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Current velocity and food supply as factors affecting the composition of macroinvertebrates in bryophyte habitats in karst running water

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In the lotic aquatic biotopes on a tufa barrage in the Plitvice cascade lake system macroinvertebrate samples associated with a calcareous substrate covered with bryophytes and accumulated organic detritus were collected seasonally in four habitats with different current velocities. The aim was to investigate the interaction between the community features of macroinvertebrates and bryophyte cover associated with the selective retention and accumulation of particulate organic matter affected by different water flow conditions. In the tufa barrage habitats, depending on current velocity, bryophyte biomass varied seasonally from 55 g AFDW m^{-2} to 256 g AFDW m^{-2}. Bryophyte biomass decreased in the tufa habitats exposed to higher current velocity. In the temporal succession from spring to autumn bryophyte biomass decreased, whereas in winter the biomass increased in all studied rheotopes. Regression analysis suggested that the bryophyte biomass significantly decreased linearly with an increase in current velocity. The bryophyte mats, which retained coarse (CPOM), fine (FPOM) and ultra fine (UPOM) benthic particulate organic matter as a food source for the detritial benthic macroconsumers, were significantly related to current velocity. CPOM and FPOM content of the bryophyte mats showed a tendency to increase in habitats with a lower current velocity. Conversely, UPOM content increased in bryophyte habitats with a higher current velocity. Regression analysis suggested that CPOM and FPOM increased whereas UPOM decreased significantly in habitats with a greater bryophyte biomass. In bryophyte habitats the community composition of macroinvertebrates was characterized by small forms of oligochaetes, dipterans and coleopterans constituting from 64.1% to 98.7% of the total number of macroinvertebrate individuals. Regression analysis suggested that macroinvertebrate density increased in faster water flow conditions associated with a decrease in bryophyte biomass, CPOM and FPOM, and an increase of UPOM. Macroinvertebrate community composition and species diversity showed significant differences among the four seasons and four water flow conditions associated with selective retention and accumulation of POM. In bryophyte habitats macroinvertebrate functional feeding composition was characterized by collector fauna increasing their density with faster water flow conditions. In spring and summer collector-gatherers were dominant whereas collector-filterers dominated in autumn and scrapers showed a maximum in winter. Regression analysis, using the power model ($y = ax^b$), suggested that densities of collectors and predators showed a positive relationship with the quantity of their food sources.

Key words: aquatic bryophytes, macroinvertebrate community, functional feeding composition, karstic tufa biotopes, Croatia.

Introduction

Benthic habitats on calcareous tufa barrage are widespread biotopes in karstic running waters of the Dinarid area. A tufa substrate covered with bryophytes or periphyton, calcite precipitation, high current velocity and oxygen concentrations are the main environmental variables affecting the composition and functional feeding group composition of macroinvertebrates. According to many recent studies, in benthic habitats establishing the ecological importance of bryophyte cover is focused on the physical architecture of bryophyte mats defining: (i) the environmental conditions of protection in microhabitat refugia against predator, water currents and passive drift (GURTZ & WALLACE, 1984; BRUSVEN et al., 1990; HABDIJA et al., 2000), and (ii) the retentive capability of a stream and spatial distribution of different size fractions of particulate organic matter (FINLAY & BOWDEN, 1994). STEWART & DAVIS (1990), PROCHAZKA et al. (1991) and SUREN (1991) considered that the architecture and thickness of bryophyte mats associated with current velocity play an important role in retention and trapping of POM. SUREN & WINTERBOURN (1992) reported that bryophytes provide a food source for invertebrates in the form of trapped detritus and periphyton. With respect to the significant positive correlation between the functional organization of the macroinvertebrate community and food availability in the framework of the River Continuum Concept (VANNOTE et al., 1980; HAWKINS & SEDELL, 1981; BASAGUREN et al., 1996) we considered, that in bryophyte habitats on the tufa substrate the interaction between current velocity and retention of POM would have marked implications for species diversity and changes of community and functional feeding group composition of the macroinvertebrates. Supporting the concept of a river continuum in limnological research of the Turiec river basin (West Carpathians, Slovakia) KRNO & ŠPORKA (1996) emphasized the importance of transport and retention of POM as factors affecting the quality of food sources and the composition of macroinvertebrate functional feeding groups.

Despite the several recent studies investigating the community composition of macroinvertebrates associated with bryophytes, the functional organization of the macrobenthic community is poorly known in bryophyte habitats of calcareous tufa in karstic running waters. For this reason the present study deals with current velocity as a factor regulating: (i) the selective retention and accumulation of organic detritus in bryophyte mats and (ii) the community composition of macroinvertebrates. Our hypothesis was that in tufa barrage habitats various current velocity conditions associated with selective retention of organic detritus in bryophyte mats are the main factors affecting changes in: (i) population density, (ii) species diversity, and (iii) macroinvertebrate community and functional feeding group composition.

Study area

Macroinvertebrate community and functional feeding group composition were studied in the Plitvice lakes located in the karstic region of the NW Dinarid Mts (Fig. 1). This cascade lake hydrosystem consists of 16 oligotrophic, dimictic lakes in which the water flows from one lake to the other over tufa barrages. Our four sampling sites (L1, L2, L3 and L4), placed at depths of 10 cm to 20 cm, were located in a channel on the first big tufa barrage through which the water flows from Prošće lake to other lakes located downstream. Current velocity, clean and unpolluted water, physical oxygenation, precipitation of calcite (50000 tons of calcite pro year: according to KEMPE & EMEIS, 1985, in FORD & PADLEY, 1996) and well-developed bryophyte vegetation (according to PAVLETIC, 1957, predominantly *Cratoneurum commutatum* Roth, *Bryum ventricosum* Dicks., *Didymodon tophaceus* Jur. and *Platyhypnidium rusciforme* Fleischr.) are the main ecological determinants in the tufa barrage habitats. Water chemistry on our four sampling sites was determined by chemical and physical characteristics associated with the thermal regime of the epilimnetic water in Prošće lake (HABDIJA et al., 1986). As seen in Table 1, the seasonal change in temperature was characterized by summer maximum and winter minimum. The highest oxygen concentrations were associated with winter tem-

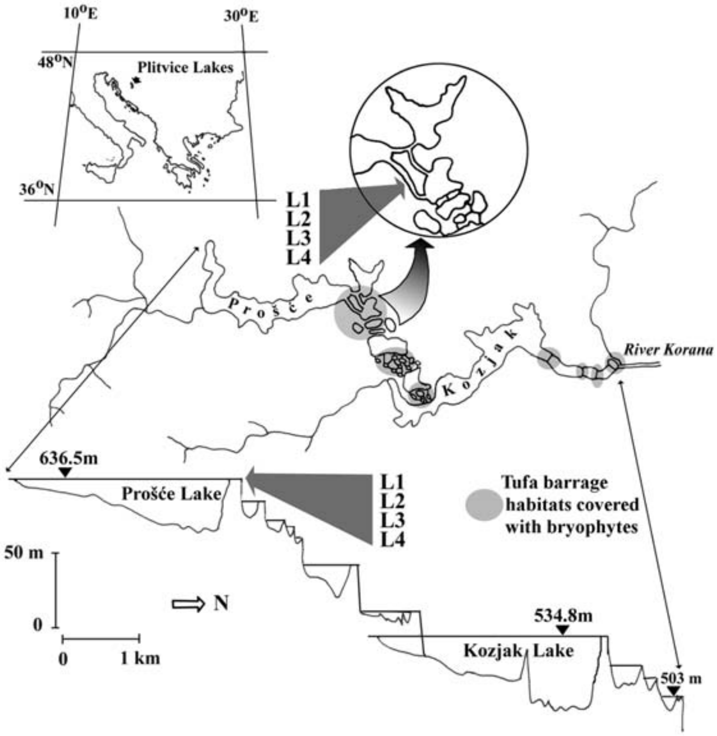

Fig. 1. Map of Plitvice cascade lake system with four locations (L1, L2, L3, L4) for the benthic sampling.

perature. Percentage O_2–saturation varied from 80% to 115% approximately. COD, as indicator of organic matter, was under 3 mg O_2 L^{-1}. Its increased values were associated with the summer months. Concentration of ortho-phosphate exhibited an identical seasonal change. Alkaline earth ions varied seasonally in a narrow range.

