

et al. 1992). Thus fatty acids are good indicators of long-term feeding patterns. Sampling was done during early rainy season, just after the productive period with high nutrient loading and high turbulence (Patterson and Kachinjika 1995). If these have resulted in plankton blooms and opportunistic feeding behavior in Malawian cichlids, it has not been sufficient to unify the fatty acid signatures. It seems highly probable that the ecological niches of the species studied here are clearly differentiated. This conclusion is further supported by the clear separation of species in discriminant analysis (Fig. 2).

Similar questions of Malawian cichlids have been studied using entirely different technique, stable isotope ratios (Bootsma et al. 1996; Genner et al. 1999). Tests of concordance of these two methods might be a very powerful way of unraveling trophic interactions in these and other systems. The present results encourage the use of chemometric methods, especially fatty acid studies, for studying ecological relationships among freshwater fauna and investigating the ongoing evolutionary processes.

Liisa Kuusipalo¹
Reijo Käkälä

Department of Biology
University of Joensuu
P.O. Box 111
FIN-80101 Joensuu, Finland

References

ACKMAN, R. G. 1994. Animal and marine lipids, p. 292–328. In B. S. Kamel and Y. Kakuda [eds.], *Technological advances in im-*

¹ Corresponding author (liisa.kuusipalo@joensuu.fi).

Acknowledgments

We thank G. F. Turner for the species identification and the referees for their comments.

Invertebrate recolonization patterns in the hyporheic zone of a gravel stream

Abstract—Invertebrate recolonization at short-term exposures (2–192 h) in the hyporheic zone of a gravel stream revealed significant depth-specific differences. In the shallow hyporheic zone (0–20 cm), mean meiofaunal density increased asymptotically stabilizing within 66 h, a similar but nonsignificant pattern was found for macrofauna. Permanent meiofaunal members (e.g., rotifers, chironomids, cyclopoids) were the fastest colonizers of the traps. At the deeper hyporheos (20–50 cm) meiofauna and macrofauna entered the pipes rapidly (2 h) but neither a power curve nor an asymptotic curve described their colonization pattern. Nonlinear regression analysis indicated a significant relationship between amounts of interstitial sediment entering the pipes and abundances of macrofauna and meiofauna.

- proved and alternate sources of lipids. Blackie Academic and Professional, Chapman and Hall.
- ALLISON, E. H., K. IRVINE, A. B. THOMPSON, AND B. P. NGATUNGA. 1996. Diets and food consumption rates of pelagic fish in Lake Malawi, Africa. *Freshw. Biol.* **35**: 489–515.
- BOOTSMA, H. A., R. E. HECKY, R. H. HESSLEIN, AND G. F. TURNER. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analysis. *Ecology* **77**: 1286–1290.
- ECCLES, D. H., AND E. TREWAVAS. 1989. Malawian Cichlid fishes. The classification of some haplochromine genera. *Lake Fish Movies*, H. W. Dieckhoff, Arenbergstrasse 27, 4352 Herten.
- FOLCH, J., M. LEES, AND G. H. SLOANE-STANLEY. 1957. A simple method for the isolation and purification of total lipides from animal tissues. *J. Biol. Chem.* **226**: 497–509.
- GENNER, M. J., G. F. TURNER, S. BARKER, AND S. J. HAWKINS. 1999. Niche segregation among Lake Malawi fishes? Evidence from stable isotope signatures. *Ecol. Lett.* In press.
- LINKO, R. R., M. RAJASILTA, AND R. H. HILTUNEN. 1992. Comparison of lipid and fatty acid composition in vendace (*Coregonus albula* L.) and available plankton feed. *Comp. Biochem. Physiol.* **103A**: 205–212.
- MUJE, P., J. J. ÅGREN, O. V. LINDQVIST, AND O. HÄNNINEN. 1989. Fatty acid composition of vendace (*Coregonus albula* L.) muscle and its plankton feed. *Comp. Biochem. and Physiol.* **92**: 75–79.
- PATTERSON, G., AND O. KACHINJIKI. 1995. Limnology and phytoplankton ecology. The fishery potential and productivity of the pelagic zone of Lake Malawi, p. 1–68. Njassa. [ed.] A. Menz. U.K. SADC, Natural Resources Institute, ODA.
- TURNER, G. F. 1996. *Offshore cichlids of Lake Malawi*. Cichlid Press, Germany. 240 pp.
- , A. S. GRIMM, O. K. MHONE, R. L. ROBINSON, AND T. J. PITCHER. 1991. The diet of *Oreochromis lidole* and other chambo species in Lakes Malawi and Malombe. *J. Fish Biol.* **39**: 15–24.

