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Effect of riverbed morphology, stream order and season on the structural and functional attributes of caddisfly assemblages (Insecta: Trichoptera)

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We tested the individual and joint effects of stream order, riverbed morphology (i.e. pool-riffle sequence), and season on the structural (i.e. species composition, density and richness) and functional (i.e. percent ratio of shredders, collectors, scrapers, and predators) properties of caddisfly assemblages in a closely natural headwater system (Börzsöny Mts., North Hungary). Each factor, both individually and in interaction had a significant effect on caddisfly assemblages as shown by MANOVA analyses. To clarify the effects of stream order, riverbed morphology and season on caddisflies, assemblage properties were also separately studied by ANOVAs. Percent ratio of shredders and collectors were strongly affected by all factors, whereas other attributes were not always sensitive to stream order, season and riverbed morphology. In contrast, species compositions of the reaches differing in stream order and riverbed morphology were significantly different. Our findings on the contrasting differences in shredder composition between riffles and pools may suggest that not only riparian vegetation, but also instream habitat features could shape the accumulation and retention of particulate organic matter (in streams with pool-riffle heterogeneity).

Keywords : Trichoptera, assemblage structure and function, channel unit, riffle, pool, stream.

Introduction

The abiotic habitat template is generally considered as the major determinant of community organisation in running waters, at many spatial and temporal scales (Hynes 1970, Townsend 1989, Ward 1989, Allan 1995, Townsend et al. 1997, Boyero 2003a, Parson et al. 2003). In headwater streams particularly, the physical habitat of benthic animals show contrasting changes at relatively small scales, thus generating considerable spatial heterogeneity (Boyero 2003b, 2003c). This spatial heterogeneity strongly influences the distribution of stream-dwelling organisms (Allan 1995). Studies conducted at the reach scale (linear spatial scale: several tens of metres, Giller & Malmqvist 1998) showed that stream order (Strahler 1952) had a broad capability of predicting the structural and/or functional properties of macroinvertebrate communi-

ties (Vinson & Hawkins 1998), including caddisflies (Wiberg-Larsen et al. 2000, Park et al. 2003, Céréghino et al. 2003). Beside stream order, environmental heterogeneity may strongly influence the assemblage characteristics of macroinvertebrate communities at the mesohabitat scale (i.e., a few metres, Vinson & Hawkins 1998, Bournaud et al. 1998, Beisel et al. 1998, 2000; Usseglio-Polatera et al. 1999).

While many studies focused on the structure of stream macroinvertebrate communities at the mesohabitat (Beisel et al. 1998) and the reach (e.g. González et al. 2003) scales, the number of investigations at the subreach (channel unit, or pool-riffle) spatial scale (i.e. between the mesohabitat and the reach, Giller & Malmqvist 1998) remain somehow limited (but see Brown & Brussock 1991, Brussock & Brown 1991, Carter & Fend 2001, Rabeni et al. 2002). At the subreach spatial scale, riverbed morphology shows an alternating sequence of pool and riffle habitats. By definition pools are slowly flowing depositional zones dominated by fine particles of mineral substrates; while

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riffles are turbulent, shallower, fast flowing and erosional zones dominated by large particles of mineral substrates (Brussock & Brown 1991, Gordon et al. 1992, Giller & Malmqvist 1998). The contrasting differences in abiotic (e.g. current velocity, substrate composition, water depth) as well as biotic (e.g. food sources, predation) factors between riffles and pools may exert a strong effect on the organisation of macroinvertebrate assemblages (Allan 1995, Rabeni 2002). In fact, riffles are generally considered to support higher densities of benthic macroinvertebrates contrast to pools (Hynes 1970, Kerans et al. 1992, Allan 1995, Weigel et al. 2003, Townsend et al. 2004). However, information on the similarities and differences in assemblage diversity of certain taxonomical groups remains too sporadic to allow general conclusions (Vinson & Hawkins 1998).

In this paper, we examined the individual and joint effects of (1) season, (2) stream order and (3) riverbed morphology (i.e. pools vs. riffles) on the structural and functional properties of caddisfly assemblages in a closely natural, headwater stream system receiving deciduous litter input in the Börzsöny Mts, Hungary. Caddisflies (Insecta: Trichoptera) were selected as study organisms because they inhabit different kinds of substrates (Higler 1975, Habdija et al. 2002) within various flow regime (Bacher & Waringer 1996), and represent a variety of functional feeding groups (Cummins 1973, Giller & Malmqvist 1998).

