1. Introduction

The hyporheic zone plays an important role for the stability and functioning of stream ecosystems. Within the interstices, organic matter and nutrients may be retained, transformed and/or stored (e.g. Gibert *et al.*, 1990; Vervier *et al.*, 1992; Hendricks, 1993). Furthermore, the hyporheic zone may function as a distinct habitat that offers benthic organisms sufficient oxygen concentrations and low water velocities within a rather stable substratum (e.g. Bretschko, 1981; Godbout and Hynes, 1982; Pennak and Ward, 1986; Mc Elravy and Resh, 1991). Due to its high resistance and resilience to disturbances, the hyporheic zone may act as a refuge for benthic organisms (e.g. Sedell *et al.*, 1990; Grimm *et al.*, 1991; Griffith and Perry, 1993; Dole-Olivier *et al.*, 1997).

However, the role of the hyporheic zone as a habitat for the stream fauna largely depends on the size of the interstitial space available (e.g. Godbout and Hynes, 1982; Mc Elravy and Resh, 1991; Maridet *et al.*, 1996). Fine sediment accumulations may clog the interstices and restrict hyporheic water exchange, leading to a decrease of oxygen within the sediments (Brunke, 1999). Due to the erosiveness of their geological basement, sandstone streams, like the Weidlingbach, transport high loads of fine particles during storms that are deposited within the channel when the water level falls (Weigelhofer and Waringer, 2000). Thus, sediments in the midreaches are extremely heterogeneous, consisting of a coarse frame of pebbles and stones filled by fine particles which clog the interstices. This clogging of sediments largely depends on channel morphology and the pattern of hydrological exchange of each stream reach (Brunke, 1999). In the present study we therefore focused on the effect of channel

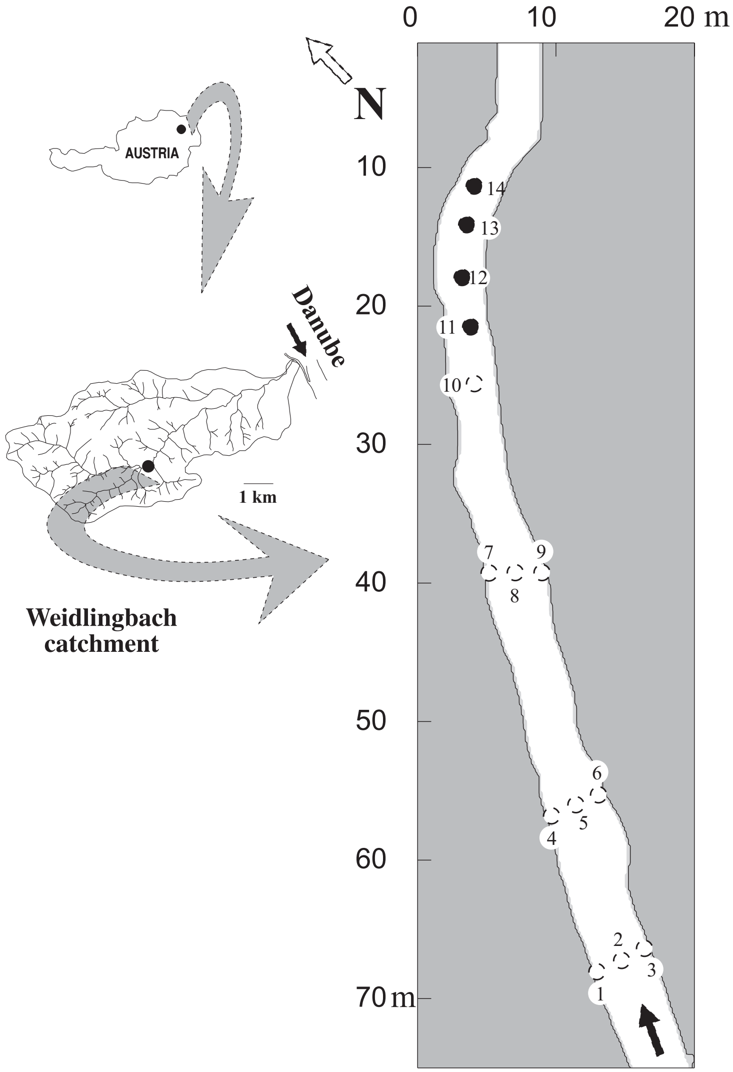


Figure 1. Study area in the Weidlingbach (Lower Austria), showing the locations of 15 standpipes. Open dots 1–10: riffle section; full dots 11–14: run section.

