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SPECIAL REVIEW

The ecological significance of exchange processes between rivers and groundwater

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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 zone, 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 zone 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 geological 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, and decreased permeability of the stream bed. Consequently, colmation can hinder exchange processes between surface water and groundwater.
4. Physicochemical gradients in the interstices result from several processes: (i) hyporheic flow pattern and the different properties of surface and groundwaters; (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 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–groundwater 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.

Micro-organisms 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 connectivity; (ii) by altering exchange processes; and (iii) by toxic or organic contamination.

Introduction

Groundwater 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 groundwater. 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 groundwater 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 waters and groundwaters are very closely connected (Castro & Hornberger, 1991; Bencala, 1993; Stanford & Ward, 1992, 1993).

3 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, Hynes & Telang, 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 emphasizing the significance of interactions for the water balance and metabolism of streams. Simultaneously, the interactions with surface water have become important in 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 towards a comprehensive ecological understanding of the hydrological continuum.

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 ‘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 zone as an integral part of the fluvial ecosystem (Bretschko & Klemens, 1986; Bretschko, 1991b; Danielopol & Marmonier, 1992) and he 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 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 groundwater 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 stream bed, 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 containing 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 of 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. Thus Gibert *et al.* (1990) and Vervier *et al.* (1992) developed a dynamic ecotone model which distinguishes two variants, one where groundwater flows into the river and one where the river recharges the groundwater. 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 zones, 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 led Bretschko (1981, 1991b, 1992; Bretschko & Klemens, 1986) to term this area 'bed sediments', 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 groundwater has been attempted 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 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 groundwater can be distinguished from other waterbodies by its stable environmental conditions, the transition between rivers and groundwater 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 a subterranean area where the groundwater 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 subterranean 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 floodplain (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.

Hydrological exchange processes

Hydraulic conductivity and porosity

The permeability of ecotones is of fundamental importance for the exchange processes between ecological systems (Wiens, Crawford & Gosz, 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 flowpath 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 only a function of the medium (Davis, 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 °C corresponds to 0.77 times that of water at 20 °C and K at 30 °C is 1.25 times that of water at 20 °C. In small streams with significant diel variations in stream temperature, Constantz, Thomas & Zellweger (1994) were able to show that reduced afternoon stream flows were caused mainly by increased infiltration rates due to increased hydraulic conductivity.

Porosity is the ratio of pore volume to the total volume of a given sample (Davis, 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 (Davis, 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 stream 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 stream bed 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, grain size distribution and shape of suspended particles; the hydraulic gradient of 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 microorganisms developing a biological layer with adhesive capacities (Beyer & Banscher, 1975; Banscher, 1976; Geldner, 1982; Cunningham, Anderson & Bouwer, 1987; Schälchli, 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 (Schälchli, 1992). Colmation is removed under natural conditions during spates involving bedload movements. These induce resuspension of deposited fine material. In stream reaches with upwelling groundwater the upward hydraulic force reduces siltation and thereby tends to maintain hydraulic conductivity (Schälchli, 1993).

Large-scale exchange processes

The dimension of exchange processes between rivers and groundwater 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, soil and bedrock type, and patterns of 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 hydraulic head, whereas flow (volume/unit time) depends on sediment 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 subterranean flow (infiltration, downwelling, stream-fed aquifer, recharge of aquifer);

2 the effluent situation: groundwater drains into the stream (exfiltration, upwelling, aquifer-fed stream).

Under conditions of low precipitation baseflow originates from groundwater. In many streams this exfiltration constitutes the discharge for 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 groundwater (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, successive discharge and recharge of the aquifer has a buffering effect 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 baseflow, which is determined by the groundwater level. In perennial streams baseflow is more or less continuous, whereby they are primarily effluent and flow continuously throughout the year (Gordon, McMahon & Finlayson, 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 water move-

