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The metabolism of organic matter in the hyporheic zone of a mountain stream, and its spatial distribution

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Abstract

Community respiration in hyporheic sediments (HCR) was studied in a characteristic riffle-pool-sequence of a mountain stream. HCR activity at the riffle site strongly exceeded that at the corresponding pool site with a mean ratio of 5.3. The vertical distribution of HCR activity was homogeneous in the pool, while there was a distinct maximum in the uppermost layer in the riffle. Similarly, the spatial distribution of certain fractions of particulate organic matter (POM), and their turnover, was largely determined by stream morphology. Mean annual HCR per unit area of stream bed was estimated as 1.71 g O_2 m^{-2} d^{-1}. Hence, HCR contributes significantly to total heterotrophic activity in streams, thus enhancing the relative importance of heterotrophic processes in running waters containing hyporheic zones.

Introduction

The running waters of the world transport a total load of about 1 billion (10^9) tons of total organic carbon (TOC) per year towards the sea. About 60% of this is dissolved organic carbon (DOC), with the remainder particulate organic carbon (POC) (Eisma, 1993). This organic matter constitutes a potential basis for heterotrophic activity in running water ecosystems. The extent of the biological utilization of resource is still a topic of discussion. While some authors stress the function of running waters as transport systems (Winterbourn, 1986; Winterbourn & Townsend, 1991), others emphasise the importance of biological processes for the balance of nutrients in running waters (Cummins *et al.*, 1983; Paul *et al.*, 1989; Triska *et al.*, 1989).

In non-polluted highland streams, biological decomposition of organic matter takes place nearly exclusively in association with the surfaces of sediment particles (Minshall *et al.*, 1983; Naiman *et al.*, 1987; Paul *et al.*, 1989). These are generally covered by a microbial biofilm (e.g. Bärlocher & Murdoch, 1989). In order to assess the degradation rate of organic matter, chamber techniques have been used to measure heterotrophic activity in the benthic zone of various streams (e.g. Bott *et al.*, 1978, 1985; Naiman *et al.*, 1987; Paul *et al.*, 1989; Hedin, 1990).

However, many streams run within an alluvial floodplain including a deep layer of unconsolidated sediments below the stream bed. These hyporheic sediments are connected with the surface waters by vertical water exchange, and may be densely populated by interstitial fauna (Schwoerbel, 1961; Hynes, 1983; White *et al.*, 1987). Grimm & Fisher (1984) were the first to show that the hyporheic zone contributes significantly to the metabolism of stream ecosystems: They found that, in a desert stream in Arizona, hyporheic community respiration (HCR) was about equal to benthic community respiration. They stated that "exclusion of deep sediment respiration gives an erroneous picture of desert stream metabolism", and recommended that future investigators include deep sediments in models of stream metabolism.

The activity of HCR in a single layer within the hyporheic zone of a temperate stream, and its seasonal variation, was reported by Pusch & Schwoerbel (1994). Pusch (in press) examined the coupling of heterotrophic activity with hydraulic properties of stream sediments. The present paper shows the spatial extension of heterotrophic activity in the hyporheic zone. Additionally, the data on temporal and spatial variation of HCR are combined, so that overall HCR activity of the stream can be estimated.

Materials and methods

Study site

The study was conducted in a third order reach of the Steina (47° 47′ N, 8° 19′ E), a soft water mountain stream in the Black Forest, southern Germany. In a distance of about 9 km from the source, the stream channel has a mean gradient of 1.6%, and is approximately 4.5 m wide. It cuts about 1 m into the approximately 100 m wide alluvial floodplain, which is mostly vegetated by pastures and riparian trees. Mean discharge was 0.64 m^3 s^{-1} (years 1986–1988, 1990, 1991), and mean water temperature was 7.8 °C (years 1986–1988; Meyer *et al.*, 1990). The sediments consist of gneiss and sandstone, with occasional calcareous particles. They are poorly sorted, with the coarse sediment fractions 16–63 mm (sieve analysis) and that >63 mm (rough estimation) constituting 25% of hyporheic sediments, respectively. Stream morphology is characterised by sequences of riffles and pools, the latter occurring with mean intervals of 73 m (N = 7). The sparsely-populated watershed is used for forestry and some stock farming. For further details on the Steina see Meyer *et al.* (1990), Pusch (1993), and Pusch & Schwoerbel (1994).

Table 1. Base flow characteristics of the riffle and pool sections of the Steina studied. Water depths and flow velocities are means of 24 measurements on one transect. Velocities are averages of one measurement at the surface and one near the bottom

	Riffle	Pool
Gradient of water surface [%]	1.8	<0.1
Mean (maximal) water depth [cm]	7 (16)	29 (40)
Mean flow velocity [cm s^{-1}]	7.6	1.3
Wetted cross-sectional area [m^2]	0.34	1.15
Percentage of stream length [%]	80	20

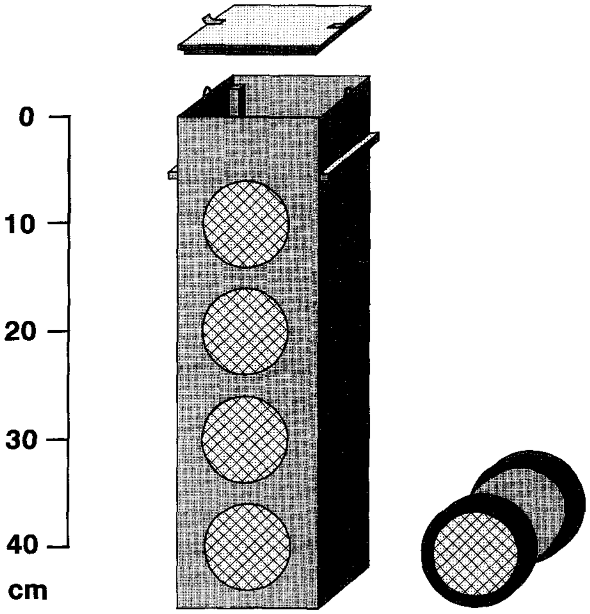

Fig. 1. Vertical incubation container for exposure of sediment pipes, and a single sediment pipe.