morphology on clogging of the hyporheic interstices and the influence of fine sediment accumulations within the hyporheic zone on colonization patterns by stream invertebrates.

2. Method

The Weidlingbach is a 12 km long tributary of the Danube, northwest of Vienna (Fig. 1; 48°17′N, 15°16′E; altitude: 440–164 m above sea level; WEIGELHOFER and WARINGER, 1999). The geology of its mostly forested, 32 km^2 catchment is dominated by calcareous sandstone, marl and slate. Mean grain size in the river bed ranges from 29.3 to 31.0 mm and mean porosity is approximately 20%. During

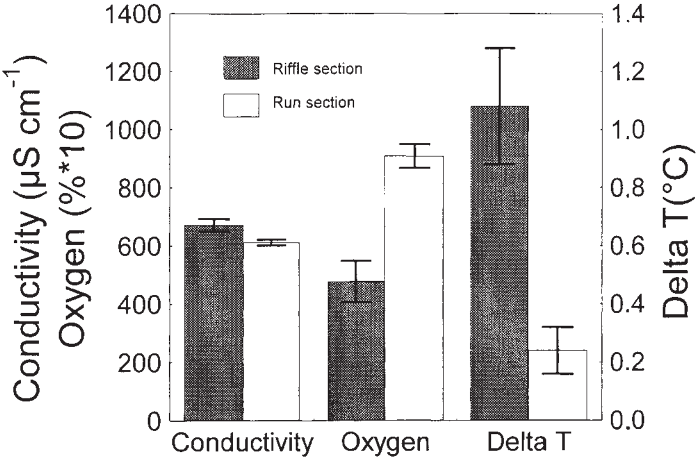


Figure 2. Conductivity (µS cm^{-1}), oxygen concentration (‰) and deviation of interstitial water temperature from surface water temperature (Delta T °C) (±95% C. L.) within the riffle and the run section.

base flow, the third order study site is divided into a wide, fast-flowing and shallow riffle section (sites 1–10; Fig. 1) and a narrow, slow-flowing and deep run section (sites 11–14). Chemical data obtained by 15 plastic standpipes (70 cm long, 5 cm ID) at 40 cm depth yielded significantly higher conductivity values, significantly higher deviations from surface water temperature and significantly lower oxygen values in the riffle section than in the run section (Fig. 2; WEIGELHOFER and WARINGER, 2000).

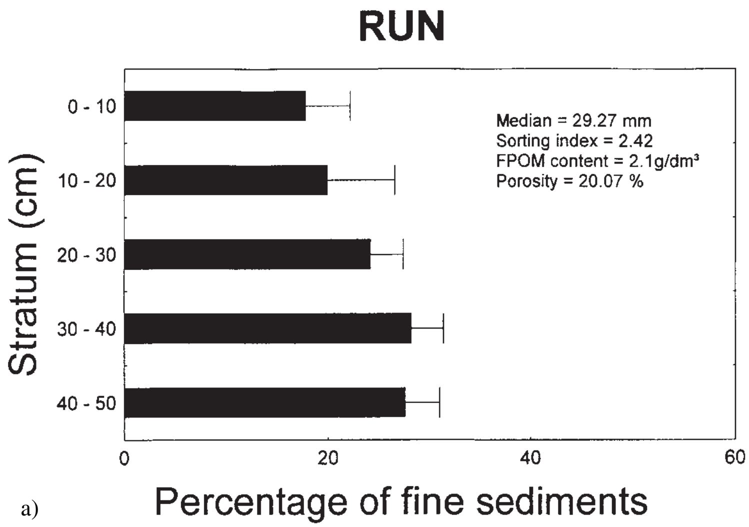
For the study of vertical grain size distribution and hyporheic invertebrates, sediments were sampled to a depth of 60 cm every second to third month from October 1997 to October 1998, using the freeze-coring-technique with previous electropositioning (BRETSCHKO and KLEMENS, 1986). On each date, 11 cores were taken at sites 1–6 and 10 within the riffle section and at sites 11–14 within the run section approximately 0.5 m upstream of each reference standpipe (Fig. 1). The samples were analysed for pore volume (as percentage of interstitial water of the total sample volume), grain size and the amount of fine particles with a diameter <2 mm (FPC). For the estimation of FPC, stones >6.3 cm in diameter were excluded from total weight in order to eliminate stochastic effects of irregularly distributed, heavy sediment particles that may bias the proportion of sediment fractions. Fine particulate organic matter (FPOM <2mm in this study) was estimated after combusting FPC at 450 °C in a muffle furnace for 4 hours. Before sieving, organisms over 100 µm body size were elutriated from the sediments, preserved in 95% ethanol and counted and identified to the lowest possible taxonomic level.

