

## Fish assemblage structure, habitat and microhabitat preference of five fish species in a small stream

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**A b s t r a c t.** Fish assemblage in the Úpoř brook was observed. The stream was inhabited by 13 fish species and *Lampetra planeri*. The abundance reached the mean value of 12175 spec.ha<sup>-1</sup> and the mean biomass 395 kg.ha<sup>-1</sup>. *Salmo trutta* dominated, *Cottus gobio* was also very abundant and inhabited preferably riffles as well as *Barbatula barbatula*. *Leuciscus cephalus* and *L. leuciscus* were resident in pools. Other species occurred occasionally. Preferences in habitat and microhabitat use were evaluated using RDA and FE test. Two first axes of RDA explain 27.8% of total variability of all species, and 95.3% of relationship between the species and the environmental variables. These factors significantly correlated with the axes: distance from the mouth, maximum depth, presence of mud, presence of stones as shelters, presence of rocky shelters, and presence of the deposits. The character of substrates was the most important factor influencing the distribution of *S. trutta*, *L. cephalus*, *L. leuciscus* and *B. barbatula*, whereas *C. gobio* were greatly influenced by character of shelters. Also the distance from the mouth play a role in distribution of two last species. Seasonal changes in habitat preference of *C. gobio* were recorded.

**Key words:** microhabitat, brown trout, dace, chub, bullhead, stone loach

### Introduction

An important aim of ecology in the last few decades has been to find relationships between environmental variables and biocenosis. Knowledge of ecological variables of these biocenoses such as abundance, biomass and species composition is important for understanding functional roles of the biota in ecosystems (B r o s s e & L e k 2 0 0 0 ). These variables also indicate the population status of common species useful for assessing the quality or stresses at a local scale (A n g e r m e i e r & D a v i d e a n u 2004). This information is often the basis for species conservation and ecosystem management (L a m o u r o u x & S o u c h o n 2002, E r ö s et al. 2003, L a b o n n e et al. 2003).

Two scales that have been used to analyse variables shaping fish communities in streams: microscale conditions and regional factors. The most well known microscale method is the Physical Habitat Simulation Model (PHABSIM, B o v e e 1982) that treats streams as a collection of habitat patches determining the composition and distribution of fish (E r ö s et al. 2003). Strong preferences of different aquatic organisms to habitat variables have been repeatedly shown in a variety of flow waters (e.g., L a m o u r o u x et al. 1999). The most common variables influencing the use of stream habitats by species are substrate, water depth, and current velocities (P i r e s et al. 1999, L a m o u r o u x & S o u c h o n 2002, M a g o u l i c k

2004). In addition, cover or shelter (Erös et al. 2003), riparian vegetation (Paller et al. 2000), and relative water level have been found to be predictors of fish composition in streams. Microhabitat models are regarded as limited in applicability to different streams and systems (Lamouroux et al. 1999, Magalhães 2002) and too simplistic in analysing high habitat diversity in streams (Lamouroux & Souchon 2002).

The regional scale approach addresses characteristics of the stream setting in the context of an aquatic system and their influence on the composition of a stream biocenosis (Peter 1998, Labonne et al. 2003). Relationship between local habitats and regional scale variables (e.g. water temperature, oxygen saturation) and the role of rainfall and contiguous waters have been studied (Magalhães et al. 2002). The Regional Model of Lamouroux et al. (1999) uses these variables with the aim of creating universal relations for species. Additional variables of a stream system might also be influential. Predation threat known to a factor influencing the habitat use by fish (Schlosser 1988, MacKenzie & Greenberg 1998, Pires et al. 1999, Mathis & Chivers 2002, Jackson et al. 2001, Erös et al. 2003, Magoulick 2004) as well as interspecific (Albertová 1982, Gatz et al. 1987) or intraspecific competition (Cattanéo et al. 2002).

Our contribution focuses on the fish assemblage of the Úpoř brook. It evaluates the basic variables of this assemblage, the preferred habitat and microhabitat of particular fish species and their seasonal changes as well as larger scale variables influencing the distribution of the species in this stream.

