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Vegetation Cover and Substrate Type as Factors Influencing the Spatial Distribution of Trichopterans along a Karstic River

key words: macroinvertebrates, functional feeding groups, community composition, karstic freshwater

Abstract

In the longitudinal continuum of the Kupa River the vegetation cover and substrate type were the important environmental factors influencing the spatial differences in the biomass and community composition. Of total macroinvertebrate biomass, a significantly greater percentage of trichopterans was found on boulder and cobble substrata covered with moss (54.3% on boulders, 55.8% on cobbles) than on substrata covered with periphyton (9.9% on boulders, 14.8% on cobbles). In the potamal, trichopterans were markedly reduced (<2.5% of total macroinvertebrate biomass) on gravel substrata.

A comparison of the Shannon diversity index values suggested that for trichopteran species diversity the substrate type was a more influential factor than vegetation cover. On the other hand, multidimensional scaling analysis showed that trichopteran community composition was related more significantly to vegetation cover and river area than to substrate type.

In the rhithral the vegetation cover was an important factor influencing the functional feeding group composition of trichopterans. The spatial distribution of scrapers and filtering collectors depended significantly on the vegetation cover associated with substrate type, and shredder trichopterans were related to vegetation cover only. Predatory trichopterans made up 17–65% of total predator biomass, and in the rhithron area they were correlated significantly only with vegetation cover. On gravel substrata in the potamal, vegetation cover did not affect the spatial distribution of shredder and collector-filterer trichopterans significantly.

1. Introduction

In lotic environments the biomass of trichopteran larvae varies seasonally and spatially depending on temperature, current velocity, substrate type, source of food, and other abiotic and biotic factors. According to CIANFICCONI *et al.* (1991) the trichopteran fauna constituted 2.8% of the total density of macroinvertebrates and 12.7% of the insect fauna in the Umbrian Tiber River. In the Danube River, the percentage of trichopterans varied from 0.01% to 59.7% depending on substrate type and temporal fluctuations of organic load (RUSSEV, 1977). In addition, in a tributary of Lake Scadar (Montenegro), JACOBI (1978) found that the biomass of trichopteran larvae accounted for approximately 38% of total benthic macroinvertebrates on boulder substrate. Considering these spatial differences in trichopteran biomass, we hypothesised that the trophic role of trichopteran larvae in the functional feeding organisation of macroinvertebrate communities will also spatially differ. Their importance in the benthic community, and especially their feeding strategies and food preferences, have been documented by many authors (WALLACE *et al.*, 1977; PETERSEN, 1987; DOLÉDEC and TACHET, 1989; PETERSEN, 1989; BECKER, 1990; MALICKY, 1990; MUOTKA, 1993). However, the spatial distribution of trichopteran biomass in lotic biotopes of karstic

streams and rivers with boulder, cobble and gravel substrates covered predominantly by moss and periphyton is still poorly known.

The objectives of our study were: (1) to investigate the spatial changes in the community composition of the trichopteran assemblage along the longitudinal gradient of a karstic river, (2) to examine if the observed spatial differences in biomass, community composition and species diversity depend on vegetation cover and substrate type, (3) to establish if the functional feeding composition of trichopteran larvae is dependent on vegetation cover and substrate type along the karstic rivers.

2. Study Area

The Kupa River is a karstic river, 296 kilometres in length, located in the north-western Dinaric area of Croatia. Based on physiographic variables (discharge regime, type of substrate, morphology of river bed and its declivity) and the longitudinal distribution of functional feeding groups of macroinvertebrates, three successive river sections may be distinguished (BELINIĆ *et al.*, 1993): a limnocrenal source with first order headwater streams, the upper and the lower course. In each of the three pre-defined river sections, four stations were established (Fig. 1). Along its upper course the river flows through a calcareous bed and in

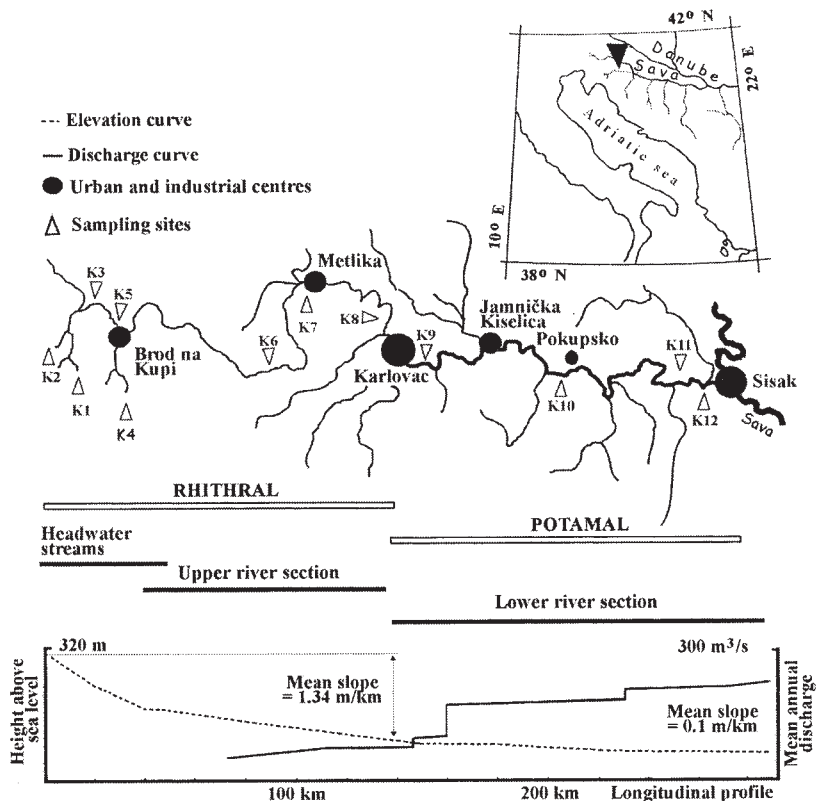


Figure 1. Elevation curve, discharge curve and location of sampling sites K1–K12.

