

## DO DIEL VARIATIONS IN STREAM FISH ASSEMBLAGES DEPEND ON SPATIAL POSITIONING OF THE SAMPLING SITES AND SEASONS?

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The effect of diel period (i.e. day vs night) and its dependence on the spatial position of the sampling site were evaluated on the assessment of fish assemblage attributes in a wadeable lowland stream (Hajagos stream, Hungary). Species richness, composition and abundance data of two 150 m long reaches, one situated directly at the tributary mouth and one 6 km upstream were compared using three pass removal by electrofishing in three seasons (summer, autumn and spring) to test the effect of spatial position on day and night patterns. No differences in any assemblage level variables were found between day and night. Although fish assemblages showed large temporal variations, spatial position of the sampling site had the most influential effect on fish assemblage attributes compared with seasonal and/or day night patterns. Consequently, the diel period had rather negligible effect in the studied stream. Daytime electrofishing data seems to be highly representative for the accurate assessment of fish assemblages in relatively small (less than 5 m wide) wadeable streams and maybe used reliably for any model of community organization (e.g. food web studies).

Key words: day vs night, sampling, electrofishing, spatial position, tributary mouth.

### INTRODUCTION

The accurate estimation of assemblage level attributes (e.g. species richness, species composition and abundance) is a fundamental requirement in ecological research and environmental monitoring and assessment (MAHER *et al.* 1993, CAO *et al.* 2003, MEADOR *et al.* 2003, KENNARD *et al.* 2006). However, most of our knowledge about the structure and organization of ecological assemblages is based on daytime samples. It has been shown, that the activity of animals can be different between day and night, which may influence sampling effectiveness (CRAIG 1977, PIERCE *et al.* 2001, ANDERSON *et al.* 2007). Movement of animals among different habitat patches can also differ between day and night (NIELSEN 1984, HELFMAN 1993, DAVID & CLOSS 2003, RAILSBACK *et al.* 2005). Therefore, samples collected either at day or night may reveal different pictures of assemblage structure, which can substantially influence our inferences on patterns and processes in ecosystems.

Structure of fish assemblages have been long recognized to show contrasting day and night pattern. In freshwater systems for example, diel changes have been found to be significant in the littoral zone of lakes and reservoirs (BAUMANN & KITCHELL 1974, LEWIN *et al.* 2004, RIHA *et al.* 2015) and rivers (SANDERS 1992, COPP & JURAJDA 1993, ARRINGTON & WINEMILLER 2003, ERŐS *et al.* 2008). Several studies showed that night time samplings yielded more species and specimens and greater biomass than day time samplings in the near-shore habitats of rivers because of higher catching efficiency, diel migration of many species to the littoral zone and higher movement activity by night (COPP & JURAJDA 1993, WOLTER & FREYHOF 2004, ERŐS *et al.* 2008). It was concluded that both diurnal and nocturnal samplings are required to adequately characterize fish assemblages, especially in large rivers, which are difficult to sample representatively (WOLTER & FREYHOF 2004, COPP *et al.* 2005, BAUMGARTNER *et al.* 2008).

Interestingly, much less research has been devoted to diel changes and their effect on estimating fish assemblage variables in smaller (i.e. wadeable) streams (but see e.g. COPP 2010, SALAS & SNYDER 2010). This is probably because these habitats are considered to be more easily and representatively sampled using e.g. electrofishing or seine netting (see MURPHY & WILLIS 1996, MATTHEWS 1998) compared with large rivers (GROSSMAN & RATAJCZAK 1998, LAPOINTE *et al.* 2006). In fact, diel differences in the habitat use and activity of certain fishes are relatively well known (REEBS 2002, SALAS & SNYDER 2010). For example, salmonids have been shown to use different habitats for feeding and hiding and habitat selection can differ between seasons and diel periods (e.g. CUNJAK *et al.* 1998, HISCOCK *et al.* 2002). However, it is much less known how differences in the habitat use and/or sampling effectiveness of individual species scale up to the assemblage level causing differences in the estimation of assemblage level attributes between day and night samples.

Day and night differences in fish assemblage samples may also depend on the spatial position of the sampling site. Daytime samplings showed that tributary mouths are more intensively used by mainstream fishes as refuge and feeding areas than more upstream reaches (OSBORNE & WILEY 1992, SCHLOSSER & ANGERMEIER 1995, THORNBRUGH & GIDO 2010). Therefore, assemblages close to the mouth may be more variable than more upstream sites (ERŐS & SCHMERA 2010, ROBERTS & HITT 2010). Since fish migration patterns can be more intense downstream and may show a diel pattern, it can be hypothesized that differences between day and night samples will be the most contrasting close to the tributary mouth and may mitigate upstream as the number of migrants from the species pool outside the focal stream diminish. However, to our knowledge, no study to date has quantified day and night differences and the effect of the spatial positioning of the sampling site on estimating assemblage level variables for stream fishes.

