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Comparison of Fish Assemblage Diversity in Natural and Artificial Rip-Rap Habitats in the Littoral Zone of a Large River (River Danube, Hungary)

key words: riverine fish, habitat modification, sampling effort, biological traits diversity, beta diversity

Abstract

We studied day-night patterns in fish diversity in natural, gravel-sand stretches and boulder covered rip-rap habitats in the littoral zone of the River Danube. Sample-based rarefaction indicated marked differences in species richness between day and night, and smaller differences between habitats for both day and night. Whereas, individual-based rarefaction indicated no such substantial differences in species richness. However, distinct fish assemblages were found based on relative abundance data, and species of great conservation concern tended to link to natural habitats. The diversity of biological traits/attributes were generally higher in rip-rap habitats. The differences in fish assemblage characteristics between habitats revealed the importance of gravel-sand habitats in maintaining natural assemblages and that rip-rap sections increase compositional beta diversity at the mesohabitat scale.

1. Introduction

Exploring and understanding spatial and temporal patterns in diversity is one of the central themes of ecology and conservation biology (MAGURRAN, 1988). Habitat modification is one of the most important factors affecting the diversity and integrity of freshwater biota (KARR *et al.*, 1985; ALLAN and FLECKER, 1993; RICHTER *et al.*, 1996), and this is particularly true for large lowland rivers. The natural and dynamic riverine landscape diversity (*sensu* ROBINSON *et al.*, 2002) has been seriously altered by intensive land use practices, such as diversions for irrigation, damming, drainage, and various catchment conversion through urbanization, transportation, deforestation and agriculture (POFF *et al.*, 1997; SAUNDERS *et al.*, 2002). In large floodplain rivers, flood control projects have shortened, narrowed, straightened and regulated many river systems, resulting in reduced connectivity between the main channel and the adjacent flood plain (PETTS *et al.*, 1989; DYNESIUS and NILSSON, 1994; POFF *et al.*, 1997). These large scale modifications have led to abrupt declines in the diversity of riverine fauna, and especially fishes (KARR *et al.*, 1985; COPP, 1990; MOYLE and LEIDY, 1992; WELCOMME, 1994; SCHIEMER *et al.*, 2001; HOLČÍK, 2003).

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Although the destructive effects of larger scale (*i.e.*, landscape scale) river regulation on the diversity of fish assemblages have been well documented, much less is known about how smaller (*i.e.*, meso-) scale habitat modifications affect the distribution and diversity patterns of fishes in large rivers. Amongst the meso-habitat scale modifications, shoreline embankment (*i.e.*, the strengthening of the bank with boulder coverage, so called rip-rap) can be one of the most important factors that affects fish assemblage organization (BACALBASA-DOBROVICI, 1985; SCHIEMER and SPINDLER, 1989; JURAJDA *et al.*, 2001). The main function of shoreline embankments is to increase the stability of the bank to combat flooding, waving, and natural bank erosion. In addition, shoreline embankments do not allow natural flow meandering, and therefore preferred over natural reaches for inland navigation (WOLTER and ARLINGHAUS, 2003). However, rip-rap sections may increase meso-habitat level physical diversity and complexity, since boulders, rocks and large stones provide different and more complex substrate material over sand or gravel, which are the general bed materials in the main channel of large rivers (GORDON *et al.*, 1992). If there is a general relationship between habitat structure/complexity and fish diversity (*e.g.*, GORMAN and KARR, 1978; SCHLOSSER, 1991; ERŐS and GROSSMAN, 2005a), then rip-rap sections should increase fish diversity at the meso-habitat scale.

There are contradictions in the few studies that aimed to compare fish assemblage structure between natural and artificial (*i.e.*, rip-rap) shorelines. For example, within the waterways with predominantly artificial bank substrata (rip-rap and sheet pile wall), a significant negative correlation was found between the percentage of artificial sections and species richness of fishes in lowland waterways of North-Germany (WOLTER and VILCINKAS, 1998). Similarly, the highest population density and species richness of 0+ fish was observed along shallow gravel beaches in the Austrian portion of the Danube, and poor 0+ fish assemblages occurred along boulder banks (SCHIEMER and SPINDLER, 1989; SCHIEMER *et al.*, 1991). In contrast, a contrasting pattern was reported for the nursery habitats of 0+ fish in a lowland stretch of the River Morava, Czech Republic, where boulder banks were intensively utilized by fishes in both spring and late summer (COPP and JURAJDA, 1993; JURAJDA, 1999), and this use was size structured (COPP and JURAJDA, 1999). Clearly, more studies are necessary for the generalizations about the role of rip-rap habitats in the diversity of running water fish assemblages. Such studies would increase our knowledge on how fish assemblages react to physical habitat modifications and, in addition, could aid the design of restoration works.

In this paper, we examine patterns in the diversity of fish assemblages in the littoral zone of the River Danube, Hungary, with special regard to the similarities and differences between natural and artificial (*i.e.*, rip-rap) shorelines. Specifically, we examine how three important aspects of diversity, 1) species richness, 2) community composition, and 3) biological trait (*i.e.*, attribute) diversity varies between natural and rip-rap banks, based on a data set collected in the frame of an intensive spatial survey carried out both day and night at two sampling periods in the Hungarian Danube section.

As rip-rap shorelines provide a habitat type which is different from natural littoral zone habitats, we predicted differences in all metrics of diversity between gravel-sand and rip-rap shorelines. However, it was a question how (at what extent) the metrics/variables differ between habitats in relation to sampling effort and how the time of the day (day *vs.* night) and the season affect the diversity-sampling effort relationships. Finally, we were also interested to examine how results based on the recently used indices of biological trait diversity (*e.g.*, BADY *et al.*, 2005) can be used as a surrogate of the more conventionally used indices of species diversity in characterizing mesohabitat level fish assemblage diversity in the River Danube.

2. Methods

2.1. Study Area and Sampling

With its 2847 km length and a drainage area of 796 250 km², the Danube is the second largest river in Europe. In Hungary (Middle-Danube section) the river runs 415 km and has a mean annual discharge of 2000 m³ s⁻¹. The main channel has a width of 300–600 m and its substrate is dominated by gravel and sand.

Data on fish and meso-habitat features were obtained at 43, 500 m long stretches from five sites along the littoral zone of the Danube main channel during two sampling periods in 2004: spring-to-early summer (April to early July), and mid-to-late summer (late July to late September) (ERŐS *et al.*, 2005). To be representative for the Middle-Danube and to embrace landscape level heterogenities the sites/stretches were scattered along a 300 km long section (Fig. 1). The sites were 134 km (\pm 122 S. D.) apart on average from each other and 5–12 stretches were examined at each site depending on the general representativeness of the site to the Middle-Danubian riverine habitat. Note, that except one site further downstream (*i.e.*, 160 km), no sites were selected below Budapest (the capital of Hungary with 2 million people) to avoid possible perturbation effects. Further, the habitat types (*i.e.*, natural or artificial) were equally well distributed in the longitudinal profile of the river, and hence spatial effects did not affect our comparisons. Each stretch was surveyed during day and night-time at 100-m intervals, which were delineated using a GPS unit. Both abiotic and biotic data were compiled at the 100 m level but were subsequently pooled, due to the relatively homogenous nature of each 500 m stretch (see ERŐS *et al.*, 2005), in further analysis except where noted. Finally, the same stretches were surveyed day and night within a sampling period, but not between sampling periods because of the differences in water level between the seasons. The latter determined the availability of inshore areas for effective electrofishing.

