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Fine spatial scale patterns of fish assemblage structure and environmental factors in wadable small streams

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1. BACKGROUND AND OBJECTIVES OF THE STUDY

The diversity of watercourse habitats plays a fundamental role in the coexistence of different fish species. The habitat quality has a significant impact on the long-term survival and integrity of fish communities, contrary to environmental and human impacts at a given habitat. Habitats with different environmental characteristics ensure the survival of fish species depending on their life activities (e.g., feeding, spawning, perennation), life stages (larvae, fry, juveniles, adults), and the individual body size. Therefore, fish prefer habitats where they can maximize their survival (e.g., avoidance of predation, shelter from extreme climatic events). Consequently, the individuals prefer different habitats.

The habitat diversity of watercourses (habitat heterogeneity) can be interpreted on several spatial scales. At the landscape level, the landform and hydrological characteristics of the catchment determine the environmental diversity from the stream source to the estuary of large rivers. At the meso-scale, the habitat heterogeneity of large rivers is determined by the main stem, the tributaries, and the associated potamal habitat types, while in the case of small submountain and highland watercourses at the reach level, it is determined by hydro-geomorphological units (pools, runs, and riffles). The micro-scale habitat heterogeneity within the watercourse reach is determined by the variability of the substrate composition, the characteristics of water flow and depth, the accumulation of woody and herbaceous plant debris, and the vegetation type. At the same time, the significance of the pattern-forming effects of biotic and abiotic factors influencing the spatial distribution, habitat use of fish, and the assemblage structure also varies in a spatial manner, interacting hierarchically with each other.

In Hungary, small watercourses can be classified into three main groups according to their catchment size, channel slope, substrate composition, flow conditions, and channel morphology: submountain, highland, and lowland small streams. Small watercourse types have been severely affected by the extreme climatic and weather conditions experienced in recent years. As they are habitat to many native, protected, and Natura 2000 species, they deserve special attention from a nature conservation perspective.

Fish undergo substantial changes in body size during their life cycle, resulting in size-structured fish assemblages. As fish grow in body size, their ecological requirements, feeding habits, and strategy for successful predation avoidance change. Consequently, changes in feeding and social behavior related to body size are often accompanied by changes in habitat use. This phenomenon is known as ontogenetic habitat change or ontogenetic habitat shift. During ontogenetic habitat changes, fish gradually try to find new optimal habitats, which differ from each other to a greater or lesser extent and best suit their current needs. However, the habitat shifts are generally not large contrasting changes as environmental quality varies; rather, they are gradual transitions along environmental gradients as the fish grow. If the habitat diversity of a stream reach is low, there are few opportunities for ontogenetic habitat shifts, so survival chances and, ultimately, assemblage composition may vary within the local fish assemblage depending on species and body size group.

Taking all this into account, it is particularly justified to examine fish-environment associations on multiple spatial scales, taking into account size structure. This approach can reveal ecological patterns that can provide a basis for understanding the mechanisms behind the patterns that determine the organization and ecological resilience of fish populations in small watercourses.

The relative effects of variables at different spatial scales that affect the spatial patterns of fish assemblages have typically been studied in large rivers, and numerous studies have also been conducted to explore the relationships between body sizes and habitat variables. However, to our knowledge, the relative impact of spatial scales in the context of small stream reaches has not been studied yet, and research on fish habitat use depending on body size has typically been conducted using coarse size groupings (e.g., juveniles and adults). Furthermore, we are not aware of any studies that have quantified ontogenetic habitat shifts and whether the extent of habitat shifts may be related to the maximum adult body size of species.

The doctoral research examines the relationship between fish community structure and environmental factors. Our goal was to examine the spatial organization of species assemblages within a stream reach on a fine spatial scale, paying particular attention to the size structure of fish assemblages. Our investigations consisted of three main research topics. Our specific objectives are described below for each topic.

1. Fish faunistical survey on the main watercourses of the upper (submountain) and middle (highland) Tarna catchment.
2. A fish fauna overview of the three main streams of the Tarna basin (Tarna, Ceredi-Tarna, and Parádi-Tarna) by synthesizing the knowledge available about the streams, supplementing it with our own fish faunistical data.

Research questions:

2.a What fish species currently characterize the habitats of the submountain and highland areas of the Tarna?

2.b How many species and what species have been detected in the Tarna, Ceredi-Tarna and Parádi-Tarna streams in the last 50 years, between 1979 and 2020?

2.c What is the temporal and spatial distribution of species detections, and have these variables changed over the decades?

2.d What extent can the species observed in given streams be considered a characteristic faunal element of the stream?

Hypothesis:

Over the past 50 years, both the intensity of fish faunistical research in streams and the research methods have changed (e.g., instead of hand-seine fishing, electrofishing is used now). During the last 50 years in Hungary, several non-native fish species have appeared in watercourses and lakes. Because of this, non-native fish species also may have gained ground in the Tarna watershed. Based on this, our prediction is that the number of detected species and their detection frequency over time, as well as the detection frequency of non-native species and the cumulative number of detected non-native species, will increase over time.

3. Comparison of the relative pattern-forming importance of meso- and micro-spatial habitat variables in the spatial distribution pattern within a stream reach of a size-structured fish assemblage of a submountain small stream and a highland small stream.

   Research questions:

   3.a What meso-scale and micro-scale habitat variables explain the spatial distribution of species-specific, body-size-grouped fish assemblages within stream reach in submountain and highland stream habitats?

   3.b What is the relative importance of habitat variables at the two spatial scales in describing spatial patterns of fish species size classes within a stream reach?

   3.c Do the habitat variables of the two spatial scales have similar relative pattern-descriptive importance in the two stream types (habitats)?

   3.d What habitat use can be characterized by the size-grouped fish assemblage within the species in the two stream types?

   Hypothesis:

   The relative pattern-forming role of habitat variables is not scale-independent. Since micro-spatial scale habitat factors (e.g., substrate, water depth) can directly affect fish assemblages as opposed to meso-spatial scale variables (e.g., stream width), we assume that the general relative pattern-explaining role of micro-spatial scale variables is more significant than that of meso-spatial scale variables. However, in different small stream types (submountain and highland), which specific habitat variables are significant for a given spatial scale may differ. Habitat variables that contribute more to habitat diversity within a stream reach and are characterized by high variance provide wider habitat gradients and, overall, more diverse microhabitat types for fish than habitat variables with low variance within a reach. Thus, we expect that differences in the spatial distribution of fish assemblages within the submountain and highland regions are also linked to habitat variables that distinguish stream types, such as substrate characteristics and hydro-geomorphological variability.

4. Explanatory and descriptive study of the microhabitat use of fish species living in submountain small streams, taking into account the individual body size of the fish (species size classes) and ignoring the body size (species).

   4.a Which habitat variables most influence the micro-spatial distribution patterns of fish, and what is the relative pattern-explanatory role of each habitat variable in relation to each other?

4.b Are the relative pattern-explanatory roles of habitat variables the same or different in shaping the micro-spatial distribution patterns of species and species size classes?

4.c Are there interspecific and intraspecific differences in microhabitat use?

4.d Are there preferences for some range of values of micro-spatial scale habitat variables?

Hypothesis:

Research conducted at larger spatial scales (catchment and sub-catchment levels) has found water depth and water velocity to be the most important habitat predictors explaining the spatial distribution of fish. Therefore, we assume that these will also be the most significant habitat variables in shaping the distribution patterns of fish at small spatial scales (micro-spatial scale). Large individuals find more favourable hiding and resting places in deeper habitat patches than in shallower waters and have better swimming ability against strong water currents than small individuals. Therefore, we expect that the habitat use of juvenile and adult individuals of large-bodied species will differ to a greater degree than in the case of small-bodied species, and there may be greater intraspecific differences in habitat preference in the case of large-bodied species.

