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The boundaries of river systems: the metazoan perspective

J. V. WARD
Department of Limnology, EAWAG/ETH, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

G. BRETSCHKO
Institute of Limnology, Biological Station Lunz, Austrian Academy of Sciences, A-3293 Lunz am See, Austria

M. BRUNKE
Department of Limnology, Limnological Research Center, EAWAG, CH-6047 Kastanienbaum, Switzerland

D. DANIELOPOL
Institute of Limnology, Mondsee Austrian Academy of Sciences, A-5310 Mondsee, Austria

J. GIBERT
Université Lyon I, Laboratoire d'Ecologie des Eaux Douces et des Grands Fleuves, Equipe Hydrobiologie et Ecologie Souterraines, 43 Blvd du 11 Novembre 1918, F-69622 Villeurbanne Cédex, France

T. GONSER
Department of Limnology, Limnological Research Center, EAWAG, CH-6047 Kastanienbaum, Switzerland

A. G. HILDREW
School of Biological Sciences, Queen Mary and Westfield College, University of London, London E1 4NS, U.K.

SUMMARY

1. This overview of metazoans associated with the riparian/groundwater interface focuses on the fauna inhabiting substratum interstices within the stream bed and in alluvial aquifers beneath the floodplain. The objective is to integrate knowledge of habitat conditions and ecology of the interstitial fauna into a broad spatiotemporal perspective of lotic ecosystems.
2. Most aquatic metazoans of terrestrial ancestry, secondarily aquatic forms including insects and water mites (Hydracarina), are largely confined to surface waters (epigean), most of the time penetrating only the superficial interstices of the stream bed.
3. Primary aquatic metazoans include crustaceans and other groups whose entire evolutionary histories took place in water. Some species are epigean, whereas other members of the primary aquatic fauna are true subterranean forms (hypogean), residing deep within the stream bed and in alluvial aquifers some distance laterally from the channel.
4. The hypogean/epigean affinities of interstitial animals are reflected in repetitive gradients of species distribution patterns along vertical (depth within the stream

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Correspondence: Prof. J.V. Ward. E-mail: jvward@eawag.ch

bed), longitudinal (riffle/pool), and lateral (across the floodplain) spatial dimensions, as well as along recovery trajectories following floods (temporal dimension).

5. Fluvial dynamics and sediment characteristics interact to determine hydraulic conductivity, oxygen levels, pore space, particle size heterogeneity, organic content and other habitat conditions within the interstitial milieu.

6. Multidimensional environmental gradients occur at various scales across riparian/groundwater boundary zones. The spatiotemporal variability of hydrogeomorphological processes plays an important role in determining habitat heterogeneity, habitat stability, and connectivity between habitat patches, thereby structuring biodiversity patterns across the riverine landscape.

7. The erosive action of flooding maintains a diversity of hydrarch and riparian successional stages in alluvial floodplains. The patchy distribution patterns of interstitial communities at the floodplain scale reflect, in part, the spatial heterogeneity engendered by successional processes.

8. Interstitial metazoans engage in passive and active movements between surface waters and ground waters, between aquatic and riparian habitats, and between different habitat types within the lotic system. Some of these are extensive migrations that involve significant exchange of organic matter and energy between ecosystem compartments.

9. The generally high resilience of lotic ecosystems to disturbance is attributable, in part, to high spatiotemporal heterogeneity. Habitat patches less affected by a particular perturbation may serve as 'refugia' from which survivors recolonize more severely affected areas. Mechanisms of refugium use may also occur within habitats, as, for example, through ontogenetic shifts in microhabitat use. Rigorous investigations of interstitial habitats as refugia should lead to a clearer understanding of the roles of disturbance and stochasticity in lotic ecosystems.

10. Development of realistic 'whole river' food webs have been constrained by the exclusion of interstitial metazoans, which may in fact contribute the majority of energy flow in lotic ecosystems. A related problem is failure to include groundwater/riparian habitats as integral components of alluvial rivers. A conceptual model is presented that integrates groundwater and riparian systems into riverine food webs and that reflects the spatiotemporal complexity of the physical system and connectivity between different components.

11. Interstitial metazoans also serve as 'ecosystem engineers,' by influencing the availability of resouces to other species and by modifying habitat conditions within the sediment. For example, by grazing on biofilm, interstitial animals may markedly stimulate bacterial growth rates and nutrient dynamics.

