The influence of hydrological exchange patterns on environmental gradients and community ecology in hyporheic interstices of a prealpine river

Author(s):
Brunke, Matthias

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The Influence of Hydrological Exchange Patterns
on Environmental Gradients and Community Ecology
in Hyporheic Interstices of a Prealpine River

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Matthias Brunke
Diplom-Biologe (University of Freiburg, Germany)
born on 24 Oktober 1964 in Castrop-Rauxel, Germany

accepted on the recommendation of
Prof. Dr. J. V. Ward, examiner
Prof. Dr. J. Schwoerbel, coexaminer
Dr. T. Gonser coexaminer

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SUMMARY

1. In this study the hyporheic invertebrate community was the system property of interest. Hydrological exchange patterns between streams and ground water were used as the starting point for the investigation of environmental gradients that are decisive for the structure of this community. These abiotic habitat variables encompass physicochemical parameters, organic matter and sedimentological properties. The most influential of these habitat characteristics for hyporheic bacteria and hyporheic meio- and macrofauna were elucidated by factor analyses.

2. Following the introduction, there is a literature review on the ecological significance of exchange processes between rivers and ground water. Based on this knowledge, three basic types of hydrological exchange (infiltration, horizontal advection, exfiltration) were used to test the role of hydrology on hyporheic ecology.

3. The study was conducted at the Töss River, a prealpine gravel-bed stream in northern Switzerland. At the sampling site ground water exfiltrates into the stream at the left margin (exfiltration zone), whereas surface water infiltrates into the sediment at the opposite bank (infiltration zone). In midstream the dominant interstitial flow direction is along the river channel (horizontal advection zone). Twelve piezometers were installed in three clusters of four sediment depths (20-, 50-, 100- and 150-cm) in each of these 3 hydrological exchange zones. The samples (255) were taken with a hand pump (hyporheos) and with an electric pump (environmental parameters). Additionally nine freeze cores were taken to document sediment texture.

4. Hydrological exchange patterns determined the steepness of physicochemical gradients within the hyporheic interstices of the Töss River. In the upper sediment layers of the infiltration zone, physicochemical conditions resembled those of the surface water and showed high temporal variability, especially at a depth of 50 cm. In contrast, in the exfiltration zone physicochemical conditions were influenced by the more stable properties of upwelling ground water. Therefore, gradients in the exfiltration zone were steepest in the uppermost sediments. Physicochemical conditions in the horizontal advection zone were in between those of the infiltration zone and exfiltration zone; however, they tended to resemble the conditions within the infiltration zone more, especially in their thermal characteristics.

5. The sediment grain size class smaller than 1 mm seems to be the ecologically most important particle parameter. The median grain size of these mobile fine particles (fines) was about 0.03 mm. The content of fines tended to increase with depth, although higher accumulations were found at intermediate depths in sediments influenced by exfiltrating ground water. The content of particulate organic carbon increased down to a depth of 50 cm in all three hydrological exchange types. However, the differences between 50 and
100 cm were only significant in the region of exfiltrating ground water. Frequent flood events caused high temporal variability of interstitial particle parameters.

6. **Bacterial abundances** ranged between 0.163 to $478 \times 10^6$ cells/ml and differed significantly between upper and deeper sediment strata. This change with depth was significantly modulated by the type of hydrological exchange. The bacterial carbon portion of particulate organic carbon varied between 0.06% and 5.3% and tended to decrease with depth. Bacteria were most numerous at sediment depths where inflow of stream water occurred, but had been attenuated. Bacterial production was highest in hyporheic interstices dominated by surface water inflow. Bacterial abundance and production were strongly correlated to interstitial particulate organic matter; the best predictor for both was the content of particulate nitrogen. The predictive power of statistical models was substantially improved by the introduction of the 'hyporheic position', defined by sediment depth and hydrological exchange type, which integrated information on flowpath connections. Flowpath connections were particularly relevant when one uses dissolved organic carbon and interstitial fine sediment as explanatory variables.

7. Several hyporheic metazoan taxa and collective properties of the invertebrate community showed a strong correspondence with bacterial distribution patterns.

8. The **hyporheic fauna** exhibited a biotic gradient between interstitial positions influenced by surface water and those dominated by phreatic ground water. Sixty taxa were identified, the most abundant of which were cyclopoid copepods, ostracods and chironomids. All other groups combined accounted for the remaining third of individuals found. Total faunal density patterns were strongly related to the ratio of particulate organic carbon to total fine particles (POC/TP), which explained 61% of the variation in abundance within the sediments. Taxa richness and temporal persistence in species composition were also significantly correlated with the POC/TP ratio. The gradient in hyporheic community structure corresponded most with changes in the POC/TP ratio as well as to hydrological variables and distance between the surface and phreatic habitats. The POC/TP ratio optima for individual taxa indicate that the depth to which epigean taxa penetrate sediments may be restricted by the availability of the food resource, which decreased with decreasing POC/TP ratios. Therefore, the interstitial content of fine inorganic particles appears to be a critical determinant of the availability of food resources for interstitial invertebrates.

9. The coupling of sediment depth and hydrological exchange type in factor analyses revealed **flowpath connections** as being superimposed vectors in determining hyporheic abiotic and biotic gradients.
ZUSAMMENFASSUNG


5. Die Sedimentfraktion kleiner 1 mm ist die ökologisch wichtigste. Der Median der Korngrössenverteilung dieser mobilen Matrixfeinsedimente lag bei 0,03 mm. Der Gehalt an Feinsedimenten nahm tendenziell mit der Tiefe zu. Nur in der Exfiltrationszone wurden in einer Tiefe von 50 cm höhere Akkumulationen gefunden, verursacht durch den


8. Die Struktur der interstitiellen Invertebraten-Biozönose änderte sich graduell zwischen hyporheischen Positionen die durch Oberflächenwasser beeinflusst waren zu solchen die durch Grundwasser dominiert wurden. Von den 60 identifizierten Taxa hatten cyclopoide Copopoden, Ostracoden und Chironimiden die grösste Dominanz; alle anderen Taxa stellten zusammen ein Drittel der Besiedlungsdichte dar. Die faunistische Besiedlungsdichte korrelierte am stärksten mit dem Verhältnis zwischen partikulärem organischen Material und den gesamten Feinpartikeln (POC/TP); allein dieses Verhältnis erklärte 61% der Variabilität der Besiedlungsdichte. Auch die Taxazahl und die Persistenz korrelierten signifikant mit dem POC/TP. Die POC/TP-Optima individueller Taxa weisen darauf hin, dass die unterirdische Ausbreitung epigäischer Taxa durch die Verfügbarkeit des organischen Materials eingeschränkt wird, welche mit abnehmendem POC/TP sinkt. Daher erscheint der Gehalt an mineralischen Feinsedimenten als eine kritische Größe für die Verfügbarkeit von Nahrungsressourcen für interstitielle Invertebraten.

CHAPTER 1

Introduction

The ecotone concept has gained much attention in ecology during the last decade (Wiens et al., 1985; Di Casta et al., 1988; Naiman & Decamps, 1990), and it has been shown that aquatic-terrestrial ecotones are of particular importance for fluvial systems (Naiman et al., 1988). Lotic ecosystems, which are an integral part of the surrounding landscape (Hynes, 1975), are interactive along three spatial dimensions, longitudinal, lateral and vertical, on which time, regarded as fourth dimension, superimposes a temporal hierarchy (Amoros et al., 1987; Ward, 1989a). Resource gradients along river courses (Vannote et al., 1980) and transition zones of hydraulic forces (Statzner & Higler, 1986) structure environmental conditions and biotic patterns along the longitudinal dimension. Interactions between rivers and flood plains/riparian zones occur along the lateral dimension (Chauvet & Decamps, 1989; Junk et al., 1989; Ward, 1989b; Naiman & Decamps, 1997). Interaction between surface waters and ground waters occur along the vertical dimension, which also has a subterranean lateral component (Gibert et al., 1990; Stanford & Ward, 1993; Brunke & Gonser, 1997).

The existence of interactions between two or more ecosystems is fundamental for the ecotone concept. Ecotones are defined by exchange processes that do not exist in either of the adjacent ecosystems, but between these systems: "The ecotone is a zone of transition between adjacent systems, having a set of characteristics uniquely defined by space and time scales and, by the strength of the interactions between adjacent ecological systems" (Holland, 1988).

In addition, ecotones are often important regulators of ecosystem functions (Ward, 1989a; Coleman & Dahm, 1990; Valett et al., 1994; Brunke & Gonser, 1997). The internal properties of an ecotone result through an interplay between large-scale external and small-scale internal processes (Odum, 1990). The permeability of the ecotone determines the degree to which the landscape elements can be viewed as closed or open systems (Wiens et al., 1985).

The ecotone between lotic ecosystems and ground water are the hyporheic interstices of permeable sedimentary deposits. This transition zone was first recognized as a distinct habitat by Orghidan (1959). The hyporheic interstices are important sites for processes on ecological as well as on evolutionary time-scales (Ward & Palmer, 1994). Schwoerbel (1961a, b, 1962, 1964a, b, 1967a, b) demonstrated the role of the hyporheic habitat as a refuge against extreme temperature, current, and bedload movement. Furthermore, he
showed the importance of preadaptations for the colonization and the initial evolution of interstitial water mites in terms of ongoing adaptations.

Exchange between rivers and ground waters necessitates permeable and porous interstices, in which throughflow transports matter. An understanding of the ecology of the hyporheic habitat and its significance for ground waters and streams requires the incorporation of hydrology as a vector of various transfers (Danielopol, 1989; White, 1990; Rouch, 1992; Dole-Olivier & Marmonier, 1992a; Williams, 1993; see also "Perspectives on the hyporheic zone", Journal of the North American Benthological Society 1993, volume 12, 10-99pp). A thorough overview of the ecological significance of exchange processes between rivers and ground water is given in Chapter 2 of this thesis.

In this study the system property of interest is the hyporheic invertebrate community and the environmental factors that structure this community. Twin goals of community ecology were emphasized by Townsend (1989) as follows: (a) to recognize the patterns that exist in composition, diversity, trophic organization, and stability of species assemblages in nature, and (b) to understand the processes that determine these patterns. An understanding of the environmental conditions characterizing the habitat, and a careful description of such conditions, is a prerequisite for any explanatory inferences on the biota (Southwood, 1988; Fisher, 1994). Therefore, much of the work of this thesis is focussed on abiotic habitat variables.

As an ecotone, the hyporheic habitat is characterized by various gradients. The thesis begins with the higher hierarchical levels of hydraulic and sedimentological gradients; this is followed by consideration of physicochemical and organic matter gradients. The starting point for the field study was to identify the major hydrological exchange patterns within hyporheic interstices at the study reach. Specific hypotheses and objectives are formulated in the introductions of Chapters 3 - 8. Chapter 3 depicts the influence of hydrological exchange on vertical gradients of physicochemical variables. Chapter 4 deals with sedimentological gradients. The first part of this chapter provides an analysis of the mechanisms underlying the transport and retention of the fine particles, which are mobile within the interstices of the framework of coarser sediment. The second part of Chapter 4 analyses the characteristics of fine particles in terms of grain size composition and distribution within the habitat. In Chapter 5 the approach used in Chapter 4 for mineral sediments are examined for particulate organic matter, the food resource for most hyporheic invertebrates. Chapter 6 provides a multivariate synthesis of the importance of hydrological exchange on the steepness of environmental gradients within the hyporheic habitat.

The final chapters are factor analyses of the environmental gradients which are of most relevance for the distributions of bacteria and invertebrates in the hyporheic interstices of
the Töss River. Chapter 7 assesses the relationships between bacteria and resources and the potential role of subsurface flowpath connections. Distributional relationships between hyporheic bacteria and invertebrates are depicted for the first time. Chapter 8 highlights the transitions in the hyporheic invertebrate community structure along flowpaths and the importance of organic matter resource gradients relative to sedimentological gradients. A model of the invertebrate community organization within the hyporheic habitat of the Töss River is presented. This conceptual model includes the likely role of biotic interactions and stochasticity. The clinal nature of the hyporheic community structure is discussed from three perceptive scales and their corresponding models of community organisation (sensu Townsend 1989, 1991). It is concluded that the nature of hyporheic interstices is represented better by aspects of gradients and transitions than by static delineations in zones with distinct boundaries. Due to inherent dynamics the clinal perspective is more appropriate than attempts to define boundaries on distinct temporal and spatial scales. Indeed, the discoverers of the 'Hyporheal' - Orghidan and Schwoerbel - were themselves far from a zonation perspective and Bretschko (1991, 1992) even proposes dissolving the vertical differentiation between the benthal and the hyporheal.

References


CHAPTER 2

The ecological significance of exchange processes between rivers and groundwater

SUMMARY

1. This review focuses on the connectivity between river and groundwater ecosystems, viewing them as linked components of a hydrological continuum. Ecological processes that maintain the integrity of both systems and those that are mediated by their ecotones are evaluated.

2. The hyporheic habitat, as the connecting ecotone, shows diverse gradients. Thus it can be characterized by hydrological, chemical, zoological, and metabolic criteria. However, the characteristics of the hyporheic habitat tend to vary widely in space and time as well as from system to system. The exact limits are difficult to designate and the construction of static concepts is inadequate for the representation of ecological processes. The hyporheic interstices are functionally a part of both the fluvial and groundwater ecosystems.

3. The permeability of the ecotone depends on the hydraulic conductivity of the sediment layers which, because of their heterogeneity, form many flowpath connections between the stream and the catchment, from the small-scale of a single microhabitat to the large-scale of an entire alluvial aquifer. Local up- and downwellings are determined by geomorphologic features such as streambed topography, whereas large-scale exchange processes are determined mainly by the geologic properties of the catchment. Colmation - clogging of the top layer of the channel sediments - includes all processes leading to a reduction of pore-volume, consolidation of the sediment matrix, decreased permeability of the streambed. Consequently, colmation can hinder exchange processes between surface water and ground water.

4. Physicochemical gradients in the interstices result from several processes: (i) hyporheic flow pattern and the different properties of surface and ground waters; (ii) retention, caused by the filtering effect of pore size and lithologic sorption as well as the transient storage of solutes caused by diminished water velocities; (iii) biogeochemical transformations in conjunction with the local residence time. Each physicochemical parameter may develop its own vertical dynamics laterally from the active channel into the banks as well as longitudinally because of geomorphologic changes.
5. The river-ground water interface can act as a source or sink for dissolved organic matter, depending on the volume and direction of flow, dissolved organic carbon concentrations and biotic activity.Interstitial storage of particulate organic matter is influenced mainly by grain size distribution and by spates involving bedload movement that may import or release matter, depending on the season. After initial transient and abiotic storage, hyporheic organic matter is mobilized and transformed by the biota. Microorganisms account for over 90% of the community respiration. In subterranean waters most bacteria are attached to surfaces and remain in a biofilm.

6. Hyporheic interstices are functionally significant for phreatic and riverine metazoans because they act as a refuge against adverse conditions. The net flow direction exerts a dominant influence on interstitial colonization, but many other factors also seem to be important in structuring the hyporheos.

7. The hyporheic corridor concept emphasizes connectivity and interactions between subterranean and surface flow on an ecosystem level for floodplain rivers. It is a complementary concept to others which focus on surficial processes in the lateral and longitudinal dimensions.

8. The ecological integrity of groundwater and fluvial systems is often threatened by human activities: (i) by reducing the connectivity; (ii) by altering exchange processes; and (iii) by toxic or organic contamination.

2.1 Introduction

Ground water and rivers have traditionally been treated as distinct entities in most ecological research. Interest has been focused on intra-system patterns mainly due to historical perspectives, but also because of differences in the accessibility and nature of rivers and ground water. Rivers are characterized by a current creating turbulent hydraulic forces, brief retention times of the water masses, varying discharge, changing chemical conditions, unidirectional transport of material, bedload transport, and a dynamic channel morphology. In contrast, the environmental conditions of an alluvial groundwater ecosystem are more stable, they have laminar flow, long residence times, a largely constant sediment structure, and permanent darkness.

However, a separate approach to the study of rivers and ground water is unsatisfactory for the following reasons:

1 The characteristics of running waters are controlled significantly by their interactions with their surroundings (Hynes, 1975; Ward, 1989).
2 Hydrologically, surface water and ground water are very closely connected (Castro & Hornberger, 1991; Bencala, 1993; Stanford & Ward, 1992, 1993).
Groundwater ecosystems depend on energy transfer from the surface in the form of dissolved and particulate organic matter (Ghiorse & Wilson, 1988; Madsen & Ghiorse, 1993) and conversely many streams receive considerable inputs of nutrients from groundwater (Wallis et al., 1981; Rutherford & Hynes, 1987; Ford & Naiman, 1989; Fiebig & Lock, 1991).

Many flowpath connections between the stream and the catchment exist, from the small-scale of a single microhabitat to the large-scale of alluvial aquifers. Although these interactions have been documented by hydrologists for some time, river ecologists have only recently begun to recognize the significance of these exchanges for the biota and the metabolism of lotic ecosystems. Hynes (1983) was the first to give prominence to the hydrological connectivity between running waters and groundwater, by emphasising the significance of interactions for the water balance and metabolism of streams. Simultaneously, the interactions with surface water have become important for groundwater ecological research because the upper layers of porous aquifers are biologically the most active (Danielopol, 1980, 1989).

Currently the boundaries between river and groundwater ecological research are dissolving and both fields are beginning to merge toward a comprehensive ecological understanding of the hydrologic continuum.

2.2 The hyporheic zone as the ecotone between streams and groundwater

The transition between groundwater and streams was first recognized as a distinct zone by Orghidan (1959), who termed this the 'the hyporheic biotope', although Karaman (1935), Chappuis (1942), and Angelier (1953) had begun faunistic investigations in this zone some years earlier. Modern ecological research in the hyporheic zone began with Schwoerbel (1961a,b, 1964, 1967). He was the first to describe the community and hydrology of the hyporheic habitat as an integral part of the fluvial ecosystem (Bretschko & Klemens, 1986; Bretschko, 1991b; Danielopol & Marmonier, 1992) and characterized its environmental conditions. He developed the perspective of the hyporheic interstitial zone and coined the term "hyporheal" for this habitat. Schwoerbel named the epigean and hypogean organisms that colonize the hyporheal 'hyporheos', and obligate dwellers were specified as 'hyporheobionts'. Further detailed accounts of the historical developments of subterranean ecological research are given by Danielopol (1982), Danielopol & Marmonier (1992), and Gibert (1992).

As a transition zone, the hyporheic habitat shows features of both adjacent areas. The general definition of groundwater relates to subterranean water coherently filling the
cavities (Thienemann, 1925). The hyporheic zone is also a saturated, subterranean matrix of interstitial spaces characterized by permanent darkness, low current velocities, and high substrate stability; but in contrast to phreatic ground water it is partially composed of surface water with other qualities. Accordingly, White (1993) proposed a conceptual definition of the hyporheic zone as being the saturated interstices beneath the streambed, and into the stream banks, that contain some proportion of channel water, or that have been altered by surface water infiltration. Using tracer experiments Triska et al. (1989b) defined two hyporheic zones of differing mixing ratios: a surface hyporheic zone directly beneath the channel zone, containing more than 98% of advected surface water and an underlying interactive hyporheic zone with a proportion of 98 - 10% advected surface water. The latter is characterized by gradients of nutrients and dissolved gases. A different perspective is advanced by Vervier et al. (1992). They consider the model by Triska et al. (1989b) as not being sufficiently flexible because it bases boundaries between zones on modifications of water quality that are hard to localize (Danielopol, 1980), and because it does not integrate temporal changes in the extent of the zones. Therefore, Gibert et al. (1990) and Vervier et al. (1992) developed a dynamic ecotone model which distinguishes two variants, one where ground water flows into the river and one where the river recharges the ground water. They emphasize the significance of the permeability of the ecotone as a photic, mechanical, and biochemical filter.

Williams (1984) points out that the exact limits of the hyporheic zone are difficult to define, because they may vary in time and space. Its upper boundary, the boundary between the benthic and hyporheic zone, can be delineated relatively easily by the decline in light intensity and current velocity (Schwoerbel, 1964). Thus the depth of the benthic zone is restricted to a few centimetres or tens of centimetres. Although this definition corresponds with the spatial limits of autotrophic production, the dispersal capacities of the macrozoobenthos within the sediments do not allow such an exact delineation of the upper border of the hyporheic zone. Epigean macroinvertebrates leaving the benthic zone and migrating into deeper interstices lead Bretschko (1981, 1991b, 1992; Bretschko & Klemens, 1986) to term this area 'bedsediments', which can be considered as being roughly equivalent to a combination of the benthic zone and an upper hyporheic zone.

A distinction between the hyporheic zone and ground water has been attempted by using various criteria, but few correlations exist between them (White, 1993; Williams 1989, 1993). The connecting hydrological processes which maintain the extent of the hyporheic zone are highly variable (Bencala, 1993). Individual abiotic or biotic indicators appear to be unsuitable, because they do not allow an integrated consideration of the ecological aspects. Since many ecological parameters develop their own vertical dynamics (Danielopol, 1991), the concept of the hyporheic habitat has been criticized (Motas, 1963; Danielopol, 1991). Although phreatic ground water can be distinguished
from other water bodies by its stable environmental conditions, the transition between rivers and ground water represents a hydrological continuum, preventing a clear separation. Danielopol (1980) and Palmer (1993) have suggested leaving it to individual researchers to describe their particular system according to the scientific questions being asked. In this manner Stanford & Ward (1993) delineate the hyporheic zone in their ‘hyporheic corridor concept’ in a zoological, metabolic, and hydrological context. They regard it as a groundwater zone penetrated by epigean organisms with hyporheobiont life history stages (amphibionts), where microbial activities exert controls on the nutrient cycles of lotic and riparian systems, and as subterranea areas where the ground water is hydrologically interactive with the channel water over short time intervals.

In conclusion, the hyporheic zone can be distinguished from its surrounding environments because it combines features of both, although each parameter develops its own gradients. Thus an exact designation is too static and does not contribute to a functional understanding. Especially the slow current velocity, the reduced daily and annual temperature amplitudes, the gradients of physicochemical parameters, and the high stability of colonizable substrates distinguish this habitat from the benthic zone and demonstrate its unique characteristics. Because of the heterogeneous nature of the sediment matrix and discharge variability, the characteristics of the hyporheic zone tend to vary widely in space and time, as well as from system to system. This formation of gradients with their inherent variability and spatial expanse characterizes the hyporheic zone as an ecotone between two more uniform, yet contrasting, ecological systems. This zone plays a critical role in mediating different exchange processes between surface and subterranea water that are of importance for ecosystem functions, such as the mass transfer of water, nutrients and organic matter, including its transformations. Furthermore, it functions as a filter which buffers against physical and chemical influences, it is within the dispersal range of many benthic organisms and it is the contact zone between stygobiont metazoans and the nutrient rich surficial habitat. In a four-dimensional perspective of lotic ecosystems (Amoros et al. 1987; Ward, 1989), the hyporheic zone extends vertically as well as laterally (Schwoerbel, 1961b; Stanford & Gaufin, 1974; Stanford & Ward, 1988), and is of functional and structural significance for the hydrology and ecology of the alluvial flood plain (Stanford & Ward, 1993). Thus, this ecotone is functionally a part of the fluvial as well as the groundwater ecosystem. The ecologically important processes are described in detail below.
2.3 Hydrological exchange processes

Hydraulic conductivity and porosity

The permeability of ecotones is of fundamental importance for the exchange processes between ecological systems (Wiens et al., 1985; Gibert et al., 1990; Vervier et al., 1992). The permeability of the hyporheic zone depends on the hydraulic conductivity of the sediment layers, which, because of their heterogeneity, form many flow-path connections between the stream and the catchment. However, biologists should be aware that, in hydrological terminology, permeability ($K$) refers to an intrinsic material characteristic of resisting forces against a specific fluid motion and is a function of the medium (Davies, 1969). Detailed explanations of hydraulic conductivity, Darcy's Law and hydraulic gradients are given in Freeze & Cherry (1979).

The viscosity and density of water are temperature dependent, thus the hydraulic conductivity varies with temperature: a $K$ value of water at $10^\circ C$ corresponds to 0.77 times that of water at $20^\circ C$ and a $K$ of $30^\circ C$ to 1.25 times that of water at $20^\circ C$. In small streams with significant diel variations in stream temperature, Constantz et al. (1994) were able to show that reduced afternoon streamflows were caused mainly by increased infiltration rates due to the increased hydraulic conductivity.

Porosity is the ratio of pore volume to the total volume of a given sample (Davies, 1969). It is not determined exclusively by grain size and grain size distribution, but also by grain shape, surface roughness and the type of packing. A smooth surface of similar sized grains creates small cavities, in contrast to rough surfaces or a bulky packing (Marcinek & Rosenkranz, 1989).

The storage capacity of a sediment deposit can be calculated from the volume of the cavities (porosity) while its hydraulic conductivity is derived from the size, shape, and interconnectivity of the voids (Beyer, 1964; Allen, 1985; Marcinek & Rosenkranz, 1989). Although both terms (porosity and hydraulic conductivity) are related to the content of cavities, in unconsolidated clastic sediments, as is the case with fluvial deposits, these factors vary inversely with grain size; porosity increases as grain size declines, whereas conductivity decreases with grain size. However, fluvial deposits are generally heterogeneous, whereby the porosity can be relatively uniform while conductivity may vary widely (Davies, 1969). Of the various sediment parameters that can be measured, e.g. roundness and sphericity (Köster, 1964; Allen, 1985), grain size and grain size distribution are the most influential ecologically (Bretschko, 1994).

Reductions in porosity and hydraulic conductivity due to intrusion of fine sediments into a gravel bed depend more on particle size than on the hydraulic situation. In the experiments carried out by Beschta & Jackson (1979) sand particles were trapped in the
interstices within the upper 10 cm of an initially clean gravel layer, forming a barrier to further intrusion. Thus the streambed acts as a mechanical filter and, depending on the flow characteristics and particle loads, its composition and hydraulic properties may change, and a progressively reduced pore space causes a decreased seepage rate. This clogging of the top layer of channel sediments - colmation (from German: die Kolmation) - is influenced by:

1. **Physical variables**: shear stress, representing the flow conditions; the suspended load, the grain size distribution and shape of suspended particles; the hydraulic gradient of the seepage flow and its direction;

2. **Chemical variables**: type and quantity of dissolved organic matter (DOM) controlling sorption processes;

3. **Biological variables**: the activity of epilithic algae and microbial organisms developing a biolayer with adhesive capacities (Beyer & Banscher, 1975; Banscher, 1976; Geldner, 1982; Cunningham et al., 1987; Schächlchi, 1992, 1993).

Clogged sediments are characterized by tight packing and a compact texture with a low porosity, a high stability against increasing discharge, and reduced permeability (Schächlchi, 1992). Colmation is removed under natural conditions during spates involving bedload movements. These induce resuspension of deposited fine material. In stream reaches with upwelling ground water the upward hydraulic force reduces siltation and thereby tends to maintain hydraulic conductivity (Schächlchi, 1993).

**Large-scale exchange processes**

The dimension of the exchange processes between rivers and ground water is determined by the geological and anthropogenic genesis of the catchment area, hydrology, climate and geomorphology. The surface and subsurface discharge regimes are influenced by precipitation, evapotranspiration, relief, the soil and bedrock type, and patterns of human land use.

Hydrologic interactions between rivers and their subterranean environment occur by interflow through the unsaturated soil and by in- or exfiltration into the saturated zones. The direction of the exchange processes varies with the hydraulic head, whereas flow (volume/unit time) depends on sediments permeability. Precipitation events and seasonal precipitation patterns can alter the hydraulic head and thereby induce changes in flow direction. Two net directions of water flow can be distinguished:

1. **The influent situation**: surface water contributes to the subterranean flow (infiltration, downwelling, stream-fed aquifer, recharge of aquifer);

2. **The effluent situation**: ground water drains into the stream (exfiltration, upwelling, aquifer-fed stream).
Under conditions of low precipitation baseflow originates from ground water. In many streams this exfiltration constitutes the discharge most of the year (Hynes, 1983). In contrast, under conditions of high precipitation, surface runoff and interflow gradually increase, leading to higher hydraulic pressures in the lower stream reaches which cause the river to infiltrate its banks and recharge the aquifer (Matthess & Ubell, 1983). This process is important to the water budgets of rivers and ground water (Baumgartner & Liebscher, 1990), particularly in alluvial and lowland rivers (Ubell, 1987). During a spate the river loses water to bank infiltration, which reduces the flood level and recharges the aquifer. The volume of the bank storage depends on duration, height, and shape of the flood hydrograph as well as on the transmissivity and storage capacity of the aquifer. During a dry season the release of stored water compensates for a decrease in stream discharge. In some river reaches the water released to the river from bank storage originating from flood runoff can exceed groundwater discharge under baseflow conditions. Bank storage may also exceed groundwater regeneration by precipitation (Baumgartner & Liebscher, 1990). Thus, the successive discharge and recharge of the aquifer has a buffering affect on the runoff regimes of rivers.

Groundwater exfiltration may occur diffusely or at discrete locations. Perennial, intermittent, or ephemeral stream discharge conditions depend on the regularity of the baseflow, which is determined by the groundwater level. In perennial streams the baseflow is more or less continuous, whereby they are primarily effluent and flow year round (Gordon et al., 1992). Intermittent streams receive water only at certain times of the year and are either influent or effluent depending on the season. In ephemeral streams the groundwater level is always beneath the channel, so they are exclusively influent when they are flowing (Gordon et al., 1992).

From a catchment perspective, the relationship between discharge and recharge generally develops a tendency along a decline in slope. In steeper and coarser degrading headwater reaches exfiltration will prevail, while in aggrading lowland reaches infiltration will gain in importance (White, 1993). However, subdividing a fluvial system may appear artificial because sediments are stored, eroded and transported in all zones (Schumm, 1977) and on this scale other factors also have a major influence on the water movements. Of major importance are subterranean geomorphology and catchment surface area, the stream order, and the intensity, frequency, duration, amount, and distribution of precipitation. Geological formations cause the slope to be irregular and degradation and aggradation zones often alternate. Geological constraints can effect an incision and the development of narrow valleys, which can change at knick points into deep basins filled with fluvial (and/or glacial) sediments (alluvium). Below such a knick point large-scale downwelling zones may exist, while ground water will tend to upwell at the downstream end of the alluvium (Fig. 1).
Figure 1. Schematic representation of large-scale downwelling (D) and upwelling (U) zones, at the upstream and downstream ends respectively, of an alluvial basin. Small-scale up-(u) and downwelling (d) zones are indicated as they appear in the riffle-pool sequence of an alluvial river.

Three cross-sectional types of potential surface-groundwater interaction can be distinguished, depending on the volume of sediment deposition over which a stream flows (White, 1993):

1. Surface water flowing over an impermeable stratum without any surficial-subterranean exchange processes.
2. The channel consists of a more or less extended sediment layer over an impermeable layer and is influenced only by advected surface water maintaining a hyporheic zone.
3. A large sediment deposition with a groundwater zone which is in contact with the surface water mediated by a hyporheic zone.

Within a geomorphological continuum four types of sinuosity can be distinguished (Ferguson, 1987) and have been described by Amoros et al. (1987) as functional sectors arising from the integration of geomorphological processes and ecological functions. These patterns influence the potential amount of water exchange within a river segment:

1. A gorge stream flowing in a single, stable and straight channel in a deep valley. The high transport capacity and dominant erosional activity in streams of this type result in unstable sediments. Lateral and vertical exchange processes are of minor significance.
2. A braided pattern is characterized by highly mobile multiple channels with unstable bars and islands above an alluvial fill. The shallow, stony channel has a high transport capacity and shows large bedload transport. This results in highly variable erosional and
depositional zones. Rapid lateral channel migration and high permeability of the sediments allow for maximum exchange processes vertically as well as laterally.  

3 Anastomosed rivers develop multiple channels, but in contrast to braided patterns the current velocity and transport capacity are attenuated and the positions of the channels are relatively stable. They appear as a series of subchannels that split and rejoin on a longitudinal scale many times the width of the channel (Collinson, 1986). The relatively stable streambed consists of fine grained sediments with low permeability. Nevertheless, on a floodplain scale, with numerous upwelling and downwelling zones, the interactions with the ground water and surface water are manifold. The braided and anastomosed geomorphic patterns of an alluvial flood plain often appear together since the latter develops in aggradation zones with low slope at the margins of braided sections.  

4 The meandering river develops a sinuous pattern, that is typically regular with a ‘wavelength’ related to channel width (Collinson, 1986). The streambed form of meandering rivers is similar to that of anastomosing rivers, characterized by a deep channel with low current velocities due to the low slope, and a mainly suspended load. However, it has only one continuous winding channel with considerable lateral migration over time. Even in meandering river segments intense hydrological interactions take place, but the fine particulate load can cause clogging of the sediments. Erosional forces can have long-term effects during flood discharge conditions by removing siltation and thereby enhancing infiltration.

Channels within gorges are controlled mainly by the characteristics of geologic formations (‘bedrock-controlled’). The geomorphic patterns of the other channel forms are controlled predominantly by fluvial flow processes (‘alluvium-controlled’) (Gordon et al., 1992). The streambed and bank material of alluvial rivers consist of materials transported under recent flow conditions, and the entire alluvium is composed of debris deposited by the stream (Schumm, 1977) or fluvioglacial outwash (Huggenberger et al., 1994a) over geologic time scales. In some regions alluvial fans are a typical landscape feature (Collinson, 1986). During the genesis of an alluvial deposit the former migrations of the river channel also create a heterogeneous sediment matrix, resulting in a complex mosaic of subterranean flowpaths (Huggenberger et al., 1988). This can have an enormous impact on the exchanges between surface water and ground water. The deposits of braided, anastomosed and meandering river segments differ in their textural composition (lithofacies) and hydraulic properties (Allen, 1970; Collinson, 1986). For instance, rare erosion enables the development of a mature vegetation cover on the interchannel and floodplain surfaces, filtering suspended material and enhancing soil formation. After an aggradation on the flood plain during highvolume flow conditions the soil will remain as a relict and appear as a subterranean layer of low hydraulic conductivity. In contrast, in a highly dynamic braided river system (e.g. the Alpine
Rhine), seems to leave gravel deposits of rather low structural diversity, compared with other braided river systems (Siegenthaler & Huggenberger, 1993). Preservation of sedimentary structures under low discharge conditions is inhibited in the braided river deposits of the Alpine Rhine River. Any sediments deposited at elevated locations such as floodplain deposits or bars, are successively destroyed by channel formation and are replaced by channel deposits, which in turn may be reworked by pools which operate at the lowest geometric levels (Siegenthaler & Huggenberger, 1993). An active channel that becomes uniformly filled during an aggradation event can result in a zone of high permeability. Such a paleochannel represents a structure of preferential subterranean flow, which can act as a downwelling zone at the upstream end and as an upwelling zone at the downstream end. The succession of aggrading and degrading processes creates a characteristic mosaic of deposit facies with heterogeneous hydraulic conductivities (Freeze & Cherry, 1979). An exemplary three-dimensional analysis of the evolution of a fluvial system is given by Garcia-Gil (1993).

The variability and distribution of the hydraulic conductivities of streambed deposits and alluvial sediments act as key factors determining the volume of large-scale and small-scale exchange processes, as well as the residence time of water within the riverine aquifer. Ground-penetrating radar appears to be a good tool for estimating the textural composition of deposits (Huggenberger et al., 1994 a,b).

**Small-scale exchange processes**

Local up- and downwelling processes are determined by geomorphologic features such as discontinuities in slope and depth, riffle-pool sequences as well as changes in the direction of flow. Advection is promoted by high permeability and roughness of the streambed as well as by obstacles that protrude into the channel (White, 1990; Williams, 1993). The hyporheic zone actually consists of multiple flow paths (Triska et al., 1989b; Bencala, 1993).

The significance of streambed topography for hydrological exchange processes has been demonstrated for riffle-pool sequences (Vaux 1968; Thibodeaux & Boyle, 1987; Savant et al., 1987): decreasing stream depth causes a high pressure zone at the end of a pool, where surface water downwells into the sediments, displacing interstitial water. The porewater travels for some distance as underflow beneath the riffle (Jackman et al., 1984; Munn & Meyer, 1988). At the end of the riffle increasing stream depth effects a low pressure zone, causing an upwelling. Tracer experiments by Harvey & Bencala (1993) indicate that these convexities and concavities in streambed topography control the interactions between subsurface and channel flow. River water infiltrates locally and flows in well-defined flowpaths through the alluvium. These surface water-filled
substreams returned to the stream 1 - 10 m downstream and appear to be isolated from
the large-scale system of groundwater delivery to the stream. However, an advective,
longitudinal underflow in porous media generally induces dispersion in all dimensions
(Freeze & Cherry, 1979; Cerling et al., 1990).

Obstacles like gravel bars, boulders, debris dams, log jams, lamprey nests, macrophyte
aggregations and beaver dams create localized differences in head pressure which induce
complex subsurface flow patterns (Hendricks & White, 1988; White, 1990). Salmonid
fish flush out fines when preparing their spawning sites (Lisle, 1989; Kondolf et al.,
1993), thereby altering advective flow (Cooper, 1965).

Obstacles and streambed roughness tend to cause an influx of channel water into the
hyporheic zone, even in effluent stream reaches. A thermally induced, density dependent
mechanism causing convection of surface water into the interstices has been proposed by
Whitman & Clark (1982). Cooler stream water should tend to displace warmer interstitial
water seasonally during winter and diurnally during the night in summer and autumn. In
spring and summer, warming of the surface water during the day will inhibit this mixing
process.

In general, it must be emphasized, that the hydrological exchange and mixing
processes in the hyporheic zone are highly variable and may change on anything between
daily and seasonal time scales.

Influence of ground water on channel morphology

Effluent seepage may have a minor impact on channel roughness, by decreasing the flow
resistance, as well as on the bedform and sediment transport in sandy-bottomed streams.
In contrast, the dewatering of saturated banks after floods can cause substantial bank
erosion (Keller & Kondolf, 1990). Furthermore, these authors distinguish the direct
influences of ground water on stream channel form and processes from indirect
influences, mainly on the riparian vegetation. The importance of groundwater levels that
sustain the riparian vegetation is emphasized, because the vegetation enhances bank
stability against erosive forces by increasing the shear strength of the bank material.