For each 500 m long stretch, habitat measurements were made during daytime to estimate mean values for distance from bank, water velocity and depth, with substratum composition, large woody debris and macrovegetation coverage estimated visually as a proportion of the 500 m stretch (ERŐS *et al.*, 2005). Mean distance from the bank (m) was determined by averaging the visual estimates made by the three team members at 20 m intervals (the inter-individual estimates were highly consistent, accurate to within 1 m). Mean water velocity (cm s⁻¹) was calculated from water velocity measurements (FP201



Figure 1. Sampling locations in the River Danube, Hungary. The number of 500 m long study stretches at each location (43 altogether) are given in parentheses.

Global Flow Probe; Global Water Instrumentation, Inc) taken at 20 m intervals, with the boat held stationary in the flow. Mean water depth (cm) was measured with a metre stick at 20 m intervals. The substratum was estimated visually at 20 m intervals and categorized as fine alluvia (silt and sand), gravel and stone (stones and rocks). Percent area covered by large woody debris (LWD) or macrovegetation (predominantly willow sprouts *Salix* sp.) was estimated visually along the approximate 1 m wide strip where the fish samples were taken at each study stretch.

Study stretches were electrofished from a boat, using a DEKA 3000 electrofishing unit (350–450 V, PDC), in a single pass moving slowly downstream as per WOLTER and BISCHOFF (2001) and WOLTER and FREYHOF (2004). At the end of each 100 m section, captured fish were identified, counted and measured in cm for standard length (SL). Fishes were returned into the water \approx 50 m upstream from the next sampling reach in order to avoid recapture (ERŐS *et al.*, 2005). All age groups were considered in the sample, although the method was rather effective in catching juvenile to intermediate age classes and ineffective in catching fish below 2 cm (see Table 1; ERŐS *et al.*, unpublished data). Therefore the abundance of 0+ fish which usually occupy hardly accessible, very shallow habitats (*i.e.*, < 30 cm), and that of old/large specimens which prefer offshore areas, may be underrepresented in the sample. Although this is a well-known bias in boat electrofishing (see SIMON, 1999; GOFFAUX *et al.*, 2005), it should be emphasized that our results are confined to samples collected with the conventional technique of boat electrofishing in the littoral zone of rivers (see Table 2 for general physical characteristics of the habitat types). Note that we used a battery-powered gear with relatively low capacity, which could have affected sampling efficiency. Nevertheless, the standardization techniques used in the statistical analyses (see below) allowed for the unbiased comparison of fish diversity between natural and artificial rip-rap habitats.

2.2. Trait Data Base

We used literature data (*e.g.*, POFF and ALLAN, 1995; LAMOUREUX *et al.*, 2002; SANTOUL *et al.*, 2005; ERŐS, 2005), regional fishery text books (*e.g.*, HARKA, 1997), www.fishbase.org, our own expertise, and additional information from other fish biologists, in this order, to construct a data base of the biological traits of fishes collected during this study. (Note that we use the word “biological trait” throughout the text to be consistent with recent literature, although “biological attribute” can be a more valid expression.) Trait variables were classified in a hierarchical manner. Three main trait groups were defined that may provide the most significant information on the structural and functional composition of fish assemblages (POFF and ALLAN, 1995; GOLDSTEIN and MEADOR, 2004, 2005; SANTOUL *et al.*, 2005): (1) life-history traits, (2) functional (*i.e.*, trophic) traits, and (3) habitat preference. Life-history trait variables were as follows (see Table 1 in ERŐS, 2005): age at maturation, maximum age, maximum length, egg size, mean fecundity, parental care. No exact values were found for the larvae of *Eudontomyzon mariae*, *Zingel zingel* and *Zingel streber* in the literature, as well as for a hybrid. Consequently, we gave approximate values for the *Zingel* species in order to include the Genus in the analysis, but the larvae of lamprey and the hybrid were excluded from the analysis due to insufficient (or absence of) data on their biological traits. We combined and simplified the categorization system of POFF and ALLAN (1995) and GOLDSTEIN and MEADOR (2004) for trophic trait factors and determined five traits: herbivore-detritivore, invertivore, piscivore, planktivore and parasite. No parasitic fish species was found, however during the surveys. For determining habitat trait diversity, three traits were established based on the adaptation and combination of the system of POFF and ALLAN (1995), SCHIEMER *et al.*, (1994), SPINDLER (1997), and GOLDSTEIN and MEADOR (2004): large scale habitat preference, vertical position, and substratum preference. For the large scale habitat preference, five categories were established that provided information on the longitudinal habitat use of species in the Carpathian Basin: small highland stream, small lowland stream, medium river, large river, lentic. For the vertical position two categories were established: benthic, nonbenthic. For the substratum preference four categories were defined: rubble, gravel, fine and various. Finally, while most data, measured on ratio scale could be used for life-history variables (ERŐS, 2005), a fuzzy coding system (CHEVENET *et al.*, 1994) was adopted for constructing the data base of functional and habitat preferences (see Appendix I). Fuzzy scoring allows the more detailed (*i.e.*, finer) classification of species to the biological attribute categories compared with a simple ‘0’ or ‘1’ coding. For example, since fish can be plastic in feeding (food content) in many cases it is hard to force a species to just only one feeding category (*e.g.*, planktivore). In the fuzzy coding system the numbers refer to the approximate affinity of the fish to the trait variable with ‘0’ values indicating no affinity to the highest values (*e.g.*, ‘3’) indicating high affinity. The fuzzy coded data table

therefore inform on the approximate distribution of the species' affinities among the trait variables. For further details see *e.g.*, CHEVENET *et al.* (1994) or BADY *et al.* (2005).

2.3. Statistical Analysis

Of the 43 stretches surveyed, 25 could be categorized as relatively natural (a total of 12.5 km), 12 as boulder covered rip-rap (6 km) and 6 as transitional (3 km) based on a principal component analysis of physical habitat data (see Fig. 2 in ERŐS *et al.*, 2005). For the purpose of this study, transitional stretches were omitted from further analyses. Then a canonical discriminant function analysis (DFA) was performed to validate the separation of the habitat stretches into natural and rip-rap habitats. The environmental data were \log_{10} (mean velocity, mean depth) or square root arcsine transformed (% substratum composition, % woody debris and macrophytes) prior to the DFA analysis. As such, the fish-habitat evaluations were undertaken using the 'habitat categorization approach' (*e.g.*, JURAJDA, 1999; ERŐS and GROSSMAN, 2005b) instead of the 'habitat-gradient analysis approach' (*e.g.*, ERŐS and GROSSMAN, 2005a; ERŐS *et al.*, 2005) to permit the use of randomization procedures for within-category comparisons of fish assemblages and to find indicator species for the habitat categories.

