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STREAM HABITATS, BENTHIC MACROINVERTEBRATES, LOTIC FISH AND THEIR RELATIONSHIPS: A MULTI-SCALE APPROACH

ABSTRACT: A natural reach of montane stream (length 96 m and 7 m width) was grided into 150 cells (2 × 2 m). Density and biomass of fish (*Salmo trutta* L. and *Cottus poecilopus* Heckel) were estimated at each cell, as well as stream depth, current velocity, Froude number, bed granulation and its roughness were measured, and benthic samples from exposed bricks were collected from mid August to early October. The analysis of spatial patterns of seven variables (five abiotic and two biotic ones) and fish occurrence from the period of highest organisms' abundance confirmed that two fish species were separated within the stream space and sculpin showed close association to benthic prey. The PCA pointed to the highest loadings of abiotic habitat variables (64% of the total variance) indicating importance of hydraulics (stream velocity and Froude number) and bed characteristics (stream depth and bed roughness) in distribution of fish communities in pristine low order streams.

KEY WORDS: stream, spatial heterogeneity, spatial patterns, habitat, ecological scale

1. INTRODUCTION

Streams are particularly pertinent systems for examining issues about scaling because their structure poses some clear spatial gradients (Downes *et al.* 2000). First, rivers are linear systems that change relatively predictably in discharge, water temperature, substrate size and channel size between river sections. Collectively these changes are thought to cause large differences in biotic composition between locations along rivers (Vannote *et al.* 1980). Second, because rivers can have particular and distinct flow regimes. Discharge and its associated measures of water velocities, depths and turbulence have strong influences on stream communities (Hynes 1970, Allan 1995). Consequently, the geomorphological and hydrological features of catchments (and channel morphology) are often assumed to set most of the spatial scales that affect stream biota (e.g. Frissell *et al.* 1986).

However, if considering the rivers on different ecological scales there is a lack of basic information on small scales in lotic systems reporting spatial correlations between fish and their prey in the contexts of habitat variability. Especially there is a need of such studies on a closer examination of organisms' distribution and habitat heterogeneity with the hydraulic key factors (Statzner *et al.* 1988, Lamouroux *et al.* 1999a).

Theoretical concepts focusing on habitats are of major interest for ecologists. The one of the most important is the habitat template concept (Southwood 1977) which predicts that spatial and temporal features of the habitat are the major determinants of species traits (i.e. life–histories, morphological and behavioural adaptations) observed. For example, aquatic species that are relatively small and fecund are expected to dominate in temporally variable environments with low spatial heterogeneity.

A study of lotic fish on a short temporal scale and a small spatial scale appeared to be appropriate for evaluating the power of physical habitat variability. This study spatial (ten weeks) and temporal (about six hundred square meters) scales corresponded well to the time and space used as habitat by small and young fish (Schiemer *et al.* 1991, Schiemer and Zalewski 1992). The upper part of stream course has extreme, unpredictable natural hydrological variations in relation to rains in summer or to snow melting in spring. The morphology of the selected stream and the condition of surrounding riparian forest are natural, i.e. humans have not yet changed the spatial variability of the stream (which is the rare case in most running waters in Europe). Thus, such stream reach seems to be ideal for studying the effect of the state and variability of abiotic factors on macroinvertebrates and fish community.

Because streams are heterogeneous ecosystems where organisms exhibit patchy distributions on a spatially and temporally variable physical area (Townsend 1989) it seems obvious that fish–habitat relationships, as well as associations between fish species, should be examined across multiple ecological scales (Muotka *et al.* 1998). In this study we are presenting such comprehensive and intensive sampling strategy. The results from our field study are employing an "ecological landscape approach" to examine habitat selection by stream fishes (sectional/local scale, *sensu* Habersack 2000) in relation to spatial variation in physical habitat variables and benthic macroinvertebrates (point scale) as prey resources.

2. STUDY AREA

The field study was conducted in the Kamienica, a second order montane stream (32 km long, drainage basin 129.5 km^2) in the Dunajec River basin, southern Poland. The investigated stream stretch of 96 m in length and 7.25 m mean width (N 49°25'10", E 20°13'13", altitude 720 m, 11 km from the source, watershed area of 24.3 km^2, mean annual discharge about 0.5 m^{3}s^{-1}) was chosen in its upper natural part located in the Gorce Mts National Park (GNP; Gorczański Park Narodowy) (Fig. 1).

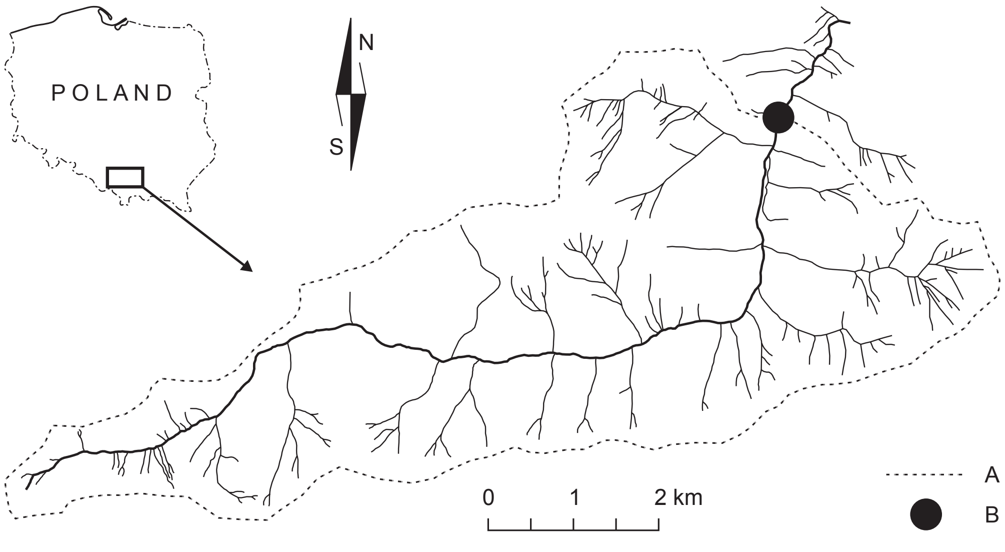

Fig. 1. The drainage basin of the upper course of the montane Kamienica stream with the location of the investigated stretch: A – border line of the Kamienica watershed, B – study reach.