the lower course through alluvium. The first four sampling sites (K1–K4) were located in the headwater streams, 1 to 2 m wide, 0.3 to 0.8 m deep, and with a mean discharge below $0.5 \text{ m}^3 \text{ s}^{-1}$ during summer flow conditions. Deciduous (beech) or coniferous (spruce) bank vegetation provides dense shading of stream section. The substrata consist mostly of boulders and large cobbles covered with moss or periphyton. In the upper river section, the second set of sampling sites (K5–K8) was located on the right or left side of the river at an average water depth of 0.5 m. The width of the river varied from 10 to 40 m. The substrate was composed mostly of boulders and cobbles covered by moss or periphyton. The headwater streams and the upper river section are characterised by fast-flowing, turbulent and unpolluted water, and summer water temperatures were always below 15°C . At all sampling sites and in all seasons, oxygen concentrations were high (8 to 10 mg l^{-1}). According to the classification of ILLIES (1961), the headwaters and the upper river section belong to the rhithral area (Povž *et al.*, 1998).

In the lower river section 4 sampling sites (K9–K12) were placed in shallow areas 0.5 m deep on the right or left side of the river. The river bottom consisted mainly of gravel covered with periphyton and macrophytes. Summer water temperatures were $>20^\circ \text{C}$, and oxygen concentrations ranged from 8 to 14 mg l^{-1} . Based on physiographic characteristics, temporal changes of water temperature, and composition of the fish assemblage, the lower river section can be classified as potamal (Povž *et al.*, 1998).

3. Methods

Our investigation of the spatial distribution of the Trichoptera fauna was carried out as a part of a research programme dealing with benthic community organisation in karstic running waters. At each site in each of the three river sections (headwater, upper and lower) of the Kupa River, macroinvertebrate samples were taken every two months between January 1988 and February 1989. On each sampling date two replicate samples were taken with a Surber sampler (0.1 m^2 , 0.5 mm mesh size) from two substrate types (boulder and cobble in headwater and upper, and gravel in lower river section) at each site.

Macroinvertebrate samples were taken either from randomly selected locations along a transect across the bottom in the headwater streams, or in the shallow biotopes near the river bank in the upper and lower river sections. Substrate habitat types were boulders and cobbles covered with moss or periphyton in the headwater and upper river sites. In the lower river sites macroinvertebrate samples were collected from gravel substrate covered with macrophytes or periphyton.

Thus, three substrate types and two types of vegetation cover combined to six habitat types. In the rhithral: boulders (RBM) and cobbles (RCM) covered with moss, boulders (RBP) and cobbles (RCP) covered with periphyton, and in potamal: gravel covered with periphyton (PGP) and gravel covered with macrophytes (PGM). The total number of macroinvertebrate samples was 288 (2 replicates \times 4 sites \times 6 sampling periods \times 6 habitats).

All macroinvertebrate material retained by the net was removed from dead vegetable detritus and other non living bottom material, and preserved with 5% formaldehyde. In the laboratory, samples were hand-sorted, and macroinvertebrates identified to the lowest possible taxonomic category. Before weighing, cases were removed and all specimens of a species in a sample were dried with absorbent tissue for about 10 sec. Wet biomass was determined on a technical balance accurate to 1 mg. Biomasses were not corrected to fresh biomass because it was assumed that the formaldehyde-preserved biomass was approximately the same as the wet biomass of fresh material (*sensu* MACKAY and KALFF, 1969).

In our study we carried out three summarizations of biomass data: (1) For the review of species composition and species diversity the biomass data of each species were summarized as a mean (2 replicates \cdot 4 sites \cdot 6 sampling periods) for each of six habitats, (2) The arithmetic means of 2 replicates and 4 sites taken, resulting in a total of 36 means, were a basis for all subsequent analyses of temporal changes in biomass, (3) The means (2 replicates \cdot 6 sampling periods) calculated for each of sites and habitats, resulting in 24 mean samples, were a basis for the analysis of spatial changes in trichopteran biomass depending on substrate type and vegetation cover. The statistical significance of differences in spatial changes of trichopteran biomass depending on substrate type and vegetation cover along the river

gradient was calculated using Kruskal-Wallis ANOVA by ranks as the nonparametric alternative to one-way analysis of variance. Similarity among trichopteran assemblages were determined using multidimensional scaling analysis (MDS). This analysis was based on a similarity matrix from Pearson correlation coefficients (r) (KRUSKAL and WISH, 1978). ANOVA and MDS were carried out using STATISTICA (StatSoft Inc. 1995) software. As an index of species diversity, the Shannon-Wiener function was used (KREBS, 1989).

Trichopteran larvae were classified into functional feeding groups according to the literature. It must be emphasised that no consistent system has been adopted for the convenient classification of trichopteran larvae into functional feeding groups based on their feeding strategies. Moreover, the literature information on feeding behaviour is copious and often contradictory. For this reason, we explain in detail our classification of trichopteran larvae identified with respect to their trophic status and feeding strategy.