Material and methods

In the running water aquatic biotopes on a tufa barrage in the Plitvice cascade lake system a total of 48 samples of macroinvertebrate and organic detritus were collected during four seasons in 1999. In each season three replicates were taken at each of four sites (L1, L2, L3 and L4) with different ranges of water flow speed (L1: 20–40 cm s^{-1}, L2: 40–70 cm s^{-1}, L3: 70–100 cm s^{-1} and L4: $>$ 100 cm s^{-1}). Water velocity was measured with a flow meter (manufactured by firm Rost, Vienna). Before macroinvertebrate sampling, current velocity was measured at depths of 20 to 30 cm, and $\approx$ 3 cm above the surface of moss mats selected for sampling. Tufa substrates (1 dm^2) covered with bryophytes and together with the macroinvertebrates, different size fractions of particulate organic matter (POM) and epiphytic algae and microzoobenthos were cut out with a sharp trowel to a depth of 10 cm and transported in PVC dishes to the laboratory. The cut soft and porous tufa substrate was used to determine bryophyte biomass, population density of macroinvertebrates and different size fractions of benthic detritus: coarse (bCPOM), fine (bFPOM) and ultra fine (bUPOM) particulate organic matter. CPOM was defined as material $>$ 1 mm diameter, FPOM as 0.045 mm – 1 mm and UPOM as particles $<$ 0.045 mm.

During laboratory treatments, first, the bryophytes were hand-separated from the tufa substrate. Then, benthic detritus and macroinvertebrates were removed by rinsing from the bryophyte mat. After washing, the bryophytes were dried at 104 ℃ and ashed at 400 ℃. Benthic particulate organic matter (bCPOM and bFPOM) and macroinvertebrates were separated from the mineral sediments by repeated washing and decanting through three sieves (1 mm, 0.5 mm and 0.045 mm mesh opening). For the determination of bUPOM (including epiphytic algae) by filtration on a preweighed 0.45 μm pore size membrane filter, three subsamples were taken from the filtered water (after determination of FPOM) with suspended material (size class $<$ 0.045 mm). The sestonic particulate organic matter (sPOM) was determined by filtering water through a membrane filter (0.45 μm, Sartorius). The three replicate determinations of sPOM were conducted once monthly between January and December 1999 at all four sites (L1, L2, L3 and L4). The results were summarized as monthly means (3 replicates $\times$ 4 sites).

Using a stereomicroscope (Stemi 2000, C. Zeiss) all macrozoobenthic material retained by the sieves was picked by hand and preserved in 5% formaldehyde.

Table 1. Seasonal changes of the main physical and chemical features of water (mean ± SD) in tufa barrage habitats during 1999 (mean values of 4 habitats L1, L2, L3 and L4).

Month	Temperature (°C)	Dissolved oxygen (mg O_2 L^{-1})	O_2-saturation (%)	COD ($KMnO_4$) (mg O_2 L^{-1})	Phosphate (mg P L^{-1})	Alkaline earth ions (meq L^{-1})	Discharge (m^3 s^{-1})
January	3.1 ± 0.0	12.4 ± 0.8	95.3 ± 6.1	0.95 ± 0.2	0.01 ± 0.003	4.4 ± 0.00	7.93
February	3.2 ± 0.0	12.7 ± 0.9	97.8 ± 6.8	1.05 ± 0.3	0.01 ± 0.003	4.4 ± 0.05	7.71
March	7.7 ± 0.0	12.2 ± 0.8	109.0 ± 7.0	1.42 ± 0.2	0.02 ± 0.003	4.5 ± 0.00	7.76
April	12.9 ± 0.02	10.8 ± 0.7	109.7 ± 6.9	1.34 ± 0.3	0.02 ± 0.004	4.5 ± 0.05	7.47
May	16.9 ± 0.03	10.0 ± 0.9	113.2 ± 8.0	2.10 ± 0.3	0.03 ± 0.002	4.4 ± 0.05	6.96
June	17.8 ± 0.05	9.1 ± 1.0	103.7 ± 11.4	2.34 ± 0.3	0.02 ± 0.002	4.3 ± 0.00	6.68
July	18.4 ± 0.06	7.5 ± 0.5	84.0 ± 5.6	3.00 ± 0.4	0.04 ± 0.003	4.4 ± 0.05	6.43
August	18.5 ± 0.06	8.6 ± 0.5	98.0 ± 6.2	3.29 ± 0.4	0.02 ± 0.003	4.5 ± 0.05	6.27
September	15.3 ± 0.05	10.1 ± 0.5	108.3 ± 5.4	3.08 ± 0.2	0.03 ± 0.002	4.5 ± 0.00	6.26
October	12.0 ± 0.5	8.9 ± 0.4	93.0 ± 4.8	2.45 ± 0.2	0.02 ± 0.002	4.7 ± 0.00	6.53
November	8.9 ± 0.6	10.4 ± 0.7	101.0 ± 5.0	2.45 ± 0.2	0.04 ± 0.004	4.4 ± 0.00	7.02
December	8.0 ± 0.4	10.4 ± 0.8	95.0 ± 7.3	1.90 ± 0.2	0.01 ± 0.002	4.4 ± 0.00	7.07

Macroinvertebrates were hand-sorted, counted and identified to the lowest possible taxonomic category. Classifying identified macroinvertebrates into five functional feeding groups (shredders, scrapers, collector-gatherers, collector-filterers and predators) was performed according to the literature. Fauna Aquatica Austriaca edited by MOOG (1995) was the basic source. In addition, other recent literature sources were used (MERRITT & CUMMINS, 1978; SCHWANK, 1981; WARD & WILLIAMS, 1986). The macroinvertebrate material, sPOM, and separated size fraction of bPOM were dried at 104 °C and ashed at 400 °C in order to determine the ash-free dry weight (AFDW).

In this study a total of 48 macroinvertebrate, bryophyte and bPOM samples (3 replicates × 4 sites × 4 seasons) were collected. For each season and site (i.e. ranges of water flow) the macroinvertebrate population density and AFDW of bryophyte biomass and of the detritus size fractions were calculated as a mean of the three replicates. Mean values of macroinvertebrate density more than 1,000 ind. m^{-2} were rounded to 10^1, 10^2 and 10^3.

The level of similarity among patterns of macroinvertebrate community composition, expressed as population density (untransformed data of ind. m^{-2}), was determined using cluster analysis. The tree clustering and complete linkage methods were based on 1-Pearson r as a measure of the distance among the macroinvertebrate composition patterns. With a view to evaluating the functional association between changes in food sources (bCPOM, bFPOM, bUPOM and sPOM) associated with water flow conditions and macroinvertebrate population density we used regression analysis. The models: $y = ax \pm b$, $y = ax^b \pm c$ and $y = ax^b$ showed the best goodness of fit. In the regression analysis 16 data values were included (4 seasons × 4 sites, i.e. 4 ranges of water flow). Each of the 16 data values was calculated as a mean of 3 replicates. Regressions were tested for significance by using the coefficient of determination, R^2 (i.e. Pearson R) to estimate an F ratio: $F = R^2(N - k - 1)/(1 - R^2)k$, where k is number of regression parameters and N is number of samples (SOKAL & ROHLF, 1995). Regression and cluster analysis were carried out using Statistica software (STATSOFT, 1998). The Shannon index of diversity (H') (KREBS, 2000) was used as index of macroinvertebrate community diversity.