Seasonal changes (e. g. floods vs. droughts, differences in stream temperature) are one of the most important factors influencing assemblage organization and movement patterns of fish (SCHLOSSER 1991). For example, movement activity of fish increases in spring due to spawning. Diel changes in activity and habitat use of fish may also be affected by seasonality (CRAIG 1977, CUNJAK *et al.* 1988, HEGGENES *et al.* 1993). Although diel variation in movement patterns may be as important as seasonal differences at the species level, seasonal changes are presumably more significant at the assemblage level, especially in small streams. For these reasons we hypothesized that seasonal differences in fish assemblages will be more significant than diel changes, and diel patterns of fish movement will be determined by seasons.

The aim of this study was to test the effect of seasonal differences, site spatial positioning and diel differences on fish in a tributary system in term of species richness, composition and abundance of fishes standardized for unit area.

## MATERIAL AND METHODS

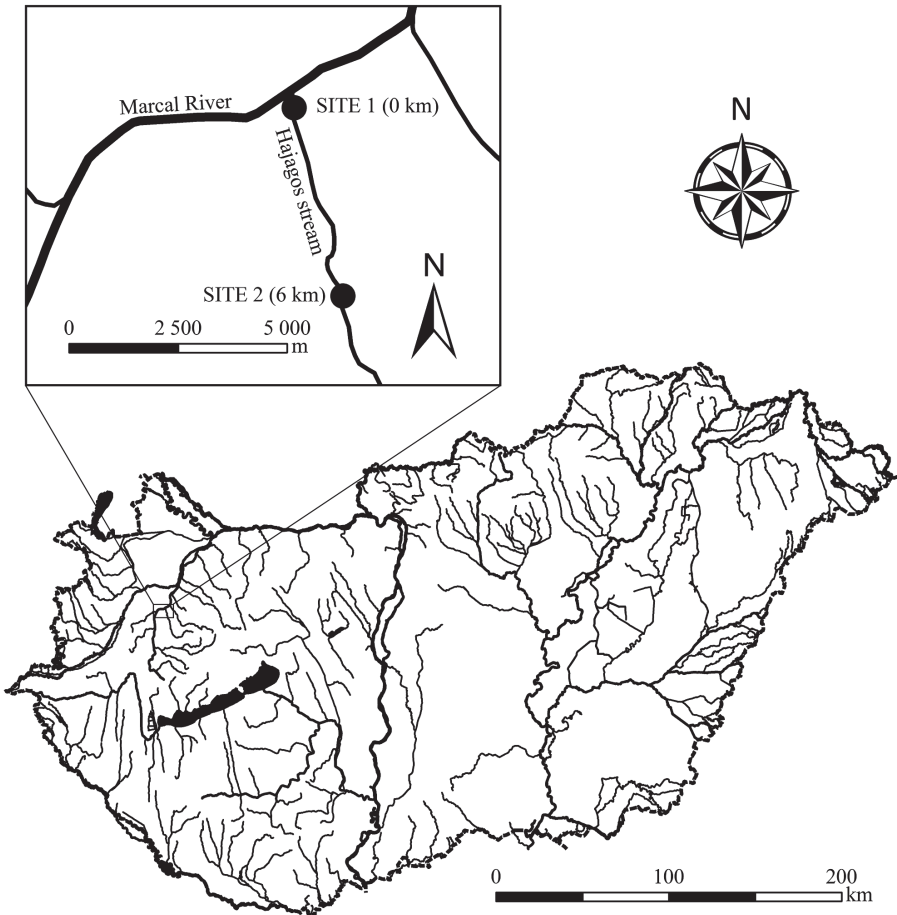
### *Study area and field sampling*

The study was conducted in the Hajagos stream, a right side tributary of the 100.4 km long lowland Marcal River, situated in North-Western Hungary (Fig. 1). The Hajagos has a length of 33.3 km, an average slope of 4.3 m km<sup>-1</sup> and a total drainage area of 188 km<sup>2</sup>. The riverbed is covered by diverse substrate dominating by coarse-gravel, fine-gravel, sandy-silt and organic debris. The middle and downstream parts of the stream run through a predominantly agricultural landscape. Like the majority of lowland streams in Hungary, the Hajagos was channelized, which does not allow meandering. The macrophytes were dominated by emergent plants, such as reed (*Phragmites australis*), bulrush (*Typha* spp.) and sedge (*Carex* spp.), which can dramatically increase their biomass in the vegetation period covering even 100% of the riverbed.