Sampling procedure and respiration measurements

Natural sediment from the Steina was dried and sieved into particle size fractions of 1–2 mm and 2–4 mm, which served as quasi-natural substrata. Polyvinyl chloride pipes (15 cm in length, 8 cm in diameter, 0.754 dm^3 volume) were filled with one or other sediment fraction, and the ends closed by nylon mesh of 1 mm mesh size; the pipes were fully described by Pusch & Schwoerbel (1994).

In order to study the vertical distribution of HCR in the hyporheic zone, four pipes each were inserted vertically into incubation containers (Fig. 1), which were buried in the stream bed. Incubation containers had four openings on two opposite sides, and when in use were 10, 20, 30 and 40 cm beneath the sediment surface. The openings provided contact between sediment pipes and hyporheic sediments. The long axes of the sediment pipes were parallel to the longitudinal axis of the stream. As longitudinal flow velocity in the hyporheic zone was much higher than that in vertical direction (Pusch & Schwoerbel, 1994), it is assumed that the interstitial flow of water through the pipes was not obstructed much by that design. Six vertical incubation containers were buried in a riffle, and six more were buried in a pool 20 m upstream (Table 1, Fig. 2). In total, 48 sediment pipes were set out, among them 24 containing particles of each size.

By using these vertical incubation containers, the surrounding hyporheic sediments did not have to be disturbed when retrieving pipes for measurements. In order to ensure that biological colonization of buried sediments matched that in undisturbed sediments (cf. Rounick & Winterbourn, 1983; Stock & Ward, 1989), the pipes were incubated for more than a year (16 and 20 months). Unfortunately, during that period some fine POM accumulated in the hollow space of several vertical incubation containers in the riffle section. Although the sediment samples themselves were not in direct contact with this POM (cf. Fig. 1), some sediment pipes at the lowermost depth (40 cm) might have been affected somehow by this occurrence.

After exposure, the sediment pipes were retrieved and inserted into a portable device used for measuring HCR. This device simulated the continuous flow of water through hyporheic sediments, with a flow rate close to that found *in situ* (Pusch & Schwoerbel, 1994). Half the pipes were retrieved in spring (21 March to 5 May) when discharge was close to average, and stream water temperature 5 °C. The other half were retrieved in summer (15 August to 11 September), at base flow conditions when stream temperature was 16 °C. During the measurements, which took several hours for each pipe, the concentration of dissolved oxygen within the measuring device declined continuously. This provides a measure of the respiration activity of the sediment biota.

Processing of samples after incubation

After termination of HCR measurements, the organic content of sediments was analysed. Particulate organic matter (POM) was determined separately: POM which was loosely associated with the sediment (LAPOM), and the POM fraction which remained on rinsed sediments i.e. the POM fraction strongly associated with the sediment (SAPOM). The latter was determined by combusting the sediments in a muffle oven for 4 h at 550 °C. The LAPOM fraction was removed by thoroughly agitating and rinsing the sediments. The resulting suspension was then filtered on glass fiber filters, which were then combusted for 2 h. In the LAPOM fraction, the protein content was determined with the biuret method according to Rausch (1981), using bovine serum albumine as a standard. Extraction of protein from POM was done by filling a POM subsample corresponding to about 1 mg of ash-free organic matter into a test tube. Protein was then extracted in 0,5 n NaOH two times at 80 °C for 10 min, and once at 100 °C for 10 min. All POM values are given as ash-free dry mass. Parallel to the removal of POM from sediments, macro- and meiofauna was separated using a 100 μm gauze screen.

Calculations

HCR and POM values were converted to carbon equivalents assuming a respiratory quotient of 0.85 (Bott & Kaplan, 1985) and 40% carbon content of organic matter (Cahill & Autrey, 1987). The theoretical turnover rate of carbon, k [yr^{-1}] (Fisher, 1977), was calculated as the ratio of the respiration rate [$\mathrm{g\ C\ dm^{-3}\ yr^{-1}}$] to the standing stock of POM [$\mathrm{g\ C\ dm^{-3}}$] (Minshall *et al.*, 1993; Naiman *et al.*, 1987). The respiration rate of the hyporheic fauna at ambient temperature in the hyporheic zone was estimated using the equations given by Lampert (1984) for meiofauna, and following to M. Kussmaul (unpubl. results) for macrofauna, using a Q_{10} value of 2. Analysis of variance was performed on original data using the GLM procedure of SAS software (SAS Inst., 1987). Data were not transformed before ANOVA, but the main effects would be identical if data were subject to log-transformation. For further details on methods see Pusch (1993) and Pusch & Schwoerbel (1994).