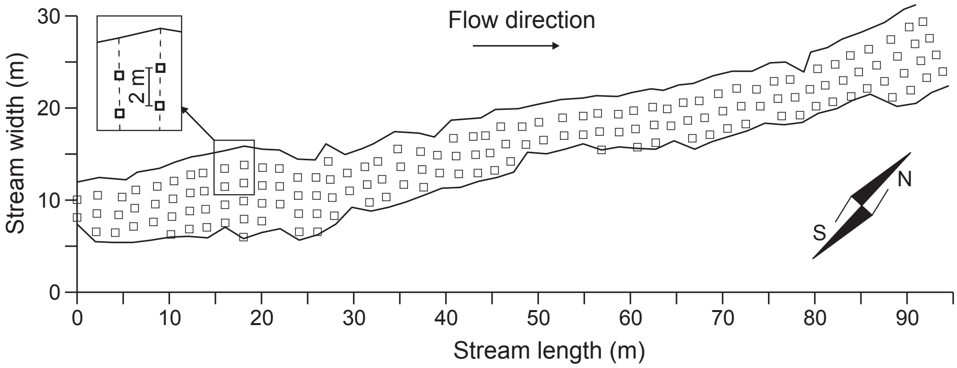

Fig. 2. Positions of colonization substrates (n = 150) used as sampling points for macroinvertebrates and fish sampling and for measurements of abiotic stream variables within the investigated reach of the Kamienica stream (see Fig. 1). Distance among sampling points of 2 m.

The upper Kamienica drains a montane basin covered mainly by coniferous and mixed forest. Main bedrock in this area is Tertiary sandstone with an addition of calcite. The stream discharge is characterized by wide flow fluctuations with the peak flow in summer what is characteristic of the Carpathian montane watersheds. The stream bed is very variable and consists of large blocks (> 1 m), stones (5–25 cm), coarse and fine gravel (2–50 mm), and of sand (<2 mm) with fine organic matter in small pools. No aquatic macrophytes occur in the investigated stretch. The stream bed is covered only by microalgae. This part of the Kamienica course is still kept in a natural status, and remains unaffected by human activity.

Within the boundaries of the GNP two fish species occur in the Kamienica, brown trout, *Salmo trutta* L. (only stationary population) and Siberian sculpin, *Cottus poecilopus* Heckel. In the lower stream course the fish community is richer, beside brown trout and sculpin there occur grayling, *Thymallus thymallus* (L.), European minnow, *Phoxinus phoxinus* (L.), spotted barbel, *Barbus petenyi* Heckel, stone loach, *Barbatula barbatula* (L.) and bullhead, *Cottus gobio* L. (J. Starmach, unpubl.)

3. MATERIAL AND METHODS

Within the study stretch (96 m long) we delineated a grid of 150 cells with each cell size of 2 × 2 m (Fig. 2). The cell size was chosen to reduce any disturbances caused by sampling of invertebrates and fish in adjacent cells. The benthic invertebrates and fish were sampled from mid August to early October. This period was chosen to avoid early/mid summer flooding events and to reduce the possible effect of fish behaviour connected with spawning periods (sculpin in April, and brown trout in October/November). To avoid the undesirable interactions between macroinvertebrate and fish sampling these samplings were done separately with at least one week intervals between them (i.e. four times for macroinvertebrates and fish, in total eight terms).

The fish sampling was carried out four times: on 5, 20 September and on 4, 11 October 2001). The entire study area was electrofished using a DEKA–Lord (Germany) backpack electroshocker with anode 10 cm in diameter. To locate fish the point electrofishing method (Moyle and Baltz 1985, Heggenes 1989) was used to minimize the “fright bias”, which may cause displacement of individual fish from their original position (Copp and Garner 1995, Muotka *et al.* 1998). The unit sampling area of the sampling point covered 3.1 m^2 (see also Bischoff and Wolter 2001). The species, number and approximate size of fishes located at each cell were recorded in the field. Fishes were assigned to size categories according to their total length. The length of brown trout was estimated in 5-cm intervals while sculpins were divided into two categories, the small and large ones separated arbitrarily by the limit of 7 cm. In Carpathian populations of brown trout the size range 5–10 cm roughly corresponds to age class 0+, while the classes 10–15 cm to 1+, 15–20 to 2+, and 20–25 to 3+ (Solewski 1960, 1961, 1962, 1963, 1964, 1965). The maturity threshold is within the range 14–28 cm depending on localv feeding and environmental conditions (Solewski 1964). In this study the trout individuals <15 cm were regarded as immature and called "small" in contrary to "large" ones which may be mature. In the case of sculpin it was assumed that the size classes <7 cm and ≥ 7 cm correspond to age classes 0+–1+ and 2+ or older, respectively (Starmach 1965). The individual fish biomass for trout was estimated using length-weight relationship based on data provided by Backiel (1964). The weight of Siberian sculpin was estimated from data presented by Brylińska (1986). The total fish biomass *FB* was calculated per 1 m^2.