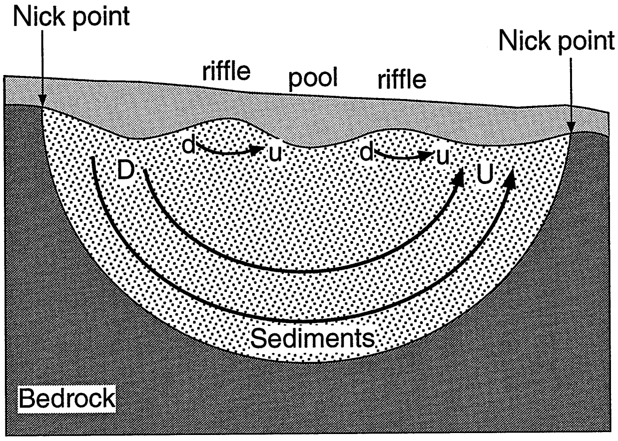

Fig. 1 Schematic representation of large-scale downwelling (D) and upwelling (U) zones, at the upstream and downstream ends, respectively, of an alluvial basin. Small-scale up- (u) and downwelling (d) zones are indicated as they appear in the riffle-pool sequence of an alluvial river.

ments. 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, leading to the development of narrow valleys which can change at nick points into deep basins filled with fluvial (and/or glacial) sediments (alluvium). Below such a nick point large-scale downwelling zones may exist, while groundwater will tend to upwell at the downstream end of the alluvium (Fig. 1).

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 stream bed consists of fine-grained sediments of low permeability. Nevertheless, on a floodplain scale, with numerous upwelling and downwelling zones, interactions between the groundwater and surface water are manifold. The braided and anastomosed geomorphic patterns of an alluvial floodplain often appear together since the latter develops in aggradation zones with low slopes 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 geological 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 consists 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, Meier & Puguin, 1994a) over geological 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, Siegenthaler & Stauffer, 1988). This can have an enormous impact on exchanges between surface and groundwaters. 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 floodplain during high volume flow conditions, the soil will remain as a relict and appear as a subterranean layer of low hydraulic conductivity. In contrast, 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 palaeochannel 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 be a good tool for estimating the textural composition of deposits (Huggenberger *et al.*, 1994a; Huggenberger, Rauber & Stauffer, 1994b).

Small-scale exchange processes

Local up- and downwelling processes are determined by geomorphologic features such as discontinuities in slope and depth, riffle-pool sequences, and changes in the direction of flow. Advection is promoted by high permeability and roughness of the stream bed as well as by obstacles that protrude into the channel (White, 1990; Williams, 1993). The hyporheic zone actually consists of multiple flowpaths (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, Reible & Thibodeaux, 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, Walters & Kennedy, 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, Sale & Wolman, 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 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 groundwater on channel morphology

Effluent seepage may have a minor impact on channel roughness, by decreasing flow resistance, as well as on bed form 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 groundwater 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.

Physicochemical gradients at the surface–groundwater interface

Gradients between surface water and groundwater develop by the mixing of water with different physicochemical characteristics and by biogeochemical processes in conjunction with the local residence time of water. As a result of small-scale exchange processes, heterogeneous 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 filtering effect of pores and lithologic adsorption (Gölz, Schubert & Lieblich, 1991; Vervier *et al.*, 1992; Younger, Mackay & Connorton, 1993). Biological processes are responsible for transformations of organic material and most anthropogenic micropollutants (Hoehn, Zobrist & Schwarzenbach, 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–groundwater 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

Surface–interstitial exchanges determine temperatures in the hyporheic zone because groundwater temperatures 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, Elzinga & Hendricks, 1987; Crisp, 1990; Evans, Greenwood & Petts, 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, Fisher & Stanley, 1990). In effluent reaches, the temperature in the hyporheic zone corresponds to the groundwater temperature, and temperature fluctuations are absent or minimal (Shephard, Hartmann & Wilson, 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 groundwater 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 waterbodies lateral to the main stream of the river are heated in summer and cooled in winter to temperatures which depend on the ambient air temperature, solar irradiance, the size of the waterbody, 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 groundwater they receive. A schematic representation of the water temperatures that can be encountered on a temperate alluvial floodplain in summer and in winter is given in Fig. 2.

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 groundwater (Schwoerbel, 1961a, 1964; Poole & Stewart, 1976; Pennak & Ward, 1986; Valett *et al.*, 1990; Triska, Duff & Avanzino, 1993a). Decreases in dissolved oxygen correspond with interstitial flow, community respiration rates 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, Schmidt & Marxsen, 1993). The filtering effect for matter in an ecotone with clogged interstices is governed by aerobic and anaerobic processes, and not hydrodynamics as in permeable aquifers (Vervier *et al.*, 1992). Anaerobic zones within the hyporheic zone are not exceptional (Dahm, Carr & Coleman, 1991) and can be significant for the riparian vegetation since such conditions increase nutrient concentrations (Dahm, Trotter & Sedell, 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 relationships between photoautotrophic uptake, respiration, the dynamic equilibrium with carbonate