Extrapolation of the original results for HCR activity and related parameters to a unit area of stream bed involved a 3-step calculation:

- First, the vertical distribution of HCR was taken into account. The mean values for HCR over the whole profile at the riffle site were compared to the data on seasonal HCR activity at 30 cm (25 to 35 cm) sediment depth, which were reported by Pusch & Schwoerbel (1994). Thus, a 'vertical ratio' was calculated as the ratio between the mean activity in the whole profile and that at a specific depth within the sediment (Table 2). On this basis, mean annual HCR at 25 to 35 cm sediment depth was extrapolated to a hyporheic sediment layer 5 to 45 cm deep.
- Next, horizontal variability of HCR was taken into consideration. A weighted mean of the HCR activity in the riffle and the pool sections was calculated according to the respective proportions of each in stream length (80% riffle, 20% pool). A 'topographic ratio' was calculated as the ratio between HCR activity in the riffle and that in the pool site (cf. Table 2).
- Finally, the percentage of sediments that actually contributed to the formation of interstitial pore

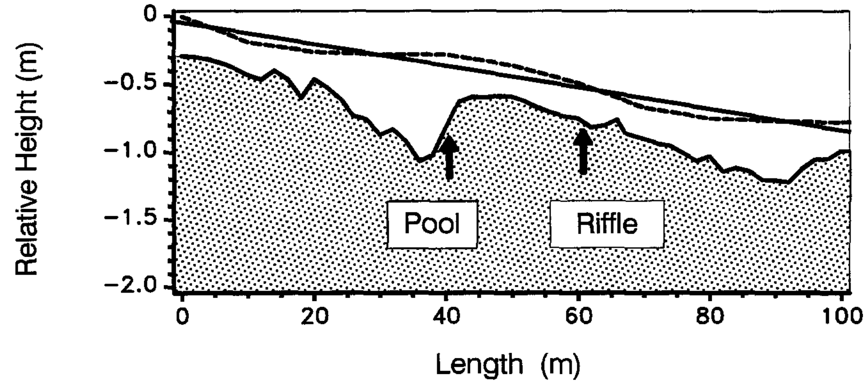

Fig. 2. Longitudinal section through the riffle-pool-sequence of the Steina in the reach studied. Relative heights of the stream bed and of the water table, and the mean gradient (regression line) of the water table are shown. Arrows indicate the locations of vertical incubation containers in riffle and pool sections.

space in the stream bed, and thus enabling HCR activity, was estimated. It was assumed that the coarse 'skeleton' fraction >16 mm hardly contributed to metabolic activity. Consequently, the calculated values for HCR and the other parameters (cf. Table 2) were finally reduced by 50% (cf. description of study site).

Results

Hyporheic community respiration (HCR)

HCR was much higher in the riffle than in the pool: Mean values differed by a topographic ratio of 7.2 in spring, and 3.4 in summer (Table 2, Fig. 3a). In the pool, the vertical distribution of HCR was very homogeneous. Activity averaged there at 0.07 mg O_2 dm^{-3} h^{-1} in spring, and 0.20 mg O_2 dm^{-3} h^{-1} in summer. In the riffle, however, highest activity was measured in the uppermost layer, which was followed by a sharp decline with a minimum at 20 cm sediment depth. HCR minima were less than half the respiration values measured at 10 cm (Wilcoxon Signed Rank Test, $p < 0.05$). At greater depths within the riffle bed, HCR activity increased again. HCR in the riffle averaged at 0.47 mg O_2 dm^{-3} h^{-1} in spring, and 0.67 mg O_2 dm^{-3} h^{-1} in summer. Unfortunately, HCR activities at the lowermost depth in spring may not be reliable because of POM accumulation in the incubation containers (cf. methods).

In order to enable a direct comparison to be made between HCR profiles obtained in spring and summer, seasonal values were adjusted to a temperature of

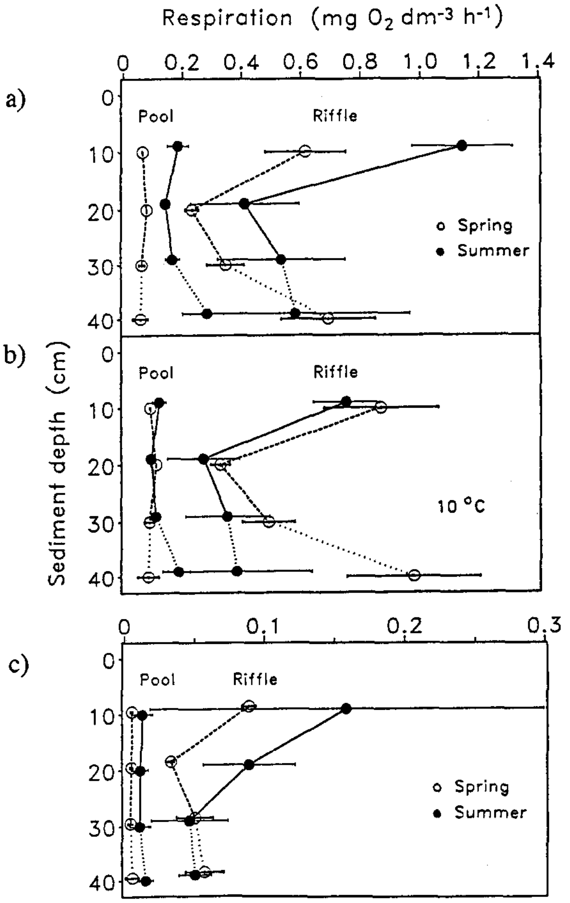

Fig. 3. Vertical distribution of hyporheic community respiration (HCR) (means ± 1 standard error) a) at ambient temperatures; b) standardized to a uniform temperature of 10 °C; c) respiration of hyporheic fauna at ambient temperatures.