For density and biomass assessment of benthic invertebrates we used 150 numbered gray-colored cuboid bricks (20 × 10 × 7 cm) as colonization substrates (Douglas and Lake 1994). The color of bricks was similar to natural stream bed substrate at the study site. To enable macroinvertebrate colonization the bricks were placed at the center of each of 150 cells on 2nd August 2001, two weeks before the first sampling. In total, the benthic organisms were sampled four times with two-week intervals (on 16, 30 August and on 13, 27 September, 2001).

The benthic macroinvertebrate samples were taken by placing a frame (25 × 25 cm) with a net (mesh size 0.1 mm) behind a brick and against the flow. Next, the brick was quickly moved into a net. After the sampling each brick was returned to its place in a given cell. In total, 600 samples were collected on four sampling occasions. The collected animals were preserved in 4% formalin in the field. They were picked up under binocular microscope and all individuals in each sample were enumerated (i.e. expressed as a macroinvertebrate density ind. per 200 cm^2 of brick area, *MD*), measured to the nearest 0.5 mm using a graduated eyepiece (body length without cerci), and identified to lowest practicable taxonomic level, normally genus. The total macroinvertebrate biomass (*MB*) was estimated as a sum of all individual biomasses calculated from length–dry weight relationships for each taxon (Meyer 1989, Burgherr and Meyer 1997).

During the study period, five hydraulic and habitat variables (water depth, Froude number, water velocity, substrate size, and substrate roughness) were measured in each of 150 cells. Water depth (*D*) was measured to the nearest cm with a wading rod. Water velocity (*V*) was measured with a Schiltknecht (Switzerland) MiniAir2 type flow meter fitted with a 22 mm propeller. Current velocity was recorded in the centre of each cell at the top of the brick. Moreover, for each sampled area the Froude number (*Fr*), a dimensionless index of turbulence, was calculated according to the formula: $Fr = V/(gD)^{0.5}$ where: V – mean flow velocity, g – acceleration due to gravity, and D – mean depth of water.

Fig. 3. The stream bottom roughness measurement device (see methods for explanation).

Mineral substrate was assessed by taking at each cell a digital picture from the stream bed with the use of white frame (25 × 25 cm) observed with a box with Plexiglas plate to avoid light reflexes on water surface. The digital pictures were analyzed with the use of image analysis (Carnoy 2.0 software). To estimate a substratum size we applied Heggenes *et al.* (1990) particle size classification with class reduction to five substrate size categories: <2 mm (sand), 2–10 mm (fine gravel), 10–50 mm (coarse gravel), 50–250 mm (stones), and > 250 mm (boulders). A fraction of areas of each substrate category was measured from the images and a weighted mean of substratum size class (i.e. representative granulation, G expressed in mm) was estimated using the formula $G = (\Sigma\ di\ Pi)/100$ where: di – diameter of i-th substrate size category in mm, and Pi – percentage of i-th category (Bajkiewicz-Grabowska *et al.* 1993).

The substrate roughness was measured with the use of a manual profile device (55 cm width) based on Gore (1978) and Gore and Nestler (1988) ideas. Our tool consisted of 25 vertical movable metal rods (length 40 cm, diameter 4 mm) and a horizontal metal bar with holes (rod intervals of 2 cm) (Fig. 3). In the field, the device was placed in each cell perpendicular to the bed and to the bank line and pressed against the bottom so that the rods were allowed to fall freely to the bottom. The positions of the rods were then fixed with an additional metal bar with silicon band. Then the device was removed and the position of rods was recorded by a digital camera. On the picture the distance (in mm) of each rod end from the margin of horizontal bar was measured with the use of Carnoy software. The mean values of 25 rod lengths were calculated and used as measure of the substratum roughness R (i.e. roughness height, Gore 1978, Statzner *et al.* 1988).

The data were presented as overlay maps showing the spatial distributions of variables within the sample space (coordinates: X – site length, Y – site width, Z – measured parameter) *versus* fish species size and their distribution within the grid. For the spatial data analysis we used the kriging (SURFER, Golden Software Inc.), a geostatistical method which is effective in the study interpolation of spatial patterns among ecological data (Rossi *et al.* 1992).

All multivariate analyses were conducted using STATISTICA 6.0 (StatSoft Inc. 2001). Variation in spatial fish abundance and biomass with habitat and prey variables from Kamienica stream was summarized through principal components analysis (PCA). To present the PCA results we calculated eigenvalues, loading factors (at level > 0.7) and projected them onto two first factors presented as factors biplot. Because the frequency of fish in sampled cells was low it was not possible to utilize the data of species or their size category in the PCA analysis (in total we had only 18 cases for nine variables). We analyzed the data by the PCA in two steps: (1) including all variables, and (2) excluding benthic macroinvertebrate variables to assess the highest variance explanation. This approach allowed us to interpret the strongest associations between the fish community and habitat variables.

4. RESULTS

As previously planned we scheduled start of our field survey in mid July to avoid fish autumn migrations and macroinvertebrate emergence in the end of the season. Nevertheless, a high flood occurred in early July and we decide to shift our experiments (mainly the setup of bricks colonization by invertebrates) to beginning of August (Fig. 4). During the experiment we observed a continuous increase of benthic fauna (according to exponential model) and a low changes in fish community densities along with decreasing of the water level. Because the density of benthic fauna was very low in the first three terms of ecosystem recovering after flooding we limited our data set only to the last period at turn of September and October (i.e. for fish the third and for benthic fauna the last sampling occasion) to get appropriate data set for the interpretation and statistical analyses.