Material and methods

Study area and field sampling

The study was carried out in the northern part of the Börzsöny Mountains, Hungary (47°50' -48°05'N, 18°45' -19°05'E): The Kemence stream system belongs to the Danube drainage basin. It meanders through an oak-hornbeam woodland (*Quercus-Carpinetum*) with riparian vegetation dominated by alder (*Alnus glutinosa*). The canopy provides extensive shading and leaves little light for instream primary production. Hence, the primary production of the Kemence stream system is mostly based on allochthonous leaf litter from the surrounding riparian vegetation. Two study sites were chosen: one site was in the tributary of the Kemence stream (i.e. the second order Bernecei stream), and the other site was in the third order section of the Kemence mainstream. These sites were randomly taken from the pool of possible candidate sites that represented the diversity of habitats in the stream system (see Erős et al. 2003 for a detailed methodology). The Bernecei and the Kemence have a well developed riffle-pool morphology with gravel as the dominant substratum (Erős et al. 2003), and basically the same physical and chemical characteristics (Table 1). Riffle-pool riverbed morphology however, is more contrasting in the third order (i.e. Kemence) than in the second order (i.e. Bernecei) section. The Kemence stream system is among the reasonable representative of the closely natural submontane streams of the Carpathian region in Central Europe.

Table 1. Chemical and physical characteristics of the Bernecei and Kemence streams. Note that habitat data describe the average characteristics of the studied sites.

	Bernecei stream	Kemence stream
pH	7.8-8.6	7.7-8.5
Conductivity $\mu\text{S}/\text{cm}$)	450-580	310-550
Dissolved Oxygen (mg/l)	7.3-11.1	8.5-11.8
Salinity (%)	0.02	0.01-0.02
Stream order	2 nd	3 rd
Width (m)	1.4-4.1	3.5-7.0
Average current velocity (m/s)	0-30	1.5-50
% Silt (<0.005 cm)	10	15
% Sand (0.005-0.2 cm)	20	15
% Gravel (0.2 - 6 cm)	50	45
% Stone (6 - 30 cm)	13	20
% Rock (>30 cm)	5	2
Claystone (%)	2	3

Caddisfly larvae were collected on three sampling dates (April, August and October) in 2001. At every sampling occasion, three replicates of Surber samples (area: 0.0625 m², mesh size 500 µm) were randomly taken from the mid-channel of riffle and pool habitats at each site. Hence, altogether 36 samples were taken over the whole year [3 (replicates) x 2 (pool and riffle) x 2 (stream order : 2nd order Bernecei stream, 3rd order Kemence stream) x 3 (season: April, August and October)]. We acknowledge that the number of replicate samples per date per channel unit was rather limited. However, other studies successfully demonstrated the patchy distribution of stream macroinvertebrates at the riffle-pool scale using a similar procedure and number of replicates (Boyero 2003a, 2003b). The pooled sampled areas per habitat unit (i.e. riffle) was 0.1875 m² against 0.0675 m² in Boyero (2003a, 2003b). Consequently, the number of replicates and the area sampled in our study appeared to be representative for comparing the characteristics of caddisfly assemblages.

To dislodge caddisflies from the substrate and allow the streamflow to force them into the Surber net, the substrate within the Surber sampler's quadrat frame was agitated by hand to a depth of about 5 cm, followed by careful wiping by hand of all cobble and gravel pieces. Each sample was placed in a container with 5% formalin and identified based on Waringer & Graf (1997). The list of species, and the corresponding functional groups are given in Appendix 1. Unfortunately, two samples were lost, thus they should be omitted from the analyses.