2.4 Physicochemical gradients at the surface-ground water interface

Gradients between surface water and ground water develop by the mixing of water with
different physicochemical characteristics and by biogeochemical processes in conjunction
with the local residence time of the water. As a result of small-scale exchange processes,
inhomogeneous interstitial flow patterns establish gradients even without groundwater
influence. The properties of downwelling channel water are altered in the hyporheic zone. In the course of the first metres of infiltration major retention of material is caused by the filter effect of the pores and lithologic adsorption (Gölz et al., 1991; Vervier et al., 1992; Younger et al., 1993). Biological processes are responsible for the transformations of organic material and most anthropogenic micropollutants (Hoehn et al., 1983; Schwarzenbach et al., 1983). These processes within the sediments are of major significance for stream metabolism because of the much longer residence times of subsurface water and a high ratio of attached biofilms to water volume. Longitudinal flowpaths along a riffle-pool sequence (Hendricks & White, 1991, 1995) and lateral flowpaths into the bank (Williams, 1989, 1993) create three-dimensional physicochemical patterns. For the above reasons flow patterns are the major controlling factor of the physicochemical gradients, that can be observed at the surface water-ground water interface.

**Light and current velocity**

The gradients of light intensity and current velocity are the sharpest at the surface water-sediment water interface. In a uniform sediment light does not penetrate beyond depths of 4-5 times the diameter of the grain size (Schwoerbel, 1964). However, in natural sediments fine particles enter the cavities between larger particles and detritus is stored there, reducing light penetration further (Schwoerbel, 1964; Tilzer, 1969).

The current velocity is reduced as soon as the water infiltrates the benthic layer. In general, interstitial flow is around one-thousandth that of the surface water velocity, although it can vary locally and with depth (Williams & Hynes, 1974; Bretschko, 1991a; Pusch & Schwoerbel, 1994).

**Temperature**

Surficial-interstitial exchange determines the temperature in the hyporheic zone because groundwater temperature generally (excepting geothermic influences) vary according to mean annual air temperatures, while rivers display pronounced diel and seasonal fluctuations. Along an infiltration gradient, the annual thermal amplitude of the water declines, with downwelling water cooling down in summer and warming up in winter, but the annual temperature cycle remains (Schwoerbel 1961a, 1967; Williams & Hynes, 1974; Pennak & Ward, 1986; White et al., 1987; Crisp, 1990; Evans et al., 1995). Generally there is no sudden decrease in temperature and the fluctuations become lagged and attenuated with increasing depth and distance from the infiltration site. In lateral, sun-exposed parafluvial sections, the temperature of the interstitial water (particularly of
the capillary fringe) can be higher than in the stream (Schwoerbel, 1961b; Valett et al., 1990). In effluent reaches, the temperature in the hyporheic zone corresponds to the groundwater temperature, and temperature fluctuations are absent or minimal (Shephard et al., 1986).

The temperature regime in the interstices is important for the groundwater and fluvial system because invertebrate development and microbial activity are temperature dependent (Ward & Stanford, 1982). This can cause annual variations of other physicochemical parameters such as pH, redox potential and concentrations of nutrients and trace metals (Von Gunten & Kull, 1986; Von Gunten et al., 1991).

The interstitial flow through a heterogeneous sediment matrix interacts with the river water and the groundwater to various degrees along its complex flowpaths. Water composed of a wide spectrum of mixing ratios and subterranean residence times is thereby distributed within the alluvium. The hydraulic head pressure and localized differences in sediment permeability cause near-surface ground water to erupt in springbrooks and fill, and/or flow along floodplain depressions created by the surficial scouring of flooding events in conjunction with the riparian vegetation, large woody debris and geomorphic features. These diverse surficial water bodies lateral to the main stream of the river are heated in summer and cooled in winter to temperatures depending on the ambient air temperature, solar irradiance, the size of the water body, and the volume and temperature of groundwater influx. In this way aquatic habitats with wide ranging temperatures can be encountered on alluvial floodplain surfaces, especially during the summer months (Gonser, 1994). Their annual temperature regimes show characteristic fluctuations depending on the temperature and volume of ground water they receive. A schematic representation of the water temperatures that can be encountered on a temperate alluvial flood plain in summer and in winter is given in Fig 2.

**Figure 2.** (next page) Temperature diversity of aquatic habitats along the lateral dimension of an idealized alluvial flood plain caused by surface-groundwater interactions in a temperate region during summer (a) and winter (b). Terminology of the subunits of the fluvial hydrosystem according to Amoros et al. (1987), Copp (1989), and Ward & Stanford (1995), is as follows: eupotamon, lotic channels of various geomorphological origin; parapotamon, semi-lotic channels of various geomorphological origin, upstream end abandoned; paleopotamon, abandoned anastomosed and meander channels; plesiopotamon, abandoned braided channels.
Dissolved oxygen

The existence of dissolved oxygen in the hyporheic zone is evidence for a significant exchange between stream and subterranean water, since photosynthesis is impossible in the interstices and diffusion rates are low (Schwoerbel, 1967; Grimm & Fisher, 1984). In general, the oxygen content declines with increasing depth and lateral distance from the channel until it reaches the more constant conditions of ground water (Schwoerbel, 1961a, 1964; Poole & Steward, 1976; Pennak & Ward, 1986; Valett et al., 1990; Triska et al., 1993a). Decreases in dissolved oxygen correspond with the interstitial flow, community respiration rate and residence times of the water. Thus the oxygen content is normally higher in downwelling zones than in upwelling zones (Valett, 1993).

The respiration rates of interstitial communities can approximate benthic respiration rates on an area basis (Grimm & Fisher, 1984). Hyporheic metabolic activity can cause reductions in the oxygen saturation from 100% in surface water to 0% in the interstices, depending on the residence time of the water. Hyporheic import of degradable organic material in streams contaminated by sewage effluents can induce oxygen depletion and anaerobic conditions (Pieper 1976; Mestrov & Lattinger-Penko, 1977/78, 1981; Kirchengast, 1984). In fine-grained sediments, or those with pore spaces sealed by fine particulate matter, anoxic conditions can prevail below a small oxygenated layer a few millimetres thick, especially during summer (Strommer & Smock, 1989; Wagner et al., 1993). The filtering effect for matter in an ecotone with clogged interstices is governed by aerobic and anaerobic processes, and not hydrodynamics as it is in permeable aquifers (Vervier et al., 1992). Anaerobic zones within the hyporheic zone are not exceptional (Dahm et al., 1991) and can be significant for the riparian vegetation since such conditions increase nutrient concentrations (Dahm et al., 1987). The relationship between biological oxygen demand and oxygen import determines the redox conditions, which affect the mobility of trace metals (Mn, Cu, Zn, Cd, Fe, Hg) in the interstices (Von Gunten & Kull, 1986; Von Gunten et al., 1991; Younger et al., 1993; Trémolières et al., 1993).

Carbon dioxide and pH

The relationship between photoautotrophic uptake, respiration, the dynamic equilibrium with the carbonate minerals, and atmospheric exchange processes determine the content of dissolved carbon dioxide in natural waters. In the hyporheic zone, the CO2 concentrations are determined mostly by the community respiration rates, to which microbial activity contributes more than 90% (Pusch, 1993; Pusch & Schwoerbel, 1994). CO2 level are elevated in the hyporheic interstices (Husmann, 1971; Williams & Hynes, 1974; Pieper, 1976; Whitman & Clark, 1982) due to the lack of photosynthetic activity.
and atmospheric exchange, the long residence time of the throughflow, and the large area colonized by microbial biofilms.

Linked to the CO2 content is pH, which is lower in the interstices than in the channel water. In highly permeable sediments, diel cycles caused by the photoautotrophic activity may appear delayed in the hyporheal depending on the water's travel time (Schwoerbel, 1961a, 1967).

**Nitrate and ammonium**

The flood plain, hyporheic zone, and riverine aquifer as interconnected components of the fluvial system play a decisive role in the transfer of nitrogen in and between landscapes. They act as buffering zones between the terrestrial and aquatic environments for nitrogen compounds as well as other nutrients (e.g. orthophosphate, Fe, Ca, Mg), because of their high retentive and transformative properties. Thus this riverine transition zone clearly has the filtering qualities of an ecotone (Schlosser & Karr, 1981; Yates & Sheridan, 1983; Lowrance et al., 1984; Peterjohn & Correl, 1984).

Intense nitrogen processing occurs in heterogeneous hyporheic zones with anaerobic regions, especially at the aerobic-anaerobic interface, due to the interplay of nitrification and denitrification (Duff & Triska, 1990; Triska et al., 1993b). Both processes are related to the gradients of dissolved oxygen, dissolved organic carbon (DOC), ammonium and nitrate, and thus to the fluxes between ground water and surface water (Hill, 1990; Triska et al., 1990a; Triska et al., 1993a). Triska et al. (1993b) proposed a model in which hyporheic ammonium adsorbed to clay sediments is in equilibrium with the interstitial ammonium, which in turn is influenced by the exchange with surface water. Under aerobic conditions, nitrifying bacteria oxidize ammonium to nitrate. In anaerobic zones the nitrate can either be denitrified to nitrogen or reduced to ammonium by the degradation of bioavailable DOC. However, in general oxygen seems to be the dominant regulator of the denitrification process, with a threshold of at least 10 μmol L⁻¹ (Tiedje, 1988), although there is evidence for aerobic denitrification (Robertson & Kuenen, 1984), and even nitrate-ammonification does not appears to be an obligatory anaerobic process (Brons & Zehnder, 1990). Dinitrogen can be fixed by symbiotic bacteria associated with alder (Alnus spp.), otherwise it disappears from the system. Nitrate entering the stream can be taken up by epiphyton and may have a positive influence on the recovery rates of benthic algae which have been impacted by disturbances, especially in nutrient poor streams (Grimm et al., 1991; Valett et al., 1992, 1994).
2.5 Retention and metabolism of organic matter at the surface groundwater interface

Organic matter is present within the sediments in three forms: as dead organic particles and dissolved molecules, as living organisms and as biofilm (Leichtfried, 1988, 1991). The amount and distribution of organic matter depends on the input rate, abiotic as well as biotic processing, hydraulic transport capacity, retentive structures, and the channel morphology (Naiman & Sedell, 1979). The process of retention is the connecting link between input and storage, and thus opposes to the transporting character of streams (Speaker et al., 1984). Retention enables the utilization of organic matter by the stream biota and consequently is decisive for the metabolism of fluvial ecosystems (Lush & Hynes, 1978; Dahm, 1984; Triska et al., 1990b). Solutes are generally retained initially by physical and chemical transient storage, while biotic uptake dominates the process of retention later on (Bencala et al., 1984; McDowell, 1985; Triska et al., 1989a, Kim et al., 1992).

Conceptually retention can be viewed as taking place on three spatial scales:

1. On a large-scale in relationship to the extent and structure of the flood plain (constrained vs unconstrained), the hyporheic corridor and the length of the water course.
2. On a meso-scale relating to morphological structures such as riffle-pool sequences, streambed roughness, and obstacles like boulders or log jams, the condition of the riparian vegetation, changes in flow patterns and sedimentologic features of the alluvium.
3. On a micro-scale influenced by the development of biofilms and lithologic properties of the sediment as well as the sorptive capacities of previously stored organic matter. The latter are so strong that where the organic matter exceeds 1% of the mineral sediments by weight its sorption far outweighs that of the mineral surfaces (McCarty et al., 1981; Karickhoff, 1984; Younger et al., 1993).

Microorganisms have a controlling function on fluvial metabolism as they can be responsible for more than 90% of the community respiration (Pusch & Schwoerbel, 1994), although their biomass may not be large (Fenchel & Jorgensen, 1978; Findlay & Meyer, 1984). In the hyporheic interstices of a third order Black Forest mountain stream the ratio of total particulate organic carbon to bacterial carbon was up to 562 : 1 (Fischer et al., 1996). However, in the loosely attached particulate organic matter (POM) fraction (sensu Pusch, 1996) this ratio ranges between 28 and 23 : 1. Furthermore, 7.6% to 14.2% of the bacteria within the loosely attached POM fraction were active. This is significantly higher than within the POM fraction that was strongly associated with the sediments, where the active percentage ranged from 1.4% to 4.7% (Fischer et al., 1996). The proportion of actively respiring cells in benthic samples has been found to be less than 25% (Bott & Kaplan, 1985), whereas in groundwater samples Marxsen (1988b) found the proportion ranging from 0.66 to 7.4%. With short generation times, a wide-ranging
metabolic potential and high metabolic activity rates, bacteria play the major role in biochemical degradation and transformation of DOM and POM. Many of these processes are mediated exclusively by heterotrophic bacteria because of specifically required enzyme systems (Chróst, 1990; Chróst & Overbeck, 1990). Bacteria are important not only as decomposers of organic compounds, but also as a food resource for primary consumers (Marxsen, 1988a; Meyer, 1988). They are free-living or attached to particles, associated with biofilms (Aufwuchs). In the ground water habitat most bacteria are attached to surfaces (Wolters & Schwarz, 1956; Hirsch & Rades-Rohkohl, 1983; Husmann et al., 1988). Marxsen (1982) found that in the ground water of sandy sediments interstitial bacteria contributed less than 1% of the total number of bacteria; the remainder was associated with biofilms. The latter are superficial biological layers consisting of consortia of bacteria, cyanobacteria, algae and fungi which are embedded in a polysaccharide matrix secreted by the microorganisms themselves (Lock et al., 1984). Protozoa and micrometazoa can graze these biofilm (McFeters et al., 1984; Bott & Kaplan, 1989, 1990). The composition of, and the relationship between, autotrophic and heterotrophic organisms vary according to the ambient environmental conditions, especially with respect to light intensity and algal DOC release (Rounick & Winterbourn, 1983). Complex biotic interactions occur within the biofilm as internal food webs and cross-feeding, but no consistent trends concerning microbial physiology have been determined (Ghiorse & Wilson, 1988; Loosdrecht et al., 1990).

In Bärlocher & Murdoch's (1989) study on hyporheic biofilms on artificial surfaces, bacterial cells contributed up to 20% of the total carbon content. Intruding organic molecules are depolymerized by the extracellular enzymes that bacteria excrete (Jones & Lock, 1989; Chróst, 1990) into this extensive, highly porous polymer matrix (> 95% water; Charakis, 1984). The polyanionic nature of the extracellular polymers effects a high adsorption capacity for inorganic and organic molecules that diffuse into the matrix (Lock et al., 1984). However in turbulent waters minute 'channels' inside the biofilm matrix might enable advective solute movements (Lock, 1993). Thus on a molecular level the material uptake by biofilms represents a retention process, where abiotic and biotic immobilizations are combined (Fiebig & Marxsen, 1992; Freeman et al., 1995) and the polysaccharide matrix may buffer varying supplies of dissolved organic substrates (Freeman & Lock, 1995). Bretschko & Leichtfried (1988) found that in riverine bedsediments the biofilm appears to incorporate most of the organic matter.

Bacterial uptake is restricted to the low-molecular-weight fraction of the DOM pool, and only the labile, larger compounds can be depolymerized by extracellular enzymes (Chróst, 1990). Bacterial production is controlled more by the composition of the organic matter than by its absolute amount (Bärlocher & Murdoch, 1989; Münster & Chróst, 1990). Biochemically recalcitrant compounds constitute most of the ambient DOM
(Thurman, 1985); however, their exact proportions and their chemical identities are hard to determine because of the inherent complexity of DOM composition (Fiebig & Lock, 1991). Even the analytic distinction between dissolved and particulate organic matter is arbitrary and does not consider its origin and ecological function (Steinberg & Melzer, 1985; Münster & Chróst, 1990). Furthermore, by considering the scale of complex DOM fluxes this differentiation loses significance (Pusch & Schwoerbel, 1994).

Although occurring in low concentrations, the labile fraction seems to be in a rapid state of turnover (Fiebig, 1992), imparting a major impact on the trophic structure of the ecosystem. Ladd et al. (1982) found a higher metabolic activity of interstitial groundwater bacteria than in drifting bacteria, and that the former could utilize DOM more readily. DOM has been regarded as the lowest trophic level of a foodweb in aquatic ecosystems, nourishing heterotrophic microorganisms which thrive as the next trophic level (Münster & Chróst, 1990). This microbial uptake of DOM and its transformation renders the DOM available for consumer organisms (Dahm, 1984). DOM is the major energy source in the heterotrophic phreatic and hyporheic systems and POM gains importance in upper sediment layers. Thus the interstitial biota are dependent on inputs from autotrophic, surface habitats. However, various studies emphasize the quantitative importance of DOM input from ground water into streams (Wallis et al., 1981; Hynes, 1983; Naiman et al., 1987; Rutherford & Hynes, 1987; Triska et al., 1989ab; Marxen, 1988; Stanford & Ward, 1988; Ford & Naiman, 1989; Fiebig & Lock, 1991; Fiebig, 1992, 1995; Fiebig & Marxsen, 1992) as well as from soil water (Wallis et al., 1981, Rutherford & Hynes, 1987; McDowell & Likens, 1988; Cronan, 1990; Fiebig et al., 1990; Gregory et al., 1991). Although the microorganisms must be induced in order to be enzymatically prepared for the utilization of a pulse of DOM (Kaplan & Bott, 1985), Fiebig (1995) has shown that even short-term pulses of DOM may be immobilized and processed in upwelling hyporheic zones. Groundwater DOM and its degraded products can also be transported to the benthic zone and used by the periphyton (Stanford & Ward, 1988, 1993; Ward, 1989; Coleman & Dahm, 1990). On the other hand the DOC of infiltrating stream water may be metabolized in the hyporheic zone (Bott et al., 1984; Triska et al., 1989b; Findlay et al., 1993; Marmonier et al., 1995). Consequently, the hyporheic zone can act as a source or a sink for DOC, depending on the volume and direction of flow, DOC concentrations and biotic activity (Vervier et al., 1992; Kaplan & Newbold, 1993). In general, solute concentrations are enriched in the hyporheic zone relative to surface waters (Grimm & Fisher, 1984; Crocker & Meyer, 1987; Ford & Naiman, 1989; Valett et al., 1990; Valett, 1993; Wagner et al., 1993), but may vary in detail depending on the redox potential (Triska et al., 1989b). The local conditions are influenced substantially by channel topography (Vervier & Naiman, 1992; Findlay et al., 1993; Vervier et al., 1993), and the permeability and roughness of the sediments (Triska
et al., 1989b; Meyer, 1990; Vervier et al., 1992), and are subjected to diurnal fluctuations due to photoautotrophic production, especially during summer (Kaplan & Bott, 1983, 1989; Rutherford & Hynes, 1987).

The significance to fluvial metabolism of transformations in interstitial water increases with the sediment permeability, and with the stream water velocity, both of which increase water velocity in the deeper interstitial layers. Thus biofilms in deeper zones are exposed to the mass transport rates of the water column and contribute to the removal of solutes (Gantzer et al., 1988).

A disturbance regime can prevent or hinder the development of benthic algal mats which can cause a gradual external colmation that diminishes the uptake of solutes by underlying gravel. This layer reduces inflow and can consume labile DOC. Finally, this process can lead to a depletion of nutrients and organic components in the interstices, which hinders the development of an active interstitial microbial community (Mickleburgh et al., 1984). On the other hand, exudates from epilithic algae are a source of high quality DOM that can increase hyporheic metabolism if sufficient water exchange is provided (Hedin, 1990; Findlay et al., 1993).

The temporal distribution of interstitially stored organic matter is a consequence of its type, the hydrological regime, season, and the mechanism of transport (Leichtfried, 1988). Maximum storage occurs during high discharge and surface runoff, which imports allochthonous material from the soil, and also during autumn after defoliation. The fine POM (FPOM) and coarse POM (CPOM) < 10 mm fractions especially are transported into the sediments during spates (Leichtfried, 1988; Bretschko, 1991; Bretschko & Moser, 1993; Naegeli et al., 1995). Surprisingly, in a porous gravel stream in Austria more than 80% of the annual POM input does not enter the sediment in autumn, but rather between April and August when high discharge fluctuations occur, and less than 10% enters after defoliation (Bretschko & Moser, 1993). However, depending on the season, floods involving bedload movement may release stored organic matter from the hyporheic zone. In a sandy-bottomed stream the removal of organic matter due to scouring during a spate in late summer had an enduring effect that was not compensated for by the following autumnal input of detritus (Metzler & Smock, 1990). In this stream the annual hyporheic storage of detritus to a depth of 20 cm was approximately an order of magnitude greater than on the surface. In general, fine-grained stream sediments contain larger amounts of stored detritus than streams with coarse sediments (Metzler & Smock, 1990; Wagner et al., 1993). This concurs with Leichtfried's (1985) finding that POM concentrations in the sediments decrease with increasing grain size.

However, conclusions that the retention of POM in sandy-bottomed streams is more efficient than in gravel-bed streams must be made cautiously. The data must be related to the overall volume as well as to the area of the hyporheic interstitial. Therefore it is
necessary to include the maximum and average depths of the sediment which is integrated into the exchange process between the channel and interstitial water during floods as well as during low discharge periods. In coarse-sediment streams the vertical and lateral extent of this exchange zone is expected to be much larger than in sand-bottomed streams, where solutes or particles are prevented physically from intrusion in deeper layers. Valett et al. (1990) measured the concentrations of organic matter in the hyporheic zone of a sandy, fine-gravel desert stream and estimated the hyporheic storage. This was possible because there was no groundwater zone present due to adjacent bedrock. Thus, the conversion from concentration per volume to storage per area is not arbitrary. This hyporheic zone stored about three times more organic matter than the benthic surface. In this desert stream the average interstitial water volume was nearly four times that of the channel water, but the subsurface discharge rates were an order of magnitude lower than those for the channel water (Valett et al., 1990). In order to assess the retentive abilities of the hyporheic zone, the hydrological relationship between the surface and subterranean flow must be considered (Hendricks, 1993; Findlay, 1995), because of the information it provides on the potential rates of input, throughflow and output (Fig. 3), especially of DOM, which in natural waters are about one order of magnitude greater than of POM (Steinberg & Stabel, 1978; Münster & Chróst, 1990). Organic matter concentrations in the interstices must be related to annual transport in the river. However, data on POC fluxes in streams over longer periods and a broad range of discharges are rare (Hope et al., 1994). Organic matter is entrained in the sediments especially during high discharge, although the ratio between interstitial import and surficial organic matter transport may be low. To date, most investigations on interstitial POM content have failed to distinguish between upwelling and downwelling zones, although exfiltration tends to prevent deposition of fine material, and infiltration may result in interstitial pores being filled. Furthermore, the overall volume of flow through the sediments of a stream reach must be taken into account, because this increases nutrient retention by increasing the residence time relative to surface transport. Using tracer experiments, Munn & Meyer (1988) concluded that diminished interstitial flow depresses retention and results in longer nutrient spirals.

2.6 Functional importance of the river-groundwater ecotone for the biota

Metazoans within the river-groundwater transition zone include hyporheobiont species, which complete their entire life cycle in hyporheic interstices and normally do not occur in the benthic zone (permanent hyporheos), as well as hyporheophile species advancing
into this intermediate zone between their usual habitats (occasional hyporheos: epigean aquatic insects and fish embryos; stygobiont crustaceans) (Orghidan, 1959; Schwoerbel, 1961ab, 1964; Williams & Hynes, 1974). A third group consists of 'amphibionts': epigean insects that obligatory complete their larval development in the hyporheic interstices (Stanford & Ward, 1993). The term stygobiont was coined for the groundwater fauna (Thienemann, 1925; Orghidan, 1959). Further information on the classification of the aquatic subterranean fauna is provided in Gibert et al. (1994).

Figure 3. An ecosystem perspective of factors controlling hyporheic throughflow and metabolism.

The composition and distribution of the hyporheos is controlled abiotically by the usable pore space, interstitial flow rates and hydrological exchange processes, which lead to the decisive environmental conditions (Fig. 4). Fluctuations of environmental conditions in the hyporheic interstices are dampened in comparison with riverine habitats, but conditions are not as balanced as in the phreatic zone. Thus the hyporheic
habitat is characterized by complex physicochemical gradients, yet higher temporal stability of physicochemical conditions and substrate than the benthic zone. This causes a shift in the ecologically significant time scales, and this is manifested by the prolonged development of stygobiont species (Schminke & Glatzel, 1988), as has been demonstrated for the subterranean Candoninae (Ostracoda) (Danielopol, 1978). This may lead to diminished metabolism (Botosaneanu, 1986), and to a compromise with lower mobility compensating for the high energy expenditure required for oxygen regulation under hypoxic conditions. This has been demonstrated for hypogean isopods (Danielopol et al., 1994).

Figure 4. Factors influencing the composition of the hyporheos.

Some of the permanent hyporheic dwellers, especially the water mites, have undergone intense evolution and adaptation to the subterranean environment, facilitated by preadaptations resulting from the periodically adverse conditions in streams (Schwoerbel, 1964, 1967; Danielopol, 1989). Further discussion on the evolutionary colonization of the interstices, biogeography, and speciation of the stygion is provided by Rouch & Danielopol (1987), Botosaneanu & Holsinger (1991) and Coineau & Boutin (1992). Considering evolutionary time scales, Ward & Palmer (1994) proposed a global interstitial highway model as a long-term route for meiobenthic taxa along a continuous
alluvial aquifer system connecting different subterranean habitats and ultimately surficial aquatic habitats.

The biodiversity of an ecotone is generally believed to be higher than in the adjacent areas (edge effect), due to overlap as well as to communities being specific to the ecotone (Naiman et al., 1988). The contrasting characteristics of rivers and ground water result in substantially higher local species richness in the surface habitat than within the ecotone and the phreatic zone. Therefore Gibert et al. (1990) suggested an intermediate species richness caused by deteriorating conditions for fluvial species, arising from decreases in oxygen and organic matter contents, the absence of a photoautotrophic production and primary consumers as well as filter feeders, and reduced pore spaces. Other reasons might be the increased environmental variability for stygobiont species that are adapted to stable conditions, and the low number of hyporheobiont species. However, comparative considerations on subterranean biodiversity remain uncertain at present, because, on a global scale, the groundwater biota are hardly known (Gibert et al., 1994). On a regional scale endemic species probably exist, and biodiversity can be expressed at many levels of biological organization (Noss, 1990). These have not been investigated comprehensively in groundwater ecosystems.

The hyporheic zone is used functionally by early instars of benthic insects as a refuge against strong currents (shear stress), extreme temperatures (during winter ice formation on the stream bottom, and physiologically dangerous surface temperatures in summer), and offering stable substrates during bedload movement (Schwoerbel, 1964, 1967). In high altitude streams with frequent bedload movement, the whole biocoenosis of the benthic zone may persist in the hyporheic interstitial (Schwoerbel, 1962). Furthermore, the interstices act as an aquatic refuge during droughts (Bishop, 1973; Williams, 1977; Sedell et al., 1990; Griffith & Perry, 1993). However, Townsend (1989) points out the lack of research on the proportion of the benthos that actually migrates into the hyporheic habitat during disturbance events. For a sandy-bottomed stream with small interstices Palmer et al. (1992) demonstrated that the hyporheic zone cannot explain the recovery rates after spates for some meiofaunal components (Rotifera, Chironomidae, Oligochaeta, Copepoda). In flume experiments only copepods and chironomids demonstrated significant downward movement induced by increased water velocity (Palmer et al., 1992). In general, the mechanism and dynamics of refugium use remain uncertain (Lancaster & Hildrew, 1993).

The hyporheic zone offers its inhabitants protection against high discharge, desiccation and extreme temperatures (Ward, 1992). It provides predictable conditions for the development of fish embryos, for the immobile life stages of insects (eggs, pupae) and diapausing organisms (Pugsley & Hynes, 1986), and protection from large predators. It also acts as a shelter against anthropogenically induced toxic pulses (Jeffrey et al.,
In conclusion, the epigean component of the hyporheos can function as a reservoir capable of recolonizing decimated benthic zones (but see Palmer et al., 1992). Benthic insects that migrate into the hyporheic interstitial to avoid adverse conditions during spates and re-emerge afterwards, contribute to population resilience on a microscale level, to resistance at the stream segment level (Townsend & Hildrew, 1994), and to species persistence over evolutionary time scales. Even algae that are transported into the subterranean water may stay viable; they are protected during unfavourable periods and may even reproduce in some cases (Poulícková, 1987).

The metazoans themselves influence sediment permeability. In less dynamic alluvial sediments the interstitial detritivores may contribute to the maintenance of an open interstitial system through their ‘pelletization’ of the silty material, which could cause colmation (Husmann, 1975, 1978, 1982; Danielopol, 1984). On the other hand, faecal pellets can accumulate and alter local sediment porosity (Danielopol, 1989).

Although the hyporheic abundance of invertebrates in a sandy-bottomed stream was up to an order of magnitude lower than in higher gradient streams with coarse sediments, the hyporheic zone accounted for 65% of the total invertebrate production (Strommer & Smock 1989; Smock et al., 1992). Transient abiotic storage and biotic uptake of organic matter and nutrients, as well as additional conversion by the alluvial foodweb, can enhance lotic secondary production by the immigration of prey invertebrates from the hyporheal, and increase nutrient supply for primary producers in upwelling zones. This hyporheic retention combined with a delayed and gradual release, enhances the stability of fluvial ecosystems.

Exfiltration of subterranean water is ecologically important over a broad spectrum of functions and spatial scales:

1 Upwelling water can be enriched in nutrients by storage and mineralization. Benthic algal communities may be subsidized by the upwelling of nutrient-rich interstitial water in oligotrophic streams (Coleman & Dahm, 1990). This hyporheic delivery can increase algal standing crop and shorten the recovery time after disturbance, and thus enhance the resilience of primary producers (Grimm et al., 1991; Valett et al., 1992, 1994). The grazing consumers may benefit from this supplementation, and hence the upwelling exerts a control on secondary production (Ward, 1989). This demonstrates a significant boundary control on ecosystem function. The small-scale distribution of some aquatic macrophytes is influenced by the upwelling of ground water as well as by interstitial water originating from the infiltrating surface water, because of their different physicochemical properties and specific requirements (Fortner & White, 1988; White et al., 1992).

2 Upwelling water can differ in temperature from the surface water, being cooler in summer and warmer in winter. In the Chilkat River (Alaska, USA) the upwelling of
ground water prevents freezing and enables the chum salmon (*Oncorhynchus keta*) to spawn during winter. These are preyed upon by the bald eagle (*Haliaeetus leucocephalus*) during this critical season for this predatory bird. They migrate from their breeding grounds hundreds of kilometers away specifically to exploit this event, rendering the world's largest eagle population dependent on the exfiltration of ground water (Hansen et al., 1984, in Keller & Kondolf, 1990). Upwelling zones in warm climates can provide cool water which is essential for the survival of juvenile salmonids, as is the case for anadromous steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*) in northern California (USA). Pools that are kept cool in summer by exfiltration might also be a critical refuge for anadromous fish (Keller & Kondolf, 1990).

3 Upwelling may prevent siltation. Lithophilous fish using gravely sediments for their spawning redds require open interstices with high oxygen content. The permeability of the sediment is not only inversely related to the content of fine substrate, but is also directly related to the survival of salmonids during their intragravel embryonal period. Thus colmation can induce higher mortality of eggs and alevins by diminishing throughflow and dissolved oxygen content, and excessive sedimentation can also physically entrap emerging alevins (Crouse et al., 1981; Moring, 1982; Carling & McCahon, 1987; Olsson & Persson, 1988; Reiser & White, 1988). Effluent ground water reduces siltation and provides a stabilized temperature regime, but may import oxygen-poor water. A 50% survival of pre-emergent embryos of *Oncorhynchus mykiss* is ensured when interstitial velocity exceeds 100 cm/h and oxygen concentrations exceed 8 mg/L (Coble, 1961; Sowden & Power, 1985). In the river studied by Benson (1953) groundwater exfiltration controlled the selection of trout redd locations and the lack of upwelling ground water prevented spawning. In contrast, Hansen (1975) found that the density of redds was the same in zones with or without groundwater exfiltration. Spawning salmon can produce topographic streambed alterations which promote convective flow, and this enhances ova survival rates (Cooper, 1965). By accumulating small stones, and thereby enlarging the inflow of surface water, lampreys build a highly permeable nest for spawning and hatching (White, 1990).

**Metazoan distribution patterns caused by river-groundwater exchange processes.**

Aquatic macroinvertebrates may respond sensitively to the prevailing flow direction and complex interstitial water patterns: The existence of some fluvial Odonata is linked to groundwater exfiltration (Castella, 1987), and some oligochaete species react sensitively to surface-groundwater interactions (Lafont et al., 1992). The distribution and composition of the benthos is possibly influenced by advective exchange (Boulton,
Increased infiltration during floods shifts the lower boundaries of the hyporheic zone into deeper sediment layers. The behaviour of benthic and hypogean crustaceans corresponds to this altered mixing pattern of surface water and ground water, and is reflected in spatial distribution patterns of the biota. For instance, benthic *Gammarus*, an indicator of surface water, intrudes into deeper sediment layers after a spate, while during low flow conditions the hypogean *Salentinella* appears in the upper layers (Gibert et al., 1990; Marmonier & Creuzé des Châtelliers, 1991; Marmonier et al., 1992; Dole-Olivier & Marmonier, 1992b; Stanley & Boulton, 1993). Channel topography also determines the positions of up- and downwelling zones and thus influences the spatial distribution of the interstitial fauna, in combination with other factors such as the content of fine substrate, POM, and dissolved oxygen (Godbout & Hynes, 1982; Williams, 1989; Creuzé des Châtelliers & Reygrobellet, 1990; Creuzé des Châtelliers, 1991; Marmonier, 1991; Boulton et al., 1992; Creuzé des Châtelliers et al., 1992; Dole-Olivier & Marmonier, 1992a). The abundance and species richness of stygobiont species increases gradually from influent to effluent zones (Dole-Olivier et al., 1993).

Local hydraulic conditions in combination with sediment characteristics appear to be more influential than altitude in structuring interstitial communities (Ward & Voelz, 1990, 1994).

Because of their high hydraulic conductivity and short residence times, preferential subsurface flowpaths, such as paleochannels, can transport water with physicochemical properties similar to the surface water into deeper alluvial layers underneath the flood plain. These subflows extend the direct connections between rivers and ground water into the subterranean landscape, and may sustain a high interstitial biodiversity and biomass by delivering resources. Ward et al. (1994) propose that paleochannels in the alluvium of the Flathead River (Montana) are a significant factor influencing the spatial distribution of crustaceans. For stygobiont metazoans the hyporheic interstitices are the contact zone to the nutrient rich surface habitat. Danielopol (1991) describes hypogean metazoans as active individuals that normally live in the temporally fluctuating and spatially heterogeneous upper sediment layers, where they disperse steadily and form aggregates according to their physiological requirements. The mobility of hypogean dwellers is illustrated by a harpacticoid copepod (*Limnocamptus echinatus* Mrázek) moving through the interstices in vertically oscillating cloud-like patches (Kowarc, 1992). The colonization of traps exposed in the upper sediment layers (30 cm) of a desert stream appears to be extremely rapid (Boulton et al., 1991). Although 90% of the organisms exist within the upper 40 cm of the highly permeable sediments of an alpine gravel stream (Bretschko, 1991a), the migratory activity of the organisms increases to a sediment depth of 70 cm, below which no measurements were made (Panek, 1991). The hyporheophilous species-rich chironomid community in this stream seems to be
organized around rapid changes in species composition, different life history strategies, resource utilization and species-specific dispersal patterns in connection with the influence of riverine disturbance, which creates dynamic resource patches and induces random colonization (Schmid, 1993). Nevertheless, we do not know how far the hyporheal is colonized by a community characterized by a specific structure and biological interactions, or whether it merely offers environmental conditions that can be exploited by an array of different interacting taxa, resulting in local assemblages of species.

An appreciation of the significance of biological interactions, such as trophic relationships and competition, for community structure and distribution patterns of the hyporheos has yet to be developed. The possible contribution of biotic interactions is assumed (Strayer, 1988; Danielopol, 1992), but their significance relative to abiotic controls is unknown.

The distributional changes of the fauna appear to be gradual on the macroscale of a cross-section from a river along the flood plain and into the depth of an alluvial aquifer, but on a microscale of individual sampling units faunal distributions may appear patchy because of site-specific discontinuities (Bretschko, 1991a; Marmonier et al., 1992; Ward et al., 1994).

In conclusion, ecological studies concerning the faunal composition, distribution, and abundance of the river-groundwater interface reveal an extraordinary patchiness and variability, owing to the inherent heterogeneity of the physical parameters. The main determinants of the interstitial habitat of alluvial rivers seem to be the usable pore space, dissolved oxygen concentrations, temperatures, organic matter and nutrient contents, which are influenced on a higher hierarchical scale by the sediment facies, the hydrology and climate (Fig. 4).

2.7 An ecosystem perspective

The hyporheic corridor concept

An ecosystem model for alluvial rivers has been developed by Stanford & Ward (1993). The hyporheic corridor concept emphasizes and discusses the connectivity and interactions of subterranean flow with different geologic and geomorphic formations. The authors point out the determining significance that alluvial flowpaths have for floodplain structure and function regarding biodiversity patterns and ecosystem metabolism.

Along a longitudinal transect, the Flathead River (Montana, USA) is characterized by deeply incised (constrained) river reaches, where bedrock reaches the surface, alternating with reaches developing wide (unconstrained) flood plains on fluvio-glacial deposits.
Surface water infiltrates the alluvium in large-scale downwelling zones at the upstream end of an alluvial basin. The interstitial water in the unconfined aquifer flows advectively, mainly along preferential pathways created by zones of high sediment permeability, and exfiltrates in large-scale upwelling zones at the downstream end of the alluvium. Depending on bedrock geomorphology and sediment permeability, ground water in the upper layers may upwell directly into the channel or into floodplain springbrooks according to the local hydraulic head pressure. A subsurface aquatic continuum is formed (the hyporheic corridor) containing a lateral component extending up to 3 km from the main channel in the case of the Flathead River (Stanford & Ward, 1988). The interactions (connectivity) between the river and the subterranean body of water, and between the river and the riparian zone, create a wide array of landscape features. The upwelling of ground water to the surface and the convergence of waters of different origins and physicochemical properties form diverse aquatic habitats within the landscape, demonstrating temporal variability according to the degree of connectivity with the discharge regime. The convergence zones promote ecological connectivity between the heterogeneous components of alluvial flood plains. They are highly productive and contribute significantly to landscape biodiversity, for which the exchanges and transformations of resources between adjacent features are of major importance. Thus the hyporheic corridor is composed of serial convergences between surface water and ground water and it alternately constricts and expands because of site-specific geomorphic features. The differences in the capacities between constrained reaches and unconstrained alluvial reaches, with their flood plains, for nutrient retention and turnover, biological production and biodiversity patterns is expressed by conceiving the alluvial reaches as ‘beads on a string’.