Rarefaction-based randomization techniques (UGLAND *et al.*, 2003) were used to compare how estimated species richness changes in the function of sample size (here 100 m long units) between natural and artificial habitats for both sampling periods and for day and night samples separately. This yielded four species-accumulation curves per sampling period (*i.e.*, two habitat categories, each with one day and night curve). We also standardized our catches according to the number of individuals collected and produced individual-based species richness accumulation curves for the two habitat categories (see GOTELLI and COLWELL, 2001; UGLAND *et al.*, 2003), which also yielded four rarefaction curves per seasonal sample. The advantage of these methods is that they make species richness comparisons independent of the actual sample size or number of individuals collected. In addition, the curves also provide information about how sampling effort affected our estimates.

We applied the recently-developed method of CAO *et al.* (2002, 2003) to compare how sample representativeness, measured as average similarity among replicate samples randomly drawn from a community (*i.e.*, autosimilarity, hereafter AS) changes in the function of sample size in each habitat category. For this purpose, Jaccard's coefficient (JC) was used for sample comparisons based on species presence/absence data, whereas the Bray and Curtis coefficient (BC) was used for sample comparisons based on abundance data (*i.e.*, here, number of individuals collected per species per 100 m long stretch: CPUE data). Consequently, we constructed eight community similarity curves per sampling period (*i.e.*, two habitat categories, each with one day and night curve and two similarity/dissimilarity measures). It should be recognized that beside getting an estimation about how well our samples may represent the 'target community' we wanted to characterize, this method can also be used for the measurement of spatial heterogeneities between samples based on community composition (*i.e.*, compositional beta diversity, see KOLEFF *et al.*, 2003). For example, the more dissimilar the samples from each other at a standardized level of sampling effort in a certain habitat category (*e.g.*, natural stretches) as compared with the samples from another habitat (*e.g.*, rip-rap shorelines) the more diverse their fish assemblages spatially. Finally, similarly to species richness comparisons, the advantage of the AS method was that we could compare the fish assemblage composition of the two kinds of habitats based on a standardized level of community similarity.

Canonical discriminant function analysis (DFA) was performed to investigate whether fish assemblage composition (square root arcsin transformed relative abundance data) between natural and artificial habitats and in day and night were different. To obtain robust and readily interpretable results, samples were pooled according to sampling periods and therefore, four groups of fish assemblages were compared in the final DFA graph (day-natural, day-artificial, night natural, night artificial). Finally, indicator species analysis (DUFRENE and LEGENDRE, 1997) was applied to find indicator species for the different states of habitats and daytime. A conservative confidence limit of $P = 0.01$ was taken in order to increase the sensitivity of the analysis.

Biological trait diversity (BTD) was calculated for life-history traits, trophic guilds and habitat preferences separately. For each calculation, we used RAO's (1982) quadratic entropy index:

$$BTD = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j,$$

where i and j are two species in the sample with S species; d_{ij} is the dissimilarity between species i and j ; and p_i and p_j are the relative abundance vectors of species i and j , respectively. We used Bray and Curtis dissimilarity index to calculate d_{ij} values, thereby expressing the trait dissimilarity between species i and j , using the following formula:

$$d_{ij} = \frac{\sum_{k=1}^T |a_{ik} - a_{jk}|}{\sum_{k=1}^T (a_{ik} + a_{jk})},$$

where k is a biological trait out of T traits defining a group of traits (*i.e.*, life history traits, trophic traits or habitat preference traits), a_{ik} is the affinity value of species i to trait k , and a_{jk} is the affinity value of species j to trait k . Before the calculation, affinity values (see Table 1 in ERŐS, 2005 and Appendix I in this paper) of the species to the traits were standardized to the maximum value within the group of traits observed. Although this transformation was meaningless in calculating trophical or habitat trait diversity (as all of these values varied between 0 (no affinity) to 3 (high affinity), see Bady *et al.*, 2005), its application was necessary to avoid weighting differences in life history traits, which were measured at ratio scale (see ERŐS, 2005, for values). For each sample size (n , number of 100 m long stretches), n number of sample units were drawn randomly and then biological trait diversity was calculated. This process was repeated 1000 times to obtain mean biological trait diversity value for each level of sample size and for each data set.

The DFA-s were performed using STATISTICA (Statsoft, Inc 2000), and the indicator species analysis was undertaken by PC-ORD computer programs (McCune and Mefford, 1997). Finally, self-produced Excel® macros were used for calculating sample representativeness and the diversity of biological traits as a function of sample size.

3. Results

A total of 11 754 specimens were collected and identified to 41 species and one hybrid (Table 1). Of the 42 taxa collected, golden loach (*Sabanejewia aurata*), Danubian roach (*Rutilus pigus*), Danube streber (*Zingel streber*) and rudd (*Scardinius erythrophthalmus*) were collected only at natural shorelines, whereas common carp (*Cyprinus carpio*), pumpkinseed (*Lepomis gibbosus*), rainbow trout (*Oncorhynchus mykiss*), spirlin (*Alburnoides bipunctatus*), and European catfish (*Silurus glanis*) were caught at rip-rap sections exclusively.

Natural and rip-rap stretches were clearly separated along the first canonical discriminant axis based on their habitat characteristics (88.0% of variance; Eigenvalue = 5.852; Wilk's $\lambda = 0.081$; χ^2 for $\lambda = 159.57$; $P < 0.001$), with samples separated according to sampling period along the second axis (11.9% of variance; Eigenvalue = 0.793; Wilk's $\lambda = 0.555$; $\chi^2 = 37.36$; $P < 0.001$), the latter separation being more pronounced for natural stretches than for rip-rap shorelines (Fig. 2). Note, that two summer-rip-rap stretches were grouped as natural habitats since at low summer water level only the edge of the rip-rap bank could be investigated for some stretches. This is also mirrored in the summary statistics of the abiotic data (Table 2).

Sample based rarefaction curves showed similar patterns in species richness for spring and summer catches (Fig. 3a). The curves for night-time increased more dramatically with sample size, independent of habitat category; this indicated that less effort was necessary to detect new species at night than in the daytime. Although the patterns at night were generally similar for natural and artificial habitats, there were differences during the daytime, when species richness was higher in rip-rap than natural stretches. Most of the difference between the four types of curves could be largely explained (Fig. 3b) by differences in the number of individuals collected (*i.e.*, species richness curves generally covered each other as a function of number of specimens collected). Day samples of natural habitats differed

Table 1. The species composition and relative abundance of fishes (%) in day and night of spring and summer 2004 in the River Danube, Hungary. Standard length (SL) data (minimum-maximum values in cm) are also shown for each species. Note, that “–” indicates zero relative abundance.