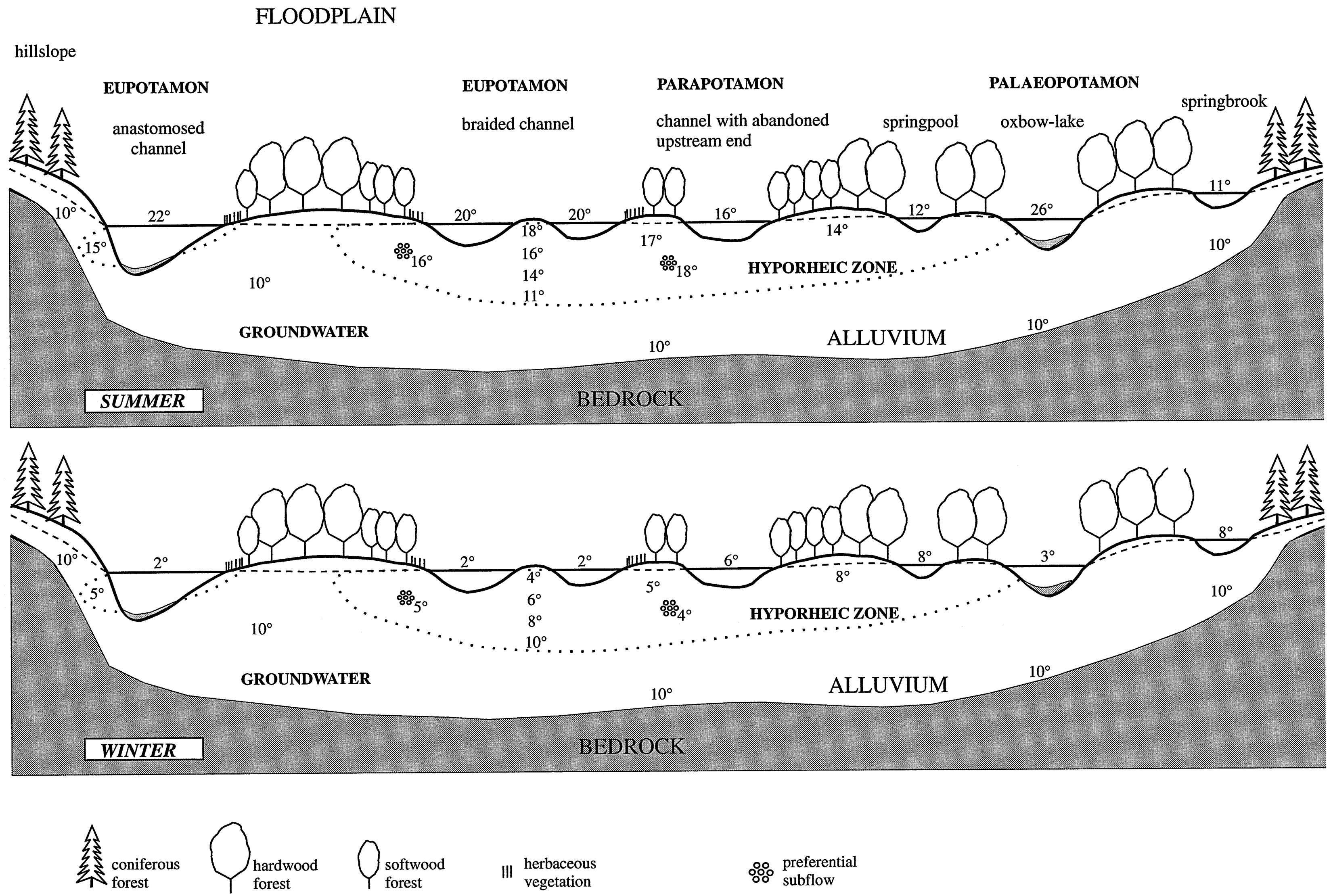

Fig. 2 Temperature diversity of aquatic habitats along the lateral dimension of an idealized alluvial floodplain caused by surface–groundwater interactions in a temperate region during summer (a) and winter (b). Terminology of the subunits of the fluvial hydrosystem, according to Amoros *et al.* (1987), 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; palaeopotamon, abandoned anastomosed and meandering channels; plesiopotamon, abandoned braided channels.

minerals, and atmospheric exchange processes determine the content of dissolved CO_2 in natural waters. In the hyporheic zone, CO_2 concentrations are determined mostly by community respiration rates, to which microbial activity contributes more than 90% (Pusch, 1993; Pusch & Schwoerbel, 1994). CO_2 levels are elevated in the hyporheic zone (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 throughflow, and the large area colonized by microbial biofilms.