For statistical analyses, environmental variables and faunistic data were log-transformed to reduce skewness and kurtosis, and the distribution was checked by probability plots. Abundances of hyporheic organisms and concentrations of fine particles were compared by t-tests. Pearson´s correlation was used to detect relationships between fine sediment accumulations and the distribution of the hyporheic fauna (statistical workpackage UNISTAT 4.5).

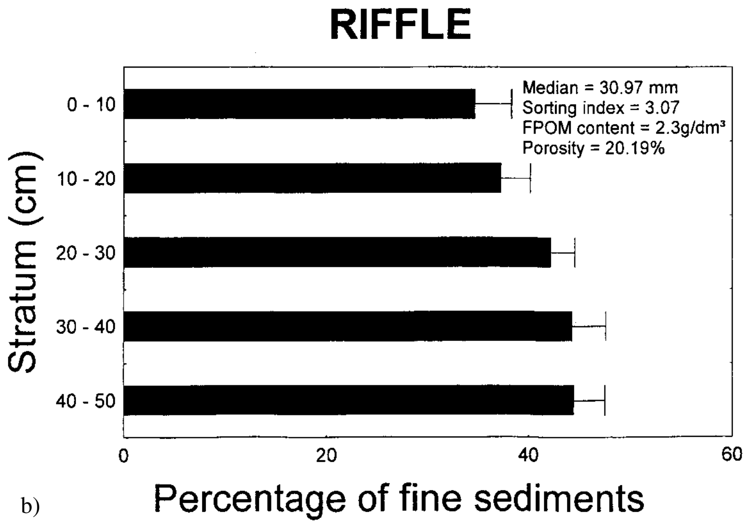
3. Results

3.1. Total Macroinvertebrate Densities within the Run and Riffle Sections

Sediments of the riffle and the run section differed significantly from each other with respect to their FPC (t-test, $p < 0.001$, df = 71). In the riffle, sediments were heavily clogged by fine particles from the top layer downwards, with FPC increasing from 35% in the first 10 cm to 45% at 60 cm depth (Fig. 3). Sediments of the run section showed significantly lower concentrations of fine particles in the topmost 20 cm stratum (<20%; t-test, $p < 0.001$, df = 71),



a)



b)

Figure 3. Vertical distribution patterns of fine sediments (grain size ≤2 mm; given as percentage of total sediment dry weight) (±95% C. L.) within the run and riffle section.

with only a slight increase downwards. However, FPC never exceeded 30% in the run section.

The FPOM content of the sediments was uniformly distributed over depths at both riffle and run. In contrast to FPC, the amount of organic particles within the sediments did not differ significantly between the two sections (t-test, $p > 0.05$, $df = 71$). Porosity given as interstitial water content of the sample showed no significant differences between sediments of the riffle and the run, either. This is due to the high amount of adhesive water within fine sediments, especially within clay fractions, which results in a high interstitial water content and, thus, in high porosity values. Although porosity within sediments of the riffle was as

Table 1. Correlation between hyporheic densities (n/dm^3) and fine particle concentration (FPC; <2 mm) of the most abundant macrozoobenthic taxa; showing the correlation coefficient and the probability level (p). Degrees of freedom = 62.