Received: 18 March 1999
Accepted: 24 November 1999
Amended: 28 January 2000

Mobile and sedentary invertebrates inhabiting streambeds are exposed to forces of flowing water and can be displaced during periods of high discharge when stones are scoured, overturned, or rolled downstream and finer substrates are stirred or shifted (Mackay 1992). These physical disturbances promote a diverse invertebrate community adapted for recolonizing denuded areas of streambeds. The process of recolonization and subsequent changes in species presence and abundance has been intensively targeted to benthic macroinvertebrates inhabiting the streambed surfaces. The rich literature on experimental studies dealing with benthic recolonization indicates that it may be a deterministic process (Cushing and Gaines 1989), where important factors include

invertebrate mobility, substrate size and texture, biological interactions, and sources of colonizers (*see* Mackay 1992). However, others have found that colonization in streams is dynamic and linked to the stochasticity of distribution and patch formation of invertebrates (Tokeshi and Townsend 1987; Schmid 1997).

The hyporheic zone, the saturated subsurface sediments beneath and lateral to the wetted channel containing some proportion of surface and groundwater, has been viewed as a major detrital storage area influencing surface stream functioning through hydrological exchange (e.g., Valett et al. 1994) and heterotrophic metabolism (Mulholland et al. 1997). From the organism perspective, the hyporheic zone may constitute a refuge (Dole-Olivier and Marmonier 1992) or a resource patch (Bretschko 1991). Hyporheic inhabitants include the meiofauna (organisms $<500\ \mu\text{m}$, Meyer 1994) with their temporary members (insect larvae of first to second instars) and permanent members (e.g., nematodes, tardigrades, rotifers). Their depth distribution can be skewed toward the surface in sandy streams (Palmer 1990) or to deeper layers in gravel streams (Schmid-Araya 1997). Their importance to stream metabolism and hyporheic functioning is still under debate, but it has become clear that their contribution to total biodiversity is substantial, and they also link the microbial and the macroinvertebrate assemblages (e.g., Schmid and Schmid-Araya 1997; Robertson et al. in press).

Small-bodied taxa characterized by short generation times have the ability to colonize new resources faster due to their high mobility (Marzluff and Dial 1991). Hence, their recolonization patterns would be expected to differ from those of large-sized invertebrates. Recolonization of small patches of defaunated hyporheic sediments by invertebrates can be as rapid as 1 d in desert streams (Boulton et al. 1991) or in gravel streams (Schmid 1997). No other studies have reported such short exposure time, and no research has examined the colonization patterns of both meiofauna and macrofauna simultaneously.

I here examined the hypothesis that short-term recolonization patterns will differ between meiofauna and macrofauna and that their patterns will vary between the streambed surface and the deeper hyporheic zone. I have also tested whether sediment input has an effect upon recolonization patterns within the shallow and deeper hyporheic zone.

Material and methods—The study site was a single 10-m riffle of the Oberer Seebach, a second-order stream in Lower Austria ($47^{\circ}51'N$, $5^{\circ}04'E$, 615 m above sea level). The stream is a calcareous, summer-cold, gravel stream with a nearly uninhabited drainage basin of 20 km². The stream has a slope ranging between 1 and 7% in the study area. Further descriptions of the hydrography and chemical parameters of the bed sediments of the Oberer Seebach can be found in Bretschko (1991).

Three samplings were conducted between August and December 1993 and two between April and September 1994 (Fig. 1), when the average water temperature was 6.7°C and 8.3°C respectively. Average water depth was 31.8 and 36.6 cm, whereas mean daily surface discharge ranged between 0.039 and 7.051 m³ s⁻¹, respectively. Temporal variations in