Lepidostoma hirtum, *Crunoecia irrorata*, *Sericostoma personatum* and *Odontocerum albicorne* were classified as shredders (MERRITT and CUMMINS, 1978). Our classification of *Sericostoma personatum* as a shredder was supported by a feeding test with larvae (MALICKY, 1990) and the examination of gut contents (THORUP and IVERSEN, 1974). In this study, the limnephilids (*Limnephilus extricatus*, *L. lunatus*, *L. rhombicus*, *Potamophylax latipennis* and *Stenophylax* sp.) were also recorded as shredders. Lepidocerid larvae of the genera *Mystacides* and *Athripsodes* are omnivores, and from the functional standpoint are considered collector-gatherers and shredders (CZACHOROWSKI, 1989). In this study, the three lepidocerid larvae identified (*Mystacides azurea*, *Athripsodes bilineatus* and *Athripsodes* sp.) were noted as shredders.

The scraper group consisted of seven taxa. According to WIGGINS and MACKAY (1978), and MERRITT and CUMMINS (1978), representatives of the families Glossosomatidae (*Glossosoma conformis* and *Agapetus* sp.) and Goeridae (*Silo* sp. and *Lithax obscurus*) were classified as scrapers. *Drusus croaticus*, *Micrasema setiferum* and *Tinodes* sp. were also included in the scraper group. Larvae of *Tinodes* forage for food by scraping stones (DANECKER, 1961; ALDERSON, 1969). *Micrasema* has an unclear trophic status. In MOLLES (1982), and WIGGINS and MACKAY (1978), species of *Micrasema* were denoted as scrapers and shredders, whereas BECKER (1990; 1994) stated that species of *Micrasema*, *Tinodes* and *Drusus* were epilithic scrapers.

Net-building hydropsychid species were placed into the collector-filterer group. The role of hydropsychids in processing suspended matter has been studied by many authors (WILLIAMS and HYNES, 1973; PETERSEN, 1987; DARROW and HOLLAND, 1989; DOLÉDEC and TACHET, 1989; PETERSEN, 1989). Into this group we placed *Psychomyia pusilla* and two brachycentrids *Brachycentrus montanus* and *B. subnubilus*. In general, the Brachycentridae and Psychomyiidae are classified as filterers (MERRITT and CUMMINS, 1978). In addition, VOELZ and WARD (1992) also found that a species of *Brachycentrus* feeds primarily by filtering organic matter from the water column.

The feeding strategies of the hydroptilids vary. According to NIELSON (1942), hydroptilids are piercers. He found that larvae of *Agraylea*, *Hydroptila*, *Oxyethira* and *Orthotrichia* fed by sucking the cells of filamentous green algae. However, VERNEAUX (1973), KAWECKA (1977), STREIT and SCHRÖDER (1978) and O'CONNOR and O'CONNOR (1980) found hydroptilids to be mixed-feeders that fed on algae and organic detritus. For this reason, we placed the genera *Hydroptila* and *Ithytrichia* into the collector-gatherer group. Last the rhyacophilid larvae *Rhyacophila vulgaris*, *Rh. nubila*, *Rh. simulatrix* and *Rh. gr. tristis* and the polycentropodid larva *Cyrnus trimaculatus* were classified as predators (THUT, 1969; MARTIN and MACKAY, 1982; MERRITT and CUMMINS, 1978).

4. Results

4.1. Spatial and Temporal Distribution in Biomass

Trichopteran biomass varied from 1% to 56% of the total macroinvertebrate biomass with highest values in February and April and lowest values in July or September (Table 1). The percentage of trichopteran biomass decreased in downstream sites. In the rhithral, i.e. the headwater and upper river sites, the greatest biomass was found in moss habitats. Trichopterans were less abundant on substrata covered with periphyton. In the potamal area (lower river section) their abundance was <1.2% of the total macroinvertebrate biomass. Seasonal

Table 1. Temporal and spatial distribution patterns of trichopteran biomass at different types of vegetation cover and substrate along the river Kupa (mg wet weight \pm S.D. m^{-2})

River area	Rhithral				Potamal	
	Headwater streams		Upper river section		Lower river section	
River section	1, 2, 3, 4		5, 6, 7, 8		9, 10, 11, 12	
Sites						
Substrate type	Boulders Moss RBM	Cobbles Moss RCM	Boulders Periphyton RBP	Cobbles Periphyton RCP	Gravel Periphyton PGP	Gravel Macrophytes PGM
Mean trichopteran biomass	9 770.2 \pm 5 265	5 113.9 \pm 3 689	3 389.3 \pm 2 366	2 340.5 \pm 1 163	779.1 \pm 691	465.8 \pm 418
Mean macroinvertebrate biomass	18 004.4 \pm 7 892	9 155.5 \pm 4 467	34 136.2 \pm 15 432	15 805.7 \pm 6 583	63 638.9 \pm 26 789	18 691.2 \pm 6 583
Percentage of trichopteran biomass	54.3	55.8	9.9	14.8	1.2	2.5
Trichopteran biomass	February 17 586.5 \pm 4 504	8 880.6 \pm 1 736	5 897.4 \pm 498	4 493.8 \pm 153	1 729.6 \pm 59	922.2 \pm 60
	April 14 655.5 \pm 3 108	10 739.2 \pm 2 438	6 710.8 \pm 629	2 808.6 \pm 44	1 542.6 \pm 85	1 034.0 \pm 106
	June 7 034.1 \pm 1 930	2 454.6 \pm 502	3 050.5 \pm 129	1 966.0 \pm 204	701.2 \pm 40	447.2 \pm 54
	July 5 275.9 \pm 671	2 761.4 \pm 469	1 626.9 \pm 152	1 404.3 \pm 94	233.7 \pm 41	111.8 \pm 13
	September 4 689.7 \pm 399	2 778.9 \pm 628	1 016.7 \pm 88	1 825.6 \pm 65	186.9 \pm 16	83.8 \pm 4
	November 9 379.4 \pm 1 028	3 068.3 \pm 1 169	2 033.6 \pm 105	1 544.7 \pm 104	280.5 \pm 23	195.6 \pm 8