For the purpose of this study we chose two sampling reaches, Site 1, the downstream sampling point situated directly at the tributary mouth, and Site 2 approximately 6 km upstream from the tributary mouth (Fig. 1). Electric fishing was carried out during both daytime and nighttime in three sampling periods: summer (July) and autumn (October) 2013 and spring (April) 2014 using a back-pack electrofishing machine (Hans-Grassl IG200/2B, PDC, 75-100 Hz, 350-650 V, max. 10 kW; Hans Grassl GmbH, Germany). The stream was not sampled in winter due to the difficulties of sampling and installation of the nets in icy water. In addition, a winter sampling can disturb the resting fish and may cause high-level mortality. Each sampled reach was 150 m long and was further divided into 50 m long sampling units. Prior to electrofishing we blocked each unit at both ends with weighted nets (6 mm mesh size) to prevent fish movement in and out of the units. The nets were manipulated in the same way both during day and night samplings. Lower parts of the nets were strengthened with chains and they were fixed at the banks with steel rods. We always started sampling the most downstream unit at each site and then continued with the more upstream units. The sampling team consisted of four people: the electrofisher operator who handled the gear and caught the stunned fish with the hand-held anode (2

m long pole with a net of 30 cm diameter, mesh size 6 mm), a netter who helped to catch fish and two helpers who carried the buckets and took care of the fish. To increase the sampling efficiency each unit was electrofished three-times in the same manner. We sampled the whole stream width (moved in a zig-zag fashion) while slowly wading in an upstream direction. During each pass the fish were removed from the stream and placed immediately into a large, plastic tank filled with water. We identified the fish to species level on each pass, counted and measured their standard length and finally returned to the stream downstream of the studied sampling unit. Minimum 15 minutes were allowed to elapse between the individual passes. Data of successive removals (i.e. of individual passes) were pooled and this was used in all statistical evaluations. A minimum of six hours elapsed between day and night collections. During darkness, the sampling area was illuminated using head lamps.

We also took transect based measurements of habitat data at each unit to characterize the environmental features of the sampling sites in each season (Table 1). For this purpose



**Fig. 1.** Map showing the locations of sampling sites in Hajagos stream, Hungary.

**Table 1.** Average habitat characteristics of the 150 m long sample reaches (sites) in the Hajagos stream. Each mean value is based on the pooled mean data of sampling units (see methods for details).

	Summer		Autumn		Spring	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Width (m)	5.9	3.2	3.6	3.6	4.9	4.7
Sampled area (m <sup>2</sup> )	885	480	540	540	735	705
Depth (cm)	78.1	23.9	50.1	27.2	73.3	50.0
Velocity (cm s <sup>-1</sup> )	5.1	5.2	5.1	5.1	19.3	20.7
Silty sand (%)	31.7	20.0	50.0	10.7	13.0	3.3
Sand (%)	1.7	1.7	–	7.7	–	–
Fine gravel (%)	40.0	6.7	16.7	25.0	61.3	33.3
Coarse gravel (%)	10.0	71.7	18.3	56.7	22.3	63.3
Stone (%)	16.7	–	8.3	–	3.3	–
Rock (%)	–	–	6.7	–	–	–
Emergent plant (%)	63.3	60.0	92.3	78.3	31.7	51.7
Submerged plant (%)	6.7	–	5.0	4.0	16.7	16.7
Floating leaved plant (%)	11.7	1.7	2.7	0.2	–	–
Filamentous algae (%)	–	16.7	–	–	–	–

four transects were placed at each unit perpendicular to the main axis of the stream. We measured wet width of the channel with a tape measure, depth and current velocity with a meter stick and a water velocity meter (FP101 Global Flow Probe, Global Water Instrumentation Inc., Gold River, CA, USA), respectively, at five equally spaced points along each transect. At every transect point the occurrence and type of aquatic vegetation and substrate were recorded.