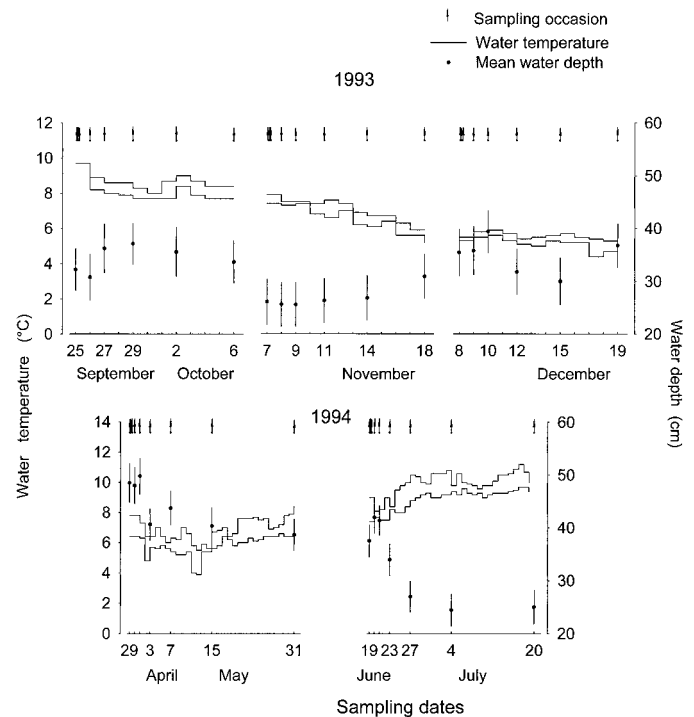


Fig. 1. Maximum and minimum water temperature and mean water depth (± 1 SE) during invertebrate colonization between 1993 and 1994 in a gravel stream. Arrows indicate sampling occasions.

the abiotic variables (water depth and water temperature) are shown in Fig. 1.

Standpipe traps (Bretschko and Klemens 1986) were used to allow the emigration/immigration of meiofauna and macrofauna and the entry of interstitial sediment and organic matter from all directions (upstream, downstream, and lateral). Previous experiments established a period of 3 d exposure for collecting macrofauna (Bretschko and Klemens 1986), and interstitial flow rates through the pipes were positively correlated with superficial water velocity, and, depending on sediment depth, they ranged between 87 and 700 ml min⁻¹ (Peter 1985).

In this study, a total of 10 standpipe traps were permanently installed between 0- and 50-cm depth in a riffle zone, two of the pipes collecting invertebrates from each of five sediment depths. The traps were spaced at least 1-m apart within the physical constraints of the riffle. The standpipe traps were made of plastic tubes (diameter 6.7 cm, total length 144 cm), with a circle of 10 catching holes (diameter 9 mm) located 10 cm from the bottom of each tube. At the bottom, the pipes were sealed from below with a timber tip with rubber seals to make them watertight. The traps were closed at the top with cylindrical cork caps, perforated to compensate for pressure differences. The catching holes (total opening area 11.06 cm²) were shut tightly between sampling occasions by sliding down a short piece of cylindrical tube (diameter 6 cm) equipped with a plastic foam, using a metal hook. On the sampling date, the cylinder was removed to allow sediment and hyporheic dwellers to enter the pipes via the catching holes over a specified period. In order to extract a sample, the catching holes were closed using an inflatable rubber col-

lar. The contents of the traps (approximate volume 250 ml) were carefully sucked up using a syringe-like pump. After a sample was taken, the trap holes were closed and the pipe was cleaned by removing the remaining interstitial water and sediment and then left open for further exposure.

Five samplings were carried out, three in 1993 and two in 1994 (Fig. 1). Two replicates were collected at each of five sediment depths (0–10, 10–20, 20–30, 30–40, and 40–50). Sampling sequence was to open the pipes, extract a sample promptly (= background densities), close, clean, and reopen for 2 hr (= first exposure). After 2 h, the traps were closed, samples were collected, pipes were cleaned and then reopened for the following exposure period (e.g., 4 h). The exposure intervals for benthic recolonization were 2, 4, 6, 12, 24, 48, 72, and 96 h for the August to December 1993 samplings. An additional exposure time of 8 d (192 h) was carried out from April to September 1994. Samples were kept cool and transported to the laboratory within 1–2 h. Samples were stirred, homogenized, and sieved into four fractions: <30, 30–100, 100–250, and >250 μm . Identification and counting were completed on each fraction on the live material within 48 h. Coarse particulate matter (size range >1 mm) and fine particulate organic material (range >0.45 μm and <1.00 mm) were dried in an oven at 65°C to constant weight and weighed to the nearest mg. Spot records of water depth were made at the side of each pipe; water temperature and surface discharge were continuously monitored by a stage-recorder throughout the study period.

Results—The amount of interstitial sediment (size range 30 μm to <9 mm) that accumulated in the traps differed significantly between depth layers and exposure time but not between sampling dates (Table 1). However, there was a significant interaction of depth \times exposure duration and exposure \times sampling dates. Traps at deeper sediment layers consistently contained more interstitial sediment than more superficial traps over time (Table 1). Consequently, the rate of sediment input (= quantity entered the pipe per hour) differed between depths (Fig. 2a). Less sediment entered the traps between 0 and 20 cm ($\bar{x} \pm 1 \text{ SE}$: $0.019 \pm 0.001 \text{ mg L}^{-1} \text{ h}^{-1}$) than those in deeper layers ($\bar{x} \pm 1 \text{ SE}$: $0.155 \pm 0.012 \text{ mg L}^{-1} \text{ h}^{-1}$). The rate of sediment input remained constant after 20 h at the streambed surface and after 50 h in deeper sediment layers (Fig. 2a). Rates of interstitial sediment input at the streambed surface were significantly and positively correlated with surface discharge (0–10 cm; $r_s = 0.304$, $n = 84$, $P = 0.005$); however, the relation was not significant for deeper sediment layers (20–50 cm; $r_s = -0.0547$, $n = 312$, $P = 0.335$).