12. Although there has been a recent surge of interest in the role of interstitial animals in running waters, the knowledge gaps are vast. For example, basic environmental requirements of the majority of groundwater metazoans remain uninvestigated. Virtually nothing is known regarding the role of biotic interactions in structuring faunal distribution patterns across groundwater/riparian boundary zones. Interstitial metazoans may contribute significantly to the total productivity and energy flow of the biosphere, but such data are not available. Nor are sufficient data available to determine the contribution of groundwater animals to estimates of global biodiversity.

13. Effective ecosystem management must include groundwater/riparian ecotones and interstitial metazoans in monitoring and restoration efforts. Evidence suggests that a 'connected' groundwater/riparian system provides natural pollution control,

prevents clogging of sediment interstices and maintains high levels of habitat heterogeneity and successional stage diversity. River protection and restoration should maintain or re-establish at least a portion of the natural fluvial dynamics that sustains the ecological integrity of the entire riverine–floodplain–aquifer ecosystem.

Keywords: groundwater/riparian ecotones, hyporheic habitat, epigean, hypogean, interstitial fauna, biodiversity, food webs

Introduction

Riverine floodplains are characterized by exchange of water, nutrients, detritus and biota between diverse habitats and by ecotones at a range of scales (Amoros & Roux, 1988; Junk *et al*., 1989; Gibert *et al*., 1990; Naiman & Décamps, 1997; Ward & Wiens, in press). Unconsolidated alluvium contains water-filled interstices inhabited by a diverse fauna. Although research on this interstitial fauna began in Europe early this century (e.g. Karaman, 1935; Chappuis, 1942), only recently has it been fully recognized that the spatial extent of river ecosystems extends well beyond the channel boundary (Stanford & Ward, 1988; Marmonier *et al*., 1992; Gibert *et al*., 1994; Ward & Stanford, 1995). According to this expanded perspective, the invertebrate fauna of river systems consists of aquatic species inhabiting surface and interstitial waters, and terrestrial species of the riparian zone.

Here we focus mainly on invertebrates inhabiting the interstices within the stream bed or in contiguous aquifers beneath alluvial floodplains. We deal with the well-known surface benthos only in terms of its interactions with the subsurface system, or where benthic forms also extend into the subsurface system. Neither is there space for us to discuss exhaustively metazoa in the above ground parts of the riparian zone and the floodplain. We thus address mainly the subsurface and lateral boundaries of river systems from the perspective of the metazoa.

Following a brief description of the fauna and its habitat affinities, we examine environmental variables and spatio-temporal dynamics. The role of the metazoans in riparian ecosystems is then approached with respect to food webs and energy flow. Research prospects and suggestions for the management of alluvial river-aquifer systems are then discussed. External forcing by the climate, vegetation and hydrology are treated elswhere in this volume. We address pattern and process within spatial and temporal limits. The floodplain reach between adjacent 'knickpoints' (Stanford & Ward, 1993) provides the upper limit to the longitudinal dimension, while the contemporary floodplain, excluding terraces, provides the lateral dimension. The vertical dimension extends from the river bed or floodplain surface, down to bedrock. The time-scale ranges from physiological responses to floodplain succession.

The fauna

General characteristics

The aquatic invertebrates of alluvial rivers consist of primary and secondary aquatic forms (Fig. 1). Secondary aquatic forms invaded fresh waters from the land. They include aquatic insects, most of which have a terrestrial adult (Ward, 1992) and water mites (Hydracarina), which coevolved with aquatic insects. Many mites are ectoparasitic on adult aquatic insects (Smith & Cook, 1991). The third secondary aquatic group, pulmonate snails, does not have a terrestrial phase, although aquatic species have lungs and most rely on surface breathing (Brown, 1991). The secondary aquatic fauna resides mainly in surface waters, penetrating only the superficial interstices of the stream bed.