The Úpoř brook is the right tributary of the Berounka River, into which it flows near to the Týřovice village. The drainage area is 39.5 km<sup>2</sup>, the length of the flow is 11.2 km and the average flow in the estuary is 0.08 m<sup>3</sup>.s<sup>-1</sup>. The brook is typically fragmented into pools, rapids and riffle

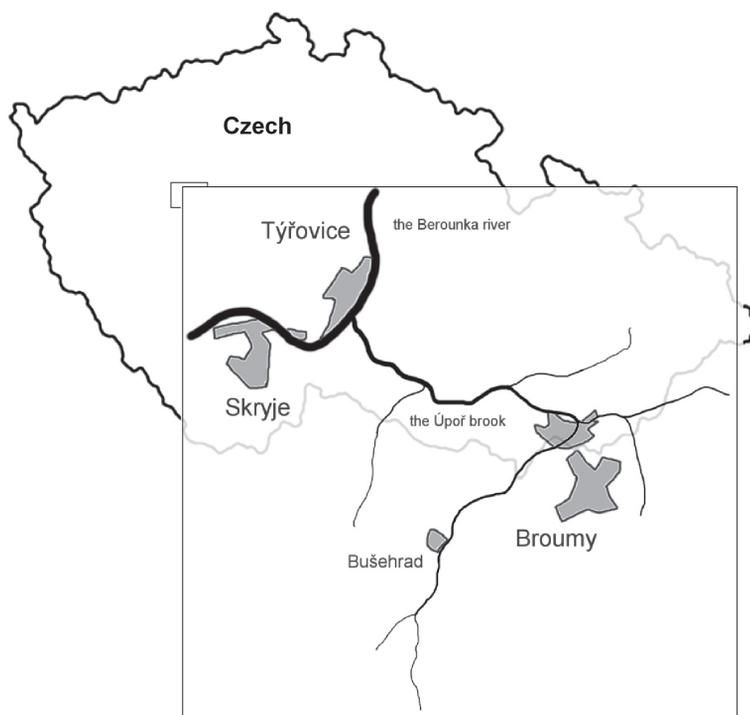


Fig. 1. Map of the locality.

areas. The brook is a part of the Landscape Protected Area Křivoklátsko, the National Natural Reservation Týřov, the Biospherical reservation UNESCO and there is no fishery management activity (Fig. 1). The lower part, flowing through the broadleaf forest, with a length of about 5 km was chosen. This study site is clearly defined as a part between the small village Broumy and the confluence with the Berounka River.

## Material and Methods

From 2000 to 2003 we conducted 167 sets of fish and habitat samples (termed profiles) at 39 locations recording more than 9000 fishes. Individual profiles were randomly chosen from the stream and their size varied between 30 and 200 m<sup>2</sup>. The fishes were caught using the method of electrofishing (devices TRA 2 – pulsed 450V; MK-1 pulsed 225/300V; LENA pulsed 225/300V). Each specimen from a particular profile was determined, measured (SL) and weighed. The abundance and the biomass were estimated using the Leslie-Davies method. A visual evaluation of the substrate was carried out in each profile in a one-metre quadrat, similar to Erős et al. (2003). The substrate was classified into three basic categories (mud, sand and gravel) as in Paller et al. (2000). The presence of deposited organic material (e.g. deposited detritus, leaf or other allochthonous material) was also recorded as well as the quality of shelters assigned to one of four categories (underwashed banks with naked roots, fallen tree or branches, rock shelters and stones). Beyond the habitat variables, local scale values were recorded: depth of water (in cm), water current (in m.s<sup>-1</sup>), the riparian cover status (4 categories: 0–25%; 25–50%; 50–75%; 75–100%), and the distance from the confluence with the Berounka River.

## Statistical analysis

All statistical analyses based on 167 sets of profile values. Seasonal changes of abundance were analysed using the one-way ANOVA. Microhabitat use was evaluated for five dominant fish species. Microhabitat preferences were evaluated using Index of electivity calculated as the difference between the expected (uniform distribution) and actual frequency of occurrence in habitats within the given environmental variable (Copp 1993, Gózlán et al. 1998, Carter et al. 2004). These frequencies were compared using the Fisher exact (FE) test. Index of electivity was not calculated for brown trout because this species was always present ( $f=1$ ). These analyses were evaluated using the STATISTICA software pack.

Microhabitat preferences were also evaluated by means of multivariate analyses relating fish assemblage and environmental variables (Cao et al. 2002). A redundancy analysis (RDA) was chosen. Correlation among all variables were computed, and maximum stream depth was deleted from use because it was closely related to others variables (water current speed, substrate). Variables were square-root transformed (Erős et al. 2003) and assembled in a matrix of environmental variables and samples. This environmental matrix was compared with a similarly organised matrix of samples and the abundance of each species (log-transformed; Penczak et al. 2004). A linear ordination analysis was conducted after a preliminary ordination (PCA – principal correspondence analysis) yielded a gradient length value of 1.8 exceeding a criterion (ter Braak & Smilauer 1998) for the use of linear rather than unimodal (CCA – canonical correspondence analysis) ordination models. The significance of the created model was tested using the Monte-Carlo randomization test with

499 permutations (Magalhães et al. 2002, Penczak et al. 2004, Marshall & Elliott 1998). These analyses were carried out by means of the CANOCO 4.5 software and biplot graphs were made using the graphic module CanoDraw.