Meiofaunal percentage contribution to the benthic assemblage colonization was higher than that of macroinvertebrates in all experiments and at all sediment depths within the hyporheic zone (Table 2, Fig. 2b). Colonists included 12 meiofaunal groups and 13 macroinvertebrate taxa. Nematodes, oligochaetes, harpacticoid copepods, and ostracods dominated the meiofaunal assemblage, whereas large-sized chironomids (\geq third instar), Ephemeroptera, Trichoptera, and Amphipoda were the most abundant macroinvertebrates (Table 2).

A highly significant effect of depth, exposure time, and

Table 1. RMANOVAs results of the effect of sediment depth, colonization time, and date of experiments on input of interstitial sediment (30 μm –9 mm) and on macrofaunal and meiofaunal densities within the hyporheic zone. Values given are F statistics for shallow hyporheos ($n = 4$; 0–10 and 10–20 cm) and deep hyporheos ($n = 6$; 20–30, 30–40, and 40–50 cm).

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i> *
Interstitial sediments				
Between subjects				
Sediment depth (<i>D</i>)	1	454.155	21.629	0.002
Error	8	20.998		
Within subjects				
Date of experiment (<i>E</i>)	4	1.930	0.958	0.399
<i>E</i> \times <i>D</i>	4	10.963	5.442	0.019
Recolonization time (<i>T</i>)	8	10.854	12.146	0.001
<i>T</i> \times <i>D</i>	8	8.225	9.204	0.002
<i>E</i> \times <i>T</i>	32	1.288	3.335	0.023
<i>E</i> \times <i>T</i> \times <i>D</i>	32	1.455	3.788	0.014
Error	256	0.386		
Meiofauna				
Between subjects				
Sediment depth (<i>D</i>)	1	212.309	38.938	0.000
Error	8	5.452		
Within subjects				
Date of experiment (<i>E</i>)	4	3.970	5.412	0.031
<i>E</i> \times <i>D</i>	4	8.602	11.733	0.003
Recolonization time (<i>T</i>)	8	0.805	9.227	0.000
<i>T</i> \times <i>D</i>	8	0.631	7.235	0.002
<i>E</i> \times <i>T</i>	32	0.227	2.680	0.052
<i>E</i> \times <i>T</i> \times <i>D</i>	32	0.127	1.505	0.226
Error	256	0.085		
Macrofauna				
Between subjects				
Sediment depth (<i>D</i>)	1	2.306	3.598	0.094
Error	8	0.641		
Within subjects				
Date of experiment (<i>E</i>)	4	10.367	18.589	0.000
<i>E</i> \times <i>D</i>	4	3.688	6.677	0.004
Recolonization time (<i>T</i>)	8	0.878	3.808	0.011
<i>T</i> \times <i>D</i>	8	0.698	3.025	0.029
<i>E</i> \times <i>T</i>	32	0.546	2.277	0.056
<i>E</i> \times <i>T</i> \times <i>D</i>	32	0.316	1.315	0.278
Error	256	0.240		

* Box's Greenhouse-Geisser correction for all the within-subjects F tests.

sampling dates and nonsignificant interaction between depth, duration of exposure, and date of sampling were found for meiofauna (Table 1). At more surficial depths (0–20 cm), meiofaunal densities increased with time, whereas at deeper sediment layers (>20 cm) densities declined with time (Fig. 3a). Macrofaunal densities did not differ between sediment depths, but there was a significant effect of duration of exposure and among experiments (Table 1). There were no significant interactions of sediment depth \times exposure time and also between depth \times exposure time \times date of experiment (Table 1). Similar to meiofauna, macroinvertebrate densities increased with time at the streambed surface and declined throughout time within the hyporheic zone (Fig. 3a).

In the shallow hyporheic zone, the pattern of meiofaunal recolonization did resemble an asymptotic curve but not significantly (Fig. 3a), and there was no significant fit for mac-