In total, we collected 19 fish individuals on the third sampling period (4th October 2001). The number of fishes was low and only in 18 cells they were captured (i.e. 12% of a total of 150 cells). The community con-

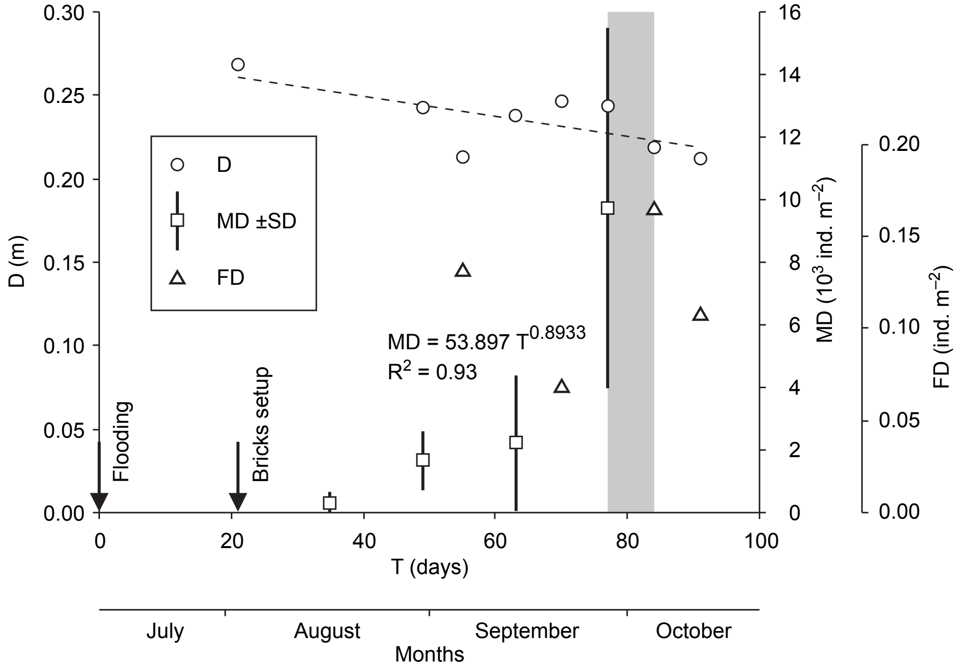

Fig. 4. Flooding situation (prior to study startup) with basic information about experiment setup, sampling periods, and measured parameters: mean stream depth (MD), mean macroinvertebrate density (D), and fish abundance (FD) within studied Kamienica stream reach on the time scale (T). Shaded area denotes time period from which the data were used for this study (i.e. end September/early October).

sisted only of two species: brown trout (*Salmo trutta* L.) and Siberian sculpin (*Cottus poecilopus* Heckel) (21% and 79%, respectively). The mean fish density accounted for 0.17 ind. m^{-2} ± 0.45 SD and mean biomass for 2.1 g WW m^{-2} ± 7.5 SD (n = 146). Both species represented two age classes: brown trout 1+ (10–15 cm) and 2+ (15–20 cm) while Siberian sculpin 1+ (<7 cm) and age class 2+ (≥ 7cm).

The benthic macroinvertebrates were collected from all available cells/bricks, on 27 of September 2001. In total the samples were collected from 121 bricks. The samples lost was caused by bricks drying up (decrease of water level) or by their movement downstream by the flow. Within studied reach mean macroinvertebrate density accounted for 195 ind. 200 cm^{-2} (±115 SD) and biomass for 8.93 mg 200 cm^{-2} (±7.86 SD). The benthic community mainly consisted of Chironomidae (56%), Ephemeroptera (30% including *Baetis alpinus* Pictet., *Baetis* sp., *B. rhodani* Pictet., and *Rhitrogena semicolorata* Curt.), Plecoptera (15% – Perlodidae, Leuctridae, and Perlidae), and others (e.g. *Dugesia gonogephala* (Duges.)). In total, including some rare species (e.g. *Baetis muticus* (L.) and *Protonemura* spp.), 25 macroinvertebrate taxa were found in the study area.

The contours of five habitat parameters (current velocity, stream depth, Froude number, granulation, and roughness) and contour plots of macroinbertebrate density and biomass in relation to two fish species and their size categories are presented in Fig. 5. The overlay maps show the tendency of both species occupied the habitats with current velocity from slow (both size classes of brown trout) to slow/medium current habitats (Siberian sculpin). The both size classes of brown trout showed a preference to intermediate/high depth stream habitats with differentiation to low Froude number (size class 2+) and to mid-gradient of Froude number (size class 1+). Siberian sculpin occurred at a medium range of stream power (Froude number 0.3–0.7). Both species occupied stream areas of mid-sized granulation, except of 2+ brown trout which was recorded in downstream habitat with large-sized substrate. Prevailing fish individuals avoided

