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Energy resources and feeding guild structure of macroinvertebrate assemblages in the hyporheic zone of calcite depositing lake outlets

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ABSTRACT

We investigated the distribution of particulate organic matter (POM) and its relation to flow velocity and tufa deposition rates (TDR) in the 4–10 cm deep zone at tufa barriers. We expected surface conditions affect the hyporheic zone, even in habitats with non-moving substrate in calcite depositing lake outlet streams. Additionally, we analyzed feeding guild structure of macroinvertebrate assemblages against environmental conditions, food resources and predatory abundance. Overall, more POM was deposited in the hyporheic zone of slow flow and low TDR habitats. Mean energy stored in the hyporheic POM was 163.4 kJ dm^{-3}. While least abundant in mass, coarse POM represented the majority of organic matter energy stock. Coarse particles accumulated more at fast flow habitats and finer particles accumulated more at slow flow habitats. We propose that fast flow partly flushes small particles and partly macroinvertebrate fauna ingests and converts them to larger particles (fecal pellets) and transports them to the hyporheic zone. Collector gatherers dominated the assemblages (76%) and as passive filterers (4%) they thrived at fast flow sites. Grazers were the second dominant feeding guild (14%) and were more abundant at slow flow sites. Surface flow and predation pressure were the most important controls of hyporheic assemblage structuring. POM content was not as important. We propose that in the stable, non-moving tufa hyporheic zone food is plenty for the scarce fauna so macroinvertebrates are more reactive to predatory pressure. Moog's functional feeding guild allocation system, while more complex, proved more suitable for our analyses than classification system derived from Cummins'.

Introduction

The hyporheic zone is metabolically connected with the surface habitats but functionally isolated from their primary production, so particulate organic matter (POM) is an energetic basis for animals dwelling in the interstices (Boulton et al., 2010). Deposition of organic matter detritus particles depends on drift forces and factors that cause flow variation (Wanner and Pusch, 2001; Cotton et al., 2006; Sertić Perić et al., 2011). Deposited POM can be buried by sediment shifting, by water force that drives small particles into the interstices or by organisms (Warren et al., 2009; Nogaro et al., 2009; Gunkel et al., 2009).

In karst areas, calcite precipitation in streams is common. The calcite deposit that encrusts all immersed objects is called tufa (Riding, 1991). Tufa does not allow for sediment movement but offers overgrowing as an additional mean of POM burial. Tufa may grow in height more than 1 cm per year. Encrusted moss stems that grow abundantly at tufa barriers subsequently die-off and are turned to detrital food source while upper, non-encrusted parts remain alive and serve as POM trapping device (Suren, 1991). Due to microbial processing of encrusted material, acidity increases locally and calcite may be dissolved. Together with subsequent decay of encrusted material, this results in a system of pores and caverns within the substrate (Chafetz et al., 1994). These can be populated by animals and/or filled with new organic particles.

Depending on its size, POM serves as a food source for different animals (Moog, 2002). The dependence of assemblage composition of macroinvertebrates on the quality and the quantity of these food sources has been thoroughly investigated both historically and recently (Hawkins and Sedell, 1981; Hoffman, 2005). Surface conditions can have a direct effect on the composition of the macroinvertebrate assemblages since, unlike POM, animals can voluntarily migrate through the layers of sediment searching for food, escaping from predators etc. (Zwick, 1996; Elser, 2001). At tufa barriers, the most important abiotic factor affecting benthic macroinvertebrate assemblages is flow velocity (Miliša et al., 2006).

The main purpose of this study was to: (1) analyze mass and energy stock of POM deposits in relation to surface flow and tufa deposition and (2) assess the factors affecting functional organization of assemblages within tufa substrate.

Since this is a specific and stable environment with largely fixed interstitial spaces we hypothesized that fine and ultrafine organic

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particles (FPOM and UPOM) would be dominant in mass over the coarse particles (CPOM). Since coarse particles are mostly plant litter that has not yet been ingested and digested, we expected CPOM to be a more pronounced part of organic matter energy stock. We expected CPOM to exhibit the opposite pattern of deposition compared to FPOM and UPOM, i.e. more CPOM at fast flow because fast currents provide more particles and moss architecture suites best for retaining CPOM. Due to the stable nature of this hyporheic zone we hypothesized that food sources would be a stable resource and that the importance of predatory pressure (as a top-down control mechanism) would have an increased importance compared to the POM stock (as a bottom-up control mechanism) in structuring hyporheic assemblages. Since surface flow positively affects benthic macroinvertebrates abundance, and many benthic organisms migrate to the hyporheic zone we expected that surface flow would positively affect hyporheic macroinvertebrate abundance as well.

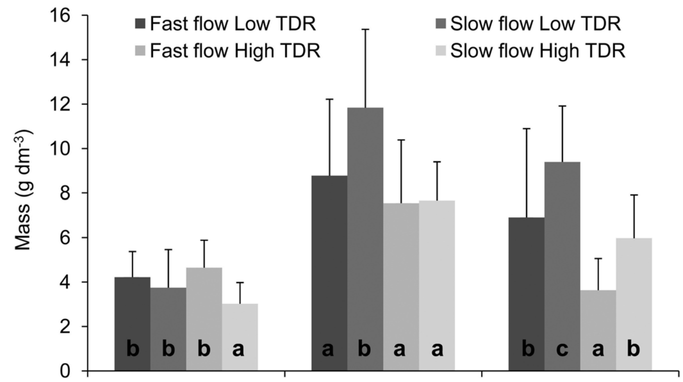

Fig. 1. Mass content (mean + SD) of three size classes of POM at four study sites. Letters denote Tukey test derived homogenous groups i.e. different letters symbolize significant differences in content of POM size classes among the sites.

