (1978). Each species population and, when possible, each age-class was analysed separately (Cowx, 1983). Mean biomass and production were calculated following Ricker (1975) and Mahon *et al.* (1979).

Statistical treatments

Stream reaches and habitat characteristics were classified by Twinspan (two-way indicator species analysis). Twinspan is a computer program designed for the classification of ecological communities. Twinspan first constructs a classification of samples and then uses this classification to obtain a classification of habitat characteristics. Twinspan also constructs a key to the sample classification by identifying one to several characteristics which are particularly diagnostic of each division in the classification (Hill, 1979).

Table II. Significant correlations (positive or negative) between habitat parameters and main stream fisheries characteristics

	Fish community		Trout population	
	Production	Biomass	Production	Biomass
Distance to source	‡ (+)	‡ (+)		
Slope	‡ (−)	‡ (−)		
Rocky surface	† (+)			
Depth		* (+)		
Pool/riffle		* (+)		
Temperature			† (−)	† (−)
Submerged vegetation				† (+)
Habitat diversity				† (−)
Benthos	‡ (+)			

* $p < 0{\cdot}1$.
† $p < 0{\cdot}05$.
‡ $p < 0{\cdot}01$.

Twinspan has been considered the best classification technique for complex data matrices (Gauch *et al.*, 1977).

Detrented correspondence analysis or Decorana (HIll, 1979) was used to analyse the ecological gradients of stream habitats and to interpret the classification according to Twinspan. Decorana removes relationships among variable axes and rescales them.

RESULTS

Habitat characterization

The relationships among the habitat parameters analysed are presented in Table II. Classification of sampling reaches together with the classification of parameters from Twinspan analysis are shown in Figure 2. The habitats of the stream reaches analysed are divided into two classes. Type A included all higher elevation reaches (Ve1, Ve2, Ve3, Ve4, Ve5, AS1, AS2, AS3, AS4, AS5, AS6, Os1, Os2 and Os3). This class of habitats is characterized by the following indicator parameter values: distance to stream source <21 km; water conductivity $<265\ \mu$S; and benthic biomass $<0{\cdot}85\ g/m^2$. Type B consisted of lower elevation sites (Ve6, Ve7, Ve8, Ve9, Ve10, Ve11, Ve12, Ve13, Ve14, AS7, AS8, AS9, AS10, AS11, AS12, AS13, and Os4). This group of sites is characterized by $<2\%$ stream channel slope and a low percentage of fine substrate.

Habitats A and B are each subdivided into two subclasses. Subtype A1 consisted of head stream habitats (Ve1, Ve2, Ve3, Ve4, AS2, AS3 and Os1), which were characterized by one or more of the following: habitat

Variable group	Variable	B1							B2										A1							A2						
		AS13	Ve14	AS7	AS8	AS11	Ve7	AS9	AS12	Ve6	Ve9	Ve8	Os4	Ve11	AS10	Ve10	Ve11	Ve13	Ve1	Ve2	Os1	Ve4	AS2	Ve3	AS3	AS1	Os3	Os2	Ve5	AS5	AS6	AS4
B1	distance	5	5	3	4	5	3	4	5	2	4	4	3	5	5	4	5	5	1	1	1	1	1	1	1	1	2	1	2	2	2	1
B1	benthos	5	2	4	3	4	2	3	4	2	5	5	1	5	5	5	2	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1
B1	WPW spaw.	-	5	5	5	5	5	5	2	4	4	5	4	5	4	-	-	1	4	5	-	1	-	4	1	1	3	1	-	-	-	-
B2	gravel	4	5	5	5	5	3	1	1	2	4	4	4	4	5	4	4	3	4	2	3	1	2	1	1	4	4	3	4	1	1	1
B2	Conductiv.	4	4	2	4	4	3	4	4	3	4	4	4	4	3	5	4	4	3	3	1	3	1	3	2	2	4	4	3	2	2	2
B2	P/R	1	3	3	3	3	4	4	4	1	5	3	1	4	5	5	5	4	1	1	4	4	1	5	4	3	1	1	1	1	2	3
B2	temperature	4	4	2	4	4	4	2	3	3	3	2	4	4	4	4	4	4	3	3	1	3	3	2	3	4	4	3	3	3	2	3
B2	hab. divers.	3	3	2	4	4	4	4	4	3	4	3	3	3	3	2	2	4	4	3	2	4	3	4	4	3	3	3	1	3	3	2
B2	width	5	4	4	4	4	4	4	5	4	4	2	3	2	2	2	2	3	1	4	1	4	4	5	4	1	1	2	2	2	2	3
B2	WPW fry	1	4	5	5	5	4	5	2	2	3	3	2	3	1	2	-	2	2	3	4	4	5	4	4	1	2	2	-	4	1	1
B2	WPW juven.	4	4	4	5	5	5	5	2	2	3	2	2	3	2	1	1	3	2	3	1	4	5	4	4	1	1	1	1	4	4	2
A1	coarse	-	1	1	1	1	4	4	5	3	1	5	1	1	1	5	1	5	2	1	1	-	1	5	3	1	1	2	1	5	5	5
A1	Refuge Ind.	1	1	1	4	4	4	4	1	1	1	5	4	3	4	2	5	3	1	1	4	5	5	5	5	2	1	3	4	5	5	4
A1	depth	1	1	1	2	4	2	4	3	2	1	4	1	4	4	2	5	5	1	1	1	3	1	4	3	3	1	3	5	5	5	5
A2	WPW adult	4	1	1	5	5	3	5	2	1	2	3	1	3	2	1	2	4	3	1	1	4	5	4	4	1	1	1	2	5	5	4
A2	slope	1	1	2	1	1	2	1	1	2	1	1	3	4	2	4	1	1	5	3	5	3	4	5	4	3	4	5	2	4	5	4
A2	fines	5	1	1	1	1	-	5	1	1	1	1	2	1	1	2	4	3	1	5	3	5	5	3	4	4	3	1	3	5	5	5