4.e Is there a relationship between the degree of intraspecific ontogenetic habitat change (preference shift along habitat gradients) and age (body length)?

Hypothesis:

The growth rate of fish (change in body length per unit time) decreases with age. As a result, during the early life stage (first and second year of life), there are larger relative increases in total body length and in the size of body parts (e.g. mouth size, fin size) than during the later life stage. We assume that the larger rate of body size changes during the young life stage provides individuals with more opportunities to exploit resources other than those they currently use (food, habitat). On the other hand, the lower relative growth at older ages limits this opportunity, and individuals may not use resources or only slightly different from those they currently use. Regarding habitat use, we therefore expect that fish belonging to young age groups will experience a greater shift in preferred environmental values along habitat gradients than in the case of older age groups of the same species.

4.f Is the maximum degree of shift along habitat gradients observed in growth transitions between successive life stages (size classes) related to the maximum adult body size of fish species?

Hypothesis:

Large bodied fish species that reach a larger maximum body length as adults grow faster in their youth than young individuals of the same age of small bodied fish species that reach a smaller maximum body length as adults. Therefore, we expect that the maximum value of ontogenetic habitat shift (preference shift along habitat gradients) of fish species is positively related to the maximum body size of the species as adults. In other words, we predict that large bodied species will show a larger degree of ontogenetic habitat shift than small bodied fish species.

2. MATERIALS AND METHODS

2.1. Fish faunistical survey of the upper (submountain) and middle (highland) Tarna watershed

In 2018, we conducted a general fish fauna survey at a total of 21 sampling sites on the Tarnán, Ceredi-Tarnán, Parádi-Tarnán, and Ilona streams. The sampling methodology followed the recommendations of the National Biodiversity Monitoring System. The length of the sampling sections varied between 150 and 200 m, depending on the sampling conditions. We also used the data from the faunistic survey (hereinafter referred to as *our own faunistic data*) to synthesise an overview of the fish fauna of the Tarna, Ceredi-Tarna, and Parádi-Tarna rivers based on literature sources.

2.2. An overview of the fish fauna of Tarna, Ceredi-Tarna, and Parádi-Tarna based on sources published over the past 50 years and our own survey

2.2.1. Collection and selection of source documents and the breakdown of the examined time interval

The type of documents containing relevant data (e.g., journal articles, conference presentations, theses, etc.) was different. Because of it, these documents will be referred to collectively as *source works* (or *sources* for short). The sources were collected from the 1970-2020 publication interval. We examined 57 sources, and from those, 47 contained usable data: observation of a given species (1 = presence, 0 = absence), name of the watercourse, species observation's calendar year or interval of years, and location of the observation. The faunistical data covered the period between 1979 and 2019, which is also the *entire examination interval* of our research. We divided the entire study period into four smaller periods (hereinafter referred to as *periods*). The first period covers the eight years between 1979 and 1986, the second period covers the 12 years between 1988 and 1999 (none of the sources contained fish fauna information for 1987), the third period covers the ten years between 2000 and 2009, and the fourth period covers the ten years between 2010 and 2019. The data for the fourth period were analysed in conjunction with our own faunistic data.

2.2.2. Analysis of spatial and temporal occurrences – Fauna integrity of species

The hierarchical classification of species was performed separately for the three streams based on the spatial and temporal occurrence data of the species. The fish species data we used for the classification were (1) the detection data for the four study periods (binary coded variable), (2) the spatial frequency of occurrence (a discrete quantitative variable), and (3) the temporal frequency of occurrence within the period (a discrete quantitative variable). The species association matrix was generated using the Gower index proposed for the analysis of mixed-scale data, and the Ward algorithm was used for the classification.

To determine the stability of species occurrence and their level of integrity in the fauna, we created the fauna integrity score (*FIS*) of the species. The FIS_i value of a given species was calculated by adding the relative spatial (Fs_i/Fs_{max}) and relative temporal (Ft_i/Ft_{max}) detection frequencies of a given species. The Fs_i is the number of detection locations of a given species, and the Fs_{max} is the number of detection locations of the species detected from the most locations. The Ft_i is the number of temporal detection years of a given species, and the Ft_{max} is the number of detection years of the species detected from the most years. The *FIS* value range is between (0, 2]. Based on the *FIS*, species were classified into three integrity categories: (1) strongly integrated, permanent, base species, primarily characteristic species of the fauna, which are frequently observed both in space and time; (2) loosely integrated, secondarily characteristic species of the fauna, which are only frequently observed in space or time; and (3) non-integrated, occasional species, which are rarely observed both in space and time. The range of values for the fauna integrity categories was defined as follows: the score for strongly integrated species was [1, 2], for loosely integrated species was [0.5, 1), and for non-integrated species was (0, 0.5). The *FIS* were calculated separately for the three streams because of the differences between the maximum values of spatial and temporal detection frequencies; therefore, a species had different *FIS* values depending on the stream.

2.3. Relative importance of meso- and micro-scale habitat variables

2.3.1. Field data collection

The study was conducted on a small watercourse in a highland stream (Tarna stream at Kápolna village) and a submountain stream (Kemence stream at Bernecebaráti village). Sampling was carried out in Kápolna between August 24 and 27, 2020, and in Bernecebaráti between August 31 and September 4, 2020, during daytime. Fish sampling was carried out in an area of approximately 1 m² (microhabitat patches) using the point abundance method by wading with backpack electric fishing gear.

Micro-spatial scale variables were recorded in microhabitat patches (sampling patches), while meso-spatial scale variables were recorded along a sampling transect perpendicular to the stream and crossed the centre of the sampling patch. The habitat variables recorded in the microhabitat patches were the water velocity; water depth; visually estimated percentage cover of aquatic vegetation (emerged, submerged, floating-leaved vegetation, filamentous algae); of living tree roots (FR: fine roots, CR: coarse roots); and of organic debris of vegetation (LWD: large woody debris, FWD: fine woody debris, MD: macrophytic detritus); and the distance from bank of the centre point of the patch. Habitat variables recorded at the two end points of the sampling transect: the type of riparian vegetation (woody and herbaceous vegetation, margin vegetation, overhanging vegetation), undercut bank, FR and CR, wetted width, bank slope, and channel side slope. Variables recorded along the transect: at five sampling transect points approximately equidistant from each other, we recorded the water depth, visually estimated the dominant substrate type, and recorded the presence of aquatic vegetation and vegetation organic debris. Water velocity for the transect was also recorded at the right middle, left middle and middle positions. The distance between the neighbouring sampling points and the length of the sampling section were measured.

2.3.2. Statistical data processing of habitat variables

For the analysis we used the field-measured (non-derived) variables and variables derived from the field-measured variables. From the field-measured and derived variables, the meso-scale variables were the wetted width, mean bank slope, bank slope asymmetry, mean channel side slope, channel side slope asymmetry, mean water velocity and velocity asymmetry, mean water depth, woody and herbaceous vegetation, overhanging vegetation, margin vegetation, large woody debris and fine woody debris, fine roots and coarse roots of living trees at transect end points. The frequency of occurrence of the following variables: bedrock, marl, clay, fine sediment, sand, fine gravel, coarse gravel, cobble, boulder, large woody debris, fine woody debris, macrophytic detritus, coarse roots and fine roots of living trees, emerged aquatic vegetation, submerged aquatic vegetation, floating-leaved aquatic vegetation, and filamentous algae.