## Results

### Fish assemblage structure

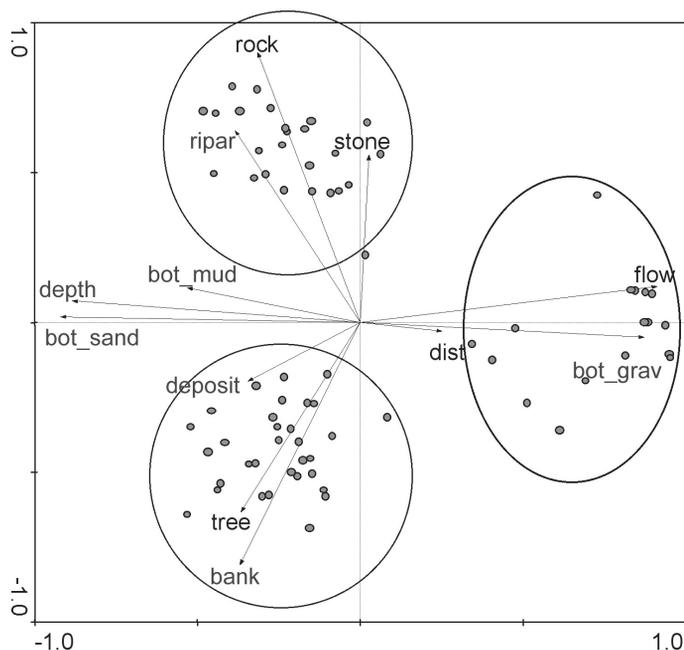
The fish assemblage of the Úpoř brook is typical for small lowland streams in the Czech Republic. Common species and sizes (total length range of most individuals) were brown trout (*Salmo trutta* L.; 50 – 300 mm), chub (*Leuciscus cephalus* (L.); 80–250 mm), dace (*L. leuciscus* (L.); 90 – 220 mm), bullhead (*Cottus gobio* L.; 40 – 120 mm), stone loach (*Barbatula barbatula* (L.); 50–130 mm). Other species recorded in low numbers were: barbel (*Barbus barbus* (L.)), grayling (*Thymallus thymalus* (L.)), minnow (*P. phoxinus* (L.)). Some fish species believed to be from an adjacent pond in the Broumy village were also captured: roach (*Rutilus rutilus* (L.)), gudgeon (*Gobio gobio* (L.)), pike (*Esox lucius* L.), carp (*Cyprinus carpio* L.) and stone maraca (*Pseudorasbora parva* (Schlegel, 1842)). The brook lamprey (*Lampetra planeri* Bloch) was recorded once.

Total fish abundance varied between 1187 spec.ha<sup>-1</sup> and 74074 spec.ha<sup>-1</sup> and reached the mean value of 12175 spec.ha<sup>-1</sup> (*S.D.*= 9507.2). Brown trout dominated with 50% (6076 spec.ha<sup>-1</sup>) of the total abundance. Bullhead was also very abundant (35.6%, 4329 spec.ha<sup>-1</sup>) and inhabited mainly riffles. Chub and dace accounted for 7.5 % (918 spec.ha<sup>-1</sup>) and 3.7% (448 spec.ha<sup>-1</sup>) respectively. Both species were resident in pools. Stone loach were 2.7% (329 spec.ha<sup>-1</sup>) of the total abundance. The abundance of other species reached the value of 76 spec.ha<sup>-1</sup> (0.6%) led by barbel. The biomass of the fish assemblage reached the mean value of 395 kg.ha<sup>-1</sup> (*S.D.*=352). The dominant species was brown trout (278.6 kg.ha<sup>-1</sup>) which accounted for 70.5% of the total biomass. Other species shared the total biomass similarly to the total abundance with respect to their average size: chub created 13.8% (54.3 kg.ha<sup>-1</sup>), bullhead 8.7% (34.7 kg.ha<sup>-1</sup>), dace 5.3% (21.3 kg.ha<sup>-1</sup>), stone loach 1% (3.91 kg.ha<sup>-1</sup>), and the remaining species 0.5% (2.12 kg.ha<sup>-1</sup>).

### Environmental setting and habitat

Using DCA (biplot of the matrix variables by samples) it can be seen that sets of variables can be divided into tree groups defined by some environmental variables (Fig. 2). One group seen on the right side of the second PCA axis consisted of shallow rapids and riffle areas with a gravelly bottom. Two groups on the left side are associated with pools. The upper one consisted of rocky, almost shaded, pools with stones. The lower one consisted of deep pools with sandy or muddy bottom, with deposits, eroded bank and fallen trees or branches.