Figure 2. Results of Twinspan classification. The sampling localities are grouped according to their habitat characteristics into habitat types. Also, the habitat variables are classified according to their values on different sampling localities. Numbers in figure represent standarized classes of the variable values

diversity higher than 1·5 bits, pool–riffle rato > 0·8, water channel width < 10 m and WPWfry > 6·5 m. Subtype A2 included stream habitats (Ve5, AS1, AS4, AS5, AS6, Os2, Os3) characterized by > 18 km to stream source. (The inclusion of AS1 in this class is explained by the fact that the Aragón-Subordán River runs from several kilometres from its source along a high plateau). Subtype B1 included stream habitats (V7, V14, AS7, As8, AS11, AS14) characterized by WPWjuv > 11 m. Subtype B2 included stations V6, V8, V9, Ve10, Ve11, Ve12, Ve13, AS10, AS12 and Os4.

Decorana analysis of habitat parameters produced the results shown on Figure 3, where the first axis separates WPWspaw, associated with gravels and benthos, from the other types of substrata. The second axis separates benthos associated with coarse substrata from fine substrata.

Considering the representation of habitat parameters on both axes simultaneously, the greatest positive values include benthos, distance to source and WPWspaw. These are the parameters that Twinspan grouped because they more clearly differentiate type A habitats in the upper reaches of the study streams from the other habitat classes. Habitat parameters with low values on both axes include fines, slope and WPWadult. These are the parameters that Twinspan grouped because they more clearly differentiate type B habitats in the lower reaches.

Once stream habitats were classified, we analysed for associations with characteristics of fish populations and communities. Only the total fish biomass and total fish production showed significant differences between habitat types (Figure 4). These characteristics distinguished type A from type B ($p < 0·01$) and type A1 from type A2 ($p < 0·05$). Habitat type B supports a greater mean fish biomass (16·5 g/m^2) than type A (6·2 g/m^2) and greater fish production (10·8 versus 4·6 $g/m^2/y$, respectively). Within type A, type A2 supports greater fish biomass (10·9 g/m^2) than type A1 (2·7 g/m^2) and greater production (7·5 versus 2·4 $g/m^2/y$, respectively).

Habitat parameter as fishery predictors

Streams in the Spanish Pyrenees support fish communities comprised mainly of brown trout (*Salmo trutta*) and reophilic cyprinids such as barbels (*Barbus graellsii*, *Barbus haasi*), nase (*Chondrostoma toxostoma*) and minnow (*Phoxinus phoxinus*). In head streams and high altitude stream reaches trout are always dominant and are often the only species present, whereas in the lower reaches, cyprinids predominate (García de Jalón, 1992).