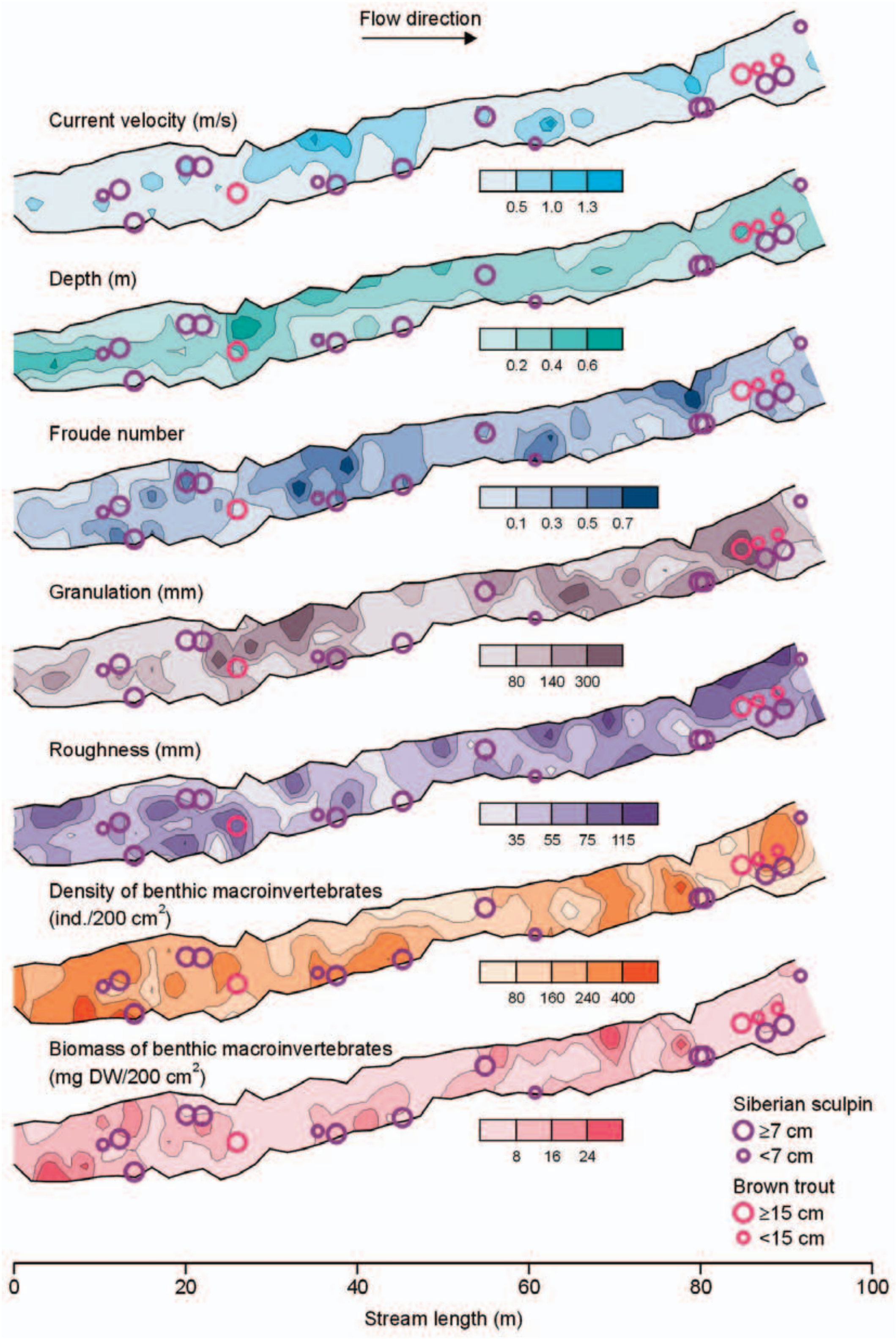

Fig. 5. Overlay maps (kriging method) showing patterns of five abiotic stream characteristics and distribution of benthic macroinvertebrates (density and biomass) against two fish species: Siberian sculpin (*Cottus poecilopus* Heckel) and brown trout (*Salmo trutta* L.) with two size categories within studied reach (96 m) of the Kamienica stream from September/October period (see Fig. 4).

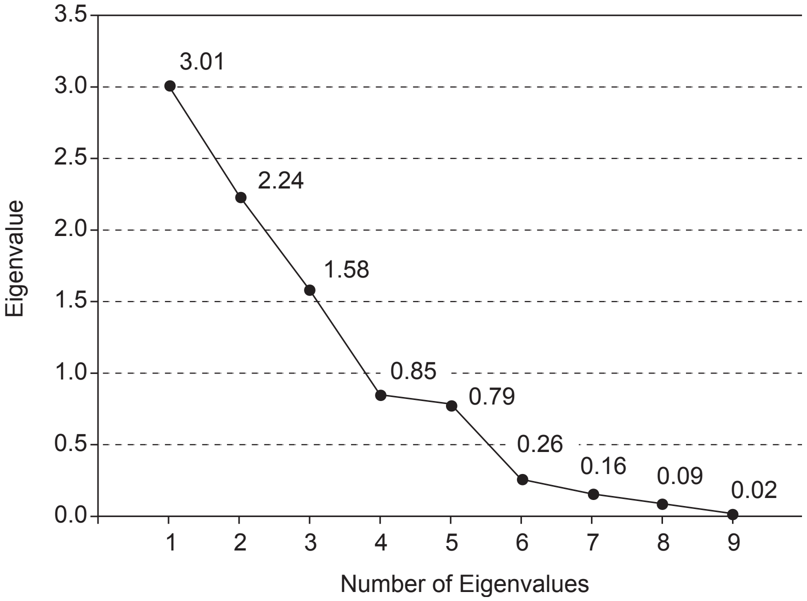

Fig. 6. Plot of eigenvalues against nine factors for nine variables with the use of PCA method. The plot refers to Table 1 and Fig. 7. For explanation see the text.