### *Data analysis*

We used three-way factorial analysis of variance (ANOVA) in a nested design with three replicates (units) to test for differences in species richness or number of individuals between seasons, between sites within seasons, and between diel periods within sites and seasons. Species richness values were also compared using individual based rarefaction analyses to control for the likelihood of collecting more species when more individuals were collected (SIMBERLOFF 1972). Individual based rarefaction curves were constructed separately for each season and day and night samples and by pooling data from the individual sampling units at each site (Fig. 4.) We used principal coordinate analysis (PCoA) to reveal patterns in species composition and abundance between sites, seasons and diel periods. The Jaccard and Bray-Curtis indices were used for comparing samples based on species composition and abundance data, respectively. Finally, nested permutational analysis of variance (PERMANOVA) was used to assess the differences in species composition and abundance data between seasons, between sites within seasons and between diel periods

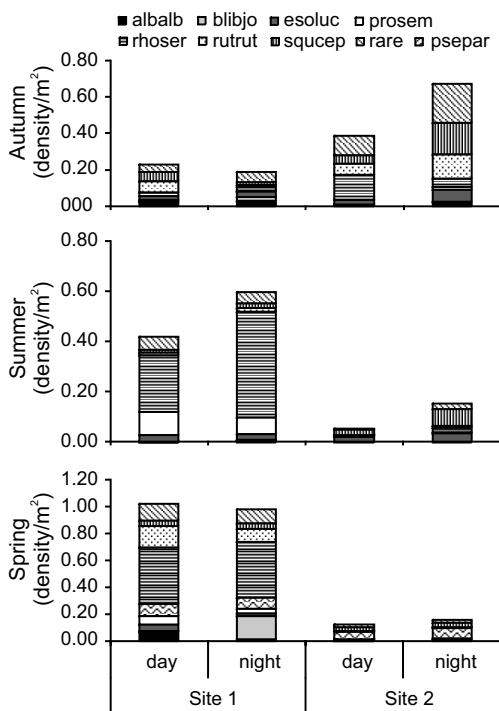
within sites and seasons. PERMANOVA uses analysis of variance using distance matrices and a permutation test with pseudo F-ratio to test difference in the multivariate data groups. Similarly to the PCoA, Jaccard and Bray-Curtis dissimilarity indices were used for species composition and abundance, respectively (LEGENDRE & LEGENDRE 1998). Abundance data were standardized for unit area before all of the analyses. All statistical analyses were performed in the R statistical environment (R CORE TEAM 2013). PERMANOVA was conducted with 'adonis' function of the R package named vegan (OKSANEN *et al.* 2013).

**Table 2.** Fish species, species codes (SC), total number of individuals and species density values (in parentheses, averaged over seasons) collected at Site 1 and Site 2 in the Hajagos stream during day and night sampling.

Species	Species code	Site 1		Site 2	
		Day	Night	Day	Night
<i>Abramis brama</i> (L.)	abrbra	1 (<0.001)	2 (<0.001)	–	–
<i>Alburnus alburnus</i> (L.)	albalb	67 (0.030)	40 (0.016)	3 (0.002)	12 (0.008)
<i>Ameiurus melas</i> (Rafinesque)	amemel	7 (0.003)	9 (0.005)	–	3 (0.002)
<i>Ballerus ballerus</i> (L.)	balbal	4 (0.002)	–	–	–
<i>Barbatula barbatula</i> (L.)	ortbar	–	2 (0.001)	15 (0.011)	9 (0.006)
<i>Blicca bjoerkna</i> (L.)	blibjo	12 (0.005)	147 (0.065)	–	–
<i>Carassius gibelio</i> (Bloch)	cargib	4 (0.002)	10 (0.005)	9 (0.006)	18 (0.012)
<i>Cobitis elongatoides</i> (Bacescu et Maier)	cobelo	12 (0.006)	9 (0.004)	4 (0.002)	9 (0.005)
<i>Esox lucius</i> (L.)	esoluc	65 (0.031)	57 (0.026)	31 (0.019)	60 (0.038)
<i>Gobio</i> sp. (L.)	gobgob	1 (<0.001)	–	13 (0.009)	17 (0.011)
<i>Lepomis gibbosus</i> (L.)	lepgib	4 (0.002)	6 (0.003)	–	2 (0.001)
<i>Leucaspis delineatus</i> (Heckel)	leudel	2 (0.001)	1 (<0.001)	–	–
<i>Leucaspis idus</i> (L.)	leuidu	4 (0.002)	26 (0.012)	–	–
<i>Leuciscus leuciscus</i> (L.)	leuleu	12 (0.006)	19 (0.007)	8 (0.005)	38 (0.024)
<i>Misgurnus fossilis</i> (L.)	misfos	–	4 (0.002)	1 (<0.001)	3 (0.002)
<i>Neogobius fluviatilis</i> (Pallas)	neoflu	19 (0.009)	13 (0.005)	–	–
<i>Neogobius melanostomus</i> (Pallas)	neomel	35 (0.017)	19 (0.009)	3 (0.002)	11 (0.008)
<i>Perca fluviatilis</i> (L.)	perflu	5 (0.002)	6 (0.003)	10 (0.005)	11 (0.007)
<i>Phoxinus phoxinus</i> (L.)	phopho	1 (<0.001)	1 (<0.001)	–	–
<i>Proterorhinus semilunaris</i> (Pallas)	prosem	99 (0.052)	64 (0.034)	1 (<0.001)	13 (0.008)
<i>Pseudorasbora parva</i> (Temminck et Schlegel)	psepar	67 (0.030)	63 (0.028)	43 (0.020)	57 (0.027)
<i>Rhodeus sericeus</i> (Pallas)	rhoser	456 (0.222)	558 (0.286)	74 (0.049)	35 (0.024)
<i>Rutilus rutilus</i> (L.)	rutrut	182 (0.079)	86 (0.040)	31 (0.021)	69 (0.045)
<i>Scardinius erythrophthalmus</i> (L.)	scaery	42 (0.019)	17 (0.008)	6 (0.004)	13 (0.009)
<i>Squalius cephalus</i> (L.)	squcep	72 (0.033)	56 (0.027)	53 (0.032)	147 (0.094)
<i>Tinca tinca</i> (L.)	tintin	4 (0.002)	1 (<0.001)	–	–