Linked to the CO_2 content is pH, which is lower in the interstices than in the channel water. In highly permeable sediments, diel cycles caused by photoautotrophic activity may appear delayed in the hyporheic zone depending on the water's travel time (Schwoerbel, 1961a, 1967).

Nitrate and ammonium

The floodplain, 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. These 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, Duff & Avanzino, 1993b). Both processes are related to gradients of dissolved oxygen, dissolved organic carbon (DOC), ammonium and nitrate, and thus to the fluxes between groundwater and surface water (Hill, 1990; Triska, Duff & Avanzino, 1990a, 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 biologically available 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 appear 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).

Retention and metabolism of organic matter at the surface water–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 the transporting character of streams (Speaker, Moore & Gregory, 1984). Retention enables the utilization of organic matter by the stream biota and is consequently 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, Jackman & Triska, 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 floodplain (constrained *v* 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, Reinhard & Rittmann, 1981; Karickhoff, 1984; Younger *et al.*, 1993).

Micro-organisms have a controlling function in 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 zone of a third-order Black Forest mountain stream the ratio of total particulate organic carbon to bacterial carbon was up to 562 : 1 (Fischer, Pusch & Schwoerbel, 1996). However, in the loosely attached particulate organic matter (POM) fraction (*sensu* Pusch, 1996) this ratio ranges between 28 : 1 and 23 : 1. Furthermore, 7.6–14.2% 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 groundwater habitat most bacteria are attached to surfaces (Wolters & Schwarz, 1956; Hirsch & Rades-Rohkohl, 1983; Husmann *et al.*, 1988). Marxsen (1982) found that in the groundwater of sandy sediments interstitial bacteria contributed less than 1% of the total number of bacteria; the remainder were 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 micro-organisms themselves (Lock *et al.*, 1984). Protozoa and micrometazoa can graze these biofilms (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; Charaklis, 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 bed sediments the biofilms appear 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 in 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 micro-organisms 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 groundwater into streams (Wallis *et al.*, 1981; Hynes, 1983; Naiman *et al.*, 1987; Rutherford & Hynes, 1987; Marxsen, 1988a; Stanford & Ward, 1988; Triska *et al.*, 1989a,b; 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, Lock & Neal, 1990; Gregory *et al.*, 1991). Although the micro-organisms 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 epiphyton (Stanford & Ward, 1988, 1993; Ward, 1989; Coleman & Dahm, 1990). On the other hand DOC in infiltrating stream water may be metabolized in the hyporheic zone (Bott, Kaplan & Kuserk, 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, Dobson & Pinay, 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 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, Rittmann & Herricks, 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, Lock & Ford, 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 the 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, 1991a; 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