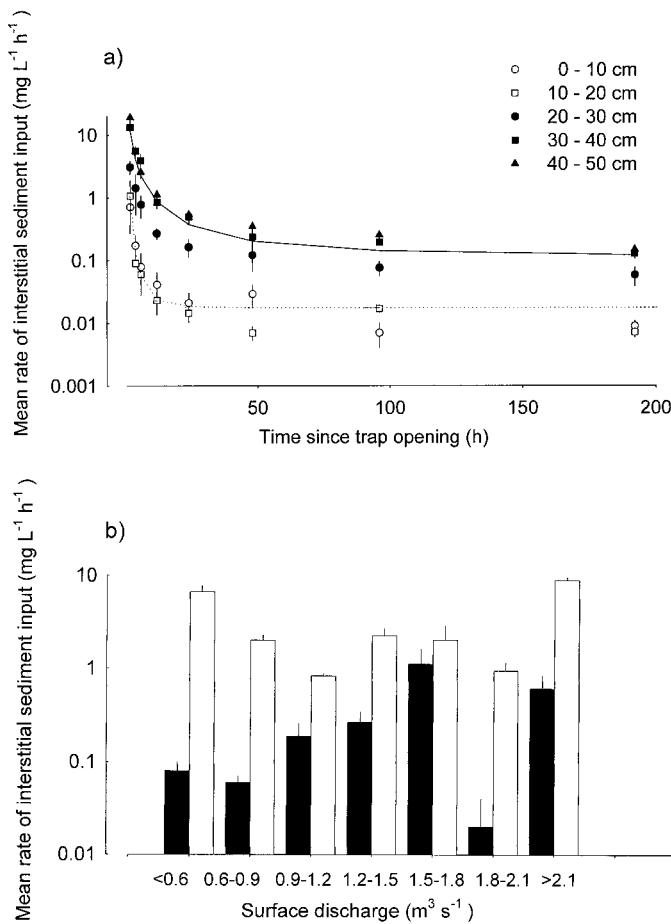


Fig. 2. (a) The mean rate of sediment input at sediment depths between 0 and 50 cm in the gravel stream Oberer Seebach. Vertical lines are ± 1 SE. (b) Mean abundance of invertebrates recolonizing the traps between 1993 and 1994 in a gravel stream. Vertical lines are ± 1 SE.

rofauna, probably due to low densities. The time for total meiofauna to reach 95% of its benthic density was 63.7 h, but it varied between taxa from 42 h (chironomids) to 126 h (harpacticoids, Table 3). The fastest meiofaunal colonists (from 42 to 51 h) were rotifers, small chironomids (instars I and II), cyclopoid copepods, and ostracods (Table 3). Estimates for abundant macrofauna taxa at the shallow hyporheos were not significant (Table 3).

In contrast, recolonization by meiofauna and macrofauna was very rapid within the hyporheic zone. After 2 h, invertebrate densities approximated or exceeded those from the initial densities then declined and remained entering the traps at a constant rate throughout time (Fig. 3a).

There was no significant relationship between total macrofauna and meiofauna, and the interstitial sediment accumulated in the traps at the streambed surface. But nonlinear regression analysis indicated a significant relationship between average amounts of interstitial sediment and colonist densities within the deeper hyporheos (Fig. 3b). Benthic invertebrates increased with greater amounts of interstitial sediment entering the traps. This pattern may indicate a passive or particle-associated colonization pattern. Furthermore,

Table 2. Percentage occurrence of meiofaunal taxa collected in standpipe traps in the hyporheic zone of the Oberer Seebach during colonization experiments in 1993 and 1994.

Taxon	Percentage	
	1993	1994
Meiofauna		
Microturbellaria	3.0	4.9
Gastrotricha	6.0	4.1
Rotifera	4.8	4.0
Nematoda	14.5	11.5
Oligochaeta	6.7	3.9
Tardigrada	0.1	0.3
Acari	0.4	1.6
Insecta		
Diptera		
Chironomidae (<250 μm)	3.3	1.8
Microcrustacea		
Cladocera	0.3	0.2
Cyclopoida	4.3	2.8
Harpacticoida	36.0	22.3
Ostracoda	17.0	27.2
Macrofauna		
Turbellaria	0.5	0.07
Gastropoda	0.1	0.4
Acari	0.04	0.2
Insecta		
Collembola	<0.04	0.01
Ephemeroptera	0.3	1.2
Plecoptera	0.04	0.2
Megaloptera	0	0.2
Trichoptera	0.02	1.6
Coleoptera	—	0.02
Diptera		
Simuliidae	—	0.01
Chironomidae (>250 μm)	2.3	10.1
Other Diptera	<0.01	—
Crustacea		
Amphipoda	0.3	1.4

dominant meiofaunal taxa included poor swimmers such as nematodes and harpacticoid copepods (Table 2).

Discussion—The study performed within the hyporheic zone of a gravel stream demonstrated a colonization pattern for macrofauna similar to those observed by other investigations at the streambed surface (i.e., Minshall et al. 1983; Ciborowski and Clifford 1984). In contrast to other studies where sterile or seminatural substrates have been exposed, these standpipe traps were free of substrate. The sump of a standpipe is analogous to an empty interstitial void or space (250 cm^3 in volume), where sediment accumulates and species can arrive over time. The size of interstitial voids in such gravel stream has been assessed using special techniques described elsewhere (Bretschko and Leichtfried 1988; Schmid 2000). However, the pattern of voids is highly unpredictable but largely interconnected, varying between 150 cm^3 and 600 cm^3 per kilogram of sediment (Schmid 2000).