## RESULTS

A total of 3,225 specimens representing 26 species were collected during the study (Table 2). Basic data about number of species and their composition and abundance reflected more the effect of spatial position of the sampling site than the effect of season (although season effect was also significant) or diel period (Fig. 2). Both mean species richness (i.e. averaged over 50 m sampling units) and mean number of individuals collected were significantly higher at Site 1 (at the mouth) than at Site 2 (6 km upstream) (Fig. 3, Table 3).



**Fig. 2.** Fish assemblage composition (standardized for unit area, averaged over 50 m sampling units) at Site 1 and Site 2 during day and night time samplings in summer and autumn 2013 and spring 2014. Rare species (species without the 8 most abundant ones) were treated together. Species abbreviations are as follows. albalb – bleak; blibjo – white bream; esoluc – pike; prosem – tubenose goby; psepar – topmouth gudgeon; rloser – bitterling; rutrut – roach; squcep – chub; rare – rare (i.e. non dominant) species.

However, neither of them differed significantly between day and night samples (Fig. 3, Table 3). Individual based rarefaction curves confirmed the results obtained on species richness at the sampling unit level (Fig. 4). Especially, they confirmed the lack of significant differences between day and night samples in species richness (except in the case of summer for Site 2 where there was a clear difference between day and night patterns). However, they also revealed the strong effect of season on the results on site level species richness. They indicated high differences in species richness between the two study sites in spring, but less clear differences in summer and autumn.

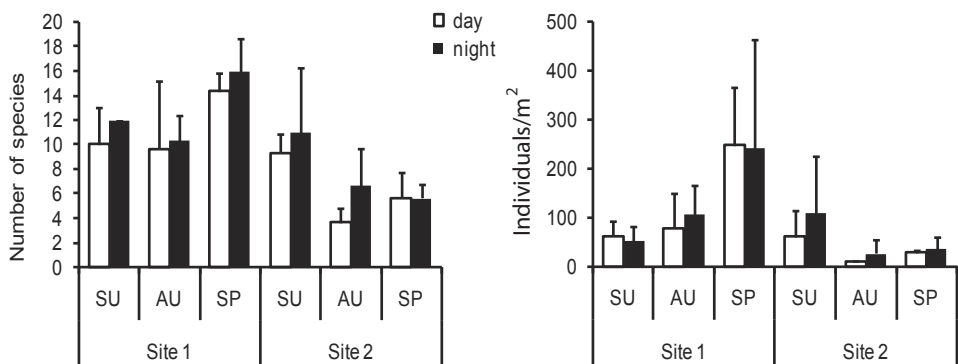
For species composition data the PCoA ordination of Jaccard dissimilarity matrix showed a clear separation of sites along the first axis (Fig. 5a). This separation was generally related to the presence of those species at Site 1 that were not caught at Site 2 (e.g. white bream *Blicca bjoerkna*) (Fig. 5c, Table 2). Some of these species prefer larger water bodies (e.g. ide

**Table 3.** Summary results of the nested three-way factorial analysis of variance (ANOVA) for species richness and number of individuals (standardized for unit area).