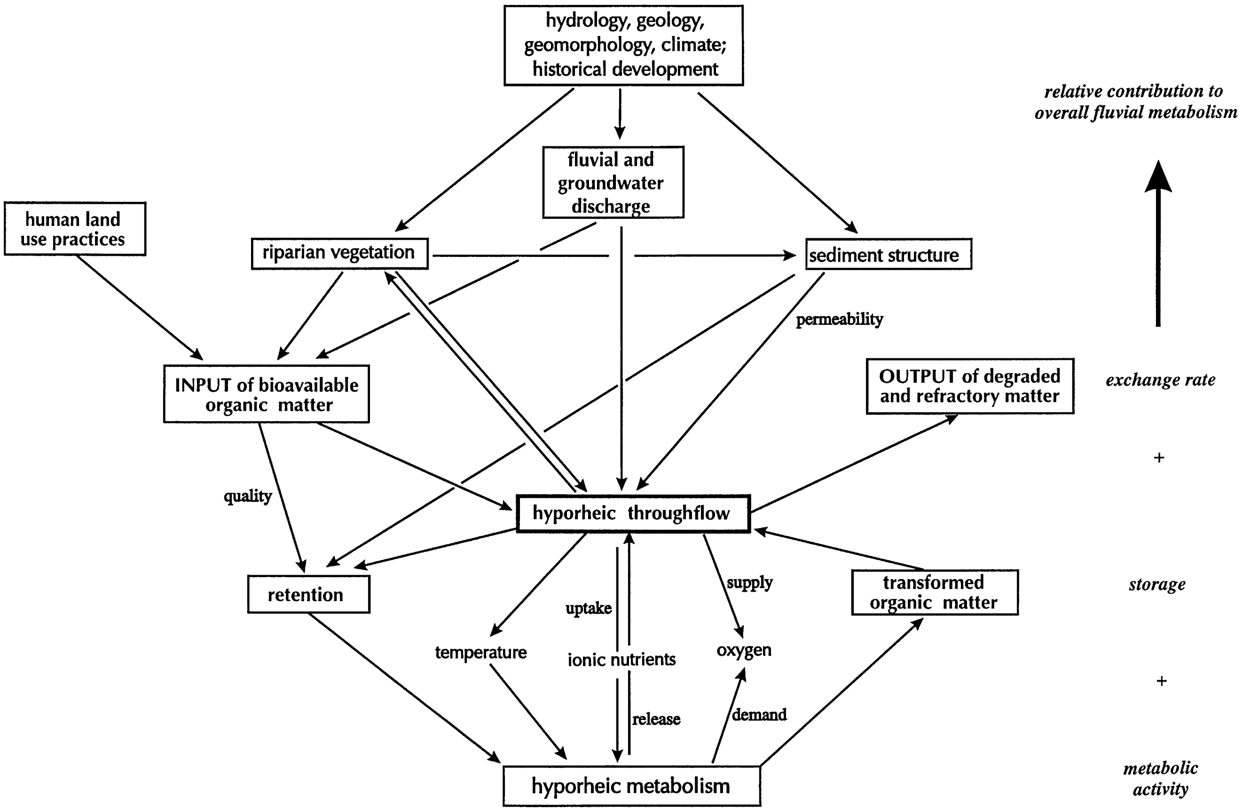

Fig. 3 An ecosystem perspective of factors controlling hyporheic throughflow and metabolism.

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 one 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 gravelbed 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 periods of low discharge. 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 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 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

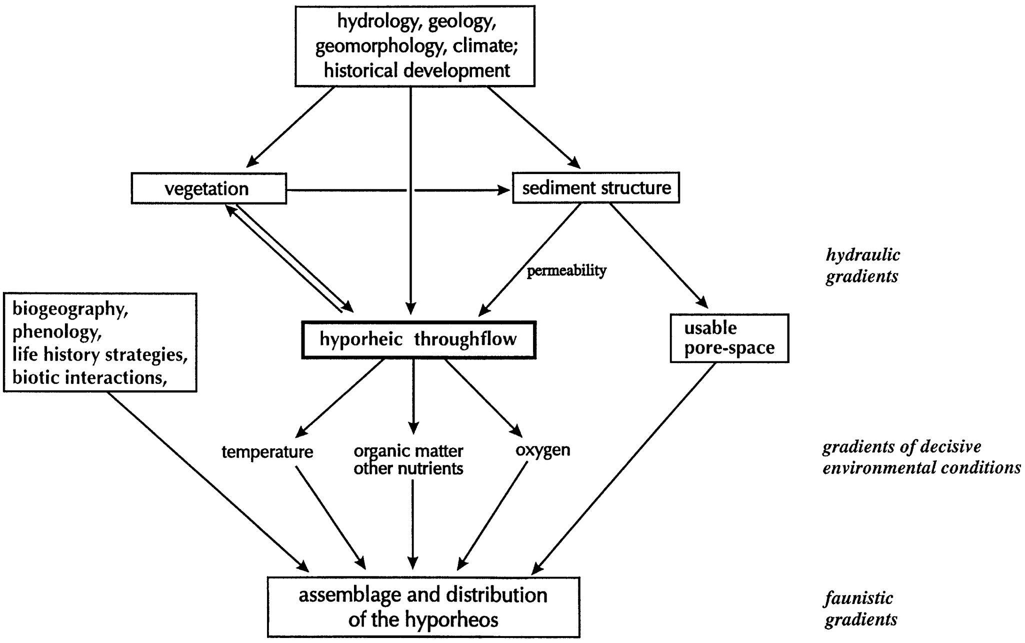

Fig. 4 Factors influencing the biotic composition of the hyporheos.

and output (Fig. 3), especially of DOM, which in natural waters are about one order of magnitude greater than those 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, Billett & Cresser, 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.