The following field-measured variables and derived variables were the micro-scale (patch) variables: distance from bank, mean water velocity, mean water depth, depth asymmetry in patch, the proportion of substrate fractions expressed as a percentage by weight, the percentage coverage of large and fine woody debris, of the macrophytic detritus, of coarse and fine living tree roots, of emerged vegetation, of submerged vegetation, of floating-leaved vegetation, and of filamentous algae.

In order to identify meso- and micro-scale variables relevant to fish habitat use and to reduce the number of variables, we performed a preliminary variable selection for the two sampling sites and the two spatial scales separately.

To generate spatial autocorrelation modelling covariates (spatial MEMs), we used the distance between directly adjacent sampling patches in space, while to generate temporal covariates (temporal MEMs), we used the sampling time of the patches in Moran's eigenvector mapping (MEM).

2.3.3. Fish size classification

Rare species, which occurred in less than 10% of sampling patches, were excluded from further analysis. Based on the body length frequency distributions of the remaining species, we performed size classes for each species. The length frequency distributions were performed from the pooled body length data from two sampling sites. The classes of individuals formed by the classification of individuals are referred to as species size classes. Rare species size classes those occurred in less than 4% of the sampling patches were also excluded from further analysis. Finally, the data of species size classes were Hellinger transformed.

2.3.4. Main statistical analyses: forward selection, variance partitioning, partial redundancy analysis (pRDA)

The main analyses were performed separately for the two study site. A multivariate forward selection procedure was used to identify relevant spatial, temporal, and habitat (micro- and meso-scale) variables.

Subsequently, we applied multivariate variance partitioning with three explanatory variable groups (species size classes vs. mesohabitat variables, microhabitat variables, and spatial and temporal covariate variables). Using this procedure, we divided the total variance of the size-grouped species community into variance proportions explained by mesohabitat variables, microhabitat variables, and spatial and temporal covariates. We used the adjusted R^2 values calculated for each variance fraction to compare the relative importance of meso-scale factors, micro-scale factors, and covariates.

Finally, we constructed a pRDA model that allowed us to assess the similarities and differences in fish–environment associations between and within species. The dependent variables of the model were species size classes, the explanatory variables were meso- and micro-scale habitat variables, and the MEM variables were included as covariates in the model. The statistical significance of the marginal effects of environmental variables and the ordination axes was examined using permutation tests, while the contribution of habitat variables to the ordination axes and the relationship between species size classes and ordination axes were examined using Pearson's correlation.

2.4. Body size-dependent fish—environment associations at micro-spatial scale in submountain small streams

2.4.1. Field sampling

Data collection was carried out at seven sampling sites in five submountain small streams in the sumer of 2016 and 2017: Kemence stream at Bernecebaráti village in the Börzsöny Mountains, Kemence stream at Kishuta and Kőkapu villages in the Zemplén Mountains, Parádi-Tarna stream in the Mátra Mountains at Sirok and Recsk villages, Szentjakabi stream in the Transdanubian Hills at Felsőjánosfa village, and Zala stream in the West Hungarian Borderland at Őriszentpéter village. The fish assemblage was sampled and the sampling patches were marked as described in Section 2.3.1.

After fish sampling, we recorded the habitat variables of the sampling patches (microhabitats): water velocity, water depth measured at five points within the patch, distance from bank of the centre point of the path, the distance between immediately adjacent patches, and the visually estimated cover of substrate fractions and of the coarse and fine woody debris.

2.4.2. Species selection and size classification

Exclusively, we included those species in the analyses which presented at least three sampling sites and presented at least ten percentages of the number of sampling patches. Six species met the criteria, and their individuals were classified into species size classes based on the body length frequency distribution by species as described in Section 2.3.3. Finally, the data of the six species and 20 species size classes were Hellinger transformed.

2.4.3. Field-recorded and derived habitat variables

Variables with low variance were either excluded from further analyses or new, pooled variables were created to avoid the loss of information resulting from their exclusion. Four pooled substrate variables were created: substr1 (fine-grained substrate category), substr2 (fine gravel substrate category), substr3 (coarse gravel substrate category), and substr4 (coarse-grained substrate category). Heterogeneity of substrate composition within patches was quantified by calculating Shannon diversity, which included all original substrate categories estimated in the field. The maximum, minimum, mean, standard deviation (SD), and coefficient of variance (CV) were calculated for water depth and water velocity. To reduce the number of correlated variables, we applied principal component analysis (PCA) to the mean values, standard deviation, and coefficients of variance of water depth, of water velocity, and of substrate diversity. From the PCA analysis, only the principal components with eigenvalues greater than the mean eigenvalue were retained: PC1 and PC2. The water depth SD and water depth CV were related to the PC1 axis, and the water velocity SD, water velocity CV, and substrate diversity were related to the PC2 axis. Thus, PC1 represented the water depth gradient, while PC2 represented the water velocity—substrate diversity gradient. The relationship between the variables was examined using Pearson’s correlation.

Finally, a base ten logarithm transformation was performed on the water depth and water velocity, their maximum, minimum, mean, SD, CV, and wetted width. The arcus sinus square root transformation was applied to the variables expressed as percentages: distance from bank, substrate fractions, combined substrate categories, LWD, and FWD. To the values of the PC1 and PC2 variables, we added the absolute value of their minimum value to avoid negative values. Multicollinearity between the variables was examined using pairwise scatter plots, Pearson’s correlation and VIFs.

2.4.4. Main data analyses: pRDA, habitat preference, ontogenetic microhabitat shift

We constructed two pRDA models to explore fish–environment patterns along habitat gradients: in the first model, fish species data (model 1, M1) were the dependent variables, while in the second model, species–size class data (model 2, M2) were the dependent variables. In both pRDA models, the explanatory variables were distance from the bank, wetted width, mean water velocity, mean water depth, substr1, substr3, substr4, PC1, PC2, LWD, and FWD variables. The sampling sites were included in the model as covariates to filter out the confounding effect of differences in fish assemblages between sites. The marginal effects of habitat variables and the significance of canonical axes were tested using permutation tests. The relationships between the canonical axes and habitat variables were examined using Pearson's correlation.

We used Ivlev’s electivity index to assess the direct relationship between habitat variables significant according to the pRDA models and individual species and species size classes. In the M1 model, the significant habitat variables were the mean water depth, the distance from the bank, substr1, substr4, and the mean water velocity. In the M2 model, in addition to the variables listed above, the substr4 substrate category was also significant. We converted the original, field-measured form of the significant habitat variables to an ordinal scale and then calculated the electivity index values of the species and species size classes for the ordinal variable categories. The significance of the preference or avoidance towards a given habitat variable category was revealed using chi-square goodness-of-fit tests.

The degree of ontogenetic habitat shift within species was quantified by Euclidean distances between the centroids of consecutive neighbouring size classes (e.g., the first size class and the second size class) along the M2 model RDA1 and RDA2 axes. Linear regression was used to explore the relationship between the largest observed ontogenetic microhabitat shift within species and the maximum adult body size of the species. The largest values of the habitat shift values calculated for each species (hereafter: the *maximum degree of habitat shift*) were considered as the dependent variable, and the logarithm (base ln) data of the maximum adult body size for each species were considered as the independent variable.

3. RESULTS AND DISCUSSION

3.1. Changes in the research coverage of watercourses and their current fish fauna based on classification and fauna integrity score

For the entire study period, we found data on a total of 42 species from the three streams, and we identified a total of 33 locations (Tarna: 39 species, 18 locations; Ceredi-Tarna: 14 species, nine locations; Parádi-Tarna: 14 species, six locations). As the research intensity increased over time, the number of detected species also increased. Before the year 2000, the number of confirmed detected species was 25, and after the turn of the millennium, it was 40. The increase in the number of detected species is probably the combined result of the increase in the number of faunistical studies and the coverage of sampling sites, as well as changes in the sampling methods used.