The concept focuses attention on: (i) the biogeochemical transformations by speciose food-webs along flowpaths through the alluvium; (ii) the control of production in the fluvial channel by the exfiltration of nutrient-rich water in large-scale as well as small-scale upwelling zones; (iii) the influence of hyporheic flow patterns on the formation, structure, and dynamics of the riparian zone, including diverse aquatic habitats; and thereby (iv) sustaining exceptionally high biodiversity within the landscape.

Comments on the hyporheic corridor concept

This concept integrates the functions of the hyporheic zone of floodplain rivers on coarse alluvia on a landscape scale. The lateral and vertical structural complexity and hydrological connectivity of the flood plain are emphasized, and these features alternate with geologically confined narrow river reaches. The lateral extent of the riparian zone is controlled by riverine floods as well as by the interstitial flow patterns, whereby the latter
forms a highly connected subterranean network - the hyporheic corridor. To date, other lotic ecosystem concepts which included flood plains emphasized only surficial events and processes as being the structurally decisive factors. Inundation, scouring and sediment transport were considered the basis for complex spatio-temporal mosaics in geomorphology, vegetation, succession, faunal distribution and migrations, and metabolism (Junk et al., 1989; Gregory et al., 1991). Although the ecosystem-level significance of subsurface flow was referred to by Amoros et al. (1987), it has been detailed explicitly in the hyporheic corridor concept by Stanford & Ward (1993). It is a complementary concept to others, integrating an often-neglected, although important, component of the fluvial hydrosystem. Therefore several concepts must be considered for a comprehensive understanding of the dynamic and hierarchical interactions between rivers and their interconnected surface and subsurface environments. For each fluvial system the relative contribution of the potential determinants must be assessed individually. For instance, permeability of sediments in rivers with a high suspended load is comparatively low, and therefore floods will tend to be the more important structural component. This appears to be the case for many streams and rivers in central Europe which have been altered by human impacts, beginning gradually with the influences of land use practices in the catchment area (Karr & Schlosser, 1978), leading to the total disconnection of the lotic water body from its environment (Brunke et al., 1994) with a consequent loss of ecological integrity.

2.8 Anthropogenically induced disruptions of hydrological exchange processes and their ecological consequences

The ecological integrity of alluvial hydrosystems is impacted by several, often interacting, human activities. Organic and toxic contamination in surface water can be transferred to the ground water in influent reaches. The quality of the downwelling surface water is normally altered during its passage through the first metres of the infiltrated sediments (Hoehn et al., 1983; Götz et al., 1991). However, this may not be the case for persistent organic compounds, e.g. chloroform and inorganic pollutants, which may contaminate extensive groundwater areas (Schwarzenbach et al., 1983; Hoehn & Santschi, 1986; Santschi et al., 1987). The retention of toxic trace metals within a more or less extended infiltration zone is not only determined by sorption capacities, but also varies with the pH and redox potential, which in turn are influenced by temperature-dependent biological activity (Von Gunten et al., 1991). Von Gunten & Kull (1986) have shown that in the Glatt river (Switzerland) the concentration of anions and metal ions in ground water was determined by the infiltration of polluted stream water up to a distance
of 110 m. In the Upper Rhine valley the springs and springbrooks fed by ground water originating from infiltrated polluted water of the canalized Rhine, have markedly altered aquatic vegetation. The macrophyte community indicates the contamination of the aquifer arising from the degree of eutrophication and the accumulation of toxic metals such as mercury. Furthermore, they integrate discontinuous releases of stored eutrophics and metals due to varying redox conditions in the aquifer (Carbiener & Trémolières, 1990; Trémolières et al., 1993). Significantly, the aquifer of the also highly polluted river III in the adjacent Alsacian Rhine valley remains uncontaminated, because replenishment of the aquifer occurs due to percolation through the active flood plain surface during high discharge. The contaminants are retained by the soil-vegetation system of the active flood plain (Trémolières et al., 1994). Thus a functional flood plain reduces the risk of groundwater contamination by a permanently or sporadically polluted river.

Metal pollution (zinc, copper) impairs invertebrate colonization, but the taxa are affected differentially (Plenet & Gibert, 1994). In streams receiving sewage the hyporheic and phreatic communities are affected gradually and can eventually be eliminated by oxygen depletion caused by the microbial degradation of imported organic matter (Husmann 1975; Danielopol, 1976; Pieper, 1976; Mestrov & Lattinger-Penko, 1978, 1981; Kirchengast, 1984). However, slight increase in organic matter supply may enhance the abundance of stygobionts which exist naturally in a nutrient-poor environment (Husmann, 1978).

Increased sewage loading can lead to external colmation by promoting the development of dense algal mats, or by causing sedimentation of an organic layer on the river bed. Internal colmation results from the intrusion of fine particulate organic or inorganic matter into the cavities (Schächli, 1993). The extent of these processes has a direct relationship with land use practices which increase seston and sediment loading (Karr & Schlosser, 1978; Platts et al., 1989). In many streams gradual colmation occurs naturally through the siltation of fine material during low discharge, alternating with a reopening of the interstices during spates or exfiltration (colmation) (Marcinek & Rosenkranz, 1989). Although increased current velocity may flush fine material out of the upper layers, only bedload movement opens deeper interstices. A balanced relationship between colmation and streambed scouring can be disturbed by increased organic and fine sediment inputs, hydroengineering, and river bank filtration for supplying drinking, industrial and irrigation water (Petts, 1988; Götz et al., 1991; Kondolf & Matthews, 1993). Each of these factors is capable of causing permanent colmation. Colmation exerts severe impacts on the renewal of ground water through river bank infiltration and the development and colonization of epigean as well as hypogean invertebrates and fish. Furthermore, alterations of the fluvial temperature regime are
possible with wide ranging implications for the biota. The mechanical opening of a colmated section of the Rhine's streambed near a drinking water bank filtration site induced a 1 m rise of the groundwater table near the river, but after a few weeks the opened section was sealed again (Gölz et al., 1991). On the other hand, a colmated bed may act as an intrusion barrier that prevents the contamination of ground water by polluted surface water (Younger et al., 1993; Komatina, 1994).

The refugial space for invertebrates is reduced by siltation of the interstices, and thus the impacts of natural and anthropogenic disturbances, such as urban stormwater runoff, are magnified (Borchert & Statzner, 1990). Sealed interstices cannot function as nurseries for the benthos. Colmation can diminish or prevent the reproductive success of fish spawning on gravel (Berkman & Rabeni, 1987; Peter, 1991; Zeh & Dönni, 1994).

Discharge fluctuations caused by hydropeaking power generation alter the mixing relationships between surface water and ground water in hyporheic interstices. This may have severe impacts on the reproductive success of gravel spawning fish (Curry et al., 1994).

River bed incision, as a consequence of bedload deficits due to sediment retention by impoundments and an increased transport capacity following channel straightening, determines the dominant subsurface flow direction and lowers the adjacent groundwater level (Galay, 1983; Kondolf & Matthews, 1993; Gölz, 1994). Desiccation of the flood plain endangers aquatic and riparian vegetation, reduces the connectivity and spatio-temporal heterogeneity of former channels, and ultimately alters biodiversity patterns (Dister et al., 1990; Allan & Flecker, 1993; Bornette & Heiler, 1994). The vegetation contributes to the resisting forces by stabilising the bank material with roots and decreasing the velocity of floodwaters. Thus, riparian vegetation which has been impacted by a lowered groundwater table, enhances the danger of stream bank erosion during spates (Keller & Kondolf, 1990). Changes from perennial to intermittent flow may alter bank vegetation and moisture content and hence fluvial geomorphology (Keller & Kondolf, 1990).

The landscape in the 'Taubergießen' riparian zone of the Rhine River has been changed dramatically induced by impoundments which have altered the relationship between groundwater flow patterns and floods as the structuring agents of the flood plain (Coch & Ewald, 1992). The pristine situation was characterized by braided patterns with many unstable gravel bars and sparse vegetation. Early anthropogenic manipulations of the water course had only a minor impact, but thalweg fixation preventing channel migration and enabled development of extensive vegetation. Nevertheless, geomorphic variability and dynamics remained manifold because of the influence of tributaries. More recently, however, raising of the river water level following the construction of impoundments prevents the surficial runoff of upwelling ground water. Today the
A riparian landscape is dominated by accumulations of exfiltrated subsurface water and an absence of the structuring force of riverine floods. This causes an absence of geomorphic dynamics, which results in the development of nothing but dense mature vegetation.

**Figure 5.** Anthropogenically induced impacts that promote the colmation of streambed sediments, and their ecological consequences.

Against the background of global climate change (Carpenter et al., 1992; Firth & Fisher, 1992), the groundwater level as a structuring landscape feature and indicator of available drinking water is of increasing concern world-wide. Simultaneously, the difficulties in identifying and ameliorating groundwater contamination caused by pollution of rivers and other point and non-point sources are becoming increasingly evident (Pye & Patrick, 1983; Edworthy, 1987; Bopp & Leiss, 1993; MacDonald & Kavanaugh, 1994). As discussed above, human impact on terrestrial and aquatic systems may lead to a reduction in the exchange processes which connect running waters to their surroundings, and thus diminish the ecological integrity of subterranean and surface water ecosystems. By preventing the communication between these systems, as mediated by their ecotones, cascading effects in ecosystem structure and function may occur (Fig.
5). It is therefore important for research and management to consider hydrological exchange processes seriously, and view streams and ground water as integrated components of a hydrological continuum.

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CHAPTER 3

The influence of hydrological exchange patterns on physiochemical gradients within hyporheic interstices

Abstract The influence of three types of hydrological exchange between a stream and ground water on interstitial water temperature and chemistry were examined in the hyporheic habitat of a prealpine gravel-bed river in Switzerland. At the study site an infiltration zone is located on the right margin of the channel and an exfiltration zone on the left margin. The midstream section is dominated by subsurface flow along the channel, which is termed as the horizontal advection zone. Sampling was conducted on 13 dates for one year by collecting interstitial water from 20, 50, 100, and 150 cm sediment depths with the use of permanent piezometer nests which were installed in 3 locations along a cross-section of the channel, each location corresponding to one of the three hydrological exchange types.

Hydrological exchange patterns determined steepness of physicochemical gradients within the hyporheic interstices of the Töss River. In the upper sediment layers of the infiltration zone physicochemical conditions resembled those of the surface water and showed high temporal variability, especially at a depth of 50 cm. In contrast, in the exfiltration zone physicochemical conditions were influenced by the more stable properties of the upwelling ground water. Therefore, gradients in the exfiltration zone were steepest in the uppermost sediments. Physicochemical conditions in the horizontal advection zone were in between those of the infiltration zone and exfiltration zone; however, they tended to resemble the conditions within the infiltration zone more, especially in their thermal conditions.

3.1 Introduction

The importance of the local hydrological exchange vectors for the ecology of hyporheic as well as benthic habitats has been recognized in recent years (Rouch, 1992; Vervier et al., 1992; Boulton, 1993; Dole-Olivier et al., 1993; Stanford & Ward, 1993; Triska et al., 1993; White, 1993; Valett et al., 1994). Several studies have focused on the influence of local upwelling and downwelling, that are induced by small-scale topographic alterations and slope discontinuities of the streambed such as riffles and pools (Vaux, 1968; Hendricks & White, 1991; Dole-Olivier & Marmonier, 1992; Hendricks, 1993; Pusch & Schwoerbel, 1994; Pusch, 1996). The stream water infiltrates locally into the bed sediment, travels within subsurface flowpaths for short distances downstream (1 - 10 m)
and exfiltrates again into the stream (Harvey & Bencala, 1993). These near-surface substreams appear to be independent of the large-scale groundwater flow pathways (Castro & Hornberger, 1991). However, river morphology and riverine processes often suffer from various encroachments by human land use and hydro-engineering (Karr & Schlosser, 1978; Bravard et al., 1986; Keller & Kondolf, 1990; Ward & Stanford, 1995; Stanford et al., 1996; Bravard et al., 1997). Many streams in central Europe are artificially constrained by straightening, bank stabilization, and weirs (Brunke et al., 1994; Bravard & Petts, 1996). In addition, obstacles like coarse woody debris are often removed, which otherwise could structure fluvial geomorphology (Keller & Swanson, 1979; Gregory & Davies, 1992). In such modified streams the extent of small-scale hydrological exchange processes is likely to be significantly reduced compared to naturally dynamic systems.

Hydraulic pressure differences between the riparian ground water and the stream water level can also induce hydrological exchange at their interface. Interactions between the surface and interstitial flow are controlled by the transmissivity of the alluvial aquifer and general flowpath directions. This large-scale system of ground water delivery is superimposed on topographically induced small-scale exchanges (Brunke & Gonser, 1997a).

The objective of this study was to examine how environmental conditions within the hyporheic interstices are influenced by different hydrological exchange vectors between riparian ground water and channel water. Three types of hydrological exchange patterns within a cross-section of the straightened Töss River were investigated: infiltration of stream water, exfiltration of riparian ground water, and prevailing subsurface flow along the channel (horizontal advection).

### 3.2 Study site, material and methods

The Töss River is a third order prealpine gravel-bed river. The study area is situated in a valley (460 m a.s.l.) upstream from the city of Winterthur, Switzerland. The formerly braided channel had been straightened and channelized by bank stabilization to a width of about 20 m early in the last century. Due to this hydro-engineering the river has downcut into its alluvial sediments and is surficially disconnected from its former flood plain. At the study site the general flow direction of the riparian ground water crosses the stream (Fig. 1). At the left margin of the stream ground water upwells into the surface water (exfiltration zone, EZ), whereas at the right margin surface water downwells into the sediments (infiltration zone, IZ). In midstream there is a horizontal advection zone (HZ) where neither infiltration nor exfiltration prevails because of neutral vertical hydraulic gradients. In each of the three zones steel piezometer pipes (internal diameter = 5 cm) were inserted to four sampling depths (20, 50, 100, and 150 cm). Interstitial water for
chemical analysis was collected by using an electric pump. Sampling was conducted at approximately monthly intervals between April 1995 and April 1996. The analysis of the physicochemical gradients was based on the following parameters: dissolved oxygen (Winkler method), Nitrite-N (standard method according to DEW, 1995), pH (Metrohm 678 EP/KF Processor), and temperature (between 10 and 11 a.m.). Measurement by ground penetrating radar (Naegeli et al., 1996) in a narrow grid of 3 longitudinal and 15 cross-sectional transects at the study site showed that no buried boulders or distinct layers of different porosities occurred (Brunke and Huggenberger, unpublished data), which could effect local inhomogeneities in throughflow patterns (Vaux, 1968).

Figure 1. Study area, showing the location within Switzerland (top), the groundwater flowpath and the location of the sampling site on the Töss River in plan view (middle), and a cross section through the sampling site (bottom). The 4 vertical lines at the infiltration, horizontal advection and exfiltration zones represent the sampling piezometers nests at these 3 locations.
3.3 Results and discussion

Temperature depth profiles in different hydrological exchange zones and seasons

Water temperature plays a central role for regional and local distribution patterns of aquatic invertebrates and fish. It controls physiology and growth, life histories, and phenologies (Ward & Stanford, 1982; Ward, 1985; Ward, 1992). Upwelling of ground water influences stream water temperature and may be important for biota inhabiting streams and flood plains. Further explanations are provided in Brunke & Gonser (1997a) and Ward et al. (in press).

In general three types of interstitial temperature depth profiles can be distinguished (Fig. 2): (A) Surface water colder than interstitial water (winter - early spring), (B) isothermal depth profiles (spring-early summer and autumn), and (C) surface water warmer than interstitial water (summer - early autumn). The change of temperature with depth was different for the hydrological exchange zones during the heterothermal phases in summer and winter. In the EZ, interstitial temperatures were warmer in winter and colder in summer at all depths, compared with the IZ and HZ. The phreatic ground water determined temperatures at depths of 100-cm and 150-cm in the EZ, whereas seasonal changes in the 20 and 50-cm depths documented mixing with inflowing surface water. The temperature amplitudes for each depth stratum were smaller in the EZ than in the other zones, and the annual mean temperature was higher (Tab. 1).

The seasonal mean temperature profiles for the IZ and HZ were only different in summer. Mean summer temperatures in the IZ were slightly higher than in the HZ at 20 and 50-cm depths, whereas mean temperatures were higher in the HZ at depths of 100 and 150-cm. Annual temperature amplitudes within all depth strata were higher in the IZ than in the HZ (Tab. 1). The comparatively narrow range of temperatures within the EZ led these sediments be the thermally more stable during the cold and warm seasons. Trout eggs incubated within the gravels of the EZ would develop faster than in the IZ and HZ, as proposed by Crisp (1990).

The importance of ground water discharge for the thermal regime of the Töss River is documented by the high stream temperatures in winter, ranging between 4.4 and 9.0°C.

Temperature profiles show the influence of surface water down to sediment depths of 150-cm in the IZ and HZ. For comparison, other studies reported stream water influx based on observed temperature patterns, at sediment depths of 10 to 30 cm (Shepherd et al., 1986), 50 cm (White et al., 1987) and 70 cm (Kirchengast, 1984).
Figure 2. Seasonal water temperature depth profiles (mean ± S.D.) within the hydrological exchange zones. n = 13.
Table 1. Mean annual temperature (°C) at depths within hydrological exchange zones; annual temperature amplitude in parentheses. n = 13.

<table>
<thead>
<tr>
<th>Sediment depth (cm)</th>
<th>Infiltration Zone</th>
<th>Horizontal Advection Zone</th>
<th>Exfiltration Zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>9.5 (13.0)</td>
<td>9.5 (13.0)</td>
<td>9.6 (11.8)</td>
</tr>
<tr>
<td>20</td>
<td>9.4 (11.4)</td>
<td>9.4 (10.7)</td>
<td>9.7 (9.2)</td>
</tr>
<tr>
<td>50</td>
<td>9.0 (10.6)</td>
<td>9.2 (10.0)</td>
<td>9.4 (6.8)</td>
</tr>
<tr>
<td>100</td>
<td>8.7 (4.9)</td>
<td>9.1 (4.5)</td>
<td>9.5 (4.3)</td>
</tr>
<tr>
<td>150</td>
<td>9.6 (7.1)</td>
<td>9.7 (5.8)</td>
<td>9.8 (4.1)</td>
</tr>
<tr>
<td>all depths</td>
<td>9.2 (13.1)</td>
<td>9.4 (13.1)</td>
<td>9.6 (11.8)</td>
</tr>
</tbody>
</table>

Interstitial dissolved oxygen concentrations in different hydrological exchange zones

In hyporheic interstices, dissolved oxygen (DO) concentrations are a consequence of the ratio between delivery by surface water and heterotrophic activity (Brunke & Gonser, 1997a). Microorganisms account for more than 90% of the interstitial community respiration (Pusch & Schwoerbel, 1994; Pusch, 1996). Therefore, severe oxygen depletion may occur in retentive and less permeable sediment (Poole & Steward, 1976; Whitman & Clark, 1982; Metzler & Smock, 1989; Wagner et al., 1993) and in subsurface water recharged by polluted streams (Pieper, 1976; Kirchengast, 1984; Malard et al., 1994). Groundwater animals have developed adaptations to cope with low DO concentrations. Hypogean taxa are more resistant to hypoxia than their epigean relatives and can recover from anaerobic stress (Malard & Hervant, in prep.). They also show different strategies in terms of oxygen consumption and ventilatory activities (Danielopol et al., 1994; Mösslacher & Creuzé des Châtelliers, 1996). Therefore, DO is a key environmental factor for hyporheic communities (Ward et al., in press). The question addressed by this study was if distinct patterns of DO concentrations occur on a small scale in different hydrological exchange zones.

A comparison of the DO depth profiles (Fig. 3) revealed that, based on annual mean oxygen concentrations, the hydrological exchange zones differ down to sediment depths of 50-cm. In the upper 20-cm, the steepest vertical DO gradients occurred in the EZ (0.082 mg/l DO per cm), intermediate gradients in the HZ (0.037 mg/l DO per cm) and minor gradients in the IZ (0.015 mg/l DO per cm). Between 20-cm and 50-cm sediment
depths, gradients were steepest in the HZ (0.072 mg/l DO per cm) and IZ (0.044 mg/l DO per cm) and less distinct in the EZ (0.024 mg/l DO per cm). Below the 50-cm depth DO gradients were negligible for the EZ and HZ, whereas in the IZ DO gradient remained distinct (0.041 mg/l DO per cm). However, despite these gradients mean DO saturation remained at high levels in all depth strata (78% - 109%), similar to the Lunzer Seebach, a comparable calcareous gravel-bed stream in Austria (Bretschko, 1991). Mean oxygen saturations above 100% in the 20-cm depth strata of the IZ and HZ demonstrate the dominating inflow of surface water, compared to the EZ with a mean saturation of 92%.

**Figure 3.** Depth profiles for dissolved oxygen concentration (mg/l) and saturation (%) within the hydrological exchange zones (mean ± S.D.). n = 13.
However, for the latter zone mixing of advected stream water with upwelling ground water is of significance too, as shown by higher DO concentrations in shallower than in deeper strata. DO is probably not a constraining factor for interstitial invertebrates due to the high concentrations throughout the hyporheic interstices of the Töss River. Nevertheless, distinct DO depth profiles within the hydrological exchange zones suggest that water circulation patterns structure the environmental milieu and metabolism within the hyporheic habitat.

In the stream water flowing above the EZ, the annual mean DO concentration was lower (11.5 ± 0.85 mg/l) than at the IZ (12.0 ± 0.97 mg/l) and the HZ (12.1 ± 0.90 mg/l). Similar patterns were also observed for pH and nitrite concentrations.

**Interstitial pH and nitrite concentration**

In hyporheic sediments the pH usually decreases with distance from the overlying stream (Schwoerbel, 1961; Husmann, 1971; Williams, 1984). The depth profiles for the hydrological exchange zones correspond to those for DO, with higher pH in the upper strata of the IZ than in the HZ and EZ (Fig. 4). Therefore, pH also reflects the relationships between surface and interstitial water mixing and heterotrophic activity.

The vertical patterns of the physicochemical conditions, as described above for temperature, DO, and pH, were even more pronounced for nitrite (Fig. 4). Nitrite, as the intermediate product during nitrification and denitrification, only occurred in trace amounts in the well-oxygenated ground water of the Töss River aquifer. The main source of ammonium is the stream water, and thus nitrite concentrations within the hyporheic interstices were indicators of surface water influx. Nitrite concentrations decreased differentially within the hydrological exchange zones towards the minimum levels of the alluvial ground water. Fluctuations of the nitrite concentration were highest at the depth of 50-cm in the IZ, similar to temperature, pH, and DO concentration. It appears that this hyporheic stratum showed widest fluctuations in its environmental conditions. This was presumably due to a varying vertical hydraulic conductivity effected by the surface flow regime resulting in different spatiotemporal degrees of colmation of the streambed (Brunke & Gonser, 1997a, b).
Figure 4. Depth profiles for interstitial pH and Nitrite-N concentrations (μg/l) within the hydrological exchange zones (mean ± S.D.), n = 13.

References


CHAPTER 4

Colmation and depth filtration within streambeds:
retention of particles in hyporheic interstices

Abstract Colmation refers to the retention processes that can lead to the clogging of the top layer of channel sediments and decolmation refers to the resuspension of deposited fine particles. Internal colmation, clogging of the interstices directly below the armor layer, may form a thin seal that disconnects surface water from hyporheic water by inhibiting exchange processes. The settling of particles under low flow conditions can cause external colmation. Colmated channel sediments are characterized by reduced porosity and hydraulic conductivity as well as by a consolidated texture. The term ‘depth filtration’ refers to the transport and storage of fine matrix sediments in interstitial layers. Depth filtration is of significance for the transport of colloidal and fine particulate inorganic as well as organic matter within the hyporheic interstices and into the alluvial aquifer. The role of depth filtration is assessed for the content (given in mg per liter) of matrix fine particles retained in the coarse framework sediment of a gravel-bed river in Switzerland. Sediment samples were taken by freeze-coring with liquid nitrogen down to 70 cm depth and by piezometers down to 150 cm depth. Seventy-two percent of the mobile matrix fine particles were smaller than 0.1 mm and 50% were smaller than 0.03 mm. The content of fines tended to increase with depth, although higher accumulations were found at intermediate depths in sediments influenced by exfiltrating ground water. Interstitial detrital particles > 90 μm showed vertical distribution patterns opposing those of total particles. These relationships revealed a differential significance of import, storage, and transport within three types of hydrological exchange zones (infiltration, horizontal advection, exfiltration) in the cross-section of the stream.

4.1 Introduction

Hyporheic interstices are the connecting ecotone between river and groundwater ecosystems and mediate the exchange processes between both of them. The permeability of this ecotone depends on the hydraulic conductivity of the sediment layers (Brunke & Gonser, 1997a). The sediment of gravel-bed rivers can be separated into two components, the framework gravel and the fine inorganic matrix particles (Petts, 1988). The proportion of these fine inorganic particles (< 2 mm: sand, silt, clay; Petts, 1988; Lisle, 1989), henceforth referred to as ‘fines’, is decisive for the hydraulic conductivity.
Fines suspended in the flowing surface water may intrude into stable gravel-beds and progressively reduce pore spaces, thereby causing decreasing seepage rates. This affects the metabolism of fluvial hydrosystems and the habitat quality for fish and aquatic invertebrates (Brunke & Gonser, 1997a; Milan & Petts, 1998).

The local retention and transport of particles < 2 mm in rivers are determined by flow conditions (shear stress, depth, kinematic viscosity, density, hydraulic gradient), by properties of the suspended load (grain size distribution, concentration, shape, settling properties, cohesivity), and by the channel sediment structure (grain size distribution, texture; Geldner, 1982; Reynolds et al., 1990; Bettess, 1992; Carling, 1992). It is generally assumed that a freely flowing stream is capable of transporting all particles < 62 \mu m which are imported to it (Jobson & Carey, 1989).

Sediment in suspension can interact with the streambed in several ways (Fig. 1):

1. Sediment may settle on the top of the streambed in areas of low water velocity (e.g. in pools, or between coarser gravels) under low flow conditions. Silt may be trapped within the structural matrix of epilithic periphyton even in turbulent water (Graham, 1990).

2. A thicker layer of fine particulate matter, that reduces the permeability of the streambed (external colmation), may develop after an extended period of low current velocity (Beyer & Banscher, 1975). These clogging processes can also be induced by algal mats in eutrophic streams as well as by cohesive depositions in rivers receiving sewage effluents (Kustermann, 1962; Beyer & Banscher, 1975).

3. Fine sediment that passes the coarse armor layer may accumulate beneath the armor layer; if low discharge continues a compact layer that reduces the porosity and hydraulic conductivity of the streambed may develop and stabilize the streambed against erosion (internal colmation) (Beyer & Banscher, 1975; Schächlchli, 1993).

4. Particles may penetrate the armor layer but not contribute to the clogging of the top layer (depth filtration); such particles undergo alternating phases of deposition and resuspension.

The objectives of this article are two-fold. The first part provides an overview on the ecological significance of fine matrix particle transport within fluvial sediments and on the mechanisms underlying deposition and transport processes. The second part focuses on the characterization and distribution of mobile matrix fines subjected to depth filtration within the interstices of the Töss River, Switzerland.
Figure 1. Factors that influence the retention of fine particles in streambeds. Numbers 1 - 4 are described in the text.

4.2 Ecological significance of colmation and depth filtration

Colmation

In general, colmation lowers the exchange processes between a river and the adjacent ground water. The alternating phases of colmation during low flow conditions and the decolmation induced by a high discharge are natural processes of sedimentation and erosion. However, the balance between colmation and decolmation may be altered anthropogenically towards an enhanced siltation, e.g. by flow regulation (Petts, 1988). In the Rhine River a mechanical opening of a colmated reach near a drinking water filtration site induced a 1 m rise of the ground water table near the river, but after a few weeks the opened section was sealed again (Gölz et al., 1991). River bank storage is a component of the ground water budget as well as of the riverine discharge regime (Baumgartner & Liebscher, 1990; Squillace, 1996). Therefore, if infiltration is inhibited, floodpeaks that cannot erode consolidated channel beds (Reid et al., 1985) are not buffered. A sealed bed can act as an intrusion barrier that prevents the contamination of ground water by polluted surface water (Younger et al., 1993; Komatina, 1994).

Increased clogging threatens the reproductive success of fish spawning on gravel (Berkman & Rabeni, 1987; Chapman, 1988; Zeh & Dönni, 1994). Sealed interstices cannot function as nurseries for aquatic insects (Gammeter, 1996). Furthermore, siltation reduces the refugial space available to invertebrates, and thus the impacts of natural and
anthropogenic disturbances, such as urban stormwater runoff, are magnified (Borchardt & Statzner, 1990). Increased loads of sand may affect the components of benthic communities differentially. It has been shown that small sized animals and the taxonomic groups Ephemeroptera, Diptera, and Coleoptera exhibit stronger declines in abundance compared to other taxa as the proportion of sand increases (Alexander & Hansen, 1986).

**Depth filtration**

The fine matrix sediment proportion of total bed sediments is increased by depth filtration. The fines enlarge the surface area that can be colonized by a biofilm. On the other hand, the interstitial throughflow and the concomitant delivery of resources, as well as the usable pore space for the interstitial fauna can be reduced. Excessive siltation has impacts on the colonization dynamics of interstitial animals (Richards & Bacon, 1994; Govedich et al., 1996; Maridet et al., 1996).

Colloidal particles contribute significantly to subsurface transport processes as carriers (DVWK, 1992) since they are important adsorbents for metals, phosphates, humic acids and organic compounds (Eggleston et al., 1991). Trace metals adsorbed to particles may accumulate in the interstitial habitat (Petts et al., 1989; Gibert et al., 1995). Suspended bacteria may be interpreted as living colloids (van Loosdrecht et al., 1990). Their transport and initial adhesion is controlled by the structure and physicochemical characteristics of the surfaces, especially by the hydrophobicity (Lindqvist & Bengtsson, 1991; Bosma & Zehnder, 1994). Algae that are transported into the subterranean water may remain viable; they are protected during unfavorable periods and may even reproduce in some cases (Poullíková, 1987; Wasmud, 1989).

The importance of fine particles for bacteria and invertebrates in unpolluted hyporheic sediments is discussed in detail in Brunke & Fischer (in prep.) and Brunke & Gonser (in prep.).

**4.3 Overview of colmation and depth filtration**

**Mechanism of filtration**

According to Herzig et al. (1970) and Beyer & Banscher (1975) two types of filtration can be defined in natural systems: Large fine particles with diameters > 30 μm are subjected to a mechanical filtration, whereby size and shape prevail in importance over surface phenomena such as positive and negative charges. Smaller particles (diameter about 1 μm) are mainly subjected to physicochemical filtration; surface phenomena prevail over volume phenomena. Medium size particles between 3 and 30 μm are
retained by both filtration mechanisms. Adhesion of colloidal particles and bacteria is exclusively due to physicochemical processes (Herzig et al., 1970; van Loosdrecht et al., 1990) (Tab. 1).

The following formula describes the effectiveness of mechanical depth filtration in relationship to the effective pore diameter of a filter medium, which is about $D_{15}/5^1$:

$$D_{15\text{particle}} < D_{15\text{filter}/5} < D_{85\text{particle}}$$

For a retention of fine particles the effective pore diameter of the filter must be smaller than $D_{85}$ of the fines, otherwise fines will pass through the filter. Furthermore, for a retention within the filter column, the effective pore diameter must to be larger than $D_{15}$ of the fines (Sowers & Sowers, 1970; Sherald et al., 1984). If the effective pore diameter is smaller than $D_{15}$ of the fines, they would accumulate on the top of the filter.

<table>
<thead>
<tr>
<th>Particle Size</th>
<th>&gt; 30 μm</th>
<th>~ 1 μm</th>
<th>&lt; 0.1 μm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Filtration Type</td>
<td>mechanical</td>
<td>physicochemical</td>
<td>colloidal</td>
</tr>
<tr>
<td>Retention Sites</td>
<td>constrictions, crevices, caverns</td>
<td>surface sites</td>
<td>surface sites</td>
</tr>
<tr>
<td>Retention Forces</td>
<td>friction, fluid pressure,</td>
<td>Van der Waals forces, electrokinetic forces,</td>
<td>Van der Waals forces, electrokinetic forces, chemical bonding,</td>
</tr>
<tr>
<td>Capture Mechanism</td>
<td>sedimentation, interception</td>
<td>interception</td>
<td>interception, diffusion</td>
</tr>
<tr>
<td>Remobilization</td>
<td>alterations in flow direction</td>
<td>increase in flow rate</td>
<td>increase in flow rate</td>
</tr>
</tbody>
</table>

**The evolution of colmation**

The formation of clogged interstices depends on the size distributions of suspended sediment, fine bedload, and channel sediments. Schächerli (1993) developed a model of the evolution of colmation in which he distinguished three phases by using the different

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1 $D_{15}$ represents the particle diameter for which 15% of the sediment is smaller
filtration mechanisms of Herzig et al. (1970) (Tab. 2). During each of these phases the retention of a different particle size fraction is decisive for the process. Larger fine particles (> 30 μm) are essential for an initial bridging of the pores, but during this first phase the hydraulic conductivity remains largely unaffected. This phase can be rapidly completed. Fine sand may be under-represented during low flow conditions with a minor transport capacity, and therefore a depth filtration of particles may prevail. However, in most streambeds a sandy fraction exists, which has been deposited contemporaneously with coarser framework particles (Lisle, 1989).

### Table 2. Processes and phases of internal colmation according to Schächli (1993).

<table>
<thead>
<tr>
<th>Phase</th>
<th>Large Particles (Ø &gt; 30 μm)</th>
<th>Medium Particles (Ø 3 - 30 μm)</th>
<th>Small Particles (Ø &lt; 3 μm)</th>
<th>Permeability of the Streambed</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>clogging of larger pores directly between and below the gravels and stones of the armor layer</td>
<td>deposition mainly in the pores of the upper subarmor layer; transport into deeper strata is possible (depth filtration)</td>
<td>partial deposition on surfaces due to physicochemical interactions; transport into framework gravel (depth filtration)</td>
<td>minor reduction of hydraulic conductivity</td>
</tr>
<tr>
<td>II</td>
<td>filling of some voids, limited deposition on the armor layer; role of large particles is largely terminated,</td>
<td>mechanical clogging of fine pores; sedimentation in voids with low current velocity</td>
<td>attachment on substrate of the filter layer effects further narrowing of pore channels</td>
<td>substantial reduction of hydraulic conductivity</td>
</tr>
<tr>
<td>III</td>
<td>only minor deposition between larger particles</td>
<td>lessened deposition further attachment effects a reduction of the interstitial velocity to a lower limit due to a decreased import of particles into the filter layer</td>
<td>hydraulic conductivity reaches a minimum value</td>
<td></td>
</tr>
</tbody>
</table>

Commonly fluvial sediments have a bimodal grain size distribution (Petts et al., 1989) characterized by the absence of the fine gravel and coarse sand. The fine material is generally missing in unimodal open framework gravel (Huggenberger et al., 1988), e.g. of fresh spawning redds (Kondolf et al., 1993). Such sediments are rapidly filled by fines from the bottom up (Einstein, 1968; Beschta & Jackson, 1979; Carling, 1984).

During the second phase the straining and sedimentation of intermediate sized particles (3 - 30 μm) effects a significant reduction of the streambed’s hydraulic conductivity, while the contribution of larger particles on the clogging process decreases continuously. The small particles (< 3 μm) still penetrate the sediment layers in which larger particles are strained (filter layer) or may adhere to surfaces due to physicochemical interactions. Below this filter layer the small particles are subjected to depth filtration.

In the third and final stage of colmation the small particles settle in the filter layer and the pore spaces are reduced to a minimum. Then the hydraulic conductivity reaches a certain minimum value (Banscher, 1976), due to an inhibited import of fines in the filter layer by lowered advection. The minimum value of hydraulic conductivity is maintained by an equilibrium of deposition and resuspension of particles at the top of the filter layer (Schälchli, 1993).

**Factors that influence colmation**

The temporal development of colmation, the clogging depth, and the lower limit of the decreased hydraulic conductivity are influenced by interactions of several factors (Tab. 3). Low flow conditions, suspended particles and fine bedload are requirements for the clogging process. A key parameter is the *dimensionless shear stress* \( \Theta \) (often termed Shields factor) (Schälchli, 1993) as the force ratio between shear stress promoting entrainment of particles and the particle size, density and gravity resisting an entrainment (Carling, 1992):

\[
\Theta = \frac{\tau}{(p_S - p)} g x D
\]

and

\[
\tau = p x g x R x S
\]

where \( \Theta \) is the dimensionless shear stress; \( \tau \) is the shear stress; \( p_S \) is the density of the sediment; \( p \) is the density of water; \( g \) is the acceleration due to gravity; \( D \) is the grain size; \( R \) is the hydraulic radius and \( S \) is the slope.
A dimensionless shear stress below a critical dimensionless shear stress ($\Theta_k$ of the beginning of decolmation, which is about 0.05) is a prerequisite for the occurrence of colmation. If $\Theta$ is below a certain minimum value, all suspended particles will be deposited. When $\Theta$ is above this minimum value only a small fraction of the fines will settle and the rest remain in suspension. At a $\Theta$ near the $\Theta_k$, colmation converts to decolmation. Thus, for a theoretically constant $\Theta$ the concentration of suspended particles and their deposition attain an equilibrium. Below a $\Theta_k$ increasing $\Theta$ effect a more dense packing of the sediment due to higher turbulent pulses and vibrations of the framework gravel (Schälchli, 1992, 1993). Therefore, higher $\Theta$ (below $\Theta_k$) accelerate the development of sealing and lower the minimum of the hydraulic conductivity.

The grain size distribution is of overriding relevance for the intrusion of fines into the bed sediments (Beschta & Jackson, 1979). The transport into the interstices of large and medium sized particles, once they have passed through the surface, is largely determined by the pore sizes (Frostick et al., 1984). Well-sorted gravel with large pores promote a deep intrusion of fines into the bed sediments, and thus more matrix sediment can accumulate increasing the clogging depth and lowering the minimum of hydraulic conductivity (Beyer & Banscher, 1975). In contrast, poorly sorted framework sediment is characterized by small pore sizes, which induce a straining of fines within a thin layer. Therefore, in such sediment less fine material is deposited, the clogging depth is comparatively shallow and the minimum of hydraulic conductivity is not raised compared with well-sorted gravel (Schälchli, 1993). However, even in poorly sorted sediment macropores may exist which can enable the transport of fines into deeper layers. In streams with a coarse armor layer and a finer subarmor layer internal colmation develops directly below the armor layer in a thin stratum due to clogging of the small pore spaces of the subarmor layer (Frostick et al., 1984; Cunningham et al., 1987).