Table 2. Summary of carbon metabolism measurements in the Steina: For each parameter, means ± 1 SD for standard sediment volumes of 1 dm^3 are given for riffle and pool sites. For the definitions of 'topographic ratio' and 'vertical ratio' see methods. The annual mean is for the hyporheic zone (5 to 45 cm depth) beneath a standard 1 m^2 of streambed. In the annual mean column values for HCR and faunal respiration are g O_2 m^{-2} d^{-1}

	Riffle [dm^{-3}]	Pool [dm^{-3}]	Topographic ratio	Vertical mean [m^{-2}]	Annual mean [m^{-2}]
Total POM [g]			1.43	1.01	2107
Spring	9.5±1.9	7.6±1.0			
Summer	9.0±1.7	5.6±1.1			
SAPOM [g]			1.08	0.97	1953
Spring	6.7±1.0	7.1±1.0			
Summer	6.3±0.7	5.2±1.0			
LAPOM [g]	2.8±1.3	0.47±0.17	5.74	1.11	171
Protein within LAPOM [g]	0.45±0.21	0.03±0.02	12.90	1.13	21.1
Protein within LAPOM [%]	16.2±2.4	7.3±2.7			
HCR [mg O_2 h^{-1}]			5.28	1.30	1708
Spring	0.47±0.28	0.07±0.02			
Summer	0.67±0.40	0.20±0.09			
Faunal respiration [mg O_2 h^{-1}]	0.067	0.010	9.02	1.50	72.5
Carbon turnover rate [yr^{-1}]			3.78	1.29	0.236
Spring	0.334±0.15	0.061±0.016			
Summer	0.507±0.310	0.245±0.104			
Carbon turnover rate for LAPOM [yr^{-1}]			0.93	1.20	2.91
Spring	1.22±0.49	0.89±0.35			
Summer	1.76±0.96	3.54±1.75			

10 °C, using a Q_{10} value of 2 (cf. Pusch & Schwoerbel, 1994). The standardized depth profiles of HCR for spring and summer were very similar (Fig. 3b).

The hyporheic fauna contributed on average 7.9% of HCR in the pool, and 14.5% in the riffle. This percentages varied little with depth, so the vertical distribution of faunal respiration rates closely resembled that of HCR (Fig. 3c).

Relative importance of physical factors

In order to obtain an overview of the relative importance of physical factors controlling the spatial distribution of HCR, the data on HCR and related parameters were subjected to variance analysis. Stream-bed topography, sediment particle size, season, and sediment depth were used as independent variables (Table 3). Stream-bed topography had a very significant effect on HCR and most other parameters, especially the LAPOM fraction, the protein content within LAPOM fraction, total POM (sum of SAPOM and LAPOM fractions), and the theoretical turnover rate of carbon *k* (Table 3). These parameters reached much higher values in the riffle than in the pool (Table 2). The most pronounced differences between riffle and pool were found for LAPOM and protein content, faunal respiration and HCR. These parameters reached topographic ratios of more than five (Table 2). HCR decreased significantly with depth, whereas sediment particle size had no detectable effect (Table 3).

Because of the higher stream temperature, HCR and *k* values were significantly higher in summer than in spring (Table 2, 3). It is noteworthy that in the time period from April to August HCR increased much more in the pool than in the riffle. In contrast to HCR, the respiratory activity of the fauna did not increase from spring to summer. In summer, the higher individual respiration rates of individuals were countered by lower biomass (Pusch, 1993).

Particulate organic matter

A previous study had shown close correlations between HCR and the sediment content of LAPOM, particular-

Table 3. Variance analysis of HCR and related parameters (N = 48). Independent variables were SEASON of sampling (spring or summer), sediment DEPTH (10–40 cm), stream TOPOGRAPHY (pool or riffle), and particle SIZE of sediments (1–2 or 2–4 mm), including their first-degree interactions (cross effects), if significant. Positive effects (+) are defined as follows: higher values in summer, in greater depth, in riffle and in coarser particle size. Significance levels are $+ = p < 0,05$, $++ = p < 0,01$, $+++ = p < 0,001$, $++++ = p < 0,0001$; for negative effects (−) and interactions (*) correspondingly.

Parameter	Season	Depth	Topography	Particle size	Topogr. and season	Topogr. and size	Season and size
Total POM	− −		+ + ++		*	*	
SAPOM	− −				*		
LAPOM		− −	+ + ++			**	
Protein within LAPOM		− −	+ + ++			*	
HCR	+ + ++	− −	+ + ++		**		
Faunal respiration			+ + ++	+		*	*
Carbon turnover rate k	+ + ++	−	+ + ++		* * *		
Carbon turnover rate for LAPOM k_{LAPOM}	+ + ++				**		

ly with the protein fraction within LAPOM (Pusch & Schwoerbel, 1994). Corresponding to these findings, the spatial distribution of LAPOM closely resembled that of HCR (Fig. 4a). Similar to HCR, the sediment content of LAPOM differed considerably between riffle and pool. Hyporheic sediments in the riffle contained a mean of 2.8 g dm^{-3}, whereas the value for the pool was 0.47 g dm^{-3}. The content of LAPOM at the lowermost sediment level (40 cm) in spring may have been overestimated somewhat due to the POM accumulation in the incubation container (cf. methods). The mean standing stock of LAPOM within the hyporheic zone was 171 g m^{-2} and clearly exceeded the mean standing stock of benthic LAPOM in the Steina, which was estimated at 50–100 g m^{-2} (unpubl. results).