Analyzing the seasonal change of plankton dynamics in the upstream located Prošće lake, ŠPOLJAR et al. (2001) found a peak of phytoplankton and zooplankton development during summer period.

Because the drift of sPOM was caused by an erosion effect, discharge was measured at a limnograph of the Meteorological and Hydrological Service. According to the three-month mean based on daily values of discharge, the hydrological regime of the Plitvice lakes was characterized by (i) high discharge in winter and at the beginning of spring period, (ii) decreased discharge in spring, (iii) low discharge in stable summer and (iv) increased discharge in the unstable autumn period (Tab. 1).

Results

Food sources

In bryophyte habitats on the tufa barrage of the Plitvice lake hydrosystem, three food sources are available for the macroinvertebrate community. Bryophytes and periphytic algae are the source for herbivorous shredders and periphyton scrapers. For detritivorous shredders and collector gatherers the food source is the leaf litter of riparian vegetation (beech predominantly), processed by physical and microbiological fragmentation into different size fractions of benthic organic detritus (bCPOM, bFPOM and bUPOM). A third food

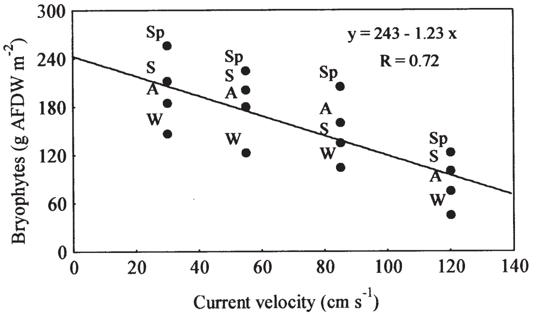

Fig. 2. Bryophyte biomass in relation to current velocity. Sp – spring; S – summer; A – autumn; W – winter.

source is the seston (sPOM), which is transported from the upstream to downstream lakes, supplying the benthic collector-filterers with food.

The biomass of bryophytes, the main ecological characteristic of tufa barrage habitats, changed seasonally depending on current velocity (Fig. 2). In all four seasons bryophyte biomass measured as AFDW decreased in tufa habitats exposed to higher current velocity. Using a linear model $y = ax \pm b$ regression analysis suggested that the bryophyte biomass decreased with an increase of current velocity significantly ($R = 0.72$, $n = 16$, $P < 0.05$).

The bryophyte mats retaining coarse (bCPOM), fine (bFPOM) and ultra fine (bUPOM) benthic particulate organic matter, a food source for the detrital benthic macroconsumers, were related also to current velocity (Fig. 3). Benthic CPOM and FPOM content tended to increase in habitats with lower current velocity. Conversely, bUPOM increased in bryophyte habitats with a higher current velocity. The greatest bUPOM content was found in autumn and winter at higher values of current velocity. According to the regression analysis carried out using the linear model $y = b \pm ax$, the content of different sized benthic POM fractions showed significant correlations with current velocity (Tab. 2). Considering the seasonal changes in detail, the greatest content of bPOM was found in autumn and winter, which can be explained by the leaf litter of riparian vegetation in autumn (Fig. 3). Sestonic particulate organic matter (sPOM) is a very important food source for macroinvertebrate collector-filterers. It varied from 28.5 mg AFDW m^{-3} to 196 mg AFDW m^{-3} through the year (Fig. 4). This temporal fluctuation of sPOM was characterized by spring (April) and autumn (September) peaks.

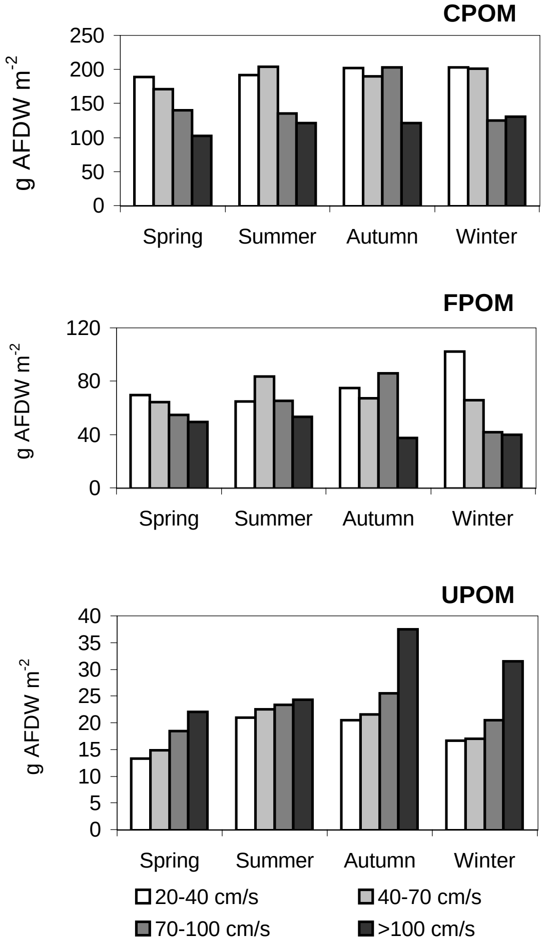

Fig. 3. Seasonal changes of bCPOM, bFPOM and bUPOM associated with current velocity.

The decrease of bryophyte biomass, bCPOM and bFPOM, and the increase of bUPOM with increased water flow conditions raised the question of whether there is a relationship between the content of different sized fractions of benthic POM and bryophyte biomass. Use of the linear model $y = ax \pm b$ regression analysis suggested that bCPOM and bFPOM increased whereas bUPOM decreased significantly in habitats with greater bryophyte biomass (Tab. 2).

Community composition

In bryophyte habitats macroinvertebrate population densities ranged from 69,900 ind. m^{-2} to 706,260 ind. m^{-2} depending on season and current velocity conditions (Fig. 5). In all current velocity conditions the lowest density was found in

Table 2. Regression analysis based on model $y = ax+b$ of the relationships: bentic POM sized fractions (bCPOM, bFPOM & bUPOM) against current velocity (v) and bryophyte biomass (bb)

Bentic POM	n	Regression equation	R	Significant level
bCPOM	16	bCPOM = 231 − 0.92 v	0.85	**
bFPOM	16	bFPOM = 85.9 − 0.32 v	0.71	*
bUPOM	16	bUPOM = 12.97 + 0.12 v	0.70	*
bCPOM	16	bCPOM = 0.402 bb + 102.6	0.60	*
bFPOM	16	bFPOM = 0.160 bb + 36.6	0.61	*
bUPOM	16	bUPOM = 33.30 − 0.076 bb	0.71	*

Key: $^{*}P < 0.05$; $^{**}P < 0.01$.

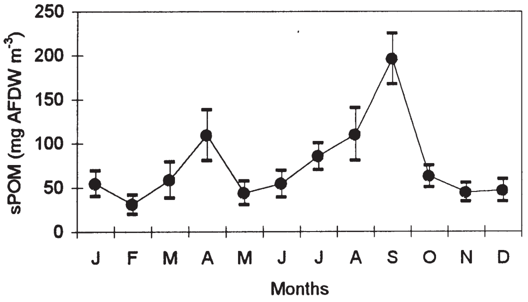

Fig. 4. Temporal changes of sestonic sPOM calculated as monthly means (4 sites × 3 replicates) ±1 SD.