In the study by Cunningham et al. (1987) the suspended particle concentration in a range of 200-1600 ppm did not have a significant effect on the degree of colmation. This is because the particle concentration does not influence the location of deposition within the filter layer (Schälchli, 1993). However, suspended particles and fine bedload are a prerequisite for the clogging process and higher concentrations of such material can accelerate the temporal development of colmation (Banscher, 1976; Carling, 1984; Diplas & Parker, 1992).

Compared with other factors the vertical hydraulic gradient (VHG) is of intermediate relevance for the development of a colmation (Schälchli, 1993). Influent conditions induce higher interstitial current velocities and particles may be transported deeper into the bed sediment. Thus, more fines can be deposited resulting in a thicker colmated layer, and thereby effect a low hydraulic conductivity (Schälchli, 1993). Effluent conditions reduce the deposition of very fine particles and only large particles intrude into
interstices, which exert a minor effect on hydraulic conductivity. However, the permeability of an already clogged streambed can only be re-established locally when the exfiltration reaches site-specific threshold levels, whereby fines are flushed out from local pore channels (Banscher, 1976).

Increasing water temperature affects colmation in a similar way as infiltration; the reduction of the cinematic viscosity promotes higher interstitial velocities. However, the relevance of temperature for colmation is comparatively low (Schålchli, 1993).

In conclusion, the colmation depth depends mainly on the grain size distribution of the bed sediment. Schålchli (1993) derives an empirical formula from his flume experiments, which can be used to roughly estimate the depth of the clogged layer \( (D_c) \) in gravel-bed streams:

\[
D_c = 3D_m + 0.01 \, [m]
\]

where \( D_m \) is the mean grain size.

A variable fluvial geomorphology integrates all these factors on a reach scale. Riffle-pool sequences induce variable flow patterns with alternating local up- and downwelling zones (Savant et al., 1987; Harvey & Bencala, 1993), and heterogeneous grain size distributions and textures (Carling, 1992). Complex flow patterns with high variability due to discharge fluctuations create different scour and depositional areas in a longitudinal and cross-sectional profile (Church, 1992). Thus, siltation may be highly variable locally resulting in a three-dimensional mosaic of differentially colmated areas within the streambed. The import of larger fine particles is increased in areas of preferential bedload movement and higher surface velocities (Frostick et al., 1984), presumably because of fine bedload (i.e. larger fine particles) that has a higher probability of intrusion into the interstices than the suspended load (Lisle, 1989) and an increased flushing of small particles relative to areas not situated in the thalweg (Frostick et al., 1984). However, the effect of imported larger fine particles may be small, since the hydraulic conductivity of the streambed is not reduced significantly.

Low flow conditions enable external colmation processes, characterized by a deposition of fines directly on the streambed. External colmation prevents an intrusion of fines into the channel sediments and thus constraints the development of internal colmation (Banscher, 1976).
Table 3. Summary of factors that influence the temporal course of colmation, the clogging depth, and the minimum value of decreased hydraulic conductivity (after (Beyer & Banscher, 1975; Schälchli, 1993) (C is the concentration of suspended particles, Re is the Reynolds number).

<table>
<thead>
<tr>
<th>Primary Influence</th>
<th>Variable</th>
<th>Key Parameter</th>
<th>Relevance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flow</td>
<td>- current velocity</td>
<td>θ</td>
<td>requirement: θ &lt; θ&lt;sub&gt;k&lt;/sub&gt;, low</td>
</tr>
<tr>
<td></td>
<td>- dimensionless shear stress</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suspended Particles</td>
<td>- concentration</td>
<td>C/p&lt;sub&gt;W&lt;/sub&gt;</td>
<td>requirement: C &gt; 0</td>
</tr>
<tr>
<td></td>
<td>- size distribution</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>- shape</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>- adhesion, cohesion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment</td>
<td>- size distribution</td>
<td>d&lt;sub&gt;10&lt;/sub&gt;/d&lt;sub&gt;m&lt;/sub&gt;</td>
<td>high</td>
</tr>
<tr>
<td></td>
<td>- armor layer</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>- texture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydraulic Gradient</td>
<td>- infiltration</td>
<td>- VHG</td>
<td>medium</td>
</tr>
<tr>
<td></td>
<td>- exfiltration</td>
<td>+ VHG</td>
<td>decolmation at</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+VHG &gt; +VHG&lt;sub&gt;k&lt;/sub&gt;</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>- kinematic viscosity</td>
<td>Re</td>
<td>low</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Secondary Influence</th>
<th>Variable</th>
<th>Key Parameter</th>
<th>Relevance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morphology</td>
<td>- riffle-pool sequences</td>
<td>VHG, θ, D&lt;sub&gt;10&lt;/sub&gt;/D&lt;sub&gt;m&lt;/sub&gt;</td>
<td>variable</td>
</tr>
<tr>
<td></td>
<td>- longitudinal and cross profile</td>
<td></td>
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<tr>
<td></td>
<td>- zones of preferential bedload movement</td>
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<td></td>
</tr>
</tbody>
</table>

Decolmation

Decolmation refers to all processes that contribute to an increase of hydraulic conductivity and to a breaking up of the bed sediment structure. Schälchli (1992, 1993) distinguished different phases of decolmation according to dimensionless shear stress: (I) At θ > 0.05 fine bedload transport begins, which may induce a partial decolmation by jostling deposited fines and removing them or, depending on the stage of colmation, fill up larger pores, e.g. of open framework gravel. (II) During a transitional phase of θ values between 0.06 and 0.072 the hydraulic conductivity of the top layer can increase by a factor of 10 due to a flushing out of fines below and beside the coarser gravels of the
armor layer and by removing individual components of the armor layer. (III) During the flushing phase (Θ between 0.072 - 0.078) at high flow conditions the armor layer breaks up locally and hydraulic conductivity increases to a maximum value. However, the development of new colmation is possible when discharge remains constant and the suspended load is high. (IV) At peak flows when Θ > 0.08 the whole river bed is mobilized and consolidated channel beds are broken up.

**Depth filtration**

Depth filtration refers to particle separation by selective straining and transport within porous media. In riverine sediments and aquifers it means transport and retention of fine inorganic and detrital particles. Moreover, fine inorganic particles may be colonized by microorganisms and contain adsorbed compounds on their surfaces. The mechanisms underlying depth filtration correspond to those occurring during colmation. It must be stressed that the role of the cohesive properties of organic matter for filtering are difficult to assess and have rarely been addressed in experiments. Since organic layers have a porosity of about 90% (Characklis, 1984), they can increase the particle size of fines enormously. However, organic layers on fines and detrital particles may have a high plasticity in form and thereby pass pore channels differentially depending on interstitial throughflow.

4.4 The retention of particles on a landscape scale

The patterns and structures within fluvial systems are the result of processes operating at different spatial and temporal scales (Frissele et al., 1986; Minshall, 1988). In systems organized in a nested hierarchy, large-scale processes determine higher levels of ecological structure, that on the other hand contain lower levels, which are governed by smaller scale processes (Wiens, 1989). Processes that take place on higher levels of organization constrain patterns and processes on lower levels. Thus, the suspended load of a stream depends not only on the local transport processes, but is also a consequence of processes occurring in the upstream drainage basin. For a holistic perspective of the retention of particles it is essential to consider processes operating on the landscape scale (Fig. 2). On this scale the physiographic characteristics of the catchment, geology, geomorphology and climate are fundamental for the pristine stream type. Geomorphological and hydrological processes are responsible for mobilizing and transporting sediment within the drainage basin (Walling, 1996). However, human land use practices and hydro-engineering have altered the connectivity between streams and the adjacent surface and subterranean landscape by transforming retentive systems into
transport systems. Agricultural and forestry practices and road construction increase erosion and thus the import of sediment into streams and rivers (Karr & Schlosser, 1978; Adams & Beschta, 1980; Likens, 1984; Lowrance et al., 1984; Cooper et al., 1987).

The stream-specific relationship between suspended solid load and discharge is also of importance. Significant amounts of sediment are often transported during short time spans (Williams, 1989). For an extensive overview of suspended sediment transport and retention processes by the surface hydrosystem see Walling (1996).

**Figure 2.** Factors determining fine particle transport and retention on a landscape scale.
4.5 Distribution of fine particles within the interstices of a calcareous gravel-bed river

Very little ecological research has been conducted on fine matrix sediments, regarding their influence on interstitial organic matter and organisms, even though they constitute the ecologically most important inorganic sediment fraction in gravel-bed rivers (Jobson & Carey, 1989; Bretschko, 1991; Ward et al., in press). For example, in two gravel-bed streams in Austria and Switzerland particles smaller than 1 mm contributed to only 6 - 9% of the total sediment, yet up to 88% of the total organic carbon (TOC) and total organic nitrogen (TON) content was associated with this component (Leichtfried, 1988; Eglin, 1990). The percentage of particles < 1 mm can be used as an indicator of habitat quality (Adams & Beschafta, 1980).

For a characterization of the mobile matrix fines the size distribution of this fraction must be examined separately from the total bed sediment. Theoretically, the interstitial content of the mobile matrix fines should increase with sediment depth simply because of gravity. It is hypothesized that the proportion of large particles (> 30 \mu m) should decrease with depth due to a straining in the topmost layer of the streambed, whereas the content of small particles (< 2 \mu m) should not change with depth, because similar physicochemical surface properties of the sediments were assumed. Therefore, the proportion of small particles should increase with depth.

Interstitial detrital particles > 90 (DPs) of allochthonous origin (i.e. mostly plant material) were used as tracers of interstitial transport of organic matter. It was predicted that the interstitial content of DPs decrease with depth, because of continuous mineralization and ingestion by interstitial animals. Furthermore it was tested if the DP content differs between three types of hydrological exchange between the stream and the interstices, i.e. infiltration of surface water, exfiltration of ground water, and prevailing subsurface flow along the channel (horizontal advection).

4.5.1 Objectives

Specific objectives were: (1) to characterize the mobile matrix fines by their grain size distribution, (2) to examine the vertical distribution of three grain size classes differing in their type of filtration, (3) to examine the vertical distribution of detrital particles, and (4) to test the influence of infiltration, horizontal advection, and exfiltration on the vertical distribution of detrital particles and all fine particles.
4.5.2 Study site, material and methods

The study was carried out in a transect across a calcareous prealpine gravel-bed river (Töss River, 460 m a.s.l., Switzerland). Due to hydro-engineering the former braided channel has been straightened and no riffle-pool morphology exists; the present channel width is about 20 m. At the study site distinct exfiltration zones (EZ) are located on the stream’s left side, whereas on the right side surface water infiltrates into the alluvial sediments (infiltration zone; IZ). In midstream neither infiltration nor exfiltration prevail, but a horizontal advection dominates the throughflow within the sediments (horizontal advection zone; HZ).

Interstitial water was extracted by steel piezometers (internal diameter = 50 mm), from 4 sediment depths (20, 50, 100, 150 cm). Piezometers were spatially organized as clusters located in each of the three hydrological exchange zones. The piezometer nests within the IZ were located 3 m from the right bank, those within the HZ were 10 m from both banks in midstream and those within the EZ were 3 m from the left bank. Total matrix particles (i.e. inorganic fine particles and particulate organic matter, given as total particle content in mg per liter of interstitial water) were collected with a submersible electric pump after taking a sample with a hand pump for faunistic investigations (Bou & Rouch, 1967; Husmann, 1971). Sampling dates were on 15 occasions between May 1995 and November 1996. The samples were filtered through Whatman GF/F filters. The filters were dried to constant weight at 60°C and weighed. The grain size distribution of the fine particles from 12 samples were measured with a SediGraph 5100 (Micrometrics) with X-rays. The detrital particles (DPs) were collected on 3 occasions in July, September and November 1996. Ten liters of interstitial water were taken with the hand pump and filtered through a 90 μm net. The DPs were extracted from the sample by a flotation technique along with the interstitial animals (Danielopol, 1976; Dole-Olivier & Marmonier, 1992a). In another step DPs and animals were separated by removing the animals individually. The DPs were separated into size classes > 300 μm and 300 - 90 μm. The allochthonous origin of the DPs from plant material was determined by examination with a microscope. The DPs were measured as ash free dry mass by loss on ignition at 500°C for 3 hours.

Additionally, 9 freeze cores (Bretschko & Klemens, 1986) were taken on November 1996, three of them in each hydrological exchange zone to measure the size distribution of framework gravel and to assess sediment porosity and hydraulic conductivity. Cores were taken to a sediment depth of 70 cm and cut into 10 cm sections. Framework grain size distribution was determined for each depth layer by passing the sediment through a set of seven sieves (mesh sizes > 20, 12.5, 8, 6.3, 2.5, 1, 0.063 mm). Rocks greater than 50 mm were excluded from the analyses as recommended by Adams & Beschta (1980) to reduce the effect of extreme values for relatively small sediment samples. The sorting
coefficient \((D75/D25)^{0.5}\) was calculated according to Schwoerbel (1994). Porosity was calculated as \((\text{total volume} - \text{grain volume}) \times 100/\text{(total volume)}\) according to Eglin (1990). Hydraulic conductivity was calculated according to Beyer (1964) and Holting (1989). A few depth layers did not freeze on some cores presumably due to high interstitial currents. Therefore, it was not possible to statistically compare framework characteristics of depth layers between hydrological exchange zones. The grain size distribution of the armor layer was assessed with two methods: (a) by measuring the intermediate axis (b-axis) of 200 mineral particles > 1 cm along a straight line in flow direction in three replicates according to Fehr (1987) and (b) by taking 6 sediment samples down to a depth of 10 cm using a Surber sampler (400 cm²) with a 90 μm net.

4.5.3 Results and discussion

Bed sediment characteristics

The porosity of the bed sediments of the Töss River tended to increase with depth (Fig. 3), though this was not statistically significant. Porosities ranged between 6.2% and 32%, with an average of 18.8% \((± 6.6 \text{ SD})\). The Thur and Neckar Rivers, two other calcareous gravel-bed rivers in Switzerland, had similar sediment porosities (Eglin, 1990; Naegeli, 1997). In the Lunzer Seebach (Austria) porosity is about 24% (Bretschko, 1991).

The D50 of the surface sediment (i.e. the grain diameter at which 50% of the sediment in weight is smaller) was 31.0 mm \((± 2.6 \text{ SD})\) measured by b-axis and 32.2 mm \((± 6.1 \text{ SD})\) measured by sieving. It was coarser at the stream margins than in midstream (Tab. 4). Not shown by the grain size analyses was that the grains in midstream tended to be more rounded and those at the margins tended to be flatter. The reason for this difference was probably that the midstream sediments were more often affected by bedload movement, where water velocities were highest in the straightened channel. Furthermore, the layering of the flatter gravels at the margins resulted in a more erosion resistant armor layer. River engineering and lateral embankments in the whole catchment of the Töss River have reduced sediment supply, which leads, in conjunction with an increased transport capacity by the straightening of the river course, to a deficiency of bedload. In flume experiments Dietrich et al. (1989) found that a reduction in sediment supply resulted in an expansion of lateral coarser 'inactive' zones in which little or no transport took place compared to finer 'active' zones in midstream. In the Töss River this is presumably a self enhancing process, since the longer a surface layer is not mobilized, the more it consolidates and becomes erosion resistant (Reid et al., 1985).

The subsurface sediment showed a finer grain size composition than the surface sediment, with a D50 = 11 mm \((± 3.6 \text{ SD})\), but ranging between 4.5 and 17 mm. The
difference in D50 values between midstream and marginal sediments is reduced (Tab. 4), due to a higher proportion of sand in the subsurface sediments. Schälchli (1993) collected larger amounts of sediment with a different technique from an upstream site of the Töss River and calculated a D50 of 16 mm, presumably for a mixture of surface and subsurface sediment. The technique of freeze coring underrepresents the coarse fraction

| Table 4. Sediment characteristics of the three positions within the channel cross-section. Means (± SD) for three freeze cores in each zone. Grain size metrics in mm. |
|---------------------------------|------------------|------------------|
|                                 | Infiltration zone (right margin) | Horizontal advection (midstream) | Exfiltration zone (left margin) |
| D50 Surface (b-axis)           | 36.5 ± 2.9        | 24.9 ± 1.8       | 32.2 ± 2.8       |
| D50 Surface (sieving)          | 38.5 ± 6.3        | 26.5 ± 0.7       | 31.5 ± 0.7       |
| D75 Subsurface                 | 16.5 ± 2.7        | 15.5 ± 2.3       | 16.2 ± 2.5       |
| D50 Subsurface                 | 11.0 ± 3.6        | 10.3 ± 3.1       | 10.9 ± 4.1       |
| D25 Subsurface                 | 3.4 ± 3.4         | 3.1 ± 1.4        | 4.4 ± 2.9        |
| D15/5 Subsurface               | 0.41 ± 0.33       | 0.21 ± 0.16      | 0.31 ± 0.45      |
| So (D75/D50)-0.5               | 2.4 ± 1.0         | 2.3 ± 0.45       | 2.9 ± 1.6        |
| Porosity (%)                   | 18.8 ± 7.8        | 19.7 ± 6.9       | 18.0 ± 5.7       |
| k\text{f}_{0-70} cm (1*10^{-3} m/s) | 16.9 ± 34         | 3.7 ± 6.8        | 11.2 ± 28        |
| k\text{f}_{0-20} cm (1*10^{-3} m/s) | 48.5 ± 63         | 9.2 ± 6.4        | 29.3 ± 51        |
| k\text{f}_{20-50} cm (1*10^{-3} m/s) | 6.2 ± 8.4         | 5.5 ± 10.6       | 1.3 ± 1.4        |
| vertical \text{vf}_{0-20} cm (1*10^{-3} m/s) | -0.92 ± 63       | 0.12 ± 6.4       | 0.44 ± 51        |
| vertical \text{vf}_{20-50} cm (1*10^{-3} m/s) | -0.94 ± 8.4      | -0.09 ± 10.6     | 0.04 ± 1.4       |

where there are cobbles and gravels (discussion by G. E. Petts in Church et al., 1987). Schälchli (1993) calculated a porosity of 25% and hydraulic conductivities ranging between $k_f = 1.5 \times 10^{-3}$ and $2.5 \times 10^{-4} \text{ m/s}$. In this study, hydraulic conductivities ranged between $1.5 \times 10^{-5}$ and $1.2 \times 10^{-1} \text{ m/s}$ and changed significantly with depth (Kruskal-Wallis test, $p < 0.05$) (Fig. 3). Hydraulic conductivity decreased continuously down to the 40-50 cm depth stratum, thereafter it increased again. On average the sediment down to 40 cm was 'highly permeable', whereas the deeper strata were 'permeable' according to Hölting (1989). The specific flux ($\text{vf}$) was calculated for the upper sediment strata by using the average $k_f$-values and the average vertical hydraulic gradients measured between April 95 and November 96 on 22 occasions (Brunke & Gonser, in prep.) (Tab. 4). These calculations indicate that in the IZ water can infiltrate down to a depth of 20-cm with an average velocity of 5.5 cm/min and in the EZ water can exfiltrate with an average of 2.6 cm/min. Therefore, by using the porosities for the IZ and EZ, 10 liters per minute could infiltrate and 4.7 liters per minute could exfiltrate on a square meter. At the
sampling site the IZ and EZ are both approximately 4 m x 24 m in size, each. Therefore, about 47 liter/m x s are exchanged throughout the sampling site, contributing to 0.67% of the annual mean surface discharge of 7 m³/s. Assuming hydrological exchange along the river course is the same as at the study site, the entire stream water would be exchanged on a channel length of 3.57 km. With an average flow velocity of 0.67 m/s complete exchange would take 1.5 hours. However, these calculations are just rough estimations, since they are based on averages and approximate calculations of hydraulic conductivity. Data from the HZ were not included in the calculations, though it contributed actively to the exchange since temperature variations can be detected down to a depth of 150 cm. Therefore, these estimates are likely to underestimate the water exchange between the stream and the subsurface water.

Figure 3. Depth profiles of sediment porosity, the proportion of fine particles < 1 mm in the sediment, the D50 (mm) and the hydraulic conductivity. Means (± SD). n = 38.
According to Schälchli's (1993) formula a thin colmated layer of the topmost streambed would be located at a depth of about 10 cm. Severe colmation only occurred at the channel margins that were rarely affected by bedload movement.

The proportion of fines < 1 mm in the sediment increased with depth, from 7.3% (± 3.2 SD) at 10 cm to 16% (± 6.7 SD) at 70 cm (Fig. 3). Adams & Beschta (1980) and Milan (1996) also found lower levels of fines near the bed surface. Adams & Beschta (1980) assumed that this might reflect a paucity of fines or the presence of an armor layer. In their study they had an average of fines of 17.4% at 0 - 10 cm, 22.3% at 10 - 25 cm, and 22.2% at 25 - 40 cm sediment depths, which were clearly higher percentages of fines than in this study. The vertical trend for fines was not reflected in the porosity; porosity and fines were not correlated. Maridet et al. (1992) concluded in their study, that only a high content of fines always leads to a low porosity, whereas porosity may be high or low when the content of fines is low. The sorting coefficient was highly correlated to the percentages of fines < 1 mm and < 2 mm ($r_s = -0.86$, $p < 0.001$ and $r_s = -0.95$, $p < 0.001$, respectively). Therefore, the depth profile of the sorting coefficient resembles the depth profile of the percentage of fines < 1 mm in the sediment (Fig. 3).

Characterization of mobile matrix sediment

For various reasons the interstitial fines fraction is a critical factor for hyporheic biota in the Töss River (Brunke & Fischer, in prep.; Brunke & Gonser, in prep.). On average it contributed 13.9% (± 6.0 SD) of the bed sediment down to a depth of 70 cm. About 72% (± 23 SD) of these fines were smaller than 0.1 mm and the median size was 0.03 mm (Fig. 4a).

The distribution of particles < 2 μm, which is exclusively filtered by physicochemical forces, did not change much with depth except for slightly higher portions at 50 cm depth (Fig. 4b). Its proportions ranged between 8.5% and 32.7% with an average of 14.5 (± 6.6 SD). The depth profile of the size fraction 2 - 32 μm was similar in shape to the depth profile of the fraction < 2 μm ($r_s = 0.88$, $p < 0.001$), but it contributed to higher proportions ranging between 16.7% and 60.4% with an average of 36.4% (± 12.9 SD). Consequently, the proportions of the fraction > 32 μm were inversely related to the fractions of 2 - 32 μm and < 2 μm ($r_s = -0.82$, $p < 0.001$ and $r_s = -0.81$, $p < 0.001$, respectively). The proportions of this fraction ranged between 5.1% and 74.9% with an average of 43.7% (± 6.4 SD). The hypothesis that the proportions of the large size fraction are greater in upper sediment strata, because of an exclusive filtering in the top layers by mechanical straining is not supported. Instead, this fraction might be responsible for the general trend that fine particles accumulate with depth (Leichtfried, 1988, 1994; Panek, 1994). In this study the content of the fine particles also increased
with depth, though strong temporal variations occurred (Fig. 5). Only in the 50-cm depth stratum of the exfiltration zone was the content of fine particles higher than in deeper strata. This is probably due to the upwelling forces of exfiltrating ground water, which likely prevented the sedimentation of particles into the deeper strata.

As discussed above, bedload movement was more frequent in midstream than at the margins because of the straightening of the channel and bedload deficits. In these midstream sediments the content of total mobile fine particles tended to be lower. In contrast, the vertical patterns of the detrital particles (DPs) (Fig. 6) were opposed to those shown by the content of total fine particles (Fig. 5). Considering the continual

Figure 4. (a) Cumulative size distribution curve for mobile matrix fines. (b) Depth profiles for three size classes which are differentially subjected to physicochemical and mechanical filtering (see text and Tab. 1 for further explanations). Means (± SD). n = 12.
degradation of DPs, higher contents of DPs in sediment depths below 50 cm in midstream sediments indicate higher import of fine particles in these sediments. Therefore, it appears that the transport of fines within midstream sediments is increased relative to the deposition when compared with sediments at the margin. In a similar way Frostick et al. (1984) found a higher ingress of matrix fines in thalweg sediments in a field experiment. Higher interstitial currents promote the transport of fines, provided there is no straining effect (Herzig et al., 1970). In contrast, in marginal areas where flow is reduced accumulation may prevail until the next flood that breaks up the sediment across the entire channel. In this context, the contrastingly low contents of DPs in the
exfiltration zone at a depth of 50-cm compared with the high contents of total particles are remarkable (Figs 5, 6). This relationship supports the interpretation that the import of particles to this stratum is reduced, but the temporal accumulation is of long duration.

**Figure 6.** Depth profiles of detrital particles > 300 μm, 300 - 90 μm, and the proportion > 300 μm to DPs > 90 μm for the infiltration, horizontal advection and exfiltration zones. Means (± SD). n = 74.
The proportion of DPs > 300 μm to DPs > 90 μm ranged between 22% and 60% and showed no clear trend with depth (Fig. 6). This suggests that the straining of DPs > 300 μm was not affected differentially by pore size than that of DPs > 90 μm. The DPs were certainly flushed (and not deposited during bedload movements) into the sediment down to depths of 100-cm and 150-cm and probably also into the upper strata, because bedload movement of a magnitude which could have buried the DPs to depths below 100-cm would have removed the piezometers.

Calculations using the formula by Sowers & Sowers (1970) demonstrate the potential mobility of most matrix fines in the Töss River streambed. The D15/5 of the subsurface sediment (Tab. 4) is about the size of the D85 of the fine particles (D85 fines = 0.28 mm) and much higher than the D15 (D15 fines = 0.002 mm).

The grain size distribution of the matrix fines reflects the absolute sizes of particles. It is likely that the effective grain size distribution is somewhat coarser due to formation of aggregates. However, even with an estimated median grain size an order of magnitude greater (i.e. about 0.3 mm), most particles could still pass the framework. This becomes even more evident considering the sampling method which in general underrepresents the gravels and cobbles, the exclusion of rocks greater than 50 mm, and the fact that the sand and silt fractions were also included in the grain size analysis of the freeze core samples.

### 4.5.4 Conclusions

Field studies in gravel-bed rivers with unregulated discharge regimes (Leichtfried, 1988; 1991; Panek, 1994; Naegeli et al., 1995; Pusch, 1996; Milan & Petts, 1998; this study) do not support the results from flume experiments in which fine particles were retained exclusively in the topmost layer of the channel bed and that further transport into deeper layers was negligible (e.g. Behnke, 1969; Beschta & Jackson, 1979; Diplas & Parker, 1992; Schächli, 1992). The presence of detrital particles > 300 μm even at sediment depths of 150 cm demonstrated the importance of transport by interstitial throughflow and the interconnectedness of voids. In the Töss River the large pore sizes of the framework sediment probably limited the significance of mechanical straining of mobile fine particles. Rather, the interplay between direction and intensity of interstitial throughflow with sedimentation in subsurface dead zones and particle inertia, as described by Herzig et al. (1970), appear to be more important for depth filtration. Finally, the intrusion of fines appears to be influenced by the location in the channel relative to the frequency of bedload movement, since it controls the composition and shape of framework gravel.
Acknowledgements

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Brunke M. & Gonser T. (in prep.) Hyporheic invertebrates - the clinal nature of interstitial communities structured by hydrological exchange and environmental gradients.


CHAPTER 5

Influence of surface and subsurface flow on distributions of particulate organic matter and fine inorganic particles in perialpine stream sediments

**Abstract** The relevance of vertical hydrological exchange processes for the retention of particulate organic carbon (POC) and fine inorganic particles in channel sediments was assessed by comparing their depth distributions at locations within the streambed that exhibited three different types of interstitial flow (infiltration, exfiltration, and horizontal advection). The POC content (defined as mg per liter of interstitial water) increased down to a sediment depth of 50 cm in all three hydrological exchange types. However, the differences between 50 and 100 cm were only significant in the region of exfiltrating ground water. Inorganic fine particle contents tended to increase down to depths of 150 cm (the greatest depth investigated), with the exception of the exfiltration type where the highest fine inorganic particle contents were found at a depth of 50 cm, indicating an influence by the net upward movement of ground water. The POC/TP ratio, defined as the ratio between POC and the total of all fine particles, decreased with depth for all types of interstitial flow. In the exfiltration type the POC/TP ratios were lower than in the other two types down to a depth of 100 cm. Frequent flood events caused high temporal variability of interstitial particle parameters.

5.1 Introduction

Particulate organic carbon (POC) is the food resource for most animals living in streams. Many temperate fluvial ecosystems depend on the mainly seasonal inputs of allochthonous POC from riparian zones (Bretschko & Moser, 1993). However, although streams are transport systems, it is their retention capacity that makes POC available to the biota year round (Speaker et al., 1984). The channel sediments form a major storage site due to their porosity and increasing stability with sediment depth (Naegeli, 1997). POC is imported into the sediments during bed-moving spates (Bretschko, 1991) and by depth filtration, i.e. the transport and deposition of particles within interstices (Brunke & Gonser, 1997b). Import is restricted by the degree of consolidation of the channel bed and also by the permeability of deeper strata. These properties of the sediment structure are markedly influenced by the proportion of fine inorganic particles ('matrix fines'; in general < 2 mm according to Petts (1988) and Lisle (1989)). These inorganic matrix fines
and the framework gravel can be regarded as two components of the bed sediment in gravel-bed rivers (Petts, 1988). Excessive amounts of fine inorganic particles may lead to a clogging of the top layer of the channel sediments (colmation). They can also fill the underlying interstitial voids, thereby reducing the available subsurface habitat (Brunke & Gonser, 1997a). However, the deposition of fine inorganic particles increases the surface area for biofilm development. Leichtfried (1988) found high correlations between fine inorganic particles and the POC contents (defined as mg/liter of interstitial water) in the bed sediments of a calcareous mountain brook; most of the POC originated from the biofilm. Consequently, studies on the POC within the interstices should be based on knowledge regarding spatiotemporal dynamics of the fine inorganic particles.

In this study, we investigated the role of vertical hydrological exchange (infiltration, horizontal advection, exfiltration), surface flow regime and season on the distribution patterns of these particle parameters within the interstices. Specific objectives were: (1) to examine the differential influence of infiltration, horizontal advection and exfiltration on the vertical distribution patterns of POC and fine inorganic particles, (2) to examine the influence of season on interstitial POC contents, and (3) to assess the affect of the surface flow regime on temporal dynamics of POC and fine inorganic particle contents.

5.2 Study site and methods

The Töss River is a third-order calcareous gravel-bed river in northern Switzerland. At the study site (460 m.a.s.l.) hydraulic gradients indicated ground water exfiltration on the left side of the stream, whereas river water infiltrates to the ground water on the right side. In midstream subsurface flow in the direction of streamflow prevails (horizontal advection). Along the margins of the stream, where the infiltration and exfiltration zones are located, the uppermost channel sediments form an erosion-resistant armor layer, whereas in midstream, frequent bedload movement creates permeable open-framework gravel. The surface sediments (top 10 cm) of the entire sampling site had a mean grain size of 31 mm (± 26 SD) and the subsurface sediments (10 - 70 cm), 11 mm (± 3.6 SD), with a mean porosity of 18.8% (± 6.6 SD). In each of the three zones steel piezometer pipes (internal diameter = 5 cm) were installed to four sampling depths (20, 50, 100 and 150 cm). Interstitial water containing the particles was collected from these sediment depths with an electric pump. Sampling was conducted at approximately monthly intervals between April 1995 and November 1996. For the analysis of the particles the samples were filtered through Whatman GF/F filters. The filters were dried at 60°C to determine total dry weight of the particles. Inorganic carbonate was removed from the filters with 3 M HCl. The POC and PN were measured with a CHNS analyser (Elementar vario EL). The POC and PN ‘contents’ refer to the amounts of particulate organic carbon.
and nitrogen in 1 liter of sampled interstitial water, whereas POC/TP and PN/TP ratios are defined as the amounts of particulate carbon and nitrogen in mg per gram dry weight of total particles ('POC concentration' sensu Leichtfried 1988). In this study, the measured fine inorganic particles were smaller than 1 mm and the size frequency distribution had a mode of 0.1 mm. The effect of the hydrological exchange type, depth and season on the particle parameters were analyzed by the Kruskal-Wallis test.

5.3 Results

Depth distribution of particles in different hydrological exchange zones

Overall, fine inorganic particles within the interstices tended to increase with depth ($p < 0.001$). In the horizontal advection zone (HZ), the fine inorganic particles increased gradually to a depth of 150 cm, whereas in the infiltration zone (IZ), the change with depth was discontinuous (Fig. 1). However, for both zones, only the fine inorganic particles of the 20-cm and 150-cm depth strata were significantly different for the IZ as a result of a high temporal variability. In the exfiltration zone (EZ), the fine inorganic particles of the 50-cm depth stratum were significantly higher than in the 20- and 100-cm depth strata in spite of large confidence limits.

In all zones the POC content increased to a depth of 50 cm and decreased in the deeper strata ($p < 0.001$) (Fig. 1). However, the difference between the upper and deeper strata was significant only for the EZ. The POC content was significantly correlated to the amount of fine inorganic particles ($r = 0.88, p < 0.001, n = 246$).

The POC/TP ratios differed significantly between the zones ($p = 0.005$) and decreased significantly with depth ($p < 0.001$) (Fig. 2). In the IZ and HZ the POC/TP ratios did not differ significantly from the 20- to the 50-cm depth strata, whereas they differed significantly between 50- and 100-cm, as well as between the 100- and 150-cm depths. In contrast, the POC/TP ratios in the EZ differed between the 20- and 50-cm depths and were similar in the depths of 100- and 150-cm.

The PN content was highly correlated with the POC content ($r = 0.96, p < 0.001, n = 286$); the POC/PN ratio did not vary significantly, neither with depth nor between the zones (Fig. 2).
The flow regime differed between the four seasons (Fig. 3a). In summer and autumn there was a moderate flood frequency and no major floods, while winter was characterized by one major flood and long periods of low discharge; during spring several small and major floods led to a high flood frequency (Figs 3a and 4).

The interstitial POC contents and POC/TP ratios varied significantly between seasons ($p = 0.002$ and $p < 0.001$, respectively) (Fig. 3b,c). The depth distribution pattern of the POC content was similar in spring, summer and autumn, with higher contents at a depth of 50 cm than at 20 cm. The POC contents were the lowest in spring and differed significantly from POC contents in autumn and winter. This might be a result of the high
flood frequency in spring relative to the other seasons. The POC contents were highest in winter, especially at a depth of 20 cm. However, the spatiotemporal variability, even down to depths of 100 cm, was very high, as indicated by the large confidence intervals (Fig. 3b).

The POC/TP ratios decreased with depth in all seasons. Except for winter the gradients between adjacent depth strata were steep. The POC/TP ratios were significantly higher in autumn compared to the other seasons (Fig. 3c). This is probably due to a higher import of POC following leaf abscission. In contrast, the high POC contents in winter were not reflected by high POC/TP ratios, thus indicating a high intrusion of fine inorganic particles into the interstices.

**Figure 2.** Depth profiles of the geometric means of the POC/TP ratio (mg/g) and the POC/PN ratio in the top 150 cm of the bed sediments in the three hydrological exchange zones. Error bars: 95% confidence intervals, calculated after logarithmic transformation.
Figure 3. Seasonal variations of the flood regime (a), the geometric means of the POC content (b) and the POC/TP ratio (c) with sediment depth. The flood peaks indicate the percentage of days with flood peaks relative to all days of a given season. The bars indicate the relative portion of flood types in the percentage of flood peaks: major floods, $Q > 80$; medium floods $Q = 40-80$; minor floods $Q = 20-40$ m$^3$/s. Asterisks indicate significant differences between seasons for the POC content and the POC/TP ratio; ** = $p < 0.01$; *** = $p < 0.001$. Error bars indicate 95% confidence intervals, calculated after logarithmic transformation.
A major flood and inorganic matrix fines

The effect of a major flood on the interstitial fine inorganic particles can be shown by the samples taken before and after the most severe spate, which mobilized the streambed sediments of the whole channel (Fig. 4). The fine inorganic particles were highest at the margins of the stream after a short period of low flow on 9 May. During the falling limb of a small spate on 16 May, the fine inorganic particles were flushed out except those in the IZ at a depth of 100 cm. After the major flood on 1 June the stream was not accessible until 19 June, due to the high water level. On 19 June the fine inorganic particle contents were low, except for higher contents at depths of 150 cm in the margins.

5.4 Discussion

The standing stock of interstitial POC is maintained by the import from the surface habitat, as well as by the microbial conversion of dissolved organic carbon to biofilms attached to sediment particles. The general spatio-temporal patterns of POC storage in the sediments of the Töss River result from a complex of interacting superimposed factors: sediment depth and structure, vertical hydrological exchange, surface flow regime and season. These factors control the loading of particles entering the interstices (Walling, 1996). In addition, interstitial currents determine deposition and mobilization within voids and the straining by pore sizes (Herzig et al., 1970). The content of inorganic matrix fines reflects physical transport processes. Gravitational forces alone would produce an increase of fine inorganic particles with depth in a porous medium. The accumulation of fine inorganic particles with depth has also been found for other gravel-bed streams (Eglin, 1990; Panek, 1994). However, the hydraulic forces of upwelling ground water may prevent the intrusion of particles into deeper sediment layers. This can result in temporary accumulations at intermediate depths in upwelling zones or in a release of particles to the surface water when thresholds of interstitial currents are exceeded (Schärlchli, 1993). We measured a concentration of particles in a spring at the stream’s left margin in the range of 130-218 mg/l. Floods may also induce a flushing effect on matrix fines by a release of fines into the stream during bedload movement or by transport into the aquifer by bank infiltration.

The interstitial POC contents are correlated to the fine inorganic particles, although this is not reflected by the general vertical patterns below a 50-cm depth, except in the EZ. There, the low POC contents are a consequence of the upwelling ground water. In the IZ and HZ the decline of POC contents below a 50-cm depth may reflect a synergetic effect of biotic degradation, a reduced import (due to a decreasing sediment permeability
Figure 4. Discharge regime of the Töss River during the sampling period and the amount of fine inorganic particles (mg/l) within the interstices of the infiltration zone (IZ), horizontal advection zone (HZ) and exfiltration zone (EZ) at sediment depths of 20, 50, 100 and 150 cm, and in the surface water on 9 May, 16 May and 19 June 1995.
from increasing amounts of fine particles) and the increasing distances from the fluctuating surface flow (which dynamically influences interstitial throughflow). The variability in the POC contents reveals the effect of discontinuous POC import. However, particle transport can be assumed to be a continual process along interstitial flow paths.

The flashy discharge regime of the Töss may be responsible for the spatio-temporal variability of interstitial POC contents. Flood peaks were most numerous in spring. Concomittantly, the interstitial POC contents were the lowest. In contrast, the discharge in winter was dominated by low flow conditions and POC contents were correspondingly high. These high contents cannot be due to the import from riparian zones because the POC/TP ratios were significantly higher in autumn, demonstrating the importance of deciduous leaf litter input during that season.