Data processing and statistical analysis

Six properties were used to characterise caddisfly assemblages. Species richness and density reflect assemblage structure, while the per cent ratio of shredders, collectors, scrapers and predators reflect func-

ional attributes of the caddisfly assemblage (Cummins 1973). The first two properties were standardised to square meter. Functional properties were determined following Moog (1995) and Cummins (1973). The effect of stream order, riverbed morphology and season on caddisflies were evaluated using Multivariate Analysis of Variance (MANOVA, Zar 1999). Stream order, riverbed morphology and season were regarded as factors (i.e. independent variables), while species richness, density, percent ratio of shredders, collectors, scrapers and predators were dependent variables. To elucidate the effects of factors on each dependent variable individually, three-way Analyses of Variance (ANOVA, Zar 1999) were performed separately. Non-metric Multidimensional scaling (NMDS, Podani 1997) using percentage difference coefficient (Podani 1997) was run to show similarity pattern of caddisfly assemblages of pool and riffle habitats in the second and third order reaches of the Kemence stream system. Multi-Response Permutation Procedure (MRPP, McCune & Grace, 2002) was used to test, whether species composition of caddisflies in second and third order reaches of pools and riffles was different. Indicator species analysis (Dufrene & Legendre 1997) was applied to find indicator species for the different states of stream order and riverbed morphology. The significance level of the indicator value was defined by Monte Carlo randomisation with 1000 runs. NMDS, MRPP and Indicator species analysis were performed using the pooled samples over the whole season. MANOVA and ANOVA were performed using STATISTICA computer program (Statsoft, Inc 2000); NMDS by SYN-TAX (Podani 1993); MRPP and Indicator species analysis by PC-ORD (McCune & Mefford 1997). The result of NMDS was visualised by STATISTICA program.

Table 2. Result of MANOVA assessing the effect of (1) season, (2) stream order and (3) riverbed morphology on the assemblage structure and function of caddisflies.

Source	Wilks' Lambda	F	Effect df	Error df	p-level
1	0.3100	2.8657	10	36	0.0099
2	0.4566	4.2842	5	18	0.0096
3	0.3802	5.8689	5	18	0.0022
12	0.2659	3.3813	10	36	0.0034
13	0.4305	1.8870	10	36	0.0799
23	0.3714	6.0936	5	18	0.0018
123	0.2921	3.0608	10	36	0.0065

Table 3. Summary of ANOVA assessing the effect of (1) season, (2) stream order and (3) riverbed morphology on the richness, density, per cent ration of shredders, collectors, scrapers and predators of caddisfly assemblages.

Dependent	Source	SS	df	MS	F	p-level
Richness	1	0.2348	2	0.1174	0.1148	0.8921
	2	1.4423	1	1.4423	1.4103	0.2477
	3	1.8526	1	1.8526	1.8114	0.1920
	12	7.5000	2	3.7500	3.6667	0.0422
	13	0.0926	2	0.0463	0.0453	0.9558
	23	2.8269	1	2.8269	2.7641	0.1106
	123	0.3533	2	0.1767	0.1727	0.8425
	Error	22.5000	22	1.0227		
Density	1	1383.3726	2	691.6863	3.3265	0.0547
	2	290.8269	1	290.8269	1.3987	0.2496
	3	416.8269	1	416.8269	2.0046	0.1708
	12	252.1904	2	126.0952	0.6064	0.5542
	13	61.0200	2	30.5100	0.1467	0.8644
	23	1495.4423	1	1495.4423	7.1920	0.0136
	123	1575.4793	2	787.7396	3.7885	0.0386
	Error	4574.5000	22	207.9320		
Shredders	1	1792.4558	2	896.2279	9.4653	0.0011
	2	1753.5037	1	1753.5037	18.5193	0.0003
	3	1208.2988	1	1208.2988	12.7612	0.0017
	12	828.4894	2	414.2447	4.3750	0.0251
	13	873.1335	2	436.5667	4.6107	0.0213
	23	2098.5044	1	2098.5044	22.1630	0.0001
	123	1934.5197	2	967.2598	10.2155	0.0007
	Error	2083.0743	22	94.6852		
Collectors	1	439.1046	2	219.5523	1.1959	0.3213
	2	2022.9249	1	2022.9249	11.0190	0.0031
	3	684.0567	1	684.0567	3.7261	0.0666
	12	928.9340	2	464.4670	2.5300	0.1026
	13	2153.1168	2	1076.5584	5.8641	0.0091
	23	1780.9567	1	1780.9567	9.7010	0.0050
	123	118.6606	2	59.3303	0.3232	0.7272
	Error	4038.8560	22	183.5840		
Scrapers	1	48.8420	2	24.4210	0.4644	0.6345
	2	27.9423	1	27.9423	0.5314	0.4737
	3	607.1969	1	607.1969	11.5471	0.0026
	12	469.8671	2	234.9335	4.4678	0.0235
	13	96.2169	2	48.1085	0.9149	0.4153
	23	5.1024	1	5.1024	0.0970	0.7584
	123	181.4641	2	90.7320	1.7255	0.2013
	Error	1156.8511	22	52.5841		
Predators	1	1083.1969	2	541.5984	1.8579	0.1797
	2	70.3606	1	70.3606	0.2414	0.6281
	3	7319.9038	1	7319.9038	25.1098	0.0001
	12	6453.2621	2	3226.6310	11.0685	0.0005
	13	2366.9561	2	1183.4781	4.0597	0.0316
	23	1.8203	1	1.8203	0.0062	0.9377
	123	1978.7222	2	989.3611	3.3939	0.0519
	Error	6413.3370	22	291.5150		