Based on hierarchical classification, the fish species identified in the Tarna were divided into two large groups, within which six further subgroups were distinguished. The first large group mainly comprised strongly integrated species, while the second large group typically included non-integrated species. Loosely integrated species were mixed in the two large groups. The following species are considered strongly integrated species: roach (*Rutilus rutilus*), pike (*Esox lucius*), chub (*Squalius cephalus*), gudgeon (*Gobio gobio complex*), monkey goby (*Neogobius fluviatilis*), Danube whitefin gudgeon (*Romanogobio vladykovi*), white bream (*Blicca bjoerkna*), stone loach (*Barbatula barbatula*), dace (*Leuciscus leuciscus*), spirlin (*Alburnoides bipunctatus*), perch (*Perca fluviatilis*), common bleak (*Alburnus alburnus*), European bitterling (*Rhodeus amarus*), tubenose goby (*Proterorhinus semilunaris*), and the spined loach (*Cobitis elongatoides* complex). Loosely integrated species are the asp (*Leuciscus aspius*), common bream (*Abramis brama*), Prussian carp (*Carassius gibelio*), ide (*Leuciscus idus*), stone moroko (*Pseudorasbora parva*), pikeperch (*Sander lucioperca*), golden spined loach (*Sabanejewia aurata*), rudd (*Scardinius erythrophthalmus*). And the non-integrated species are the white-eye bream (*Ballerus sapa*), brown bullhead (*Ameiurus nebulosus*), black bullhead (*Ameiurus melas*), Danube catfish (*Silurus glanis*), Volga pikeperch (*Sander volgensis*), sunbleak (*Leucaspius delineatus*), blue bream (*Ballerus ballerus*), zingel (*Zingel zingel*), burbot (*Lota lota*), sunfish (*Lepomis gibbosus*), common nase (*Chondrostoma nasus*), carp (*Cyprinus carpio*), brown trout (*Salmo trutta*), schraetzer (*Gymnocephalus schraetser*), Danube ruffe (*Gymnocephalus baloni*), and the ruffe (*Gymnocephalus cernua*).

The fish of Ceredi-Tarna were also divided into two large groups, which were further divided into four subgroups. The first large group included only species that were strongly integrated into the fauna, while the second large group was characterised by species that were non-integrated into the fauna but also included strongly and loosely integrated species. The species strongly integrated into the fish fauna were the chub, gudgeon, stone loach, spirlin, and the spined loach. There were no loosely integrated elements of the stream fauna. The non-integrated category included the common bream, Prussian carp, black bullhead, white bream, stone moroko, sunbleak, perch, common bleak, rudd.

Based on spatial and temporal perception patterns, fish species were divided into two large groups in the Parádi-Tarna case, within which two further subgroups emerged. The first large group consisted of strongly and loosely integrated species, while the second large group consisted of non-integrated species. The chub, gudgeon, stone loach, and the spirlin were closely integrated into the fauna. Only the stone loach actually belongs to the loosely integrated category. Species that are non-integrated into the fauna include the roach, pike, Prussian carp, white bream, sunfish, perch, pikeperch, common bleak, and the rudd.

3.2. Relative importance of meso- and micro-scale habitat variables

3.2.1. Environmental variables relevant to size-classified fish assemblages

As a result of the variable selection, eight spatial MEM variables, six meso-scale variables (mean water depth, wetted width, mean water velocity, velocity asymmetry, submerged vegetation, and bank slope), and five micro-scale variables (mean water depth, mean water velocity, submerged vegetation, distance from bank, and MD) proved to be significant in Kápolna. In the case of Bernecebaráti, two spatial MEM variables, four meso-scale variables (mean water depth, mean water velocity, FR, and wetted width), and six micro-scale variables (mean water depth, mean water velocity, FGR, water depth asymmetry, distance from bank, and FWD) were significant. Significant temporal MEM variables were not found for any of the examined sites.

3.2.2. The effects of meso-scale variables, of micro-scale variables, and of covariates

The ratio of explained variance within total variance was very similar in both sites examined. In Kápolna, the total explained variance was 24.4%. The part explained by purely meso-scale variables was 9.02% (df = 6, F-statistic = 1.477, p-value = 0.004, adjusted R2 = 0.022), the part explained by purely micro-scale variables was 38.93% (df = 5, F-statistic = 3.413, p-value = 0.001, adjusted R2 = 0.095), the part explained purely by spatial covariates (spatial MEMs) was 8.61% (df = 8, F-statistic = 1.350, p-value = 0.01, adjusted R2 = 0.021), the part explained by shared meso- and micro-scale habitat variables was 23.36%, the part explained by shared meso-scale variables and spatial covariates was 8.60%, the part explained by shared micro-scale variables and spatial covariates was 7.79%, and the part explained by shared meso-, micro-scale variables and spatial covariates was 8.61% from the total explained variance. The unexplained part of the total variance was 75.6%. In Bernecebaráti, the total explained variance was 22.96%. The part explained by purely meso-scale variables was 4.36% (df = 4, F-statistic = 1.189, p-value = 0.097, adjusted R2 = 0.010), the part explained by purely micro-scale variables was 35.71% (df = 6, F-statistic = 2.553, p-value = 0.001, adjusted R2 = 0.082), the part explained purely by spatial covariates (spatial MEMs) was 0.87% (df = 2, F-statistic = 1.102, p-value = 0.329, adjusted R2 = 0.002), the part explained by shared meso- and micro-scale habitat variables was 47.91%, the part explained by shared micro-scale variables and spatial covariates was 1.74%, and the part explained by shared meso- and micro-scale variables and spatial covariates was 9.58% from the total explained variance. The unexplained part of the total variance was 77.0% (Fig. 1).

Although the species composition of the submountain and highland sites was different, meso- and micro-scale habitat variables and spatial covariates played a similar relative role in shaping the size-structured fish assemblages' distribution within the stream reach of the two stream types. In both small stream types, the effect of purely meso-scale habitat variables was lower than both the effect of purely micro-scale habitat variables and the purely effect of shared meso- and micro-scale habitat variables, but in the case of the submountain sampling site, the purely effect of shared meso- and micro-scale variables was much greater than in the case of the highland sampling site. Furthermore, in the highland stream reach, the effect of purely micro-scale habitat variables was greater than the pure effect of shared meso- and micro-scale habitat variables, while in the submountain stream reach, the opposite was observed. A significant purely spatial effect was not detected in either case. Although micro-spatial effects had a greater influence on the spatial distribution of size-structured fish assemblages than meso-spatial effects, a significant part of the diversity of microhabitats is shaped by the heterogeneity of the meso-spatial habitat structure of the stream reach, as indicated by the relatively high values of the shared variance fraction of meso- and micro-spatial variables.

