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Primary Research Paper

The impact of aquatic macrophyte (*Salix* sp. and *Cladium mariscus* (L.) Pohl.) removal on habitat conditions and macroinvertebrates of tufa barriers (Plitvice Lakes, Croatia)

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Abstract

The effects of aquatic macrophyte (willows and sawgrass) removal on flow velocity, tufa deposition, POM dynamics, and macroinvertebrate community structure were studied in the tufa barrier habitats of the barrage system of Plitvice Lakes, Croatia. Samples were collected from two hydraulic habitats (fast > 100 cm s^{-1} and slow < 100 cm s^{-1}) at both a control (no macrophytes removed) and impact (macrophytes removed) site. Samples were collected with a core sampler (four layers in vertical profile of barrier bed) monthly on 6 dates before and 7 dates after the removal of macrophytes. Macrophytes were removed in May 2002 at the impact site. After the macrophyte removal flow velocity decreased significantly at both hydraulic habitats. Retarded flow resulted in: (a) a decrease in macroinvertebrate density and diversity since most of the taxa were rheophilic (preferring habitats with higher flow velocity) and (b) an increase in POM concentrations (FPOM and UPOM) since decreases in flow velocity facilitate particle deposition in lotic habitats. The effects of macrophyte removal were present, and diminish along the vertical sediment profile of the barrier bed. Tufa deposition was not influenced by the macrophyte removal.

Introduction

Aquatic macrophytes are common in lotic habitats in the temperate zone. Macrophytes influence hydraulic roughness, water depth, flow velocity, create habitat for invertebrates, trap detritus and influence oxygen balance (Dudley et al., 1986; Marshall & Westlake, 1990; Biggs, 1996; Newman et al., 1996; Sand-Jensen & Mebus, 1996; Kaenel et al., 2000; Dodds & Biggs, 2002; Schulz et al., 2003). Therefore, removing macrophytes from lotic ecosystems can create a disturbance that alters ecosystem function. Most previous disturbance studies have focused on natural disturbances (e.g. spates, floods, etc.) in streams (Matthaei et al., 1997; Death, 2002; Olsen & Townsend, 2005). In stream macrophyte removal studies have generally focused on the removal of water weed. Studies have shown that removing water weeds leads to increases in flow velocity and decreases in macroinvertebrate abundance, species richness, and diversity (Monahan & Caffrey, 1996; Kaenel & Uehlinger, 1998; Kaenel et al., 1998; Wilcock et al., 1999). Woody vegetation has been researched mostly in riparian habitats in terms of shadowing the stream and as an organic matter source (Behmer & Hawkins, 1986; Lester et al., 1994, 1996; Sponseller et al., 2001)

Macrophytes were removed as part of a broader study of eutrophication control in the Plitvice Lakes, Croatia. Research conducted over the last 30 years indicates that the Plitvice Lakes system is undergoing eutrophication. Increases in phytoplankton biomass (20–90 times more in 1985 than in 1954), submerged vegetation and woody vegetation in lakes and on the barriers have been well documented. Furthermore, willow roots have had deteriorating effects on the structural integrity of some barriers causing the breaking of barrier parts. Efforts to control eutrophication began in 2001 as studies focused on two research priorities: (1) control and/or elimination of the anthropogenic sources of eutrophication, and (2) elimination of macrophytes from experimental areas.

This study was conducted on tufa barriers, which are porous calcium carbonate deposits that developed in supersaturated waters of karstic, hydrothermal and/or artesian origin (Chafetz & Folk, 1984). The mineral crystals are deposited on (as opposed to within) organic tissue (Riding, 1991). Macrophyte stands comprise a significant part of the tufa depositional frameworks (Pedley, 2000). However, precise role of the biota in this process remains unresolved. Some authors have found that organisms play a central role in the precipitation of calcium carbonate (e.g. Kempe & Emeis, 1985; Srdoč et al., 1985; Chafetz et al., 1994), while others believe their role is less significant, for example at waterfall sites and in fast-flowing streams (Chen et al., 2004). However, many authors agree that organisms provide a substrate for calcite nucleation and can trap calcite, which accelerates tufa deposition (Merz-Preiß & Riding, 1999; Zhang et al., 2001; Carthew et al., 2003). Tufa barriers in the uppermost deposit are extremely porous on a micro- and macro-scale (Chafetz et al., 1994) due to bryophyte, algal and macrophyte encrustation. The greatest part of water from the accumulated lake flows over the barrier, while small part penetrates the porous structure and seeps slowly downstream (Golubic, 1969).This constructs vast variety of microhabitats differing in current velocity, depth, turbulence, organic matter deposits and light penetration. Tufa barrier macrophytes and the implications of their removal have not been studied to date.

The aim of this study was to determine the influence of macrophytes on the tufa barrier habitats as well as to establish the effects of macrophyte removal on: (1) flow velocity; (2) tufa deposition; (3) POM dynamics and (4) macroinvertebrate communities in the cross sectional area (vertical profile) of the barrier bed.

Our hypotheses were that due to increased area, the flow velocity would be retarded and hence more particles would be deposited on the site after the removal of macrophytes. Also due to a decrease in flow velocity the mainly rheophilic (preferring habitats with higher flow velocity) macroinvertebrates would seek new habitats elsewhere and their density in affected reaches would decrease. The impact of macrophyte removal was expected to be more pronounced in initially fast flow habitats than in the slow flow habitats. It was also expected that the impact of macrophyte removal would decrease along the vertical profile of the barrier bed substrate.