Table 2. Distribution of trichopteran biomass (mg wet weight \pm S.D. m^{-2}) at different substrate and vegetation type within the rhithral and potamal area the river Kupa

River area	Substrate type	Site	Vegetation cover	
Rhithral	Boulders		Moss	Periphyton
		1	9759.7 \pm 5064	3607.1 \pm 2505
		2	11096.4 \pm 6746	3133.3 \pm 2096
		3	9659.9 \pm 5694	3516.7 \pm 2575
		4	8731.7 \pm 4903	3300.0 \pm 2315
	Cobbles		Moss	Periphyton
		5	5889.7 \pm 4917	2437.0 \pm 1211
		6	4457.8 \pm 2405	2308.3 \pm 1097
7		5195.8 \pm 4079	2316.7 \pm 1164	
	8	4911.8 \pm 3649	2300.0 \pm 1195	
Potamal	Gravel		Macrophytes	Periphyton
		9	504.3 \pm 457	823.0 \pm 737
		10	460.0 \pm 420	753.3 \pm 680
		11	438.3 \pm 394	776.7 \pm 671
	12	460.4 \pm 409	763.3 \pm 677	

changes of trichopteran biomass, showed a wide range (Table 1). Distribution of trichopteran biomass depended on vegetation cover and substrate type along the river gradient (Table 2). This was confirmed by the results of parametric Kruskal-Wallis ANOVA for the effects of vegetation cover and substrate type on trichopteran biomass. We found that among three substrate types by each of the two vegetation covers the differences in biomass were significant (d.f. = 2; $H > H_0$; $P < 0.05$), as also between two vegetation covers in each of the three substrate types (d.f. = 1; $H > H_0$; $P < 0.05$).

4.2. Community Composition

Spatial differences in community composition were explained best by vegetation cover, substrate type and river area. The dominant families accounting for >75% of the total trichopteran biomass in moss habitats in the headwater streams were rhyacophilids, glossosomatids and limnephilids (Table 3). In the upper river section on periphyton habitats, rhyacophilids, hydropsychids and sericostomatids made up 56.4% of the total trichopteran biomass on boulders and 65.3% on cobbles. On the two gravel substrata with different vegetation cover, leptocerids (*Athripsodes bilineatus*, *Athripsodes* sp. and *Mystacides azurea*) constituted 60% (gravel substrate covered with periphyton) and 53.6% (gravel covered with macrophytes) of the total trichopteran biomass in the potamon.

A higher Shannon diversity index (H') of trichopteran fauna was found in habitats in the rhithral area than in the potamal (Table 4). In the rhithral the difference of diversity indices was between habitats types RBM and RCM 0.33 and 0.64 between habitats RBP and RCP. Comparing habitats with different vegetation cover but the same substrate type (in the rhithral RBM : RBP and RCM : RCP, in the potamon PGP : PGM) the differences were lower (0.40, 0.09 and 0.23 respectively). This comparison suggested that for species diversity, substrate

Table 3. Composition of trichoptera and their spatial distribution based on mean annual biomass (mg wet weight \pm S.D. m^{-2}) of 48 samples (2 replicates \cdot 4 sites \cdot 6 sampling periods). FFG – functional feeding group, Sh – shredders, Sc – scrapers, CoG – collector-gatherers, CoF – collector-filterers, P – predators.