Species richness	d.f.	MS	F	P
Season	2	<0.001	1.55	0.234
Season : Site	3	0.002	12.17	<0.001
Season : Site : Time of day	6	<0.001	0.54	0.774
Residuals	24	<0.001		
Number of individuals	d.f.	MS	F	P
Season	2	0.23	1.59	0.225
Season : site	3	1.01	6.92	0.002
Season : Site : Time of day	6	0.03	0.23	0.965
Residuals	24	0.15		

(*Leuciscus idus*), blue bream (*Ballerus ballerus*) and may use tributary mouth periodically. Overall, between site and seasonal differences in species composition were much higher than between day and night samples. The PCoA plot of Bray-Curtis dissimilarity matrix for abundance data also represented differences between Site 1 and Site 2 along the first axis, but no clear differences between day and night samples (Fig. 5b). Examples of fishes associated with Site 1 were bitterling (*Rhodeus sericeus*), black bullhead (*Ameiurus melas*) and tubenose goby (*Proterorhinus semilunaris*), while fishes associated with Site 2 were chub (*Squalius cephalus*), and perch (*Perca fluviatilis*) (Fig. 5d).

PERMANOVA analyses confirmed the results of exploratory analyses and showed that species composition and abundance of fish differed significantly between seasons and sites, but not between diel periods (Table 4).

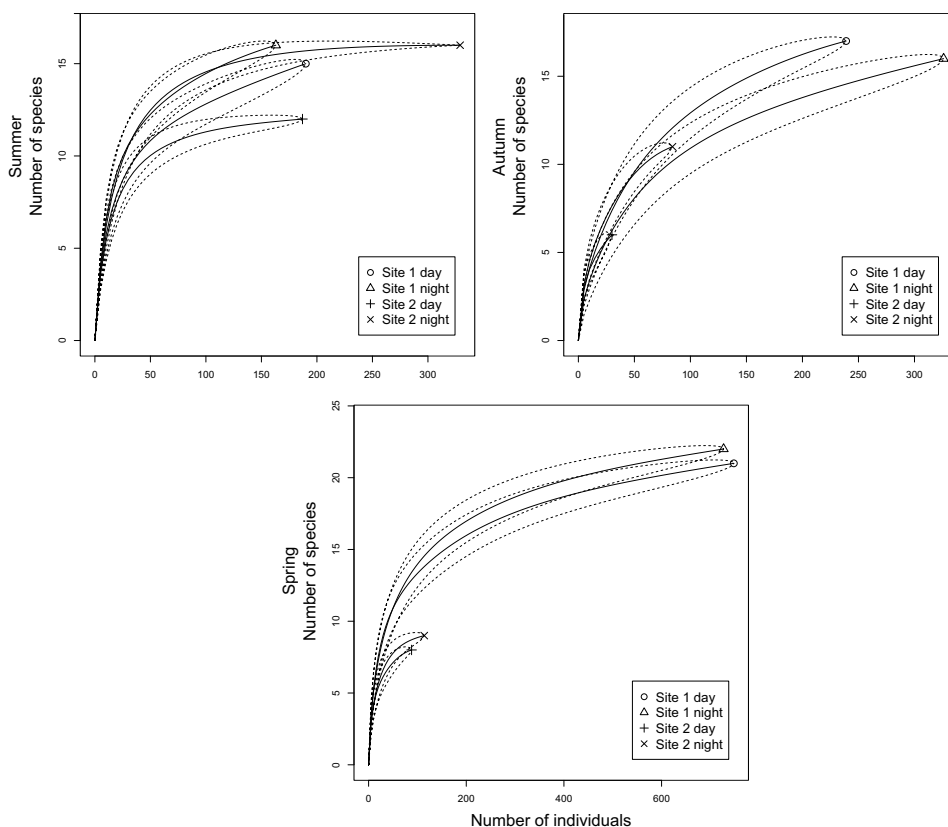


**Fig. 3.** Mean species richness (averaged over 50 m sampling units,  $\pm$ S.D.) (a) and number of individuals collected (standardized for unit area) (b) at Site 1 and Site 2 during day and night time samplings. Season abbreviations are as follows. SU – summer; AU – autumn; SP – spring.



**Table 4.** Summary results of the nested permutational analysis of variance (PERMANOVA) for species composition and abundance data (standardized for unit area).