Results

When the effects of stream order, riverbed morpho-

logy or season were studied separately, MANOVA showed that they had a significant effect on caddisfly assemblages (Table 2). When the interactions of two of

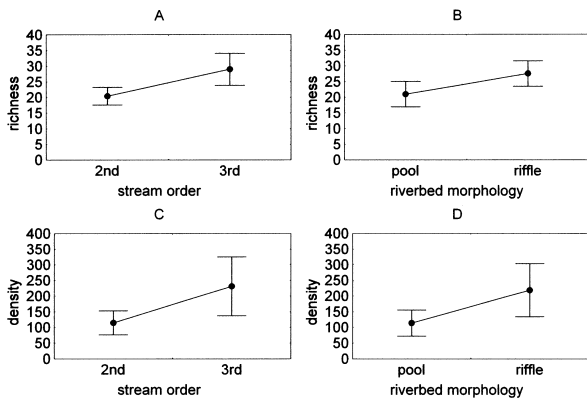


Fig. 1. Response of richness (A and B) and density (C and D) of caddisflies to stream order (A and C) and riverbed morphology (B and D). (Dots show mean values, vertical bars show standard errors).

these factors were studied, then two out of three cases showed significant results: the joint effect of season and stream order, and that of stream order and riverbed morphology. In contrast, the combined effect of season and riverbed morphology was not significant. Finally, the combined effect of season, stream order and riverbed morphology showed a significant influence on caddisfly assemblages, too (Table 2). Species richness showed dependence only on the joint effect of season and stream order; whereas density was influenced by the joint effect of stream order and riverbed morphology, and by the joint effect of season, stream order and riverbed morphology (Table 3). Neither species richness nor density of caddisflies was influenced by the

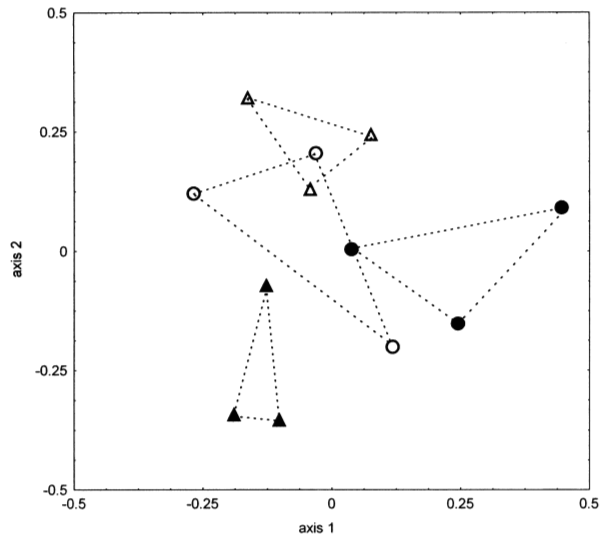


Fig. 2. Result of Non-metric Multidimensional Scaling showing the similarity patterns of caddisfly assemblages collected from pool (circle) and riffle (triangle) habitats in second (open circle or triangle) and third (filled circle or triangle) order reaches of the Kermence stream system.

individual effect of riverbed morphology or stream order (Fig 1).