The hydrograph peaks were artificially divided into minor, medium and major floods, since it was not possible to find discharge thresholds for initial motion of the bedload. This can be due to the flood history and different degrees of consolidation of the channel bed (Reid et al., 1985). The midstream sediments were moved most frequently, resulting in a permeable open-framework gravel, which facilitates the interstitial transport of particles. When such unconsolidated sediments are filled with fine particles, the deposition process begins in deeper layers and proceeds continuously to upper layers (Einstein, 1968). In agreement with these sediment properties we found higher amounts of pure organic particles (i.e. POC that was not associated with inorganic fine particles) in the HZ, which explain the higher POC/TP ratios in the HZ. These organic particles - originating from plants - cannot be buried during floods, because bedload movement to this depth would have removed our piezometers.

Flood events, vertical exchange of water, and the channel sediment structure are important determinants of the distribution of inorganic fine particles and POC to depths considerably more than 50 cm below the streambed. Thus transport and deposition of fine particles within the interstices (depth filtration) are not restricted to the upper layers of channel sediments in gravel-bed streams, where they may induce clogging of the interstices (colmation). Rather they extend further down and influence the habitat characteristics of deeper sediment layers.

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References


CHAPTER 6

Environmental gradient patterns in hyporheic interstices:  
A model based on hydrological exchange processes.

Abstract The affects of surface water infiltration, phreatic groundwater exfiltration and subsurface flow along the river channel (horizontal advection) on the environmental conditions within hyporheic interstices were studied in a transect of a prealpine gravel-bed river in Switzerland. Samples were taken from the surface water and 4 sediment depths (20, 50, 100, and 150 cm) using clustered sets of piezometers located in each of the three hydrological exchange types. We determined the depth extent of the hyporheic ecotone and the steepness of gradients by examining 8 physicochemical and 6 particle parameters with multivariate discriminant models.

Areas of steep gradients exist at sediment depths between 50 and 100 cm in the infiltration zone and between 20 and 50 cm in the horizontal advection zone. In contrast, in the exfiltration zone two areas with steep gradients exist; one between 0 and 20 cm and another between 50 and 100 cm. Physicochemical gradients function as stronger discriminators for the upper strata, whereas particle gradients distinguish the deeper depth strata. The study demonstrates the determining role of hydrological interactions for the position and steepness of environmental gradients in hyporheic interstices.

6.1 Introduction

The hyporheic interstices within alluvial sediments form the ecotone between the surface water and ground water (Schwoerbel, 1967). Generally ecotones are characterized by environmental gradients or transitions between two adjacent patches (Risser, 1990). In the hyporheic ecotone physicochemical gradients exist due to the mixing of water with different properties as well as from biogeotransformations that reflect the water’s residence time (Brunke & Gonser, 1997a). The surface discharge regime and its relationship to the solid load may also effect sedimentologic gradients within the alluvial sediments (Brunke & Gonser, 1997b). Different sedimentologic textures of framework gravel and matrix fine particles influence the porosity and hydraulic conductivity as well as the content of organic matter within the bed sediments (Leichtfried, 1985, 1988; Schälchli, 1993; Bretschko, 1994; Maridet & Philippe, 1995). In the formation of these
environmental gradients the surface and subsurface hydrological regimes as well as the interaction between them play determining roles (Brunke & Gonser, 1997a). The hydrological exchange between rivers and ground water can be subdivided into three types of net water movement: (A) The influent type of downwelling surface water (infiltration). (B) The effluent type of upwelling interstitial water (exfiltration) and (C) a neutral exchange type, where neither infiltration nor exfiltration prevails, but rather a subsurface flow along the river channel (horizontal advection).

The vertical upwelling and downwelling are caused by different hydraulic pressures of surface and interstitial water, e.g. due to changes in the streambed topography (Vaux, 1968; Thibodeaux & Boyle, 1987; White, 1990) or due to different hydraulic heads of the riparian ground water and stream water (Lee & Cherry, 1978). Mixing is also induced by the roughness of the streambed and by differences in density due to daily and seasonal temperature variations (Whitman & Clark, 1982; Hynes, 1983; Constantz et al., 1994). However, longitudinal advective flow within porous sediments also results in vertical dispersion (Cerling et al., 1990).

The objective of this study was to detect the influence of these three exchange types on the formation of environmental gradients within the hyporheic interstices (Fig. 1). A hypothetical model describing the position and steepness of gradients for each of the three hydrological exchange types has been developed. This model was then compared with the measured gradients and modified to a fitted model taking our results into account.

**Figure 1.** Model of the hydrological processes that create spatio-temporal heterogeneity in the interstitial habitat.
6.2 Study site and methods

The study was part of a multi-disciplinary research program of the EAWAG in the Töss River catchment. The Töss River is a third order prealpine gravel bed river. The study area (460 m a.s.l.) is situated in a valley upstream from the city of Winterthur, Switzerland. The formerly braided channel has been straightened and channelized by bank stabilization to a width of about 20 m. Due to this hydro-engineering the river has incised into its alluvial sediments and is surficially disconnected from its former flood plain. At the study site the flow direction of the riparian ground water crosses the stream (Fig. 2). At the left margin of the stream ground water upwells into the surface water (exfiltration zone), whereas at the right margin surface water downwells into the sediments (infiltration zone). In midstream neither infiltration nor exfiltration prevails because of neutral vertical hydraulic gradients (horizontal advection zone). In each of the three zones steel piezometer pipes (internal diameter = 5 cm) were inserted to four sampling depths (20, 50, 100, and 150 cm). Interstitial water for chemical analyses was collected by using an electric pump, after removing 2 liters from the pipe and 10 liters for faunistic investigations with a hand pump. Sampling was conducted at approximately monthly intervals between April 1995 and May 1996, with variations depending on the discharge regime.

Figure 2. Cross-sectional representation of the field site. Net flow movements are represented by arrows.

The analysis of the physicochemical gradients was conducted based on the following parameters: dissolved oxygen and BOD$_5$ (Winkler method), Nitrite-N (standard method according to DEW, 1995), Nitrate-N (standard method according to DEW, 1995), pH (Metrohm 678 EP/KF Processor), specific conductance (WTW LF91), alkalinity, and dissolved organic carbon (Shimadzu DOC-analyser). Other physicochemical parameters
were also measured (e.g. calcium and sulfate). However, these parameters showed negligible changes with depth and were therefore less relevant for the development of a model. For the particle parameters the samples were filtered through Whatman GF/F filters. The filters were oven dried at 60°C to constant weight for the measurement of fine inorganic particles. The fine inorganic particles are the freely moving matrix fines ('interstitial sediment' sensu Leichtfried, 1988). Inorganic carbon was removed from the filters with 3 M HCl. Then the dried filters with the residue were fired in a CHNS-analyser (Elementar vario EL) at 950°C for the measurement of particulate nitrogen (PN) and particulate organic carbon (POC). The POC and PN content is the particulate organic carbon and nitrogen per liter of sampled interstitial water, expressed as mg/l. The POC/TP and PN/TP ratios are the carbon and nitrogen in mg per g dry weight of all particles of the sample ('POC and PN concentrations' sensu Leichtfried, 1988).

The physicochemical and particle parameters were subjected to a multivariate discriminant analysis for two groups according to Flury & Riedwyl (1988). Within each hydrological exchange zone we compared the physicochemical and particle parameters of the adjacent depth strata, e.g. surface water and interstitial water of the 20 cm depth stratum (0/20). Prior to the statistical analysis the data were transformed and tested for normality. For the integration of the results into our model the standard distance D (Flury & Riedwyl, 1988) was calculated, which integrates the squared multiple r of the discriminant models and the number of measurements (n):

$$D = \sqrt{\frac{(n_1 + n_2)(n_1 + n_2 - 2)}{n_1 n_2}} \frac{r^2}{(1 - r^2)}$$

The dimensionless standard distance is the mean difference between two groups of data expressed in units of the standard deviation (Flury & Riedwyl 1988). The standard distance has the advantage (compared to the mean difference) that its interpretation is independent from the unit of measurement (Flury & Riedwyl 1988).

6.3 Results

Tab. 1 summarizes the results of the multivariate discriminant analysis for the comparisons between the different depth strata within each zone for physicochemical and particle parameters respectively.

For the infiltration zone no significant models could be developed for the comparison of the upper depth strata. The comparison between the 50 cm and 100 cm depths revealed
three discriminating parameters for the physicochemical and particle parameters respectively, with a similar multiple squared r (Tab. 1). The physicochemical parameters were not significantly different between the 100 and 150 cm depth strata, whereas three particle parameters discriminated these depth strata. In the horizontal advection zone only physicochemical parameters discriminate significantly between the upper strata. Contrastingly only particle parameters were different when comparing the depths of 50 and 100 cm as well as 100 and 150 cm.

Table 1. Results of multivariate comparisons between the physicochemical conditions (pc) and the particle parameters (part) between the depth strata in each zone (discriminant-analysis: within zones, between depths). The table provides the parameters that contribute significantly to models and the respective squared multiple r of the multivariate model. DO: dissolved oxygen. C/N: ratio between POC and PN. Levels of significance are as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

<table>
<thead>
<tr>
<th>Depth- Strata (cm)</th>
<th>Parameters</th>
<th>Infiltration Zone</th>
<th>Horizontal Advection Zone</th>
<th>Exfiltration Zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>0/20 pc</td>
<td>pH, BOD5, specific conductance,</td>
<td>pH, alkalinity, BOD5, specific conductance, DOC, nitrite-N,</td>
<td></td>
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<tr>
<td></td>
<td>multiple $r^2 = 0.73^{**}$</td>
<td>multiple $r^2 = 0.95^{**}$</td>
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<tr>
<td>part</td>
<td>--</td>
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<td></td>
</tr>
<tr>
<td>20/50 pc</td>
<td>pH, DOC, DO, specific conductance,</td>
<td>nitrite-N,</td>
<td>PN/TP, multiple $r^2 = 0.41^{**}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>multiple $r^2 = 0.98^{***}$</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>part</td>
<td>--</td>
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<td></td>
</tr>
<tr>
<td>50/100 pc</td>
<td>nitrate-N, DO, BOD5,</td>
<td>--</td>
<td>pH, alkalinity, DOC, DO specific conductance, multiple $r^2 = 0.88^{*}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>multiple $r^2 = 0.78^{***}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>part</td>
<td>POC/TP, PN/TP, C/N,</td>
<td>POC/TP,</td>
<td>POC/TP, PN (mg/l), multiple $r^2 = 0.57^{**}$</td>
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</tr>
<tr>
<td></td>
<td>multiple $r^2 = 0.74^{**}$</td>
<td>multiple $r^2 = 0.55^{**}$</td>
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<tr>
<td>100/150 pc</td>
<td>--</td>
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</tr>
<tr>
<td>part</td>
<td>POC/TP, PN (mg/l),</td>
<td>POC (mg/l), POC/TP,</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td></td>
<td>PN/TP, multiple $r^2 = 0.66^{**}$</td>
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</tbody>
</table>


In the exfiltration zone 6 physicochemical parameters were significantly different between the surface water and interstitial water at a depth of 20 cm. Only a single physicochemical and a single particle parameter were significantly different between the depths of 20 cm and 50 cm. However, 5 physicochemical and 2 particle parameters contribute to significant discriminant models between the depths of 50 and 100 cm. In contrast, the deeper layers were not significantly different.

The most frequent discriminating physicochemical parameters were the pH and specific conductance and for the particle parameters the POC/TP and PN/TP ratios. Generally the physicochemical parameters were important for the discrimination between the upper sediment layers, whereas particle parameters were more important for the comparisons of deeper strata. Physicochemical parameters were stronger discriminators between the strata than were particle parameters (Fig. 3). The mean difference was especially high between the depths of 20 and 50 cm of the horizontal advection zone, and between the surface water and interstitial water at a depth of 20 cm in the exfiltration zone (Fig. 3).

![Figure 3. Standard distances of the multivariate comparisons between strata of adjacent depths within each exchange zone for the physicochemical and particle parameters. The standard distance is dimensionless.](image-url)
6.4 Discussion

The hydrological interactions between surface water and interstitial water are not only influenced by channel morphology, e.g. by riffle-pool sequences. Alternating geologically constrained and unconstrained reaches with extensive alluvial aquifers may determine large-scale upwelling and downwelling zones (Stanford & Ward, 1993; Gonser, 1994). At the study site the hydraulic head differences between the riparian ground water and the stream water determined the hydrological exchange patterns. This situation appears to be common as it has already been shown to be of importance regarding pollution problems by several studies (Schwarzenbach et al., 1983; Von Gunten & Kull, 1986; Von Gunten et al., 1991; Bourg & Bertin, 1993; Benner et al., 1995).

Distinct exfiltration was located on the left side of the Töss River, whereas on the right side surface water infiltrated into the alluvial sediments. In the midstream neither infiltration nor exfiltration prevailed, but rather horizontal advection dominates the throughflow within the sediments. In each of these three zones different patterns of environmental gradients exist.

In the infiltration zone the environmental conditions of the upper sediment strata were determined by the downwelling of the surface water. Steep gradients for physicochemical and particle conditions existed between the depths of 50 and 100 cm and only weak particle gradients occurred between the 100 and 150 cm sediment layers. Our assumptions concerning the position and steepness of gradients in the infiltration zone appeared to be valid (Fig. 4).

In the horizontal advection zone steep physicochemical gradients existed in the upper strata especially between the 20 and 50 cm strata, which had not been predicted by our hypothetical model (Fig. 4). The synergistic effect of the mixing of surface water and ground water as well as biotransformations in conjunction with the residence time, might have been responsible for the formation of these gradients. Below the 50 cm stratum no statistically significant physicochemical gradients occurred; however, weak gradients of the particle parameters still indicated an influence of surface water.

In the exfiltration zone two areas of steep environmental gradients could be determined. Firstly, gradients of physicochemical parameters existed in the top layer of the channel sediment, presumably due to the mixing of the surface water and the upwelling ground water. Secondly, gradients of physicochemical and particle parameters between the 50 and 100 cm depths existed, which had not been expected by our hypothetical model (Fig. 4). These gradients indicated an influence of surface water down to a depth of 50 cm and no impact on the strata at depths of 100 and 150 cm. Thus these deeper strata were already within the phreatic ground water. However, the steep physicochemical gradients between the depths of 50 and 100 cm require further investigation, since steep gradients for the same parameters (pH, specific conductance,
Figure 4. Schematic hypothetical and fitted models of the position and steepness of environmental gradients within hyporheic interstices for three types of hydrological exchange patterns (infiltration, horizontal advection, exfiltration). The shaded areas indicate the depth extent of the ecotone and the black areas the position of steepest gradients. The fitted model is based on the hypothetical model after integrating the results of the standard distance. The two columns depicted in the representations of each zone indicate that the patterns may vary in time due to discharge fluctuations.

**HYPOTHETICAL MODEL**

**Infiltration Zone**
- benthic zone
- ecotone
- phreatic zone

**Horizontal Advection Zone**
- benthic zone
- ecotone
- phreatic zone

**Exfiltration Zone**
- benthic zone
- ecotone
- phreatic zone

**FITTED MODEL**

**Infiltration Zone**
- benthic zone
- ecotone
- phreatic zone

**Horizontal Advection Zone**
- benthic zone
- ecotone
- phreatic zone

**Exfiltration Zone**
- benthic zone
- ecotone
- phreatic zone

![Diagram](image_url)
alkalinity, DOC) also occurred between the surface water and the interstitial water of the 20 cm depth stratum.

In general terms - comparing the hydrological exchange types - the position of steep gradients shifts from deeper strata in the infiltration zone towards upper strata in the exfiltration zone, with the exception of the gradients between the 50 and 100 cm depth strata. The latter suggest the possibility of further gradients in the infiltration zone and horizontal advection zone below the 150 cm depth. The physicochemical gradients were stronger discriminators in upper hyporheic interstices, whereas particle parameters gained more importance in deeper interstices. The pH and the specific conductance appeared to be good indicators of the changing environmental conditions, since they contributed most to the discriminant models. However, the variable composition of the discriminant models shows, that each parameter may develop its own dynamics (see also Danielopol, 1991), although some parameters such as specific conductance and alkalinity are correlated (see also Williams, 1989). In the highly permeable gravel-bed of this negligibly polluted stream the interstitial water was well oxygenated at all depths, even in the deep ground water of the alluvial flood plain (Brunke unpublished data). Thus dissolved oxygen contributed only to three discriminant models in terms of the differentiation between two strata, and may not play a controlling role for biotic processes at our study site. This supports the perspective of Vervier et al. (1992), that the ecotonal permeability of highly porous sediments is controlled by throughflow, whereas in partially clogged aquifers it is governed by aerobic and anaerobic processes.

The inorganic particles do not seem to play a primary role for the statistical significance of particle gradients. This may be because of their high variability (Leichtfried, 1994; Brunke & Gonser, 1997b). However, they are integrated in the calculation of the POC/TP and PN/TP ratios. The POC/TP and PN/TP ratios were frequent discriminators between the depth strata. Although the statistical discrimination was weak for these parameters, they are expected to be critical for the distribution of hyporheic biota.

6.5 Conclusions

The discriminant model clearly revealed different patterns of environmental gradients within a cross-section of hyporheic interstices in a prealpine gravel-bed river. The different depth extent and the steepness of physicochemical and particle gradients were determined by the prevailing hydrological exchange type. The influence of surface water can be detected down to a depth of 150 cm in the case of the influent type and also in midstream in the case of the neutral exchange type. In contrast, no significant effect of
surface water could be determined at the depth of 100 cm or below for the effluent type, which is clearly influenced to a depth of 50 cm. However, the net upward movement of water in this exchange type induced strong gradients in two depth strata; in the top centimeters of the streambed as well as between 50 and 100 cm depth. In midstream steep gradients existed between depths of 20 and 50 cm, due to the mixing of surface water and ground water and biotransformations in conjunction with the residence time. These results demonstrate the necessity to include hydrological exchange patterns beside the fluvial geomorphology into studies on hyporheic metabolism and community structure as well as in those concerning salmonid reproduction.

In a conceptual perspective hyporheic interstices appear to be composed of areas with varying patterns of non-uniform vertical discontinuities due to the differential water exchange along hydrological gradients.

Acknowledgements

We thank A. Mares for the analyses of particulate organic carbon and nitrogen.

References


CHAPTER 7

Hyporheic bacteria - relationships to environmental gradients and invertebrates in a prealpine stream

Abstract Bacterial abundance and production in hyporheic interstices of the Töss River, a gravel-bed stream in Switzerland, were examined focusing on spatial distribution patterns in relationship to potential resources and meio- and macrofaunal consumers. The subsurface flow regime at the study site was characterized by a cross-sectional hydraulic gradient, with ground water exfiltration at the left margin and surface water infiltration at the right margin; in midstream, horizontal advection along the channel flow prevailed. Measurement of biotic and abiotic parameters were performed down to sediment depths of 150 cm within each hydrological exchange type.

Bacterial abundances ranged between 0.163 to 478 x 10^6 cells/ml interstitial volume containing water and fine particles and differed significantly between upper and deeper sediment strata. This change with depth was significantly modulated by the type of hydrological exchange. The bacterial carbon portion of total POC varied between 0.06% and 5.3% and tended to decrease with depth. Bacteria were most numerous at sediment depths where inflow of stream water occurred, but had been attenuated. Bacterial production was highest in hyporheic interstices dominated by surface water inflow. Bacterial abundance and production were strongly correlated to interstitial particulate organic matter; the best predictor for both was the content of particulate nitrogen, explaining 75% and 72% of the variation, respectively. Inclusion of hyporheic positions, defined by sediment depth and hydrological exchange type, substantially improved the explanatory power of models to 82 - 91%. Hyporheic positions provide information on flowpath connections, which were particularly relevant in the use of dissolved organic carbon and interstitial fine sediment as explanatory variables.

Several hyporheic invertebrate taxa, taxa richness and total invertebrate density showed positive relationships to bacterial abundance and production. The hyporheic fauna exhibited a gradient between interstitial positions influenced by surface water and those dominated by phreatic ground water. The coupling of sediment depth and

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1 in collaboration with Helmut Fischer, Institute of Freshwater Ecology and Inland Fisheries, Dept. II: Limnology of Lowland Rivers and Shallow Lakes, Müggelseedamm 260, D-12563 Berlin, Germany
hydrological exchange type revealed flowpath connections as being superimposed vectors in determining hyporheic abiotic and biotic gradients.

7.1 Introduction

Hyporheic interstices are an important compartment for the metabolism of many fluvial systems (Grimm & Fisher, 1984; Stanford & Ward, 1993; Findlay, 1995; Brunke & Gonser, 1997a; Naegeli & Uehlinger, 1997). Due to their retentiveness, these sediments form the major storage site for organic matter in streams (Metzler & Smock, 1989; Meyer, 1990), buffering the strongly seasonal input of allochthonous particulate organic matter (POM) (Herbst, 1980; Bretschko & Moser, 1993; Naegeli, 1997) upon which detritivores depend. Furthermore, inputs of dissolved organic matter (DOM) by pulses during floods and by ground water discharge are immobilized there (Fiebig & Marxsen, 1992; Fiebig, 1995). DOM is transformed into POM by microorganisms and made available to invertebrates (Dahm, 1984; Marxsen, 1988a). Microorganisms have a controlling function on fluvial metabolism, since more than 90% of the community respiration can be attributed to their biochemical degradations and transformations of DOM and POM (Pusch & Schwoerbel, 1994; Pusch, 1996). Fungi are found only rarely in ground water (Hirsch & Rades-Rohkohl, 1983; Madsen & Ghiorse, 1993), probably due to their dependence on a minimal size of dead plant particles (Sinsabaugh & Linkins, 1990). Heterotrophic bacteria mediate many conversions of organic matter exclusively, because of their specific enzyme systems (Chrost, 1990). Due to their role as decomposers of POM and as a food resource for primary consumers, bacteria play a major role in fluvial sediments.

In general, studies on stream bacterial ecology are scarce (Leff, 1994), especially for hyporheic sediments (Hendricks, 1996). Furthermore, to our knowledge no previously published study has examined the relationship between hyporheic bacteria and meio- and macrofauna. In our study, we investigated hyporheic bacterial abundance and production and their relationships to physicochemical and particle parameters as well as to invertebrate abundances. Because hyporheic interstices form an ecotone between streams and ground water, they are characterized by various environmental gradients (Schwoerbel, 1961; Brunke & Gonser, 1997a). The position and steepness of these gradients are strongly influenced by the hydrological interactions between the surface water and the ground water (Brunke et al., 1998a). Based on previous investigations (Brunke & Gonser in prep.), we distinguished three hydrological exchange types of net interstitial water movement at our study site: (A) infiltration of surface water into the sediment, (B) exfiltration of ground water into the stream, and (C) preferential subsurface
flow along the river channel, termed horizontal advection. Thus we were able to specify
the hyporheic habitat by combinations of sediment depth and hydrological exchange type.
These hyporheic positions indicate differential interstitial flowpath connections.

Our objective was to determine how bacterial abundance and production vary as a
function of depth and hydrological exchange type, which both significantly influence
possible controls of the microbiota (Sander & Kalff, 1993; Schallenberg & Kalff, 1993;
Fischer et al., 1996; Brunke et al., 1998b).

1) We hypothesized that bacterial abundance is correlated to the interstitial content of
particulate organic carbon (POC) and fine inorganic particles. Higher amounts of stored
interstitial POC should improve the nutritional conditions, e.g. by abiotic retention of
nutrients within a polysaccharide matrix (Fiebig, 1997) as well as by a release of DOC
(Crocker & Meyer, 1987). Detrital particles should provide surfaces for bacterial
colonization (Bott & Kaplan, 1985). The fine inorganic particles were expected to be an
indicator of the overall hyporheic internal surface which can be covered by a biofilm.

2) We hypothesized that bacterial production should be highest in the upper sediments of
areas with infiltration and horizontal advection, where the delivery of nutrients and DOC
by stream water is effective.

3) We hypothesized that the density of interstitial invertebrates corresponds positively
with bacterial abundance and production. The microbial loop, although being questioned
(Thomas, 1997), might function as a trophic link in streams even more than it does in
pelagic systems (Meyer, 1994). The polysaccharide matrix, bacteria and their direct
microfaunal consumers, all may be utilized by detritivorous metazoans (Fenchel &
Jørgensen, 1978; Bärlocher & Murdoch, 1989). POC colonized by bacteria may be more
attractive for invertebrate collectors, due to an enrichment of incorporated nitrogen and
other nutrients entrapped in the polysaccharide matrix.

7.2 Study site

The study was carried out in the Töss River, a calcareous gravel-bed stream in northern
Switzerland (Fig. 1). At the sampling site (3rd order, 460 m a.s.l., 0.5% gradient, MQ =
7m³/s) this prealpine stream flows in a valley which is only used by forestry. The
formerly braided stream has been straightened and channelized by bank stabilization to a
width of about 20 m. Subsequently it has incised about 3 m into its up to 20 m thick
fluvio-glacial sediments and is now surficially disconnected from its former floodplain. A
series of weirs of 20 to 40 cm height inhibits further downcutting and also prevents the
development of natural riffle-pool sequences, which could effect small-scale up- and
downwelling (Harvey & Bencala, 1993). At our study site the flow of the upper ground
water crosses the channel (Fig. 1). The different hydraulic pressures between the riparian ground water and the stream induce hydrological exchange: At the left margin of the stream ground water exfiltrates into the surface water (exfiltration zone, EZ), whereas at the right margin surface water infiltrates into the bed sediments (infiltration zone, IZ) (Fig. 1). In midstream interstitial throughflow in direction of the streamflow prevails (horizontal advection, HZ). At the margins of the stream, where the infiltration and exfiltration zones are located, the top channel sediments form an erosion-resistant armor layer, whereas frequent bed movement along the middle of the stream maintains open-framework gravel. The mean grain size of the entire sampling site was for the surface (top 10 cm) and subsurface (10 - 70 cm) sediments 31 mm (± 26 SD) and 11 mm (± 3.6 SD) respectively; the mean porosity was 18.8% (± 6.6 SD).

Figure 1. Study area, showing the location within Switzerland (top), the groundwater flowpath and the location of the sampling site on the Töss River in plan view (middle), and a cross section through the sampling site (bottom). The 4 vertical lines at the infiltration, horizontal advection and exfiltration zones represent the sampling piezometers nests at these 3 locations.
7.3 Material and methods

To detect influential factors for the biota and to characterize environmental conditions, we measured an array of abiotic parameters and collected the hyporheos from the same piezometers. Three piezometer nests were installed in each of the three hydrological exchange zones (total 36). Each piezometer nest contained 4 steel pipes (internal diameter = 5 cm) with perforations (diameter = 5 mm) which were inserted to sediment depths of 20, 50, 100, and 150 cm beneath the stream bed surface. The sampling campaign was conducted on September 2 and 3, 1997. For the collection of faunistic samples 10 liters of interstitial water was extracted by a hand pump after discarding the first two liters (Bou & Rouch, 1967; Husmann, 1971) and passed through a 90 μm mesh net. For the sampling of bacteria, physicochemical and particle parameters, the interstitial water containing the fine sediment was collected by means of an electric pump after taking the faunistic sample. The measured physicochemical parameters are: temperature, dissolved oxygen and BOD₅ (Winkler method, without inhibitor for nitrification), Nitrite-N (standard method according to (DEW, 1985), Nitrate-N (standard method according to (DEW, 1985)), pH (Metrohm 678 EP/KF Processor), specific conductance (WTW LF91), alkalinity, and dissolved organic carbon (Shimadzu DOC-analyser). Water temperature was measured by lowering a thermometer into the piezometer, which was integrated into the electric tape used to measure hydraulic heads. VHG was calculated as the difference in hydraulic head divided by depth of the piezometer (Lee & Cherry, 1978).

For the particle parameters the samples were filtered through Whatman GF/F filters. The filters were oven dried at 60°C to constant weight for the measurement of fine inorganic particles (sands, silts, clays). The fine inorganic particles are the freely moving matrix fines ('interstitial sediment', sensu Leichtfried, 1991), that together with the framework gravel represent the two components of the bed sediment in gravel-bed rivers (Petts, 1988). The differentiation between the coarser mobile matrix fines and the framework sediment is not sharp (Petts, 1988). In this study the fine inorganic particles had a grain size < 1 mm, and the grain size distribution had a median of 0.03 mm. The amount of stored interstitial POC tends to increase with decreasing grain size, and in calcareous gravel-bed sediments by far the most of the POC is in the size class < 1 mm (Leichtfried, 1988; Eglin, 1990) and mainly represents the biofilm (Bretschko & Leichtfried, 1988). Inorganic carbon was removed from the filters with 3 M HCl. Then the dried filters with the residue were fired in a CHNS-analyser (Elementar vario EL) at 950°C for the measurement of particulate nitrogen (PN) and particulate organic carbon (POC). The POC and PN content is the particulate organic carbon and nitrogen in 1 liter of sampled interstitial water. The amount of interstitial detrital particles >90 μm that originate mostly from plants had been extracted from the faunistic sample by a flotation
technique along with the interstitial animals (Danielopol, 1976; Dole-Olivier & Marmonier, 1992). In another step detrital particles and animals were separated by removing the animals individually. The detrital particles were measured as ash free dry mass by loss on ignition (550°C). The age of hyporheic water was estimated by measuring the radioactive isotope radon (222Rn) (Hoehn & von Gunten, 1989).

Bacteria were counted by the fluorescent count method of Porter and Feig (1980), which was modified according to Velji & Albright (1986), Yu et al. (1995), and Fischer et al. (1996). Subsamples of 3.6 ml interstitial water were fixed with 0.4 ml of 35% formaldehyde. Sterile filtered solutions of NaCl and pyrophosphate (Na₄P₂O₇ x 10H₂O; Sigma) were added to final concentrations of 0.85% and 1 mM, respectively. Samples were vortexed for 15 s, sonicated for 10 min in a sonication bath (Elma T 710 DH), and vortexed again for 15 sec. The samples were later diluted with a sterile filtered aqueous solution of 3.5% formaldehyde, 0.85% NaCl, and 1 mM pyrophosphate. Dilution factors ranged from 1 : 2 to 1 : 400, depending on the particle content of the samples. After dilution, each sample to be filtered should contain about the same amount of particles (ca. 100 μg per filter). This procedure was used to hold the effects of sediment masking (Schallenberg et al., 1989) constant for all samples, because previous counts have shown that the quantity of particles on the filters heavily affected the number of visible bacteria. Particle contents had been determined prior to filtration, drying and combustion (see above). DAPI (4',6-diamidino-2-phenylindol) was added to a final concentration of 10 mg/l. After 40 min of dark incubation, bacteria were filtered onto black polycarbonate filters (Nuclepore, pore size 0.2 μm). Generally, at least 200 bacteria within at least 10 microscopic fields were counted by epifluorescence microscopy (Nikon FXA Microscope, HBO 100 W, Ex 330-380, DM 400, BA 400, immersion objective CF N DIC Plan Achromate 100 x). Samples containing very few bacteria and relatively high particle amounts were examined with up to 100 microscopic fields to a count of at least 50 bacteria.

For bacterial production measurements, L-[U-14C]-leucine (Amersham Ltd.) at a specific activity of 11.2 GBq/mmol was diluted with the appropriate amount of cold L-leucine (Sigma) to achieve specific activities of 74, 148, and 296 Bq/nmol leucine. Subsamples of 3.88 ml interstitial water were poured into precombusted centrifuge vials and completed with cold and hot leucine solutions to 4 ml, achieving a final Leucine concentration of 50 μM. A previous saturation experiment had shown that a concentration of 50 μM leucine was close to saturation in interstitial water of the Töss River (Fischer & Pusch in prep.). Samples were incubated under gentle shaking for 3.5 h at a temperature of 13°C. Leucin incorporation is assumed to be linear over this time span (Marxsen, 1996, Fischer & Pusch in prep.). The incubation was stopped by the addition of 0.4 ml of 35% formaldehyde. Samples were then sonicated, and protein was extracted.
using hot trichlor acetic acid (TCA) at a final concentration of 5%. The precipitate was filtered onto 0.2 µm polycarbonate filters (Nuclepore), which were put into 20 ml scintillation vials. Subsequently, the filters were completely dissolved in 1 ml solvent (Soluene, Packard Instr. Comp.) and 10 ml of scintillation fluid was added (Hionic Fluor, Packard). Radioactive decays were measured using a Packard 1600 scintillation counter. Five controls killed with 3.5% formaldehyde (final concentration) immediately at the start of the incubation were run for each specific activity. Bacterial carbon production was calculated from leucine incorporation assuming 7.3 mol% leucine in total protein, and a carbon:protein ratio of 0.86 (Simon & Azam, 1989).

Spearman rank correlations were used to reveal relationships of bacterial data with ambient environmental conditions and invertebrate densities. Data were log-transformed to reduce skewness and kurtosis prior to further statistical analysis. Principal component analyses (PCA) were conducted for an ordination of the sampling positions within the hyporheic interstices and to explore the correspondence between the stream/interstitial water exchange gradient and the bacterial, environmental and faunal data. The general linear model (linear regression analysis; analysis of variance, ANOVA; analysis of covariance, ANCOVA) (Stahel, 1995) was applied to test effects of sediment depth, hydrological exchange type, and environmental parameters on bacterial abundance and production. Multiple comparisons were made using Tukey's test.

### 7.4 Results

**Environmental gradients within the hyporheic habitat**

The vertical hydraulic gradients (VHG) of the four sediment depths for each hydrological exchange zone are shown in Fig. 2. Negative VHG depict lower water pressure within the interstices compared to the stream indicating infiltration, positive VHG depict higher water pressure within the interstices compared to the stream indicating exfiltration. During the 2-day sampling campaign in late summer the water table of the aquifer was low due to the previous season being dry, resulting in lower VHG in the exfiltration zone (EZ) compared with the year round average (Brunke & Gonser in prep.) and a slight tendency for infiltration in the horizontal advection zone (HZ). In permeable stream sediments VHGs do not mean exclusive vertical interstitial flow. Rather, the general longitudinal flow along the channel is altered within the interstices by a vertical vector of interstitial water, resulting in a mixing of surface, hyporheic and phreatic ground water.

The interstitial temperature decreased with depth in all zones (Fig. 2). Within each depth stratum the temperature was colder in the EZ than in the infiltration zone (IZ) and
The temperature patterns of the 100-cm and 150-cm depth strata were similar in the EZ, reflecting the dominance of the phreatic ground water.

The age of the interstitial water was measured on December 9, 1997 (Fig. 2), so it may not necessarily reflect the mixing of the interstitial water on September 2, when all other measurements were conducted. Nevertheless, the interstitial temperature on September 2 was strongly correlated to age-estimations ($r_s = -0.76, p < 0.001$). In the 20-cm depth stratum water was slightly older in the EZ than in the IZ and HZ, where it was younger than one day. In 50-cm depth, water age tended to be younger in the IZ compared with the others. In the EZ age increased strongly below 50-cm, and in the IZ below 100-cm, whereas in the HZ some age-estimations indicate young water. However, these data are preliminary and provide a first attempt to assess the age of hyporheic water by the radon method (Hoehn & von Gunten, 1989).

The concentration of interstitial dissolved oxygen ranged from 4.2 to 12.2 mg/L (overall mean 8.7 ±2.3 SD) and is probably not a constraining factor for hyporheic biota in the Töss River (Brunke & Gonser in prep.). Interstitial DOC ranged from 1.0 to 2.2
mg/l. DOC concentrations tended to decrease with decreasing hyporheic water temperature ($r_s = 0.78$, $p < 0.001$), as an indicator of the mixing between surface and interstitial water. In the same way, DOC concentrations decreased with the age of hyporheic water ($r_s = -0.76$, $p < 0.001$).

The first two axes of the principal component analysis (PCA) account for 66.6% of the total variability of environmental parameters. The factorial map of the sampled positions reveals three groups (Fig. 3a). The hyporheic positions within the EZ are placed in the upper part of the factorial map; the upper sediment depth strata of all zones are situated on the right part and the lower sediment depths are located on the left side. The positions within the IZ and HZ are not distinguished by the ordination.

The first principal component depicts a gradient of hydrological exchange: Environmental parameters with higher values in hyporheic sediments due to a dominating influence of surface water (i.e. 20 and 50-cm depth positions in the IZ and HZ) are located on the right side of the ordination plot (Fig. 3b). In contrast, those environmental parameters with higher values in sediments dominated by mixing with phreatic ground water or long residence times of interstitial water were located on the left side of the plot. The VHG and nitrate-N concentrations occur in an intermediate position, because they were highest in the upper sediment depths of the EZ.

The ordination plot (Fig. 3b) reveals that bacterial production and the portion of bacterial biomass of total POC were highest in interstices with effective inflow of surface water (characterized by higher temperatures, pH and DOC concentrations).

**Depth distribution of hyporheic bacteria in different hydrological exchange zones**

In the hyporheic habitat of the Töss River bacterial numbers ranged from $1.63 \times 10^5$ to $4.78 \times 10^8$/ml. The overall means of bacterial numbers (cells $\times 10^6$/ml) for the 20-, 50-, 100-, and 150-cm depth strata were ($\pm$SD), $71.8 \pm 153.1$, $31.6 \pm 32.2$, $1.7 \pm 1.4$ and $2.3 \pm 4.1$, respectively. Assuming a mean bacterial volume of $0.127 \mu m^3$ as found in the hyporheic zone of a mountain stream (Fischer et al., 1996), and using the volume to carbon conversion factor of Simon et al. (1990), the bacterial biomass (mg C/l) in the respective sediment depths was ($\pm$SD), $1.80 \pm 3.83$, $0.789 \pm 0.805$, $0.042 \pm 0.035$, and $0.057 \pm 0.101$. Bacterial abundance and production were highly correlated ($r_s = 0.94$, $p < 0.001$) and bacterial abundance explained 88% of the variations in production ($\ln(y) = 2.671 + 0.782 \times \ln(x)$, $p < 0.001$). Bacterial parameters changed with sediment depth (Fig. 4, Tab. 1); both were significantly higher in the 20-cm and 50-cm depth strata than in the 100 and 150-cm depths (Tukey's test, $p < 0.05$).
Figure 3. PCA ordination plot of the environmental parameters. (A) Factorial scores of hyporheic positions; i, infiltration zone; h, horizontal advection zone; e, exfiltration zone; 20 = 20-cm depth; 50 = 50-cm depth; 100 = 100-cm depth; 150 = 150-cm depth. Lighter shading of dots indicates increasing groundwater influence. (B) Ordination of environmental parameters. Correlation arrows are removed to improve clarity. Values in parentheses along axes are the amounts of variation explained by the principal component.
The effect of the hydrological exchange zones on bacterial abundance and production is only evident in conjunction with the sediment depth (Tab. 1). In a two-way ANOVA, the introduction of the zone as main effect improved the one-way model of depth from 62% to 82% explained variance. The interaction between depth and zone is also significant, indicating that the exchange type modulates the effect of sediment depth on interstitial bacterial abundance. Both depth and zone also exert controls on bacterial production, but the relationship is weaker than with bacterial abundance. The one-way ANOVA model with depth as main effect, is improved by the zone in a two-way model from 59% to 76% explained variance of production. The effect of zone on production in the two-way model is not statistically significant, nor is the interaction between zone and depth. However, low p-values suggest, that more samples might have revealed statistical significance. The one-way ANOVA model with hyporheic position, specified by sediment depth and zone, as the main effect is highly significant for bacterial abundance and production.