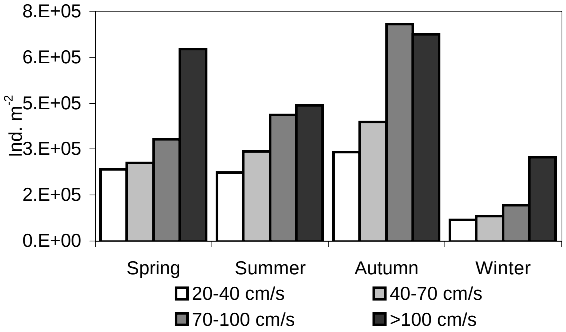

Fig. 5. Seasonal changes of macroinvertebrate population density depending on current velocity.

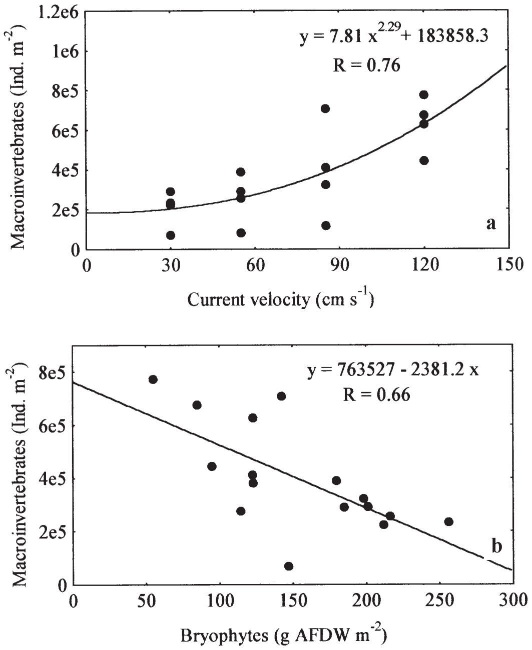

Fig. 6. Relationships: macroinvertebrate density as compared with current velocity (a) and macroinvertebrate density compared with bryophyte biomass (b).

winter and the highest during autumn. Considering the water flow we observed that higher population density was associated with an increase in current velocity (but also with decreased CPOM and FPOM and increased UPOM contents). Use of the models $y = ax^b \pm c$ and $y = ax \pm b$ regression analysis suggested that population density of macroinvertebrates increased non linearly with an increase of current velocity ($R = 0.76$, $n = 16$, $P < 0.05$) but decreased with an increase of bryophyte biomass linearly ($R = 0.66$, $n = 16$, $P < 0.05$) (Fig. 6). At our four sampling sites a total of 80 taxa were found (Tab. 3). Oligochaeta, Coleoptera, Trichoptera and Diptera were the most abundant taxa. In percentage terms they represented from 80% to 98% of the total macroinvertebrate abundance (Tab. 4). These macroinvertebrate taxa showed a seasonal succession. Oligochaeta dominated in spring, Diptera (simuliids and tanypodins mainly) in summer and in autumn, whereas in

Table 3. Macroinvertebrate community and functional feeding group composition in tufa barrage habitats in the different seasons and at different current velocity conditions (mean of three replicates, ind. m^{-2}).

Season		Spring				Summer			
Current velocity (cm s^{-1})		20–40	40–70	70–100	> 100	20–40	40–70	70–100	> 100
Acronym of habitat type		SP20	SP40	SP70	SP100	S20	S40	S70	S100
Taxa	FFG								
Gammarus balcanicus Schaeferna, 1922	Sh	0	0	100	0	450	4070	0	0
Amphinemura, div. sp.	Sh	0	5	0	0	0	0	0	0
Protonemura sp.	Sh	5000	2275	2580	400	5040	5070	16200	11400
Nemoura sp.	Sh	0	0	0	0	17	0	0	0
Limnephilidae, div. sp.	Sh	0	0	0	0	0	194	0	0
Tipula sp.	Sh	0	0	0	0	0	67	0	0
Total shredders		5000	2280	2680	400	5507	9401	16200	11400
Bythinella sp.	Sc	4700	0	0	0	400	400	0	0
Radix peregra (O.F. Müller, 1774)	Sc	33	0	0	0	15	0	0	0
Hydrobidae, div. sp.	Sc	0	0	0	0	7	5600	0	0
Naididae, div. sp.	Sc	5520	8140	9090	14670	4800	4500	7600	5600
Amphinemura, div. sp.	Sc	0	12	0	0	0	0	0	0
Baetis muticus (L., 1758)	Sc	750	1100	230	0	424	1160	3000	400
Baetis lutheri Mueller-Liebenau, 1967	Sc	350	400	233	1600	443	566	3000	400
Helodes sp.	Sc	25000	13400	21500	18000	6150	3270	6000	0
Riolus sp.	Sc	6900	13470	12150	4400	2600	21200	23200	39000
Limnius sp.	Sc	0	0	67	0	0	400	400	400
Tinodes sp.	Sc	400	105	317	0	35	1330	0	0
Lype reducta (Hagen, 1868)	Sc	0	0	17	0	0	0	0	0
Oxycera sp.	Sc	200	0	0	0	0	0	0	0
Total scrapers		43853	36627	43604	38670	14874	38426	43200	45800
Oligochaeta, div. sp.	CoG	99460	164920	205220	530660	16373	72400	146600	15900
Naididae, div.sp.	CoG	5520	8140	9090	14670	4800	4500	7600	5600
Eiseniella tetraedra (Savigny, 1826)	CoG	200	200	203	400	133	267	400	400
Amphinemura, div. sp.	CoG	0	8	0	0	0	0	0	0
Leuctra sp. (juv.)	CoG	11500	3400	2820	600	960	533	400	0
Leuctra fusca L., 1758	CoG	400	400	50	0	200	0	0	0
Torleya sp.	CoG	0	25	367	0	0	0	0	0
Leptophlebiidae, div. sp.	CoG	0	0	0	0	283	407	0	0
Paraleptophlebia sp.	CoG	0	667	167	100	0	0	0	0
Habrophlebia lauta Eaton, 1884	CoG	0	25	67	0	0	0	0	0
Hydroptilidae, div. sp	CoG	30000	4550	11050	1400	3547	5400	0	0
Bereidae, div. sp.	CoG	0	0	0	0	0	200	0	0
Psychodidae, div. sp.	CoG	300	125	0		67	0	0	0
Orthocladiinae, div. sp	CoG	10800	3000	6300	5000	96450	91800	98400	124000

Table 3. (continued)