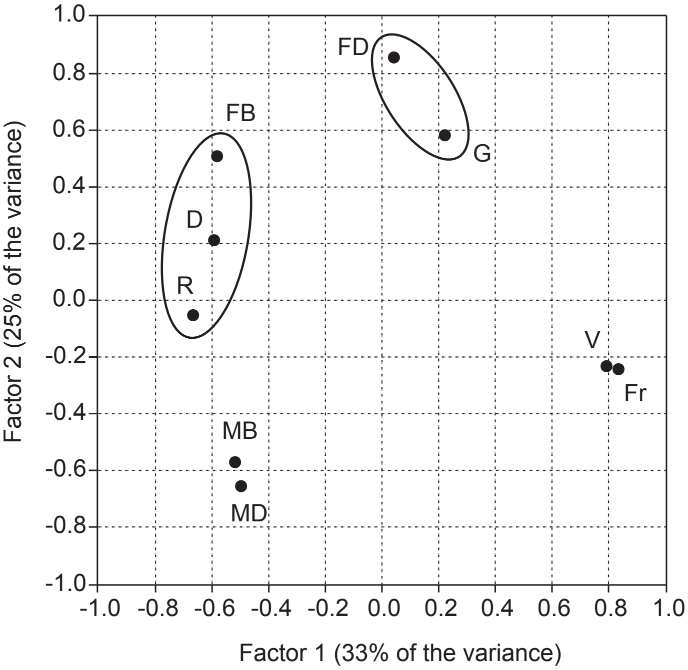

Fig. 7. Biplot of two loading factors (factor 1 *versus* factor 2) extracted by principal component analysis (PCA) for total fish density (FD) and biomass (FB) with five abiotic parameters (D – depth, R – bed roughness, G – bed granulation, V – water velocity, Fr – Froude number) and two prey variables (MD – macroinvertebrate density and MB – macroinvertebrate biomass). Factors are unrotated. In total nine variables were tested.

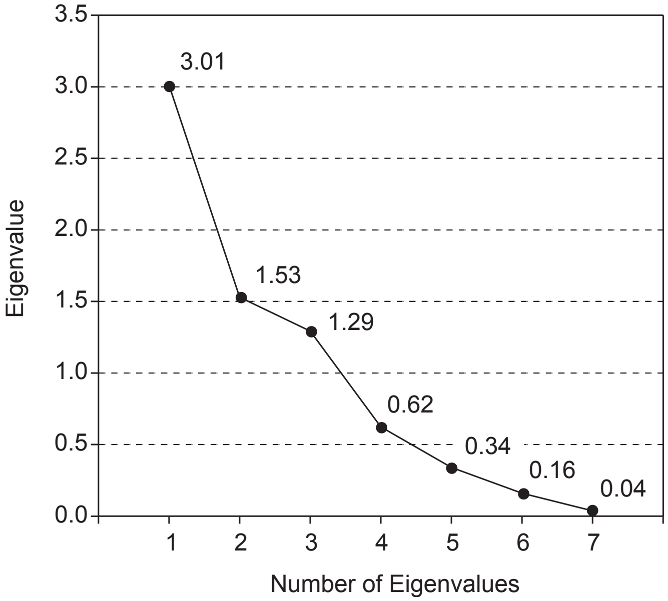

Fig. 8. Plot of eigenvalues against nine factors for seven variables with the use of PCA method. The plot refers to Table 2 and Fig. 9. For explanation see the text.

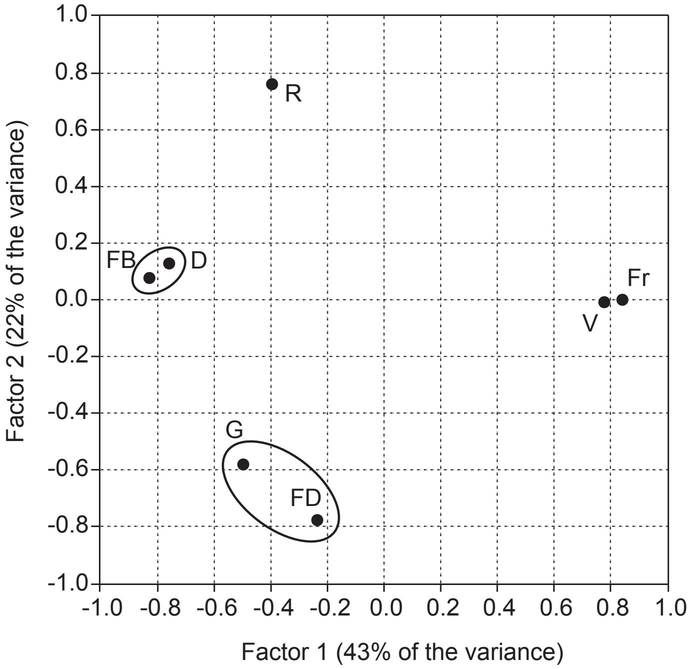

Fig. 9. Biplot of two loading factors (factor 1 *versus* factor 2) extracted by principal component analysis (PCA) for total fish density (FD) and biomass (FB) with five abiotic parameters (D – depth, R – bed roughness, G – bed granulation, V – water velocity, Fr – Froude number). Factors are unrotated. In total seven variables were tested.

low and high substrate roughness with preference 35–75 mm of roughness range for sculpin and 55–115 mm for trout.

Distribution of fish showed several relationships with their prey. Brown trout of age 2+ occupied habitats with low density and biomass of benthic fauna, while the younger 1+ fish were found in the areas of the highest macroinvertebrate density and biomas (> 240 ind. 200 cm^{-2} and > 16 mg DW 200 cm^{-2}, respectively). Despite of age, all Siberian sculpins showed a tendency to occupy stream areas mainly from intermediate to high macroinvertebrate density and biomass (80–400 ind. 200 cm^{-2} and > 8 mg DW 200 cm^{-2}, respectively).