<table>
<thead>
<tr>
<th>Bacterial variable</th>
<th>main effects</th>
<th>interaction</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Depth</td>
<td>Zone</td>
<td>Hyporheic position</td>
</tr>
<tr>
<td>Abundance</td>
<td>3/16.5***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>2/1.3</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>3/23.5***</td>
<td>2/4.7*</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>11/9.2***</td>
</tr>
<tr>
<td>Production</td>
<td>3/14.8***</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>2/0.7</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>3/17.7***</td>
<td>2/2.0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>11/6.7***</td>
</tr>
</tbody>
</table>

The bacterial biomass portion of total interstitial POC ranged from 0.06% to 5.3% (Fig. 4) and changed significantly with sediment depth (ANOVA, $F_3 = 4.5$, $p = 0.01$). It is significantly higher in the 20-cm depth than in 100 and 150-cm depths, and higher in 50-cm than in the 150-cm depth (Tukey's test, $p < 0.05$). The change with depth was gradual in the EZ, whereas it was discontinuous for the other exchange zones. The bacterial portion of POC tended to increase with increasing POC content and to be lower in the EZ than in the IZ and HZ.
Figure 4. Depth profiles of bacterial abundance, production and bacterial biomass portion of POC for the infiltration zone (IZ), horizontal advection zone (HZ) and exfiltration zone (EZ) (n = 36). Dotted line connects the averages of each depth stratum.

Relationships between hyporheic bacteria and environmental parameters

Several of the measured physicochemical parameters had high rank correlations to bacterial parameters (Tab. 2) and may indirectly reflect microbial activity, as e.g. pH due to CO₂ release, and NO₂-N as an intermediate product during nitrification. Nitrification is an important microbial process in the hyporheic interstices of the Töss River. The main source of ammonium is the surface water of the Töss River (Brunke et al., 1995) and the nitrite concentration decreased strongly to a sediment depth of 100 cm, below which it remained on a minimal level in all exchange zones. However, we did not integrate nitrite concentrations into the regression models to predict bacterial parameters. We also did not include temperature into predictive models, since temperature variations were moderate and so were likely to have only a minor influence on microbial processes (Findlay & Sobczak, 1996; Fuss & Smock, 1996); all incubations for measuring bacterial production were carried out at 13°C. Of course, interstitial temperatures indicated subsurface water mixing, as demonstrated by the depth profiles (Fig. 2) and thus might covary with predictors used in our study. Temperature is certainly of importance for seasonal
variation in bacterial activity (Sander & Kalff, 1993; Pusch & Schwoerbel, 1994; Fischer et al., 1996), which, however, was not the objective of our study.

**Table 2.** Spearman rank correlation coefficients between hyporheic bacteria and environmental parameters at all hyporheic sampling positions in the Töss River. †*P<0.1, *P<0.05, **P<0.01, ***P<0.001.

<table>
<thead>
<tr>
<th>Environmental parameters</th>
<th>Bacterial abundance</th>
<th>Bacterial production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.69***</td>
<td>0.66***</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.54***</td>
<td>0.42*</td>
</tr>
<tr>
<td>BOD5</td>
<td>0.61***</td>
<td>0.50**</td>
</tr>
<tr>
<td>pH</td>
<td>0.78***</td>
<td>0.72***</td>
</tr>
<tr>
<td>Specific conductance</td>
<td>-0.74***</td>
<td>-0.66***</td>
</tr>
<tr>
<td>Alkalinity</td>
<td>-0.61***</td>
<td>-0.51***</td>
</tr>
<tr>
<td>NO2-N</td>
<td>0.80***</td>
<td>0.70***</td>
</tr>
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<td>NO3-N</td>
<td>-0.13</td>
<td>-0.19</td>
</tr>
<tr>
<td>DOC</td>
<td>0.66***</td>
<td>0.63***</td>
</tr>
<tr>
<td>Fine inorganic particles</td>
<td>0.68***</td>
<td>0.64***</td>
</tr>
<tr>
<td>POC</td>
<td>0.84***</td>
<td>0.81***</td>
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<tr>
<td>PN</td>
<td>0.90***</td>
<td>0.87***</td>
</tr>
<tr>
<td>POC/PN</td>
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<td>-0.73***</td>
</tr>
<tr>
<td>POC/Total fine particles</td>
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<td>0.39*</td>
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<tr>
<td>Detrital particles</td>
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<td>0.85***</td>
</tr>
</tbody>
</table>

The general linear model was used for predictions of bacterial parameters in the hyporheic interstices of the Töss River: Bacterial production and abundance were significantly related to the variables we hypothesized as exerting controlling functions (Tab. 3). POC and PN explained most of the variation in bacterial parameters. In the regression models the $r^2$ for each variable is higher for bacterial abundance than for production.

In multiple regression models (Tab. 4), the combination of DOC and variables of particulate organic matter, POC, PN, and detrital particles, did not appreciably improve the coefficient of determination. The magnitude of the partial correlation coefficients indicates POM effects are greater. POM-parameters and DOC were not complementary variables, as expected. In contrast, DOC has a partial correlation coefficient that was similar to that of the fine inorganic particles in their two-dimensional regression model. Furthermore the $r^2$ is clearly higher than for both single models. However, the single regression models of POM variables explain more (POC, PN) or a similar variation
(detrital particles). POC and PN are even better predictors of bacterial parameters compared to multiple models including fine inorganic particles, DOC and the detrital particles. Since models require a minimal $r^2$ of 0.65 to be used in predictions (Prairie, 1996), the single models, whose $r^2$ are clearly higher the 0.65, are powerful enough to be used in predictions. POC, PN, and the fine inorganic particles could not be combined in multiple regression models due to a high degree of collinearity.

**Table 3. Results of simple regression models to explain bacterial abundances and production. Degrees of freedom/F-value. *P<0.05, **P<0.01, ***P<0.001.**

<table>
<thead>
<tr>
<th>Bacterial variable</th>
<th>POC</th>
<th>PN</th>
<th>POC/PN</th>
<th>Fine inorganic particles</th>
<th>DOC</th>
<th>Detrital particles</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>$1/83.6^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>$1/94.8^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>$1/36.9^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/27.4^{***}$</td>
<td>-</td>
<td>-</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/26.4^{***}$</td>
<td>-</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/55.0^{***}$</td>
<td>0.63</td>
</tr>
<tr>
<td>Production</td>
<td>$1/69.1^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>$1/83.0^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>$1/37.3^{***}$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/23.2^{***}$</td>
<td>-</td>
<td>-</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/21.6^{***}$</td>
<td>-</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>$1/48.3^{***}$</td>
<td>0.59</td>
</tr>
</tbody>
</table>

The information of sediment depths and hydrological exchange types (integrating the 'hyporheic position') is missing in above models. The effect of hyporheic position on bacterial parameters is apparent in the ANCOVA models (Tab. 5). In these the coefficient of determination ranges between 0.86 and 0.91. The effect of hyporheic position is less pronounced in models with POC and PN as covariates, compared to fine inorganic particles, DOC and detrital particles. The significance of hyporheic positions suggests that the quantities of the predictors used were not solely of importance for bacteria, but also the quality of the predictors (which is determined by their origin and change during the interstitial flowpath from the surface habitat).
Table 4. Results of multiple regression models to predict bacterial abundances and production. Coef is the regression coefficient associated with each independent variable; the t-value and associate probability (P) are given for each variable in the model. β-coef is the standardized partial regression coefficient; SE = standard error of regression coefficient. ANOVA model: Degrees of freedom/F-value. *P<0.05, **P<0.01, ***P<0.001.

<table>
<thead>
<tr>
<th>Environmental parameters</th>
<th>Bacterial abundance</th>
<th>Bacterial production</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coef±SE</td>
<td>β-coef</td>
</tr>
<tr>
<td>Constant</td>
<td>-1.89</td>
<td>0.38</td>
</tr>
<tr>
<td>POC</td>
<td>1.01</td>
<td>0.15</td>
</tr>
<tr>
<td>DOC</td>
<td>2.40</td>
<td>0.97</td>
</tr>
<tr>
<td>Constant</td>
<td>-0.92</td>
<td>0.30</td>
</tr>
<tr>
<td>PN</td>
<td>2.25</td>
<td>0.30</td>
</tr>
<tr>
<td>DOC</td>
<td>1.75</td>
<td>0.91</td>
</tr>
<tr>
<td>Constant</td>
<td>1.16</td>
<td>0.52</td>
</tr>
<tr>
<td>Detrital Particles</td>
<td>2.14</td>
<td>0.47</td>
</tr>
<tr>
<td>DOC</td>
<td>2.35</td>
<td>1.25</td>
</tr>
<tr>
<td>Constant</td>
<td>-5.26</td>
<td>1.19</td>
</tr>
<tr>
<td>Fine inorganic particles</td>
<td>0.78</td>
<td>0.19</td>
</tr>
<tr>
<td>DOC</td>
<td>4.34</td>
<td>1.05</td>
</tr>
<tr>
<td>Constant</td>
<td>-1.93</td>
<td>1.29</td>
</tr>
<tr>
<td>Fine inorganic particles</td>
<td>0.57</td>
<td>0.18</td>
</tr>
<tr>
<td>DOC</td>
<td>2.08</td>
<td>0.39</td>
</tr>
</tbody>
</table>
Table 5. Summary of ANCOVA of bacterial abundances testing the effect of hyporheic positions, with organic matter measures and fine inorganic particles as covariates. Degrees of freedom/F-value. †P<0.1, *P<0.05, **P<0.01, ***P<0.001.

<table>
<thead>
<tr>
<th>Bacterial variable</th>
<th>Hyporheic position</th>
<th>POC</th>
<th>PN</th>
<th>Fine inorganic particles</th>
<th>DOC</th>
<th>Detrital particles</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>11/2.5*</td>
<td>1/10.3**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>11/2.3†</td>
<td>-</td>
<td>1/11.4**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>11/6.7***</td>
<td>-</td>
<td>-</td>
<td>1/10.2**</td>
<td>-</td>
<td>-</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>11/6.2***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/7.8*</td>
<td>-</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>11/4.3**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/12.4**</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>11/2.3†</td>
<td>1/5.3*</td>
<td>-</td>
<td>-</td>
<td>1/3.3†</td>
<td>-</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>11/4.4**</td>
<td>-</td>
<td>-</td>
<td>1/5.6*</td>
<td>1/3.6†</td>
<td>-</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>11/3.2*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/2.9</td>
<td>1/3.8</td>
<td>1/3.1†</td>
</tr>
<tr>
<td>Production</td>
<td>11/1.7</td>
<td>1/7.8**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>11/1.5</td>
<td>-</td>
<td>1/10.7**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>11/4.5**</td>
<td>-</td>
<td>-</td>
<td>1/6.9*</td>
<td>-</td>
<td>-</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>11/5.2**</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/9.2*</td>
<td>-</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>11/2.8*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/9.0**</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>11/1.9†</td>
<td>1/3.4†</td>
<td>-</td>
<td>-</td>
<td>1/4.5*</td>
<td>-</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>11/3.6**</td>
<td>-</td>
<td>-</td>
<td>1/3.1†</td>
<td>1/5.0*</td>
<td>-</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>11/2.4*</td>
<td>-</td>
<td>-</td>
<td>1/1.5</td>
<td>1/2.6</td>
<td>1/1.7</td>
<td>0.87</td>
</tr>
</tbody>
</table>

Biotic gradients within the hyporheic habitat

The hyporheic invertebrate community was dominated by microcrustaceans, which constituted 63.3% of total invertebrates collected (10,430 individuals). Cyclopoida, the only group present in all samples, comprised 31.4% of the total faunal density. Chironomids and ostracods were codominant, contributing 16.9% and 16% of total density. Other abundant taxa were oligochaets (5.2%), the mayfly Habrophlebia lauta (5.1%) and harpacticoids (3.7%). The stygobiont taxa, Proasellus sp. (Crustacea: Isopoda), Niphargus sp. (Crustacea: Amphipoda), Bythiospeum rhenanum (Mollusca), Troglochaetus beranecki (Polychaeta) and Dendrocoelum sp. (Tricladiida) collectively contributed 4.7% of the total density.

In Fig. 5a, the first two axes of the PCA account for 63.3% of the total variability of the interstitial community. Axis 1 displays a pattern of juxtapositioning the shallower hyporheic positions at the right side and deeper positions on the left side of the factorial map. The second axis transforms this juxtaposition pattern into a gradual transition from
interstitial positions near the stream to remote, ground water dominated areas: Interstitial positions having the strongest interaction with the stream are located on the plot's lower right side (20-cm depth strata of the IZ and HZ). Along the exchange gradient, these positions are succeeded by the shallower strata within the EZ (plot's upper right side) and then by the deeper strata of the IZ and HZ (plot's upper left side). Finally, the deep strata of the EZ are placed in the lower left side of the factorial map.

The ordination of the biota reflects a pattern that separates epigean taxa (situated on the right) from hypogean groups (on the left) (Fig. 5b). Furthermore, the two-dimensional array reveals a gradient (arrow on Fig. 5b) within the hyporheic community from benthic, hyporheophile, hyporheobiont and phreatic taxa: Benthic species such as *Gammarus fossarum* and hyporheophile groups (e.g. chironomids), characterize 'upper hyporheic' interstices having intense exchange with the stream (plot's lower right side). An 'intermediate hyporheic' area (plot's upper right side) is dominated by microcrustaceans, hydracraria, oligochaeta, and other hyporheophile and permanent hyporheic taxa. 'Lower hyporheic' interstices are distinguished by the occurrence of hyporheophile hypogean taxa (plot's upper left side), whereas the archiannelid *Troglochaetus beranecki* characterizes phreatic interstices (plot's lower left side). The water-beetle *Esolus parallelepipedus* (Elmidae) is not placed directly within this community cline, because it occurred in higher densities in the upper EZ and thus spatially short-circuits the hyporheic/phreatic gradient. *Esolus* is known to be an indicator for unsilted interstices (Richoux & Forestier, 1989).

The abundances of hyporheic bacteria are highest in upper and intermediate hyporheic interstices, where inflow of stream water occurred but had been attenuated.

**Relationships between hyporheic bacteria and invertebrates**

Taxa richness and faunal density per sample is highly correlated to bacterial abundance and production (Fig. 6). Each of the 20 most common faunal groups (≥ 33% frequency of occurrence) showed correlations to hyporheic bacteria (Tab. 6). Seven taxa were highly ($r_5 > 0.7$), 8 intermediately ($r_5 = 0.69-0.50$) and 2 weakly ($r_5 < 0.50$) correlated. Only the three hypogean taxa correlate inversely to bacteria. Nematodes (typically assumed to be bacterivorous) showed no strong correlation to bacteria, as is true for oligochaetes. The dominating interstitial taxa, the cyclopoida, also only had weak correlations to bacteria. Hydracraria, being predators, are pseudo-correlated with bacteria. Most groups (15 of 20) had higher correlations to bacterial abundance than to production, which is also the case for the collective properties of the community, total density and taxa richness.
Figure 5. PCA ordination plot of hyporheic biota. (A) Factorial scores of hyporheic positions; i, infiltration zone; h, horizontal advection zone; e, exfiltration zone; 20 = 20-cm depth; 50 = 50-cm depth; 100 = 100-cm depth; 150 = 150-cm depth. Lighter shading of dots indicates increasing groundwater influence. (B) Ordination of hyporheic taxa. Arrow indicates increasing hypogean tendency. Correlation arrows are removed to improve clarity. Values in parentheses along axes are the amount of variation explained by the principal component.
Figure 6. Relationship between bacterial abundance and (A) invertebrate density, (B) invertebrate taxa richness, (C) epigean (n = 9944; 95%) and (D) hypogean (n = 486; 5%) animals, (E) microcrustaceans (n = 5431; 52%), (F) Diptera (n = 1799; 17%), (G) Ephemeroptera (n = 994; 10%), and (E) Plecoptera (n = 416; 4%) per sample.
### Table 6. Spearman rank correlation coefficients between hyporheic bacteria and invertebrates (in order of density) at sampling positions in the Töss River. \( \dagger P<0.1, \ *P<0.05, \ **P<0.01, \ ***P<0.001 \)

<table>
<thead>
<tr>
<th>Fauna</th>
<th>Bacterial abundance</th>
<th>Bacterial production</th>
<th>Bacterial biomass/POC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyclopoida</td>
<td>0.39*</td>
<td>0.35*</td>
<td>0.18</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>0.81***</td>
<td>0.76***</td>
<td>0.60***</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>0.75***</td>
<td>0.77***</td>
<td>0.39*</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>0.59***</td>
<td>0.56***</td>
<td>0.33(\dagger)</td>
</tr>
<tr>
<td><em>Habrophlebia lauta</em></td>
<td>0.81***</td>
<td>0.74***</td>
<td>0.55**</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>0.82***</td>
<td>0.78***</td>
<td>0.44**</td>
</tr>
<tr>
<td><em>Proasellus</em> sp.</td>
<td>-0.26</td>
<td>-0.30(\dagger)</td>
<td>-0.06</td>
</tr>
<tr>
<td>Hydracarina</td>
<td>0.55**</td>
<td>0.59**</td>
<td>0.31(\dagger)</td>
</tr>
<tr>
<td>Ephemerophila larvulae</td>
<td>0.60***</td>
<td>0.60***</td>
<td>0.59***</td>
</tr>
<tr>
<td>Plecoptera larvulae</td>
<td>0.76***</td>
<td>0.71***</td>
<td>0.58***</td>
</tr>
<tr>
<td><em>Gammarus fossarum</em></td>
<td>0.65***</td>
<td>0.57***</td>
<td>0.48**</td>
</tr>
<tr>
<td><em>Leuctra</em> sp.</td>
<td>0.68***</td>
<td>0.58***</td>
<td>0.61***</td>
</tr>
<tr>
<td>Caenis sp.</td>
<td>0.76***</td>
<td>0.65***</td>
<td>0.66***</td>
</tr>
<tr>
<td>Nematoda</td>
<td>0.67***</td>
<td>0.67***</td>
<td>0.40*</td>
</tr>
<tr>
<td>Cladocera</td>
<td>0.54**</td>
<td>0.63***</td>
<td>0.33*</td>
</tr>
<tr>
<td><em>Bythiospeum rhenanum</em></td>
<td>-0.46**</td>
<td>-0.38*</td>
<td>-0.28</td>
</tr>
<tr>
<td><em>Esolus parallelepipedus</em></td>
<td>0.42*</td>
<td>0.34</td>
<td>0.41*</td>
</tr>
<tr>
<td>Niphargus sp.</td>
<td>-0.41*</td>
<td>-0.34*</td>
<td>-0.23</td>
</tr>
<tr>
<td><em>Habroleptoides confusa</em></td>
<td>0.62***</td>
<td>0.61***</td>
<td>0.46***</td>
</tr>
<tr>
<td>Limnius volkmari</td>
<td>0.53***</td>
<td>0.51**</td>
<td>0.30(\dagger)</td>
</tr>
</tbody>
</table>

### 7.5 Discussion

The measurement of bacterial production and abundance

Only a few investigations have measured bacterial production in sediments with the leucine incorporation method (Tuominen, 1995; Marxsen, 1996). This method is thought to be superior over previously used techniques (Simon & Azam, 1989; Marxsen, 1996). Nevertheless, results might be biased by several sources of error which are discussed in detail in Marxsen (1996) and Fischer & Pusch (in prep.). In this study relatively high control values occurred in samples with low bacterial production and high quantities of
fine sediment. This might be due to the high abiotic sorption capacity of hyporheic biofilms for amino acids (Fiebig, 1997). The mean value of abiotic leucine binding to sediments (determined from control samples) was 25% ± 16 (n = 15) of total uptake, which is still lower than documented for thymidine incorporation measurements (37%, Hendricks, 1996). Also, the formaldehyde used for controls could alter the biofilm’s sorption capacity. Isotope dilution by external unlabelled leucine is another possible source of error, which is probably negligible in our study because of the high leucine concentration used (Marxsen, 1996). However, the addition of leucine in high concentrations might have stimulated the growth of the bacteria in their potentially carbon limited environment. Thus, the production rates presented here might be slightly overestimated. Nevertheless, the leucine method still provides a useful relative measure of bacterial activity. Underestimation of bacterial cell counts and concurrent overestimation of bacterial production might result in too short theoretical turnover times of bacterial carbon.

Estimating bacterial abundance by fluorescent counts is widely accepted for planktonic systems (e.g. Fry, 1988; Wetzel & Likens, 1991). In sediments however, these methods are flawed by sediment masking (Schallenberg et al., 1989) and by problems of completely dislodging the bacteria from sediment surfaces prior to counting. Bacteria can be almost completely dislodged from the sediments by sonication in combination with pyrophosphate as a surfactant (Meyer-Reil, 1983; Velji & Albright, 1986; Epstein & Rossel, 1995; Fischer et al., 1996), but too intense sonication can destroy them (Ellery & Schleyer, 1984). Masking by sediment particles reduces the proportion of microscopically visible bacteria. Therefore, some authors propose a correction factor depending on the particle content of the samples (Schallenberg et al., 1989), or just double their counts (Bott & Kaplan, 1985; Kasimir, 1991), assuming an equal number of bacteria on the unviewed surfaces of particles. Centrifugation, as suggested by Bott & Kaplan (1985), reduced the amount of counted cells significantly (Fischer unpublished results) and was, therefore, not applied in this study. In conclusion, we may have underestimated bacterial abundance in this study, but the masking effect was held constant by the filtration of standardized amounts of interstitial sediments.

The bacterial abundance in the hyporheic interstices of the Töss River ranged from 1.6 x 10^5 to 4.8 x 10^8 bacteria per ml interstitial water. Bacterial abundance data from the literature, based on comparable sampling and counting methods, are within this range from shallow aquifer ground water samples (7.4 x 10^4 cells/ml, Boissier et al. (1996)) intermediate hyporheic samples (0.5 - 2 x 10^6 cells/ml, Vervier et al. (1993)), and shallow and organically enriched hyporheic samples below gravel bars (ca. 2 x 10^7 - 2.7 x 10^8 cells/ml, Claret et al. (1997)).
**Prediction of hyporheic bacterial abundance and production**

At all sediment depths we found high correlations between POM measures and bacterial abundances and production. A relationship between bacteria and POM has been reported in other studies for benthic habitats (e.g. Bott & Kaplan, 1985; Meyer, 1988; Edwards et al., 1990; Schallenberg & Kalff, 1993; Claret & Fontvieille, 1997) and hyporheic interstices (Crocker & Meyer, 1987; Marmonier et al., 1995; Fischer et al., 1996; Eisenmann, 1998). In our study, interstitial PN was a slightly better predictor than POC, with 75% and 72% explained variance, respectively. The detrital particles, originating mostly from plants, were less useful as predictors, with 63% explained variance. Nevertheless, the high Spearman correlation suggests that detrital particles were heavily colonized by bacteria. The significance of detrital particles as a food source and as an available surface for colonization, is revealed by a comparison with the fine inorganic particles. In our hypothesis the fine inorganic particles were considered as an indicator of the hyporheic surface area that could potentially be covered by microorganisms. In fact, the fine inorganic particles could explain 45% of the variation in bacterial abundance. However, multiple regression models revealed that bacterial parameters were more closely related to the organic surfaces of detrital particles, though the effect of fine inorganic particles remained evident by explaining further variation and thus being of importance for hyporheic bacteria.

Interstitial DOC was significantly correlated to bacterial parameters. However, its power in explaining the variability of bacteria was on the same level as the fine inorganic particles (i.e. 44%), and thus clearly minor compared to POM measures, though not unimportant. A comparison with other studies reveals equivocal relationships between interstitial bacteria and DOC with missing, weak or medium correlations (Marxsen, 1988b; Bärlocher & Murdoch, 1989; Vervier et al., 1993; Bernard et al., 1994; Hendricks, 1996). DOC is undoubtedly the nutritional resource for bacteria, since only dissolved matter can be transferred into the cells. However, the analytical distinction between DOC and POM may loose its importance when considering hydrolyses by extracellular enzymes (Pusch & Schwoerbel, 1994). For bacteria attached to detrital particles the organic surface may be the more important source of DOC instead of DOC transported by the interstitial throughflow. Other studies have also pointed out that POM might be the major carbon source for benthic and hyporheic heterotrophic microorganisms (Hedin, 1990; Pusch & Schwoerbel, 1994; Findlay & Sobczak, 1996; Pusch, 1996; Claret & Fontvieille, 1997). Crocker & Meyer (1987) found that only interstitial DOC of high molecular weight accumulates in correspondence to POM. This DOC fraction is thought to be refractory and thus less useful for microorganisms (Münster & Chróst, 1990). However, bacteria attached to detrital particles might take up labile DOC directly before it diffuses into the interstitial water. In contrast, the significance of interstitial DOC for
bacteria was shown in conjunction with the fine inorganic particles, because both act as complementary variables in regression models, collectively explaining 64% of the variability in bacterial abundance. This is on the same level as the explained variance by detrital particles. However, considering the predominance of refractory DOC over labile DOC (Thurman, 1985), the rapid turnover of labile DOC (Fiebig, 1992), and the change of DOC in streams even on a daily scale (Rutherford & Hynes, 1987; Kaplan & Bott, 1989), the appreciable and significant correlation between DOC and bacteria is somewhat surprising. Actually, this relationship appears in a different light when the importance of hyporheic positions is considered. Hyporheic position indicates interstitial flowpath connections within which DOC decreases with distance to surface water, demonstrated by the significant inverse relationship of DOC to the age of interstitial water and the positive relationship to water temperature. The importance of hyporheic flowpaths and distance traveled from the surface water for the quality of DOC has also been emphasized by several other authors (Meyer, 1990; Vervier & Naiman, 1992; Findlay et al., 1993; Hendricks, 1993; Mammonier et al., 1995; Findlay & Sobczak, 1996).

These results suggest that two separate sources of DOC were used by hyporheic bacteria: (1) Interstitial DOC transported from the surface habitat which is mainly subjected to abiotic sorption, biotic turnover, and (in our study) by a dilution of upwelling phreatic groundwater. This results in a decrease in DOC concentration and probably in a structural change with interstitial residence time. (2) DOC leached and hydrolyzed by extracellular enzymes directly from interstitially stored POM.

The question is how do these organic matter fractions spread within the interstices and act as a resource? Interstitial DOC is transported continuously along hyporheic flowpaths and floods may induce pulses of enhanced loading (Burney, 1994). With increasing stream velocities interstitial velocities increase also and deeper sediment layers are exposed to higher mass transfer rates (Gantzer et al., 1988) and increasing nutrient flux at the biofilm-water interface (Lock, 1993). The uptake of DOC via sorption processes can be quite rapid (McDowell, 1985) and enzymatically prepared bacteria may utilize these DOC fluxes (Kaplan & Bott, 1985; Jones & Lock, 1989). Embedded within a biofilm, bacteria can benefit from DOC stored within the polysaccharide matrix (Freeman & Lock, 1995), and might respire this DOC months later (Fiebig, 1997). These factors in conjunction with varying proportions of labile DOC can make it difficult to obtain direct evidence on the importance of interstitial DOC as an energy source for hyporheic bacteria. The effect of DOC on bacterial parameters in a multiple regression model together with detrital particles was barely insignificant. The significance of DOC in conjunction with the fine inorganic particles suggest that bacteria colonizing abiotic surfaces depend on a continuous supply of DOC via interstitial throughflow. This is supported by the relevance of the hyporheic positions in those models.
Investigations over a nearly 2-year period on the storage of fine particulate matter within the porous and permeable interstices of the Töss River (Brunke et al., 1998b), suggest that the dynamics of input, throughflow and output of POM are similar to those of DOC, despite the mechanical straining by pore sizes (Brunke & Gonser, 1997b; Brunke et al., 1998b; Brunke in prep.). The Töss River has a flashy discharge regime which frequently influences the content of fine inorganic and organic particles to a depth of 50-cm and occasionally even down to 150-cm. Changes of interstitial POM seem to be induced more by the flood frequency than by the intensity of individual floods (Brunke et al., 1998b). We found particles of plant litter about 300 μm in size even at a depth of 150-cm. It is noteworthy, that these detrital particles were flushed into this sediment depth, rather than buried there during bedload movement, since floods of such magnitude would have removed our piezometers. The pattern of transport is highly discontinuous due to pulses induced by peak flows in the stream. However, our data and the results of other studies on calcareous gravel-bed streams (Eglin, 1990; Panek, 1994), indicate that there is also a continuous transport of fine sediment ('mobile matrix sediment') into deeper sediment strata, where they tend to accumulate (Leichtfried, 1997; Brunke et al., 1998b). Thus, a deposition of single particles for a long period at certain spots within the interstices is improbable and their occurrence at a given location also reflects the subsurface residence time of organic particles with the corresponding degradation. Consequently, the hyporheic position is also of significance in explaining bacterial parameters in predictive models with detrital particles as covariates. In contrast, the hyporheic position is just significant in the model with POC and barely insignificant with PN. Therefore, POC and PN are the more direct measures to explain the variability of bacterial parameters, since most of the interstitial organic matter in gravelly sediments of streams appears to be incorporated in the biofilm (Bretschko & Leichtfried, 1988; Pusch & Schwoerbel, 1994) secreted by bacteria and embedding bacteria.

Correspondence of hyporheic bacteria and invertebrate distributions

Most of the taxonomic groups of invertebrates showed strong correlations with the abundance of hyporheic bacteria. Most of these correlations were higher for bacterial abundance than for bacterial production and they were clearly higher than for the portion of bacterial biomass of POC. In comparison to most taxonomic groups, surprisingly low correlations were found for cyclopoids, the most abundant interstitial taxa, and also for oligochaets and nematodes. However, Cyclopoida are a heterogeneous group composed of epigean eurytopic forms, hyporheophile and entirely hypogean species. Therefore, this taxonomic group, as well as the Oligochaeta, comprises ecological strategies which are too diverse to show a consistent pattern. In contrast, the Ostracoda, which also exhibit
diverse ecological strategies, were highly correlated with bacteria. The correlations between nematodes and bacteria are not particularly weak, but higher degrees of correspondence were expected, since most nematodes are bacterivorous. This result is probably due to the 90 μm mesh size of the sampling net, which is inefficient in collecting nematodes.

Invertebrate taxa richness was in strong accord with bacterial abundance and showed the highest correlation in comparison with all other studied taxonomic units or collective properties of the hyporheos. The high correspondence between bacteria and the three epigean taxa, Chironomidae, Harpacticoida, and the mayfly Habrophlebia lauta, should also be emphasized.

All hypogean taxa were inversely related to bacteria. This relationship is somewhat delicate, since the inverse correlation is effected by many zero counts in the upper hyporheic positions. Ignoring the upper sediment strata would result in a weak statistically non-significant positive correlation ($r_s = 0.25, n = 22$).

The spatial correspondence between hyporheic bacteria and most invertebrates appears to support the view that those animals have dietary preferences for microorganisms. However, a spatial association between bacteria and meio- and macrofauna does not necessarily reflect a causal relationship. Other possible explanations are also in accord with the high correlations found in this study. Three basic scenarios must be considered concerning the relationships between bacteria and invertebrates:

(a) Bacterial and animal abundances simply covary because of similar responses to abiotic factors. The interstitial storage of POM could be the most important factor, which in turn is a result of a complex of interacting factors including sediment depth and structure, type and intensity of vertical hydrological exchange, surface flow regime, and season (Brunke et al., 1998b). Another aspect is the regularity of the delivery of resources, such as DOC and dissolved oxygen, and the development of physicochemical environmental conditions, such as temperature. The retention of interstitial POM and inorganic fine particles is strongly influenced by events which result in their import or flushing (Metzler & Smock, 1989; Bretschko, 1991; Brunke et al., 1998b). The supply with dissolved resources is effective by continuous transport through interstices; however, short term pulses might also play an important role in the delivery of nutrients. The quality of imported organic matter is partly a function of travel time along the flowpath. In this scenario bacteria are competing with detritivorous animals for allochthonous POM. This competition could be regulated by group-specific mobility as well as by the affinity and the activity of their enzyme systems (Thomas, 1997).

(b) A second explanation for the spatial correspondence between hyporheic invertebrates and bacteria may reflect that bacteria are a prime food source for invertebrates and/or improve the nutritional quality of POM consumed by detritivores.
Several studies have shown that bacteria are ingested by benthic animals (e.g., Edwards & Meyer, 1987; Perlmutter & Meyer, 1991; Borchardt & Bott, 1995; Hall, 1995). However, it is contentious whether bacterial cells can be digested and, if so, how much bacterial biomass can be assimilated (Thomas, 1997). Some meiofaunal groups selectively assimilate microorganisms passing the gut (Fleeger & Decho, 1987), as demonstrated for marine and freshwater harpacticoids (Carman & Thistle, 1985; Perlmutter & Meyer, 1991). In general, definitive results are difficult to obtain due to the possibility of different food niches resulting from selective feeding in terms of particle size and type of microorganism (Fenchel, 1978). Furthermore, assuming invertebrates can utilize bacteria colonizing detritus as food, the relative importance of dead plant material and bacteria as food for detritivores remains equivocal (Hildrew, 1992; Maltby, 1992; Wotton, 1994). The polysaccharide matrix, secreted by bacteria, might at least partly be used as a food resource by detritivores (Bärlocher & Murdoch, 1989). In this study, the weak correlations between invertebrates and the bacterial portion of POC do not support the assumption that bacteria improve the nutritional quality of POM. On the other hand, the high correlations of invertebrate densities with bacterial abundances support the role of bacteria as food, whether digested directly or by consuming protozoans grazing on bacteria (Carlough & Meyer, 1990; Eisenmann, 1998). In the stream studied by Borchardt & Bott (1995) the densities of meiofauna might have been too low to have had a significant impact on bacterial populations. In another study, Perlmutter & Meyer (1991) estimated that meiofauna may remove from 1 to 22% of the bacterial production in stream leaf litter. They also showed, as did Caron (1987) for two flagellate species, that bacterivores are able to graze on attached bacteria.

(c) Mutual benefits between hyporheic bacteria and invertebrates may be a third explanation for the spatial correspondence between hyporheic invertebrates and bacteria. On the one hand, invertebrates assimilate at least parts of the bacterial biomass or secreted polysaccharides. On the other hand, the grazing pressure by animals might enhance bacterial activity (Fenchel & Jørgensen, 1978). Bacteria might benefit by animal secretion and feces, losses during feeding ('sloppy feeding'), by invertebrate exuviae, and invertebrate activity increasing colonizable surface area. Reductions in the size of POM particles by invertebrates increases surface area of organic detritus and increases the release of nutrients. Bioturbation of fine sediment induces redistribution of microbial resources and breaks down diffusion gradients (Giere, 1993).

These scenarios are not mutually exclusive and each might provide partial explanations for the high correspondence in spatial distribution of hyporheic bacteria and most of the interstitial invertebrates. Individual faunal components will certainly exhibit a variety of relationships to microorganisms.
Using the minimum and maximum grazing rates determined by Perlmutter & Meyer (1991) for harpacticoid copepods we calculated that this taxon would utilize only 0.03 - 0.4% of the bacterial carbon produced in the hyporheic zone. However, if these grazing rates are applied to all microcrustaceans, 1.6 to 25.7% of the bacterial production would be grazed by this meiofaunal group alone. However, the bacteria observed on the leaf discs in their experiments were larger than those typically encountered in the hyporheic zone (Fischer unpublished results), and harpacticoid grazing seems to have been selective for large bacteria. Because of their small size, bacteria in hyporheic interstices could be subjected more to nematode and protozoan grazing. Feeding rates of benthic protozoa depend on the density of bacteria and temperature (Bott & Kaplan, 1990). The density threshold for grazing in the latter study was approximately $4 \times 10^8$ bacteria/cm$^3$ sediment, a value that was equaled only in one sample of our study. Since we lack data on protozoa, and the data reported in the literature for protozoan grazing vary by a factor of $10^5$ (e.g. Bott & Kaplan, 1990; Kemp, 1990), we cannot assess the importance of bacterivory by these organisms. However, bacterivory by protozoa in streambed sediments can be significant under certain conditions (Bott & Kaplan, 1990; Eisenmann, 1998). Reported grazing rates for nematodes range from 6 bacteria / ind. x h (Borchardt & Bott, 1995) to $3 \times 10^5$ bacteria/ind. x h (Duncan et al., 1974), and the impact of nematodes as grazers might thus range from negligible to 1.5% of bacterial production.

**Bacteria within the hyporheic biotic gradient**

The ordination method revealed a hyporheic faunal gradient along the transition from interstices dominated by inflow of surface water to those dominated by phreatic ground water. Bacteria were situated within this gradient in an intermediate position, close to harpacticoids, oligochaetes and the hyporheophile mayfly *Habrophlebia lauta*. Thus, bacteria were most numerous in the hyporheic interstices of this gravel-bed river where inflow of surface water was still evident, although apparently attenuated. Bacterial production, however, was highest in interstices influenced most by surface water advection. This difference in the spatial positioning of different bacterial parameters makes interpretation difficult, because bacterial abundance and production are interconnected and in fact are strongly correlated in our study. Therefore, it appears to be reasonable to speculate that high grazing pressures and/or hydraulic forces reduce bacterial abundance in the uppermost sediments and that the delivery of resources in somewhat greater depths is still sufficient to maintain high populations in areas where the storage of all organic matter is more protected from the flushing effects. In the Töss River, hyporheic POC storage tends to be higher in the 50-cm than in 20-cm depth strata and, as discussed above, is strongly affected by the surface flow regime even down to the
50-cm sediment depth (Brunke et al., 1998b). Hydraulic forces of the surface flow regime maybe a superimposed agent, which influences continuous transport of solutes and the more discontinuous import and export of particulate matter within the interstices.