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, 1961b, 1964; Williams & Hynes, 1974). A third group consists of 'amphibionts': epigean insects that obligatorily 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 aquatic subterranean fauna is provided in Gibert *et al.* (1994).

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 zone 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 in 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).

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 stygon 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 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 groundwater 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 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 zone during disturbance events. For a sandy-bottomed stream with small interstices, Palmer, Bely & Berg (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 had significant downward movements 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.*, 1986). 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 subterranean water may remain 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 hyporheic zone, 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 recovery times 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 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 groundwater 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, Hendricks & Fortner, 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, U.S.A.) the upwelling of groundwater prevents freezing and enables 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 kilometres away specifically to exploit this event, rendering the world's largest eagle population dependent on the exfiltration of groundwater (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 (U.S.A.). 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 gravelly 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 groundwater 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^{-1} and oxygen concentrations exceed 8 mg l^{-1} (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 groundwater 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, Durbec & Ille, 1992). The distribution and composition of the benthos is possibly influenced by advective exchange (Boulton, 1993). 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 groundwater, 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, Dole-Olivier & Creuzé des Châtelliers, 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, Valett & Fisher, 1992; Creuzé des Châtelliers *et al.*, 1992; Dole-Olivier & Marmonier, 1992a). The abundance and species richness of stygobiont species increase gradually from influent to effluent zones (Dole-Olivier, Creuzé des Châtelliers & Marmonier, 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 palaeochannels, can transport water with physicochemical properties similar to the surface water into deeper alluvial layers underneath the floodplain. These subsurface flows extend direct connections between rivers and groundwater into the subterranean landscape, and may sustain a high interstitial biodiversity and biomass by delivering resources. Ward, Stanford & Voelz (1994) propose that palaeochannels in the alluvium of the Flathead River (Montana. U.S.A.) are a significant factor influencing the spatial distribution of crustaceans. For stygobiont metazoans the hyporheic interstices constitute 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* Mràzek) 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 hyporheic zone is colonized by a community characterized by specific structures 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 floodplain 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).

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 geological 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, U.S.A.) is characterized by deeply incised (constrained) river reaches, where bedrock reaches the surface, alternating with reaches developing wide (unconstrained) floodplains on fluvioglacial deposits (details are given in Stanford, Ward & Ellis, 1994). 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, groundwater 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 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 groundwater 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 floodplains. 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 groundwater, 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 floodplains, for nutrient retention and turnover, biological production and biodiversity patterns is expressed by conceiving the alluvial reaches as 'beads on a string'.

The hyporheic corridor concept focuses attention on: (i) the biogeochemical transformations by speciose foodwebs 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 floodplain 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 floodplains 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, Bayly & Sparks, 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 the others, integrating an often-neglected, although important, component of the fluvial system. 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 effects 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, Schwoerbel & Wendling, 1994) with a consequent loss of ecological integrity.

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 groundwater 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; Gölz *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 groundwater was determined by the infiltration of polluted stream water over a distance of up to 110 m. In the Upper Rhine valley the springs and springbrooks fed by groundwater originating from infiltrated polluted water from 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 eutrophicants and metals due to varying redox conditions in the aquifer (Carbiener & Trémolières, 1990; Trémolières *et al.*, 1993). Significantly, the aquifer of the highly polluted river Ill in the adjacent Alsacian Rhine valley remains uncontaminated, because replenishment of the aquifer occurs due to percolation through the active floodplain surface during high discharge. The contaminants are retained by the soil–vegetation system of the active floodplain (Trémolières *et al.*, 1994). Thus a functional floodplain 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, 1977/78, 1981; Kirchengast, 1984). However, slight increases 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 (Schälchli, 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 (decolmation) (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

