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Primary Research Paper

The role of flow velocity in the vertical distribution of particulate organic matter on moss-covered travertine barriers of the Plitvice Lakes (Croatia)

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Abstract

We investigated the distribution patterns of particulate organic matter (POM) on travertine barriers in respect to flow velocity. Research was conducted on the barrage-lake system of the Plitvice Lakes, Croatia. Four layers were distinguished within the substrate (moss mat + three travertine layers) in three hydraulic habitats at three sites. Substrate samples were collected monthly with a core sampler. The aim of the study was to explore the ability of moss mats and travertine substrate to accumulate POM; to ascertain the role of flow velocity and to produce a model of POM distribution pattern. The average of POM deposited in the 10 cm deep zone decreased significantly in the three sites along longitudinal profile of the system. Most POM was deposited in the moss mats, and the amounts decreased exponentially with depth. This was observed for coarse particulate organic matter (CPOM), ultra-fine particulate organic matter (UPOM) and total organic matter (TPOM) while fine organic matter (FPOM) deposition appeared unaffected by depth. More POM was accumulated in hydraulic habitats of low flow velocity. Correlation between flow velocity and POM accumulation was generally negative. Positive correlations between flow velocity and deposition rates were noted for CPOM in moss mats and top travertine layers; the deposition of other POM fractions was negatively influenced by the flow velocity. The influence of flow velocity decreased with increasing depth. In the deepest layers (7–10 cm) flow velocity influenced only the deposition of the smallest particles (UPOM).

Introduction

Allochthonous organic matter, predominantly leaf litter, constitutes an energetic basis for benthic communities in forested headwater streams of the temperate zone (Cummins, 1974; Vannote et al., 1980; Hawkins & Sedell, 1981). Upon entering the stream ecosystem it is microbially transformed and consumed by detritivores or physically broken, resulting in the formation of different size-fractions, which can be subsequently utilized by other functional feeding groups (Cummins & Klug, 1979; Vannote et al., 1980; González & Pozo, 1996; Minshall et al., 2000). The community composition of invertebrates partially depends on the quality and the quantity of organic matter. The retention of organic matter particles is a function of stream bed roughness, porosity and morphology, in-stream vegetation, debris dams and filterer fauna (Bretschko, 1990; Prochazka et al., 1991; Strayer et al., 1999; Wanner & Pusch, 2001; Habdija et al., 2004). The burying of detrital particles is a very important mechanism of organic matter retention and accumulation, especially in streams with porous beds (Smock, 1990). Buried particulate organic matter (POM) provides virtually the sole energy source for interstitial fauna (Lenting et al., 1997), also enabling the interstices to act as a refugium for benthic fauna (Coleman & Hynes, 1970; Hynes, 1974; Dole-Olivier et al., 1997). Detritus also enters the interstices in the travertine substrate and within these shelters there are colonization opportunities for benthic and interstitial fauna (Pedley, 2000).

Streams originating in karstic systems are widespread in the Mediterranean, especially in the limestone mountains of the northern part of the Mediterranean basin (e.g. Dinarids). A common feature of these streams is travertine precipitation. When abundant, it can affect both biota and POM dynamics i.e. quantity and/or quality (Casas & Gessner, 1999).

The role of POM in travertine barrier building-mechanisms is dual. Chafetz & Folk (1984) state that the organisms attached to POM create the substrate for calcite nucleation. POM as an energy source partly determines the community composition of macroinvertebrates, which also play an important role in inducing calcite precipitation, according to Srdoč et al. (1985). Carthew et al. (2003) and Drysdale (1998) stress the role of aquatic insect larvae dwelling and feeding constructions in travertine deposition. However, moss mats play the most important role in inducing calcite precipitation due to their abundance. Vast areas of moss mats are colonized by periphyton secreting mucopolysaccharides – the molecules that serve as nucleation sites for calcite crystallization (Srdoč et al., 1985).

Subsequent decay of incrusted dead plant material (POM) results in an extensive system of pores and caverns within the travertine (Chafetz et al., 1994). Golubic (1969) and Golubic & Schneider (1979) proposed that the organic matter (entrapped detritus or remnants of algae, moss or macrophytes) plays an additional destructive role. As organic matter becomes subject to microbial degradation, pressure of CO_2 increases locally in the solution and some surrounding calcite is dissolved, contributing to travertine porosity.

Therefore processes affecting POM dynamics in travertine barrier habitats affect community composition and travertine formation.

Although extensive work has been done on in-stream particulate organic matter regime and dynamics, knowledge on factors influencing the vertical distribution of POM should be expanded, especially with respect to porous travertine stream beds. These porous stream beds are characteristic of channels and barriers between lakes in barrage-lake systems of some karstic areas. Plitvice Lakes are characterized by extensive calcite precipitation and the formation of porous stream bottoms corresponding to 10,000 tons of $CaCO_3$ per total lake area per year (Kempe & Emeis, 1985), with a vertical growth of the travertine barriers of 13.5 mm per year (Srdoč et al., 1985).

The main purpose of this study was to describe patterns of vertical distribution for different size-fractions of POM, and the possible influence of flow velocity on them, in travertine barrier habitats.

The hypotheses were: (1) the distribution patterns of POM would be strongly influenced by the flow velocity; (2) the influence of flow velocity would be generally negative, especially for accumulation of small particles i.e. FPOM and UPOM which are more readily resuspended; (3) the influence of flow velocity would be stronger in the top layers of the substrate and decrease with increasing substrate depth; (4) the amounts of deposited POM (especially the amounts of CPOM) would decrease with substrate depth because of the top-down increase of substrate stiffness and decrease of substrate permeability/porosity combined with lack of exposure to surface water; (5) moss mats are an important POM retention mechanism in the travertine barrier habitats.