The spatial distribution of LAPOM-protein was very similar to that of the LAPOM fraction itself (Fig. 4b). Since protein content of LAPOM was higher in riffle than pool (Table 2), protein showed relatively greater spatial inequality than the LAPOM fraction itself: it differed between riffle and pool by a topographic ratio of nearly 13:1. In contrast, the sediment content of the SAPOM fraction, showed only minor spatial variation (Fig. 4c). However, in the pool it decreased significantly (Wilcoxon Rank Sum Test, $p < 0.01$) from spring to summer (by 27%), whereas it remained nearly constant in the riffle.

Turnover rates

The mean theoretical turnover rate of carbon (k) ranged between 0.06 yr^{-1} in the pool (spring) and 0.51 yr^{-1} in the riffle (summer). Like HCR, k had a nearly homogeneous vertical distribution in pool, but sharply declined in riffle (Fig. 4d).

The close correlation between HCR and LAPOM content of sediments (Pusch & Schwoerbel, 1994) indicates that this POM fraction may serve as the main substrate for heterotrophic activity. Therefore, the mean theoretical turnover rate has been recalculated on the basis of the LAPOM content of sediments. Of course, these values (k_{LAPOM}) were much higher than those for k and usually exceeded unity (Table 2). In spring, the turnover of LAPOM in the riffle was faster than in the pool, with the reversed situation in summer (Table 2). The values for k_{LAPOM} showed nearly homogeneous vertical profiles in spring (Fig. 4e). In summer, k_{LAPOM} reached four times higher values in the pool, but increased to a lesser extent in the riffle. Especially at sediment depths of 20 to 40 cm, the values for LAPOM turnover remained nearly at their spring level. Hence, k_{LAPOM} was the only parameter investigated that ever showed clearly higher values in pool than riffle. As for HCR, turnover rates did not differ significantly between sediment particle sizes of the samples (Table 3).

HCR per unit area of stream-bed

The annual average of HCR activity at a sediment depth of 30 cm in riffle sections of the Steina was given by Pusch & Schwoerbel (1994). Based on these data, and those for spatial variation of HCR reported here, the average HCR activity per unit area of the stream bed (5 to 45 cm depth) in the Steina was estimated (Table 2).

The mean annual value for HCR in the Steina was estimated as 1.71 g O_2 m^{-2} d^{-1} = 0.545 g C m^{-2} d^{-1}, equivalent to a decomposition rate of organic matter of 497 g m^{-2} yr^{-1}. This means a carbon turnover rate (k) of 0.24 yr^{-1} (Table 2). However, if only the LAPOM fraction was subjected to degradation, POM would be depleted after 4 months (equivalent to a k_{LAPOM} value of 2.9 yr^{-1}). The annual means of HCR in the riffle and pool were 2.04 and 0.39 g O_2 m^{-2} d^{-1}, respectively. Mean respiration rate of the hyporheic fauna >100 μm was 0.0725 g O_2 m^{-2} d^{-1}. Thus, meio- and macrofauna contributed only 4.2% of total hyporheic respiration activity.

Discussion

Hyporheic community respiration

The metabolism of organic carbon can be characterised in every ecosystem by the level of physical import–export fluxes on one side, and the intensity of autotrophic and heterotrophic metabolism of organic matter on the other. Additonally, changes in the standing stock of organic matter have to be considered (Fisher, 1977; Cummins *et al.*, 1983; Minshall *et al.*, 1983; Naiman *et al.*, 1987). Studies of ecosystem metabolism in high-gradient streams and rivers depend on techniques using closed chambers (Bott *et al.*, 1978). The sediment pipe technique used in this study can be regarded as the hyporheic counterpart of the benthic chamber technique widely used for the measurement of benthic metabolism (e.g. Bott *et al.*, 1985; Hedin, 1990).

Up to now, the contribution of the hyporheic zone to the carbon metabolism of streams has been largely ignored, except by Grimm & Fisher (1985). They measured HCR activity in a warm-water desert stream (24 to 31 °C) and obtained a value of 3.5–4.7 g O_2 m^{-2} d^{-1}. The value obtained for the stream in the temperate zone (1 to 16 °C) in the present study (1.7 g O_2 m^{-2} d^{-1}) is two to three times lower. As HCR is strongly temperature-dependent (Pusch & Schwoerbel, 1994), the higher level of HCR in the desert stream can be readily explained, although other differences in the general features of both streams could have the same effect.

The estimate of mean HCR in the Steina is within the range of values for community respiration of benthic sediments in comparable, temperate streams (0.2 to 6 g O_2 m^{-2} d^{-1}; Bott *et al.*, 1985). Accordingly, the mean turnover rate of POM (k) within the hyporheic zone in the Steina (Table 2, Fig. 4e) was in the same range as estimates for benthic POM in woodland streams (~0.1 yr^{-1}; Hedin, 1990).