The primary aquatic invertebrates, in contrast, have evolved in water. They are either of ancient freshwater lineages or invaded inland waters from the sea (Notenboom, 1991). Primary aquatic species lack a terrestrial phase and some species from each of the major groups inhabit subsurface waters throughout their lives. Crustaceans are especially well represented and, for example, a large number of amphipods inhabit subsurface waters (Barr & Holsinger, 1985) and all Bathynellacea are exclusively subterra-

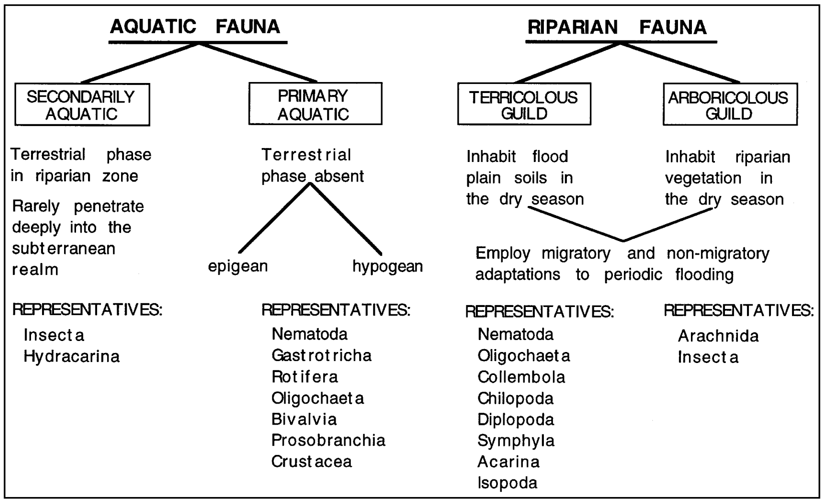

Fig. 1 The major categories of aquatic and riparian invertebrates inhabiting riverine–floodplain systems.

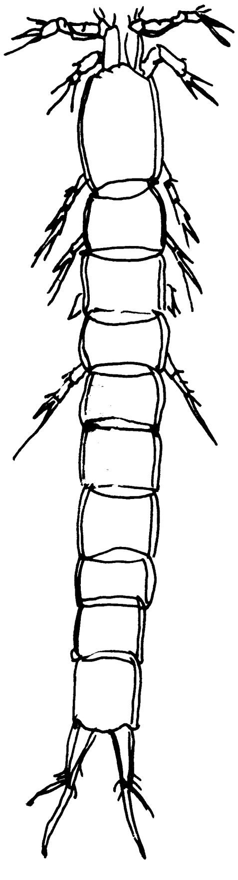

Fig. 2 *Parastenocaris dianae*, female (Harpacticoida), from the alluvial sediments of Lachein Brook; body length 0.5 mm, 360 × magnification (original courtesy of R. Rouch).

nean. See the Appendix for scientific names of species referred to in this paper.

The terrestrial invertebrates of the floodplain consist of terricolous or arboricolous guilds (Fig. 1), based on their occurrence in soils or above-ground vegetation during the dry season (Adis, 1992). They survive floodplain inundation in a variety of ways.

Hypogean/epigean affinities

Epigean and hypogean are general terms that refer, respectively, to surface and subsurface habitats or their inhabitants. Because animals residing in subsurface waters vary in their requirements for particular types of subterranean habitats, additional terms are sometimes needed to describe more precisely the hypogean affinities of different species (Gibert *et al.*, 1994). Metazoa in interstitial waters have affinities either with animals which live exclusively in subterranean habitats, the so-called stygobitic fauna, or belong to epigean groups that are widely distributed in surface water habitats, including the benthos.

Most strongly hypogean animals display morphological and/or biological adaptations to interstitial life (Ginet & Decou, 1977; Camacho, 1992). Stygobites are readily distinguishable from their epigean counterparts through traits such as reduction of eyes, loss of body pigment, small size, elongated shape and reduction of setae. These are adaptations to life in small spaces without light. Stygobite crustaceans such as the copepod *Parastenocaris* and amphipod *Niphargus* (Figs 2 and 3) illustrate these specialisations. Exclusively subterranean organisms adapted to the oligotrophic conditions and/or low oxygen concentrations found in many alluvial sediments, generally have low metabolic rates and a high tolerance of hypoxia (Mathieu, 1983; Danielopol *et al.*, 1994;