Habitat and environmental setting relations from the RDA were summarised in Fig. 3. The first axis explains 19% of the total variability of all species, and 67.3% of the relationship between the species and the environmental variables. This axis significantly correlated with the presence of mud substrates and fallen trees, but the presence of the eroded bank was not significant when taken together with the other variables (Monte-Carlo randomisation test, *P*>0.05). The second axis explains 8.9% of the total variability, as well as 28% of the relationship among the species and the environment. Significant variables were distance from the mouth of the river, depth of the patches, presence of the mud, and presence of stones as



**Fig. 2.** PCA biplot (environmental variables\_samples) abbreviations: ripar-riparian cover, dist-distance from the mouth, type of bottom: bot\_grav-gravel, bot\_mud-mud, bot\_sand- sand type of shelters: tree-fallen tree, bank-eroded bank, stone-stones.

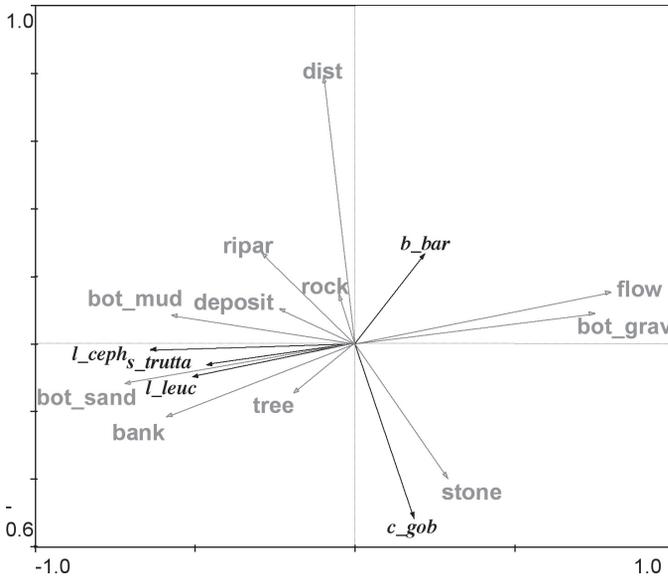
shelters for fish (Table 1). The presence of rocky shelters and organic material deposits were not significant (Monte-Carlo randomisation test,  $0.07 > P > 0.05$ ). The third and the fourth axis explain only a small amount of the total variability (2.2%, respectively 0.62%). And only the third axis significantly correlated with a level of riparian cover and the presence of stones. Other variables correlated with these axes (e.g. gravely bottom, depth of patches, water current) were other not significant individually (t-test,  $P > 0.05$ ) or as part of the total model (Table 1). The total variability of the species is characterised well by the RDA model (Monte-Carlo test,  $F=5.871$ ,  $P=0.002$ ) which explains 31.1% of the total variability and 91.1% of the relationship between the variables and species.

The character of the substrate was the most important factor influencing the distribution of brown trout (7.42% of variability). Brown trout was most often associated with a sandy or muddy bottom, whereas it avoided gravely substrate (Fig. 4). The character of the shelters (4.24%) also influenced the distribution of this species. The higher numbers of abundance were associated with the presence of stones, fallen trees or branches. Brown trout also preferred less shady places.

The distribution of chub was influenced mostly by the character of the substrate (7.95% of variability). Chub preferred profiles with a presence of eroded banks and fallen trees, whereas it avoided rocky patches. The species also preferred a muddy substrate, whereas it avoided a gravely bottom in fast moving parts of the stream. This preference of microhabitats can also be seen when evaluating the preference of shelters using the index of electivity (FE test,  $P < 0.05$ ; see Fig. 5). Chub also significantly preferred deeper microhabitats and avoided shallow sections (FE test,  $P=0.04$ ). The distribution of this species was also influenced by its distance from the mouth of the river. Chub appeared equally in the lower and central part of the stream. The migration of this species above 4 km from the mouth was blocked by a series of small dams.

**Table 1.** Correlations among environmental variables and axis of the RDA. Black colour indicates significance ( $P < 0.05$ ) individually although some were not significant within the model as explained in the text.