Study site

This research was carried out in the barrage-lake system of the Plitvice Lakes in Croatia, located in the karst region of NW Dinarid Mountains (Fig. 1). This barrage-lake system consists of 16 oligotrophic, dimictic lakes with water flowing from one lake to the other over travertine barrages. The system is approximately 8.2 km long, located at 636–503 m above sea level and divided into two sections (the upper and the lower lakes). The upper section comprising of twelve lakes flows on a dolomite valley ending with the largest lake

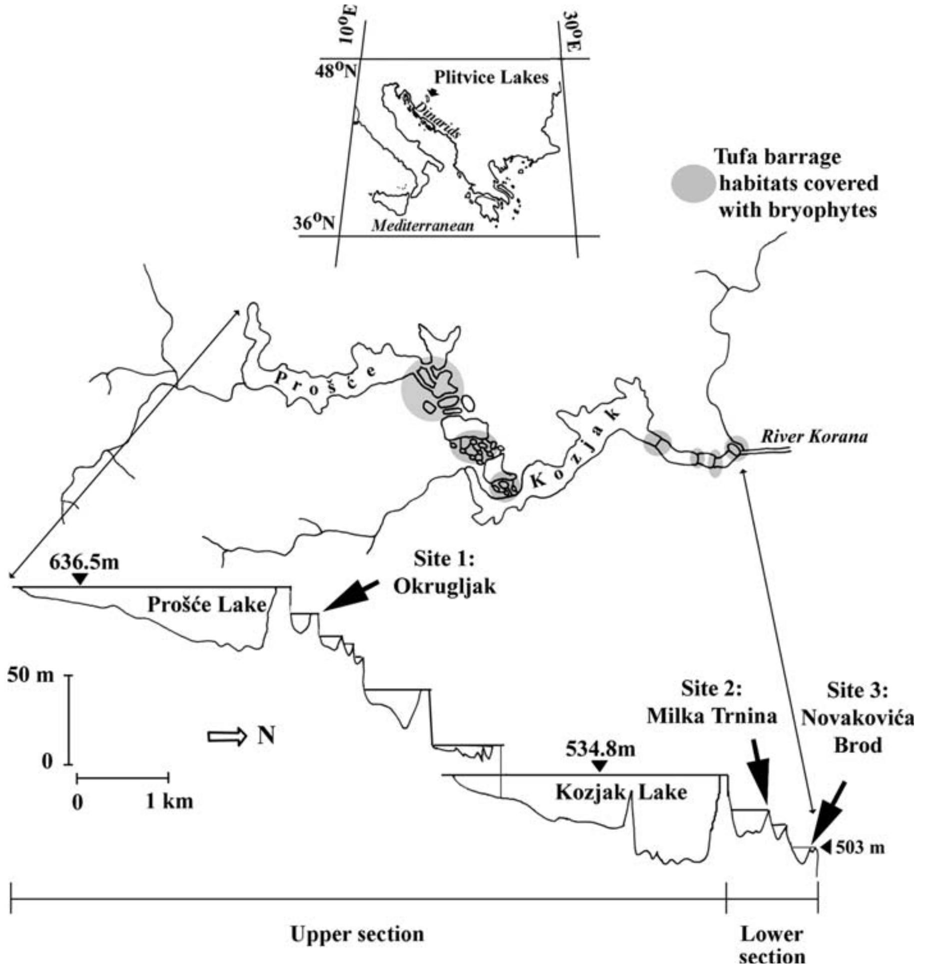


Figure 1. Map of the Plitvice barrage-lake system with the three sampling sites.

(Kozjak Lake 0.83 km^2; 46 m deep). The string of four lower lakes is located in a limestone canyon and finally joins the Korana River.

The system is supplied with water from the Matica stream formed by merging of the streams Crna Rijeka and Bijela Rijeka in the upper section. The Matica flows into the first lake of the system. There are also many minor tributaries and an undefined number of springs under the lakes. Mean discharge during the study period at two reference points, the inflow of the Matica and the overflow of Lake Kozjak, was 2.2 and 2.6 m^3 s^{-1} respectively. At the Matica the minimum discharge was 0.6 m^3 s^{-1} and maximum was 9.4 m^3 s^{-1}, while the minimum and maximum discharge on Kozjak overflow was 0.9 and 7.3 m^3 s^{-1} respectively.

Water characteristics, except alkalinity, did not vary significantly among sites. At all study sites, water was characterized by low concentration of nutrients and low COD (mean values during study period were 0.010 mg (NO_2^-) l^{-1}, 0.54 mg (NO_3^-) l^{-1}, 0.016 mg (PO_4^{3-}) l^{-1}) and 0.8 mg (O_2) l^{-1} COD). Yearly mean temperature was 12.8 °C, with a summer maximum of 21.5 °C and a winter minimum of 3.1 °C. Oxygen saturation during the study period varied between 85% and 125%, dissolved oxygen amounts ranged between 7.4 mg (O_2) l^{-1} and 15 mg (O_2) l^{-1}. Water pH was 8 ± 0.3. Alkalinity of water decreased significantly among study sites, attaining mean values of 212, 203 and 199 mg ($CaCO_3$) l^{-1} at site 1, 2 and 3 respectively. This was expected, given the calcite precipitation along the system.

Riparian vegetation, which is the major source of organic matter in this system, consists mostly of *Fagus sylvatica* L. and *Abies alba* Mill. Travertine barriers are characterized by well-developed submerged bryophyte vegetation (predominantly *Cratoneurum commutatum* (Hedw.) according to Pavletić (1957)). The bryophyte vegetation is an important mechanism of POM retention as well as a site for the travertine precipitation on the barriers.