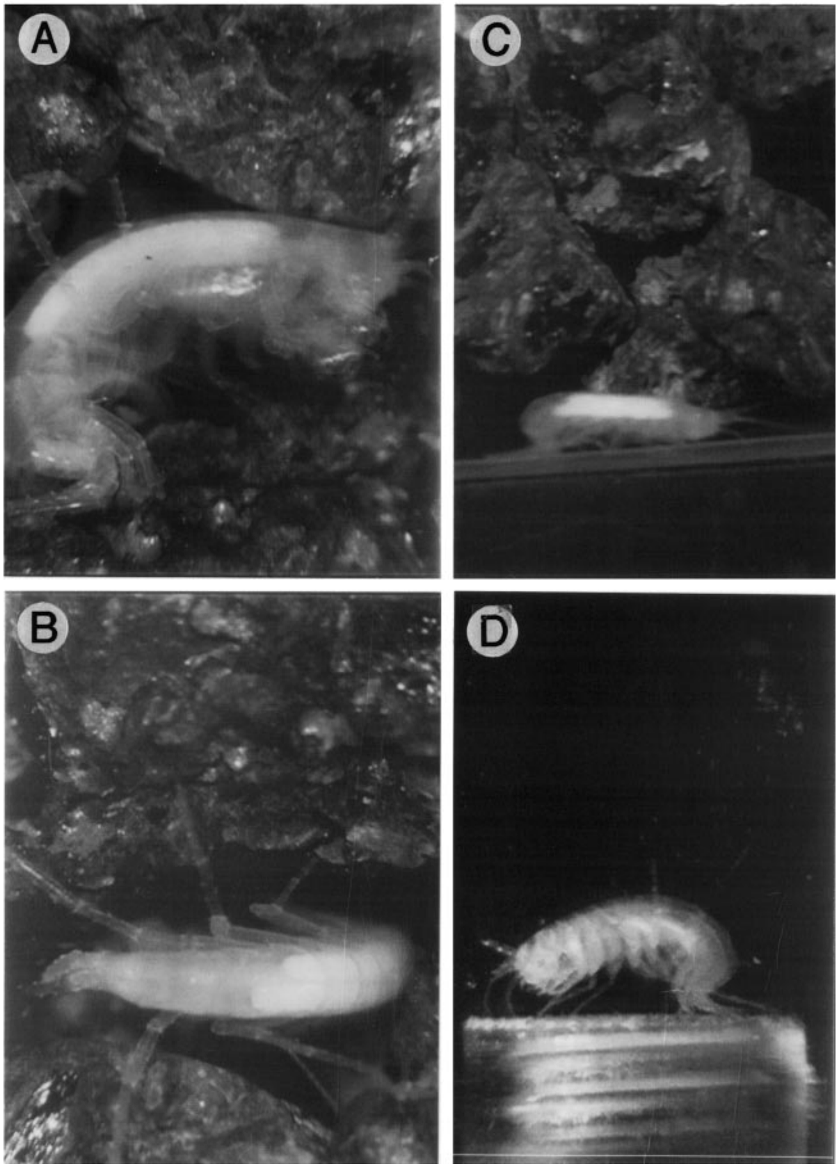

Fig. 3 *Niphargus* sp. (Amphipoda), male, body length 9 mm, from the alluvial sediments of the Danube wetland Lobau (Original; 124 × magnification in A and B; 62 × magnification in C and D).

Hervant & Mathieu, 1995). They are thigmotactic and move with agility through the labyrinthine pore space (e.g. *Niphargus* sp., Fig. 3).

Epigean animals, both terrestrial and aquatic, have well developed eyes and pigmentation and a higher metabolic rate than hypogean forms. Many insect larvae and epigean crustaceans colonise the superficial benthos of running waters (Bretschko, 1981; Danielopol, 1983). Epigean species can also, however, penetrate deeper where water circulates freely through the sediments and where much organic matter and oxygen are available. For example, some stonefly larvae live within the interstices of an alluvial floodplain, kilometres from the river channel (Stanford & Ward, 1988), and the epigean amphipod *Gammarus* migrates deeper into sediments following spates (Marmonier & Dole, 1986; Marmonier, 1988).

Some epigean animals of running waters are preadapted for subsurface life. Stonefly larvae such as *Leuctra* (Berthelemy, 1968), and the beetle *Cyphon palustris* (Klausnitzer & Pospisil, 1991) have elongate, stream-lined bodies and can penetrate 1–2 m vertically and tens of metres laterally into river alluvium.

A species-rich assemblage of epigean macrofauna and meiofauna inhabits the superficial beds and the banks of running waters. Schmid (1991) identified 70 species of chironomid larvae in a 100-m length of riverbed in Austria. Examples of species-rich meiofaunal groups include water mites (Schwoerbel, 1961a), nematodes (Andrassay, 1962; Eder, 1983), rotifers (Palmer, 1990; Schmid-Araya, 1993) and some microcrustaceans, especially Copepoda and Ostracoda. In some cases, both epigean and hypogean species contribute to the high species richness just below the surface sediments.