Taxon	Correlation coefficient	p
Ephemeroptera	−0.64	<0.01
Plecoptera	−0.58	<0.01
Chironomidae	−0.4	<0.01
Diptera without Chironomidae	−0.23	n.s.
Coleoptera	−0.19	n.s.
Trichoptera	−0.31	<0.05
Sialidae	−0.3	<0.01
Gammaridae	−0.5	<0.01
Oligochaeta	−0.18	n.s.
Asellus	+0.07	n.s.

high as that of the run (20%; Fig. 3), sediment particles were tightly packed in the riffle and colonisable pore space was low. In the run, however, sediments were loosely packed and interstices >1 cm in diameter could be frequently observed in the frozen sample. We used, therefore, the amount of fine particles (FPC) rather than porosity as a descriptor of sediment clogging and its subsequent effects on invertebrate colonization patterns.

Macroinvertebrate abundance was significantly negatively correlated with FPC (Pearson's correlation coefficient $C = -0.45$, $p < 0.01$, $df = 207$). Beneath the surface layer, the hyporheic zone of the run section showed significantly higher mean animal densities than that of the

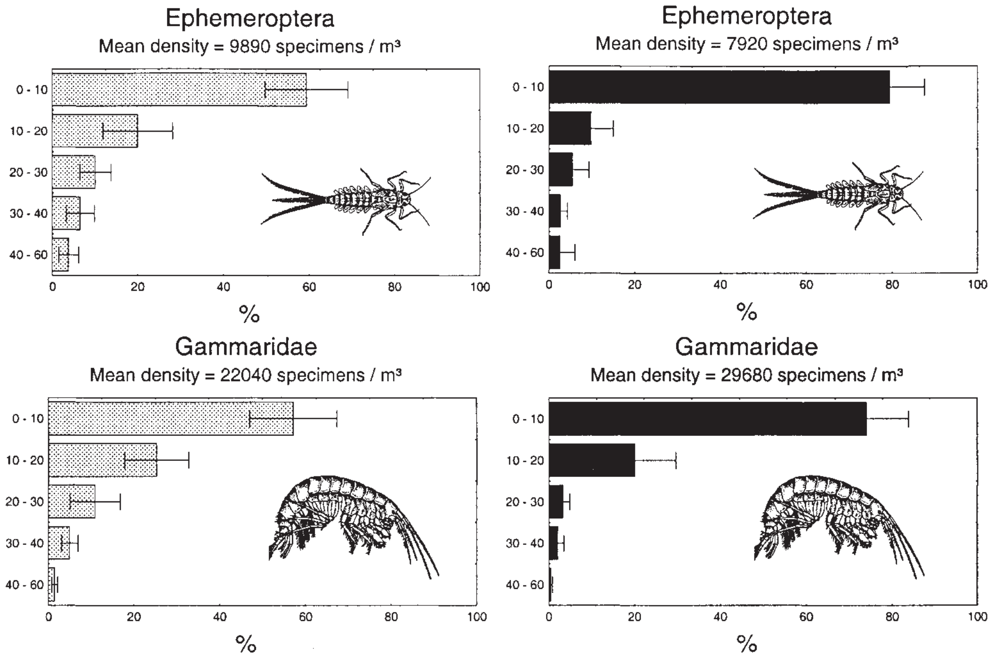


Figure 4.