Materials and methods

Sampling protocol

To exclude possible influence of other factors three sampling sites with similar environmental, physicochemical and hydraulic characteristics were chosen. The only difference within each site was flow velocity. Site 1 was located within the upper section on the barrier after Okrugljak Lake (0.04 km^2; 15 m deep). The two others were located within the lower section. Site 2 was situated on the barrier of Milka Trnina Waterfall after Milanovac Lake (0.03 km^2; 18 m deep) and Site 3 was located on the barrier Novakovića Brod after Kaluđerovac Lake (0.02 km^2, 13 m deep). These sites are representative of travertine barriers in terms of moss-cover and hydraulic characteristics i.e. flow velocity. In consideration of the flow velocity on each of the three sites, three hydraulic habitats were selected: (A) < 50 cm s^{-1}, (B) between 50 and 100 cm s^{-1} and (C) >100 cm s^{-1}. Four depth layers were selected within each hydraulic habitat for substrate sampling, based on empirical observations of the substrate consistence: three travertine layers (1) 7–10 cm; (2) 4–7 cm; (3) 1–4 cm; and (4) a moss mat layer (0–1 cm).

Substrate samples were collected in triplicate on 11 dates from January 2002 to April 2003 (3 habitats $\times$ 4 depth layers $\times$ 11 dates $\times$ 3 samples = 396 samples per site). However the number of samples was not uniform at all sites due to snow and ice in winter months (Site 1 and Site 2), elevated discharge in spring (Site 2) and the absence of high flow velocities in the summer months (Site 3). Consequently a total of 252, 330 and 384 samples were collected at sites 1, 2 and 3 respectively.

Methods

Flow velocity was measured with a flow meter approximately 3 cm above the moss mats. Samples were collected for POM content analysis with a core sampler (r = 2.25 cm, h = 10 cm, $V \approx 159$ cm^3), separated into four layers and transported in glass containers to the laboratory. Macroinvertebrates were separated from the samples under a stereomicroscope. To separate POM fractions, the samples were sieved through two different nets (1 mm and 50 μm mesh size) resulting in three size-fractions: coarse ($>$1 mm; CPOM), fine (1 mm to 50 μm; FPOM) and ultra-fine ($<$50 μm; UPOM) particles.

After separation, the POM size-fractions were dried at 104 °C, weighed, ashed at 400 °C and weighed again, the difference providing Ash-Free Dry Weight (AFDW). The mass of each size-fraction AFDW was calculated as the mean value of the three replicates and the contents of POM were expressed as concentrations (AFDW g l^{-1}).

We used analysis of variance to detect differences in the POM content in relation to hydraulic conditions. Pearson correlation coefficients were used to ascertain the relationship between the studied factors i.e. depth and flow velocity and accumulation of POM while regression analysis was used to model patterns of POM distribution. Analyses were carried out using the Statistica software (StatSoft, 2001).

Results

Upstream-downstream variations

Mean mass of deposited TPOM was highest at the uppermost site (Site 1) and decreased over the mid site (Site 2) to the lowermost site (Site 3), providing values of 27.012, 23.543 and 20.163 g l^{-1} respectively. These differences were proven significant via ANOVA (p-level < 0.001). Post hoc honestly significant difference (HSD) test for unequal samples revealed significant differences in retained POM between Site 3 and the two others, i.e. a significantly lower quantity of POM was accumulated at Site 3. No significant differences were found between Site 1 and Site 2. Accumulation of UPOM and FPOM was at the origin of the downstream decrease of

Table 1. Results of two-way analysis of variance for effects of depth and flow velocity on POM accumulation

		Site 1 (N = 84) (upstream)			Site 2 (N = 110)			Site 3 (N = 128) (downstream)		
		DF	F	p	DF	F	p	DF	F	p
CPOM	Depth	3	**35.7304**	**2.97E−14**	3	**27.3415**	**6.23E−13**	3	**18.9871**	**4.52E−10**
	Flow velocity	2	0.4294	0.6525	2	1.2926	0.2792	2	**5.6514**	**0.0046**
	Depth*Flow velocity	6	**2.5340**	**0.0278**	6	0.2723	0.9487	6	**2.4575**	**0.0284**
	Error	72			98			116		
FPOM	Depth	3	0.4745	0.7010	3	0.9739	0.4083	3	1.6357	0.1850
	Flow velocity	2	**8.0964**	**6.74E−04**	2	2.6319	0.0770	2	**3.8836**	**0.0233**
	Depth*Flow velocity	6	0.7674	0.5980	6	1.0025	0.4282	6	0.2801	0.9454
	Error	72			98			116		
UPOM	Depth	3	**18.6400**	**4.75E−09**	3	**6.1308**	**7.27E−04**	3	**3.8651**	**0.0112**
	Flow velocity	2	**19.7811**	**1.42E−07**	2	**7.3684**	**0.0010**	2	**6.9898**	**0.0014**
	Depth*Flow velocity	6	0.7487	0.6124	6	0.1406	0.9905	6	0.3821	0.8892
	Error	72			98			116		
TPOM	Depth	3	**13.343**	**5.13E−07**	3	**10.0304**	**7.97E−06**	3	**3.1648**	**0.0272**
	Flow velocity	2	**11.420**	**4.92E−05**	2	**4.2463**	**0.0170**	2	**3.1397**	**0.0470**
	Depth*Flow velocity	6	0.810	0.5655	6	0.3698	0.8965	6	0.4430	0.8486
	Error	72			98			116		

N – number of samples; DF – degrees of freedom; F – quotient of variance between samples and variance within samples; p – level of statistical significance. Bold numbers are significant.

TPOM accumulation. The accumulation of UPOM displayed the same pattern as observed for the accumulation of TPOM. FPOM accumulation was significantly higher at Site 1 than at the two other sites. No significant differences were observed in CPOM accumulation among sites.