Some aquatic invertebrates of riparian zones are able to live above the water table. Larval ceratopogonids and chironomids occur regularly in the capillary fringe along the banks of the Cimmaron River in Kansas (Ferrington, 1987; Goldhammer & Ferrington, 1992). In riparian zones of central Brazil, in the *wet campo* areas, a meiofauna of nematodes, rotifers, harpacticoid copepods and others occurs in soils which are fed by ground water (Reid, 1984). In Europe, Eder (1983) showed that some soil nematodes living between the roots of floodplain vegetation can colonise shallow groundwater. The same is true for various species of oligochaetes, especially enchytraeids (Schmid-Araya & Schmid, 1995a). Terrestrial microarthropods with aerial respiration, such as Collembola, can be found in hydromorphic soils close to the water table (Pospisil & D. Danielopol, unpublished data). From here they can passively or actively enter superficial, water-saturated layers of riparian zones where they are able to survive for short periods (Bretschko & Christian, 1989).

Habitat variables

The environment of organisms living within the boundaries of rivers is highly dynamic due to discharge fluctuations and sediment movements. Flooding events form a diversity of floodplain water bodies with differing degrees of connectivity to the river channel, resulting in a range of hydrarch and riparian successional stages (Amoros & Roux, 1988; Ward & Stanford, 1995). Sediments of groundwater and riparian zones vary in pore size, hydraulic conductivity and other physico-chemical factors (Ward & Palmer, 1994) and the sediment matrix results from the geological and climatic history of the catchment (see discussion by Huggenberger *et al.*, 1998; this volume).

Floodplain aquatic habitats

River–floodplain systems provide an array of diverse surface and subsurface aquatic habitats structured by hydrological, morphological, and biological patterns and processes. Several general gradients exist (Fig. 4) between the main channel, side arms, partially and totally abandoned channels. Deep oxbow lakes, formed in old meanders, undergo slow autogenic processes towards terrestrialization, whereas shallow backwaters, in abandoned braids, rapidly terrestrialize via allogenic processes (Amoros *et al.*, 1987; Amoros & Roux, 1988; Ward & Stanford, 1995).

The spatio-temporal variability of hydrogeomorphological processes plays an important role in determining the heterogeneity and physical stability of the habitats and thus the biodiversity patterns across the riverine landscape (Ward, 1998; Ward *et al.*, in press). A comparison between the adjacent Rhône and Ain floodplains in France illustrates the connection between geomorphic heterogeneity and the fauna (Castella *et al.*, 1991). The floodplain of the Rhône has a diversity of water bodies, formed by successive meandering and braiding phases and differential

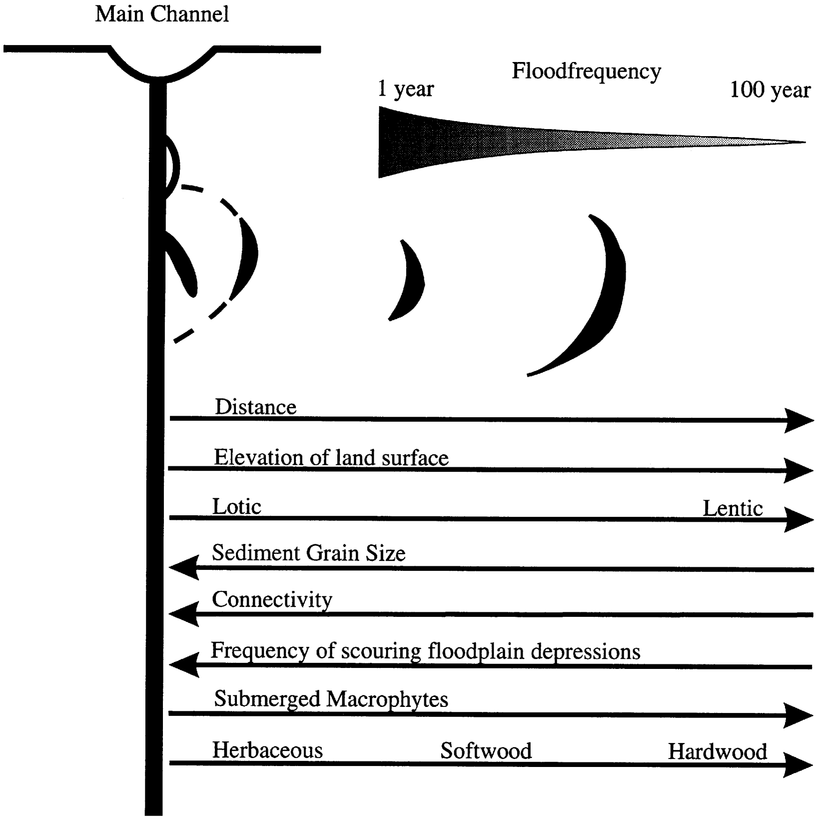

Fig. 4 Generalized gradients characterizing the lateral surficial aquatic habitat. Arrows indicate the direction of change in these variables from the main channel to the edge of the flood plain.