Materials and methods

Study site

This research was carried out on two tufa barriers that were similar in hydraulic properties, flow patterns, vegetation and size. Both sites were located in the lower lakes section of the barrage-lake system of Plitvice Lakes in Croatia (Fig. 1). The control site was situated on the barrier of Milka Trnina Waterfall after Lake Milanovac

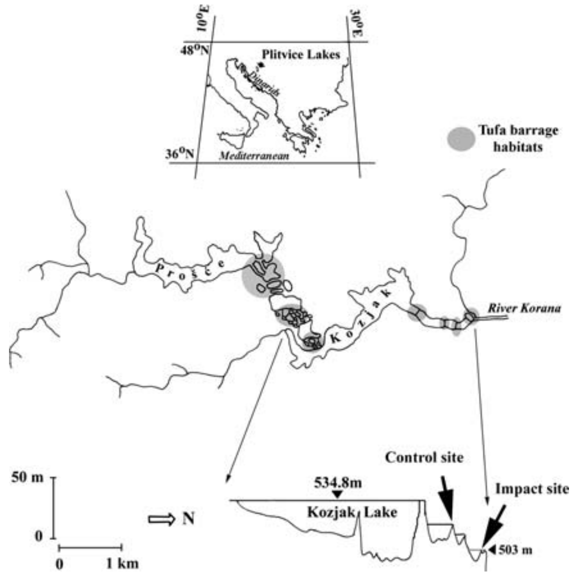

Figure 1. Map of the Plitvice barrage-lake system with marked sampling sites.

(0.03 km^2; 18 m deep) and the impact site was located on the barrier after Lake Kaluđerovac (0.02 km^2, 13 m deep). These sites were representative of travertine barriers in terms of moss cover and hydraulic characteristics.

Mean discharge during the study period at the reference point, the overflow of Lake Kozjak, was 2.5 $m^3\ s^{-1}$ (range 0.9–7.3 $m^3\ s^{-1}$). Water was characterized by low concentrations of nutrients and low COD at both sites. Mean values during the study period were 0.011 mg (NO_2^-) l^{-1}, 0.52 mg (NO_3^-) l^{-1}, 0.014 mg (PO_4^{3-}) l^{-1} and 0.83 mg (O_2) l^{-1} COD at the control site and 0.011 mg (NO_2^-) l^{-1}, 0.55 mg (NO_3^-) l^{-1}, 0.024 mg (PO_4^{3-}) l^{-1} and 0.8 mg (O_2) l^{-1} COD at the impact site. Mean temperatures were 12.8 °C (range 3.3–21.5 °C) and 11.4 °C (range 3.1–21.3 °C) on the control and impact sites, respectively.

Macrophyte cover of the barriers consisted predominantly of willows (*Salix* sp.) and sawgrass (*Cladium mariscus* (L.) Pohl.). Macrophytes were removed in the beginning of May 2002 at the impact site. The entire area of the barrier (1150 m^2) was cleared of macrophytes, 1000 m^2 of which was covered with willows and 150 m^2 with sawgrass. Willows were cut with a chainsaw and removed manually, and sawgrass was plucked and removed manually.

Sampling protocol

Sampling was conducted on moss-covered sites between the macrophytes because the flow in these sites was not impeded by the macrophytes and to avoid errors caused by loss of fauna and detritus as a result of the sheer mechanical removal of the macrophyte debris.

In order to assess the effects of macrophyte removal on flow velocity, two hydraulic habitats were selected (slow: < 100 cm s^{-1} and fast: > 100 cm s^{-1}) at both the control and the impact site. In areas of the barriers that satisfied the two aforementioned requirements (free flow between the macrophytes and flow velocity conditions) sampling was done randomly.

Four depth layers of the substrate were selected at each hydraulic habitat for sampling, based on empirical observations of the substrate consistency: three travertine layers (1) 7–10 cm; (2) 4–7 cm; (3) 1–4 cm; and (4) a moss mat layer (0–1 cm). The purpose of the vertical sampling was to determine if and to what extent the effects of macrophyte removal were present in the barrier bed profile.

Substrate samples were collected in triplicate on 13 dates (6 before and 7 after the removal of macrophytes) monthly from November 2001 to November 2002 (2 habitats $\times$ 4 depth layers $\times$ 13 dates $\times$ 3 samples = 312 samples) at the impact site. Samples were collected at the control site on the same dates. The control site was unapproachable in November 2001 and January and November 2002 due to snow and ice so the sampling was conducted on 10 dates (4 dates before and 6 dates after the removal of macrophytes at the impact site) (2 habitats $\times$ 4 depth layers $\times$ 10 dates $\times$ 3 samples = 240 samples).

Glass slides were put in the barrier bed at the impact site after macrophyte removal and simultaneously at the control site in order to determine how macrophyte removal impacted tufa deposition. The slides were exposed for periods of two weeks on six dates from 17 June to 17 September. The slides were implanted only in fast flow habitats since expected changes in flow velocity would have more (if any) impact in fast flow habitat. was not used The 'before-after' sampling that was used for macroinvertebrates and POM concentrations was not used for tufa deposition because there is a significant increase in tufa deposition in the summer months. Differences in summer and winter tufa deposition rates are large, and as a result would hinder subsequent analyses of the role of macrophytes on the tufa deposition (Matoničkin Kepčija et al., 2005). Tufa deposition was measured in the same way in the period before the macrophyte removal only to establish the upstream-downstream difference without the disturbance.

Data collection and analyses

Flow velocity was measured with a flow meter approximately 3 cm above the moss mats. Samples were collected for POM concentrations and macroinvertebrate community 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, fixed in 70% ethanol and later identified (larvae to the genus level or higher and adults to species level) and counted. The quantity of macroinvertebrates was expressed as number of individuals per volume unit of the sample (ind. dm^{-3}).

Only the top three layers of sediment were analyzed for macroinvertebrate data because the community in the first (deepest) layer was almost exclusively represented by Oligochaetes. The parameters chosen for description of macroinvertebrate communities were: number of taxa found, total density of macroinvertebrates (ind. dm^{-3}), Shannon–Wiener diversity index (bits ind.$^{-1}$) and density of most common taxa (Oligochaeta, Plecoptera, Coleoptera, Trichoptera, Chironomidae, the rest of Diptera, *Amphinemura* sp., *Riolus cupreus* (Müller), *Hydropsyche* sp., Tanytarsini, Orthocladinae, Tanypodinae, *Hemerodromia* sp.)

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 amounts of POM were expressed as concentrations (g AFDW dm^{-3}).