Depth variations

In spite of these differences among sites, the accumulation of POM size-fractions showed similar patterns with substrate depth at all the sites. Analysis of CPOM and UPOM quantities showed significant differences with increasing depth (ANOVA $p < 0.005$) at all sites (Table 1). Post hoc HSD test for unequal samples detected significant differences with more accumulation in the top layer (moss mat) than in the three other layers (travertine substrate). There were no significant differences among travertine layers. Pearson correlation index revealed negative correlations of CPOM and UPOM concentrations with increasing depth (Table 2). Hence, the concentrations of CPOM and UPOM are functions of depth. These relations were best fitted by an exponential function $f(x) = a + b{*}c^x$; x = depth; ($p < 0.05$). Relative abundances of POM size-fractions changed with increasing depth. Even though amount of FPOM did not differ significantly among layers of the substrate, the relative abundance of FPOM increased while the relative abundance and amounts of CPOM decreased (Fig. 2).

Flow velocity

The differences in POM accumulation among layers were also analyzed against flow velocity. Significant differences among layers were found for CPOM in all hydraulic habitats at all sites, with the exception of the slowest water flow at Site 3 (Table 3). Significant differences among layers were also found for UPOM, mainly with flow velocity between 50 and 100 cm s^{-1} but also in fast flows at Site 1. FPOM content showed no significant variation among layers regardless of the site or the flow velocity. When significant differences were found, post hoc HSD test for unequal samples indicated that more POM was accumulated in the top layer, i.e. moss mats, than in travertine substrate layers (Table 3). The POM fractions

Table 2. Relations, expressed as Pearson *r*, between the accumulation of POM and the depth and the flow velocity

	CPOM	FPOM	UPOM	TPOM
Site 1 (N = 84) (upstream)				
Depth	−0.55***	−0.01	−0.38***	−0.35***
Flow velocity	−0.03	−0.41***	−0.42***	−0.38***
Site 2 (N = 110)				
Depth	−0.53***	−0.15	−0.33***	−0.40***
Flow velocity	−0.09	−0.12	−0.21*	−0.16
Site 3 (N = 128) (downstream)				
Depth	−0.45***	0.07	−0.22*	−0.24**
Flow velocity	0.15	−0.21*	−0.25**	−0.13

N – number of samples. Marked correlations are significant at: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

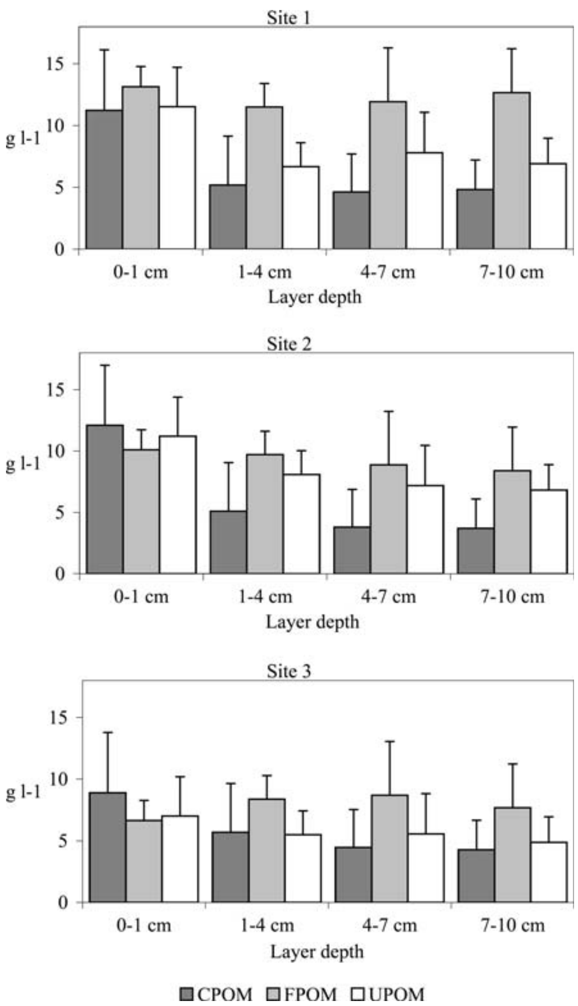


Figure 2. Mean values and standard deviation of POM fractions amounts at four different depths. 0–1 cm layer refers to moss mats, the rest are travertine layers.

generally showed a negative correlation with depth. Positive correlations with depth were found at Site 3 for FPOM regardless of flow velocity and for all POM fractions at slowest flow; however these were not significant.

Generally, the amounts of CPOM differed significantly among the hydraulic habitats at Site 3 only, while no differences were found at the two other sites. Differences in FPOM accumulation among hydraulic habitats were observed at sites 1 and 3, and UPOM distribution differed in respect to flow velocity on all the sites (Table 1). Concerning the POM fractions, post hoc HSD test for unequal samples generally separated flows <50 cm s^{-1} from others, as the most suitable for particle deposition. Also, the Pearson correlation index revealed negative correlations for FPOM and UPOM concentrations and the flow velocity on all sites, but a positive one for CPOM at site 3 (Table 2).

The impact of flow velocity on POM accumulation in the four layers was also analyzed. These analyses revealed that the impact of flow velocity on POM accumulation in the top layer was weak (Table 4). The accumulation of FPOM at site 1 and of CPOM at site 3 represented exceptions. Site 1 was the only site where FPOM accumulation was significantly influenced by the flow velocity (Table 4). Post hoc HSD test for unequal samples distinguished hydraulic habitat of flow velocity lower than 50 cm s^{-1}, as the hydraulic habitat with the highest accumulated quantity of POM. Values of UPOM content were negatively correlated with the flow velocity in all layers of the substrate at all sites. Differences in the accumulation of CPOM

Table 3. Analysis of effect of depth on POM accumulation at the different flow velocities