groundwater influence. Embankments built in the nineteenth century constrained channel migration and prevented restructuring of fluvial landforms. Each former channel has a specific fauna, the different water bodies having diverged from each other over time. Thus, in the Rhône floodplain much of the high biodiversity is attributable to beta diversity (turnover of species between habitats). In contrast, meandering in the Ain floodplain continued into the first half of this century. Rapid hydrogeomorphic processes continued to restructure aquatic habitats more recently than in the Rhône and thus created many abandoned channels, relatively similar to each other (low beta diversity) but with a high internal heterogeneity. Thus, in the Ain, taxon richness in the separate water bodies is high and the system therefore has high alpha (within habitat) diversity.

There is an important interplay between flooding and the influence of upwelling groundwater. The interstitial fauna of the Rhône floodplain is influenced by local groundwater characteristics and the particular position of each water body in the floodplain, in terms of a gradient of physical stability that is linked to the surface discharge regime and the water exchange (Marmonier *et al.*, 1992). The spatial distribution of interstitial fauna, however, only partly reflects the distance from the main channel. Local, site-specific hydrogeological and geomorphic processes may produce patchiness in the interstitial fauna that appears gradual only when visualized on a larger scale within a continuum or gradient (Marmonier *et al.*, 1992; Ward *et al.*, 1994).

Sediment structure

The nature of the sediment habitat is determined by a hierarchy of factors (Fig. 5). Sediments shape the environment of the stream and constitute the precise habitat of the interstitial community. Every stream and groundwater organism interacts in complex ways with the sediment during its lifetime. Most studies have concerned the surface and/or the topmost sediment layer (Minshall, 1984). Since the 'hyporheic zone' was identified (Angelier, 1953; Orghidan, 1959; Schwoerbel, 1961b), it has become evident that much of the epigean stream community dwells in the sediments, marking the near-surface hyporheos as an integral part of the stream ecosystem (Triska *et al.*,