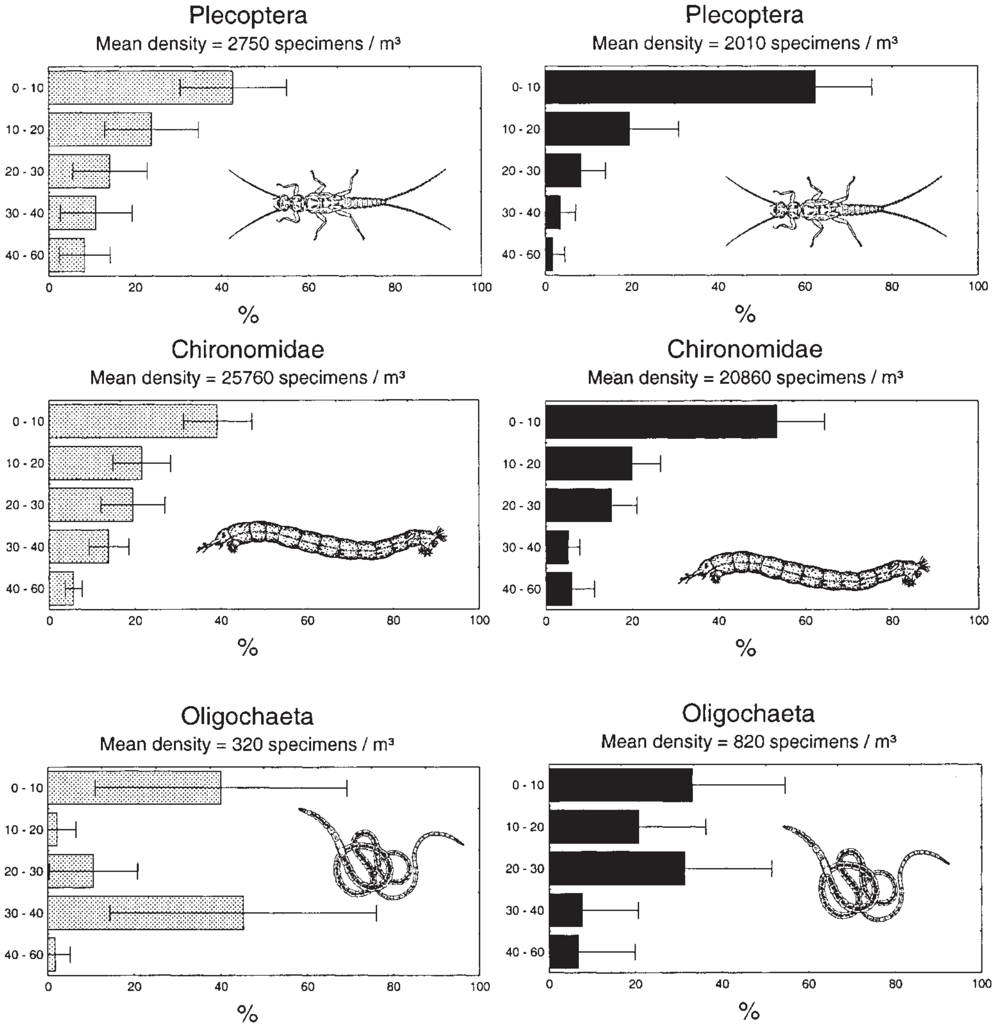


Figure 4. Vertical distribution patterns of Ephemeroptera, Gammaridae, Plecoptera, Chironomidae and Oligochaeta within the sediments of the run (light bars) and riffle sections (dark bars). Data are given as arithmetic means with 95% C. L.

riffle section (t-test, $p < 0.01$, $df = 71$), with 42.9 ind./dm^3 in the run and 34.3 ind./dm^3 in the riffle. Variability in animal density was lower in the run section.

In general, macroinvertebrate densities decreased with depth from 210 ind./dm^3 to 10 ind./dm^3 in the riffle and from 136 ind./dm^3 to 15 ind./dm^3 in the run section. Stream organisms were clearly concentrated within the top layers in riffle sediments, with more than 85% of the fauna inhabiting the first 20 cm of the hyporheic zone there. Below 30 cm, clay cells were frequent in the riffle section. While animal densities were generally low at 60 cm depth in both sections, macroinvertebrates were totally missing from such clay layers. In the run section, vertical distribution patterns were more even and stream organisms penetrated deeper into the hyporheic zone. At least 30% of the fauna was found below 20 cm in the sediments there.