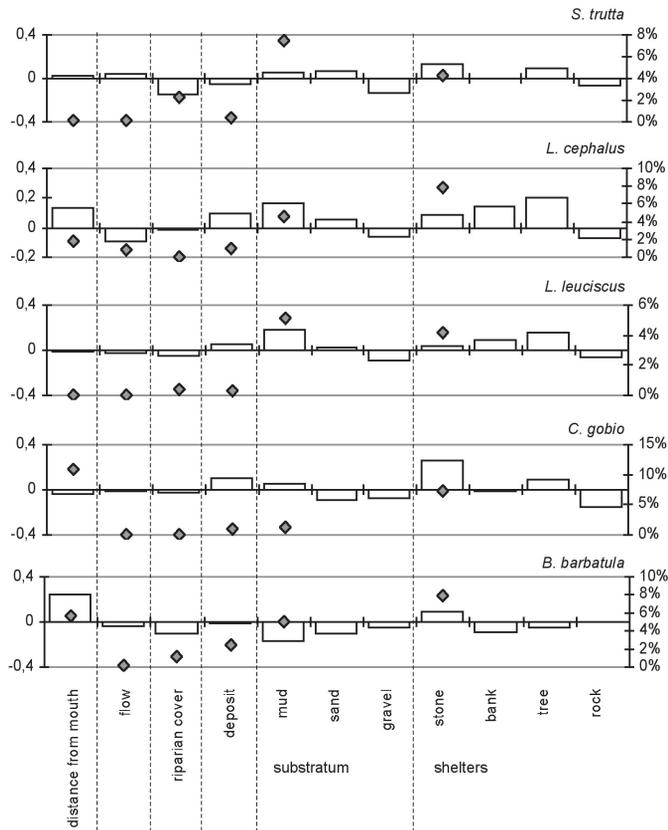
axis	AX1	AX2	AX3	AX4
eigenvalue	0.19	0.089	0.022	0.006
depth	-0.047	0.410	<b>0.710</b>	<b>-0.833</b>
distance from mouth	-0.177	0.778	<b>-0.443</b>	<b>-0.349</b>
flow	0.163	0.131	<b>0.540</b>	<b>0.498</b>
riparian cover	-0.038	-0.023	-0.558	<b>0.434</b>
bottom_gravel	0.271	0.332	<b>0.881</b>	<b>-0.395</b>
bottom_sand	<b>-0.344</b>	0.106	<b>0.785</b>	<b>0.199</b>
bottom_mud	-0.382	-0.391	0.053	<b>0.331</b>
deposit	0.148	0.300	-0.211	<b>0.323</b>
shelters_stone	-0.025	-0.523	-0.827	<b>-0.035</b>
shelters_rock	0.200	0.530	0.356	<b>0.698</b>
shelters_bank	-0.446	<b>-0.305</b>	-0.122	<b>0.005</b>
shelters_fallen_tree	0.389	0.315	0.259	<b>0.538</b>



**Fig. 3.** RDA biplot (environmental variables\_species) abbreviations: ripar-riparian cover, dist-distance from the mouth, type of bottom: bot\_grav-gravel, bot\_mud-mud, bot\_sand- sand type of shelters: tree-fallen tree, bank-eroded bank, stone- stones.

Dace had very similar demands on the environment as chub. The most important observed factor influencing its existence was the character of the substrate (5.12% variability), similarly to chub it associated with a muddy substrate (FE test,  $P=0.067$ ) and avoided gravely substrate (FE test,  $P=0.036$ ). The quality of the shelter explained 4.5% of the variability. Dace similarly to chub preferred the existence of an eroded bank and fallen trees. Dace also appeared less in the upper part of the stream (FE test,  $P=0.05$ ).

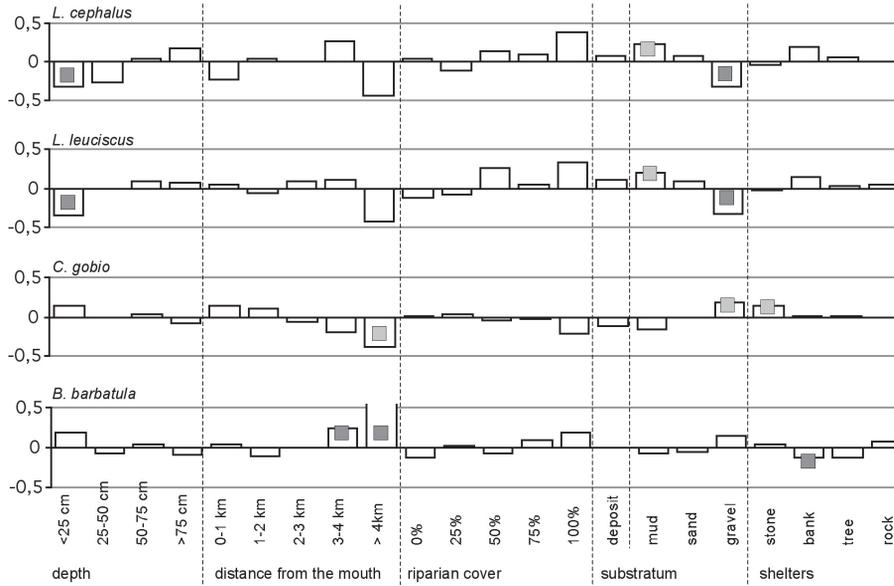
The distribution of bullhead was mostly influenced by the variable of the distance from the mouth of the river (10.96%). Although the evaluation of the frequency of occurrence does