Season		Spring				Summer			
Current velocity (cm s^{-1})		20–40	40–70	70–100	> 100	20–40	40–70	70–100	> 100
Acronym of habitat type		SP20	SP40	SP70	SP100	S20	S40	S70	S100
Taxa	FFG								
Total collector-gatherers		158180	185460	235334	552830	122813	175507	253400	145900
Hydropsyche (juv.), div. sp.	CoF	2200	11650	2980	800	2360	1900	4200	8000
Hydropsyche saxonica McLachlan, 1884	CoF	400	150	67	67	139	133	600	1200
Hydropsyche instabilis (Curtis, 1834)	CoF	1400	550	1070	200	7	0	0	0
Philopotamidae, div. sp.	CoF	1900	8225	1200	3000	667	667	6400	0
Philopotamus sp.	CoF	0	0	0	0	7	0	0	0
Wormaldia occipitalis (Pictet, 1834)	CoF	0	0	0	0	1230	1260	2400	0
Simuliidae, div. sp.	CoF	700	1500	150	400	57100	56300	46200	74400
Total collector-filterers		4000	12350	4117	1067	2506	2033	4800	9200
Hydra sp.	P	1600	200	0	0	3800	800	0	0
Dugesia gonocephala (Duges, 1830)	P	200	200	83	0	0	0	0	0
Crenobia alpina (Dana, 1766)	P	0	100	17	0	333	667	0	0
Dendrocoelum lacteum (O.F. Müller, 1774)	P	0	0	0	0	167	0	0	0
Gomphidae, div. sp.	P	0	0	0	0	33	0	0	0
Onychogomphus forcipatus (L., 1758)	P	0	0	0	0	17	67	0	0
Gyrinidae, div. sp.	P	0	0	17	0	0	0	0	0
Rhyacophila sp. (juv.)	P	1100	1175	1200	1000	200	733	2200	1200
Rhyacophila tristis Pictet, 1834	P	0	50	133	400	180	600	2600	0
Rhyacophila aurata Brauer, 1857	P	100	0	0	0	0	67	0	0
Rhyacophila fasciata Hagen, 1859	P	0	0	0	200	0	0	0	0
Rhyacophila dorsalis Curtis, 1834	P	0	0	0	0	0	133	0	0
Philopotamidae, div. sp.	P	1900	8225	1200	3000	667	667	6400	0
Philopotamus sp.	P	0	0	0	0	7	0	0	0
Wormaldia occipitalis (Pictet, 1834)	P	0	0	0	0	1230	1260	2400	0
Holocentropus sp.	P	0	0	0	0	17	0	0	0
Emphididae, div. sp.	P	9100	1775	5300	2600	223	133	5400	8400
Athericidae, div. sp.	P	300	25	282	0	203	0	0	0
Ibisia marginata F., 1781	P	0	0	0	0	7	207	0	0
Atherix ibis F., 1781	P	0	0	0	0	0	0	0	0
Ceratopogonidae, div. sp.	P	5800	400	451	600	390	1200	1600	0
Tanypodinae, div. sp.	P	2300	4650	27467	25000	13710	3600	26800	3600
Total predators		20600	16300	36050	32800	16884	8667	47400	13200

Table 3. (continued)

Season		Autum				Winter			
Current velocity (cm s^{-1})		20–40	40–70	70–100	> 100	20–40	40–70	70–100	> 100
Acronym of habitat type		SP20	SP40	SP70	SP100	S20	S40	S70	S100
Taxa	FFG								
Gammarus balcanicus Schaeferna, 1922	Sh	0	800	0	0	0	0	0	0
Amphinemura, div. sp.	Sh	400	720	1240	2980	80	40	80	2560
Protonemura sp.	Sh	1000	1400	11400	3000	300	1200	22800	17400
Nemoura sinuata Ris, 1902	Sh	0	0	0	0	0	0	0	400
Nemoura sp.	Sh	1000	733	400	1500	0	0	0	0
Haliplidae, div. sp.	Sh	0	67	0	0	0	0	0	0
Limnephilidae, div. sp.	Sh	1100	447	0	0	648	0	79	0
Total shredders		3500	4167	13040	7480	1000	1200	22900	17800
Bythinella sp.	Sc	16000	0	0	0	1100	200	200	200
Radix peregra (O.F. Müller, 1774)	Sc	300	0	0	0	100	100	100	0
Hydrobidae, div. sp.	Sc	16000	26200	0	0	200	200	0	0
Naididae, div. sp.	Sc	660	5350	3450	2340	450	670	1290	1200
Amphinemura, div. sp.	Sc	1000	1800	3200	7450	200	100	200	6400
Baetis muticus (L., 1758)	Sc	800	760	1160	4850	500	200	300	3700
Baetis lutheri Mueller-Liebenau, 1967	Sc	200	100	500	3450	300	0	0	3100
Helodes sp.	Sc	14000	15783	36800	26800	26800	37500	52800	106000
Riolus sp.	Sc	13200	16733	15600	27600	1400	5400	1700	13400
Drusus croaticus Marinković, 1971	Sc	100	220	0	0	52	0	21	0
Total scrapers		62260	66940	60710	85090	31102	44370	56611	134000
Oligochaeta, div. sp.	CoG	18680	26500	24400	17780	5200	5360	19420	19600
Naididae, div. sp.	CoG	660	850	900	910	450	670	1290	1200
Eiseniella tetraedra (Savigny, 1826)	CoG	700	667	800	500	400	0	0	0
Amphinemura, div. sp.	CoG	600	1080	1860	4570	120	60	120	3840
Paraleptophlebia sp.	CoG	0	0	0	0	0	100	0	0
Hydroptilidae, div. sp.	CoG	1000	3450	2400	1800	10500	5400	5400	3000
Psychomiidae, div. sp.	CoG	0	0	0	0	0	0	1000	0
Psychodidae, div. sp.	CoG	200	0	0	0	0	0	0	800
Orthocladiinae, div. sp	CoG	6400	1900	15200	16700	7300	7400	5500	7000
Total collector-gatherers		28240	34447	45560	42260	23970	18990	32730	35440
Hydropsyche (juv.), div. sp.	CoF	54000	54500	95600	90100	1500	5200	10100	9800
Hydropsyche saxonica McLachlan, 1884	CoF	100	67	1200	0	100	300	200	1800
Wormaldia occipitalis (Pictet, 1834)	CoF	0	50	0	0	0	0	300	0
Simuliidae, div. sp.	CoF	102000	211800	420000	449900	3800	100	0	1400

Table 3. (continued)

Season		Autum				Winter			
Current velocity (cm s^{-1})		20–40	40–70	70–100	> 100	20–40	40–70	70–100	> 100
Acronym of habitat type		SP20	SP40	SP70	SP100	S20	S40	S70	S100
Taxa	FFG								
Total collector-filterers		54100	54567	96800	90100	1600	5500	10300	11600
Hydra sp.	P	200	267	800	3200	600	0	0	0
Dugesia gonocephala (Duges, 1830)	P	300	0	0	0	0	0	0	0
Crenobia alpina (Dana, 1766)	P	400	200	0	900	0	0	0	0
Dendrocoelum lacteum (O.F. Müller, 1774)	P	700	200	200	200	2000	100	100	0
Planaria torva (O.F. Müller, 1773)	P	0	1800	0	0	0	200	0	0
Herpobdella octoculata (L., 1758)	P	0	67	0	0	100	0	0	0
Isoperla sp.	P	0	33	1000	0	0	0	200	0
Isoperla grammatica (Poda, 1761)	P	0	0	0	0	100	100	100	1000
Gomphidae, div. sp.	P	400	0	0	0	0	0	0	0
Onychogomphus forcipatus (L., 1758)	P	200	67	200	400	0	0	0	0
Gyrinidae, div. sp.	P	0	33	0	0	0	0	0	0
Rhyacophila sp. (juv.)	P	700	233	2600	4500	200	400	0	2000
Rhyacophila tristis Pictet, 1834	P	0	183	1400	600	0	600	100	1000
Rhyacophila fasciata Hagen, 1859	P	0	0	200	800	0	0	0	0
Rhyacophila dorsalis (Curtis 1834)	P	0	0	0	0	0	0	0	800
Wormaldia occipitalis (Pictet, 1834)	P	0	50	0	0	0	0	300	0
Polycentropodidae, div. sp.	P	200	217	200	400	0	0	0	0
Plectrocnemia brevis McLachlan, 1871	P	0	67	0	0	100	0	0	0
Plectrocnemia conspersa (Curtis, 1834)	P	0	0	200	0	0	0	0	0
Emphididae, div. sp.	P	12500	9700	56400	24300	3500	7400	9600	9200
Athericidae, div. sp.	P	0	0	200	0	600	600	1500	0
Ibisia marginata F., 1781	P	200	100	0	0	0	0	0	200
Atherix ibis F., 1781	P	0	0	400	0	0	0	0	0
Ceratopogonidae, div. sp.	P	200	467	200	300	0	600	500	0
Muscidae, div. sp.	P	0	267	0	0	0	0	0	0
Limnophora sp.	P	0	0	0	0	0	200	0	0
Tanypodinae, div. sp.	P	4800	8100	8400	9100	1200	700	4500	800
Total predators		19200	19584	71400	40400	5800	10600	16800	15000

Key: FFG – functional feeding group; Sh – shredders; Sc – scrapers; CoG – collector-gatherers; CoF – collector-filterers; P – predators.