According to our data both fish species were clearly non-randomly distributed within the studied sampling space. It seems that within the sampling area both species formed three clearly distinct clusters (i.e. in the upstream, midstream and downstream reach) (Fig. 5). Moreover, the two species showed a tendency toward the spatial avoidance – the aggregations of trout and sculpin were in separate sampling cells of the stream reach. Within the sampling cells we never found both species located in the same cell.

In the first step to verify the relationships between fish and environmental and prey variables (in total nine variables were tested) principal component analysis (PCA) was performed. The PCA extracted nine factors among them the first three factors showed eigenvalues > 1 (Fig. 6). The first three extracted factors explained 76% of the variance. The stream velocity and Froude number were strongly related to factor 1 (eigenvalues > 0.7), while the fish density was associated with factor 2 (Table 1). The first two factors accounted for 58% of the variance (Fig. 7). The biplot of the first two factors shows clearly positive associations of the fish biomass with stream morphometry (water depth and bed roughness) and between fish density and bed granulation. (Fig. 7). The macroinvertebrate abundance and biomass were negatively related to stream hydraulics (stream velocity and Froude number). The same opposite relationship was found between fish biomass and stream hydraulic variables (i.e. *Fr* and *V*) (Fig. 7).

Taking into account the high hydraulic stream variations and low loading factors for macroinvertebrate community (Table 1) we decided to exclude the two variables from the PCA analysis. The next step of the PCA was to analyze reduced data set with only 7 variables. The second PCA extracted seven factors with three of them having eigenvalues > 1 (Fig. 8). The first two factors accounted for 64% of the variance (Fig. 9). Four analyzed variables (stream depth, current velocity, Froude number, and fish biomass) were

Table 1. Loading values for the first three factors and nine variables (D – depth, V – stream velocity, G – bed granulation, R – substratum roughness, Fr – Froude number, MD – macroinvertebrate density, MB – macroinvertebrate biomass, FD – fish density, and FB – fish biomass) with explained variance (EV) extracted by the principal component analysis. Bolded values >0.7.

Variable	Factor 1	Factor 2	Factor 3
D	−0.59	0.21	−0.38
V	**0.79**	−0.24	−0.39
G	0.22	0.58	0.36
R	−0.67	−0.06	−0.55
Fr	**0.84**	−0.24	−0.38
MD	−0.49	−0.66	0.29
MB	−0.51	−0.57	0.43
FD	0.04	**0.85**	0.41
FB	−0.59	0.51	−0.51
EV	3.01	2.24	1.58
Total proportion	0.33	0.25	0.18

Table 2. Loading values for the three factors and seven variables ((D – depth, V – stream velocity, G – bed granulation, R – substratum roughness, Fr – Froude number, FD – fish density, and FB – fish biomass) with explained variance (EV) extracted by the principal component analysis. Bolded values >0.7.

Variable	Factor 1	Factor 2	Factor 3
D	**–0.76**	0.13	0.44
V	**0.77**	–0.001	0.59
G	–0.50	–0.57	0.52
R	–0.40	**0.76**	–0.05
Fr	**0.83**	0.002	0.45
FD	–0.24	**–0.77**	–0.32
FB	**–0.83**	0.08	0.40
EV	3.01	1.53	1.29
Total proportion	0.43	0.22	0.18

strongly associated to the factor 1, while the bed roughness and fish density were related to the factor 2 (Table 2). In the PCA biplot (Fig. 9) the relationships between fish biomass and stream depth and between fish density and bed granulation were similar but stronger (i.e. if variance of the two factors is considered and variables loading factors) as in the first PCA analysis (Fig. 7).

5. DISCUSSION

Spatial heterogeneity in streams is complex and evident across multiple spatial scales (Schlosser 1991). Stream ecosystems have very variable structure because materials are constantly moved downstream and organisms often must recolonize disturbed areas from refugia habitats (Osborne and Wiley 1992). However, in our study we did not observe apparent alternation in fish density after flood event. In contrast, we recorded relatively slow colonization of the brick substrata by macroinvertebrates after the first weeks of high flow (Fig. 4).

In the upper Kamienica stream exclusively two fish species were found. This simple fish structure is related to a conceptual model proposed by Schlosser (1987) that headwaters are represented as “colonizing” habitats that contained temporally variable assemblages due to highly variable regimes and small, structurally simple habitats. In contrast, larger downstream habitats are viewed as environmentally stable with more stable and diverse fish assemblages.

The stream-habitat PCA (including prey variables) resulted in two axes from which the first one we refer to as stream habitat. Two habitat variables (water velocity and Froude number) loaded highly on the first axis, and on the second axis was loaded fish density, for both axes explaining 58% of the variation in the original data matrix. What is also interesting from this PCA analysis that both benthic variables were not related to the total fish density and to total fish biomass. Exclusion from the PCA of benthic invertebrates resulted in two meaningful axes which we refer to as stream habitats. All four variables (depth, current velocity, Froude number and fish biomass) loaded highly on the first axis while two other variables (bed roughness and fish density) on the second axis, both accounting for 64% of total variability. The results from both PCA analyses clearly demonstrated the importance of abiotic factors for fish community distribution in the headwater natural stream. In the context of these results and if hierarchy of different factors affecting biotic components in a stream continuum is considered, Naiman and Zalewski (1985) suggested that fish communities in headwater streams are controlled by abiotic factors (e.g. by hydraulic or stream bed parameters) and lowland rivers are more controlled by biotic factors (by food availability or interspecific competition). This importance of hydraulics in stream ecosystems is common and has been demonstrated for macroinvertebrates (e.g. Gore 1978, Statzner and Higler 1986), as well for other groups of stream organisms (e.g. Biggs 1996). Therefore, hydraulic variables are suitable for predicting the characteristics of fluvial communities using the theoretically simple concept of the ecological niche. This fact demonstrates the importance of identifying and modeling key local-scale processes to understand community patterns at larger scales (Lamouroux *et al.*1999b).