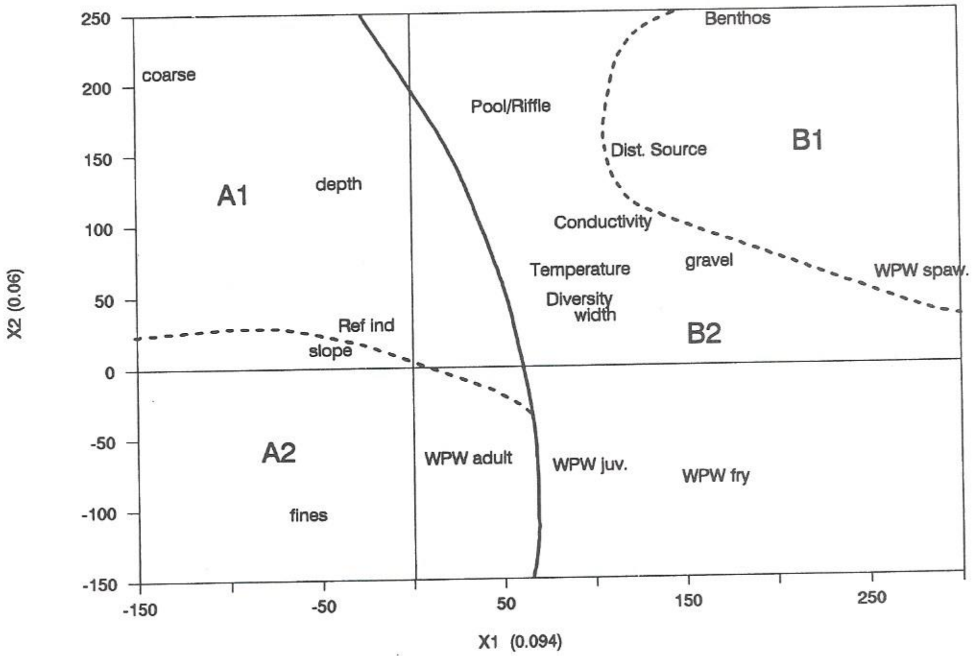

Figure 3. Decorana analysis results are represented in the two main axis. The classification of habitat variables is shown together with their ordination

Once we had analysed the structure and main components of the stream habitats, we examined them for correlations with important fisheries characteristics. We have considered three: production ($g/m^2/y$), biomass (g/m^2) and turnover ratio (P/B $year^{-1}$). We have calculated these parameters for the entire fish community and for trout population alone, as trout are a dominant species in these streams and the most sought after fisheries resource. Significative correlations among variables are shown on Table II.

Total fish production and biomass were both positively correlated ($p < 0{\cdot}01$) with distance to source and negatively correlated ($p < 0{\cdot}01$) with channel slope, indicating a general increase in fish abundance from the headwaters downstream. In addition, fish production was positively correlated with rocky surfaces ($p < 0{\cdot}05$), which is indicative of the periphyton available for grazing fishes and with the biomass of macro-invertebrates ($p < 0{\cdot}01$), another food resource. Fish biomass was also correlated with water depth and pool–riffle ratio ($p < 0{\cdot}1$), both of which are indicators of fish refuge. The turnover ratio was not correlated with any habitat parameter.

The production and biomass of trout were both negatively correlated ($p < 0{\cdot}05$) with water temperature, which reflects the adaptation of trout to cold waters. Trout biomass was also negatively correlated with habitat diversity ($p < 0{\cdot}05$), but positively correlated with submerged vegetation ($p < 0{\cdot}05$). Submerged vegetation may provide a source of food as it shelters large numbers of macroinvertebrates.

The negative correlation with habitat diversity is surprising. Our expectation was that habitats capable of supporting all trout developmental stages would be preferentially selected by trout. We suggest that floods in autumn and late spring favour migration by Pyrenean trout populations, which results in some reaches being occupied preferentially by different life stages.

These correlations were made along the entire river continuum studied. However, trout populations are most important in the upper reaches of the continuum. Therefore, we performed a second analysis which included the high altitude stations only (Table III). This analysis included correlations with total trout production and biomass as well as the biomass of 0+, 1+, 2+ and 3+ age classes.