In conclusion, a complex of interrelated processes must be considered to explain distribution patterns of hyporheic biota. Biotic interactions are impacted by superimposed abiotic processes, such as the surface and subsurface flow regimes, variations in sediment structure in terms of fine inorganic particles and seasonal inputs of organic matter, all of which interact to shape the physical habitat. Nevertheless, a remarkable correspondence between the occurrence of hyporheic invertebrates and bacterial parameters must be stressed. Particulate nitrogen was the best single predictor of bacterial abundance and production. Detrital particles, mostly originating from terrestrial plants, were important for bacteria as colonizable surface areas and as a source of nutrition. DOC and inorganic fine particles were useful as predictors of bacterial abundance and production only by including information on flowpath connections.

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CHAPTER 8

Hyporheic invertebrates - the clinal nature of interstitial communities structured by hydrological exchange and environmental gradients

Abstract In this study we investigated the environmental factors which control the local composition and distribution of hyporheic invertebrates within the sediments of a third order prealpine gravel-bed stream (Töss River, Switzerland). We focused on faunal gradients as a function of environmental conditions reflecting a) hydrological exchange patterns, b) sediment depths, c) physicochemical and fine particle gradients, and d) interactions between a), b), and c).

Three clustered sets of steel piezometers were installed at 4 depths in the sediment (20, 50, 100, 150 cm) at locations with distinctly different hydrological exchange types (infiltration, exfiltration, horizontal advection) to obtain samples of the fauna and the physicochemical and sedimentological conditions (pH, specific conductance, alkalinity, dissolved oxygen, BOD, ammonium, nitrite, nitrate, dissolved organic carbon, inorganic fine particles, particulate organic carbon and nitrogen, water age). Sampling was conducted at approximately monthly intervals from April 1995 to November 1996.

Sixty taxa were identified, the most abundant of which were cyclopoid copepods (33%), ostracods (23%) and chironomids (11%). All other groups accounted for the remaining 33%. Three characteristic hypogean taxa were frequently collected: the snail Bythiospeum rhenanum (Hydrobiidae), and the crustaceans Niphargus sp (Amphipoda) and Proasellus sp (Isopoda).

Total faunal density patterns were strongly related to the ratio of particulate organic carbon to total fine particles (POC/TP), which explained 61% of the variation in abundance within the sediment. Taxa richness and the temporal persistence in species composition at defined hyporheic positions were also significantly correlated with the POC/TP ratio. Gradients in hyporheic community structure corresponded most with changes in the POC/TP ratio as well as to hydrological variables and distance between the surface and phreatic habitats. The POC/TP ratio optima for individual taxa indicate that the depth to which epigean taxa penetrate sediments may be restricted by the availability of the food resource, which decrease with decreasing POC/TP ratios. Therefore, the proportion of fine inorganic particles appears to be a critical determinant
of the availability of food resources for interstitial invertebrates. The interstitial POC/TP ratio was determined mainly by the interaction between sediment depth and hydrological exchange type in conjunction with the season.

Based on these results, a conceptual model was developed to explain the distribution and composition of the interstitial fauna on three scales: 1) On the scale of the fluvial hydrosystem, we separate epigean and hypogean taxa in a zonation perspective. 2) On a local scale transitions in environmental conditions are evident and the community structure is clinal in nature. We assume an exclusion of hypogean taxa in areas most densely colonized by epigean taxa due to biotic interactions. 3) The upper and intermediate interstices are the proper habitat for many epigean taxa. These areas seem to be nutritionally advantageous due to their retentiveness for organic matter; however, there is a high probability of dislocation during spates. Therefore the community in these sediment strata may be organized by deterministic and stochastic factors favoring individual mobility.

8.1 Introduction

Hyporheic interstices have been viewed as a distinct habitat since Orghidan (1959) and Schwoerbel (1961a). This habitat supports a diverse fauna composed of hyporheobiont as well as by hyporheophilous species from the benthic and phreatic zones (Schwoerbel, 1961a, 1964). For many epigean species it is of functional importance during certain life cycle stages and as a refuge against adverse conditions (Brunke & Gonser, 1997a). Thus the community composition can be highly variable in space and time. Biotic gradients have been found vertically within the river bed and laterally from midstream towards the margins and into the flood plain (e.g. Schwoerbel, 1967; Bretschko, 1981; Pennak & Ward, 1986; Williams, 1989; Dole-Olivier et al., 1993). However, event induced and site-specific discontinuities are characteristic of the hyporheic interstices and often cause a patchy distribution of the hyporheos (Schwoerbel, 1967; Danielopol, 1989; Bretschko, 1991; Danielopol, 1991; Marmonier et al., 1992; Ward et al., 1994). The usable pore space and the interstitial throughflow are overriding physical factors which influence parameters such as the oxygen content, temperature and organic matter storage (Brunke & Gonser, 1997a).

Early studies on the hyporheic habitat investigated the role of the detrital-particles and pore space for the hyporheic fauna (Schwoerbel, 1961a, Husmann, 1966, Schwoerbel, 1967, Williams & Hynes, 1974), whereas recent studies focused on the role of factors on higher hierarchical levels such as the channel geomorphology, hydrological exchange patterns and the structure of the alluvial aquifer (Creuzé des Châteillers & Reygrobellet,
1990; Marmonier, 1991; Dole-Olivier & Marmonier, 1992a, b; Stanford & Ward, 1993; Boulton & Stanley, 1995). However, definitive relationships between interstitial environmental conditions and the invertebrates living in this habitat remain unclear (Ward & Palmer, 1994; Ward et al. in press). In this study we attempted to link hydrology and nutritional resources within the interstices to explain the local variability of the hyporheos. Hence, we focus on changes in the composition and distribution of hyporheic invertebrates on local and microhabitat scales from the perspectives of:

1. different hydraulic gradients: infiltration, exfiltration, and horizontal advection
2. different sediment depths: 20, 50, 100 and 150 cm
3. different environmental gradients: physicochemical and particle parameters, and
4. different interactive combinations between: subsurface hydrology, sediment depth and environmental gradients.

The investigation of hydrological exchange types superimposed on the sediment depth gradient enabled differentiation of the interstitial habitats into ‘hyporheic positions’. Hyporheic position (the specific combination of depth and hydrological exchange type) indicated interstitial flowpath connections and the age of the subsurface water.

Based on our results and theoretical considerations, we developed a hypothetical model of the community organization within the alluvial sediments of the Töss River.

### 8.2 Study site

**Geomorphology**

The Töss River, Switzerland, is a 3rd order calcareous gravel bed river. At the study site (460 m a.s.l.) the prealpine stream flows through a forested valley, has a gradient of 0.5%, a mean width of 20 m, a depth of about 20 - 40 cm at low discharge conditions, and an annual mean discharge of 7 m³/s (1921-1994). The Töss has been straightened and channelized for nearly two centuries and the banks are stabilized by large boulders. This induced river bed incision that further disconnected the stream from its former flood plain. To prevent further downcutting sills (10 - 20 cm height) were constructed at more or less regular intervals along the length of the river. The topography of the study site can be typologized as an extended riffle (Church, 1992). At the margins of the stream the channel sediments are composed of an erosion-resistant armor layer on top of a finer subarmor layer. In midstream frequent bedload movement causes the deposition of open framework gravel. The mean grain size of the entire sampling site was for the surface (top 10 cm) and subsurface (10 - 70 cm) sediments 31 mm (± 26 SD) and 11 mm (± 3.6
SD) respectively; the mean porosity was 18.8% (± 6.6 SD) and mean hydraulic conductivity was \( K = 10 (± 25 \text{ SD}) \times 10^{-3} \text{ m/s} \) (Brunke, unpublished data).

**Subsurface hydrology**

Although river engineering severed the surficial connectivity between the stream and its former flood plain, the exchange processes between the Töss River and the ground water are still interactive. River water infiltrates into the sediments about 500 m upstream of the sampling site and flows through the upper layers of the alluvial aquifer (Fig. 1). It crosses the Töss channel after a 400 m interstitial passage which takes half a year, as indicated by annual temperature patterns. At the sampling site the ground water exfiltrates into the stream at the left margin (exfiltration zone), whereas it infiltrates into the sediments at the opposite bank (infiltration zone) (Fig. 1). In midstream neither infiltration nor exfiltration prevail, because a neutral hydraulic gradient exists most of the time. Here the interstitial net flow direction is dominated by the flow along the river channel (horizontal advection zone), with a slight tendency towards infiltration on some dates. It is important to note that hydraulic gradients only indicate pressure differences and do not signify exclusively vertical subsurface flow. Rather there will also be a longitudinal component in the subsurface flow, especially near the surface. Thus the upper sediment layers within the exfiltration zone will also receive some inflow of surface water due to the general stream flow direction, streambed roughness, density differences and fluid dispersion in all directions.

Topographic variability may induce further small-scale upwelling and downwelling (Vaux, 1968; Thibodeaux & Boyle, 1987), superimposed upon the general exchange pathways between the river and the alluvial aquifer (Brunke & Gonser, 1997a). These geomorphic patterns are not, however, stable in time, resulting in shifting patterns of interstitial animals. The stabilized stream morphology in the Töss River therefore offers advantages as a system suitable for testing the affects of hydrological exchange types on the ecology of the hyporheic habitat.

**8.3 Material and methods**

In each of the hydrological exchange types (infiltration, horizontal advection, exfiltration) three clustered sets of permanent piezometers were installed to 4 depths (20, 50, 100, and 150 cm). The steel pipes (ID = 5 cm) are perforated by a series of 0.5 cm diameter holes along the distal 5 cm of the pipe.

For the collection of faunistic samples, 10 l of interstitial water were extracted by a hand pump after discarding the first two liters (Bou & Rouch, 1967; Husmann, 1971) and
Figure 1. Study area, showing the location within Switzerland (top), the groundwater flowpath and the location of the sampling site on the Töss River in plan view (middle), and a cross section through the sampling site (bottom). The 4 vertical lines at the infiltration, horizontal advection and exfiltration zones represent the sampling piezometers nests at these 3 locations.

Interstitial water for chemical analysis was collected by inserting a submersible electric pump directly after the faunistic sample was taken. The following chemical parameters were measured: dissolved oxygen and BOD$_5$ (Winkler method), Nitrite-N (standard method according to (DEW, 1985), Nitrate-N (standard method according to (DEW, 1985), pH (Metrohm 678 EP/KF Processor), specific conductance (WTW LF91), alkalinity, and dissolved organic carbon (Shimadzu DOC-analyser). For the measurement of particle parameters the samples were filtered...
through Whatman GF/F filters. The filters were oven dried at 60°C to constant weight for the measurement of fine inorganic particles. The fine inorganic particles are the freely moving matrix fines ("interstitial sediment", sensu Leichtfried, 1988). In our study the fine inorganic particles had a grain size < 1 mm, and the grain size distribution had a median of 0.03 mm. Inorganic carbon was removed from the filters with 3 M HCl. Then the dried filters with the residue were burned in a CHNS-analyser (Elementar vario EL) at 950°C for the measurement of particulate nitrogen (PN) and particulate organic carbon (POC). The POC and PN content are expressed as mg/l of interstitial water. A further measure is the portion of fine POC relative to total fine particles per liter of interstitial water, termed here as the POC/TP ratio and expressed as mg particulate organic carbon per g dry weight of the total particles of the sample ("POC concentration" sensu Leichtfried, 1988). The age of hyporheic water was estimated with the radon isotope method (Hoehn & von Gunten, 1989). Sampling was conducted at approximately monthly intervals between April 1995 and November 1996, depending on the accessibility of the river due to discharge.

The data were analyzed using the general linear model (linear regression analyses, analyses of variance, ANOVA, and analyses of covariance, ANCOVA) (Stahel, 1995) to detect relationships between hydrological exchange types, sediment depth, environmental parameters and the distribution of the hyporheic fauna. Environmental parameters and faunistic data were log transformed to reduce skewness and kurtosis and the distribution was checked by probability plots (Stahel, 1995). Community structure gradients were investigated by a linear ordination method (principal component analysis, PCA) using quantitative faunal data. Comparisons between the scores of the PCA axes 1 to 4 and the environmental variables were made by applying the general linear model. Three different statistical methods were used to assess the distribution of individual taxa in relation to the POC/TP ratio. The weighted average disregards taxa absences and so the value indicates the POC/TP ratio for which most individuals could be found at our sampling site. The logistic regression models the optimum based on presence-absence data, whereas the log-linear regression uses quantitative data. The weighted average of the POC/TP ratio of each taxon was calculated according to Jongman et al. (1995), in which taxa abundances data are included. Logistic regression and log-linear regression were used to model POC/TP ratio optima and tolerances of taxa (Jongman, et al., 1995). The parameters of the logistic regression enable one to calculate the probability of occurrence for single taxa at the estimated optimum (Ter Braak & Looman, 1986). The temporal persistence in rank species composition at hyporheic positions between successive sampling was calculated with non-parametric Kendall's tau correlation (Huhta, 1979; Schmid, 1992), as discussed by Townsend et al. (1987). Spearman correlation was used to determine the influence of POC/TP ratio on taxa richness and persistence.
8.4 Results

Physicochemical and particle parameters

Table 1 provides an overview of the values of environmental parameters in the depth strata of the hydrological exchange zones. Detailed analyses of environmental gradients within the interstices of the study site are given Brunke et al. (1995, 1998a, b)

Interstitial taxa: occurrence and abundance

The hyporheic community was dominated by microcrustaceans throughout all depths and zones. The most abundant hyporheic taxa were cyclopoid copepods (33%), ostracods (23 %) and chironomids (11 %). All other groups accounted for the remaining 33% (Fig. 2). The Acarina are almost exclusively composed of Hydrachnellae, except for a few specimens of Oribatida and the occasional Limnohalacarida. The Hydrachnellae accounted for 5.5% of the total fauna, similar to Schwoerbel’s (1961a) study. The cyclopoid copepods, ostracods, chironomids and water mites were also the most frequent. This is certainly also due to their diverse species composition with various ecological requirements (Schwoerbel, 1961b; Schmid, 1993; Rouch & Danielopol, 1997), which effect a broad distribution down to a depth of 150 cm. This is similar for other taxonomic groups composed of numerous species such as Oligochaeta, Harpacticoida and Nematoda, which are also frequent dwellers of the hyporheic interstices. The most abundant ephemeropteran and plecopteran larvae are Habrophlebia lauta, Caenis beskidensis and Leuctra sp. Three characteristic hypogean taxa were commonly encountered: the snail Bythiospeum rhenanum (Hydrobiidae), and the crustaceans Niphargus sp. (Amphipoda) and Proasellus sp. (Isopoda). The archiannelid Troglochaetus beranecki was found only rarely. Nematoda are presumably under-represented because they may pass through the nets easily due to their body shape. This is also the case for other meiofaunal groups such as Rotatoria, Gastrotricha, and Tardigrada. Table 2 provides an overview of the total densities and the abundances of important taxa at various depths in the infiltration, horizontal advection and exfiltration zones.
Table 1. Average values of environmental parameters in the four depth strata of the three hydrological zones from April 96 to November 97.
IZ = infiltration zone, HZ = horizontal advection zone, EZ = exfiltration zone; n = number of measurements; ΔH is the difference between the water level in the piezometer and the surface water level, in cm; VHG is the vertical hydraulic gradient, i.e. ΔH/sediment depth. Values in parentheses are standard errors.

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<th>Zone</th>
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Table 2. Average values of the total faunal density (per 10 l) and the densities of important taxa that contributed > 0.5% to total faunal density.  
IZ = infiltration zone, HZ = horizontal advection zone, EZ = exfiltration zone; n = number of measurements. Values in parentheses are standard errors.

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<td>(0.5)</td>
<td>(0.1)</td>
<td>(0.2)</td>
<td>(0.05)</td>
<td>(1.1)</td>
<td>(0.4)</td>
<td>(0.4)</td>
</tr>
<tr>
<td><strong>n</strong></td>
<td></td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
<td>255</td>
</tr>
</tbody>
</table>
Figure 2. Dominance and frequency of occurrence of hyporheic taxa that contributed > 0.5% of the total abundance. Based on combined data from the 3 hydrological exchange types and the 4 sediment depths.

Faunal density and environmental parameters

The alluvial aquifer of the Töss River is well oxygenated (Tab. 1); thus dissolved oxygen is probably not a limiting factor for hyporheic biota. Weak correlations do exist between the faunal density and pH ($r = 0.5$, $p < 0.001$, $n = 215$), specific conductance ($r = -0.43$, $p < 0.001$, $n = 170$), alkalinity ($r = -0.43$, $p < 0.001$, $n = 210$), Nitrite-N ($r = 0.48$, $p < 0.01$, $n = 206$), and Nitrate-N ($r = -0.53$, $p < 0.001$, $n = 196$), which likely only reflect the fact that these parameters change along flowpath connections (Brunke et al., 1995, 1998a).

In the Töss River the particle parameters were strongly correlated with the density of hyporheic invertebrates. Out of six particle parameters five can be used to develop significant regression models with faunal density patterns (Tab. 3). Only the model for the fine inorganic particles is not significant. The fine inorganic particles and the POC content were strongly correlated ($r = 0.75$, $p < 0.001$, $n = 209$). The POC content and PN content contributed to significant regression models explaining faunal density. However, the explained variance is low for both (Tab. 3).

The nutritional value of the organic matter can be estimated by the C/N-ratio. Since we measured the PN (and not PON), the ratios may be comparatively low, but the general spatio-temporal patterns may not be affected. In regression analysis the C/N-ratio revealed significant correlation to the faunal density, but the explained variance is negligible (Tab. 3).

The most important parameter for the total faunal density appears to be the portion of the POC and PN of all fine particles; in the regression analysis, the POC/TP ratio alone
explained 61% of the variation in faunal abundance (Tab. 3). In the Töss River the hyporheic faunal density correlates strongly with the interstitial POC/TP ratio, but not with the POC content (Fig. 3).

Table 3. Results of regression models between log faunal density and log particle parameters; n = number of measurements. Degrees of Freedom/F-Value. Levels of significance are *, p < 0.05; **, p < 0.01; ***, p < 0.001. POC = particulate organic carbon; TP = total particles; PN = particulate nitrogen.

<table>
<thead>
<tr>
<th>$r^2$</th>
<th>POC/TP ratio</th>
<th>PN/TP ratio</th>
<th>POC-content</th>
<th>PN-content</th>
<th>C/N-ratio</th>
<th>Fine inorganic particles</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.61</td>
<td>1/332.7***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td>220</td>
</tr>
<tr>
<td>0.40</td>
<td>-</td>
<td>1/143.8***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td>218</td>
</tr>
<tr>
<td>0.17</td>
<td>-</td>
<td>-</td>
<td>1/45.6***</td>
<td>-</td>
<td>-</td>
<td></td>
<td>226</td>
</tr>
<tr>
<td>0.16</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/42.4***</td>
<td>-</td>
<td></td>
<td>224</td>
</tr>
<tr>
<td>0.03</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/8.3**</td>
<td></td>
<td>224</td>
</tr>
<tr>
<td>0.01</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1/2.5</td>
<td>224</td>
</tr>
</tbody>
</table>

Figure 3. Relationships between the faunal density and the POC content (n = 226) (a), and POC/TP ratio (n = 220) (b). POC = particulate organic carbon; TP = total particles.

A multiple linear regression with the POC/TP and PN/TP ratios did not improve the regression model with the POC/TP ratio alone, which is due to the high collinearity between the POC and PN ($r = 0.87, p < 0.001, n = 269$). The correlation between the faunal density and the POC/TP ratio is much higher than with the PN/TP ratio.
Consequently in the following we focus on the factors affecting the local interstitial POC/TP ratio.

**Particulate organic matter and hydrological exchange types**

One-way ANOVA models revealed that the hydrological exchange types had a significant affect on the POC/TP ratio in the sediment, however, the explained variance was negligible. In contrast, the sediment depth as a main factor in an ANOVA model explained 57% of the the variability of the POC/TP ratio (Tab. 4). In a two-way ANOVA the sediment depth and the hydrological exchange type as main effects explained two thirds of the variation; the interaction between both was significant. Thus the hydrological exchange type modulates the effect of the sediment depth on the variations of the POC/TP ratio. The hyporheic position is defined by the combination between the three hydrological exchange zones and the four depths and thus the same model can be derived in a one-way ANOVA as in a two-way ANOVA with depth and exchange type as the main factors (Tab. 4). The season as a main factor also has a significant affect on the POC/TP ratio, but the explained variance is very low (Tab. 4). However, in a two-way ANOVA the combination of season and depth explains two thirds of the variation in interstitial POC/TP ratio. In this model the interaction is not significant and thus the effects of space and time are additive. Consequently the best model is derived by the main effects of the hyporheic position and season, explaining 77% of the variation in the POC/TP ratio. A further inclusion of the fine inorganic particles as covariate improves this model in an analysis of covariance slightly to 79% explained variance. The POC/TP ratio is negatively correlated to the fine inorganic particles ($r = -0.72, p < 0.001, n = 247$).

Hence, the interstitial POC/TP ratio is mainly determined by the interaction between sediment depth and hydrological exchange type in conjunction with the season. The interaction between sediment depth and hydrological exchange type indicates flowpath connections and thereby the interstitially transported distance of organic matter from the surface habitat.

**Faunal density, hydrological exchange types and organic matter**

The sediment depth, hydrological exchange type and season had significant affects on the faunal density (Tab. 5). However, depth only explained one third of variation in the faunal density. In a two-way ANOVA depth and exchange types explained 48% of the variability. The significant interaction reveals that the affect of the vertical distance to the benthic habitat on the interstitial faunal density differs between the infiltration, horizontal advection and exfiltration zones.
Table 4. Results of one-way and two-way ANOVA to detect effects on the POC/TP ratio by the 4 sediment depths, the 3 hydrological exchange zones, hyporheic position, and the four seasons. Hyporheic position is defined by a specific combination between zones and depth. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>$r^2$</th>
<th>Depth</th>
<th>Zone</th>
<th>Hyporheic Position (HP)</th>
<th>Season</th>
<th>Depth</th>
<th>Depth</th>
<th>HP</th>
<th>Fine Inorganic Particles</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.57</td>
<td>3/102.1 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.05</td>
<td>-</td>
<td>2/6.4 **</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.66</td>
<td>-</td>
<td>11/39.4 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.08</td>
<td>-</td>
<td>-</td>
<td>3/6.1 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.66</td>
<td>3/125.4 ***</td>
<td>2/16.4 ***</td>
<td>-</td>
<td>6/4.2 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.66</td>
<td>3/95.4 ***</td>
<td>-</td>
<td>3/16.8 ***</td>
<td>9/0.53</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.77</td>
<td>-</td>
<td>11/37.5 ***</td>
<td>3/21.1 ***</td>
<td>-</td>
<td>33/0.6</td>
<td>-</td>
<td>-</td>
<td>231</td>
<td></td>
</tr>
<tr>
<td>0.79</td>
<td>-</td>
<td>11/33.2 ***</td>
<td>3/22.8 ***</td>
<td>-</td>
<td>33/0.7</td>
<td>1/7.0 **</td>
<td>206</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Results of one-way and two-way ANOVA to detect effects on the faunal density by the 4 sediment depths, the 3 hydrological exchange zones, the hyporheic position, and the four seasons. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>$r^2$</th>
<th>Depth</th>
<th>Zone</th>
<th>Hyporheic Position (HP)</th>
<th>Season</th>
<th>Depth</th>
<th>Depth</th>
<th>Zone</th>
<th>HP</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.33</td>
<td>3/40.9 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.12</td>
<td>-</td>
<td>2/16.4 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.48</td>
<td>-</td>
<td>11/20.5 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.08</td>
<td>-</td>
<td>-</td>
<td>3/7.6 ***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.48</td>
<td>3/51.4 ***</td>
<td>2/26.8 ***</td>
<td>-</td>
<td>6/3.2 **</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.42</td>
<td>3/33.7 ***</td>
<td>-</td>
<td>3/12.6 ***</td>
<td>9/0.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.23</td>
<td>-</td>
<td>2/15.0 ***</td>
<td>3/9.0 ***</td>
<td>-</td>
<td>6/1.6</td>
<td>-</td>
<td>-</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>0.62</td>
<td>-</td>
<td>11/18.0 ***</td>
<td>3/17.4 ***</td>
<td>-</td>
<td>-</td>
<td>33/0.7</td>
<td>255</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Most of the variation in hyporheic faunal density (62%) is explained by a model with hyporheic position and season as main factors. Based on these results, analysis of covariance was used to combine the effects of depth, exchange type and season with the POC/TP ratio as a quantitative covariate. A model with hyporheic position (the combination of depth and exchange type) and the POC/TP ratio explained 68% of the variation of faunal density (Tab. 6). A further inclusion of the season improved this model to 72%, however, the influence of the season is not significant, because much of the seasonal information is already contained in the model due to the temporal trends in the POC/TP ratio. Thus, the variability of the hyporheic faunal density is explained mostly by the interaction between the sediment depth, hydrological exchange type, and the interstitial POC/TP ratio.

Table 6. Results of analysis of covariance (ANCOVA) to detects main effects on faunal density by the hyporheic position and season together with the POC/TP ratio as the quantitative covariable. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>r²</th>
<th>main effects</th>
<th>interaction</th>
<th>covariate</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hyporheic position (HP)</td>
<td>Season</td>
<td>HP *</td>
<td>POC/TP ratio</td>
</tr>
<tr>
<td>0.68</td>
<td>11/4.2***</td>
<td>-</td>
<td>-</td>
<td>1/73.9***</td>
</tr>
<tr>
<td>0.72</td>
<td>11/2.7**</td>
<td>3/0.9</td>
<td>33/0.8</td>
<td>1/42.8***</td>
</tr>
</tbody>
</table>

Relationships of taxa richness and community persistence to the POC/TP ratio

The taxa richness of each faunal sample was strongly correlated to the POC/TP ratio ($r_s = 0.78$, $p < 0.001$) (Fig. 4a). This relationship becomes even stronger when neglecting temporal variability and comparing the average of taxa richness and POC/TP ratio for each hyporheic position ($r_s = 0.97$, $p < 0.001$) (Fig. 4b). Taxa richness increased gradually from the deeper interstitial strata, dominated by phreatic ground water to the upper hyporheic positions. The order of hyporheic positions is comparable to those of the PCA factorial map, though temporal variations exist as indicated by the error bars (Fig 6b).

The persistence in rank species composition is correlated to the average POC/TP ratio ($r_s = 0.75$, $p = 0.005$) (Fig. 5a). Persistence is lowest in the 100-cm and 150-cm depth strata of the EZ. In contrast, persistence in the 150-cm depth strata of the IZ and HZ are clearly higher, in spite of minor increases in POC/TP ratios. Thereafter, the increase in persistence with increasing POC/TP ratio is comparatively small for all hyporheic positions. There is also a relationship between relative variability in persistence and
POC/TP ratio ($r_s = 0.87$, $p < 0.001$) (Fig. 5b); both increase from upper to deeper hyporheic positions.

**Figure 4.** Relationship between the POC/TP ratio and taxa richness for each sample (a), and for the averages at the hyporheic positions (b). Bars represent standard errors. POC = particulate organic carbon; TP = total particles.

**Figure 5.** Relationships between the persistence in species composition (Kendall's tau) and the average POC/TP ratio at the hyporheic positions (a), and between the coefficients of variance for persistence and the POC/TP ratio (b). Bars represent standard errors. POC = particulate organic carbon; TP = total particles.
Hyporheic community structure and environmental gradients

Principal component analysis (PCA) permits the investigation of gradients in hyporheic community structure due to changes in species composition and abundance. The resulting ordination plot of the first two axes accounts for 46% of the total variability of the community (Fig. 6a). All epigean taxa are placed on the right side of the PCA-plot, whereas the hypogean taxa *Bythiospeum rhenanum*, *Proasellus* sp., *Niphargus* sp., and *Troglochaetus beranecki* are placed at the left side. Furthermore, the plot demonstrates the intermediate position of three epigean insect taxa with an amphibiontic tendency. These amphibiontic taxa are scattered along the PCA-axis 2, similar to the other diverse groups of epigean and hypogean taxa. *Esolus parallelepipedus* is known as an indicator for permeable stream sediments (Richoux & Forestier, 1989). The plecopteran larvae *Leuctra cf. major* and the dipteran larvae *Ibisia marginata* are found in even deeper parts of the alluvial aquifer (Brunke, unpublished data). *Esolus* and more clearly *Ibisia* are not directly placed within the community cline, because they occurred in higher densities in the upper EZ and thus spatially short-circuit the hyporheic/phreatic gradient. The factorial map of hyporheic positions reflects the faunal gradient from interstices dominated by surface water inflow to those dominated by phreatic ground water as indicated by the arrows (Fig. 6b).

Only the scores of the first PCA-axis have several significant correlations between environmental variables (Tab. 7). Some of the variables even have no correlations to the axes 2, 3, and 4. The pH has the highest correlations of the physicochemical parameters to axis 1. However, the highest correlations of all variables are achieved by the POC/TP and PN/TP ratios. In two-way ANOVA models the hyporheic position and the season as main factors explain 78% and 53% of the variability of the scores of axes 1 and 2 (Tab. 8). These models are improved by the inclusion of the POC/TP ratio as a quantitative covariate, and explain 82% and 61% of the first two axes (Tab. 9). Thus changes in the hyporheic community structure correspond most with changes in the POC/TP ratio as well as to hydrological variables and the distance between the surface and phreatic habitat, both of which indicate flowpath connections.

Figure 6. (next page) PCA ordination of interstitial invertebrates. (a) Ordination diagram (Factor 1 x Factor 2) of taxa. Correlation arrows were removed to improve clarity. Arrows indicate faunal gradient from interstices dominated by surface water inflow to those dominated by phreatic ground water; lighter shading of dots indicate increasing hypogean tendency of taxa. Values in parentheses along axes are the amount of variation explained by the principal component. (b) Mean factorial scores of hyporheic positions; i, infiltration zone; h, horizontal advection zone; e, exfiltration zone; 20 = 20-cm depth; 50 = 50-cm depth; 100 = 100-cm depth; 150 = 150-cm depth. Bars represent standard errors.
HYPOGEAN  EPIGEAN

Bythiospeum  Leuctra major
Proasellus  'intermediate
'lower  hyporheic'
thyporheic'

'phreatic'

Troglochaetus  Ibsis

'upper  hyporheic-
benthic'  

Niphargus

Ostracoda  Acari
Cladocera  Oligochaeta
Habrophlebia  Habroleptoides
Harpacticoida  Chironomidae
Plec. Larvulae  Leuctra sp.
Gammarus  Trichoptera

Factor 1 (34%)

Factor 2 (12%)

(a)

(b)
Table 7. Pearson correlation coefficients between the scores of PCA axes 1 to 4 and environmental variables. Percentages refer to the proportion of variance in faunal data explained by the synthetic gradients. Missing values indicate that correlation was zero. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Axis 1 (34.1%)</th>
<th>Axis 2 (11.8%)</th>
<th>Axis 3 (7.8%)</th>
<th>Axis 4 (5.6%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.11</td>
<td>-</td>
<td>0.13</td>
<td>-0.29</td>
</tr>
<tr>
<td>pH</td>
<td>0.67***</td>
<td>-0.11</td>
<td>0.13</td>
<td>-</td>
</tr>
<tr>
<td>Alkalinity</td>
<td>-0.54***</td>
<td>-0.10</td>
<td>0.21</td>
<td>-</td>
</tr>
<tr>
<td>Conductivity</td>
<td>-0.40***</td>
<td>-0.20</td>
<td>0.27</td>
<td>0.14</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.50***</td>
<td>-0.27*</td>
<td>-</td>
<td>0.18</td>
</tr>
<tr>
<td>BOD5</td>
<td>0.43**</td>
<td>-0.17</td>
<td>-0.18</td>
<td>-</td>
</tr>
<tr>
<td>DOC</td>
<td>0.36*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ammonium</td>
<td>0.28</td>
<td>-0.21</td>
<td>-0.32</td>
<td>0.19</td>
</tr>
<tr>
<td>Nitrite-N</td>
<td>0.49***</td>
<td>-0.17</td>
<td>-</td>
<td>0.23*</td>
</tr>
<tr>
<td>Nitrate-N</td>
<td>-0.55***</td>
<td>-0.24*</td>
<td>0.27*</td>
<td>-</td>
</tr>
<tr>
<td>PO4-P</td>
<td>0.46**</td>
<td>0.19</td>
<td>0.11</td>
<td>-0.19</td>
</tr>
<tr>
<td>Silicate</td>
<td>-0.38</td>
<td>-</td>
<td>-</td>
<td>-0.33</td>
</tr>
<tr>
<td>Fine inorganic particles</td>
<td>-0.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>POC/TP ratio</td>
<td>0.78***</td>
<td>0.14</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PN/TP ratio</td>
<td>0.71***</td>
<td>0.12</td>
<td>-0.21</td>
<td>-0.11</td>
</tr>
<tr>
<td>POC content</td>
<td>0.46***</td>
<td>0.17</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PN content</td>
<td>0.51***</td>
<td>0.16</td>
<td>-0.10</td>
<td>-</td>
</tr>
<tr>
<td>POC/PN-ratio</td>
<td>0.09</td>
<td>-</td>
<td>0.20</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Table 8. on next page

Table 9. Results of analysis of covariance on the effect of hyporheic position, season and the POC/TP ratio on the scores of PCA axes 1 and 2. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>axis</th>
<th>r²</th>
<th>Hyporheic position (HP)</th>
<th>Season</th>
<th>HP * Season</th>
<th>POC/TP ratio</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>197</td>
</tr>
<tr>
<td>Axis 1</td>
<td>0.77</td>
<td>11/9.9***</td>
<td>-</td>
<td>-</td>
<td>1/36.7***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.82</td>
<td>11/6.9***</td>
<td>3/0.5</td>
<td>33/1.2</td>
<td>1/25.9***</td>
<td></td>
</tr>
<tr>
<td>Axis 2</td>
<td>0.47</td>
<td>11/13.8***</td>
<td>-</td>
<td>-</td>
<td>1/39.8***</td>
<td>196</td>
</tr>
<tr>
<td></td>
<td>0.61</td>
<td>11/14.6***</td>
<td>3/2.6</td>
<td>33/1.3</td>
<td>1/30.1***</td>
<td>196</td>
</tr>
</tbody>
</table>
Table 8. Results of one-way and two-way analysis of variance on the effects of sediment depth, hydrological exchange type, hyporheic position and season on the scores of PCA axes 1 and 2. Levels of significance as in Table 3.

<table>
<thead>
<tr>
<th>$r^2$</th>
<th>Depth</th>
<th>Zone</th>
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<th>Season</th>
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Hyporheic taxa: Optima and tolerances of the POC/TP ratio

The previous statistical analyses have shown the strong relationship between the POC/TP ratio and variations of faunal density and hyporheic community structure. Consequently the relationship between single taxa and the POC/TP ratio was assessed, since individual taxa respond differentially to environmental variables. In Fig. 7 the interstitial taxa are ordered accordingly to their weighted average optimum (WA) of the POC/TP ratio. The four hypogean taxa have the lowest WA, they are followed by the epigean taxa with an amphibiontic tendency. Epigean hyporheophile taxa have the highest WA, e.g. *Sericostoma personatum* (Trichoptera), *Cladocera*, *Habroleptoides confusa* (Ephemeroptera) and *Gammarus fossarum* (Crustacea).

The optima estimated by logistic and log-linear regression models are highly correlated with the WA ($r = 0.88, p < 0.001$, and $r = 0.89, p < 0.001$, respectively) and are correlated with each other as well ($r = 0.77, p < 0.001$). For all epigean taxa the optima estimated by the regression models are higher than the WA. The WA is lower than the tolerances estimated by both regressions only for *Caenis beskidensis* (Ephemeroptera). For *Gammarus fossarum* and *Habrophlebia lauta* the WA is at the level of the lower tolerances estimated by the log-linear regression.

*Figure 7. (next page) Weighted average values as well as optima and tolerances of the POC/TP ratio estimated by logistic (presence/absence) and log-linear (absolute abundances) regression models for interstitial taxa. Diamond: weighted average, bars: optima estimated by regression, error bars: lower tolerances, shaded bars for quantitative data (density), unshaded bars for qualitative data (presence/absence). *, epigean taxa with an amphibiontic tendency; **, hypogean taxa. The probability of occurrence for single taxa at the estimated optimum by logistic regression is given in parenthesis. The dotted lines indicate the average of the POC/TP ratio in 20, 50, 100 and 150 cm sediment depths. Missing bars indicate that it was not possible to develop regression models for those taxa.*
POC/TP ratio (mg/g)

- **Sericostoma sp. (0.69)**
- **Cladocera**
- **Habroleptoides confusa**
- **Gammarus fossarum (0.49)**
- **Habrophlebia lauta (0.92)**
- **Chironomidae (0.98)**
- **Oligochaeta (0.98)**
- **Ostracoda (1.0)**
- **Caenis beskddensis (0.85)**
- **Ephemeroptera larvalae (0.61)**
- **Leuctra sp. (0.77)**
- **Nematoda (0.88)**
- **Plecoptera larvalae (0.38)**
- **Limnius volckmari (0.47)**
- **Cyclopoida (1.0)**
- **Harpacticoida (0.81)**
- ***Esolus parallelepipedus (0.63)**
- ***Leuctra major (0.27)**
- ****Proaseilus sp. (0.50)**
- ****Bythiospeum diaphanum (0.53)**
- ****Niphargus sp. (0.60)**
- ****Troglochaetus sp. (0.15)**

- Weighted Average
- **regression: quantitative data**
- **regression: qualitative data**

-150 -100 -50 -20 cm sediment depth
8.5 Discussion

Fluvial systems can be viewed as mosaics of habitat patches along a longitudinal continuum (Pringle et al., 1988; Townsend, 1989; Ward, 1989; Townsend, 1996). In the vertical dimension of fluvial systems the hyporheic habitat is a functional component of stream as well as of groundwater ecosystems in terms of energy flow, nutrient dynamics and invertebrate communities (Brunke & Gonser, 1997a). The hyporheic throughflow connects the surface water and the ground water, and these flowpath connections define the extent of the hyporheic interstices. This study shows the relevance of small-scale hydrological exchange for the cline in interstitial invertebrate communities along environmental gradients. A model on the role of hydrological exchange for the formation of environmental gradients within the ecotone is given in Brunke et al. (1998a).

Factor analysis of hyporheic invertebrate distribution

Many studies have recognized that collective faunistic parameters such as total density and composition change with sediment depth in the hyporheic interstices (e.g. Bishop, 1973; Danielopol, 1976; Marchant, 1988; Maridet et al., 1996). This was also found in the hyporheic interstices of the Töss River. Abundances of insect larvae decreased with sediment depth, hyporheophile microcrustaceans developed highest densities in the upper and intermediate layers of the hyporheic interstices, whereas the distribution of hypogean taxa was more dense in intermediate and deeper areas than in phreatic interstices. However, the distribution patterns of all taxonomic units differ between the hydrological exchange zones.