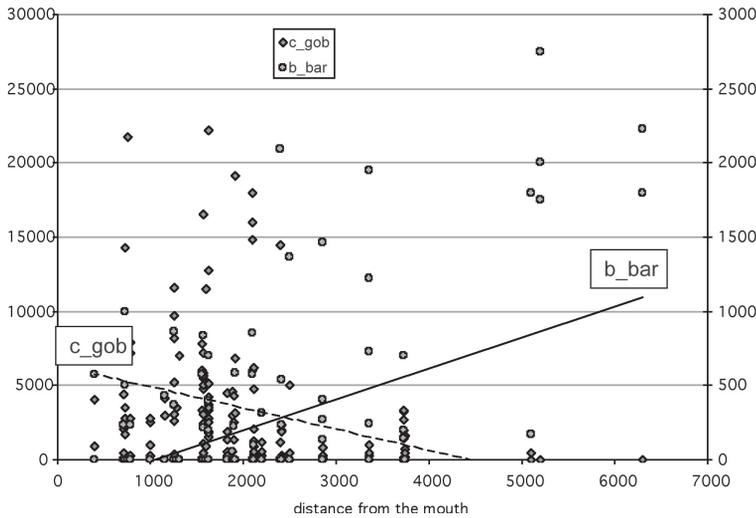
**Fig. 4.** Importance of the environmental setting variables for species abundance (histograms - RDA-score for the given variable without co-variables (pure influence); markers -percentage of explanation of fishes variability).

not show differences, the abundance of bullhead decreased with the distance from the mouth of the river according to the trend  $y = -1.4369x + 6371$  ( $R = 0.14$ ) (Fig. 6). Bullhead seemed to be indifferent to the type of substrates; this variable explained only 1.15% variability. The use of gravelly substrates was not significant (FE test,  $P=0.067$ ). The quality of shelter played a considerably larger role than the type of substrates (7.24%). Bullhead associated itself mainly with large stones, whereas it avoided rocky shelters. The occurrence of this species was influenced by neither the speed of the flow or by its depth, because they appeared in great numbers in both rapids and pools.

The variable of distance from the mouth also greatly influenced the appearance of stone loach (5.71%); the distribution of this species however, had the opposite gradient, the abundance increased with the increasing distance from the mouth according to the trend  $y = 0.2093x - 218.26$  ( $R = 0.23$ ) and stone loach appeared more frequently in the upper sections of the stream (FE test,  $P=0.05$ ) (Fig. 6). They preferred sites with large stones (shelter explains 4.14% variability), and appeared less frequently in deeper sections with eroded banks (FE test,



**Fig. 5.** Importance of habitat variables of select fishes using index of microhabitat electivity (markers – significance of FE test; light grey ( $P < 0.07$ ), dark grey  $P < 0.05$ ).



**Fig. 6.** Distribution of bullhead and stone loach in the longitudinal profile of the Úpo\_brook. c\_gob-*Cottus gobio*, b\_bar-*Barbatula barbatula*.

$P = 0.05$ ). The type of substrates explains 3.93% variability. Stone loach associated negatively with muddy substrates and appeared more frequently in gravelly substrates.

### Seasonal changes

We did not detect large differences in abundance and the distribution of species by season with the exception of dace being more abundant in September and October (ANOVA,  $P < 0.001$ ) and

bullhead less abundant in July and August (ANOVA,  $P < 0.05$ ). Variation in habitat preferences by season were also largely absent except that bullhead were concentrated in pools with muddy substrates and organic deposits in summer and otherwise them. Also, the strong preference for large stones by bullhead decreased in the summer months (marginal significance, FE test,  $P = 0.07$ ).

## Discussion

Small streams may be characterised by great changes in environmental conditions along the gradient of stream size and discharge. They are also organised into alternating pools and fast flowing sections (Inoue & Nunokawa 2002) and this breakdown creates typical microscale changes in depth and speed of current (Erös et al. 2003). Fish preference of different stream of specific depths have been discussed in literature many times (Pires et al. 1999, Šedivá et al. 2000, Erös et al. 2003) and likewise to the speed of flow (Paller et al. 2000, Penczak et al. 2004). Results of our study indicate that the distribution of species is influenced by a combination of environmental conditions such as stream depth and the available small scale microhabitats.