Significant and noticeable were the different colonization patterns found for the shallow and deeper hyporheic dwellers. At the streambed surface, only meio-invertebrates seemed to approach an asymptote, whereas invertebrates

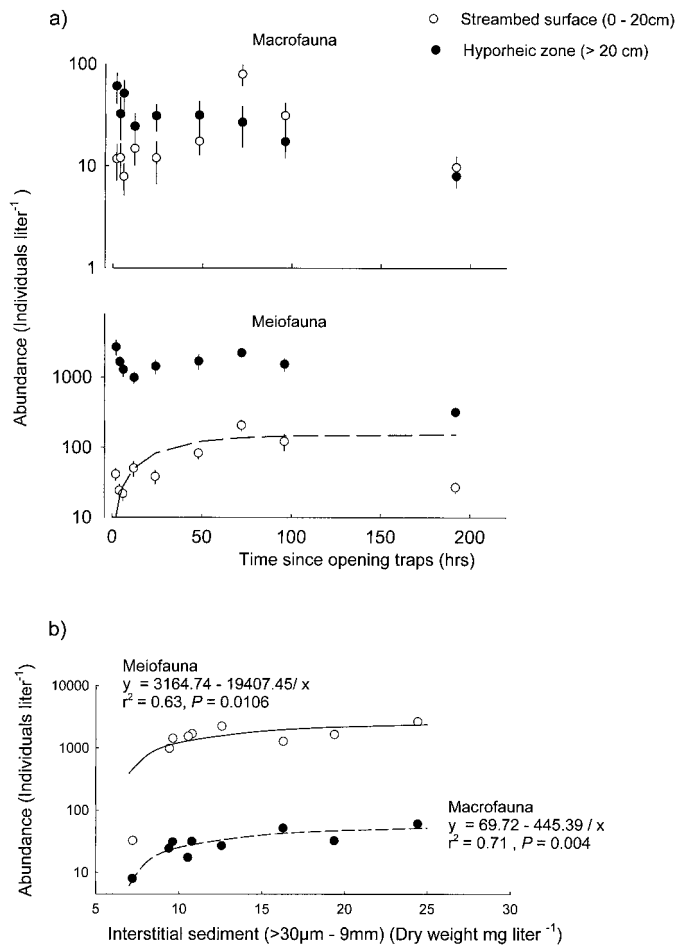


Fig. 3. (a) Mean abundance of invertebrates recolonizing the traps at the streambed surface and within the hyporheic zone in a gravel stream. Vertical lines are ± 1 SE. Meiofauna at the streambed surface $Y = 108.67(1 - \exp^{-5.11x/108.67})$, $r^2 = 0.342$, $P = 0.09$. (b) The relationship between mean abundance of macrofauna and meiofauna and the interstitial sediment entering the traps within the hyporheic zone of the Oberer Seebach.

within the deeper hyporheic zones colonized the pipes rapidly (2 h) and declined with time. Time required for stabilization of benthic abundances varied among taxa, ranging from 42 h (1.8 d) for small chironomids to 126 h (5.3 d) for harpacticoid copepods at the surface. In contrast, in the deeper hyporheic zone benthic densities were reached after 2 h. At the streambed surface, the apparent colonization period of macrofauna has been as short as 4–6 d in some experiments (Townsend and Hildrew 1976; Lake and Doeg 1985), whereas usual estimates ranged between 10 and 30 d (i.e., Mackay 1992). These rather long estimated values are probably due to the minimum chosen exposure time of 2–3 d. Only three studies have investigated the faunal colonization patterns within the hyporheos. Results from exposed substrate ranged between 1 and 2 d (Boulton et al. 1991; Schmid 1997). The colonization and consequently dispersal was faster in deeper sediment layers than at the surface in the gravel stream Oberer Seebach.

Peter (1985) estimated that mean interstitial flows can vary

Table 3. Time to reach 95% of the density for dominant invertebrates recorded in traps ($=K$) calculated as $T = -K \ln 0.05/C$, where C is the constant in an asymptotic equation $N_{(t)} = K(1 - \exp^{-Ct/K})$, in colonization experiments.