Common name	Scientific name	Spring		Summer		SL	
		Day	Night	Day	Night	Min	Max
Common bream	<i>Abramis brama</i> (LINNAEUS, 1758)	0.24	0.17	0.11	0.21	3	31
White-eye bream	<i>Abramis sapa</i> (PALLAS, 1814)	–	0.19	–	0.15	4	17
Spirlin	<i>Alburnoides bipunctatus</i> (BLOCH, 1782)	0.12	0.26	–	–	3	5
Bleak	<i>Alburnus alburnus</i> (LINNAEUS, 1758)	57.54	50.42	42.99	41.60	1	22
Asp	<i>Aspius aspius</i> (LINNAEUS, 1758)	5.39	2.97	3.82	3.72	3	40
Barbel	<i>Barbus barbus</i> (LINNAEUS, 1758)	1.64	2.28	1.01	0.56	2	53
Silver bream	<i>Blicca bjoerkna</i> (LINNAEUS, 1758)	0.55	5.40	0.56	4.41	2	30
Gibel carp	<i>Carassius gibelio</i> (BLOCH 1782)	0.30	0.51	0.11	0.31	2	35
Nase	<i>Chondrostoma nasus</i> (LINNAEUS, 1758)	5.45	5.38	3.03	3.33	2	45
Carp	<i>Cyprinus carpio</i> (LINNAEUS, 1758)	0.06	0.06	–	–	9	39
Pike	<i>Esox lucius</i> (LINNAEUS, 1758)	0.06	0.02	–	0.10	7	25
Lamprey	<i>Eudontomizon mariae</i> (BERG, 1931)	0.06	0.04	–	0.03	17	–
Whitefin gudgeon	<i>Romanogobio albipinnatus</i> (LUKASH, 1933)	–	1.26	0.22	4.21	2	11
Gudgeon	<i>Gobio gobio</i> (LINNAEUS, 1758)	–	–	0.11	0.03	7	10
Balon's ruffe	<i>Gymnocephalus baloni</i> (HOLCIK and HENSEL, 1974)	0.06	0.04	–	0.13	5	10
Ruffe	<i>Gymnocephalus cernuus</i> (LINNAEUS, 1758)	–	0.02	–	0.05	3	7
Yellow pope	<i>Gymnocephalus schraetser</i> (LINNAEUS, 1758)	0.12	0.68	–	1.62	3	15
Hybrid	<i>A. aspius</i> × <i>L. idus</i> ?	0.06	0.51	0.22	0.08	5	13
Pumpkinseed	<i>Lepomis gibbosus</i> (LINNAEUS, 1758)	0.06	–	–	0.10	7	9
Chub	<i>Leuciscus cephalus</i> (LINNAEUS, 1758)	4.24	2.18	3.03	2.77	4	38
Ide	<i>Leuciscus idus</i> (LINNAEUS, 1758)	13.33	8.88	14.70	7.95	2	43
Dace	<i>Leuciscus leuciscus</i> (LINNAEUS, 1758)	–	0.17	–	0.08	5	14
Burbot	<i>Lota lota</i> (LINNAEUS, 1758)	0.06	0.02	1.01	0.36	8	40
Monkey goby	<i>Neogobius fluviatilis</i> (PALLAS, 1814)	0.73	1.11	1.35	2.41	3	14
Kessler goby	<i>Neogobius kessleri</i> (GÜNTHER, 1861)	3.15	3.43	6.29	6.31	2	18
Round goby	<i>Neogobius melanostomus</i> (PALLAS, 1814)	1.82	6.68	18.52	12.95	2	16
Rainbow trout	<i>Oncorhynchus mykiss</i> (WALBAUM, 1792)	–	0.04	–	–	25	26
Eurasian perch	<i>Perca fluviatilis</i> (LINNAEUS, 1758)	0.85	0.41	0.45	1.10	4	20
Tubenose goby	<i>Proterorhinus marmoratus</i> (PALLAS, 1814)	0.24	0.19	–	0.08	2	7
Topmouth gudgeon	<i>Pseudorasbora parva</i> (TEMMINCK and SCHLEGEL, 1842)	0.36	0.15	0.67	0.10	2	5
Bitterling	<i>Rhodeus sericeus</i> (PALLAS, 1776)	–	0.09	–	–	2	5
Danubian roach	<i>Rutilus pigus</i> (HECKEL, 1852)	0.06	0.36	–	0.05	5	12
Roach	<i>Rutilus rutilus</i> (LINNAEUS, 1758)	2.54	4.65	0.67	2.82	2	28
Golden loach	<i>Sabanejewia aurata</i> (FILIPPI, 1865)	–	–	–	0.03	8	–
Brown trout	<i>Salmo trutta m. fario</i> (LINNAEUS, 1758)	0.12	0.02	–	–	11	35
Pikeperch	<i>Sander lucioperca</i> (LINNAEUS, 1758)	–	0.79	0.11	1.41	4	44
Volga pikeperch	<i>Sander volgensis</i> (GMELIN, 1788)	0.06	0.13	–	0.10	3	12
Rudd	<i>Scardinius erythrophthalmus</i> (LINNAEUS, 1758)	0.06	–	–	–	7	–
European catfish	<i>Silurus glanis</i> (LINNAEUS, 1758)	0.18	0.02	0.56	0.23	8	20
Vimba	<i>Vimba vimba</i> (LINNAEUS, 1758)	0.48	0.41	0.11	0.56	4	11
Danube streber	<i>Zingel streber</i> (SIEBOLD, 1863)	–	0.02	0.22	–	8	16
Zingel	<i>Zingel zingel</i> (LINNAEUS, 1758)	–	0.04	0.11	0.05	13	16
Total number of fish		1651	5313	891	3899		

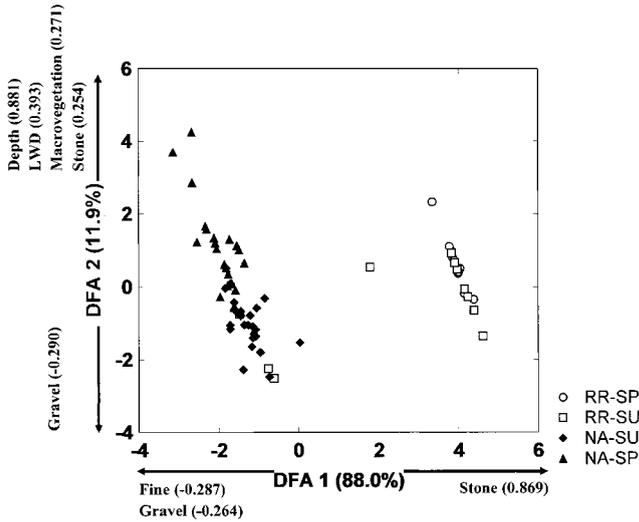


Figure 2. Canonical discriminant function ordination of 500 m-long stretches based on physical habitat characteristics. The stretches were sampled in spring and in summer in the littoral zone of the River Danube, Hungary. Abbreviations are: RR-SP, rip-rap spring ($N = 12$); RR-SU, rip-rap summer ($N = 12$); NA-SP, natural spring ($N = 25$); NA-SU, natural summer ($N = 25$). Only variables showing axis correlation > 0.2 are presented. Note, that physical habitat surveys were carried out only daytime.