Dace and chub associated themselves only with slower and deeper water, living only in pools. This fact was also noted by Lamouroux et al. (1999), Lamouroux & Souchon (2002) and Carter et al. (2004), and in other species of the *Leuciscus* genus furthers Inoue & Nunokawa (2002). At a more fine scale, dace oriented to faster flowing parts in the front part of the pools (self-observation). Similarly, Penczak et al. (2004) did not find dace frequently using backwaters. Other species we studied did not respond to speed of flow, except for stone loach, which preferred faster flowing stream sections (evaluated by FE test); a result also reported by Lamouroux & Souchon (2002).

The character of the substrates is a variable which strongly influenced the distribution of fish in our study stream at both scales, and other (Gozlan et al. 1998, Marshall & Elliot 1998, Pires et al. 1999, Paller et al. 2000, Erös et al. 2003, Carter et al. 2004) have emphasised the importance of substrate. Substrate also has influences on many other variables which causes differences among habitats (Inoue & Nunokawa 2002). In the Úpoř stream are two main types of pools: stony pools with a gravely bottom and large stones, and pools with a sandy or muddy substrates and deposits (Fig. 2). The first type was inhabited by fish less often, especially by both species of the *Leuciscus* genus, the other type of pool showed a high abundance of fish and was inhabited by dace and chub in great quantities. The type of substrates greatly influenced the abundance of brown trout, which preferred finer substrates. This preference was caused by the fact that most trout were tied to the pools, which contained sandy or muddy substrates. Both species of the *Leuciscus* genus also preferred the finer substrates as Carter et al. (2004) presented. On the other hand bullhead associated with rougher substrates (Lamouroux et al. 1999, Carter et al. 2004).

Substance flowing in the stream are often deposited in pools e.g. vegetation, detritus, etc. These particles then form deposit which influences the makeup of the benthic fauna and increases the microhabitat diversity (Johnson et al. 2001) or it acts as cover over primarily for juvenile fish (Carter et al. 2004). The association of certain fishes with organic deposits was reported by Pires et al. (1999). We found no clear relations with organic deposits.

The existence of sunken objects such as roots, fallen trees and eroded banks, increase the diversity of sites and provide shelters for fish (Lamouroux & Souchon 2002, Erös et al. 2003). Here the shelters were divided into four categories. Brown trout, dace, and

chub preferred eroded banks and sunken objects (roots, trees) while bullhead and stone loach were associated with stones presumably providing shelter.

Criticism of the habitat models such as the PHABSIM (B o v e e 1982) focus on the difficulty in using results for streams or locations different from where the models were developed (A l b e r t o v á 1982, L a m o u r o u x et al. 1999, L a m o u r o u x & S o u c h o n 2002). The alternative approach of developing regional models with environmental setting variables may fail to provide sensitivity to local habitat conditions. Our findings show that both large scale environmental variables, like distance from mouth, interact with micro-scale habitat variables in explaining fish numbers on our very small study stream. We especially clearly found this for substrate that varied at both scales and was often well related to species distributions. Further research linking microhabitat and regional variables will be needed in more streams, a larger range of stream sizes, and a wider array of species to confidently understand how to combine these two classes of variables to predict flowing water biocenoses.

#### A c k n o w l e d g e m e n t s

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## L I T E R A T U R E

- ALBERTOVÁ O. 1982: The food of rainbow trout and brown trout in the water-supply dam reservoirs Lučina and Římov. *Práce VÚRH Vodňany 11*: 127–134.
- ANGERMEIER P.L. & DAVIDEANU G. 2004: Using fish communities to assess streams in Romania: initial development of an index of biotic integrity. *Hydrobiologia 511*: 65–78.
- BOVEE K.D. 1982: A guide to stream habitat analysis using the instream flow incremental methodology. *Instream Flow Information Paper 12*, U.S. Fish and Wildlife Service, Fort Collins, CO.
- BROSSE S. & LEK S. 2000: Modelling roach (*Rutilus rutilus*) microhabitat using linear and nonlinear techniques. *Freshwat. Biol.* 44: 441–452.
- CAO Y., LARSEN D.P., HUGHES R.M., ANGERMEIER P.L. & PATTON T.M. 2002: Sampling effort affects multivariate comparisons of stream assemblage. *J. N. Am. Benthol. Soc.* 21(4): 701–714.
- CARTER M.G., COPP G.H. & SZOMLAI V. 2004: Seasonal abundance and microhabitat use of bullhead *Cottus gobio* and accompanying fish species in the River Avon (Hampshire), and implications for conservation. *Aquatic Conserv.: Mar. Freshw. Ecosyst.* 14: 395–412.
- CATTANÉO F., LAMOUREUX N., BREIL P. & CAPRA H. 2002: The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Can. J. Aquat. Sci.* 59: 12–22.
- COPP G.H. 1993: Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the upper River Rhône, France. *Folia Zool.* 42: 153–164.
- ERÖS T., BOTTA-DUKÁT Z. & GROSSMAN G.D. 2003: Assemblage structure and habitat use of fishes in a Central European submontane stream: a patch-based approach. *Ecol. Freshwat. Fish* 12: 141–150.
- GATZ A.J. JR, SALE M.J. & LOAR J.M. 1987: Habitat shifts in rainbow trout – competitive influences of brown trout. *Oecologia* 74: 7–19.
- GOZLAN R.E., MASTRORILLO S., DAUBA F., TOURENQ J.N. & COPP G.H. 1998: Multi-scale analysis of habitat use during late summer for 0+ fishes in the River Garonne (France). *Aquat. Sci.* 60: 99–117.
- INOUE M. & NUNOKAWA M. 2002: Effects of longitudinal variations in stream habitat structure on fish abundance. *Freshw. Biol.* 47: 1594–1607.
- JACKSON D.A., PERES-NETO P.R. & OLDEN J.D. 2001: What controls who is where in freshwater fish communities – the role of biotic, abiotic, and spatial factors. *Can. J. Fish Aquat. Sci.* 58: 157–170.
- JONSSON M., MALMQVIST B. & HOFFSTEN P.-O. 2001: Leaf litter breakdown rates in boreal streams: does shredder species richness matter? *Freshw. Biol.* 46: 161–171.