River area	Rhithral			Potamal		
	Headwater streams			Lower river section		
	Boulders Moss RBM	Cobbles Moss RCM	Boulders Periphyton RBP	Cobbles Periphyton RCP	Gravel Periphyton PGP	Gravel Macrophytes PGM
River section	Upper river section			Lower river section		
Sites	1, 2, 3, 4			5, 6, 7, 8		
Substrate type						
Vegetation cover						
Acronym of habitat type						
FFG						
<i>Rhyacophila nubila</i>	P	152.0 \pm 45	167.0			
<i>Rhyacophila simulatrix</i>	P			316.1 \pm 233	75.0 \pm 43	
<i>Rhyacophila vulgaris</i>	P	591.9 \pm 256	811.4 \pm 321	339.0 \pm 243	369.0 \pm 201	
<i>Rhyacophila gr. tristis</i>	P	61.0 \pm 45	50.0 \pm 32	84.8 \pm 50		
<i>Glossosoma conformis</i>	Sc	2964.7 \pm 1678	212.6 \pm 65	125.5 \pm 76	154.8 \pm 45	
<i>Agapetus</i> sp.	Sc	452.0 \pm 245	434.2 \pm 176			
Hydroptilidae, non det.	CoG			4.3 \pm 3	5.8 \pm 3	45.8 \pm 20
Hydropsychidae, non det.	CoF	400.0 \pm 189	20.5 \pm 9	487.2 \pm 277	676.3 \pm 222	
<i>Cynus trimaculatus</i>	P			194.3 \pm 120	47.0 \pm 32	
<i>Psychomyia pusilla</i>	CoF	305.0 \pm 150	69.8 \pm 35	262.9 \pm 134	97.1 \pm 45	
<i>Tinodes</i> sp.	Sc	66.6 \pm 30	3.4 \pm 2	2.1 \pm 1	5.6 \pm 3	
<i>Brachycentrus montanus</i>	CoF	100.0 \pm 67	106.7 \pm 56	30.1 \pm 15	30.0 \pm 14	
<i>Brachycentrus subnubilus</i>	CoF			24.5 \pm 12	42.3 \pm 20	48.0 \pm 31
<i>Micrasema setiferum</i>	Sc	556.7 \pm 301	215.2 \pm 123	114.3 \pm 45	185.3 \pm 78	
<i>Drusus</i> sp.	Sc	130.0 \pm 52	697.5 \pm 51			
<i>Linnephilus extricatus</i>	Sh	1579.8 \pm 897	1500.0 \pm 986	42.4 \pm 20		
<i>Linnephilus lunatus</i>	Sh	1245.7 \pm 567	1100.0 \pm 888	85.9 \pm 56		
<i>Linnephilus rhombicus</i>	Sh					
<i>Potamophylax latipennis</i>	Sh	184.3 \pm 102	10.8 \pm 7			134.0 \pm 56
<i>Stenophylax</i> sp.	Sh	104.2 \pm 87				
<i>Micropterna</i> sp.	Sc	20.3 \pm 15				
<i>Lithax obscurus</i>	Sc	222.3 \pm 122				257.0 \pm 123
<i>Silo</i> sp.	Sc	62.0 \pm 45	7.1 \pm 3			
<i>Lepidostoma hirtum</i>	Sh			14.2 \pm 13	3.8 \pm 2	
<i>Crunoecia trrorata</i>	Sh			20.7 \pm 15		
<i>Athripsodes bilineatus</i>	Sh			217.9 \pm 100	6.9 \pm 2	
<i>Athripsodes</i> sp.	Sh			68.5 \pm 24		
<i>Mystacides azurea</i>	Sh			59.6 \pm 50		
<i>Sericostoma personatum</i>	Sh	400.0 \pm 321	20.7 \pm 13	4.9 \pm 3	31.1 \pm 10	23.1 \pm 11
<i>Odontocerum albicorne</i>	Sh	173.3 \pm 89	313.9 \pm 221	5.7 \pm 3	5.6 \pm 2	153.3 \pm 99
				682.8 \pm 456	408.8 \pm 350	103.5 \pm 57
				205.7 \pm 98	196.3 \pm 98	

Table 4. Percentage functional feeding structure of trichopteran biomass and Shannon's diversity index (bit per mg wet weight m⁻²)

River area		Rhithal				Potamal	
River section		Headwater streams		Upper river section		Lower river section	
Sites		1, 2, 3, 4		5, 6, 7, 8		9, 10, 11, 12	
Substrate type		Boulders	Cobbles	Boulders	Cobbles	Gravel	Gravel
Vegetation cover		Moss	Moss	Periphyton	Periphyton	Periphyton	Macrophytes
Acronym of habitat type		RBM	RCM	RBP	RCP	PGP	PGM
Total trichopteran biomass (mg m ⁻²)		9770.3	5114.9	3389.3	2340.5	779.1	465.8
Percentage trophic structure of trichopteran biomass	Shredders	38.5	57.7	34.1	27.7	86.6	88.8
	Scrapers	45.1	18.3	14.6	14.9		
	Collector-gatherers			0.1	0.2	5.9	0.9
	Collector-filterers	8.2	3.8	23.7	36.2	7.5	10.3
	Predators	8.2	20.2	27.5	21.0		
Shannon's diversity index (H') based on trichopteran biomass composition	H'	3.3	3.0	3.7	3.1	2.4	2.1
	H'_{\max}	4.2	4.1	4.6	4.1	2.6	2.6
	H'/H'_{\max}	0.8	0.7	0.8	0.8	0.9	0.8

types were a more influential factor than vegetation cover. It was evident that maximum possible diversity (H'_{\max}) was a function of species number ($H'_{\max} = \log_2 S$, where S = number of species). The ratio between observed diversity and calculated maximum diversity (H'/H'_{\max}), as a measure of evenness, suggested that the trichopteran assemblages displayed a uniform level of equability ($x = 0.8 \pm 0.063$) along the river continuum.

A two-dimensional configuration of the six habitats derived using MDS analysis suggested that the change in trichopteran community composition was a response to vegetation cover, substrate type, and physical river gradient (rhithral and potamal). The two-dimensional scatterplot (Fig. 2) showed that in dimension 1, trichopteran assemblages of headwater and upper river sites (rhithral area) were separated from those in the lower river section (potamal area). In dimension 2, trichopteran assemblages on boulders and cobbles covered with moss were separated from those on boulders and cobbles covered with periphyton.

4.3. Functional Feeding Group Composition

Because in the headwater and upper river sites a marked percentage of macroinvertebrate biomass belonged to trichopteran fauna, it was to be expected that its trophic importance would be considerable. The functional feeding group composition of trichopteran biomass (Table 4) revealed that in moss habitats of headwater streams, shredders and scrapers represented a major part of trichopteran total biomass. In periphyton habitats of the upper river section, collector-filterer trichopterans were abundant whereas scrapers decreased. On the two gravel substrates in the potamal, we found only shredder and collector-filterer trichop-