Site/Flow velocity	ANOVA p[a]			Pearson r[b]			POM accumulation comparison[c]		
	CPOM	FPOM	UPOM	CPOM	FPOM	UPOM	CPOM	FPOM	UPOM
Site 1 (N = 28) (upstream)									
<50 cm s^{-1}	**0.007**	0.571	**0.037**	−0.43*	−0.01	−0.42*	4 > 3,1	n.s.	4 > 3
50–100 cm s^{-1}	**8.5E−07**	0.930	**0.005**	−0.72***	0.11	−0.45*	4 > 3,2,1	n.s.	4 > 3,2,1
>100 cm s^{-1}	**3.6E−08**	0.366	**1.4E−08**	−0.76***	−0.18	−0.71***	4 > 3,2,1	n.s.	4 > 3,2,1
Site 2 (N = 36)									
<50 cm s^{-1}	**0.028**	0.561	0.391	−0.44*	−0.24	−0.28	4 > 2	n.s.	n.s.
50–100 cm s^{-1}	**1.6E−08**	0.579	**2.7E−06**	−0.71***	−0.26	−0.69***	4 > 3,2,1	n.s.	4 > 3,2,1
>100 cm s^{-1}	**8.6E−08**	0.370	0.106	−0.78***	−0.16	−0.43*	4 > 3,2,1	n.s.	n.s.
Site 3 (N = 42) (downstream)									
<50 cm s^{-1}	0.215	0.490	0.673	0.08	0.39	0.07	n.s.	n.s.	n.s.
50–100 cm s^{-1}	**5.5E−05**	0.950	**0.005**	−0.44*	0.11	−0.45*	4 > 3,2,1	n.s.	4 > 3,1
>100 cm s^{-1}	**2.3E−04**	0.173	0.364	−0.58**	0.39	−0.36	4 > 3,2,1	n.s.	n.s.

N – number of samples.
[a]The effect of depth on POM accumulation at different flow velocities was analyzed via analysis of variance. Bold p-levels denote significant differences in POM accumulation among layers.
[b]Relationship between the depth and POM accumulation at different flow velocities was ascertained via Pearson correlation coefficient (r). Marked correlations are significant at: *p < 0.05; **p < 0.01; ***p < 0.001.
[c]The combined results of post hoc HSD test for unequal samples and Pearson correlation coefficients explaining differences found by ANOVA. Amounts of POM are compared among layers e.g. 4 > 3, 2, 1 means significantly more POM is accumulated in layer 4 than in layers 3, 2 and 1; n.s.– no significant difference in POM amounts among layers. Layers depth: (4) 0–1 cm (moss mat); (3) 1–4 cm; (2) 4–7 cm; (1) 7–10 cm.

among hydraulic habitats were detected at sites 1 and 2 in layer 3 (4–7 cm) and at site 3 in layer 1 (0–1 cm). At sites 1 and 2 post hoc HSD test for unequal samples differentiated the slowest flow velocity from the others and at site 3 only from the mid-fast velocity (50–100 cm s^{-1}). While CPOM accumulation was negatively correlated with the flow velocity at site 2 and in deeper layers at sites 1 and 3, it was positively correlated in the top two layers of the two latter sites. The only significant positive correlation however, was noted in the top layer of Site 3. FPOM accumulation in the given layers was marginally influenced by flow velocity, i.e. a significant difference was found only at site 1 in the top two layers between hydraulic habitats A and C (slower than 50 cm s^{-1} and faster than 100 cm s^{-1}) and was negatively correlated with the flow velocity.

To give a more plastic image of the situation at hand we combined this data into 3D quadratic fit diagrams i.e. models of POM distribution as a function of depth and flow velocity: $f(x,y) = (a + b*x + c*y)^2 + (d*x + e*y)^2$; x = depth, y = flow velocity ($p < 0.05$) (Fig. 3).

Also, porous travertine substrate and moss mats were examined separately. Differences in POM accumulation were found both for moss mats and travertine substrate at site 1 in regard to flow velocity (Table 5). Flow velocity negatively influenced the accumulation of particles within the substrate. The impact of flow velocity in travertine decreased downstream. At site 2 the impact was detected only for the accumulation of the smallest particles (UPOM) and it was also negative, while no impact of flow velocity was observed at Site 3. However, flow velocity assumed a significant and 'positive' role (the accumulation was positively correlated with the flow velocity) at site 3 for the deposition of larger particles in moss mats.

Discussion

POM accumulation decreases significantly along the barrage-lake system, even though sites were of the same order (according to Vannote et al. (1980)), with similar water chemistry, bed structure and the riparian and in-stream vegetation, as

Table 4. Analysis of effect of flow velocity on POM accumulation along the vertical profile

Site/Layer	ANOVA p^a			Pearson r^b			POM accumulation comparison[c]		
	CPOM	FPOM	UPOM	CPOM	FPOM	UPOM	CPOM	FPOM	UPOM
Site 1 (N = 21) (upstream)									
0–1 cm (moss)	0.265	**0.012**	0.160	0.35	−0.62**	−0.26	n.s.	A > C	n.s.
1–4 cm	0.601	**0.010**	**0.003**	0.23	−0.62**	−0.65**	n.s.	A > C	A > B,C
4–7 cm	**0.021**	0.695	**0.010**	−0.51*	−0.2	−0.53*	A > B,C	n.s.	A > B,C
7–10 cm	0.127	0.116	**0.001**	−0.38	−0.46	−0.72***	n.s.	n.s.	A > B,C
Site 2 (N = 28)									
0–1 cm (moss)	0.675	0.238	0.399	−0.23	−0.34	−0.24	n.s.	n.s.	n.s.
1–4 cm	0.309	0.221	**0.013**	−0.13	−0.27	−0.48*	n.s.	n.s.	A > B
4–7 cm	**0.036**	0.414	0.174	−0.46*	0.08	−0.42*	n.s.	n.s.	n.s.
7–10 cm	0.210	0.193	**0.002**	−0.35	−0.31	−0.53**	n.s.	n.s.	A > B,C
Site 3 (N = 32) (downstream)									
0–1 cm (moss)	**0.013**	0.310	0.394	0.36*	−0.22	−0.11	B > A	n.s.	n.s.
1–4 cm	0.113	0.955	0.482	0.20	−0.06	−0.21	n.s.	n.s.	n.s.
4–7 cm	0.895	0.238	0.154	−0.04	−0.31	−0.33	n.s.	n.s.	n.s.
7–10 cm	0.728	0.567	**0.025**	−0.07	−0.19	−0.48*	n.s.	n.s.	A > C