Table 2. The general physical characteristics of natural and artificial (*i.e.*, rip-rap) habitat stretches (mean \pm SD) in spring and summer in the River Danube, Hungary.

	Natural		Rip-rap	
	Spring	Summer	Spring	Summer
Depth (cm)	67.1 (22.3)	45.0 (8.4)	66.2 (6.0)	54.7 (12.2)
Velocity (cm/s)	13.0 (17.9)	10.9 (11.3)	11.3 (13.9)	6.7 (3.9)
Ratio of fine substratum (%)	54.6 (35.5)	39.2 (39.6)	0.0 (0.0)	13.6 (30.3)
Ratio of gravel substratum (%)	43.8 (35.5)	58.5 (38.1)	0.0 (0.0)	14.7 (30.6)
Ratio of rocky substratum (%)	0.0 (0.1)	2.3 (4.0)	100.0 (0.0)	71.6 (46.1)
Macrovegetation (%)	10.3 (23.9)	2.5 (8.0)	0.2 (0.6)	0.0 (0.1)
Large woody debris (%)	13.2 (26.7)	0.0 (0.0)	1.3 (3.2)	0.0 (0.1)
Distance from shore (m)	6.6 (3.6)	5.5 (3.0)	1.4 (0.5)	2.6 (2.1)

the most from the other collections and showed the lowest species richness independent of season (Fig. 3b).

Autosimilarity values were generally higher for night than for day catches for species presence/absence data (Jaccard coefficient), indicating lower beta diversity and higher sample representativeness (*i.e.*, smaller heterogeneities in species composition between samples) in night catches (Fig. 4a). Further, data based on species presence/absence reached lower mean similarity values than those based on abundance and these patterns were independent of season. In addition, AS curves covered each other in case of abundance data, indicating that samples based on abundance data represent equally well the fish assemblages of the two habitat categories (Fig. 4b).

Distinct fish assemblages were found for natural and rip-rap habitats (Fig. 5). The first axis delineated samples based on habitat category (Eigenvalue = 2.974; Wilk's $\lambda = 0.048$;

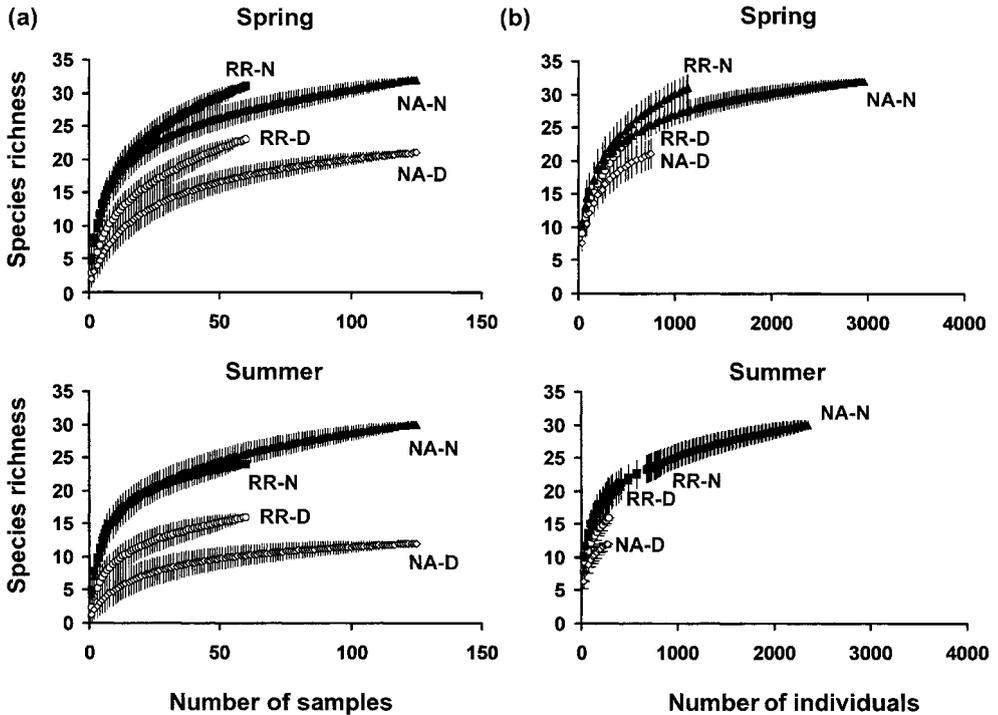


Figure 3. Estimated species richness (\pm SD ranges) as a function of (a) sample size (sampling effort) and (b) number of individuals collected in spring and summer in the River Danube, Hungary. Abbreviations are: RR-N, rip-rap night; RR-D, rip-rap day; NA-N, natural night; NA-D, natural day. See Methods for further details. Note, that number of samples refers to the number of 100 m long sampling units.

$\chi^2 = 378.894$; $P < 0.001$), whereas the second axis (Eigenvalue = 2.018; Wilk's $\lambda = 0.192$; $\chi^2 = 206.412$; $P < 0.001$) further separated day and night samples.

Of the 42 taxa, 18 proved to be a highly sensitive indicator for a certain habitat category and/or daytime, and/or daytime and habitat categories combined (Table 3). No species was found that would have been an indicator of daytime, although several species were found to be an indicator species for night-time. Of these, whitefin gudgeon (*Romanogobio albipinnatus*) showed the highest indicator value followed by roach (*Rutilus rutilus*) and pikeperch (*Sander lucioperca*). More species were found to be an indicator of artificial habitats than for natural habitats. More exotic and/or invasive species were found in the rip-rap group (e.g., gibel carp *Carassius gibelio*, topmouth gudgeon *Pseudorasbora parva*, pumpkinseed, bighead goby *Neogobius kessleri*) than in the natural habitat group (monkey goby *N. fluviatilis*). The most important indicator species of the night natural habitats was yellow pope (*Gymnocephalus schraetser*), an endemic percid of the Danube basin, whereas common, bigger bodied cyprinids (e.g., gibel carp, silver bream *Blicca bjoerkna*, ide *Leuciscus idus*, chub *Leuciscus cephalus*) and the pikeperch (*S. lucioperca*) were the important indicators of the night rip-rap category.