Taxon	T (h)	K	C	r^2	$F_{1,36}$	P
Meiofauna	63.7	108.7	5.11	0.34	3.61	ns
Rotifera	50.3	5.47	0.33	0.31	16.17	0.001
Nematoda	121.7	3.86	0.10	0.19	8.30	0.007
Diptera						
Chironomidae (<250 μm)	42.4	7.81	0.55	0.06	2.44	ns
Microcrustacea						
Cyclopoida	51.3	3.00	0.18	0.22	10.30	0.003
Harpacticoida	126.0	6.86	0.16	0.17	7.20	0.011
Ostracoda	49.2	7.74	0.47	0.20	9.26	0.004
Macrofauna	66.2	34.68	1.57	0.23	2.10	ns
Insecta						
Diptera						
Chironomidae (>250 μm)	118.3	7.81	0.55	0.14	2.44	ns
Crustacea						
Amphipoda	4.2	0.35	0.25	0.01	0.37	ns

between 234 and 375 ml min^{-1} between 0- and 60-cm sediment depth using Rhodamine dye. These experiments also showed that the dynamics of interstitial flow in areas deeper than 20 cm are not related to superficial water velocity, water depth, or discharge. The results obtained here confirmed the former findings and those of Panek (1991) using the cage-pipe method. He speculated that organisms inhabiting deeper hyporheic sediments may be more motile due to harsh conditions such as higher variability of interstitial flows that may displace them or restrict their food search. In the gravel stream Oberer Seebach, invertebrate colonization and the amount of particles transported within the sediments per hour declined with time in the deeper hyporheos (>20 cm). Further, nonlinear regression analysis indicated a significant relationship between amounts of transported interstitial sediment and colonist densities. Nematodes and harpacticoid copepods proved to be sediment bound and poor swimmers (Palmer 1992). In the Oberer Seebach, Panek (1991) examined the movement dynamics of invertebrates within the hyporheic zone. Direction of migrations (upstream, downstream, or laterally) did not differ between sediment depths and four dominant species (two permanent and two temporary inhabitants). He also demonstrated that macroinvertebrates' migratory activity increased with increasing sediment depths. In the uppermost sediment layer, flow pattern is governed by surface discharge, whereas in deeper layers the water flow is influenced by the hydraulic head of the riparian groundwater (Bretschko 1992).

The results of my study confirm that the mobility or displacement of fine-grained interstitial particles (<1 to 5 mm) has been found to depend on surface discharge down to sediment depth of 30 cm. In deeper sediment layers the variability of the interstitial through-flow increases dramatically, and faunal depth penetration may be limited. My data are consistent with the conclusion of Boulton et al. (1991) that fine particulate organic matter accumulates and levels off

after some time. In addition, it was found here that nematodes and harpacticoids were associated with these sediment inputs, which indicates mainly passive transport mechanisms. The results stress contrasting patterns of recolonization between invertebrates inhabiting superficial depths and those in deeper sediment layers. Hyporheic variability has been noted in other studies, and it has been recognized as a spatially heterogeneous environment. Hyporheic and surface subsystems are integrated by complex hydrological linkages that vary in space and time (Valett et al. 1994). The data from these experiments support the following conclusions: (1) there were significant depth-specific differences (superficial versus deeper hyporheic depths) in meiofaunal and macrofaunal colonization patterns, (2) meiofaunal taxa were faster colonizers and probably more mobile compared with macrofauna in the same sediment depths, and (3) sediment input, in turn influenced by surface discharge, has a greater effect on both macrofaunal and meiofaunal colonization pattern within the hyporheos. The dynamics of sediment transport and accumulation in the pore spaces may have an indirect effect upon species settling rates, species interactions, and trophic structure.

*J. M. Schmid-Araya*¹

Biologische Station Lunz
Institute of Limnology
Austrian Academy of Sciences
Seehof 4
A-3293 Lunz am See, Austria