N – number of samples.
[a]The effect of flow velocity on POM accumulation at different depths was analyzed via analysis of variance. Bold p-levels denote significant differences in POM accumulation among hydraulic habitats.
[b]Relationship between the flow velocity and POM accumulation at different depth was ascertained via Pearson correlation coefficient (r). Marked correlations are significant at: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.
[c]The combined results of post hoc HSD test for unequal samples and Pearson correlation coefficients explaining differences found by ANOVA. Amounts of POM are compared among hydraulic habitats e.g. A > B, C means significantly more POM is accumulated in hydraulic habitat A than in the hydraulic habitats B and C; n.s.- no significant difference in POM amounts among hydraulic habitats. Flow velocity: (A) <50 cm s^{-1}; (B) 50–100 cm s^{-1}; (C) >100 cm s^{-1}.

the source of POM and the retention mechanism respectively. The downstream decrease of POM deposited on the travertine barriers may be attributed to particle deposition in lakes. Lentic parts of the system i.e. lakes, are sites at which POM sinks (Goldman & Kimmel, 1978) because flow velocity drops below the level required to keep the particles in suspension (Speaker et al., 1984). Sites 2 and 3 are situated downstream of the largest lake and hence are the major site of POM sinkage in the system, which could be an explanation for the decrease of POM amounts found on these sites. This aspect of POM transport through barrage-lakes should be studied further.

The dynamics of POM, however, tend to result in similar patterns of vertical distribution in travertine barriers, regardless of general differences in total POM accumulation at each site. Up to 45% more POM is accumulated in the moss mats than in the travertine substrate. The study of POM retention in non-precipitating New Zealand streams showed that the moss mats accumulate an order of magnitude more POM than the gravel stream bed (Suren, 1991). Both, these results confirm that moss mats are an important retention mechanism.

Quantities of POM in travertine barriers decrease exponentially with depth, contrasting with the studies of POM dynamics in karst streams with gravel beds where more POM was accumulated in deeper layers (Leichtfried, 1985; Mathieu et al., 1991). The ratios of POM fractions also change with depth. The relative abundance of FPOM increases, although the total quantities of FPOM do not change significantly. A significant increase in the relative abundance of FPOM is due to the decrease in CPOM content. These findings can be attributed to pore-size and flexibility of the substrate decreasing from the moss mat to deeper travertine layers as well as to dramatic change in flow conditions in moss (Suren, 1991) and the

Table 5. Comparison of flow velocity influence on accumulation of POM in moss mats and travertine substrate via Pearson r

Substrate	Site 1 (N = 21) (upstream)		Site 2 (N = 28)		Site 3 (N = 32) (downstream)	
	Travertine	Moss mat	Travertine	Moss mat	Travertine	Moss mat
CPOM	−0.39	0.35	−0.25	−0.23	0.06	0.36*
FPOM	−0.62**	−0.62**	−0.11	−0.34	−0.19	−0.22
UPOM	−0.72***	−0.26	−0.50**	−0.25	−0.34	−0.11
TPOM	−0.80***	−0.24	−0.35	−0.26	−0.21	−0.01

Marked correlations are significant at: *p < 0.05; **p < 0.01; ***p < 0.001.