The slides encrusted with tufa (calcite) were dried, weighed, treated with the 18% HCl which dissolves calcite, dried and weighed again. Tufa deposition was measured as a mass difference of the slides before and after the treatment with the 18% HCl and expressed as mass of calcite per area per day (mg dm^{-2} day^{-1}).

Mann–Whitney *U*-tests were used to detect changes in hydraulic conditions, tufa deposition rates, detritus concentrations and invertebrate density before and after removal of the macrophytes. Exact *p* values were reported for borderline cases ($0.05 < p < 0.09$) to avoid type II errors (Zar, 1996). The before-after changes were compared between control and impact sites to determine which were caused by the macrophyte removal and which can be attributed to normal dynamics. Spearman rank correlation coefficients were used to ascertain the relationship of the flow velocity and the POM concentrations, tufa deposition rates and taxa density as well as the relationship between the POM concentrations and taxa density. Analyses were carried out using Statistica software (StatSoft, 2001).

Results

Hydraulic conditions and tufa deposition

Mean discharge measured at the reference point upstream of the study sites was 3056 dm^3 s^{-1} in the period before the macrophyte removal and 2141 dm^3 s^{-1} in the period after the removal. The decrease in discharge at the reference point before and after the macrophyte removal was not significantly different ($p > 0.05$).

Before the removal of macrophytes, flow velocities within the two studied habitats were similar at the control and the impact site. In the hydraulic habitat with the slow flow, mean velocities were 74.33 and 75.75 cm s^{-1} at the control and impact sites, respectively. In the habitat with the fast flow, mean flow velocities were 147.13 and 112.82 cm s^{-1} at the control and impact site, respectively. In both slow and fast habitats, there were no significant differences in flow velocity between the control and impact sites.

After the removal of macrophytes the flow velocity decreased significantly at the impact site especially in the hydraulic habitat with the faster flow ($p_{slow} = 0.0043$; $p_{fast} = 0.0023$). A slight decrease in flow velocity was recorded at the control site, but this was not statistically significant (Fig. 2).

In the period after the macrophyte removal tufa deposition rate was slightly higher at the impact site than at the control site (Fig. 3) but the difference was not significant. This was also noted in the colder period of the year, before the macrophyte removal, when the tufa deposition rates were low (0.22 and 0.47 mg dm^{-2} day^{-1} were mean deposition rates on control and impact site, respectively) and the difference was also not significant. The correlation between the flow velocity and tufa deposition rate was negative ($R = -0.78$; $p < 0.001$), while a positive correlation was found between temperature and tufa deposition ($R = 0.74$; $p < 0.001$). Similar results were found at the control site ($R = -0.67$; $p < 0.5$ and

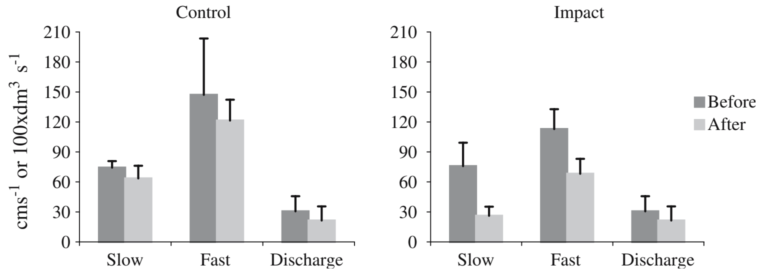

Figure 2. Mean flow velocity and discharge (+SD) at control and impact site before and after the macrophyte removal. Slow-habitats with flow velocity < 100 cm s^{-1}; fast-habitats with flow velocity > 100 cm s^{-1}. Note that the *Y*-axis values are dual (cm s^{-1} for flow velocity and $100 \times dm^3\ s^{-1}$ for discharge).

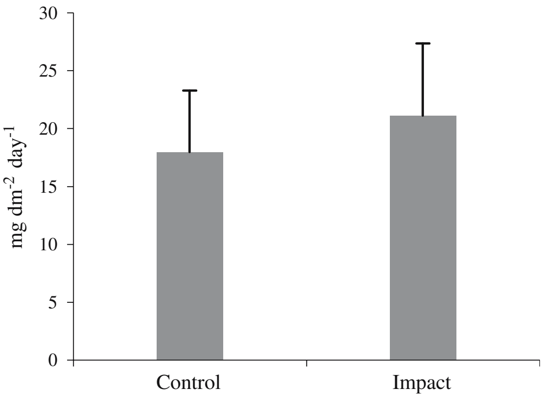

Figure 3. Mean tufa deposition rates (+SD) on control and impact site after the macrophyte removal.

$R = 0.89$; $p < 0.01$ for correlation of tufa deposition rate with flow velocity and temperature, respectively).

Organic matter

The organic matter concentration was analysed for each substrate layer separately and also for the entire 10 cm vertical profile of the barrier bed. The before-after differences in POM concentrations in the entire 10 cm deep vertical profile of the barrier bed were generally not significant at the control site. However, there was a pattern in the POM dynamics: in habitats with slow flow, the concentrations of all POM size fractions increased in the period after the removal while they decreased in habitats with fast flow. These differences were not significant except for the decrease of concentration of CPOM (Fig. 4). At the impact site only CPOM concentration decreased in both hydraulic habitats, while FPOM and UPOM concentrations increased in both habitats. Most of these differences were statistically significant (Fig. 4).

The differences between control and impact sites regarding POM concentrations i.e. the impact of macrophyte removal, was most obvious in layer 4 (surface layer). At the control site most of the POM size fractions concentrations decreased in the period after the removal. Only the CPOM concentration in slow flow habitats increased. None of these changes were proven significant (UPOM decrease in fast flow habitat was borderline: $p = 0.088$). At the impact site the situation was reversed. Only the CPOM concentration in the slow flow habitat decreased (not significant), while FPOM and UPOM concentrations increased in both hydraulic habitats as well as the CPOM concentration in the fast flow habitat (at least borderline significant) (Fig. 4).