Diversity values of biological traits saturated quite early in the function of sampling effort, independent of season, daytime or habitat category (Fig. 6). All three forms of diversity curve (i.e., life-history, habitat and trophic trait diversity) were saturated at higher values in rip-rap habitats than in natural ones, with trophic guild and habitat preference values show-

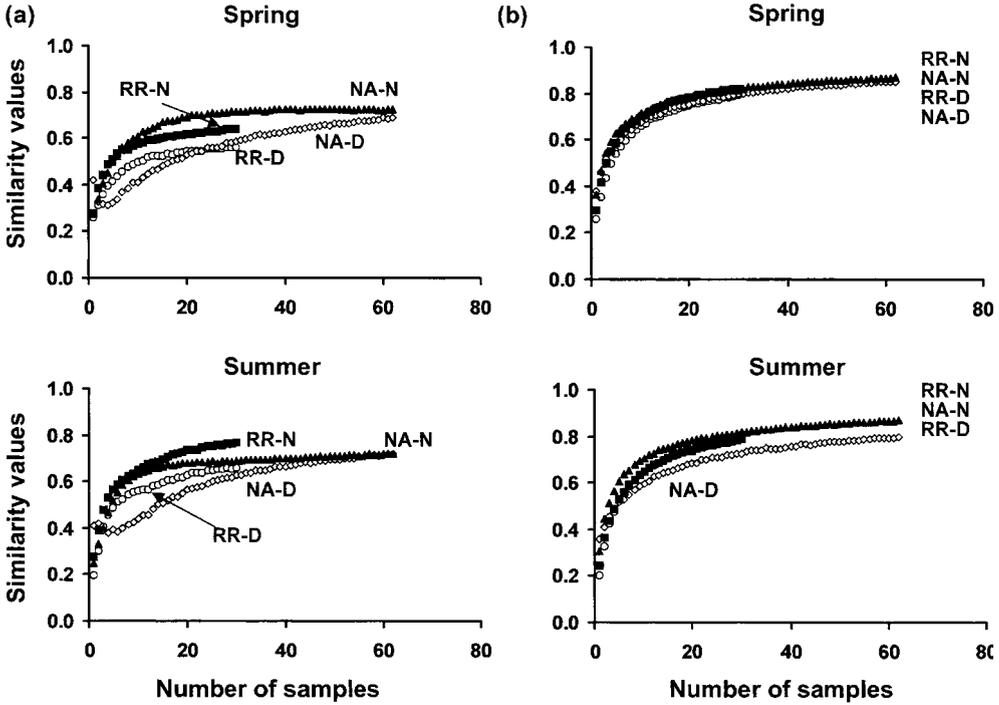


Figure 4. Changes in community similarity (*i.e.*, autosimilarity) values as a function of sample size based on (a) Jaccard and (b) Bray-Curtis similarity indices for spring and summer data. Standard deviation ranges have been omitted for clarity. Abbreviations are: RR-N, rip-rap night; RR-D, rip-rap day; NA-N, natural night; NA-D, natural day. See Methods for further details.

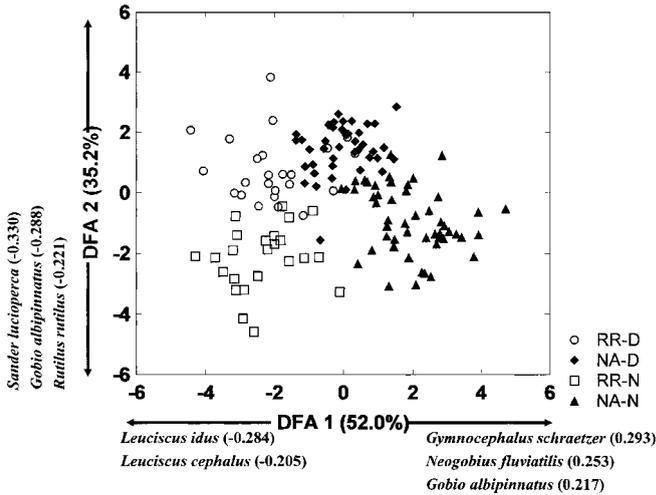


Figure 5. Canonical discriminant function ordination of 500 m long stretches based on relative fish abundance data. Abbreviations are: RR-D, rip-rap day ($N = 24$); RR-N, rip-rap night ($N = 24$); NA-D, natural day ($N = 50$); NA-N, natural night ($N = 50$). Only variables showing axis correlation > 0.2 are presented. See Methods for further details.

Table 3. Indicator value of fishes and the corresponding significance levels. Three separate analyses were run according to time of day (day, D or night, N), habitat (natural, NA or rip-rap, RR), and day-habitat (DNA, DRR, NNA, NRR) groups. Indicator value of species with the highest between analysis value is indicated with bold.

	Daytime			Habitat			Daytime and habitat		
<i>Abramis sapa</i>	N	13.5	<i>P</i> < 0.001						
<i>Alburnus alburnus</i>				NA	62.6	<i>P</i> < 0.001	DNA	33.7	<i>P</i> < 0.001
<i>Barbus barbuis</i>				RR	32.8	<i>P</i> < 0.001			
<i>Blicca bjoerkna</i>	N	35.7	<i>P</i> < 0.001				NRR	36.3	<i>P</i> < 0.001
<i>Carassius gibelio</i>	N	19.4	<i>P</i> < 0.01	RR	19.9	<i>P</i> < 0.01	NRR	22.3	<i>P</i> < 0.01
<i>Gobio albipinnatus</i>	N	48.6	<i>P</i> < 0.001				NNA	36.3	<i>P</i> < 0.001
<i>Gymnocephalus schraetser</i>	N	32.0	<i>P</i> < 0.001	NA	24.9	<i>P</i> < 0.001	NNA	43.5	<i>P</i> < 0.001
<i>Lepomis gibbosus</i>				RR	8.3	<i>P</i> < 0.001			
<i>Leuciscus cephalus</i>				RR	39.1	<i>P</i> < 0.01	NRR	24.3	<i>P</i> < 0.01
<i>Leuciscus idus</i>				RR	60.5	<i>P</i> < 0.001	NRR	34.4	<i>P</i> < 0.001
<i>Lota lota</i>				RR	20.1	<i>P</i> < 0.001			
<i>Neogobius fluviatilis</i>	N	37.0	<i>P</i> < 0.001	NA	48.1	<i>P</i> < 0.001	NNA	42.3	<i>P</i> < 0.001
<i>Neogobius kessleri</i>	N	42.3	<i>P</i> < 0.01	RR	44.1	<i>P</i> < 0.01			
<i>Pseudorasbora parva</i>				RR	16.0	<i>P</i> < 0.01	DRR	16.2	<i>P</i> < 0.01
<i>Rutilus rutilus</i>	N	41.1	<i>P</i> < 0.001						
<i>Sander lucioperca</i>	N	37.8	<i>P</i> < 0.001				NRR	23.4	<i>P</i> < 0.01
<i>Silurus glanis</i>				RR	18.8	<i>P</i> < 0.001			
<i>Vimba vimba</i>	N	18.0	<i>P</i> < 0.01				NNA	22.8	<i>P</i> < 0.01

ing the highest between habitat differences. Because the most contrasting differences in trait diversity were found in the habitat and trophic attributes, we performed more detailed comparisons on these attributes (Fig. 7). The distribution (%) of variables weighted by the relative abundance of species showed the same pattern in all four occasion (day and night of spring and summer) for both habitats.