Our observation that large trout occupied the deepest stream sections (Fig 5.) is related to the "bigger fish – deeper habitat" relationship which has been well documented in numerous studies of habitat selection by stream fish (Harvey and Steward 1991, Muotka *et al.* 1998). All trout individuals (both size classes) in our stream reach avoided high current speed and preferred velocities <0.5 m/s. However, if other abiotic habitats are considered it appeared that larger trout (age 2+) preferred deeper areas (> 0.4 m) with larger bed granulation (> 140 mm) and higher bed roughness height (> 75 mm). Beside abiotic factors, many authors have pointed out the importance of food availability as a limiting factor for salmonids (e.g. Poff and Huryn 1998). Food availability is often defined as a overall abundance or biomass of benthic invertebrates (Jowett 1995). However, salmonids are visual and size-selective feeders that partially use drifting invertebrates (Bannon and Ringler 1986). This phenomenon of using drifting organisms is confirmed in our study by large trout occupying habitats with lower and intermediate benthic invertebrate density and biomass while the smaller trout, which feed mainly on the stream bottom, preferred downstream area with the highest bentic fauna abundances. In general, brown trout habitat use and diet vary according to trout size, suggesting that relative importance of traits that make prey vulnerable may also vary according to trout size (De Crespin de Billy *et al.* 2002). Thus, the further analysis of prey traits predominantly used by small, medium and large trout should enable to determine better the factors that may affect trout foraging behavior and to improve estimates of trout habitat suitability. Because of flooding event and low trout densities in presented studies these detailed analyses were not possible.

We found apparent patterns in microhabitat selection by Siberian sculpin in relation to physical stream habitats. The bullhead clearly avoided extreme physical conditions in the Kamienica stream. It preferred rather intermediate habitats of depth, stream power (Froude number), average bed granulation and mid roughness. Most of sculpins were found in the shallow stream areas. In contrast, Hesthagen and Heggenes (2003) found that small (56 mm) and large (88 mm) Siberian sculpin preferred the large gravel, and did not change their substratum preferences much with increasing densities, suggesting higher tolerance for 'crowding'. In that study the large Siberian sculpin preferred the coarser substratum, and the largest individuals were consistently found on it.

In our study, large bullheads seemed to prefer areas with high-intermediate densities of invertebrates. This distribution is related to their foraging behavior. In general, bullhead is bottom-feeder and relies on tactile or hydrodynamic cues for prey detection (Hoekstra and Jansen 1985). Additionally, there is some evidence that sculpins are size-selective predators, favoring the largest prey types available (Englund and Olsson 1997). Two groups of stoneflies: Perlodidae and Perlidae (> 2 cm in body length) were certainly among the largest food organisms for fish in our study reach. These slow moving larvae are easy to capture, but probably not for small bullhead consumers. Our observations on bullhead distribution and their prey patterns need more laboratory or field experiments on the mechanisms of prey selection by sculpins. In some studies (e.g. Hesthagen and Heggenes 2003) habitat selection by large Siberian sculpin appeared to be unaffected by species composition and density. In our study reach it seems that small Siberian sculpins were displaced to finer substrata (in upper and mid stream sections) when comparing with large ones, suggesting plausile intraspecific competition of bulldeads for habitats (Fig. 5). Nevertheless, this observation needs further extended examination. There are available only few studies indicating that Siberian sculpin are potential habitat competitors for young brown trout (Hesthagen and Heggenes 2003). In the investigated reach we never found both species in the same cell. This may explain the mutually exclusive avoidance in space of bullhead and brown trout. The cited above authors have found that in sympatry experiments with large Siberian sculpin, habitat displacement of brown trout occurred, indicative of interspecific competition.

An attractive approach for the prediction of community patterns is to identify key processes at the local scale of individuals which persist over larger scales (Levin 1992). Local scale processes are generally easier to identify and more interpretable or mechanistic than large-scale processes. Therefore, models of local scale processes potentially provide predictive tools which are transferable across ecosystems. Nevertheless, as the scale of investigation varies dramatically, the results obtained from various analysis tools are very different. Several attempts to incorporate scales in river classifications have been made in the past (Frisell *et al.* 1986, Naiman *et al.* 1992). Recently, a new river scaling concept have been proposed by Habersack (2000) as a basis for ecological assessments and to integrate stream processes "acting" on different scales. The five spatial scales have been proposed: regional (> 1000 km), catchment-wide (100–10000 km), sectional (1–100 km), local (0.01–1 km), and point scale (0.001–0.0001 km). In our study, fish populations may predominantly reflect the sectional scale, although, of course both larger and smaller scales are relevant too. Benthic invertebrates may show the smallest bed habitats and therefore reflect the smallest spatial scale, with dominance at the point scale. Future research must be directed at improving scaling methods in ecology (Peterson *et al.* 1998). The development of detailed down- and upscalling procedures is necessary (Habersack 2000). Through the investigation of the interdependences between abiotic and biotic scaling, objective criteria for defining ecological integrity have to be found. In our study, the grid used should be dense enough to allow an accurate estimation of invertebrates at point scale. Nevertheless, since different variables vary across different scales, any sampling grid will unavoidably track them to a different accuracy. For example, stream fishes and benthic macroinvertebrates can rarely be sampled to the same accuracy with the same grid. However, it is difficult to determinate a priori an appropriate scale for a study, it may be advisable to conduct further studies on a variety of spatial scales (Levin 1992).

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