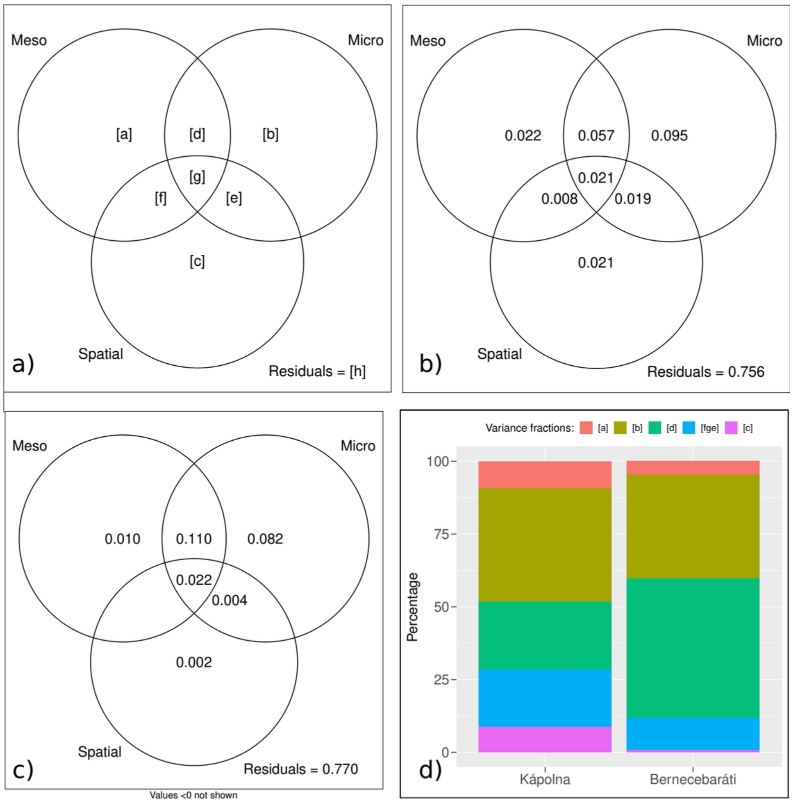

Figure 1. The results of variance partitioning on the relative role of meso-scale, micro-scale, and spatial covariates in the spatial distribution pattern of species size classes within a stream reach. a) Variance fractions identified from a three-table variance partitioning procedure: [a] pure meso-scale, [b] pure micro-scale, [c] pure spatial, [d] spatially unstructured, shared meso-micro-scale, [e] spatially structured micro-scale, [f] spatially structured meso-scale, [g] spatially structured, shared meso-micro-scale, [h] unexplained (residual) variance. b) and c) Results of the three-table variance partitioning procedures: variance fractions as adjusted proportions (adjusted R^2) of the total variance: b) Kápolna and c) Bernecebaráti (the variance proportion at the intersection of 'Meso' and 'Spatial' is not shown due to its negative value, –0.0004). d) Variance fractions as percentages of the total explained variance.

3.2.3. Fish–environment associations, habitat gradients

After controlling for spatial covariates, habitat variables explained 23.7% of the total variance at Kápolna (adjusted $R^2 = 0.175$) and 28.0% at Bernecebaráti (adjusted $R^2 = 0.202$). At both sites, the RDA1, RDA2, and RDA3 axes were significant ($df = 1$, $4.210 \leq F$-

statistic $\leq$ 15.572, 0.0002 $\leq$ p-value $\leq$ 0.0198). At Kápolna, the RDA1 axis corresponded to the habitat gradient formed by the variables of the distance from bank and water velocity of the patch, and the submerged plant and macrophytic detritus of the patch. On the RDA2 axis, the wetted width and the distance from bank of the patch gradient was represented. On the RDA3 axis, a water velocity—water depth gradient was represented; in the formation of it, both meso- and micro-scale habitat variables participated (Fig. 2). At Bernecebaráti, on the RDA1 axis, an environmental gradient formed by the water depth and depth asymmetry of the patch, and both meso- and micro-scaled water velocity was represented. Along the RDA2 axis, the gradient was formed by the distance from bank and water velocity of the patch and the wetted width. On the RDA3 axis, the fine gravel substrate fraction of the microhabitat patch gradient was depicted (Fig. 3).

Because the selection of environmental variables included meso-scale water depth, wetted width, and water velocity, and the micro-scale water depth, water velocity, and distance from bank were selected for both sampling sites, we assumed that the wetted width, water velocity, and water depth variables are universal habitat characteristics independent of the stream type, which most affect the spatial distribution pattern of fishes within reach. However, based on the results of the partial redundancy analysis, the meso-scale wetted width and the micro-scale water depth and submerged vegetation variables proved to be significant in the highland stream type, while in the submountain stream type, there were not any significant meso-scale variables, but from the micro-scale variables, distance from bank, water depth, fine gravel substrate fraction and fine woody debris were significant. However, there were only two habitat variables (micro-scale water depth and distance from bank) that seemed to be decisive in terms of the spatial organisation of the size-structured fish assemblages of both examined stream reaches. The difference in significant environmental variables may stem from the different character of the two stream reaches.

In general, many species showed size-dependent relationships with the RDA axes at both sites, but for some species, there was a strong or slight separation of size classes within species (Fig. 2), while in some cases all size classes of a given species showed similar associations along habitat gradients. For species that had multiple size classes, we typically observed a gradual shift in their habitat requirements with increasing body size (Fig. 2). However, for some species that also had size classes that overlapped in habitat, smaller size classes had slightly wider niches along habitat gradients, and this niche width gradually decreased with increasing body size, thus we observed a kind of niche narrowing (Fig. 3).

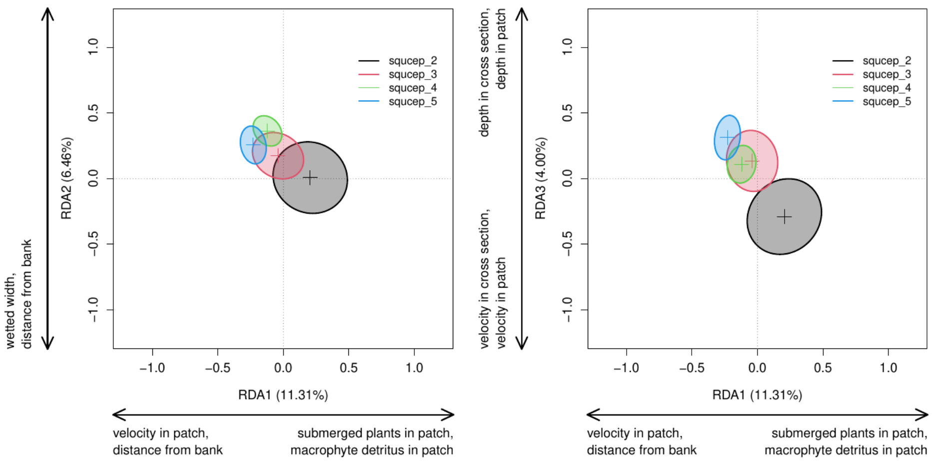

Figure 2. Example of ordination plots of partial redundancy analysis with species size classes at the Kápolna sampling site. This example plot shows the size classes of the chub, the number in the size class designation is in increasing order with increasing body size or size class from the smallest (squcep_2) to the largest (squcep_5). The left plot shows the ordination space location of the species size classes formed by the RDA1 and RDA2 axes, while the right plot shows the ordination space location of the species size classes formed by the RDA1 and RDA3 axes. The percentage value in parentheses next to the RDA axis labels shows the percentage of the total explained variance covered by the given axis. The arrows after the RDA axis labels indicate the gradients formed by the meso- and micro-scale variables. Meso-scale variables: wetted width, velocity in cross section, depth in cross section. Micro-scale variables: distance from bank, velocity in patch, submerged plants in patch, macrophyte detritus in patch.