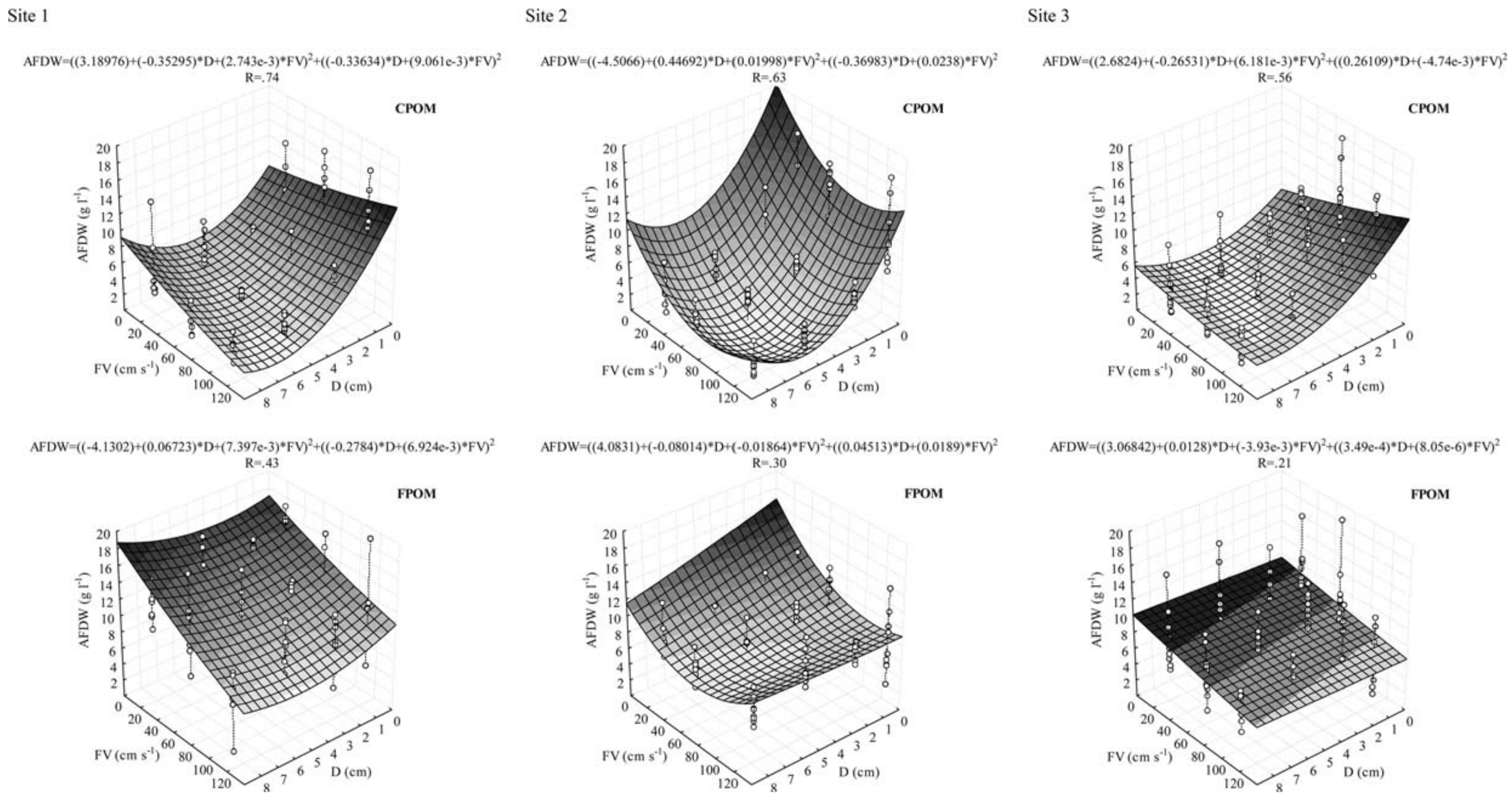
interstices (Wagner & Bretschko, 2002). Also, moss mats are exposed to the surface water that carries the majority of POM particles in stream ecosystems. Flow velocity among moss stems is greatly reduced enabling the deposition of particles. Contrary, inputs of POM for deeper layers are poor. Deeper layers depend for POM input on the burying of some POM (Smock, 1990) accumulated in moss mats, decaying remnants of cemented material (mostly moss) (Chafetz et al., 1994) or to a lesser extent on a hypogean input i.e. POM (UPOM and FPOM) transported longitudinally by slow interstitial currents (Mathieu et al. 1991).

Generally, flow velocity was found to be an important factor influencing distribution and accumulation of organic particles in travertine substrate corroborating prior studies on POM dynamics (Bretschko, 1990; Smock, 1990; Habdija et al., 2004). This influence changes considerably among substrate layers i.e. microhabitats and in respect to particle size and study site location considering the length of the preceding lakes.

CPOM accumulation in moss mats and travertine up to depth of 4 cm is positively correlated with the flow velocity at sites 1 and 3 (the barriers following shorter lakes). We attribute this to a less significant deposition of particles in smaller lakes preceding sites 1 and 3, i.e., more POM remains in the current and is available for deposition in moss mats. Also, CPOM is commonly larger than the spaces between moss stems and is hence retained by moss mats. Subsequently some CPOM is deposited in the top layer of the travertine substratum too in addition to POM originating from cemented moss.

FPOM and UPOM showed a different pattern of accumulation in comparison to CPOM and more was deposited in moss mats at slower flow velocities, as reported by Finlay & Bowden (1994) and Martinez et al. (1998). Thin and permeable moss mats are obviously not a sufficient mechanism to retain the large amounts of FPOM and UPOM that are present in faster currents. Faster flow velocities increase the downstream transport by resuspension of small particles in particular and decrease the storage capacity of moss mats. The total retention capacity of moss mats is therefore lower than that of debris dams and macrophytes reported by Smock (1990), Wanner & Pusch (2001) and Schulz et al., (2003). These larger retention mechanisms significantly enhance water residence time enabling the deposition of more POM (Schulz et al., 2003). However, in evaluating the significance of moss mats as POM retention mechanisms one should consider the distribution of mosses along the travertine barrier. While macrophytes and debris dams are scattered, mosses cover the entire barrier area homogenously. Mosses therefore enable homogenous distribution of POM and hence of macroinvertebrates and calcite precipitation along the barrier.

Generally, flow velocity shows a significant and negative influence on accumulation of POM in the travertine substrate, which is far less porous, more rigid and less exposed to temporary hydraulic disturbances than moss, thus being a long term accumulation site for POM. As expected, the influence of flow velocity on POM accumulation decreases with increasing depth (and the substrate becomes less permeable and more rigid) because interstitial flow is no longer dependant of that on the surface (Wagner & Bretschko, 2002). In the same way, the influence of flow velocity decreases with the increase of the size of organic particles. This result can be attributed to the decrease of pore size in the travertine substrate. Significant impact of flow velocity on accumulation and dis-


Site 1
AFDW=((3.18976)+(-0.35295)*D+(2.743e-3)*FV)^2+((-0.33634)*D+(9.061e-3)*FV)^2
R=.74
CPOM
AFDW=((-4.1302)+(0.06723)*D+(7.397e-3)*FV)^2+((-0.2784)*D+(6.924e-3)*FV)^2
R=.43
FPOM
Site 2
AFDW=((-4.5066)+(0.44692)*D+(0.01998)*FV)^2+((-0.36983)*D+(0.0238)*FV)^2
R=.63
CPOM
AFDW=((4.0831)+(-0.08014)*D+(-0.01864)*FV)^2+((0.04513)*D+(0.0189)*FV)^2
R=.30
FPOM
Site 3
AFDW=((2.6824)+(-0.26531)*D+(6.181e-3)*FV)^2+((0.26109)*D+(-4.74e-3)*FV)^2
R=.56
CPOM
AFDW=((3.06842)+(0.0128)*D+(-3.93e-3)*FV)^2+((3.49e-4)*D+(8.05e-6)*FV)^2
R=.21
FPOM
AFDW (g l-1)
FV (cm s-1)
D (cm)