3.2. Faunal Composition

Hyporheic communities were clearly dominated by stream organisms also common at the sediment surface, with the dipteran family Chironomidae being the most abundant (50.3%), followed by Gammaridae (30.7%), Ephemeroptera (11.4%) and Plecoptera (2.5%). Independently of their actual distribution pattern within the hyporheic zone, all taxa showed a significantly higher proportion of organisms beneath the top 20 cm stratum in the run than in the riffle section (for examples, see Fig. 4). Furthermore, the densities of Gammaridae, Ephemeroptera, Plecoptera, Trichoptera, Chironomidae and Sialidae were significantly and negatively correlated with FPC (Table 1). In most taxa the percentage of specimens decreased with increasing depth, but not so in Oligochaeta (Fig. 4).

Gammaridae were exclusively presented by the species *Gammarus fossarum* KOCH. Ephemeroptera consisted of 5 families (ranked in decreasing numbers): Baetidae (*Baetis rhodani* PICTET, *Baetis* spp.), Heptageniidae (*Ecdyonurus starmachi* SOWA, *Rhithrogena picteti* SOWA, *Electrogena uyhelii* SOWA), Leptophlebiidae (*Haproleptoides confusa* SARTORI and JACOB), Ephemeridae (*Ephemera danica* MÜLLER) and Ephemerellidae (*Ephemerella mucronata* (BENGTSSON)). Except the rare *E. mucronata*, all ephemeropteran families were found down to 60 cm depth, with maximum densities generally within the topmost layer of both sections. *E. danica* was more or less uniformly distributed over all depth strata in the run section, with a slight peak at 30 cm depth. Highly significant ($p < 0.01$) negative correlations (r) with FPC were observed in Ephemeridae ($r = -0.7$), Baetidae ($r = -0.4$), Heptagenidae ($r = -0.5$) and Leptophlebiidae ($r = -0.7$). Within Plecoptera, only Leuctridae inhabited all depth layers, while Nemouridae did not penetrate below 40 cm. Leuctridae were significantly and negatively correlated with FPC ($r = -0.4$, $p < 0.01$). Diptera comprised 8 families, but only Chironomidae were frequent in the sediments. Of the remaining families, Ceratopogonidae, Anthomyidae and Limnobiidae were detected throughout the sampling depths. Trichopteran species were rare in the sediments and generally concentrated within the topmost layer. However, single individuals of *Hydropsyche saxonica* MCLACHLAN, *Rhyacophila fasciata* HAGEN and *Philopotamus variegatus* (SCOPOLI) were recorded below 30 cm. Among the aquatic Coleoptera, only larvae of *Elmis maugetii* LATREILLE and *Riolus* sp. inhabited the deeper sediment layers in the Weidlingbach. They attained maximum densities within the top layer, decreased downwards to 40 cm and slightly increased again in the deepest stratum (40–60 cm).

4. Discussion

The hyporheic zone has been defined as part of the interstices of the fluvial sediments (ORGHIDAN, 1959). The distribution of sediment grain sizes and the volume of the interstices strongly influence the character of the hyporheic zone and, by this, become determinant for hyporheic exchange patterns and the colonization by biota (VERVIER *et al.*, 1992). Studies within highly porous gravel streams have shown that the numbers of stream organisms beneath the top sediment layer may exceed those of the sediment surface by far (e.g. BRETSCHKO, 1981; GODBOUT and HYNES, 1982; MARIDET and PHILIPPE, 1995). In contrast, STROMMER and SMOCK (1989) and WAGNER *et al.* (1993) found extremely low organism densities in the hyporheic zone of sandy bottomed, low porous streams. The amount of fine particles within stream sediments seems to be crucial for the colonization of the hyporheic zone, both on the large and small scale. The decrease of stream organisms with increasing sediment depth as a result of fine inorganic particle accumulation in deeper layers of the sediments is well documented (e.g. GODBOUT and HYNES, 1982; MC ELRAVY and RESH, 1991; STERBA *et al.*, 1992). However, MARIDET *et al.* (1996) detected that hyporheic densities were correlated with porosity only in less porous sites, whereas in coarse substrata other factors seemed to limit the penetration of stream invertebrates. STRAYER *et al.* (1997) showed that animals were more frequent within well-oxygenated porous sediments, albeit correlations between animal density and environmental parameters were generally weak, and BRUNKE and GONSER (1999) reported that fine inorganic particles did not directly correlate with hyporheic invertebrate distribution, but played an important role for the FPOM supply of the biota.