Table 4. Percentage of total population density of macroinvertebrate taxa on tufa barrage habitats covered with bryophytes found per sampling site and seasons (mean of three replicates).

Season	Taxa	Current velocity (cm s^{-1})			
		20–40	40–70	70–100	>100
Spring	Turbellaria	0.1	0.2	0.03	
	Gastropoda	2.2		0.01	
	Oligochaeta	29.4	36.1	75.3	88.8
	Crustacea	2.9		0.03	
	Ephemeroptera	0.7	2.2	0.3	0.3
	Plecoptera	7.9	3.7	1.8	0.2
	Coleoptera	15.0	22.5	11.4	3.5
	Trichoptera	18.5	28.3	6.1	1.1
	Diptera	23.2	7.0	5.1	6.1
Summer	Turbellaria	0.4	0.3		
	Gastropoda	0.02	2.7		
	Oligochaeta	18.7	38.1	37.4	50.7
	Crustacea	0.3	1.9		
	Ephemeroptera	0.8	1.0	1.5	0.05
	Plecoptera	4.4	0.7	4.1	0.02
	Coleoptera	6.3	11.6	6.8	2.5
	Trichoptera	6.0	5.0	6.7	0.6
	Diptera	63.1	38.8	43.6	46.2
Autumn	Turbellaria	1.0	1.2		0.1
	Gastropoda	11.3	14.0		
	Oligochaeta	24.1	15.5	35.5	33.2
	Crustacea	3.9	0.6	1.9	
	Ephemeroptera	0.7	0.1	0.3	0.9
	Plecoptera	2.8	2.0	2.9	2.3
	Coleoptera	18.9	17.5	17.4	7.6
	Trichoptera	12.0	5.0	11.2	4.2
	Diptera	25.3	44.1	30.8	51.8
Winter	Turbellaria	4.1	0.5	0.7	
	Gastropoda	1.2			
	Oligochaeta	1.2	1.1	1.5	0.8
	Crustacea	0.2			0.6
	Ephemeroptera	1.8	0.2	0.2	2.4
	Plecoptera	1.6	2.2	2.3	14.6
	Coleoptera	25.1	51.6	70.9	42.0
	Trichoptera	26.9	18.7	13.0	34.6
	Diptera	37.8	25.7	11.3	5.1

winter Coleoptera (represented by scirtids and dryopids) and Trichoptera (represented by rhyacophilids), constituted a marked proportion of the total macrobenthic fauna.

Species diversity, an important feature of community structure, decreased in all four seasons with an increase in current velocity (Fig. 7). With respect to the temporal changes, we observed that the macroinvertebrate communities associated with current velocity conditions from 20 to 40 cm s^{-1} showed very homogenous values of Shannon's species diversity index ($H' = 2.89 \pm 0.27$) whereas at higher current velocities Shannon's index increased in the temporal succession from spring to winter.

An important question was if the macroinvertebrate species composition showed significant differences in the four seasons and the four microhabitats influenced by the different current velocity conditions. Cluster analysis based on Pearson's r, as a similarity measure among macroinvertebrate composition patterns, illustrated the clus-

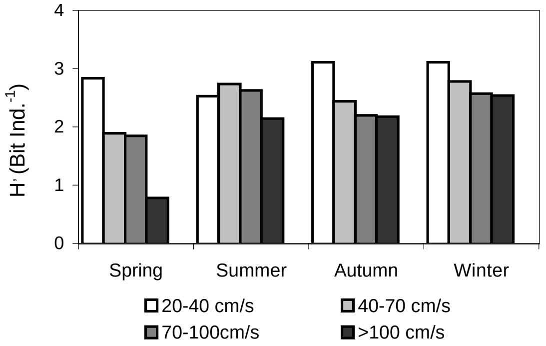

Fig. 7. Seasonal changes of species diversity (H') depending on current velocity.

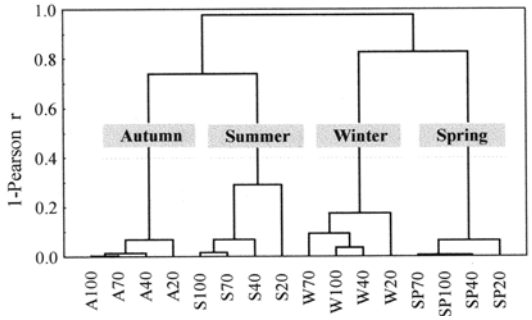

Fig. 8. Clustering of macroinvertebrate collections based on composition patterns depending on the seasons and current velocity conditions. SP – spring; S – summer; A – autumn; W – winter. 20: 20–40 cm s^{-1}; 40: 40–70 cm s^{-1}; 70: 70–100 cm s^{-1}; 100: >100 cm s^{-1}.

tering of our 16 macroinvertebrate sampling collections defined by four current velocity conditions and four seasons (Fig. 8). At the first step of clustering (Pearson $R > 0.02$), the winter and spring macroinvertebrate composition patterns were separated from autumn and summer. At the second step (Pearson $R > 0.18$), four clusters of seasonal macroinvertebrate composition patterns were formed. At the third step of clustering (Pearson $R > 0.71$) within the seasonal separated clusters the macroinvertebrate community composition patterns were grouped according to current velocity conditions.

Functional feeding composition

Changes of macroinvertebrate functional feeding composition showed temporal succession (Tab. 3). In all the analyzed rheotopes collector-gatherers, represented by oligochaetes, ephemerid and dipterous larvae dominated during spring and summer. Their population densities ranged from 1×10^6 to 6×10^5 ind. m^{-2} approximately, and increased in rheotopes with a higher current velocity. A general decrease in collector-gatherer abundance was found in the autumn and winter period. In these seasons we did not observe an increase of collector-gatherer population density with increased current velocity. In the autumn period, the collector-filterers hydropsychids and simuliids were abundant and characterized the functional organization of the benthic community in bryophyte mats whereas in the winter period scraping coleopterans (*Helodes* and *Riolus*), ephemeropterans (*Baetis muticus* L., 1758 and *B. lutheri* Mueller-Liebenau, 1967) and gastropods (*Bythinella*, *Lymnaea* and Hydrobiidae) constituted a major percentage of the macroinvertebrate fauna.

Depending on current velocity conditions in spring, summer and autumn periods shredders (amphipod *Gammarus balcanicus* Schaeferna, 1922 and detritivorous plecopterans, *Protonemura* and *Nemoura*) represented less than 4.44% of the total. In the winter the population density had a wider range (from 1.57% to 16.43%). The highest abundance (from 40.74% to 64.88% of the total) of scrapers was obtained in the winter period. In the autumn, collector-filterers varied from 22.54% to 38.13% of the total, and in spring and summer their percentage abundance was below 20% of the total.