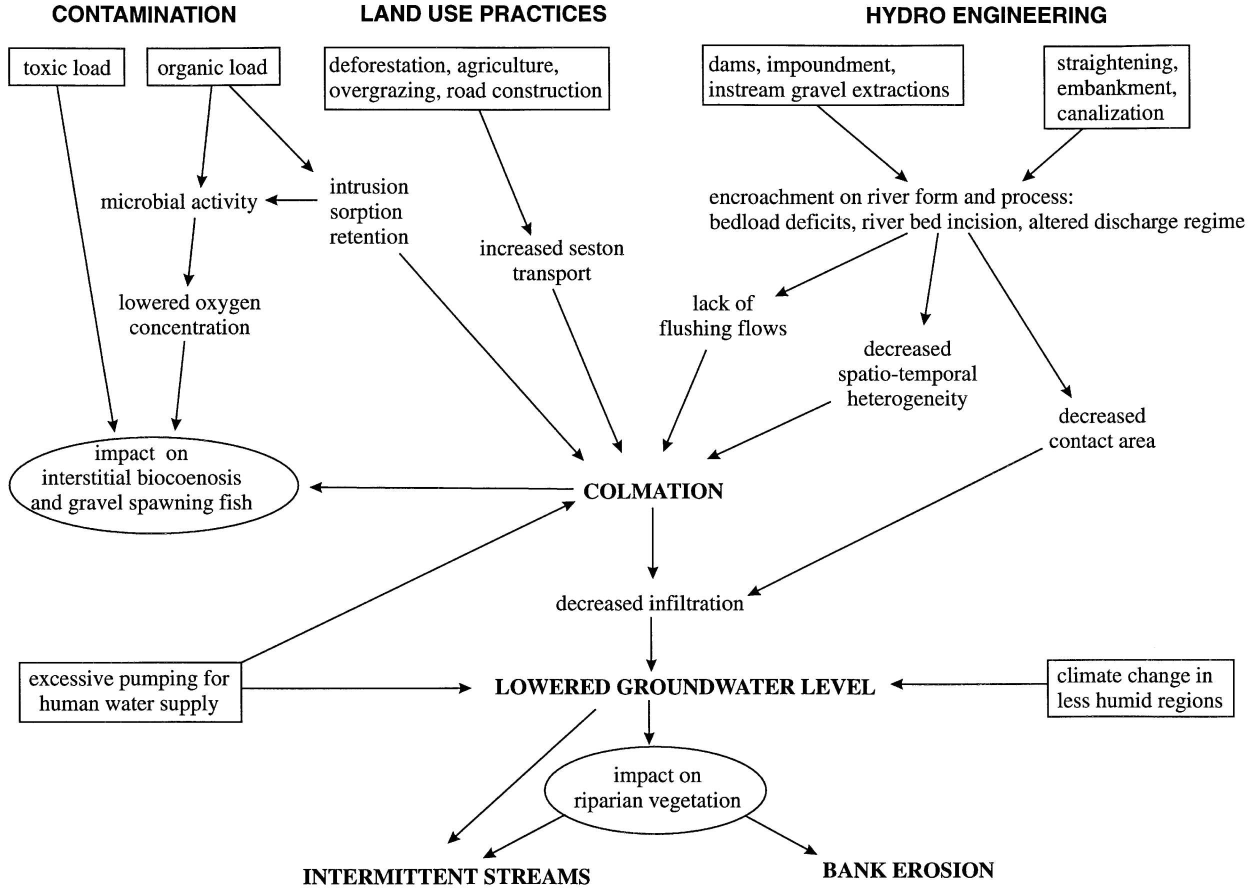

Fig. 5 Anthropogenically induced impacts that promote colmation in stream bed sediments, and their ecological consequences.

and fine sediment inputs, hydroengineering, and increased river bank filtration for supplying drinking, industrial and irrigation waters (Petts, 1988; Gölz *et al.*, 1991; Kondolf & Matthews, 1993). Each of these factors is capable of causing permanent colmation. Colmation exerts severe impacts on the renewal of groundwater 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 stream bed near a drinking water bank filtration site induced a 1 m rise in the groundwater table near the river, but after a few weeks the opened section had become sealed again (Gölz *et al.*, 1991). On the other hand, a colmated bed may act as an intrusion barrier that prevents the contamination of groundwater 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 hydroelectric power generation alter the mixing relationships between surface water and groundwater in the hyporheic zone. 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 floodplain 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 stabilizing 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 River Rhine has been changed dramatically by impoundments which have altered the relationship between groundwater flow patterns and floods as the structuring agents of the floodplain (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 prevented 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 from becoming upwelling groundwater. Today the 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 only dense mature vegetation.

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 impacts on terrestrial and aquatic systems may lead to reductions in 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 groundwater as integrated components of a hydrological continuum.

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