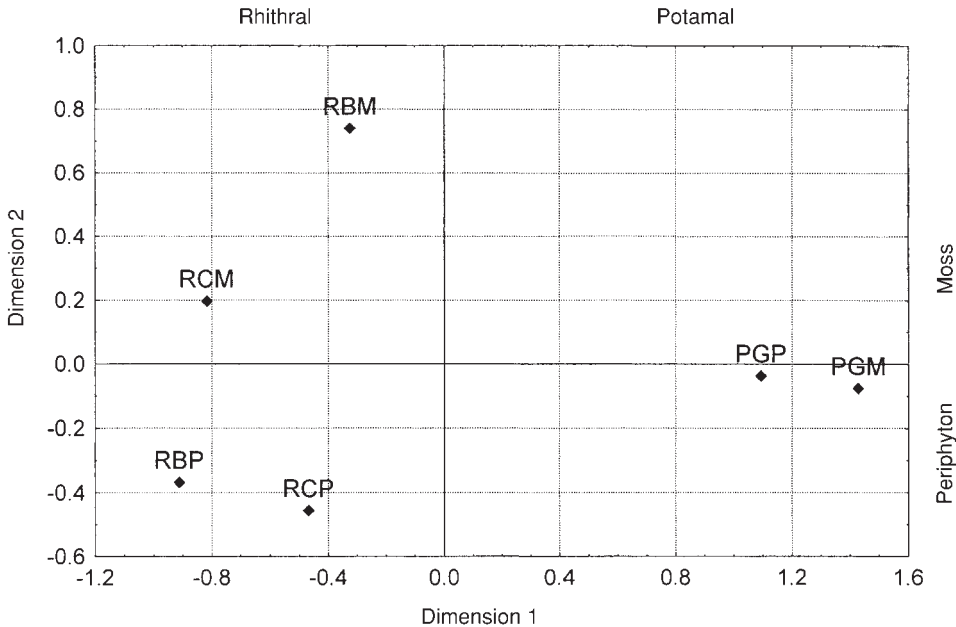


Figure 2. Two-dimensional configuration diagram of six habitats (based on trichopteran biomass composition) associated with longitudinal zonation (rhithral and potamal) (dimension 1) against vegetation cover (dimension 2). RBM rhithral, boulders covered with moss; RCM = rhithral, cobbles covered with moss; RBP = rhithral, boulder covered with periphyton; RCP = rhithral, cobbles covered with periphyton; PGM = potamal, gravel covered with macrophytes and PGP = potamal, gravel covered with periphyton.

terans. In the rhithral area a greater relative abundance of predators was associated with periphyton habitats.

Results of Kruskal-Wallis ANOVA suggested that in the rhithral the spatial distribution of shredders, scrapers and collector-filterers depended significantly on vegetation cover and substrate type (Table 5). Predators showed no substrate preference in the rhithral. In the potamal, the distribution of shredders and collector-filterers also did not show a significant response to vegetation cover.

The percentage of trichoptera in the macroinvertebrate functional feeding group varied, depending on the vegetation cover associated with substrate and longitudinal river zonation (Fig. 3). Within the macroinvertebrates, trichopteran larvae played an important functional role as shredders (represented by limnephilids), scrapers (represented by glossosomatids) and collector-filterers (represented by hydropsychids, psychomyids and brachycentrids) on boulders (RBM) and cobbles (RCM) in headwaters. Collector-gatherer trichoptera represented by hydroptilids were not included because their percentage in total macroinvertebrate biomass was less than 5%. On both substrate types in the rhithral, the role of predators was taken by rhyacophilid larvae, and in terms of biomass, they made up to 65% of all total macroinvertebrate predators.

On boulders and cobbles covered with periphyton (rhithral), the percentage of trichoptera in particular macroinvertebrate functional groups was considerably reduced, especially in scrapers and even more so in collector-gatherers, which were only minimally present. Shredder trichoptera constituted 18.5% on boulders (RBP) and 28.9% on cobbles (RCP)

Table 5. Results of Kruskal-Wallis ANOVA for effect of substrate type and vegetation cover on distribution of trichopteran functional feeding groups (FFG: Sh – shredders, Sc – scrapers, CoF – collector-filterers, P – predators) in the rhithral and potamal (mg wet weight \pm S.D. m^{-2}). Probability of differences (* = $P < 0.05$; ** = $P > 0.01$; NS = no significant) among means was based on H value. Degree of freedom = 1 (substrate); 1 (vegetation cover)

River	FFG	Substrate type		P	Vegetation cover		P
area		Boulders	Cobbles		Moss	Periphyton	
Rhithral	Sh	2453.1 \pm 1477	1800.8 \pm 1251	NS	3351.1 \pm 679	902.7 \pm 326	*
	Sc	2453.7 \pm 2117	642.4 \pm 327	*	2644.0 \pm 1886	422.1 \pm 85	*
	CoF	804.4 \pm 37	521.8 \pm 353	**	501.1 \pm 326	824.6 \pm 74	**
	P	808.5 \pm 80	760.0 \pm 289	NS	868.5 \pm 80	760.0 \pm 289	*
Potamal	FFG	Gravel	Gravel		Macrophytes	Periphyton	
	Sh	413.8 \pm 66	675.0 \pm 92		413.8 \pm 66	675.0 \pm 92	NS
	CoF	48.0 \pm 31	58.3 \pm 26		48.0 \pm 31	58.3 \pm 26	NS

of total macrozoobenthos shredder biomass. Collector-filterers showed a greater percentage on boulders (47.2%) than on cobbles (25.7%). In addition, the proportion of predatory trichopterans in total predatory macroinvertebrate biomass was significantly reduced (boulders: 27.6%, cobbles: 17.1%).