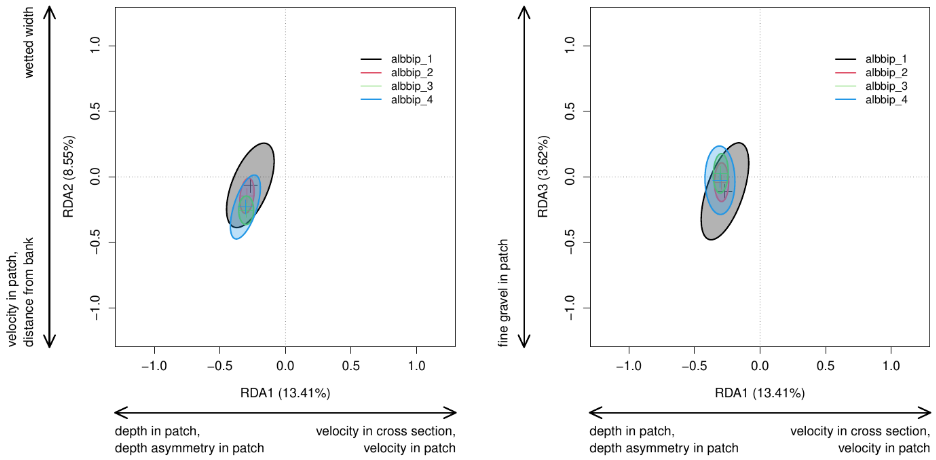

Figure 3. Example of ordination plots of partial redundancy analysis with species size classes at the Bernecebaráti sampling site. This example plot shows the size classes of the spirlin, the number in the size class designation is in increasing order with increasing body size or size class from the smallest (albbip_1) to the largest (albbip_4). The left plot shows the ordination space location of the species size classes formed by the RDA1 and RDA2 axes,

while the right plot shows the ordination space location of the species size classes formed by the RDA1 and RDA3 axes. The percentage value in parentheses next to the RDA axis labels shows the percentage of the total explained variance covered by the given axis. The arrows after the RDA axis labels indicate the gradients formed by the meso- and micro-scale variables. Meso-scale variables: wetted width, velocity in cross section. Micro-scale variables: distance from bank, velocity in patch, depth in patch, depth asymmetry in patch, fine gravel in patch.

Because we examined only one sampling reach from each of the small stream types (i.e., one submountain stream reach and one highland stream reach), there is no statistical repetition from the habitats, so the present results can only be considered a case study. However, the results may provide a basis for more targeted continuation of the research.

3.3. Relationships of fish body size and habitat variables in submountain small streams

3.3.1. Pattern of species in ordination space

In the case of the M1 model, 28.82% of the total variance was explained by the confounding effect of sampling sites, 15.17% by habitat variables, and 56.01% by residuals. The two significant axes (RDA1: p-value < 0.001, df = 1, F-statistic = 39.831; RDA2: p-value < 0.001, df = 1, F-statistic = 13.505) together accounted for 85.99% of the total explained variance: RDA1 accounted for 64.22% of the total explained variance, while RDA2 accounted for 21.77%.

According to the model, significant habitat variables were mean water depth, substr1 substrate category, distance from bank, and mean water velocity. The RDA1 axis was associated with mean water depth ($r_p = 0.585$), while the RDA2 axis was associated with mean water velocity ($r_p = 0.341$) and the substr1 substrate category ($r_p = 0.327$); hence, the first axis represented a water depth gradient, while the second axis represented a water velocity–substrate gradient.

Along the main environmental gradients, the fish species were relatively well separated from each other: three groups were visible along both gradients. At low water depths, the stone loach was located; in an intermediate position were the gudgeon, European minnow (*Phoxinus phoxinus*), and Carpathian barbel (*Barbus carpathicus*), while at high water depths the chub and spirlin were located. Along the water velocity–substrate gradient, the spirlin was oriented towards the parts with high water velocity and coarser substrate; the European minnow and stone loach were located in the intermediate position; and the chub, gudgeon, and Carpathian barbel were located in the parts with low water velocity and fine-grained substrate (Fig. 4).

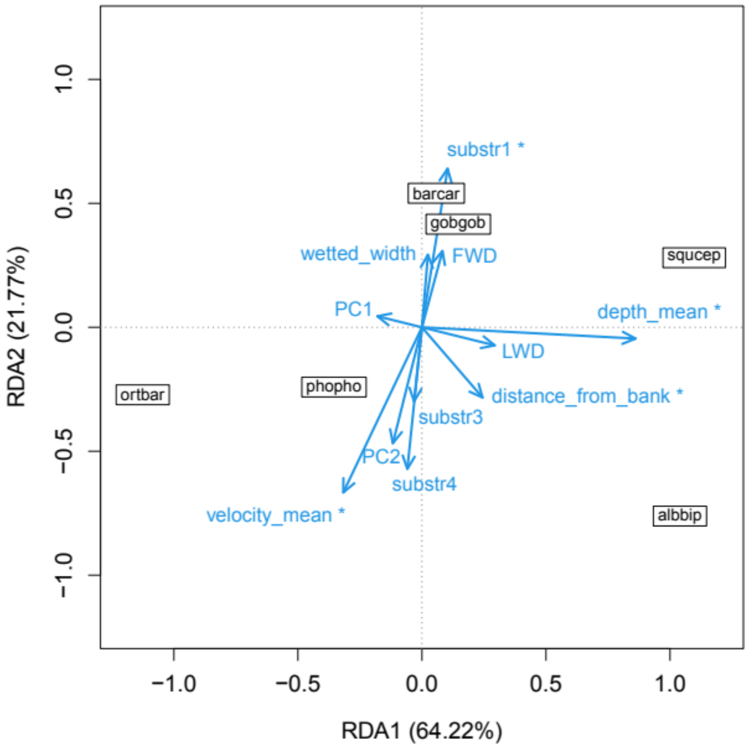

Figure 4. Ordination biplot of the species partial redundancy analyses model (non-size-dependent aspect, M1). Arrows represent the habitat variables. Asterisks denote statistically significant habitat variables. Framed labels represent species. Percentages in the axis labels are the proportions that the given canonical axis explains purely (i.e. without the sampling sites) by habitat variables of the model. Species labels: stone loach (ortbar), European minnow (phopho), Carpathian barbel (barcar), gudgeon (gobgob), chub (squcep), spirlin (albbip).

3.3.2. Pattern of species size classes in ordination space

In the case of the M2 model, 15.72% of the total variance was explained by the confounding effect of sampling sites, 12.53% by habitat variables, and 71.75% by residuals. The two significant axes (RDA1: $p\text{-value} < 0.001$, $df = 1$, $F\text{-statistic} = 21.505$; RDA2: $p\text{-value} < 0.001$, $df = 1$, $F\text{-statistic} = 6.923$) together covered 72.68% of the total explained variance: RDA1 accounted for 54.98% of the total explained variance, while RDA2 accounted for 17.70%.

According to the model, significant habitat variables were mean water depth, substr1, substr4, distance from bank, and mean water velocity. The RDA1 axis was associated with mean water depth ($r_p = -0.701$), while the RDA2 axis was associated with mean water velocity ($r_p = -0.450$) and the substr1 substrate category ($r_p = 0.571$), so that the first axis represented a water depth gradient, while the second axis represented a water velocity–substrate gradient.

For most species, the smallest size classes were located at the lower values of the water depth gradient, while the largest size classes were oriented towards the higher values of the gradient. The intermediate size classes were located between the smallest and the largest size classes. The smallest size classes of the Carpathian barbel, chub, gudgeon, and stone loach were located at the shallow part of the gradient. The smallest size classes of the European minnow and of the spirlin were oriented somewhat towards deeper waters compared to the smallest of other species along the gradient, while the largest size classes of the chub, Carpathian barbel, gudgeon, and spirlin were located at the highest water depth values. The exception to this pattern was the stone loach and the European minnow, as their small and large size classes were located close to each other along the water depth gradient. Along the water velocity–substrate gradient, the smallest size classes of the different species were typically more markedly separated from each other. The smallest size classes of the Carpathian barbel and chub were oriented towards low water velocity and fine substrate; the smallest individuals of the gudgeon were somewhat located at the higher water velocity and slightly rougher substrate but were still closer to the two species mentioned above, and the smallest size classes of the European minnow and of the spirlin were located at the intermediate position of the gradient. Among the smallest size classes, the smallest individuals of the stone loach were oriented toward the higher water velocity and coarser substrate (Fig. 5).