In the three deeper layers of the sediment at the control site POM concentrations were mostly level before and after the removal. There was a significant increase in FPOM and UPOM concentrations in the layer 2 in the slow flow habitats, and a significant decrease in CPOM concentration in layer 1 of the fast flow habitat. Generally in layers 2 and 3 POM concentrations increased in the slow flow habitats and decreased in the fast flow habitats. In layer 1 concentrations of all POM size fractions decreased.

At the impact site there was a tendency for CPOM concentration to decrease and FPOM and UPOM concentrations to increase after the macrophyte removal regardless of the hydraulic habitats in the three deeper layers. The majority of these changes were significant or borderline significant (Fig. 4).

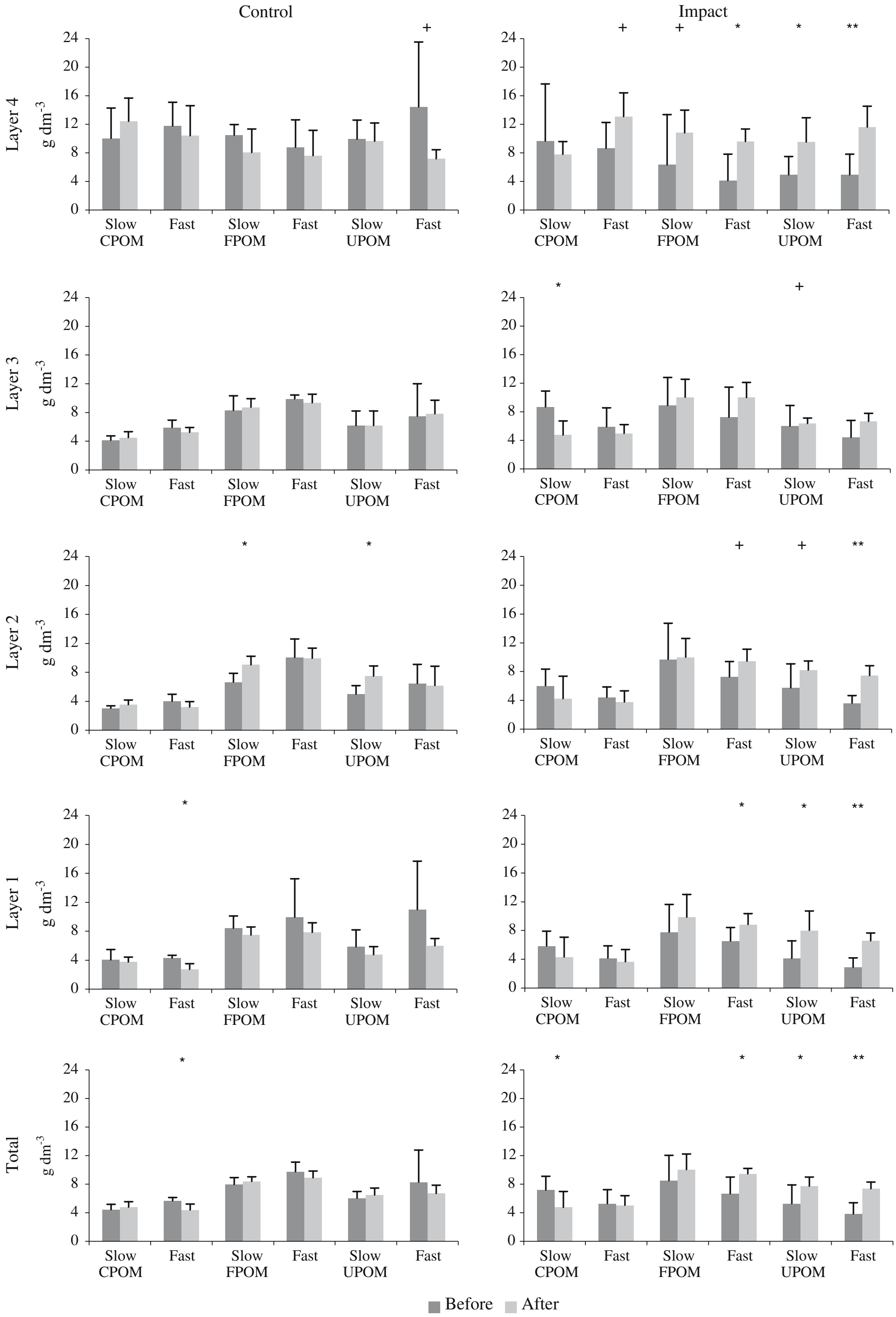
Control
Impact
Layer 4
Layer 3
Layer 2
Layer 1
Total
g dm-3
24
20
16
12
8
4
0
Slow
Fast
CPOM
FPOM
UPOM
+
*
**
Before
After

Figure 4. Mean concentrations of POM size fractions (+SD) for the layers along the vertical profile and the entire profile of the barrier bed at control and impact site before and after the macrophyte removal. Significant and borderline significant changes are marked: + $0.09 > p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

The concentrations of all POM fractions were generally negatively correlated with the flow velocity. The correlations were most pronounced and statistically significant in the top layer of the fast flow habitat. The significance of correlations expectedly decreased with layer depth. In the slow flow habitat the correlations were less significant throughout the vertical profile of the barrier bed (Table 1).