References

- BOULTON, A. J., S. E. STIBBE, N. B. GRIMM, AND S. G. FISHER. 1991. Invertebrate recolonization of small patches of defaunated hyporheic sediments in a Sonoran Desert stream. *Freshw. Biol.* **26**: 267–277.
- BRETSCHKO, G. 1991. The limnology of a low order alpine gravel stream (Ritrodat-Lunz study area, Austria). *Verh. Int. Ver. Limnol.* **24**: 1908–1912.
- . 1992. Differentiation between epigeic and hypogeic fauna in gravel streams. *Reg. Rivers* **7**: 17–22.
- , AND W. KLEMENS. 1986. Quantitative methods and aspects in the study of the interstitial fauna of running waters. *Stygologia* **2**: 279–316.
- , AND M. LEICHTFRIED. 1988. Distribution of organic matter and fauna in a second order, alpine gravel stream (Ritrodat-Lunz study area, Austria). *Verh. Int. Ver. Limnol.* **23**: 1333–1339.
- CIBOROWSKI, J. J. H., AND H. F. CLIFFORD. 1984. Short-term colonisation patterns of lotic macroinvertebrates. *Can. J. Fish. Aquat. Sci.* **41**: 1626–1633.
- CUSHING, C. E., AND W. L. GAINES. 1989. Thoughts on recolonization of endorheic cold desert spring-streams. *J. N. Am. Benthol. Soc.* **8**: 277–287.
- DOLE-OLIVIER, M. J., AND P. MARMONIER. 1992. Effects on the vertical distribution of the interstitial community. *Hydrobiologia* **230**: 49–61.
- LAKE, P. S., AND T. J. DOEG. 1985. Macroinvertebrate colonization in two upland southern Australian streams. *Hydrobiologia* **126**: 199–212.
- MACKAY, R. J. 1992. Colonization by lotic macroinvertebrates: A review of processes and patterns. *Can. J. Fish. Aquat. Sci.* **49**: 617–628.
- MARZLUFF, J. M., AND K. P. DIAL. 1991. Life history correlates of taxonomic diversity. *Ecology* **72**: 428–439.
- MEYER, J. L. 1994. The microbial loop in flowing waters. *Microb. Ecol.* **28**: 195–199.
- MINSHALL, G. W., D. A. ANDREWS, AND C. Y. MANUEL-FALER. 1983. Application of island biogeographic theory to streams: Macroinvertebrate recolonization of the Teton River, p. 355–395. *In* J. R. Barnes and G. W. Minshall [eds.], *Stream ecology: Application and testing of general ecological theory*. Plenum.
- MULHOLLAND, P., E. R. MARZOLF, J. R. WEBSTER, D. R. HART, AND S. P. HENDRICKS. 1997. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnol. Oceanogr.* **42**: 443–451.
- PALMER, M. A. 1990. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *J. N. Am. Benthol. Soc.* **9**: 17–25.
- . 1992. Incorporating lotic meiofauna into our understanding of faunal transport processes. *Limnol. Oceanogr.* **37**: 329–341.
- PANEK, K. L. J. 1991. Dispersionsdynamik des Zoobenthos in den Bettsedimenten eines Gebirgzbaches. Ph.D. thesis, Univ. Vienna.
- PETER, B. 1985. Sedimentwasserströmungen und Bettsedimentfauna. Master's thesis, Univ. Freiburg.
- ROBERTSON, A., S. RUNDLE, AND J. M. SCHMID-ARAYA. Putting the meio- into stream ecology: Current findings and future directions for lotic meiofaunal research. *Freshw. Biol.* In press.
- SCHMID, P. E. 1997. Stochasticity in resource utilisation by a larval Chironomidae (Diptera) community in the bed sediments of a gravel stream, p. 21–28. *In* J. Gibert, J. Mathieu, and F. Fournier [eds.], *Groundwater/surface water ecotones: Biological and hydrological interactions and management options*. Cambridge Univ. Press.
- . 2000. Fractal properties of habitat and patch structure in benthic ecosystems. *Adv. Ecol. Res.* **30**: 339–401.
- , AND J. M. SCHMID-ARAYA. 1997. Predation on meiobenthic assemblages: Resource use of a tanypod guild (Chironomidae, Diptera) in a gravel stream. *Freshw. Biol.* **38**: 67–91.
- SCHMID-ARAYA, J. M. 1997. Temporal and spatial dynamics of meiofaunal assemblages in the hyporheic interstitial of a gravel stream, p. 29–36. *In* J. Gibert, J. Mathieu, and F. Fournier [eds.], *Groundwater/surface water ecotones: Biological and hydrological interactions and management options*. Cambridge Univ. Press.
- TOKESHI, M., AND C. TOWNSEND. 1987. Random patch formation and weak competition: Coexistence in an epiphytic chironomid community. *J. Anim. Ecol.* **56**: 833–845.
- TOWNSEND, C. R., AND A. G. HILDREW. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *J. Anim. Ecol.* **45**: 759–772.
- VALETT, H. M., S. G. FISCHER, N. B. GRIMM, AND P. CAMILL. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* **75**: 548–560.

Received: 31 May 1999

Accepted: 16 December 1999

Amended: 8 February 2000

¹ Present address: School of Biological Sciences, Queen Mary and Westfield College, University of London, Mile End Road, London E1 4NS, U.K.

Acknowledgments

The study was supported by funds of the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung" (P9822-BIO). I thank members of the Biological Station Lunz, M. Leichtfried, A. Leichtfried, E. Lanzenberger, and E. Kronsteiner for diverse assistance during the experiments.

I am grateful to G. Bretschko and P. E. Schmid for valuable discussions concerning aspects of this study. I also acknowledge the comments of anonymous referees on a previous draft.