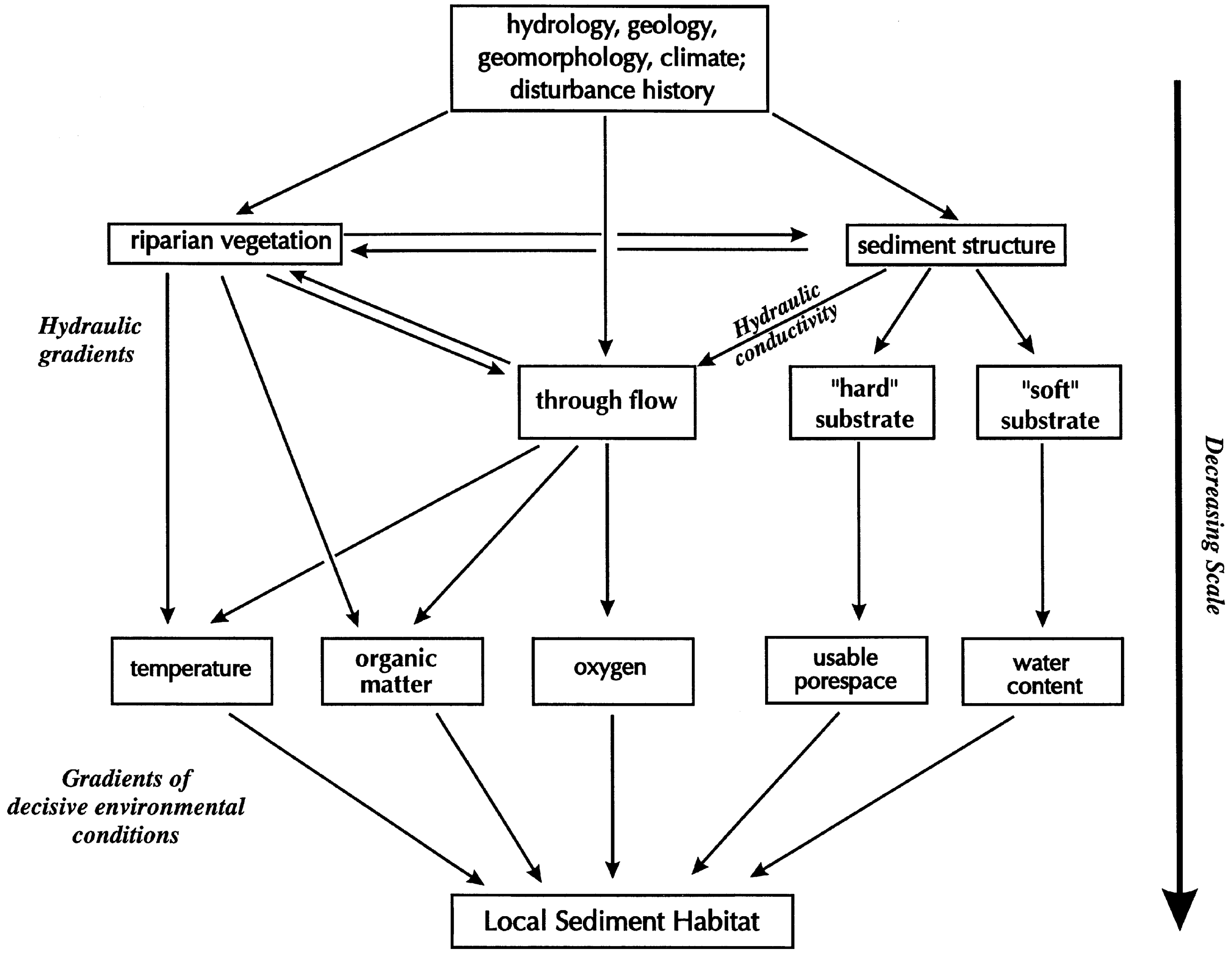

Fig. 5 Hierarchial conceptualisation of factors controlling local sediment habitat conditions of major importance to interstitial metazoans.

1989; Klemens, 1991; Bretschko, 1992, 1995). Furthermore, it has been suggested that the hyporheic zone plays 'a pivotal role in the functioning of lotic ecosystems' (Palmer, 1993).

Porosity is the relationship between the volume of water contained in a sample of sediment and the total sample volume. Little is known, however, about the actual sizes of and connections between the voids, which are the most ecologically important variables. With decreasing diameter, sediment grains approach a globular shape (Zingg, 1935), although quartzites may have irregular grains. For geometric reasons, therefore, pore spaces are small in fine-grained sediments, but water content is high. Most water is attached to the large surface area of the small sediment grains (Leichtfried, 1985) and the sediment consistency becomes more and more fluid ('soft-ground'; Schlieper, 1972), at least in surficial layers. Benthic animals can then move sediments and burrow through them.

Fluviatile pebbles, cobbles and smaller gravel tend to be rounded and globular or disc-like in shape (Bretschko, 1994). Because of the geometry of grains, pores are large in well-sorted sediments but the overall water content is lower than in fine sediments (Bretschko & Klemens, 1986). Most water moves freely through the voids and very little adheres to surfaces, because grain surface area decreases dramatically with increasing grain diameter. Permeability is high and interstitial animals cannot alter the size or arrangement of pores. Animals can swim through the larger pores, or cling and crawl over grain surfaces as they do at the surface of the stream bed.

Natural stream sediments are rarely well-sorted and normally contain an array of grain sizes. The fraction of grains smaller than 1 mm seems ecologically the most important. Large amounts of small grains clog larger interstices, increase the resistance to water flow and reduce the habitat space for the sediment community. These adverse effects may be counterbalanced by the large area of biofilm associated with fine sediment grains. (Leichtfried, 1988). The limited information indicates that highest faunal densities are supported by an admixture of up to 10% of fines to gravel sediments (Bretschko, 1994).

The sediments beneath the streambed are regarded as an ecotone between surface water and groundwater (Marmonier & Dole, 1986; Gibert *et al*., 1990; Ward & Wiens, in press) and described as the 'hyporheic zone' (Schwoerbel, 1961a, 1961b, 1964, 1967). The surface system is vertically delimited by the penetration of light. However, the faunal community of the adjacent dark interstitial system in many riverbed systems consists mainly of stream species (e.g. insect larvae), plus some species occurring only there (ecotonal species such as the amphipod *Niphargopsis*), and occasionally of blind crustaceans and worms from the 'true' groundwater, an abiotically comparable environment (Pennak & Ward, 1986; Gibert *et al*., 1990; Ward & Voelz, 1994).