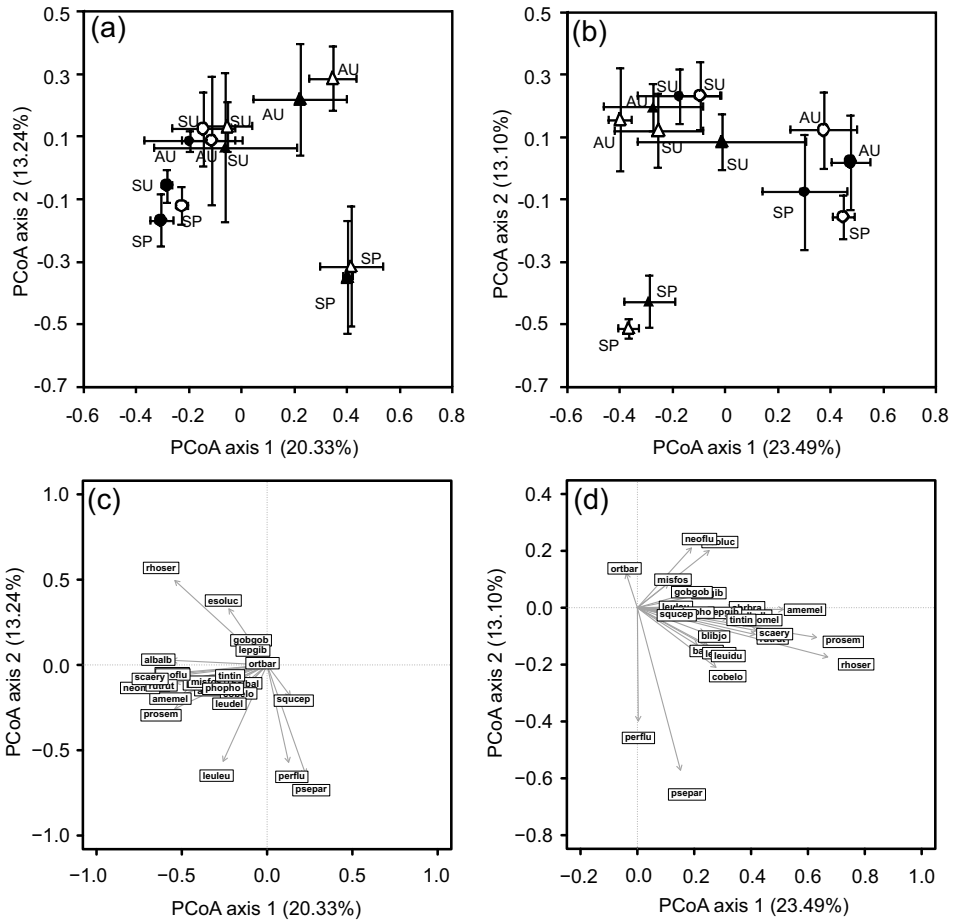
Species composition	d.f.	MS	<i>F</i>	R <sup>2</sup>	<i>P</i>
Season	2	0.79	5.97	0.21	<0.001
Season : site	3	0.69	5.23	0.27	<0.001
Season : Site : Time of day	6	0.12	0.93	0.10	0.620
Residuals	24	0.13		0.42	
Total	35			1.00	
Abundance	d.f.	MS	<i>F</i>	R <sup>2</sup>	<i>P</i>
Season	2	0.92	5.69	0.19	<0.001
Season : site	3	1.05	6.49	0.32	<0.001
Season : Site : Time of day	6	0.16	0.96	0.10	0.529
Residuals	24	0.16		0.40	
Total	35			1.00	

**Fig. 4.** Individual based rarefaction curves for summer, autumn and spring.

DISCUSSION

Contrary to our hypothesis, we found no significant effect of diel period on the assemblage level attributes of stream fish assemblages at any spatial position of the sampling sites. We can conclude therefore, that neither sampling effectiveness nor fish migration and/or differential habitat use influenced significantly the differences in fish assemblage structure between day and night, when compared with the effect of seasonal and spatial (between site) changes.

Spatial position of the sampling site had the most influential effect on fish assemblage attributes compared with seasonal and/or day night patterns.



**Fig. 5.** Principal Coordinate Analysis (PCoA) summarizing the variation across sites (averaged over 50 m sampling units,  $\pm$ S.D.) and diel periods for (a) species composition and (b) abundance data (standardized for unit area) and their associated species loaded (c and d).  $\circ$  – Site 1-day;  $\bullet$  – Site 1-night;  $\triangle$  – Site 2-day;  $\blacktriangle$  – Site 2-night. Season abbreviations are as follows. SU – summer; AU – autumn; SP – spring. For species code abbreviations see Table 2.