- LABONNE J., ALLOUCHE S. & GAUDIN P. 2003: Use of generalised linear model to test habitat preferences: the example of *Zingel asper*, an endemic endangered percid of the River Rhône. *Freshw. Biol.* 48: 687–697.
- LAMOUREUX, N. & SOUCHON Y. 2002: Simple predictions of instream habitat model outputs for fish habitat guilds in large streams. *Freshw. Biol.* 47: 1531–1542.
- LAMOUREUX N., CAPRA H., POUILLY M. & SOUCHON Y. 1999: Fish habitat preferences in large streams of southern France. *Freshw. Biol.* 42: 673–687.
- MACKENZIE A.R. & GREENBERG L. 1998: The influence of instream cover and predation risk on microhabitat selection of stone loach *Barbatula barbatula* (L.). *Ecol. Freshwat. Fish* 7: 87–94.
- MAGALHAES M.F., BATALHA D.C. & COLLARES-PEREIRA M.J. 2002: Gradients in stream fish assemblages across a Mediterranean landscape: contributions of environmental factors and spatial structure. *Freshw. Biol.* 47: 1015–1031.
- MAGOULICK D.D. 2004: Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia* 527: 209–221.
- MARSHALL S. & ELLIOT M. 1998: Environmental influences on the fish assemblage of the Humber Estuary. *U.K. Estuarine, Coastal and Shelf Science* 46: 175–184.
- MATHIS A. & CHIVERS D.P. 2002: Overriding the oddity effect in mixed-species aggregations: group choice by armored and nonarmored prey. *Behav. Ecol.* 3(14): 334–339.
- PALLER M.H., REICHERT M.J.M., DEAN J.M. & SEIGLE J.C. 2000: Use of fish community data to evaluate restoration success of a riparian stream. *Ecological Engineering* 15: 171–187.
- PENCZAK T., GALICKA W., GLOWACKI L., KOSZALIŃSKI H., KRUK A., ZIEBA G., KOSTRZEWA J. & MARSZAL L. 2004: Fish assemblage changes relative to environmental factors and time in the Warta River, Poland, and its oxbow lakes. *J. Fish Biol.* 64: 1–19.
- PETER A. 1998: Interruption of the river continuum by barriers and the consequences for migratory fish. In: Jungwirth M., Schmutz & Weiss S. (eds), Fish migration and Fish bypasses. *Fishing News Books, Oxford*: 99–112.
- PIRES A.M., COWX I.G. & COELHO M.M. 1999: Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin, Portugal. *J. Fish Biol.* 54: 235–249.
- SCHLOSSER I. J. 1988: Predation rates and the behavioral response of adult brassy minnows *Hybognathus hankinsoni* to creek chub and smallmouth bass predators. *Copeia* 1988: 691–698.
- ŠEDIVÁ A., KOVÁČ V. & COPP G.H. 2000: Growth variability of morphometric characters in perch *Perca fluviatilis* and its relation to microhabitat use. *Folia Zool.* 49: 123–132.
- TER BRAAK C.J.F. & ŠMILAUER P. 1998: Canoco reference manual and user's guide to Canoco for Windows: software for Canonical community ordination version 4.0. *Microcomputer Power, Ithaca, New York*.