Due to its ever-changing channel morphology, the Weidlingbach near Vienna provides a good opportunity to study the effects of clogging of interstices by fine sediments. In narrow and deep channel sections (runs), increased shear stress during spates removes fine particles from the upper sediment layers down to about 40 cm. The larger interstitial space enables downwelling of surface water into the sediments which is clearly demonstrated by positive hydraulic heads and oxygen concentrations of about 90–100% at 40 cm depth (WEIGELHOFER and WARINGER, 2000). Although, at baseflow, water velocities at the sediment surface are low in such run sections (2–5 cm s^{-1}), this is obviously sufficient to prevent siltation and maintain a high level of pore volume. At the riffle section, where the streambed is broad and uniform, the increase in shear stress during spates is much lower than in the narrow run section. This probably results in a reduced flushing of fine particles out of the sediments at riffle sections. At baseflow, the situation is quite different: below a given threshold of water velocity, SCHÄLCHLI (1992) observed a positive correlation between current velocity and intrusion of fine particles into the interstices. This observation seems to be also applicable to the Weidlingbach riffle section where, at baseflow, water velocities at 40% water depth range from 20 to 60 cm s^{-1}, resulting in a tight packing and compact texture of the sediments along the whole cross-section of the stream. Hyporheic exchange is largely restricted there, leading to highly variable oxygen concentrations down to a minimum of 10% at 40 cm depth.

Due to the restricted sampling depth of 60 cm in this study, most organisms within the sediments of the Weidlingbach originated from the sediment surface. Despite this, hyporheic abundance and penetration depth was high in larvae of Leuctridae, Chironomidae and Elmidae and most of the ephemeropteran species which was also observed by WILLIAMS and HYNES (1974). Only Oligochaeta had their maximum densities below the topmost sediment layer of both riffle and run. With their long, slender and flexible bodies and their tolerance towards low oxygen concentrations they are well adapted to burrow into deeper and more clogged layers of the hyporheic zone (WILLIAMS and HYNES, 1974).

Although macrozoobenthic densities at the sediment surface of the Weidlingbach were much lower in the run than in the riffle section, density within the hyporheic zone of the former was significantly higher. This was observed in all taxa, whether they were almost totally restricted to the surface layer in the riffle section, like Trichoptera, or also showed higher densities in deeper strata there (e.g. Oligochaeta). Despite this clear reaction of organisms to a porous sediment, correlations between animal densities and accumulations of fine particles were lower than expected. This may have been caused by the high spatial and temporal variability and patchiness of the hyporheos in most stream sediments (e.g. BRETSCHKO, 1981; GODBOUT and HYNES, 1982; STAYER *et al.*, 1997). Other factors may additionally influence hyporheic densities, for example channel geomorphology and patterns of hydrological exchange (STERBA *et al.*, 1992; STANLEY and BOULTON, 1993; BRUNKE and GONSER, 1999), organic matter content (STRAYER *et al.*, 1997; BRUNKE and GONSER, 1999), oxygen concentration (STROMMER and SMOCK, 1989; WAGNER *et al.*, 1993), disturbance regime (GRIMM *et al.*, 1991; GRIFFITH and PERRY, 1993; DOLE-OLIVIER *et al.*, 1997) or life cycles (PENNAK and WARD, 1986; STERBA *et al.*, 1992). Nevertheless, most workers agree that the penetration of organisms into deeper sediment layers depends mainly on the availability of the hyporheic habitat as shown by MARIDET *et al.* (1996), rendering the amount of fine particles within the interstices a key determinant for hyporheic colonisation.

5. Acknowledgements

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