Methods

Study site and sampling protocol

This study was conducted at two tufa barriers at lake outlets of Plitvice Lakes (see details in Miliša et al. (2006) and Miliša et al. (2010). The barriers are characterized by well-developed submerged bryophyte vegetation of species: *Pellia calycina* (Tayl) Nees, *Cratoneurum commutatum* (Hedw.) Roth, and *Brachythecium rivulare* (Br.) Br. We have set up our sampling design considering that the hyporheic zone in the stable tufa substrate exhibits hysteresis toward surface conditions of water flow and tufa deposition rates (TDR): The fauna being more dependent on current surface condition and POM stock being mainly dependent on prevailing (mean) conditions over a longer period of time.

The low TDR site had at least two times lower TDR than the high TDR site at all times (Miliša et al., 2010). At each site sampling was done at two habitats with different flow conditions: high flow velocity – with flow velocity higher than 70 cm s^{-1} at all times and low flow velocity – with flow velocity lower than 60 cm s^{-1} at all times; measured with Dostmann Electronic P670 flow meter. In total four sampling sites were chosen to combine high and low TDR with high and low flow.

We used a core sampler with 5 cm diameter to extract 6 cm thick triplicate samples of substrate from depth of 4–10 cm in monthly intervals on 12 sampling dates. This depth was chosen because moss mat thickness can vary in height among sites so full tufa encrustation at all sites is found at 4 cm. Below 10 cm virtually no animals occur (Miliša et al., 2006). In total we have obtained 48 triplicate samples (4 sampling habitats × 12 sampling dates).

The macroinvertebrates were separated from the samples using a stereomicroscope (Zeiss Stemi 2000). Then, samples were sieved through two nets (1 mm and 50 μm mesh size) resulting in three size categories: coarse (>1 mm; CPOM), fine (1 mm to 50 μm; FPOM) and ultra-fine (<50 μm; UPOM) particles. Separated size categories were dried at 104 °C, weighed, ashed at 400 °C and reweighed, the difference providing ash-free dry mass (AFDM). The mass of each size-category AFDM was expressed as mass per volume of substrate (AFDM g dm^{-3}).

Fauna was counted and indentified to the lowest taxonomic level that allowed the categorization to functional feeding guilds (FFG) according to Moog (2002). Moog (2002) FFG allocation system does not allocate all individuals of a taxon solely and exclusively to one single FFG. Rather it recognizes that: (i) individuals of each taxon may feed using more strategies and more resources but also, (ii) they may switch their feeding habits according to the stage in their life cycle and habitat conditions. The FFG data was expressed as a mean number of individuals per volume of substrate (I dm^{-3}).

Additional triplicate samples were taken during each season for the energy content analysis (36 triplicate samples in total). Samples were treated with 18% HCl to remove calcite and washed in running water. Then the organic matter was sieved and dried as described above and the size categories were burnt using IKA 2000 calorimeter. The energy content of the respective size category was calculated as a mean of all samples and expressed in kilojoules per gram of respective size category of POM (kJ $g_{(dr\ matter)}{}^{-1}$).

Data analyses

Our sampling design allowed us to treat our study site conditions as categories (factors) in terms of TDR and flow. To remedy the possibility that samples may be considered pseudoreplicates, we used repeated measures analysis of variance (ANOVA) with post hoc Tukey test performed where significant difference among the four combinations of studied categories were found.

Additionally, we performed detrended canonical correspondence analysis (DCCA) to explore which of the environmental data affected abundances of different FFGs. For these analyses we considered predatory pressure as a factor controlling abundances of other FFGs. So we performed DCCA on 48 data points for 5 FFGs and 7 environmental factors. Statistica 9.1 (Stat Soft Inc, 2010) was used to carry out ANOVA and Canoco for Windows 4.02 (ter Braak and Smilauer, 1999) was used for DCCA. All data was log transformed.

Results

Mass standing stock

Higher average amount of total POM was found at sites with low TDR. The most total POM was found at the habitat with slow flow (peak for both FPOM and UPOM). Mass of POM at this site was significantly higher than at other three sites and this habitat was separated from others by Tukey HSD post hoc test. At habitat with the opposite conditions (fast flow and high TDR) the deposited amounts were the lowest (Table 1).

Analysis of variance showed that flow and TDR conditions affected all size categories of POM differently (Table 2). Flow velocity was the significant factor for CPOM deposits and significantly more CPOM was found in the hyporheic zone at fast flow habitats (Fig. 1). For FPOM and UPOM deposits significant differences were found between both TDR and flow (Table 2).

The lowest mass of CPOM was deposited in the hyporheic zone of the site with slow flow and high TDR, while its amounts were similar at the other three sites (Fig. 1). More CPOM was deposited at fast flow sites, but the difference was statistically significant only at high TDR (post hoc Tukey test $p = 0.032$). FPOM was significantly