Based on the results, the key variables influencing the microhabitat use of fish communities in submountain small streams are water depth, water velocity, and substrate composition, which reflect the physical habitat structure resulting from the hidro-geomorphology. The habitat variables predicting habitat use were essentially the same regardless of whether or not the body size of the individuals was taken into account; however, the body size approach revealed a significantly more nuanced pattern.

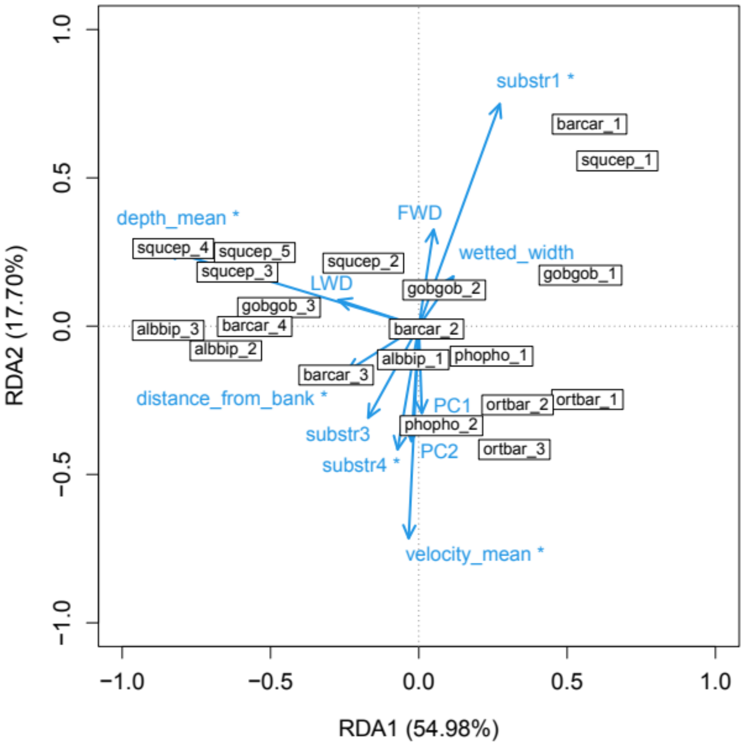

Figure 5. Ordination biplot of the species size class partial redundancy analyses model (size-dependent aspect, M2). Arrows represent the habitat variables. Asterisks denote statistically significant habitat variables. Framed labels represent species size classes. Percentages in the axis labels are the proportions that the given canonical axis explains purely (i.e. without the sampling sites) from the variance explained by habitat variables of the

model. For the species labels see Fig. 4. The number in the size class designation is in increasing order with increasing body size or size class from the smallest to the largest.

3.3.3. Ontogenetic habitat shifts: differences between size classes, and the relationship between the degree of maximum habitat shift and maximum body size of species

In general, the greatest degree of ontogenetic microhabitat shift within a species was observed at the body size transition between the smallest and the next size class of the species. The degree of habitat shift decreased at the next ontogenetic size class transition, i.e., from the second to the third size class (Table 1). The largest differences occurred between the successive smallest size classes, while these differences gradually decreased with further increase in body size. This can be explained by the ecological and biological growth principle related to the asymptotic growth of fish, according to which the relative change in body proportions and functional characteristics is much greater in the juvenile stage of individuals than in adulthood. Consequently, young individuals are more capable of exploring and utilising new habitats, while in older life stages, microhabitat use stabilizes.

Table 1. The degree of ontogenetic habitat shift between successive species size classes (sc). The first column contains the common name of the species. Columns 2–5 contains the degree of habitat shifts between successive size classes (sc). For example, the degree of transition from the first size class to the second size class due to the increase in body size and the corresponding shift in habitat preferred by the second size class in the case of the chub is 0.936, which is a unitless indicator. The 'Na' in the columns indicate that since the given species does not have more size classes, the degree of ontogenetic habitat shift could not be calculated. The values highlighted in bold indicate the maximum value of the habitat shift for a given species.

Species	1. sc → 2. sc	2. sc → 3. sc	3. sc → 4. sc	4. sc → 5. sc
Chub	**0.936**	0.428	0.218	0.265
Carpathian barbel	**0.883**	0.342	0.348	NA
Stone loach	**0.186**	0.151	NA	NA
Spirlin	**0.634**	0.199	NA	NA
Gudgeon	0.462	**0.560**	NA	NA
European minnow	**0.364**	NA	NA	NA

The maximum value of ontogenetic habitat shift within species tended to be higher in fish species with larger maximum adult body size. However, the relationship was not statistically significant (F-statistic = 6.524, df = 4, p-value = 0.063, adjusted R^2-value = 0.525). The equation of the line estimated by the model is $Y = -1.6733 + 0.4321 \times \log(X)$ (Fig. 6). The relationship between the degree of ontogenetic habitat shift and the maximum adult body size of species may indicate that growth strategy and behavioural adaptations (e.g., benthic *vs.* pelagic lifestyle) together shape habitat use patterns. We note that as for the investigation of the relationship between the degree of ontogenetic habitat shift and the growth characteristics of fish species, which was based on the analysis of a small sample size (only 20 size classes of six species), further targeted research is needed to clarify the relationships.

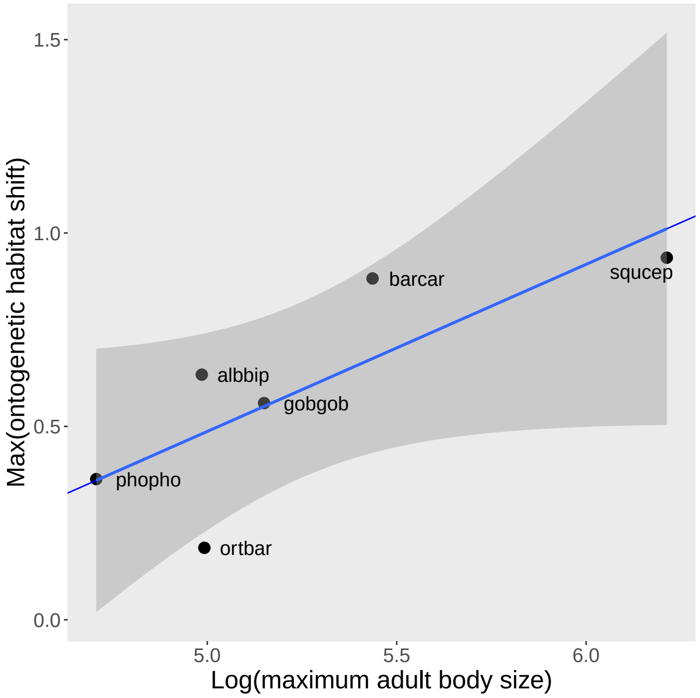

Figure 6. Maximal degree of the within-species ontogenetic shift as a function of the maximal body size of six fish species in submountain streams in Central Europe. The solid blue line represents the expected value (i.e. mean), and the grey band is the 95% confidence interval for the mean. The estimated model of the relationship is $Y = -1.6733 + 0.4321 \times \log(X)$ *(adjusted R2 = 0.5249). Labels of species: European minnow (phopho), stone loach (ortbar), spirlin (albbip), gudgeon (gobgob), Carpathian barbel (barcar), chub (squcep).*

4. CONCLUSIONS AND RECOMMENDATIONS

4.1. The importance of the long-term faunistical data collection and the properly designing monitoring system

Properly planned and implemented monitoring can shed light on changes in the fish fauna of waters. The decline or possible disappearance of a species, the appearance of a new (non-native, invasive) fish species, or the monitoring of the fish assemblage composition of a water body in a given area and the nature and dynamics of the changes occurring in it can provide a more accurate view of the situation by operating a monitoring system with appropriate coverage (i.e., the designation of sampling sites with an appropriate number and density in space) carried out at long-term, regular intervals – preferably at the same sampling sites. The monitoring system can be supplemented by the application of the fauna integrity score, which can help experts to explore changes not only in a given species but also in a local fish assemblage (for example, identifying species that are disappearing or expanding). The integrity score can draw attention to a species that is "problematic" in some way, thereby bringing it into the focus of conservation experts and helping to develop targeted conservation management.