In the lower river section (potamal), the proportion of shredder leptoцерid larvae, represented by the *Athripsodes bilineatus*, *Athripsodes* sp. and *Mystacides azurea* was very low (4.9% of total shredder biomass on gravel substrate with periphyton, 16.3% on the gravel substrate covered by macrophytes). In addition, the proportion of collector-filterers was low on both gravel substrates. On the whole longitudinal profile the percentage of trichopteran collector-gatherers of total collector gatherer biomass was very low and for this reason it was not presented in Fig. 3.

5. Discussion

Our results showed that for total macroinvertebrate biomass the percentage of trichopterans decreased along the longitudinal gradient. In studies of macrozoobenthic communities, CIANFICCONI *et al.* (1991) and DOLÉDEC (1989) also found a decrease in trichopteran fauna in downstream river sections. In addition, CÉRÉGHINO *et al.* (1997) noted a decrease in density and biomass for six trichopteran species in a downstream section of a Pyrenean stream. The decrease of trichopteran biomass and species diversity in downstream river sections can be associated with a downstream increase in substrate uniformity. DE MARCH (1976) also observed that macroinvertebrate species richness may decrease as interstitial spaces are filled in by sediment and detritus. On the other hand, habitat diversity increases with increased substrate size and, consequently, invertebrate biomass, density, and species richness also increase (REICE, 1980; MEYERHOFF and LIND, 1987). In periphyton habitats in the rhithral the increased trichopteran diversity was supported by the fact that overall species diversity is related positively to periphyton biomass (MEYERHOFF and LIND, 1987).

In our study, significant differences in trichopteran community structure depended on vegetation cover associated with substrate type and river area. In MDS analysis the spatial

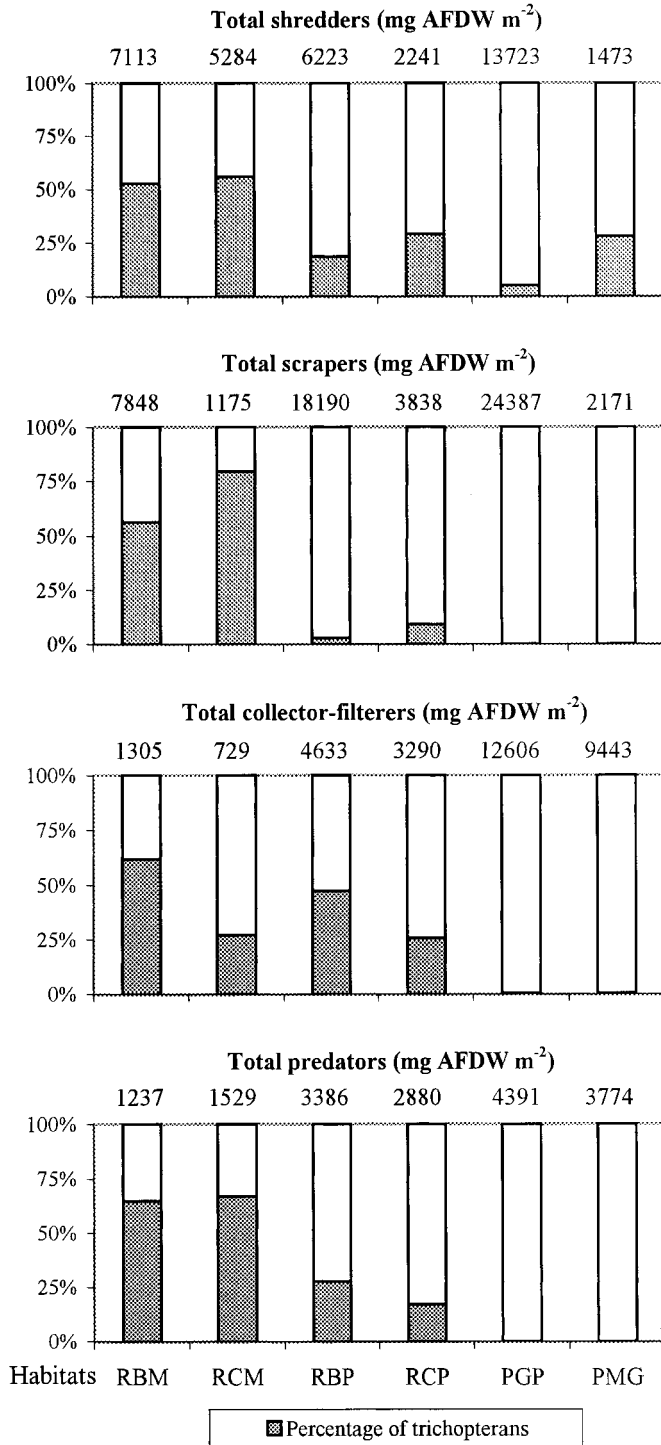


Figure 3. Percentage of trichopteran functional feeding group biomass in total macrozoobenthic functional feeding group biomass. Habitat types as in Fig. 2.

ordination of the six habitat types suggested that community composition of trichopterans responded to ecological determinants of river course classification, as described by ILLIES (1961). Because the association of community composition with vegetation cover (moss in the headwater streams and periphyton in the upper river section) was more highly expressed than with the different substrate types, we considered vegetation cover to be an important common determinate of trichopteran composition. This means that vegetation cover may influence the retention, deposition and distribution of particulate organic detritus, and consequently the functional feeding composition of trichopterans. Many recent studies have focused, from various points of view, on the analysis of the relationship between vegetation cover and invertebrate communities. Differences in macroinvertebrate composition have often been explained by differences in vegetation cover, morphology, and architecture, and thus the degree of protection and food availability (HIGLER, 1975; KEAST, 1984; ROOKE 1984).