However, some things indicated that the HCR level measured in this study might be somewhat underestimated:

- The measurement device consisted of a recirculating system, so that there was no renewal of water during measurements. Consequently, no supply of fresh, easily degradable DOM, or other nutrients was available to the microbiota, as might occur in hyporheic sediments *in situ*.
- The hyporheic zone probably extends vertically to greater sediment depths than the 45 cm maximal depth that was investigated in this study.
- Studies on organic matter (OM) metabolism in streams are influenced by discharge history (Cummins *et al.*, 1983). The HCR estimate for the Steina given here was for a year in which an extraordinarily high spate occurred. It seems likely that HCR activity in this year was unusually low (Pusch & Schwoerbel, 1994). The recovery of meio- and macrofauna after that spate apparently was even slowlier than that of microbiota: The percentage of faunal respiration in total HCR was significantly higher in 1992 (13.4% ± 9.4 at 30 cm within the sediment at the riffle site) compared to an average of 4.3% ± 2.0 in 1990/91 (Pusch & Schwoerbel, 1994; Wilcoxon Rank Test, $p < 0.001$). The temporal increase of the contribution of hyporheic fauna to total community respiration clearly indicates a successional process in the hyporheic zone.

Additionally, there is a fourth aspect which might have influenced HCR levels: In this study measurements were performed using sieved sediments, whereas in the hyporheic zone of the Steina the sediments are highly mixed. However, the two particle size classes used did not have significant effects on HCR activity or turnover rates (Table 3, cf. also Pusch & Schwoerbel, 1994). Furthermore, natural stream sediments contain

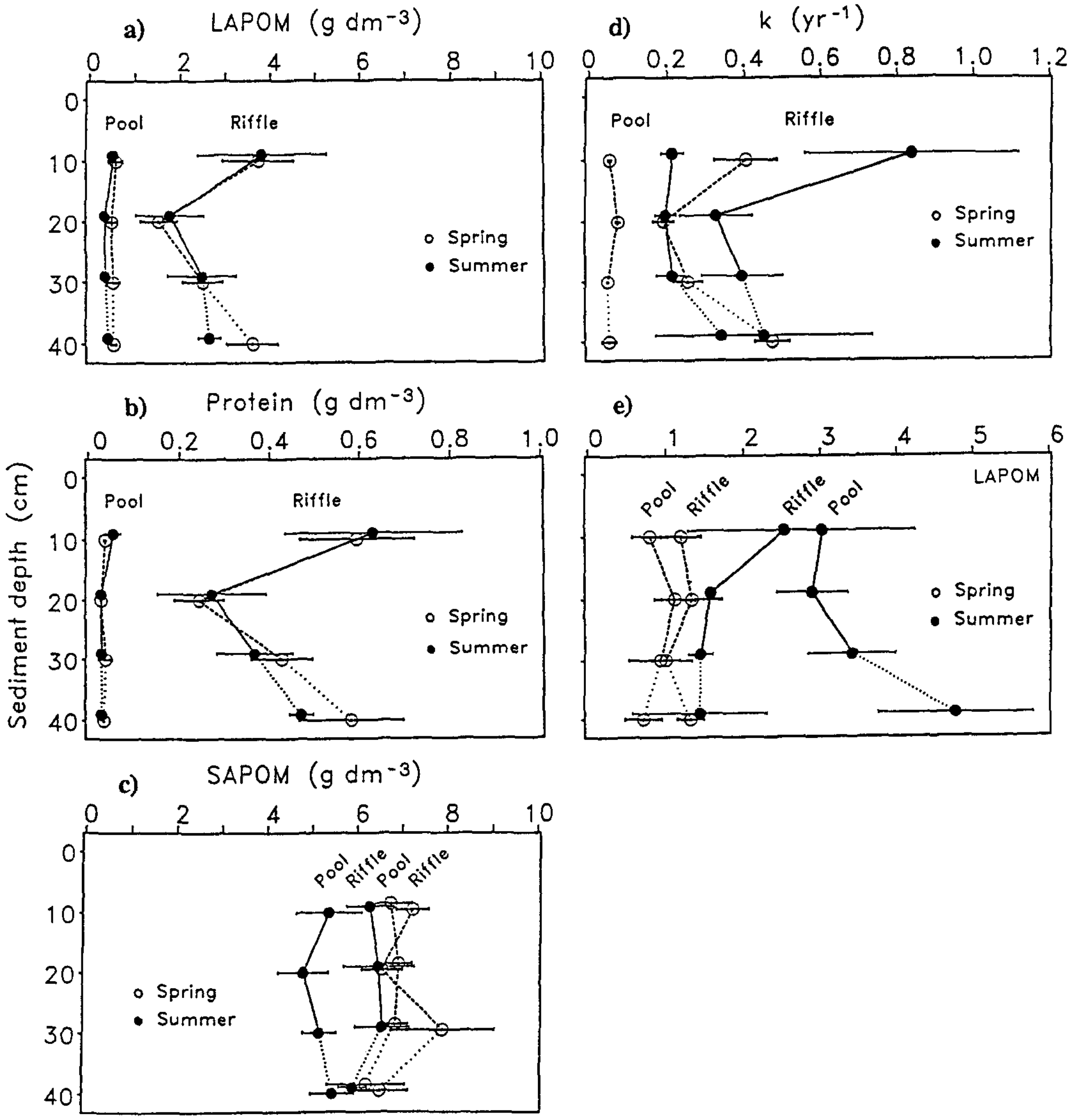

Fig. 4. Vertical distribution of organic matter parameters in the hyporheic sediments of the riffle and pool sites in spring and summer (means ± 1 standard error). a) Loosely associated particulate organic matter (LAPOM); b) Protein within the LAPOM fraction; c) Strongly associated particulate organic matter (SAPOM); d) Theoretical turnover rate of carbon, k; e) Theoretical turnover rate of carbon for LAPOM, k_{LAPOM}.

pieces of very coarse POM (i.e. twigs, branches) which are buried during spates (Metzler & Smock, 1990), and were not included in my sediment samples.