4. Discussion

Natural and artificial shorelines maintained generally the same species pool, although clear differences were found between the species richness of day and night samples. These differences between day and night collections correspond with other studies and may be attributable to differences in diel activity and resource use of fishes, and the ability of fish to perceive investigators earlier during daytime than night, and escape (COPP and JURAJDA, 1993; WOLTER and FREYHOF, 2004; ERŐS *et al.*, 2005). Although day catches may be more affected by sampling bias (*i.e.*, reduced sampling efficiency), our results for night catches suggest that there are no marked differences in species richness between natural and artificial shorelines. In addition, considering the much greater differences in the shape and magnitude among sample based rarefaction curves compared with individual based ones, it is clear that species richness between habitats and day or night samples could be mainly (but not exclusively) related to a passive sampling effect (*i.e.*, patterns in species richness depended largely on the number of individuals collected; see GOTELLI and COLWELL, 2001). Although largely underutilized, these latter results plea for a more intensive application of both sample based and individual based rarefaction in the species diversity comparison of running water fishes. In addition, the further advantage of rarefaction curves is that they provide information on abundance relations to an attentive reader (see OLSZEWSKI, 2004), and hence, they give a more accurate information on species diversity than the conventional

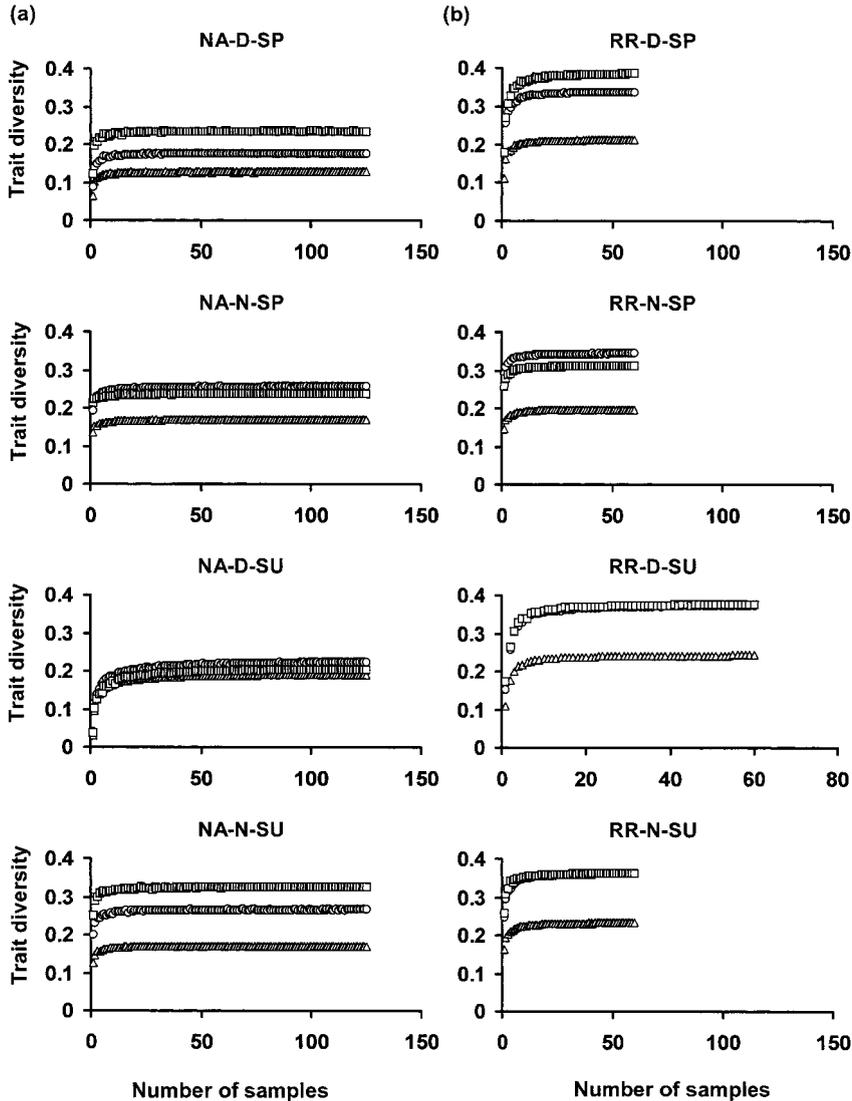


Figure 6. Changes in the diversity values of biological traits/attributes as a function of sample size in (a) natural and (b) rip-rap habitats. Triangles represent diversity of life-history traits, circles represent diversity of habitat preferences, and squares represent diversity of trophic guild. 95% C. L. ranges have been omitted for clarity. See Methods for further details.

diversity indices, which are generally hard to standardize by sample size (GOTELLI and COLWELL, 2001).

Ecological assemblages exhibit heterogeneity in both species composition and abundance at all spatial and temporal scales (KOLASA and PICKETT, 1991; CAO *et al.*, 2003). This heterogeneity, together with the rarity of many species, and the fact that it is generally impossible to take an absolutely representative sample (*i.e.*, which equals with the original assemblage for each variable) from large running waters, makes it necessary to use stan-

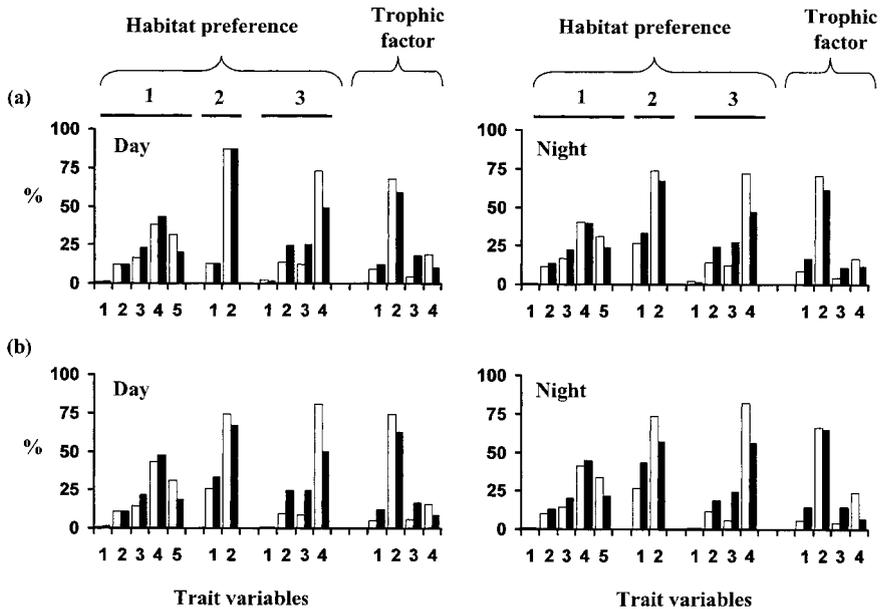


Figure 7. Percentage distribution of attributes (%) in natural (white bars) and rip-rap (black bars) habitats in (a) spring and (b) summer, and day and night. For the habitat preferences, three subgroups were established: (1) large scale habitat use (categories: 1) small highland stream, 2) small lowland stream, 3) medium river, 4) large river, 5) lentic); (2) vertical position (categories: 1) benthic, 2) non-benthic); and (3) substratum preference (categories: 1) rubble, 2) gravel, 3) fine, 4) various). For trophic guild, four categories were defined: 1) herbivore-detrivore, 2) invertivore, 3) piscivore, 4) planktivore. Note, that the percentage distribution of attributes is weighted by the relative abundance of species.