4.2. The relationship between meso- and micro-spatial scales and their impact on the organization of fish assemblages

According to our results, regardless of the type of watercourse, the combined effect of microhabitat variables and micro- and mesohabitat variables played a greater role in shaping the spatial distribution pattern of fish than mesohabitat variables alone. This suggests that micro- and meso-scale characteristics do not act independently of each other, i.e., the explanatory power of habitat variables depends on the spatial scale of the given variable within a given small stream reach. The effect of meso- and micro-scale environmental factors is typically hierarchical: habitat characteristics interpreted at the meso-scale determine what microhabitat characteristics can develop in a given cross-section. In other words, although microhabitat characteristics can directly influence the choice of fish habitat depending on the species and body size of the individuals, a significant part of the variability of microhabitats is fundamentally derived from the meso-scale characteristics of the stream reach.

At the microhabitat level, the spatial organization of fish assemblages (with and without taking into account body size) is mostly determined by water depth, flow velocity, substrate composition and distance from bank. Comparing all this with the results of previous research at larger spatial scales, independent of the dissertation research, it seems that the pattern-forming significance of these habitat variables for species assemblage structure applies regardless of spatial scale, so these three key variables can be universal predictors of habitat use by stream fish at multiple spatial scales. The body size analysis further refined the interpretation of these relationships and highlighted that the habitat requirements of different size classes – especially young, first-year individuals – can differ significantly from those of adults. Furthermore, taking into account individual body size within a species revealed ontogenetic habitat shifts. Heterogeneous habitats support inter- and intra-species (size-dependent) habitat differentiation and life-stage-dependent habitat changes. Because shifts in habitat use occur gradually, the streams with diverse habitats support the full completion of the life cycle of individuals through favourable living conditions. However, small-scale habitat diversity is a function of larger-scale environmental characteristics, so larger-scale variables can indirectly affect the structure and spatial pattern of local (small-scale, within-reach) fish assemblages.

Extreme weather events caused by climate change and other direct human impacts also threaten the biological integrity of fish assemblages in submountain and highland small streams. The severity of these events can be exacerbated if the physical habitat structure of the streambed is homogeneous. Focusing on maintaining and restoring the heterogeneity of the mesohabitat structure (e.g., meandering course, pools, and riffles) appears to be an effective conservation strategy for the local protection of size-structured fish populations, as mesoscale hydro-geomorphological diversity can also encompass significant micro-scale habitat variability, which is necessary for different size classes. One way to preserve and restore mesohabitat diversity is to protect or restore natural riparian forest bands along watercourses, giving preference to native tree species where possible. Where the preservation or restoration of riparian forest bands may pose a flood risk to urban areas, it is advisable to concentrate rehabilitation on sections between settlements, while ensuring longitudinal connectivity so that fish can move freely between restored and modified watercourse sections. In order to ensure the longitudinal permeability of watercourses, the function of drop structures on small watercourses should be reviewed and, if possible, dismantled or replaced with structures that are more passable for fish, such as block ramps.

Overall, natural channel morphology and substrate heterogeneity, as well as the presence of riparian vegetation, are essential for maintaining meso- and micro-scale habitat diversity within the watercourse section necessary for fish. However, nature conservation measures aimed at achieving habitat diversity for the effective conservation and/or restoration of habitats should be extended to other spatial scales, such as the riparian zone along watercourses and the landscape characteristics of the catchment area. A complex approach, understanding the wider environment of the local habitat, and exploring the relationships between them are essential for effective local conservation measures.

5. NEW SCIENTIFIC THESES

1) Using the spatial and temporal occurrence frequencies of fish species, I created a simple numerical indicator – the fauna integrity score – which is suitable for concisely and numerically characterizing the occurrence frequency relationships of species in an area (e.g., watershed, sub-watershed) for a given spatial and temporal interval, based on systematic surveys repeated in space and time.

2) Based on literature data and own faunistical survey data, I have identified the primary or basic species of the fish fauna of the three main watercourses of the Tarna catchment. The basic species of the Tarna stream (between Jászjákóhalma and Sirok villages): roach, pike, chub, gudgeon, monkey goby, whitefin gudgeon, white bream, stone loach, dace, spirlin, perch, common bleak, European bitterling, tubenose goby, spined loach. The basic species of the Ceredi-Tarna stream (between Sirok and Cered villages): chub, gudgeon, stone loach, spirlin, spined loach. The basic species of the Parádi-Tarna stream (between Sirok and Parádsasvár willages): chub, gudgeon, stone loach, spirlin.

3) I explored the most important habitat variables influencing the spatial organization of size-structured fish assemblages in a submountain and a highland small stream at reach-level in the late summer period, which were identical in both types of habitat (water depth within the habitat patch and the distance from bank of the habitat patch).

4) My results indicate that microhabitat variables related to the type differences of stream reaches can also be significant predictors of the spatial distribution of fish within a reach in relation to body size (submerged vegetation within the habitat patch in the case of highland stream type, and grain size of substrate and woody plant debris within the habitat patch in the case of submountain stream type).

5) I have explored the microhabitat variables (water depth, water velocity, substrate composition, distance from bank) that most effectively explain the spatial distribution of size-structured and non-size-structured fish assemblages within submountain small streams during the late summer period. I have pointed out that the microhabitat use of size classes within species is primarily separated along water depth and distance from bank, while the microhabitat use of the smallest size classes among species is typically separated in terms of water velocity and substrate composition. My results confirm that, similarly to large rivers, the distance from bank is also a significant pattern-forming factor in wadable small streams that are only a few metres wide.

6) I found that the degree of ontogenetic microhabitat shift typically decreases with increasing body size. I pointed out that the maximum degree of ontogenetic microhabitat shift may be related to the maximum adult body size of the species.

7. PUBLICATIONS ON THE TOPIC OF THE DISSERTATION

Maroda Á. & Sály P. (2025): Interspecific differences and ontogenetic shifts in body size-related microhabitat use by fishes in small, Central European submountain streams. *Journal of Vertebrate Biology* 74: 25078

Maroda Á. & Sály P. (2023): Relative importance of meso- and microhabitat features in the within-reach spatial distribution of size-structured fish assemblages in small streams. *Ecology of Freshwater Fish* 32: 656–672.

Maroda Á. & Sály P. (2022): Link between present day studies and future researches: Methodological issues of fish faunistical reviews and the importance of uniform publication. *Pisces Hungarici* 16: 33–44.

Maroda Á. & Sály P. (2022): Review of the fish fauna of the Tarna, Ceredi-Tarna and Parádi-Tarna streams on the basis of published data collected between 1979 and 2019 and the data of a faunistic survey conducted in 2018. *Állattani Közlemények* 107/1–2: 21–70.

Maroda Á. & Sály P. (2018): Size dependent microhabitat use of fishes in sub-mountain streams. *Pisces Hungarici* 12: 111–122.