In the spring, summer and winter period collector-filterers varied from 0.17% to 7.39% of the total depending upon current velocity. In autumn, this percentage was markedly higher (from 32.34% to 35.52%). On the travertine barriers in the benthic community the most abundant predators were tricladid planarians, hydras, the leech *Erpobdella octoculata* Linnaeus 1758, predatory trichopterans (rhyacophilids and philopotamids), dipterans (empidids, athericids, ceratopogonids and tanipods) and plecopterans. Depending on current velocity their macroinvertebrate abundance was below 13% of the total.

Consideration of the results, illustrated in Tab. 3, showed that the relationship between the population density of macroinvertebrate functional feeding groups (FFG) and current velocity conditions changed depending on the seasons. The significance of the relationships between the population density of FFG and current velocity conditions was determined by regression analysis using a linear model $y = ax \pm b$ (Tab. 5). In the spring and summer period, the population den-

Table 5. Regression analysis, based on model FFG = av ± b, of the relationship: population density of macroinvertebrate functional feeding groups (FGG) against current velocity (v) associated with seasons.

FGG	Season	n	Regression parameters		
			a	b	R
Shredders	Spring + summer	8	−156.5	18733.2	0.95*
	Autumn + winter	8	207.4	−22415	0.79**
Scrapers	Spring + summer	8	79.8	23108.6	0.29 ns
	Autumn + winter	8	550.4	21247	0.73*
Collector-gatherers	Spring + summer	8	3200	21105.3	0.82*
	Autumn + winter	8	2015	19734	0.75*
Collector-filterers	Spring + summer	8	80.9	28740.2	0.09 ns
	Autumn	4	4599.9	36325	0.95*
	Winter	4	92.54	1865.7	0.96*
Predators	Spring + summer	8	−0.073	29.9	0.38 ns
	Autumn + winter	8	0.073	20.1	0.19 ns

Key: * $P < 0.05$; ** $P < 0.01$; ns – non significant.

sity of shredders decreased significantly with an increase in current velocity, whereas in autumn and winter we observed a significant tendency to increase in habitats with a higher velocity. In habitats with a higher current velocity scrapers showed a significant increase in their population density in the autumn and winter period. In all seasons a higher density of collector-gatherers was associated significantly with a higher current velocity. A significant increase in collector-filterer population density with an increase in current velocity was observed in autumn and winter whereas in spring and summer this relationship was not significant. In all four seasons the highest population density of predators was found in habitats with a current velocity from 70 cm s^{-1} to 100 cm s^{-1} (Tab. 3) but according to the regression analysis predators did not show a significant response to current velocity (Tab. 5).

The described and illustrated relationships of food sources (Figs 3–5) and population density of FFG compared with current velocity (Fig. 9, Tabs 3, 5) suggested that in bryophyte mats a causative correlation could also exist between the population density of FFG and the availability of accumulated food. Regression analysis, using a non-linear model $y = ax^b$ confirmed a significant correlation between the abundance of FFG and quantity of food. As seen in Fig. 9 population density of shredders (Sh) against measured values of CPOM (defined as function: Sh = a CPOM^{b}) did not show a significant correlation ($R = 0.28$, $n = 16$, $P > 0.05$). Collector-gatherers against fine and ultra fine particulate organic matter showed a significant relationship ($R = 0.70$, $n = 16$, $P < 0.05$) according to a non-linear regression model: CoG = a (fine & ultra fine $\text{POM})^{\text{b}}$. Collector-filterers compared with sestonic POM also showed a significant relationship ($R = 0.73$, $n = 16$, $P < 0.05$). Using the linear $y = ax \pm b$ and non-linear model $y = ax^b$ we did not find a significant relationship between predators and each of the three non-predatory consumer groups separately, but the predators related significantly to the total population density of all three non-predatory FFG ($R = 0.73$, $n = 16$, $P < 0.05$).

Discussion

The major findings of this study were the significant interactions among current velocity, retention and accumulation of different detritus size fractions in the bryophyte habitats (termed bryorheal by WULFHORST, 1994) influencing the macroinvertebrate community and functional feeding group composition on a tufa barrage in karst lotic biotopes. The temporal and spatial changes of bryophyte biomass are an important factor in the explanation of these relationships. In travertine barrier habitats studied, bryophyte biomass (represented by the species *Cratoneurum commutatum* Roth and *Platyhypnidium rusciforme* Fleischr. predominantly) varied from 55 g AFDW m^{-2} to 256 g AFDW m^{-2} ($\overline{x} = 153.59 \pm 61.37$ g AFDW m^{-2}) whereas in a Pyrenean stream DAWSON (1973) found a standing crop of bryophytes with a

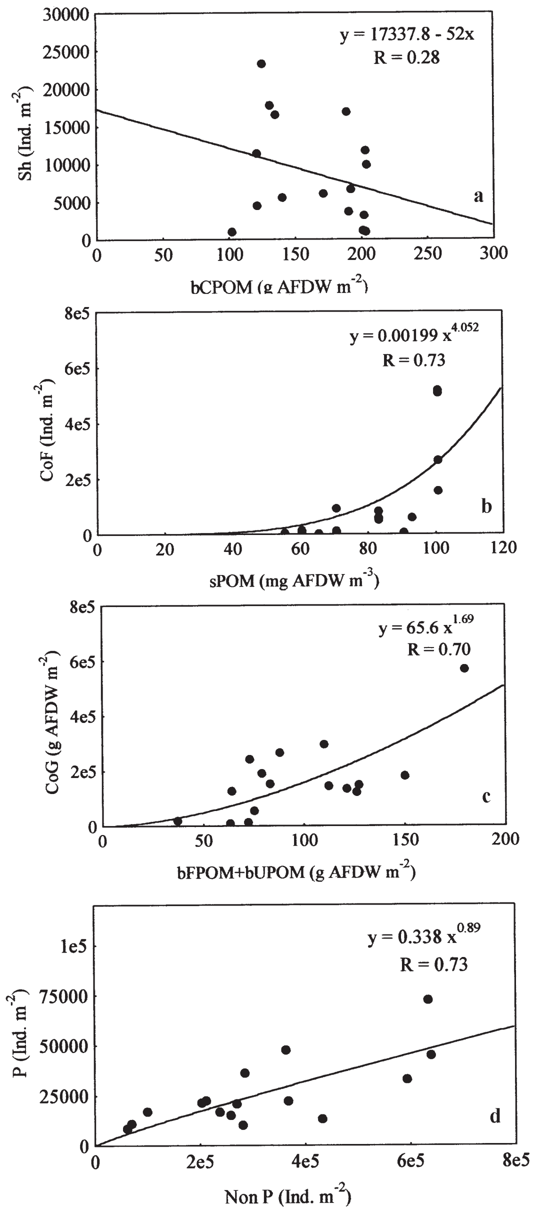

Fig. 9. Relationships: a t shredders compared with bCPOM; b t collector-filterers compared with sestonic sPOM; c – collector-gatherers compared with bFPOM+bUPOM and d – predators compared with non predatory invertebrates.

range from 9 g dry wt m^{-2} to 411 g dry wt m^{-2}, which approximately corresponds to our data. In view of the spatial microdistribution in benthic habitats, using the DECORANA analysis, SUREN & ORMEROD (1998) found that altitude, slope and conductivity of water are the main stream features regulating the community composition and spatial distribution of aquatic bryophytes in Himalayan streams. In our study, which was conducted in an entirely different geographic area, the bryophyte biomass was also associated with current velocity. The finding that bryophytes were restricted to areas of high water velocity in the two New Zealand alpine streams (SUREN, 1991) does not correspond with our results. In four water flow conditions (from 20 cm s^{-1} to $>$ 100 cm s^{-1}) we found a decrease in bryophyte biomass with an increase in current velocity. Considering the seasonal changes, in a Yorkshire hill stream, PENTECOST (1991) found a maximum of bryophyte biomass in winter. In travertine barrier habitats we also found the maxima in the winter period in the four water flow conditions.