standardization procedures for sample comparisons at all levels of data treatment (CAO *et al.*, 2003). Our results revealed that different sampling effort (*i.e.*, number of samples) is necessary to characterize assemblages (*i.e.*, composition) with the same accuracy and precision based on species presence-absence data than those based on relative abundance (Fig. 3), corroborating studies elsewhere of riverine fishes (*e.g.*, ANGERMEIER and SMOGOR, 1995). Further, sample representativeness depended strongly on time of the day and habitat category in case of species presence-absence data. However, no differences were found between natural and artificial habitats when applying AS standardizations for relative abundance data indicating the same level of spatial heterogeneities and beta diversity between samples in both habitat categories.

Relative abundance data showed substantial differences in fish assemblage composition between the natural and artificial habitats, and these were greater than the differences between day and night samples (Fig. 5). Further, subtle variations in species composition coupled with differences in relative abundance indicated that species of great conservation concern (*e.g.*, yellow pope, golden loach, Danube streber, Danubian roach) were relatively dominant in natural shorelines, whereas exotic species (*e.g.*, pumpkinseed, topmouth gudgeon, gibel carp) and species requiring high mesohabitat level complexity (*i.e.*, hiding places; *e.g.*, burbot *Lota lota*, European catfish) were relatively more frequent in rip-rap shorelines. These results indicate the importance of gravel-sand stretches over rip-raps in maintaining natural fish assemblages.

It is interesting that several species proved to be indicators of night, but no species was a strong indicator of day. These results support other studies which showed that most fish

in the littoral zone are more active during the night and/or that the littoral zone of rivers is a more intensively utilized habitat for fish at night (*e.g.*, COPP and JURAJDA, 1999; WOLTER and FREYHOF, 2004). Activity at night can be an advantageous behavioral reaction to avoid day-time feeding predatory birds (*e.g.*, herons), which are common in the littoral zone of the River Danube. In addition, COPP and JURAJDA (1999) showed that river shorelines can represent important night-time refuges for fishes from predation by their predatory counterparts. Although there are various speculations on the factors (both abiotic and biotic) that could explain diurnal distribution patterns (*e.g.*, COPP and JURAJDA, 1993; WOLTER and FREYHOF, 2004 and references herein), a more mechanistic understanding of the utilization of shorelines by riverine fishes is still missing. These results highlight the importance of the time of day in the generalization of any quantitative model of fish assemblage organization in rivers.

To our knowledge, this study is the first which examines changes in biological trait diversity of fishes in the function of sampling effort. Moreover, differences in trait diversity has not been comparatively studied for gravel-sand beach and rip-rap stretches, notwithstanding that this variable may be equally important to conventional diversity metrics (*e.g.*, species richness, diversity indices) in evaluating the importance of these habitats for meso-habitat level fish diversity. Compared with species richness accumulation curves, the curves for biological trait (*i.e.*, attribute) diversity accumulated much sooner as a function of sampling effort. Therefore, our results on fish assemblages are in accordance with the results of BADY *et al.* (2005) who found that biological trait diversity of macroinvertebrate assemblages is a more reliable measure than taxon richness in describing communities using a small number of samples. In addition, our results further support the argument that a loss of species richness may not severely affect the functional diversity of running water assemblages (BADY *et al.*, 2005), although this may depend on the functional characteristics of the extirpated species (*i.e.*, the extirpation of keystone species may severely affect ecosystem function *e.g.*, JORDÁN *et al.*, 1999).

Diversity of biological traits was higher in artificial than in natural habitats. These differences were especially marked for the habitat preference and the trophic diversities. Further, between-habitat differences for these two biological diversity measures were higher for day than night. Our method of calculating biological trait diversity was sensitive to 1) differences in species richness and therefore the number of possible trait combinations, which could increase trait diversity, 2) species abundance relations, and 3) species specific differences in biological trait attributes. Although differences in species richness may be largely responsible for the great differences in diversity between natural and rip-rap habitats for day samples, the lack of marked between-habitat differences in species richness for night may suggest that differences in species abundance relations between habitats and species specific differences in biological trait attributes also affected our results. In addition, there were a more even distribution of attributes in rip-rap habitats (Fig. 7), which could also increase trait diversity in this habitat type compared with natural shorelines. Consequently, all the above mentioned factors could have contributed to the observed differences in biological trait diversity between habitats. However, the calculation of biological trait diversity for freshwater fishes is still at an early stage. Further studies should address how calculation method (*e.g.*, distance measure used) and the number and type of trait variables influence patterns in trait diversity in a variety of habitats and assemblages. The results prove the application of indices based on biological trait diversity, since they can contribute to a more holistic understanding of both spatial and temporal changes in the diversity of riverine fish assemblages.

In conclusion, our findings demonstrate that rip-rap habitats have a significant impact on mesohabitat level fish diversity in the littoral zone of the River Danube. Whether this impact is negative, neutral or positive (*i.e.*, increase diversity which is not necessarily positive!) depends on the assemblage property studied. We found no substantial differences in the species richness of fish assemblages between natural and artificial shorelines, but the rela-

tive abundance composition of the two habitat types were different. Nevertheless, species of great conservation concern tended to bound to natural habitats, whereas exotics were more frequent along artificial shorelines. Diversity of biological traits/attributes (*i.e.*, life-history traits, habitat preferences and trophic guild) were generally higher in rip-rap habitats. The differences in compositional (*i.e.*, relative abundance) and functional (*i.e.*, trait diversity) aspects of fish diversity between habitats reveal that rip-rap sections increase beta diversity (spatial heterogeneities in fish assemblages) at the mesohabitat scale. Since rip-rap shorelines may represent a relatively novel, but increasingly widespread habitat resource, species that prefer such a kind of habitat structure could take advantage of mesoscale habitat modifications (*e.g.*, invasive gobiids; ERŐS *et al.*, 2005). Changes in local diversity and assemblage composition are expected to have strong influences on a variety of ecosystem processes and services at a hierarchy of scales. Nevertheless, the longer scale effects of habitat modifications on ecosystem function, and community processes is largely unknown and an urgent research need (SAX and GAINES, 2003). Considering the spatio-temporal environmental complexity of running waters and the methodological difficulties to sample large river habitats, understanding these long time changes will present a big challenge for freshwater fish ecology.

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