NMDS could clearly distinguish the four groups of assemblages, although a limited overlap appeared in the ordination space for riffle and pool assemblages collected in the second order reaches (Fig. 2). MRPP showed that caddisfly assemblages collected at 2nd and 3rd order streams were different ($T=-2.0729$,

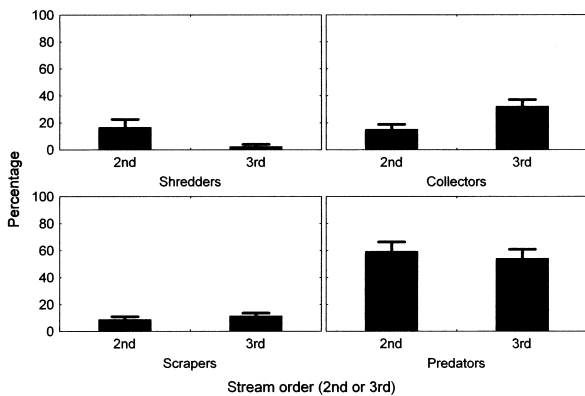


Fig. 3. Response of functional attributes of caddisflies (shredders, collectors, scrapers and predators) to stream order.

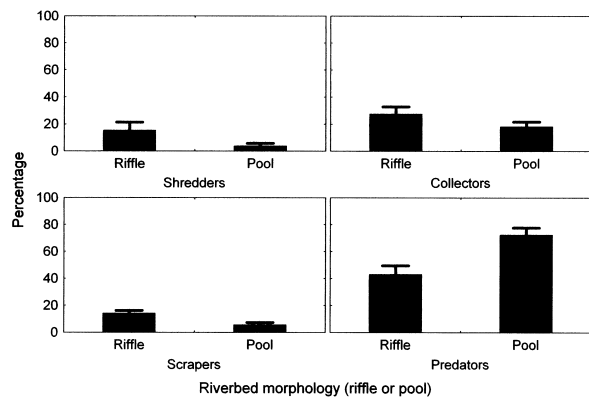


Fig. 4. Response of functional attributes of caddisflies (shredders, collectors, scrapers and predators) to riverbed morphology.

$\Delta_{\text{observed}}=0.8051$, $\Delta_{\text{expected}}=0.8519$, $R=0.0549$, $p=0.0287$), while assemblages collected from pools and riffles were not ($T=-0.6976$, $\Delta_{\text{observed}}=0.8361$, $\Delta_{\text{expected}}=0.8519$, $R=0.0184$, $p=0.2310$). In addition, MRPP showed that the joint effects of riverbed morphology and stream order had a significant effect on the species composition of caddisflies assemblages ($T=-1.9651$, $\Delta_{\text{observed}}=0.7660$, $\Delta_{\text{expected}}=0.8519$, $R=0.1008$, $p=0.0427$). Of the 12 caddisfly species identified (Appendix 1), only *Hydropsyche instabilis* Curtis 1834 proved to be a significant indicator species of the third order stream reach (Indicator value: 83, $p=0.015$). No species appeared as a significant indicator of pool or riffle habitats.

Functional properties of caddisfly assemblages were sensitive to the effects of season, stream order and riverbed morphology (Table 3). The percent ratio of shredders showed significant dependence upon season, stream order (Fig. 3) and riverbed morphology (Fig. 4, Table 3). In addition, the joint effects of the examined factors showed significant effect on caddisfly assemblages (Table 3). The percent ratio of shredders was significantly higher in the second order reach than in the third order one (Fig. 3). Furthermore, shredders were represented by a significantly higher ratio in riffles than in pools (Fig. 4). Percent ratio of collectors was affected by the individual effect of stream order (Table 3, Fig. 3), by the combined effect of season and riverbed morphology; and by the joint effect of stream order and riverbed morphology (Table 3). The percent ratio of collectors was significantly higher in the third order reach than in the second one (Fig. 3). Percent ratio of scrapers was significantly higher in riffles (Table 3, Fig. 4). Neither the individual effect of stream order nor the season affected the ratio of scrapers, whereas their combined effect influenced their ratio (Table 3). Percent ratio of predators was significantly higher in pools (Table 3, Fig. 4) and showed significant dependence on the interaction of season and stream order; and upon the season and riverbed morphology (Table 3).