At the higher altitude stations, trout production was positively correlated with rocky surface ($p < 0{\cdot}01$) and benthic macroinvertebrates ($p < 0{\cdot}1$) and negatively with slope ($p < 0{\cdot}1$). Trout biomass was again

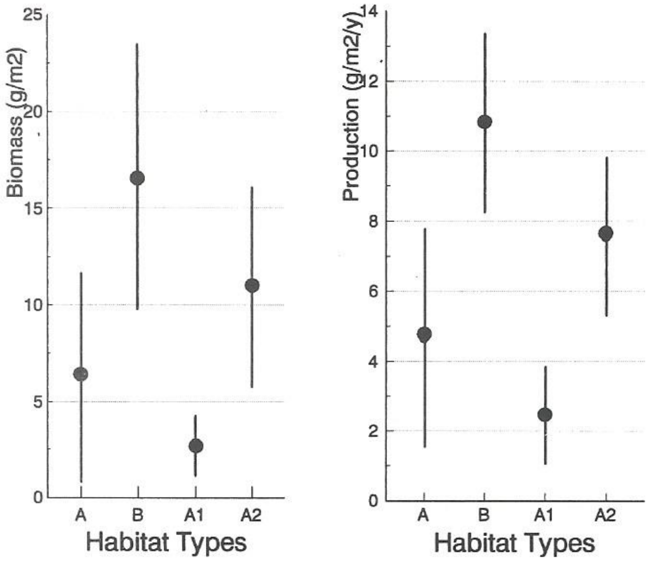

Figure 4. Fisheries characteristics of principal habitat types. Mean values and standard deviation of fishery biomass and their annual production are represented

Table III. Significant correlations between habitat parameters and main trout population characteristics, at high altitude localities

	Production ($g/m^2/y$)	Trout biomass (g/m^2)	0+ (g/m^2)	1+ (g/m^2)	2+ (g/m^2)	3+ (g/m^2)	P/B (y^{-1})
Slope	* (−)						
Rocky surface	‡ (+)						
Benthos	* (+)						* (+)
Depth		† (+)	† (+)	* (+)	† (+)		
Diversity		† (−)			* (−)		
Gravels							‡ (+)
WPW spawning			* (−)				
Submerged vegetation			* (+)				
WPW juvenil						* (−)	

* $p < 0{\cdot}1$.
† $p < 0{\cdot}05$.
‡ $p < 0{\cdot}01$.

Table IV. Statistical characteristics of the regression models for total fish production and biomass

Independent variable	Coefficient	Standard error	*t*-Value	Significance level
Model fitting results for total fish production ($p < 0{\cdot}0005$)*				
Constant	−11·393041	3·522067	−3·2348	0·0079
Benthos	5·326225	2·580107	2·0643	0·0634
Distance to source	7·577638	3·615777	2·0957	0·0600
Model fitting results for total fish biomass ($p < 0{\cdot}0008$)				
Constant	−18·101398	6·9844	−2·5917	0·0236
Distance to source	24·46037	5·513999	4·4360	0·0008

* R-SQ. (ADJ.) = 0·7012; SE = 2·415815; MAE = 1·698754; DurbWat = 1·957.
† R-SQ. (ADJ.) = 0·5896; SE = 5·422800; MAE = 4·059933; DurbWat = 1·323.

positively correlated with water depth ($p < 0{\cdot}05$) and negatively with habitat diversity ($p < 0{\cdot}05$). Trout turnover ratio (P/B y^{-1}) was positively correlated with benthos ($p < 0{\cdot}1$) and gravel substrate ($p < 0{\cdot}01$).

The separate analysis of age groups 0+ to 3+ presented some surprising results. Younger age classes were positively correlated with depth, a well-known refuge for large fish (Beard and Carline, 1991), whereas the oldest age was not. Potential habitat widths were negatively related with their respective age classes: WPWspaw with 0+, WPWjuv with 3+. Factors other than potential habitat widths must control the abundance of trout age classes.

Predictive models

Two linear regression models were fitted to the data to predict fish biomass and production from those habitat variables that were significantly correlated with them. A stepwise selection criteria was applied to the variables. The models obtained are presented in Table IV. Production is predicted by a combination of two variables: distance to source and biomass of benthic invertebrates. The model has an adjusted R^2 greater than 0·70 ($p < 0{\cdot}07$). Biomass is predicted by distance to source and the model has an adjusted R^2 greater than 0·58 ($p < 0{\cdot}03$).

DISCUSSION

The fish community should be considered as an integrated unity that responds to the same habitat features along the river continuum. Our results showed how distance to source and channel slope correlate significantly with both fish community production and biomass. Both variables are indicators of position along the longitudinal gradient of the river continuum. The classification of habitat features into habitat types also differentiated between head stream habitats (A1), intermediate reach habitats (A2) and lower reach habitats (B). We also found that fish production and biomass increase from A1 to A2 and from A2 to B. These downstream increases along the river continuum indicate that the carrying capacity of the habitat increases downstream.