Table 1. Spearman rank correlation coefficients between flow velocity and concentrations of POM size fractions for four layers along the vertical profile and the total vertical profile of the barrier bed in slow flow habitat and fast flow habitat

	Slow flow		Fast flow	
	R	*p*	*R*	*p*
Layer 4				
CPOM	−0.19		−0.69	**
FPOM	−0.64	*	−0.75	**
UPOM	−0.57	*	−0.66	*
TPOM	−0.52		−0.86	***
Layer 3				
CPOM	0.60	*	0.09	
FPOM	−0.24		−0.36	
UPOM	−0.42		−0.49	
TPOM	0.07		−0.34	
Layer 2				
CPOM	0.28		0.29	
FPOM	−0.17		−0.50	
UPOM	−0.69	**	−0.77	**
TPOM	0.01		−0.65	*
Layer 1				
CPOM	0.11		0.20	
FPOM	−0.43		−0.61	*
UPOM	−0.66	*	−0.74	**
TPOM	−0.50		−0.67	*
Total				
CPOM	0.38		−0.19	
FPOM	−0.41		−0.59	*
UPOM	−0.68	**	−0.74	**
TPOM	−0.18		−0.59	*

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

Macroinvertebrates

The 'before-after' changes in macroinvertebrate community structure in the the10 cm deep vertical profile of the barrier bed were markedly different at the impact site compared to the changes at the control site (where the changes were regarded as normal community dynamics). At the control site in the slow flow habitat there were significant changes (increases) in some community parameters while in the fast flow habitat there was a significant change (decrease) only in the Tanytarsini density. At the impact site changes were more pronounced (changes of almost all community parameters were statistically significant). Furthermore, all changes of community parameters at the impact site at both hydraulic habitats were based on the decrease of their values (Table 2 and see Electronic Supplementary Material[1]).

In the layer-by-layer community analyses at the impact site all of the community parameters decreased after the macrophyte removal in all studied layers in both hydraulic habitats. The only exceptions were the densities of Coleoptera, Trichoptera, Diptera and *Riolus cupreus* in the layer 4 (top layer) of the fast flow habitat. At the control site statistically significant changes in community parameters between the periods before and after the removal of macrophytes were found only in layer 4 (the top layer). In the slow flow habitat, statistically significant or borderline significant changes were based on the increase of the values of community describing parameters, and in the fast flow habitat the only significant change was the decrease of Chironomidae density (Tanitarsini). Most of the community parameters showed the same dynamics (increase or decrease) in layers throughout the vertical profile of the barrier bed. The number of statistically significant changes of community parameters decreased with depth of the respective layer on both sites (Table 2 and see Electronic Supplementary Material).

The only overlapping statistically significant changes (i.e. the changes that can be attributed to

[1] Electronic supplementary material is available for this article at http://dx.doi.org/10.1007/s10750-006-0271-4 and accessible for authorised users

Table 2. Comparison of community structure on control and impact site before and after the macrophyte removal (via Mann–Whitney *U*-test)

				TMD	*H′*	Oligochaeta	Plecoptera	Coleoptera	Trichoptera	Chironomidae	Diptera	*Amphinemura*	*R. cupreus*	*Hydropsyche*	Tanytarsini	*Hemerodromia*
Control site	Layer 4	Slow	Before	2473.45	1.68	531.86	210.62	1131.86	88.79	476.99	33.33	33.33	1131.86	55.46	421.53	0.00
			After	2683.44	3.03	324.95	408.81	220.13	744.23	681.34	262.05	335.43	209.64	461.22	408.81	83.86
			p	n.s.	**0.011**	n.s.	n.s.	n.s.	0.051	n.s.	**0.017**	0.061	n.s.	n.s.	n.s.	n.s.
		Fast	Before	5649.56	2.45	1221.83	888.20	920.06	366.37	2053.10	166.67	588.79	920.06	288.79	1776.11	100.00
			After	2840.67	2.78	356.39	324.95	492.66	702.31	639.41	314.47	262.05	492.66	566.04	482.18	167.71
			p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.032**	n.s.	n.s.	n.s.	n.s.	**0.010**	n.s.
	Layer 3	Slow	Before	209.98	0.72	151.16	0.00	29.41	22.06	7.35	0.00	0.00	29.41	7.35	7.35	0.00
			After	314.47	1.61	139.76	27.95	10.48	76.87	38.43	6.99	6.99	6.99	27.95	0.00	3.49
			p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		Fast	Before	483.20	1.24	176.70	132.84	33.12	33.24	107.30		132.84	33.12	33.24	66.62	
			After	419.29	0.77	342.42	0.00	17.47	6.99	52.41		0.00	17.47	0.00	17.47	
			p	n.s.	n.s.	0.055	0.068	n.s.	n.s.	n.s.		0.068	n.s.	0.068	n.s.	
	Layer 2	Slow	Before	128.94	0.25	84.64	0.00	33.19	0.00	11.11			33.19		11.11	
			After	125.79	0.28	104.82	3.49	0.00	6.99	10.48			0.00		6.99	
			p	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			n.s.		n.s.	
		Fast	Before	349.85	0.00	349.85			0.00							
			After	331.94	0.15	328.44			3.49							
			p	n.s.	n.s.	n.s.			n.s.							
	Total	Slow	Before	441.95	1.62	173.39	26.91	152.07	18.20	67.48	3.91	6.11	152.07	9.10	61.37	0.00
			After	452.83	3.01	137.32	54.51	26.21	109.01	84.91	29.35	35.64	24.11	65.41	44.03	9.43
			p	n.s.	**0.033**	n.s.	n.s.	n.s.	0.084	n.s.	**0.017**	n.s.	n.s.	**0.049**	n.s.	0.054
		Fast	Before	1086.87	2.30	400.04	165.76	121.60	61.51	311.95	21.24	128.71	121.60	51.55	262.35	12.57
			After	545.07	2.37	271.49	32.49	54.51	74.42	79.66	31.45	26.21	54.51	56.60	53.46	16.77
			p	n.s.	n.s.	n.s.	0.087	n.s.	n.s.	0.054	n.s.	n.s.	n.s.	n.s.	**0.019**	n.s.