Results from a calcareous stream of similar size (Oberer Seebach, Austria), which was sampled with the freeze-core technique (Leichtfried, 1988), indicate that the results obtained with sieved substrates were close to the levels of the surrounding sediments. The total amount of POM in the hyporheic zone (5 to 45 cm sediment depth) of the Steina (2107 g C m^{-2}, cf. Table 2) is well within the range reported for the Oberer Seebach (1550–3320 g C m^{-2} TOC from 0 to 60 cm sediment depth). A comparable amount of subsurface detritus (1920 g C m^{-2}) was reported by Metzler & Smock (1990, recalculated) for a first-order, fully canopied blackwater stream at 0 to 20 cm sediment depth.

Balance of organic matter

The amount of total hyporheic POM could theoretically support HCR activity for more than four years.

However, the standing stock of total POM, and also the LAPOM fraction, showed no detectable seasonal variability (Pusch & Schwoerbel, 1994), despite intensive degradation activity at the riffle site. Hence, it can be concluded that a continuous supply of organic matter is being made available to the hyporheic zone. Indeed, Metzler & Smock (1990) showed that POM can be transported into subsurface sediments during mean discharge conditions even in a sand-bottomed stream. If it is presumed that the sediment content of POM is in a steady state, the rate of input of OM into the hyporheic zone will correspond to the rate of degradation of organic matter within this layer at least. Consequently, hydrologic transport of POM should be higher in the hyporheic zone of riffle sections than in pool sections. This agrees with the higher hyporheic flow velocities in the riffle compared to the pool site (Pusch, 1993). In the pool, the relatively high values for k and k_{LAPOM} in summer, and the significant decrease of SAPOM in summer (Fig. 4c, d, e) might be interpreted to indicate the limitation of HCR by insufficient supply.

In reality, hydrological transport of POM not only regenerates metabolised substrates in a specific quantum of hyporheic sediments, but additionally effects a permanent dislocation of POM. Hence, the biological turnover in the hyporheic zone is paralleled by the physical throughput of POM, as in the benthic zone (Cummins *et al.*, 1983; Minshall *et al.*, 1983). However, flow velocities in the hyporheic zone were about 1000 times lower than in surface waters (Pusch, 1993). Thus, the residence time of POM within a given stream section must be much higher in the hyporheic zone than the benthic zone, since POM dynamics will not be as dominated by the hydrological regime.

Considering the complex spatial structure of hyporheic biofilms in the Steina (Pusch, 1993), it may be hypothesized that POM fractions with differing degree of association to sediment surfaces (e.g. LAPOM and SAPOM) are transported with different velocities. As LAPOM probably forms a preferential substrate for heterotrophic organisms, hydrological transport velocity and biological turnover rate are probably correlated within POM fractions.

Horizontal distribution of HCR

Stream morphology affected the horizontal distribution of the parameters that were investigated in different ways. Total POM varied relatively little between riffle and pool, but was processed much faster at the riffle than at the pool site. The higher metabolic rate in the riffle may be explained in a proximate sense by the higher LAPOM and protein contents there. However, as indicated by the respective interactions in the variance analysis (Table 3), the effect of stream morphology on HCR and turnover rates was significantly modulated by a parameter related to season. It is likely that, besides morphology, seasonal changes in hyporheic hydraulics constitute a second ultimate factor determining spatial distribution of HCR, as discussed by Hendricks (1993) and Williams (1993).

Stream-bed sediments are able to trap particulate organic matter (POM) by the downward flow of stream water (White *et al.*, 1987; Williams, 1993). Additionally, dissolved organic matter (DOM) is supplied both by epigeic and hypogeic pathways (cf. Rutherford & Hynes, 1987; Fiebig & Lock, 1991). Knowing the relative importance of these two pathways is fundamental to understanding the total OM balance of the hyporheic zone. It also forms a basic question for the understanding of hydraulic links and energetic dependencies between soil, phreatic zone, hyporheic zone, and both benthic and pelagic zones of running waters (Hendricks, 1993). The results of the present study give some background on the relative utilization of different POM fractions in the hyporheic zone:

- In the hyporheic zones of the Steina, close correlations were found between HCR and both LAPOM-protein and LAPOM (Pusch & Schwoerbel, 1994). As POM can't originate in groundwater, it must have been supplied by surface waters. This indicates an important energetic link between the epigeic and hyporheic zones of the stream primarily at the riffle site, which is possibly created by microspatial variation of hydraulic head (cf. Williams, 1993).
- HCR activity was much higher in the riffle than the pool. Differences in the hydraulic heads at these sites indicate that the sampling site in the pool should be identified with a downwelling zone, and the sampling site in the riffle rather with an upwelling zone (Fig. 2). Thus, high HCR activity possibly was correlated with upwelling of hyporheic water which may have an elevated DOM concentration (cf. Hynes, 1983; Rutherford & Hynes, 1987; Fiebig & Lock, 1991). This suggests that the high HCR activity at the riffle site might have been based partially on groundwater DOM.