Consistent with these results, our best predictive models for biomass and production includes a single physical habitat variable: distance to source (Table IV). The biomass of benthic macroinvertebrates also made a significant contribution to the production model.

However, not all fish populations increase their biomass and production downstream. The habitat requirements of stream fish vary considerably between species and may show marked ontogenetic and seasonal variations (Swales, 1994). In these Pyrenean streams, species composition is controlled by water temperature, which is also negatively correlated with trout production and biomass. In Mediterranean mountain streams small changes in summer temperature may cause significant shifts in fish community composition (García de Jalón, 1992). However, in the upper reaches where trout populations dominate, other habitat variables (channel slope, rock surface, habitat diversity, macroinvertebrate biomass) were predictive of trout production and biomass.

In analyses of fisheries habitat we can recognize five main components: spawning areas, food production areas, refuge zones, flow regimes and water quality. Fisheries require good spawning habitat. For this, trout, barbels and nase populations depend on the quality and quantity of substrate in their spawning beds, especially gravel substrates (Bear and Cardine, 1991). However, in the present study gravels correlated only with the trout turnover ratio. Apparently spawning habitat does not strongly limit fish populations in our study streams.

Benthic macroinvertebrates are often the most important food resources for river fish. Macroinvertebrate density, biomass and diversity are higher in riffles than in pools (Brown and Brussock, 1991; Logan and Brooker, 1983) and so riffles act as food supply areas. In our study streams we found that the biomass of macroinvertebrates is significantly correlated with total fish production (Table II) and in higher reaches with trout production (Table III). Thus we can consider benthic secundary productivity in riffles as a habitat factor with significant influences on fish abundance.

Refuge areas are those that provide protection from swift currents, high temperatures and predators. This protection may be provided by vegetation, boulders, undercut banks or by depth or turbulence. In our streams, turbulence produces a predominance of white water, whereas riparian vegetation is scarce, specially in summer. In our study streams refuges are provided mainly by depth and rocky surfaces, whereas refuges for trout populations are also provided by submerged macrophytes.

Water quality is mainly unpolluted in the studied streams, but water temperature controls species composition. Stream flow is important to fisheries as it provides an adequate aquatic space for them. Fisheries flow requirements greatly vary with species composition and between seasons depending on the development stages. Life histories are adapted to natural flow regimes that are torrential and poorly predictable.

The IFIM has been developed to evaluate fisheries physical habitat at different flow intensities and takes into account the habitat needs of the different life stages of trout. Our IFIM variables were only significantly correlated with fish population characteristics when we restricted our analysis to higher reaches where trout populations are dominant. Even within these reaches, few features of trout age classes were correlated with IFIM variables (Table III), even though they were created to match the habitat requirements of different life stages. Further, the few significant correlations obtained were opposed to expectations (WPWspaw inversely correlated with 0+ fry and WPWjuv inversely correlated with 3+ cohort).

Fish displacements during high flows and subsequent migration provides a reasonable explanation for these patterns. Fry are especially vulnerable during brief periods that are difficult to observe and measure without continuous recording systems. Population recovery from hydraulic disturbance in these streams may take more time than is available between disturbance events. In other words, the disturbance interval may be shorter than the time required for recovery. Gore and Nestler (1988) have shown that the IFIM evaluates potential stream habitat, but that this habitat may not actually be used by fish because limiting factors other than habitat hydraulics may control their populations.

Finally, we emphasize the importance of our results to fisheries management, especially in regard to the potential enhancement of fish populations with physical habitat improvement. Our results have shown that the refuge capacity for larger fish, which are of the main interest to anglers, is limited by water depth. Depth can be enhanced by the construction of small transverse dams (Reeves *et al.*, 1991; García de Jalón, 1995). For small fish, habitat is limited by rocky surfaces, and therefore their habitat can be improved by placing large boulders in the stream channel. In addition, these boulders can withstand high flows, provide fish cover and may increase the rearing habitat (Wesche, 1985). These habitat enhancements should be used only when other factors are not limiting and when the habitat quality is poor.

We have also shown that fish production in these Pyrenean streams is controlled by benthic invertebrates, which are a major food resource. Therefore the rehabilitation techniques for the restoration of food supply areas, such as those presented by White and Brynildson (1967) and Wesche (1985), can be applied to further enhance fisheries.

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