Impact site	Layer 4	Slow	Before	1247.38	2.69	230.61	164.22	96.09	108.32	508.39	96.09	73.38	96.09	97.83	267.30	48.92
			After	584.01	0.86	413.30	0.00	8.98	26.95	44.92	53.91	0.00	0.00	17.97	8.98	0.00
			p	n.s.	**0.004**	n.s.	**0.004**	0.050	0.071	**0.010**	n.s.	**0.015**	**0.014**	**0.029**	**0.016**	n.s.
		Fast	Before	3427.67	2.81	838.57	492.66	99.58	352.90	1411.60	179.94	167.71	94.34	330.19	803.63	31.45
			After	2066.49	2.50	646.90	26.95	143.76	386.34	637.92	197.66	17.97	143.76	305.48	386.34	26.95
			p	**0.046**	n.s.	n.s.	0.051	n.s.	n.s.	0.061	n.s.	**0.042**	n.s.	n.s.	n.s.	n.s.
	Layer 3	Slow	Before	644.12	1.79	377.04	20.56	9.94	17.50	131.51	85.82	17.20	9.94	14.00	50.02	19.92
			After	200.66	1.07	143.76	2.99	2.99	5.99	11.98	8.98	0.00	2.99	2.99	8.98	0.00
			p	**0.022**	n.s.	**0.020**	n.s.	n.s.	n.s.	**0.007**	**0.013**	**0.042**	n.s.	n.s.	**0.031**	**0.015**
		Fast	Before	837.18	1.94	494.41	57.65	12.23	67.09	149.20	49.62	45.42	12.23	60.10	55.90	3.49
			After	413.30	0.20	395.33	0.00	0.00	2.99	2.99	8.98	0.00	0.00	0.00	0.00	0.00
			p	0.074	**0.006**	n.s.	**0.042**	**0.042**	**0.010**	**0.002**	**0.018**	**0.042**	**0.042**	**0.004**	**0.014**	n.s.
	Layer 2	Slow	Before	301.73	0.87	249.95			1.75	12.86	10.80				1.91	
			After	104.82	0.46	41.93			0.00	2.99	0.00				2.99	
			p	**0.026**	n.s.	**0.021**			n.s.	n.s.	**0.042**				n.s.	
		Fast	Before	390.99	0.91	298.74			5.24	66.04	19.22			1.75	19.22	
			After	182.69	0.06	179.69			2.99	0.00	0.00			0.00	0.00	
			p	n.s.	**0.034**	n.s.			n.s.	**0.015**	n.s.			n.s.	n.s.	
	Total	Slow	Before	475.37	2.39	253.14	27.25	13.10	19.39	108.49	39.83	14.68	13.10	16.25	52.41	11.01
			After	199.46	1.63	110.51	0.90	2.70	4.49	10.78	8.09	0.00	1.80	2.70	4.49	0.00
			p	**0.010**	**0.046**	0.063	**0.008**	**0.030**	**0.027**	**0.002**	**0.031**	**0.015**	**0.019**	**0.050**	**0.003**	**0.015**
		Fast	Before	833.33	2.57	378.41	89.62	13.63	61.32	241.09	41.40	30.92	13.10	56.08	125.79	5.77
			After	410.60	1.89	261.46	2.70	14.38	40.43	65.59	22.46	1.80	14.38	30.55	39.53	2.70
			p	**0.003**	**0.046**	n.s.	**0.013**	n.s.	n.s.	**0.003**	n.s.	**0.020**	n.s.	0.086	**0.015**	n.s.

Bold p values, significant difference; regular font p values, borderline cases; n.s., not significant. TMD, mean total macroinvertebrates density; H', Shannon–Wiener diversity index. Mean taxa densities are given in ind. dm^{-3}; H' in bits ind.$^{-1}$.

normal temporal dynamics rather than to the effect of macrophyte removal), at both the control and the impact site, were found in the fast flow habitats. These changes amounted for layer 3 to the decrease of Plecoptera (*Amphinemura* sp.) and *Riolus cupreus*, for layer 4 to the decrease of Chironomidae density and for the entire profile to the decrease of Plecoptera and Chironomidae (Tanitarsini) density (Table 2 and see Electronic Supplementary Material).

Most community parameters were positively correlated with the flow velocity. The correlations were most pronounced in layer 3 of both hydraulic habitats. The only taxa negatively correlated with flow velocity were Oligochaeta and Coleoptera (Table 3 and see Electronic Supplementary Material).

The correlations between POM concentrations and community parameters were stronger in the fast flow habitats and also most pronounced in layer 3. Most taxa were positively correlated with CPOM concentration and negatively correlated with the FPOM and UPOM concentrations. Significant correlations were found almost exclusively in the top two layers (Table 3 and see Electronic Supplementary Material). In the control site there were virtually no significant correlations of community parameters with either flow velocity or the concentration of POM deposited. The correlations with the flow velocities were generally positive, and the correlations with the POM concentrations were heterogeneous.

Discussion

The purpose of this research was to assess the effects of macrophyte removal on the hydraulic conditions of tufa barrier habitats, tufa deposition rates, POM dynamics and benthic macroinvertebrates. Ours is the first study to determine how macrophyte removal affects tufa barrier habitats.

The most important impact of macrophyte removal was the significant decrease in flow velocity. Before the macrophyte removal, flow was restricted to areas between the macrophytes and hence flow velocity was fast in these areas (Sand-Jensen & Mebus, 1996). By removing the macrophytes, the area of flow increased while the volume of the water overflowing from the lake (i.e. discharge) remained the same resulting in a slower flow over the tufa barrier. Previous studies have found that macrophyte removal from streams resulted in faster flows (Kaenel et al., 1998). The contrasting results obtained in our study may be attributed to the hydrological self-regulating properties of the barrage lake system, where lakes contribute to the control of the magnitude of downstream discharge (Ford & Pedley, 1996; Riđanović & Božičević, 1996). Also, a different type of macrophytes (submerged) were removed in these previous studies. Submerged macrophytes do not reduce the volume of the lake outlet to the degree that willows do, so there would not be a significant increase of flow area after their removal. The removal of submerged macrophytes reduced bed roughness, thereby increasing flow.