Numerous studies have reported that the degree of retention and storage of particulate organic matter is determined by various substrate type (PROCHAZKA et al., 1991; MINSHALL et al., 2000; WANNER & PUSCH, 2001), and by discharge regime and stream hydrology (NAIMAN & SEDELL, 1979; WEBSTER et al., 1987; BRETSCHKO, 1990; STEWART & DAVIES, 1990; SMOCK, 1990; MATHIEU et al., 1991; POZO et al., 1994). Aquatic macrophyte and bryophyte mats (of varying degrees of compactness) can also play an important role in the spatial distribution and accumulation of various size POM fractions in benthic habitats.

In this study, our regression analyses suggested that in bryophyte habitats on a tufa barrage, retention and accumulation of different detritus size fractions were significantly affected by current velocity. Our results showed that a greater content of CPOM and FPOM was associated with bryophyte habitats exposed to current velocity < 70 cm s^{-1} and a greater content of UPOM with a current velocity > 70 cm s^{-1}. The findings that the reduction of water flow within bryophytes results in the accumulation of periphyton and detritus between their stems (MAURER & BRUSVEN, 1983; DEVANTRY, 1987; SMITH-CUFFNEY, 1987) and a greater detritus accumulation in bryophytes in slow-flowing biotopes reported by FINLAY & BOWDEN (1994) confirmed our results. However, we explained the greater UPOM retention in fast flowing biotopes ($>$ 70 cm s^{-1}) by the architecture of the bryophyte clumps. Under the influence of greater current velocity the moss mats will be compact and thicker and for this reason the retention and deposit of UPOM will be more effective than in the less compact bryophytes developed in slower current conditions. BRUSVEN et al. (1990) found that in lentic habitats bryophytes grow more horizontally than vertically. MAURER & BRUSVEN (1983) proposed that bryophyte cover filters POM from the water. Seven years later, BRUSVEN et al. (1990) and SUREN (1991) found that this selective filtering and POM accumulation depends on the physical architecture of the bryophyte mats.

Our opinion is that the relation between the physical architecture of bryophyte mats and the degree of retention and storage of particulate organic matter (POM) is a very important interaction in the tufa barrage, because the trapped detritus represents an important food source for macroinvertebrates. The relationship between bryophyte cover and composition of macroinvertebrates has been investigated in several recent studies (SUREN, 1991, 1992, 1993; ORMEROD et al., 1994). Investigations of macroinvertebrates associated with bryophytes have focussed: (i) on the accumulation and retention of detritus in bryophyte mats, in this way providing a food source in the form of trapped detritus and periphyton, and (ii) on the bryophyte mats as potential flow refugia for benthic invertebrates (sensu WINTERBOTTOM et al., 1997; LANCASTER & HILDREW, 1993; SLACK & GLIME, 1985). Because bryophyte cover has various degrees of detritus retention, we hypothesized that in bryophyte habitats the spatial distribution of macroinvertebrates will be dependent upon current velocity and the POM retention effect. In this study the results showed that the highest abundance of benthic macroinvertebrates (706,260 ind. m^{-2} except Nematoda) was at the greatest content of UPOM in the bryophyte mats associated with current velocity > 70 cm s^{-1}. Regression analysis suggested that macroinvertebrate density increased with an increase in current velocity and decreased with an increase in bryophyte biomass. Generally, higher macroinvertebrate densities are more associated with bryophyte-covered than with bryophyte-free habitats (MAURER & BRUSVEN, 1983; BRUSVEN et al., 1990). In unshaded bryophyte habitats of two New Zealand alpine streams SUREN (1991) found about ten times more invertebrates (218,400 ind. m^{-2}) than on the gravel substrate (20,900 ind. m^{-2}). In our research the maximum macroinvertebrate density was higher significantly (625,767 ind. m^{-2}).

In bryophyte habitats on a tufa barrage macroinvertebrate community composition was characterized by small forms of oligochaetes, dipterans and coleopterans. Depending on seasons and current velocity associated with different size fraction of accumulated POM, their joint percentage varied from 64.1% to 98.4% of the total macroinvertebrate density. In some recent studies it has been found that dipterans also constituted the highest percentage of the total macroinvertebrate density (GLIME & CLEMONS, 1972; BRUSVEN et al., 1990; SUREN, 1991).

Based on our 16 macroinvertebrate composition patterns, the cluster analysis suggested that in bryophyte habitats changes in macroinvertebrate composition were more markedly under the influence of current velocity conditions than of season. Among our four sampling sites water chemistry, and water depth were not significant different among seasons whereas water temperature was significantly different among seasons. For this reason, we considered that seasonal changes in water temperature associated with life cycles of invertebrates and water flow conditions associated with retention of POM in bryophyte cover and its role as flow refugia, are the main environmental variables affecting the community composition in bryophyte habitats. According to SUREN (1991) it may be concluded that community composition depends upon the current velocity and concentration of accumulated POM in bryophyte mats. His DECORANA ordination of samples, collected from unshaded (associated with faster water flow and higher content of POM) and shaded (associated with slower water flow and lower content of POM) bryophyte biotopes showed significant differences between these two invertebrate communities.

In a study on the role of bryophytes as a habitat for stream insects, GLIME & CLEMONS (1972) found that on artificial substrata species diversity (H') of the insect community was 1.8 bit $ind.^{-1}$ in bryophyte (*Fontinalis* spp.) habitats. Because in our calculations all taxonomic groups were included, we found significantly higher values of species diversity on tufa bryophyte habitats. Depending on season and current velocity, associated with concentration of accumulated POM, it varied from 0.77 to 3.11. ($\overline{x} = 2.32 \pm 0.57$). SUREN (1991) suggested also that variations in taxonomic richness were best explained by the positive association with FPOM.

Analyzing the role of aquatic bryophytes on insect community composition, BRUSVEN et al. (1990) found that functional feeding group composition in bryophyte mats of *Fontinalis neomexicana* was also characterized by insect collectors. They generally represented more than 80% of the insect community while predators comprised 12–20% and shredders and scrapers made up < 10% of the insect community. In bryophyte habitats our analysis of the functional feeding group composition of macroinvertebrates at higher current velocity suggested that collector-gatherer oligochaetes and small dipteran larvae (consumers of FPOM and UPOM) constituted a considerable percentage of the total macroinvertebrates. Compact bryophyte mats filled with FPOM and UPOM offer a rich food source and various refuges against current velocity for small detritivore invertebrates. In bryophyte biotopes exposed to current velocity < 70 cm s^{-1} as well as the collector-gatherer invertebrates a greater percentage of scraper and collector-filterer (hydropsychids and simuliids) invertebrates were found. This can be explained by the less compact architecture of bryophyte mats overgrown with epiphytes and by the considerable transport of sestonic POM. According to Krno et al. (1996) sPOM and transport of organic matter (TOM) by fluvial drift is an important food source for the collector-filtering macroinvertebrates, and in this connection Krno & Šporka (1996) found that the relationship between sPOM and discharge varied seasonally. With regard to the discharge regime our results showed that: (i) increased sPOM correlated with increased values of discharge during the beginning of spring and at beginning of autumn season, and (ii) the higher abundance of collector-filterers corresponded with increased sPOM caused by higher discharge.

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