Discussion

Our results show that season, stream order, riverbed morphology (i.e. pool-riffle geomorphology) and the interaction of these factors had a significant effect on the assemblage organisation of caddisflies in the Kemence stream system. Among the studied structural and functional properties, the percent ratio of shredders was influenced the most by the examined factors. The reach scale investigations did not show differences between the second and third order reaches ba-

sed on the structural properties (richness and density) of caddisfly assemblages. Nevertheless, NMDS and MRPP showed differences between the species composition of caddisfly assemblages. *Hydropsyche instabilis*, a stream-dwelling caddisfly usually inhabiting low-ordered streams (Higler & Tolkamp 1983, Schmera 2003), proved to be a significant indicator of the third-order site.

Literature data (Brown & Brussock 1991, Carter & Fend 2001, Rabeni et al. 2002, Townsend et al. 2004) stating that richness and density of macroinvertebrates were higher in riffles than in pools were not statistically supported for Trichoptera, although field data suggested that species richness and density of caddisflies were higher in riffles than in pools. Even if MRPP and NMDS did not distinguish contrasting riffle and pool caddisfly assemblages at a site, riverbed morphology had a significant effect on caddisflies when its joint effect with stream order was tested, suggesting that pool-riffle level heterogeneity also influenced structural properties of caddisfly assemblages. Although our study did not underpin statistically the differences in richness and density of caddisflies in riffle and pool habitats (in agreement with Scullion et al. 1982), the unique species composition of riffles and pools received support.

In general, scrapers and collectors tend to inhabit riffles, whereas predators occupy pools (Merritt & Cummins 1996, Weigel et al. 2003). In our study area, ratio of scrapers was significantly higher in riffles whereas ratio of predators in pools. The percent ratio of shredders showed strong dependence on season, stream order and riverbed morphology in the Kemence stream-system. The contrasting ratio of shredders in pool and riffle habitats might be explained by the differences in the accumulation and retention of coarse particulate organic matter in pool and riffle habitats. According to Brussock & Brown (1991), coarse particulate matter accumulates on riffles due to the rough and uneven bottom profile of these channel units. Consequently, the amount of particulate organic matter in streams is not only affected by the riparian vegetation (Friberg et al. 2002, Graca 2001) but also by instream habitat features, which may shape the assemblage structure and function of organisms living there (Arscott et al. 2003, González et al. 2003, Jonsson et al. 2001).

In conclusion, this study demonstrated that season, stream order and riverbed morphology both individually and in interaction influenced the structural and functional attributes of caddisfly assemblages in the Kemence stream system. Our results support the view

on the complex nature of fauna organisation in streams and pay attention to the examination of multifactor effects in our understanding the spatial and temporal patterns of caddisfly assemblages.

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Appendix 1:

List of collected caddisfly species and their partition into the main functional groups (Cummins 1973)

SPECIES	FUNCTIONAL GROUP
Rhyacophilidae	
<i>Rhyacophila fasciata</i> Hagen, 1859	predator
Hydropsychidae	
<i>Hydropsyche contubernalis</i> McLachlan, 1865	collector
<i>Hydropsyche instabilis</i> Curtis, 1834	collector
<i>Hydropsyche saxonica</i> McLachlan, 1884	collector
Limnephilidae	
<i>Anabolia furcata</i> Brauer, 1857	shredder
<i>Potamophylax rotundipennis</i> (Brauer, 1857)	shredder
Philopotamidae	
<i>Philopotamus montanus</i> (Donovan, 1813)	collector
Polycentropodidae	
<i>Cyrnus trimaculatus</i> (Curtis, 1834)	predator
<i>Plectrocnemia conspersa</i> (Curtis, 1834)	predator
<i>Polycentropus flavomaculatus</i> (Pictet, 1834)	predator
Beraeidae	
<i>Beraeodes minuta</i> (Linnaeus, 1761)	scarper
Leptoceridae	
<i>Athripsodes bilineatus</i> (Linnaeus, 1758)	shredder