The reduced flow velocity associated with macrophyte removal did not impede the tufa deposition. The recorded higher tufa deposition rate on the downstream barrier (impact site) corresponds with the findings of Golubic (1969) and Matoničkin Kepčija et al. (2005) who reported a downstream increase in tufa deposition rates in the Plitvice lakes. The impact of waterfall effects and temperature increase on the tufa deposition reported by Zhang et al. (2001) and Drysdale et al. (2003) probably prevail over the impact of flow velocity decrease. The waterfall effects are a combination of physical mechanisms of calcite precipitation. When a body of water approaches the waterfall its velocity increases and thus the pressure within the water reduces (Bernoulli's effect). Dissolved gases are released from water at lower pressures (Henry's law). Secondly, with increased flow velocity the turbulence of water is increased which results in larger air–water surface. Both phenomena facilitate CO_2 outgassing which results in (1) supersaturation of water with respect to calcite and consequently (2) precipitation of calcite. Increased temperature increases the CO_2 outgassing to the atmosphere contributing further to the precipitation of calcite.

Macrophyte removal had a significant impact on the POM dynamics and macroinvertebrate community structure. The retarded flow resulted in elevated deposition of POM at the impact site which is consistent with previous studies (Speaker et al., 1984; Martinez et al., 1998). Increase in POM deposition was more pronounced in the fast flow habitat where the decrease in flow velocity was most pronounced. Also, the macrophyte removal affected the deposition and retention of smaller organic particles (FPOM and UPOM) more than the retention of CPOM, which was almost unaffected. Since small particles are more prone to resuspension in fast flowing conditions, more is deposited when the flow velocity decreases (Finlay & Bowden, 1994). Several previous studies have shown that the flow-retarding effect of dense macrophyte stands enhances the deposition of fine sediments (Marshall & Westlake, 1990; Sand-Jensen, 1998) and the retention of organic detritus (Dudley et al., 1986; Schulz et al., 2003). Our results support the finding that flow velocity influences particle deposition; however, the flow-retarding effects in our study were the result of macrophyte removal rather than the presence of macrophyte stands. The impact of macrophyte removal was expectedly stronger in the top layers of the tufa vertical profile of the barrier bed but the significant increase of deposited POM was recorded throughout the vertical profile of the barrier bed (mostly for FPOM and UPOM in the fast flow habitat).

In contrast to the increase of POM concentration at the impact site, the macroinvertebrate densities decreased after the macrophyte removal. The decreases of the values of community parameters after the macrophyte removal were most pronounced in the top two layers and decreased along the vertical profile of the barrier bed. A decrease in macroinvertebrate numbers was also recorded in previous studies of macrophyte removal (Dawson et al., 1991; Kaenel et al., 1998; Kaenel & Uehlinger, 1999) but mostly for the taxa that used the macrophytes as habitat (macroinvertebrates were removed together with the macrophytes). In this study, the decrease in macroinvertebrate density should be associated mostly with the flow velocity decrease since the research was conducted in areas between the macrophyte stands.

The increase (or at least unchanged values) of the taxa densities after the macrophyte removal was found only in the top layer in the fast flow habitats. Simultaneously, the decrease of the density of the same taxa was found both in the slow flow habitats and the deeper layers of the substrate in the fast flow habitats (Table 2 and see Electronic Supplementary Material). This could be the result of the migration of these taxa both from the slow flow habitats and from the deeper layers of the fast flow habitat to the top layer in the fast flow habitats. Both lateral (Lancaster, 1999) and vertical (Dole-Olivier et al., 1997) migration during the flow disturbance events was reported. The taxa that exhibited these dynamics were rheophilic (*Hydropsyche* and *Hemerodromia*) or highly mobile (*Riolus*). The density of the highly rheophilic taxa (*Amphinemura*) decreased as their preferred hydraulic habitats no longer existed. The decrease of Chironomidae density after the macrophyte removal found in our study was reported in studies of macrophyte removal in streams as well (Dawson et al., 1991; Kaenel et al., 1998). The upward migration of the macroinvertebrates might be the reason for more pronounced changes in their densities in layer 3 (1–4 cm deep) than in the top layer, which is directly exposed to the flow. The migration pathways of macroinvertebrates in tufa barriers will be studied further.

Since most of the taxa densities were positively correlated with the flow velocity the flow velocity decrease was probably the reason for the decrease of taxa densities. The correlations of taxa density with POM concentrations were relatively uniform (generally negative) at the impact site but these results could be a product of the simultaneous decrease of taxa density and increase of POM concentrations under the influence of decreased flow velocity. Furthermore, positive correlations between the CPOM concentration and taxa densities were found only where the CPOM concentration decrease was accompanied by the flow velocity decrease. However, these results in comparison with the results acquired at the control site (stable environment) where virtually no significant correlations were found between macroinvertebrates and POM may show that the impact was not only in sheer changes of macroinvertebrate numbers and POM concentration but also in their relations. The lack of statistically significant correlations in the layer 2 corroborates this since deeper layers were not as affected as the top layers.

Number of taxa, total density of macroinvertebrates and consequently the diversity (H') all

Table 3. Spearman rank correlation coefficients between flow velocity and concentrations of POM size fractions and community parameters for top three layers along the vertical profile and the total vertical profile of the barrier bed