Dole-Olivier & Marmonier (1992a) have emphasized the influence of the upwelling and downwelling for the distribution of interstitial animals. They also showed the functional importance of the hydrological patchiness within the interstices for the use as refugia during floods (Dole-Olivier et al., 1997). However, the question is whether geomorphology, sediment depth and hydrological exchange types are proximate factors that shape hyporheic communities or if they are superimposed vectors controlling other environmental gradients that primarily influence interstitial animals?

Thus, in our factor analysis we first distinguished the effects of sediment depth, hydrological exchange type and environmental gradients, and then tested for interferences between the factors. We specified the hyporheic habitat by combinations of sediment depth and hydrologic exchange type, termed 'hyporheic position', that provides information on flowpath connections. In the case of environmental gradients we also distinguished between physicochemical and particle parameters.
Physicochemical gradients and faunal density

Physicochemical parameters are more important as discriminators between the upper strata of hyporheic interstices, whereas particle parameter gradients are steeper in deeper areas (Brunke et al., 1998a). Nevertheless, each parameter may develop differentially with depth especially the physicochemical parameters. Williams (1993) points out that there has been little research on the relationship between the hyporheic fauna and the interstitial chemistry. At his study sites many of the taxa showed no correlations with the measured parameters, although at one site the overall faunal density was negatively correlated with specific conductance and alkalinity (Williams, 1989). In the Töss River the total faunal density correlates significantly with some of the physicochemical variables. However, none of these parameters changes strongly enough throughout the interstices to be critical for hyporheic invertebrates. Thus single physicochemical parameters are not prime causal factors structuring this local hyporheic community, in spite of their variations with sediment depth and between hydrological exchange zones (Brunke et al., 1998a).

Particle gradients and faunal density

All POM metrics, including POC and PN content, POC/TP and POC/PN ratios, were significantly related to hyporheic faunal density. Hyporheic interstices are the major storage site for POM in streams (Meyer, 1990). The input of most POM into holarctic streams is strongly seasonal due to autumnal defoliation (Moser, 1991; Bretschko & Moser, 1993), whereas storms induce an import and transport of fine organic matter eventually (Walling & Webb, 1992). Depending on flood frequency and intensity, as well as retentive structures such as debris dams, much of the benthic POM is subjected to erosion (Smock, 1990; Maridet et al., 1995; Ratcliffe et al., 1995). In contrast, interstitially stored POM is more protected during spates and may serve as a reservoir for detritivores (Herbst, 1980; Pusch, 1996). Allochthonous POM enters the interstices more or less continuously by depth filtration, i.e. transport and retention of particles in porous media, or is buried eventually by spates (Metzler & Smock, 1989; Bretschko, 1991; Brunke & Gonser, 1997b; Brunke et al., 1998b). Our method only partly enabled the sampling of coarse POM, which is incorporated into the sediment mostly during spates (Herbst, 1980; Naegeli, 1997). We measured FPOM as POM associated with inorganic fine particles and as detrital particles. The amount of this fraction is mobile or loosely attached to the framework gravel. Past flood events and periods of low discharge are important determinants of the actual fine particle contents and depth distributions within the interstices (Pusch & Schwoerbel, 1994; Naegeli et al., 1995; Brunke et al., 1998b).

Not only the FPOM is subjected to depth filtration, but also the fine inorganic particles. The fine inorganic particles alone did not correlate significantly with hyporheos
distribution, however, in conjunction with the supply of FPOM the fine inorganic particles were important in our study. In general, the fine inorganic particles are ecologically important, because they provide surfaces for biofilm development and thereby promote the microbial conversion of DOC into POC (Dahm, 1984; Fiebig & Marxsen, 1992). Most of the interstitial organic matter is incorporated into the biofilm, which can be used as a food source for interstitial animals (Bretschko & Leichtfried, 1988; Bärlocher & Murdoch, 1989). In two calcareous gravel-bed streams the interstitial fine particles contained up to 90% of all organic matter, although they contributed to less than 10% of the sediment (Eglin, 1990; Leichtfried, 1991). In our study the fine inorganic particles and the POC content were strongly correlated and demonstrated the same vertical dynamics down to a depth of 50-cm (Brunke et al., 1998b).

On the other hand, increasing amounts of fine inorganic particles reduce the pore spaces. In general, the proportion of the small grain size of the sediment framework and the amount of mobile matrix fines increase with depth (Leichtfried, 1988, 1991; Eglin, 1990; Panek, 1994; Brunke et al., 1998b). Excessive siltation plays a role in the colonization dynamics of interstitial invertebrates (Shiozawa, 1986; Richards & Bacon, 1994; Govedich et al., 1996; Maridet et al., 1996). In the Lunzer Seebach, the migration activity of hyporheic invertebrates increases significantly with higher loading of mobile matrix fines which accumulated due to slower water movement with increasing depth (Panek, 1994). Panek (1994) assumed direct negative effects of the fine inorganic particles on the epigean fauna by injuring the animals, and Kowarc (1992), working in the same stream, concluded that high accumulations of fines might lead harpacticoid copepods to higher activity rates to avoid sedimentation. Husmann (1966) was the first to emphasize silation by depth filtration (‘intragrauläre Filtration’), and he highlighted a further aspect, that extreme accumulations of fine inorganic particles may fill up larger pore spaces and thereby create habitats for phreatic psammal-fauna near the riverbank, because the decreased permeability reduces the inflow of surface water. Furthermore, those areas might act as refugia, e.g. for tiny hypogean taxa such as archiannelids and bathynellaceans, against predators or stronger competitors by preventing the colonization by superior, larger epigean animals. In our study, however, we could not detect a direct relationship of fine inorganic particles to invertebrate distributions. The gravelly sediments of the Töss River provide a permeable and porous habitat with highly interconnected voids (Brunke in prep.). Thus, it would be difficult to detect the extreme effect of fines which fill up pore spaces and reduce the available interstitial habitat.

Nevertheless, fine inorganic particles indirectly played a pivotal role for the hyporheos of the Töss River. This becomes more obvious by taking a close look at the relationship between POC and faunal density. Though the density is significantly related to POC and PN contents, only a minor portion of the variability in density is explained by
those variables. This seems to be surprising, since POM is the major nutritional resource for most interstitial animals. Other studies also could not detect an effect of the total interstitial organic matter on the hyporheic faunal density (Godbout & Hynes, 1982; Bretschko & Leichtfried, 1988; Cooling & Boulton, 1993; Creuzé des Châtelliers & Marmonier, 1993; Rulik, 1995) or found equivocal relationships (Williams, 1989; Marchant, 1995; Lenting et al., 1997; Strayer et al., 1997). For this reason Bretschko & Leichtfried (1988) concluded that organic matter itself cannot be a limiting factor, which is supported by our results. Also the C/N-ratio, as an indicator of the nutritional value of the organic matter, explained only a negligible portion of density variations, thus food quality does not seem to be a determining factor either. Interstitial POC correlates strongly to fine inorganic particles, as mentioned above; however, the POC content increased to a depth of 50-cm, decreasing thereafter, whereas fine inorganic particles tend to increase with depth (Brunke et al., 1998b). The accumulation of fine inorganic particles with depth was stronger than the increase of POC content with depth, due to the continuous degradation of detrital particles and DOC transported from the surface habitat along interstitial flow paths (Brunke & Fischer in prep.). Consequently, the portion of FPOM of total fine particles decreased strongly with depth. This POC/TP ratio was the best predictor for faunal abundances and explained 61% of the variability in abundances.

We assume that the POC/TP ratio is an indicator of the availability of POM for detritivorous sediment feeders as well as selective particle feeders: High POC/TP ratios indicate high assimilation rates, whereas low POC/TP ratios necessitate the consumption of large amounts of sediment to achieve proper nutrition. For particle feeders large amounts of fine inorganic particles will act as a disruptive factor in selecting particles of high nutritional value. The POC content is the nutritional resource, but the fine inorganic particles, as an environmental factor, limit the organic portion of fine particulate matter within the interstices. Therefore, the availability of the resource, i.e. POM, is defined by the investment of energy into its acquisition, which might be controlled by the portion that is not assimilated, i.e. fine inorganic particles and refractory organic matter. A common feature in ecology, since most resources become limited in part because their acquisition may require too great of an energy investment on the part of the organism (Hall et al., 1992).

The POC/TP ratio decreased significantly with depth (Brunke et al., 1998b) and this vertical gradient was modulated by the hydrological exchange type. The hyporheic position, defined by the interaction between sediment depth and exchange type explained two thirds of the variability in POC/TP ratio. The POC/TP ratio was influenced by flowpath connections mainly in three ways; (a) by the residence time of detrital particles and the balance between import and degradation, (b) by framework sediment properties, porosity and conductivity, as well as by hydraulic gradients, which together determine the
depth filtration of fine particles, and (c) by the quality and quantity of interstitial DOC used by microorganisms within the biofilm and converted into particulate form. Thus the POC/TP ratio is strongly site-specific, but not exclusively: Nearly 80% of the variance of interstitial POC/TP ratio is explained by an extensive model comprising (i) hyporheic positions, which indicate flowpath connections, (ii) the content of fine inorganic particles in conjunction with (iii) the season, as an external factor providing information on temporal variations due to leaf litter input (Tab. 4).

Consequently, due to these results, flowpath connections and the season had also significant effects on the faunal density; they explain as much as the POC/TP ratio, i.e. 62% (Tab. 5). However, the relevance of season seems mainly to be due to its influence on POC, because in ANCOVA models together with the POC/TP ratio it becomes insignificant (Tab. 6). Therefore, the POC/TP ratio exerts the strongest effect on the density, although flowpath connections further influence faunal density. Together both explain more than two thirds of the variations in faunal density (Tab. 6). Flowpath connections integrate information on the interstitial residence time of organic matter and thereby its quality (Brunke & Fischer in prep.). By this they may provide information on the quality of organic matter for consumers (i.e. the potential for assimilation).

**Taxa richness and persistence**

The relationship of taxa richness to the POC/TP ratio corresponded with that of the faunal density to the POC/TP ratio, in part because higher taxa richness generally corresponded with a higher animal density. In our study, density and taxa richness were strongly correlated ($r = 0.81$, $p < 0.001$). Nevertheless, the remarkable correlation between average taxa richness and the average POC/TP ratio has to be stressed, since it substantiates the role of the availability food as a basis for colonization of the interstices by epigean animals.

The persistence in species rank composition was lowest in the deepest sediment strata, which was also found by Dole & Chessel (1986), Danielopol (1991) and Schmid (1993). Danielopol (1991) stated that those sediment layers with the most fluctuating interstitial environmental conditions had persistent homogeneous assemblages, whereas deeper layers with less fluctuating conditions had more variable assemblages. However, the relative variability in environmental conditions (here the POC/TP ratio), might be more influential than the absolute fluctuations, since we found a strong correlation between the coefficients of variation for persistence and POC/TP ratio. Schmid (1993) also assumed that increased variation in POM sedimentation with depth causes decreasing persistence.
Coenocline of the hyporheic community

The transitions in the community structure appear to be more abrupt than gradual, while focussing on epigean taxa, species with an amphibiontic tendency and the hypogean representatives. In Fig. 6a the first PCA axis clearly separates these three groups. However, the second PCA axis reveals that these groups are not distinct entities. Rather they form a gradient between ‘benthic-upper hyporheic’ to ‘phreatic’ interstices. The latter is characterized by the phreatobiont Troglochaetus beranecki, whereas benthic Gammarus fossarum and Leuctra sp. intrude into ‘upper hyporheic’ interstices. Cyclopida and Ostracoda make ‘intermediate hyporheic’ interstices the most densely colonized interstitial habitat at sediment depths of 50-cm. Three hypogean taxa, Bythiospeum rhenanum, Proasellus sp., Niphargus sp., characterize a ‘lower hyporheic’ habitat. These ‘indicators’ develop their highest densities in those hyporheic areas, but there is a considerable faunal overlap of ‘indicator’ taxa in other hyporheic areas and of taxa between these areas as habitat-crossers. For example, the larvae of Ibisia marginata occurs preferentially in the ‘upper’ strata of the EZ and thereby short-circuits the path from ‘upper hyporheic’ to ‘phreatic’ interstices. The amphibiontic plecopteran larvae of Leuctra cf. major occurs in both ‘lower’ and ‘intermediate hyporheic’ habitats. Several epigean taxa inhabit ‘upper’ and ‘intermediate’ interstices.

The hyporheic/phreatic gradient is also depicted by the ordination of the hyporheic positions, showing two trends (Fig. 6b): a short path along the strata of the EZ, and a transition from the 20-cm depth strata of the IZ and HZ along the 50-cm and 100-cm depth strata. However, there are temporal variations in the ordination of the hyporheic positions. Thus it seems impossible to precisely delineate distinct areas or boundaries. It is more important to emphasize the existence of transitions in species composition along flowpaths.

The analysis of the scores of the first PCA axis confirms the relationship between the hyporheic fauna and the three predominating factors; the POC/TP ratio (Tab. 7), sediment depth, and hydrological exchange type (Tab. 8). The sediment depth as well as the interaction between sediment depth and hydrological exchange type had a strong effect on the changes in hyporheic community structure. This is also the case for the POC/TP ratio as a single environmental factor. Flowpath connections and POC/TP ratio individually explain nearly the same variation in the shift of the community structure. Here it is necessary to consider that a large proportion of the changes in the interstitial POC/TP ratio is already explained by distance from the surface habitat (Tab. 4). However, analysis of covariance revealed that the POC/TP ratio explains most of the variations of the PCA axes scores, but still the effect of depth and exchange type remains significant (Tab. 9). Thus the POC/TP ratio seems to be one of the important proximate
factors for the hyporheic animals, but still the depth and hydrological exchange type exert some influence directly or indirectly on the hyporheos; a complex of factors.

The effect of season is of indirect importance by explaining temporal variations of the POC/TP ratio (Tab. 4). Variations due to different life cycles could not be detected in our analysis. These results indicate a predominance of abiotic factors in determining faunal gradients in the hyporheic interstices. This conclusion was also reached by Bretschko (1992) when comparing depth profiles of hyporheic throughflow, interstitial fines, and total fauna down to a sediment depth of 70 cm. However, we still are not able to assess the role of biotic factors such as predation and competition. Furthermore, unexplained variability remains, which might indicate the role of stochastic factors, which were shown to be of importance for the coexistence of interstitial chironomids (Schmid, 1993). Also, a niche separation for food particle size can be assumed (Fenchel, 1978). However, we could not detect a clear trend for changes with depths of particles in various size fractions between 100 μm and 2 μm (Brunke in prep.), but this measure might be too rough to assess the role of particle sizes and their interaction with attached POM.

**POC/TP ratio optima of interstitial invertebrates**

We are aware that a single factor or as here the interactive effect of two factors, can only describe reality in a simplistic way, even when represented against the background of stochastic determinants such as the flow regime. Further studies might show that the role of the POC/TP ratio depends on the range of other variables such as sediment permeability or of the POC content. However, the analysis of the total faunal density, taxa richness, persistence, and the hyporheic community structure revealed empirical evidence that the POC/TP ratio is a primary determinant of the distribution of animals in the hyporheic sediments of the Töss River, based on a study conducted over a 1.5-year period. Therefore, it should be possible to arrange the interstitial taxa according to their optima of the POC/TP ratio, using empirical data. This approach assumes that the animals are mobile enough to find their preferred or best possible realized microhabitat, that is defined by their resource demands. Several studies emphasized the capability of interstitial animals for vertical and horizontal movements (Pugsley & Hynes, 1986; Danielopol, 1989; Boulton et al., 1991; Danielopol, 1991; Panek, 1991; Kowarc, 1992; Ward et al. in press). In our study the order according to the POC/TP ratio optima follows the distinction between epigean, amphibiotic and hypogean taxa (Fig. 7). Except for *Caenis beskidensis* (Ephemeroptera), nearly all taxa stay within their estimated tolerance along the POC/TP gradient. However, all epigean taxa develop their highest densities at POC/TP ratios below their optimum modeled by two different non-linear regressions. These optima were rarely present within the interstices when comparing the averages of
the POC/TP ratios at 20-cm and 50-cm depths, except for those epigean taxa with an amphibiontic tendency. This would explain why benthic and hyporheophile epigean taxa do not advance far away from the surface habitat. Mobile and permanent hyporheic taxa as cyclopoids and ostracods may be visualized as moving individually and randomly through the interstices, and forming aggregations in locations of appropriate nutritional conditions and thereafter scattering again within the sediment. By this means they may be able to exploit newly developed resource patches.

The estimated maximum probabilities of occurrence at the optimum are a consequence of the density and the activity. Thus, the probabilities of occurrence differ between taxa. Low probabilities may indicate that those taxa are not fast colonizers of newly developed resource patches or that they have low densities. Furthermore, within a given species-specific tolerance range of POC/TP ratios the microdistribution may be influenced by other factors besides sediment depth and hydrological exchange type.

8.6 Synopsis: A model for the community organization within the hyporheic interstices of the Töss River aquifer

An approach using a single factor for explaining the hyporheic community structure is obviously misleading. Therefore, we integrated different hierarchically organized factors. The surface and subsurface flow regimes in conjunction with the season (hierarchical tier I) determined the contents of fine organic and inorganic particles (hierarchical tier II) within a given sediment structure (Brunke et al., 1998a, b). These fine particles are ecologically the most important sediment fraction. The interstitial residence time influences the degradation state of particulate organic matter and thereby shifts the ratio between FPOM and fine inorganic particles, which exerted a control on hyporheic invertebrates at our study site. The interstitial residence time of particles is affected by the flowpath connections, which are defined, from the perspective of allochthonous organic matter, by the distance traveled from the surface habitat. This was addressed in our study by the interaction between sediment depth and hydrological exchange type, i.e. hyporheic position, and evidenced by age estimations using Radon. Nevertheless, other factors must also be considered for explaining the cline in community structure, since unexplained variance remained. This raised questions concerning further stochastic and deterministic factors. These questions led us to develop a hypothetical model on the community organization of the Töss River alluvial sediments. Our ideas are summarized diagrammatically in Fig. 8.

Our results might explain, why the distribution of epigean invertebrates within the subsurface habitat is restricted to the upper sediment layers, a question recently asked by
Bretschko (1992). However, they do not explain why hypogean animals do not or only occasionally protrude into the topmost sediment layers, since better food quality and availability should improve the energy balance of individuals and the whole population. Two explanations seem to be appropriate for this restriction. (A) The physical habitat might be too adverse in terms of instability of the sediment due to bedload movement and of fluctuations of factors such as temperature, which are of importance at least partly for certain life cycle stages. However, some findings weaken the plausibility of this hypothesis. Danielopol et al. (1994) pointed out that a strong exploration activity appears to be a special adaptation of hypogean isopods. This should result in a wide distribution. Hypogean animals should be found in upper sediments at least during low flow periods and “taking risks” while profiting from a rich food supply and in autumn and spring during isothermal temperature depth profiles. Indeed, hypogean animals (Niphargus sp.) have been found as benthos in springs and acid streams, where the epigean relative (Gammarus sp.) is missing (Lasar, 1989, personal observation). By using colored food, Kureck (1967) was able to show that Niphargus aquilex feeds in springbrooks; individuals migrated out of the spring at night and returned into the rock crevices by upstream movement. These springbrooks dried out periodically and were therefore not a habitat for epigean Gammarus. Also hypogean snails like Bythiospeum species can be found frequently in springs (Zollhöfer, 1997). These findings lead us to the potential role of biotic interactions limiting the spatial existence of hypogean invertebrates (B). Strayer (1994) assumed that the absence of hypogean taxa in surficial sediment was due to epigean predators. In our study, the most abundant predators were water mites, which were ubiquitous and, therefore, should exert a similar pressure throughout the hyporheic habitat except for small pores which might be used by Troglochaetus in deep and marginal areas of the hyporheic interstices. Tanypodinae and other predators seem to be generalist feeders which also consume FPOM (Schmid-Araya & Schmid, 1995). It appears that competitive interactions might be more important than predation, since epigean animals are assumed to be competitively superior (Lasar, 1989; Creuzé des Châtelliers & Reygrobellet, 1990) and intraspecific competition seems to structure spatial distributions even within Niphargus populations (Mathieu & Turquin, 1992).

For many epigean animals it might be advantageous to stay in the sediments during their whole life cycle or larval development, when they are strongly affected by currents such as limnophilic microcrustaceans (Creuzé des Châtelliers & Marmonier, 1990), are preadapted by small size or long body shape (Schwoerbel, 1967), and might profit from a temporarily balanced storage of large POM contents in retentive upper sediment layers of streams. The reduction of POM in quality and availability becomes species-specifically effective with increasing distance along flow paths from the surface habitat towards suboptimal conditions.
We hypothesize that the coexistence of epigean and hypogean taxa is governed by tradeoffs. Epigean taxa are protected from hydraulic forces and bedload movement, but energy assimilation is constrained increasingly with flowpath distance from the surface habitat determining nutritional supply. Hypogean physiology is adapted to low nutritional supply (Hüppop, 1985); however, a higher availability of organic matter remains attractive, but the energy gain is limited by biotic interactions (sensu Hall et al., 1992) with abundant epigean animals in resource-rich interstices. It is important to note, that invertebrate abundances are highest at intermediate depths which are most retentive and on average correspond to higher amounts of stored POM (Brunke et al., 1998b). Hyporheic interstices can often be viewed as a densely colonized habitat (Strayer et al., 1997) which suggests biotic interactions are important. Therefore hypogean taxa might be outcompeted in nutrient rich areas. Below those areas (i.e. along flow paths) abundances of epigean taxa decrease and biotic interactions do not affect coexistence with hypogean animals. The density of hypogean invertebrates is highest in areas in which the resource supply becomes insufficient for epigean animals. Thereafter the density of hypogean taxa tends to decrease (e.g. Danielopol, 1982; Dole & Chessel, 1986; Mathieu & Turquin, 1992, this study), except for phreatobites like *Troglochaetus* which might be most susceptible to predation. Thus as a generalization, it appears that epigean distributions within interstices tend to reflect fundamental niches, whereas hypogean distribution tends to reflect realized niches. Probably biotic interactions are much more complicated and differential for certain species pairs as has been shown for hypogean taxa inhabiting caves by Culver (1994). A general understanding of competitive interactions in aquifers is still lacking (Strayer, 1994).

The upper and intermediate hyporheic interstices are colonized most densely, especially by microcrustaceans and chironomids. We speculate that these patches are organized more by stochastic factors due to stronger influences of the disturbance regime of the Töss River, which creates mosaics of local concentrations of organic matter. Here it might be important for individuals to possess a high mobility to exploit newly formed patches rich in resource content, quality, and availability.

To conclude, the community organization within the hyporheic interstices of this gravel-bed river can be visualized on three scales (Fig. 8): (I) On the scale of the fluvial hydro-system we separate epigean and hypogean taxa into a zonation perspective, simply by properties such as pigmentation and life cycle. (II) A closer examination reveals the importance of transitions, i.e. the existence of an ecotone. In our study we found a clinal community structure within a gradient of habitat subunits along flowpaths. Various spatiotemporal faunal overlaps existed and ‘discontinuity crossers’ make the clinal perspective more viable than a zonation perspective. We assume an exclusion of hypogean taxa by dominance of epigean taxa in areas most densely colonized by highly
mobile epigean animals. (III) Upper and intermediate hyporheic interstices are the proper habitat for many epigean hyporheic taxa, which was also found in another calcareous gravel-bed river by Bretschko (1991, 1992). These areas seem to be advantageous due to their POM retentiveness and protection for animals; however, dislocation during spates might still be effective. Therefore, the community might be organized by deterministic and stochastic factors favoring individual mobility. Herein our model partly concurs with observations made by Schmid (1993, 1997) concerning stochasticity in organisation of hyporheic chironomid communities.

Much of the high spatio-temporal complexity is formed along flowpaths which are rarely taken into account in hyporheic studies, and also by other proximate factors, which might be a consequence of random processes. Thus, detected stochasticity may partly be due to the neglect of attention given to the evolution of patchiness. The pumping device used in this study is a more integrative method compared to freeze coring since a greater volume of colonizable habitat, i.e. the interstitial space is sampled. A small sample volume relative to distribution patterns will tend to show apparent randomness, whereas larger volumes will tend to show more uniform patterns (Elliott, 1977). As a final remark, we would like to stress that we might have developed other conclusions, if samples had only been taken down to a depth of 20 to 50 cm, which is common for many hyporheic investigations.

**Figure 8.** (next page) Conceptual model for the community organization in the sediments of the Töss River. Physical instability, absolute fluctuations of environmental factors and mean POC/TP ratio generally decrease along flowpath connections or with sediment depth from the surface water into the aquifer, whereas relative fluctuations of the POC/TP ratio increase. Perspectives of community organization are given on three spatial scales: (I) On the fluvial hydrosystem scale niche control is of importance, resulting in a zonation between epigean and hypogean taxa. (II) The hyporheic ecotone perspective recognizes the faunal gradients structured by dominance and tradeoffs. (III) The channel sediment perspective emphasizes the stochasticity in abiotic and biotic patterns in upper and intermediate hyporheic interstices, and therefore the importance of individual mobility of epigean animals resulting in continuous redistributions and patchy distribution patterns. POC = particulate organic carbon; TP = total particles.
ENVELOPMENTAL GRADIENTS

- physical instability
- absolute fluctuations of environmental factors
- mean POC/TP ratio
- relative fluctuations in POC/TP ratio

ENVIRONMENTAL GRADIENTS:

- (I) Spatial Scale: fluvial hydrosystem
- Perspective: surface/subsurface Zonation
- Community Organization: Niche control

- (II) Spatial Scale: hyporheic ecotone
- Perspective: Cline
- Community Organization: Dominance control

- (III) Spatial Scale: channel sediments
- Perspective: Patchiness
- Community Organization: Mobility control

FLOW PATH CONNECTIONS

- surface water
- interstitial water

- physical instability
- absolute fluctuations of environmental factors
- mean POC/TP ratio
- relative fluctuations in POC/TP ratio

- epigean-abundance
- fundamental niche of epigean taxa
- exclusion of hypogeon—competition—coexistence—exclusion of epigean
- realized niche of hypogeon taxa

- population surplus/loss
- epigean hyporheobions
- deterministic and stochastic factors
- continuous redistribution
- amphibiotic tendency
- benthic immigration
- hypogeon immigration
Literature


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CHAPTER 9

Synopsis

The research of this thesis focuses on the hyporheic invertebrate community and on which environmental factors are most decisive for its structure. Different hydrological exchange patterns between streams and ground water were used as the starting point for the investigation to set the location of the sampling sites where the positions and steepnesses of abiotic and biotic gradients within the hyporheic ecotone were determined. The measured abiotic habitat variables encompass several physicochemical parameters (e.g. dissolved oxygen, pH, temperature), organic matter (DOC, POC) and sedimentological properties (fine inorganic particles). The most influential of these habitat characteristics for hyporheic meio- and macrofauna and also for hyporheic bacteria were elucidated by factor analyses.

The Review

The study starts with an extensive literature review on the ecological significance of exchange processes between rivers and ground water. By viewing rivers and groundwater ecosystems as linked components of a hydrological continuum several ecological processes that maintain the integrity of both systems and those that are mediated by their ecotones are evaluated. Of specific importance are small and large scale hydrological exchange, sedimentary structures, the metabolism of fluvial systems and their communities, since all of these together define the characteristics of the hyporheic ecotone and its function within the fluvial landscape. Furthermore, the consequences of anthropogenic disruption of vertical connectivity are analysed.

The Study Site

Based on the knowledge obtained by the literature review, three basic types of hydrological exchange (infiltration, horizontal advection, exfiltration) were used to test the role of hydrology on hyporheic ecology.

The study was conducted in the Töss River, a third order prealpine gravel-bed stream in northern Switzerland. At the sampling site (460 m a.s.l.) ground water exfiltrates into the stream at the left margin (exfiltration zone), whereas surface water infiltrates into the sediment at the opposite bank (infiltration zone). In midstream the dominant interstitial flow direction is along the river channel. This section is termed as the horizontal
advected zone. Twelve piezometers were installed in three clusters of four sediment depths (20-, 50-, 100- and 150-cm) in each of these 3 hydrological exchange zones. The samples (255) were taken with a hand pump (hyporheos) and with an electric pump (environmental parameters). Additionally nine freeze-cores were taken to document sediment texture.

**The Physicochemical Conditions**

Hydrological exchange patterns controlled the steepness of physicochemical gradients within the hyporheic interstices of the Töss River. In the upper sediment layers of the infiltration zone, physicochemical conditions resembled those of the surface water and showed high temporal variability, especially at a depth of 50 cm. In contrast, in the exfiltration zone physicochemical conditions were influenced by the more stable properties of upwelling ground water. Therefore, physicochemical gradients in the exfiltration zone were steepest in the uppermost sediments (0 - 20 cm). Physicochemical conditions in the horizontal advection zone were in between those of the infiltration zone and exfiltration zone; however, they tended to resemble the conditions within the infiltration zone more, especially in their thermal characteristics.

**Fine Inorganic Particles and Particulate Organic Carbon**

The interstitial content of mobile fine particles (fines) tended to increase down to depths of 150 cm (the greatest depth investigated), with the exception of the exfiltration zone where the highest fine inorganic particle contents were found at a depth of 50 cm, indicating the influence of the net upward movement of ground water. These particles were smaller than 1 mm, and their median grain size was about 0.03 mm. This sediment grain size class seems to be the ecologically most important.

Accumulations of fine particles are responsible for colmation, i.e. the clogging of the top layer of channel sediments. Colmated sediments are characterized by a consolidation, a reduction of pore volume and lower hydraulic conductivity. Colmation can hinder the exchange processes between surface water and ground water and thereby diminish the integrity of both ecosystems. The transport and storage of fine matrix sediment within interstitial layers is described as 'depth filtration'. Depth filtration is of significance for the transport of colloidal and fine particulate inorganic as well as organic matter within the hyporheic interstices and into the alluvial aquifer.

The content of particulate organic carbon increased down to a depth of 50 cm in all three hydrological exchange types. However, the differences between 50 and 100 cm were only significant in the region of exfiltrating ground water.
The ratio between particulate organic carbon to total fine particles (POC/TP ratio) decreased significantly with depth, because the accumulation of fine inorganic particles with depth was higher than even partial increase of POC content with depth. The POC/TP ratio differed significantly between the hydrological exchange zones; it was lowest in the exfiltration zone.

Frequent flood events caused high temporal variability of interstitial particle parameters. Of specific importance are the areas of prefential bedload transport during floods, because in those areas even consolidated sediment can be mobilized and hence the vertical connectivity is reestablished.

In conclusion, flood events, vertical exchange of water, and the channel sediment structure are important determinants of the distribution of inorganic fine particles and POC to depths considerably deeper than 50 cm below the streambed. Thus, the transport and deposition of fine particles within the interstices (depth filtration) are not restricted to the upper layers of channel sediments in gravel-bed streams, where they may induce clogging of the interstices (colmation), but rather these processes also influence the habitat characteristics of deeper sediment layers.

A MULTIVARIATE PERSPECTIVE OF ENVIRONMENTAL CONDITIONS

In a multivariate perspective, areas of steep gradients exist at sediment depths between 50 and 100 cm in the infiltration zone and between 20 and 50 cm in the horizontal advection zone. In contrast, in the exfiltration zone two areas with steep gradients exist; one between depths of 0 and 20 cm and another between 50 and 100 cm. Physicochemical gradients function as stronger discriminators for the upper strata, whereas particle gradients distinguish the deeper depth strata.

HYPORHEIC BACTERIA

Hyporheic bacterial abundance and production were strongly correlated to interstitial particulate organic matter and inorganic fines; the best predictor for both bacterial parameters was the content of particulate nitrogen. The predictive power of statistical models was substantially improved by the introduction of the 'hyporheic position', defined by sediment depth and hydrological exchange type, which integrated information on flowpath connections, the age of water and the quality of organic matter. Flowpath connections were particularly relevant when one uses dissolved organic carbon and interstitial fine sediment as explanatory variables.

Bacterial abundances ranged between 0.163 to 478 x 10^6 cells/ml and differed significantly between upper and deeper sediment strata. This change with depth was
significantly modulated by the type of hydrological exchange. The bacterial carbon portion of particulate organic carbon varied between 0.06% and 5.3% and tended to decrease with depth.

Bacteria were most numerous at sediment depths where inflow of stream water occurred, but had been attenuated. Bacterial production was highest in hyporheic interstices dominated by surface water inflow. It is hypothesized that high grazing pressures and/or hydraulic forces reduce bacterial abundance in the uppermost sediments and that the delivery of resources in somewhat greater depths is still sufficient to maintain high populations in areas where the storage of all organic matter is more protected from flushing effects.

**Hyporheic Bacteria and Invertebrates**

Several hyporheic metazoan taxa and collective properties of the invertebrate community showed a strong correspondence with bacterial distribution patterns. Most of the correlations between bacterial and faunal parameters were higher for bacterial abundance than for bacterial production and they were clearly higher than for the portion of bacterial biomass of POC.

Estimates of invertebrate grazing rates indicate that interstitial microcrustaceans might consume 1.6 to 25.7% of the bacterial production.

**Hyporheic Invertebrate Community**

The hyporheic community was dominated by microcrustaceans at all depths and zones. The most abundant hyporheic taxa were cyclopoid copepods (33%), ostracods (23%) and chironomids (11%). All other groups accounted for the remaining 33%. The Acarina are almost exclusively composed of Hydrachnellae, except for a few specimens of Oribatida and the occasional Limnohalacarida. The Hydrachnellae accounted for 5.5% of the total fauna. The cyclopoid copepods, ostracods, chironomids and water mites were also the most frequent. Oligochaeta, Harpacticoida and Nematoda were also common dwellers of the hyporheic interstices. The most abundant ephemeropteran and plecopteran larvae were Habrophlebia lauta, Caenis beskidensis and Leuctra sp. Three characteristic hypogean taxa were commonly encountered: the snail Bythiospeum rhenanum (Hydrobiidae), and the crustaceans Niphargus sp. (Amphipoda) and Proasellus sp. (Isopoda). The archiannelid Troglochaetus beranecki was found only rarely.

Altogether 60 taxa were identified which colonized the hyporheic habitat.
The hyporheic fauna exhibited a biotic gradient between interstitial positions influenced by surface water and those dominated by phreatic ground water. The gradient in hyporheic community structure corresponded most with changes in the ratio of particulate organic carbon to total fine particles (POC/TP ratio) as well as to hydrological variables and distance between the surface and phreatic habitats.

Total faunal density patterns were also strongly related to the POC/TP ratio, which explained 61% of the variation in abundance within the sediments. Taxa richness and temporal persistence in species composition were also significantly correlated with the POC/TP ratio.

All epigean taxa developed their highest densities at POC/TP ratios below their optimum modeled by two different non-linear regressions. These optima were rarely present within the interstices. Hence, the POC/TP ratio optima for individual taxa indicate that the depth to which epigean taxa penetrate sediments may be restricted by the availability of the food resource, which decreased with decreasing POC/TP ratios. The interstitial content of fine inorganic particles appears to be a critical determinant of the availability of food resources for interstitial invertebrates.

It is hypothesized that the coexistence of epigean and hypogean taxa is governed by tradeoffs. Epigean taxa are protected from hydraulic forces and bedload movement within the interstices, but energy acquisition is increasingly constrained with flowpath distance from the surface habitat providing the nutritional supply. Hypogean physiology is adapted to low nutritional supply (Hüppop, 1985); however, a higher availability of organic matter remains attractive, but the energy gain may be limited by biotic interactions (sensu Hall et al., 1992) with abundant epigean animals in resource-rich interstices. (It is important to note, that invertebrate abundances are highest at intermediate depths which are most retentive and on average contain to higher amounts of stored POM). Therefore, hypogean taxa might be outcompeted by epigean taxa in nutrient rich areas. Below those areas (i.e. along flow paths) abundances of epigean taxa decrease as do biotic interactions with hypogean animals. The density of hypogean invertebrates is highest in areas in which the resource supply becomes insufficient for epigean animals. Thereafter the density of hypogean taxa tends to decrease except for phreatobites like Troglochaetus which might be most susceptible to predation.

A conceptual model was developed to explain the distribution and composition of the interstitial fauna on three scales: 1) On the scale of the fluvial hydrosystem, the epigean and hypogean taxa were separated in a zonation perspective. 2) On a local scale transitions in environmental conditions are evident and the community structure is clinal in nature. An exclusion of hypogean taxa in areas most densely colonized by epigean taxa is assumed to be due to biotic interactions. 3) The upper and intermediate interstices are
the proper habitat for many epigean taxa. These areas seem to be nutritionally advantageous due to their retentiveness for organic matter; however, there is a high probability of dislocation during spates. Therefore, the community in these sediment strata may be organized by deterministic and stochastic factors favoring individual mobility.

References

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Curriculum Vitae

Matthias Brunke
born on 24 Oktober 1964 in Castrop-Rauxel, Germany

home address: Humperdinckstr. 80, D-55543 Bad Kreuznach.

1975 - 1985 High school (Gymnasium) in Castrop-Rauxel, Nordrhein-Westfalen, and Bad Kreuznach, Rheinland-Pfalz, Germany. Abitur.

1985 - 1986 Army basic training

1986 - 1993 Study of Biology at the Albert-Ludwigs-Universität, Freiburg, Germany.
Main subject: Limnology.
Subsidiary subjects: Microbiology, Biochemistry, Hydrology.

1993 - 1994 Zoobenthic and chemical investigations in commission of the Environmental Ministry of Rhineland-Palatinate, Germany, at 106 stations of streams and rivers in the Upper Rhine valley and the highlands of the Pfälzer Wald, Germany.
Electrofishing work in the catchment of the River Nahe in commission of the Agricultural Ministry of Rhineland-Palatinate, Germany.

June 1994 - May 1998 Dissertation at the Swiss Federal Institute of Technology (ETH) in Zürich, Switzerland, conducted at the Swiss Federal Institute of Environmental Science and Technology (EAWAG).
Title: The influence of hydrological exchange patterns on environmental gradients and community ecology in hyporheic interstices of a prealpine river. Supervision: Professor Dr. J. V. Ward und Dr. T. Gonser.

since July 1998 Postdoc on biodiversity of aquatic habitats in floodplains of a southern alpine river, the Brenno, Ticino, Switzerland, at the EAWAG.
Publications in peer reviewed journals and books


In press


Submitted

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In preparation

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Other publications


Papers presented at scientific meetings


Leer - Vide - Empty