It is well known, that stream fish assemblages are influenced by the position of the site along the upstream-downstream gradient (OSBORNE & WILEY 1992, SCHLOSSER & ANGERMEIER 1995, THORNBRUGH & GIDO 2009, CZEGLÉDI *et al.* 2015). Increasing complexity and size of the habitat downstream, differential rates of immigration and extinction are some of the most possible factors responsible for this typical longitudinal pattern (SCHLOSSER 1982, POWER *et al.* 1988, MIYAZONO & TAYLOR 2013). We found significantly higher species richness and collected more individuals (on average) at Site 1 than at Site 2 suggesting preferential habitat use and maybe higher immigration and lower emigration rates at Site 1. Dissimilarity of species composition and abundances were also significant between the two sites. This is in accordance with the presence and higher abundance of mainstem fishes at Site 1 (e.g. bleak *Alburnus alburnus*, white bream, tubenose goby) and more upstream species at Site 2 (e.g. spined loach *Cobitis elongatoides*, stone loach *Barbatula barbatula*, chub, gudgeon *Gobio* sp.). It seems that mainstem fishes use only the most downstream reaches of the Hajagos. There may be two possible explanations for this pattern. First, reduced habitat size in an upstream direction (shallower water depth and narrower width) limits the movement possibility and represent unsuitable habitat for mainstem fishes (SCHLOSSER 1982, MATTHEWS 1998). Second, in the vegetation period (i.e. from late spring to autumn), heavy macrovegetation coverage may restrict upstream movement of large bodied fish (ERŐS & GRANT 2015).

Seasonal differences in fish assemblage structure were also significant at both sites. Of these, the most contrasting were the changes in species composition and abundance per unit area over seasons. Spawning migration and more increased activity of fish in spring can be the two most important factors for shaping these patterns. Species which did not appear in summer and autumn samples but were detected in the spring sample both at day and night were for example blue bream and stone moroko (*Pseudorasbora parva*). However, most of the dominant tributary species (e.g. bitterling, stone moroko, roach *Rutilus rutilus*) are common in both the Hajagos and the mainstem Marcal, so we cannot really disentangle the effect of mainstem-tributary migration on seasonal changes.

Although day and night changes were relatively minor for all assemblage attributes (species richness, composition and abundance of fish), the basic data (Fig. 2) suggested some differences between day and night samples in all seasons and at both sites. Contrary to many studies which use only single pass electrofishing, we used three pass removals to maximize sample representativity. Therefore, we believe the data suggest more the rate of movement of the different species in and out of the sampling site, rather than differences in sampling effectiveness between day and night (see Appendix 1). The most noteworthy difference was the 25 times increase in the abundance of white bream by night at the mouth (Site 1) in spring. This may suggest the spawning migration of white

bream at night in this period of the year and/or the use of the tributary mouth for habitat (i.e. feeding, refuging). In fact white bream has been shown to move to the littoral zone of rivers by night (WOLTER & FREYHOF 2004, ERŐS *et al.* 2008).

Although our knowledge about diel activity and diel habitat use in fish other than salmonids is limited in small streams, it seems that looking for hiding and feeding place are two factors that may influence diel changes in fish distribution (HEGGENES *et al.* 1999, LEWIN *et al.* 2004, COPP *et al.* 2005, 2008). One of the most general factors responsible for the movement between the relatively safe tributary mouth and more hazardous river is a trade-off between predator avoidance and resource use (COPP & JURAJDA 1993, BECKER *et al.* 2011). One possible reason for the lack of significant effect of diel period in this system could be that mainstem fish find similarly suitable area for resting and hiding in the near shore habitat, which is also densely vegetated. Aquatic vegetation also provides food resources for algivorous and invertivorous fishes (WERNER *et al.* 1983).

In conclusion, our study suggests that fish assemblages in tributaries are more influenced by the spatial position of the sampling site than by the diel period, which had rather negligible effects in the Hajagos. The study also suggests that daytime electrofishing is highly effective for the accurate assessment of stream fish assemblages in this stream and could be a reliable method for any model of community organization (e.g. food web studies).

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**Appendix 1.** Cumulative catches of fish removals at Site 1 and Site 2 during day and night in summer and autumn 2013 and spring 2014. Species abbreviations are as follows: albal – bleak; blibjo – white bream; esoluc – pike; prosem – tubenose goby; psepar – topmouth gudgeon; rhoser – bitterling; rutrut – roach; squcep – chub; rare – rare (i.e. non dominant) species. Note that the diagram of spring samples has a different scale on the y axis.