Vertical distribution

The vertical distributions of the sediment contents of LAPOM, and LAPOM-protein, were very similar to that of HCR activity. At the riffle site, near-surface maxima were followed abruptly by minima at 20 cm sediment depth, with the levels at greater depths inbetween. There are basically two possibilities for the formation of such concurring patterns:

- The pattern could be the result of governing hydrological and sedimentological processes that were active at the time when the stream-bed sediments were formed. In the Steina, scouring and re-sedimentation of hyporheic sediments probably occurs only during spates that have recurrence times of several decades (Pusch & Schwoerbel, 1994; Cummins *et al.*, 1983; Metzler & Smock, 1990).
- On the other hand, there was remarkable temporal constancy of the vertical distribution of parameters that are assumed to be subject to rapid metabolism (LAPOM, protein in LAPOM), a finding also made by Metzler & Smock (1990). The same was true for temperature-standardized HCR activity.

This temporal constancy indicates that the vertical profile was a consequence of governing factors which were working continuously. Possibly, the sharp decline of the LAPOM content in the riffle with sediment depth was formed because two different pathways of POM supply existed. In the uppermost LAPOM-rich layer, as discussed above, POM could be supplied by downwelling of surface water, and in deeper layers by upwelling of interstitial water.

Trophic significance for hyporheic fauna

The occurrence of considerable respiration activity in the hyporheic zone also indicates significant production of microbial biomass (Benner *et al.*, 1988; Middelboe *et al.*, 1992), which may be ingested by hyporheic detritivores (Bärlocher & Murdoch, 1989; Decho & Moriarty, 1990). Thus, the occurrence of HCR in a stream ecosystem does not solely produce a quantitative metabolic effect, i.e. an increase of the respiratory flux of organic matter. Additionally, the production of biomass by heterotrophic microbiota provides high-quality food for detritivores permanently or temporarily living in the hyporheic zone. Because of the high stability and retentiveness of the hyporheic zone, temporal shifts of this nutritional supply are relatively smooth. Accordingly, an abundant hyporheic fauna was found in the Steina (cf. Pusch & Schwoerbel, 1994), which differed sharply between the riffle and pool sites with respect of quantity and taxonomic structure (Pusch, 1993).

Significance for the Steina ecosystem

The fact that the hyporheic zones of streams contribute to their metabolism provides an important but neglected insight into the energetics of stream ecosystems. In the case of the Steina ecosystem, epigeic input of POM into the stream reaches nearly 1000 g m^{-2} yr^{-1}, about one quarter being autochthonous (Meyer & Schwoerbel, 1991). Of this moment, 497 g m^{-2} y^{-1} are respired by HCR alone. If it is assumed that benthic community respiration reaches about the same level (Grimm & Fisher, 1984; Bott *et al.*, 1985), total respiration would equal allochthonous and autochtonous inputs of POM. This would mean that, in this ecosystem, organic matter would be used very effectively by stream biota. In other words, the stream metabolism index, SMI (Fisher, 1977), that is the ratio between community respiration and organic inputs, would approach unity. Without consideration of HCR, Naiman *et al.* (1987) found that SMI closely approached unity in fifth to sixth order rivers in North America. However, since great amounts of organic matter are exported from the Steina watershed as seston (Schwoerbel, pers. comm.), there must be substantial organic inputs into the ecosystem which have not yet been identified. In the case of the Steina, these input sources might be

- DOM produced and secreted by epilithic algae (Rutherford & Hynes, 1987; Kaplan & Bott, 1989),
- the input of organic matter within the watershed during spates (cf. Cummins *et al.*, 1983),
- and DOM from exfiltration groundwater (Hynes, 1983; Naiman *et al.*, 1987; Fiebig & Lock, 1991).

Significance for stream ecology

It is evident that the metabolism of organic matter in all running waters containing hyporheic zones cannot be characterized adequately if the contribution of the hyporheic zone is ignored. The spatial extent of the metabolically active sediment layer depends largely on stream morphology, which controls benthic-hyporheic exchanges (White *et al.*, 1987; Hendricks, 1993; Williams, 1993).

With inclusion of the hyporheic zone, the ratio between heterotrophic and autotrophic processes within stream ecosystems is shifted towards heterotrophy. Consequently, the proportion of stream reaches in which autotrophic processes predominate, for example those in the middle and downstream parts of a typical river continuum (Vannote *et al.*, 1980; Bott *et al.*, 1985; Naiman *et al.*, 1987), will be smaller than formerly presumed. Likewise, the efficiency of stream ecosystems with respect to the retaining and processing of organic matter will be clearly higher.

In the case of polluted streams and rivers, biological self-purification capacity may be roughly doubled by the contribution of an intact and active hyporheic zone. On the other hand, self-purification capacity will probably be greatly reduced if hydraulic exchange of surface and hyporheic waters is reduced artificially. Hence, the removal of riffle-pool-sequences by channelization of streams not only reduces biological diversity (e.g. Pusch *et al.*, 1991), but probably greatly decreases hyporheic self-purification capacity, too.

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