In the rhithral (headwater and upper river sites), boulders provided microhabitat refuges enriched with coarse particulate detritus thereby creating good conditions for shredder trichopterans. In addition, moss mats with epiphytes and well-oxygenated swift water provided favourable abiotic conditions and sufficient food for the epilithic scraper trichopterans, represented by stenotopic rheophiles. In the rhithral, collector-filterer trichopterans (hydropsychids) showed a preference for boulder substrate rather than cobbles. Predatory trichopterans (rhacophilids) showed no substrate type preference. The greatest biomass was associated with moss cover. According to BELINIĆ (1991) and HABDIJA *et al.* (1997) the predator – prey relationship was a more decisive factor for predators than substrate type.

In moss habitats in the rhithral, trichopteran shredders included the limnephilid larvae, *Odontocerum albicorne* and *Sericostoma personatum*, on boulders, and mostly *Odontocerum albicorne* on cobbles. In periphyton habitats, trichopteran shredders had a higher species diversity than in moss habitats. On both substrate types (boulders/cobbles) the dominant trichopterans were *Sericostoma personatum* and *Odontocerum albicorne*. Shredder leptocerids (*Athripsodes* and *Mystacides*), and the lepidostomatid larvae (*Crunoecia* and *Lepidostoma*) were collected in small numbers only. In the potamal, leptocerid larvae were the only shredders. MALICKY (1990) found that of the 40 species of Trichoptera known from Crete only 12 are potential shredders and only seven of these are widespread and abundant enough to play a significant role in total shredder biomass. Based on these findings and the observed change of the proportion of trichopteran biomass in total shredder macroinvertebrate biomass along the longitudinal profile of the Kupa River, we concluded that the importance of trichopteran larvae for CPOM processing decreases downstream.

On moss boulder habitats (rhithral), trichopteran scrapers constituted a high percentage of total macroinvertebrate scraper biomass. In rhithral periphyton habitats, trichopteran scraper biomass clearly decreased, whereas scraper trichopterans were not found in the potamal. LAMBERTI and RESH (1983), LAMBERTI *et al.* (1987), BECKER (1990), and FEMINELLA and RESH (1991) found that periphyton communities in streams are significantly influenced by grazing invertebrates. This trophic importance of scrapers and the scraper biomass of trichopterans in lotic karstic biotopes supports the idea that they can play an important role in the consumption of periphytic and epiphytic algae only in the headwater streams. The low abundance of trichopteran collector-gatherers i.e. hydroptilids at all sites along the longitudinal profile suggests that their trophic role as fine detritus processors is minor in karstic rivers.

Collector-filterers have been the object of many trichopteran studies (CUMMINS, 1973; WALLACE, 1975; WALLACE *et al.*, 1977; DARROW and HOLLAND, 1989; PETERSEN, 1989; VOELZ and WARD, 1992; DOWNES and JORDAN, 1993). In karstic habitats of the Kupa River, besides shredders and scrapers the high biomass of collector-filterer hydropsychid and psychomyiid larvae suggests that the processing of suspended organic matter is important in energy transfer in the rhithral. The dominant trichopteran collector-filterers were hydropsychids and *Psychomyia pusilla*. Two species of *Brachycentrus* were present in less abundance.

Because in moss habitats in the rhithral, predatory trichopterans, represented mainly by rhyacophilids, constituted more than 50% of the total predatory biomass, we considered that predatory trichopterans were the most important predators on other macroinvertebrates. In the potamal we found no predatory trichopterans. This means that other taxonomic groups of macroinvertebrates play predatory role. Decrease of trichopteran predatory pressure in the potamal was also described in many recent studies dealing with the predation effects of trichopteran larvae on the spatial and temporal dynamics of benthic macroinvertebrates (MECOM, 1972; HILLDREW and TOWNSEND, 1980; MARTIN, 1985; DUDGEON and RICHARDSON, 1988; BASAGUREN and ORIVE, 1989; LANCASTER *et al.*, 1990; MUOTKA, 1993; HABDIJA *et al.* 1997).

It must be also taken into consideration that vegetation cover and substrate are physical factors defining the environmental conditions of protection in microhabitat refugia against water current and passive drift. It is known that the development of periphytic algae, a food source for scrapers, depends on the physical structure of the substrate and on current velocity. In addition, the deposition and spatial distribution of different size fractions of particulate organic detritus are influenced by the physical structure of the substrate, the physical architecture of vegetation cover and current. According to HAWKINS and SEDELL (1981) these interactions can be generalised in the River Continuum Concept (RCC), which suggests that stream morphology, current velocity, substrate composition, temperature and allochthonous and autochthonous energy inputs interact to influence the availability of food to invertebrate consumers.

This study of macroinvertebrate fauna in the karstic river Kupa clearly showed that the community and functional feeding composition of the trichopteran assemblage changes spatially along the river continuum. Because the functional feeding composition of trichopterans did not show the longitudinal distribution as predicted by the RCC (ANDERSON and SEDELL, 1979; VANNOTE *et al.*, 1980), which states that community and trophic composition of benthic macroinvertebrates is a functional continuum, we concluded that the RCC hypothesis does not provide a framework for changes in trichopterans with respect to functional feeding structure along the river gradient of a karstic river. This means that the trichopteran association will also be organised according to its evolutionary adaptability to food strategy, food availability and to other environmental biotic and abiotic conditions defining the vegetation cover associated with substrate type.

6. Acknowledgements

The study was supported by a grant from the Ministry of Science and Technology of the Republic of Croatia.

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