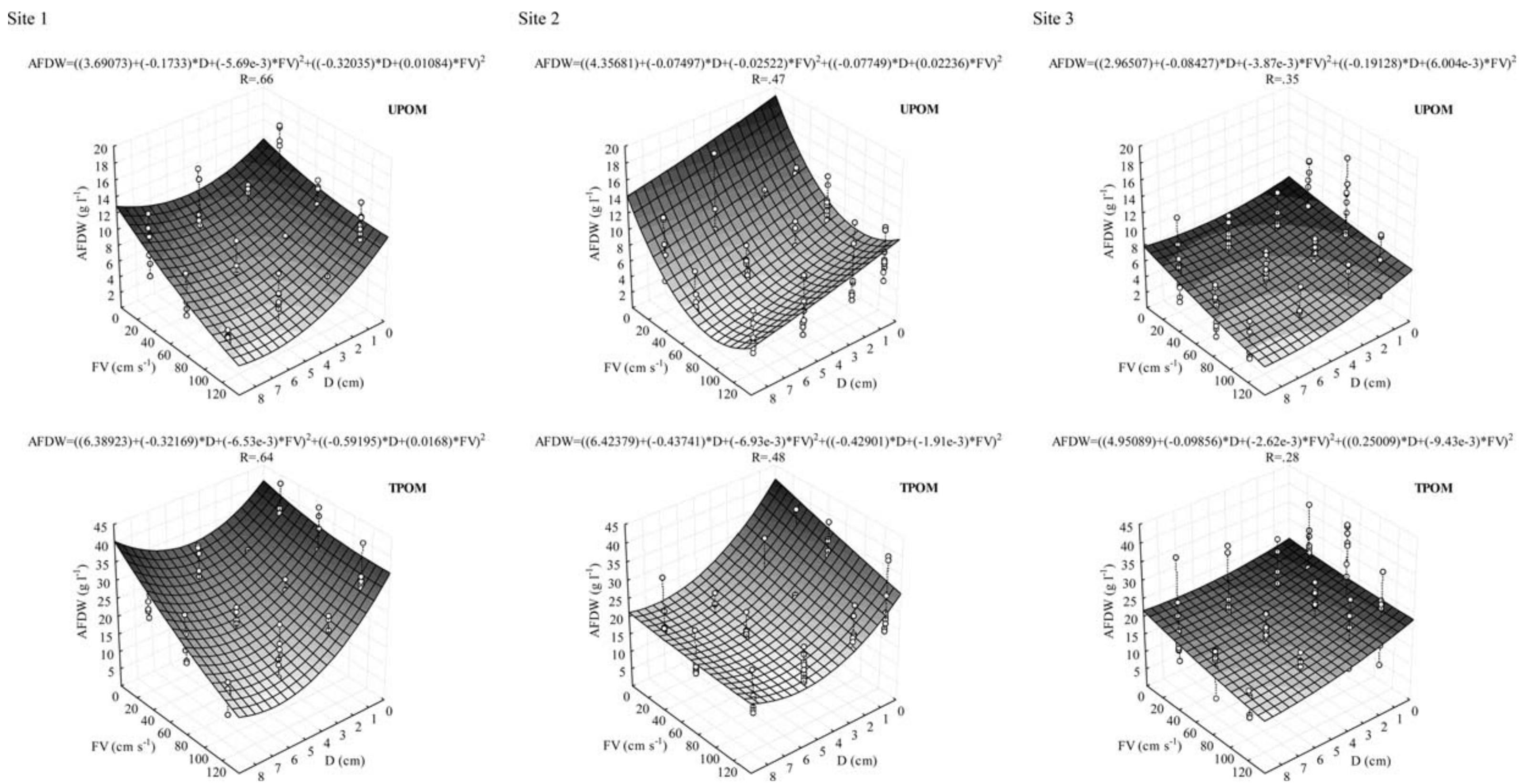


Figure 3. 3D models of vertical distribution of POM in travertine barriers of the barrage-lake system, in respect to flow velocity ($p < 0.05$). Values of POM are attributed to mean depth for each layer and mean flow velocity for each hydraulic habitat. Depths up to 1 cm refer to moss mats. Note that the scales for TPOM AFDW are different.

tribution of POM in general is detected up to depths of 7 cm in the travertine, while in deeper layers the impact is detected for small particles (UPOM) only.

In previous studies of detrital dynamics no relationship was evident between rates of leaf litter (CPOM) decomposition and the abundance of macroinvertebrates both in non-precipitating (Meyer, 1980; Stockley et al., 1998) and precipitating streams (Vivas & Casas, 2002). However, the sheer abundance of macroinvertebrates in moss mats (70000–700000 ind/m^2 according to Habdija et al. (2004)) could also hinder the deposition of POM. This aspect should be subjected to further studies.

Since it has been shown that substrate depth and flow velocity are parameters that strongly influence POM amounts, we have derived a model combining these factors (Fig. 3).

The proposed model may be used for predicting POM supplies in the top section of the vertical profile of moss-covered travertine barriers.

Conclusion

The role of flow velocity in POM accumulation in travertine barriers is dual. Increased flow velocity increases the amounts of CPOM in the moss and top travertine layer and decreases it in deeper layers. FPOM and UPOM deposition is negatively correlated with flow velocity along the vertical profile. As exposure to surface water and structure of the substrate changes with depth, the influence of flow velocity on POM accumulation is reduced. Significantly less POM is deposited with increased depth. FPOM amounts do not change with depth. Moss mats are an important POM retention mechanism in travertine barrier habitats, controlling both the quantity and quality (size structure) of POM. The role of lakes in the transport of POM along barrage-lake system as well as the role of invertebrate assemblages in POM accumulation should be studied further.

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