		Slow flow habitat				Fast flow habitat			
		Flow velocity	CPOM	FPOM	UPOM	Flow velocity	CPOM	FPOM	UPOM
Layer 4	Macroinvertebrates	0.23	0.29	0.13	−0.25	0.55	−0.14	−0.35	−0.38
	H′	0.62*	−0.28	−0.14	−0.37	0.59*	−0.54	−0.66*	−0.12
	Oligochaeta	−0.37	0.41	0.36	0.30	−0.25	0.62*	0.43	−0.01
	Plecoptera	0.82***	0.01	−0.40	−0.67*	0.69**	−0.38	−0.40	−0.19
	Coleoptera	0.29	−0.02	0.12	−0.15	−0.39	0.35	0.35	0.29
	Trichoptera	0.28	−0.41	−0.08	−0.21	0.52	−0.32	−0.59*	−0.44
	Chironomida	0.52	−0.02	−0.06	−0.22	0.60*	−0.26	−0.32	−0.27
	Diptera	0.14	0.56*	0.37	0.10	0.21	−0.13	−0.06	0.11
	Riolus cupreus	0.46	−0.13	−0.07	−0.38	−0.42	0.36	0.37	0.31
	Tanytarsini	0.49	−0.13	−0.05	−0.29	0.46	−0.21	−0.20	−0.11
	Amphinemura sp.	0.72**	−0.21	−0.27	−0.73**	0.69**	−0.72**	−0.72**	−0.62*
	Hydropsiche sp.	0.44	−0.30	−0.22	−0.22	0.75**	−0.42	−0.83***	−0.78**
	Hemerodromia sp.	0.46	0.21	−0.39	−0.20	0.46	−0.39	−0.39	−0.31
Layer 3	Macroinvertebrates	0.81***	0.73**	−0.15	−0.55*	0.67*	−0.25	−0.18	−0.17
	H′	0.42	0.17	−0.39	−0.60*	0.88***	0.21	−0.54	−0.58*
	Oligochaeta	0.81***	0.77**	0.00	−0.29	0.32	−0.37	0.23	0.27
	Plecoptera	0.41	0.34	−0.21	−0.07	0.69**	−0.13	−0.72**	−0.68*
	Coleoptera	0.25	0.31	−0.03	−0.18	0.70**	−0.19	−0.74**	−0.66*
	Trichoptera	0.59*	0.14	−0.21	−0.50	0.73**	0.22	−0.55	−0.51
	Chironomida	0.71**	0.71**	−0.15	−0.40	0.89***	0.03	−0.49	−0.55*
	Diptera	0.76**	0.52	−0.49	−0.61*	0.76**	0.37	−0.61*	−0.64*
	Riolus cupreus	0.25	0.31	−0.03	−0.18	0.70**	−0.19	−0.74**	−0.66*
	Tanytarsini	0.62*	0.68*	−0.17	−0.44	0.69**	0.11	−0.78**	−0.82***
	Amphinemura sp.	0.57*	0.53	−0.12	−0.13	0.69**	−0.20	−0.73**	−0.65*
	Hydropsiche sp.	0.60*	0.07	−0.34	−0.49	0.75**	0.19	−0.65*	−0.67*
	Hemerodromia sp.	0.66*	0.53	−0.43	−0.44	0.46	0.15	−0.39	−0.46

Layer 2	Macroinvertebrates	0.62*	0.31	−0.29	−0.24	0.50	−0.44	0.03	−0.34
	H′	0.18	0.53	0.54	0.18	0.61*	0.09	−0.23	−0.50
	Oligochaeta	0.71**	0.23	−0.18	−0.26	0.42	−0.49	0.05	−0.28
	Plecoptera								
	Coleoptera								
	Trichoptera	0.16	0.39	−0.39	−0.39	0.39	−0.28	0.12	−0.07
	Chironomida	0.36	0.46	−0.02	−0.06	0.60*	0.22	−0.25	−0.58*
	Diptera	0.62*	0.30	0.07	−0.51	0.48	−0.10	−0.07	−0.28
	Riolus cupreus								
	Tanytarsini	0.07	0.31	0.41	0.26	0.48	−0.10	−0.07	−0.28
	Amphinemura sp.								
	Hydropsiche sp.					0.27	0.08	0.31	−0.15
	Hemerodromia sp.								
Total	Macroinvertebrates	0.83***	0.48	−0.30	−0.72**	0.88***	−0.23	−0.49	−0.68*
	H′	0.32	−0.04	−0.40	−0.56	0.77**	0.07	−0.65*	−0.48
	Oligochaeta	0.58	0.56	−0.04	−0.49	0.39	−0.53	0.09	−0.36
	Plecoptera	0.77**	0.28	−0.59	−0.75**	0.83***	−0.14	−0.55	−0.51
	Coleoptera	0.38	0.18	0.01	−0.38	−0.14	−0.39	0.07	0.12
	Trichoptera	0.52	−0.03	−0.20	−0.45	0.57*	0.16	−0.43	−0.40
	Chironomida	0.69**	0.45	−0.28	−0.57	0.87***	−0.26	−0.42	−0.63*
	Diptera	0.78**	0.32	−0.66	−0.86***	0.68*	−0.22	−0.32	−0.41
	Riolus cupreus	0.46	0.31	−0.05	−0.45	−0.14	−0.39	0.07	0.12
	Tanytarsini	0.66	0.51	−0.18	−0.55	0.71**	−0.35	−0.11	−0.37
	Amphinemura sp.	0.72**	0.23	−0.44	−0.72**	0.82***	−0.39	−0.52	−0.48
	Hydropsiche sp.	0.53	−0.03	−0.05	−0.25	0.61*	0.19	−0.44	−0.46
	Hemerodromia sp.	0.64*	0.47	−0.69**	−0.62*	0.54	−0.02	−0.34	−0.24

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

decreased after the macrophyte removal while these parameters increased at the control site in the same period. These findings corroborate the results of disturbance studies in streams that found that disturbance in streams usually reduces invertebrate species richness (Englund, 1991; Matthaei et al., 1996, 1997). The effects of macrophyte removal decline along the vertical profile of the barrier bed and the 7–10 cm and even the 4–7 cm deep layers are virtually negligible. In contrast to the aforementioned flow disturbance studies the deep layers of the substrate do not serve as refugia during the flow retarding disturbance events (as in this study) and macroinvertebrates that are normally present in these habitats emigrate.

Conclusion

Aquatic macrophytes are an important feature in tufa barrier habitats. They directly control the flow velocity on the barriers and indirectly the community structure and POM deposition in the sites between the macrophyte stands. The removal of macrophytes is a disturbance that primarily decreases the flow velocity. Through the decrease of flow velocity this disturbance causes significant changes in POM dynamics and also the community structure. POM concentrations (FPOM and UPOM) increase in affected habitats, while macroinvertebrate (which are mainly rheophilic in these habitats) density and the diversity decrease. The impact of the macrophyte removal both on POM concentrations and on macroinvertebrate density decreases along the vertical profile of the barrier bed. This vertical gradient is more pronounced for the POM concentrations than for the macroinvertebrates, which leave their habitats throughout the vertical profile of the barrier bed. The tufa deposition is unaffected by the macrophyte removal probably due to the pronounced waterfall effect on tufa barriers.

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