Temperature

Temperature exerts the primary controls on phenologies and life histories, physiology, behaviour and local distribution patterns of aquatic organisms, and sets the limits of their distributional range (Vannote & Sweeney, 1980; Ward & Stanford, 1982; Ward, 1992). In addition, because invertebrate energetics and growth are strongly influenced by temperature, the energy balance model of Hall *et al*. (1992) probably applies to the interstitital fauna. Temperature patterns also relate to aspects such as migration, refugia and life histories that are addressed in later sections of this paper.

Factors controlling the thermal regime of running waters include climate, insolation and hydrology (Ward, 1985). Hydrology and, especially, insolation are in turn influenced by the riparian zone. Stream reaches receiving little groundwater tend to track air temperatures, while streams receiving much groundwater are thermally buffered in their seasonal and daily regimes (Mosley, 1982). The sediments of upwelling zones have stable temperatures, while the temperature of sediments in downwelling zones varies with that of the stream (Shepherd *et al*., 1986).

The influence of large groundwater inputs and dense riparian vegetation are analogous, both forming summer-cool/winter-warm temperature regimes. Within the sediments of alluvial rivers, due to heterogeneity in permeability and hydraulic head, the water may show a wide array of temperature regimes, depending on localized rates of downwelling from the surface, mixing ratios with the groundwater, residence times and upwelling from the groundwater (Stanford & Ward, 1993; Brunke & Gonser, 1997).

Oxygen

Dissolved oxygen (DO) is a key environmental parameter in interstitial habitats. Oxygen is utilized by the respiration of most metazoans and many bacteria and its depletion in the environment produces notable qualitative and quantitative changes in metazoans assemblages.

Molecular oxygen is much less soluble than other gases (e.g. carbon dioxide), the amount in solution depending on temperature, the partial pressure of the gas and the presence of other dissolved substances. Arbitrarily defined, aerobic or oxic environments have more than 1–3 mg/L of DO, while lower concentrations down to about 0.3–0.1 mg/L are termed dysaerobic (dysoxic). Following Fenchel & Finlay (1995), hypoxic conditions refer to oxygen concentrations that limit the rate of respiration. Most metazoans inhabitating interstitial riparian habitats are aerobes while a few, such as the nematode *Tobrilus gracilis*, are facultative anaerobes that can withstand anoxic conditions for a limited time.

Dissolved oxygen in subsurface sediments depends on the permeability and porosity of the sediments, the saturation of pore spaces with water and the intensity of sediment respiration. The latter is related to bacterial activity, which depends on the availability of assimilable carbon in the sediment. Because of high diffusion rates in the gaseous phase, oxygen concentrations in the unsaturated zone below the soil surface exceed those in saturated sediment layers (i.e. groundwater *sensu stricto*).

Sediments with low porosity and permeability generally have low oxygen concentrations. This is the case in alluvial sediments of floodplains, where pore spaces between gravel and cobbles are filled with silt, clay and fine particulate organic matter. An example would be the bed sediments of large rivers, especially behind dams, and such conditions exist along the Danube. At such sites animal assemblages are impoverished, often dominated by relatively few species, belonging to the Oligochaeta and Nematoda, that tolerate low oxygen concentrations (Danielopol, 1976; Eder, 1983; Herzig *et al.*, 1987). In contrast, oxygen concentrations are high in well sorted and coarse sediments, situations commonly encountered in mountain streams such as the Seebach in Austria (Bretschko, 1991) and in the Flathead River, Montana (Stanford *et al.*, 1994), where the strong subsurface flow supplies well oxygenated water. In such situations, diverse assemblages of interstitial metazoans develop and groups common in well oxygenated surface waters may occur deep in alluvial sediments.

Dissolved oxygen concentrations within sediments are not uniform. For instance, areas close to surface running waters are usually well oxygenated, whereas concentrations decrease during the subsurface passage of water (Marmonier & Dole, 1986; Findlay *et al.*, 1993), mainly because of sediment respiration (Chapelle, 1993). Accordingly, the fauna consists largely of oxyphilous species in superficial sediments, whereas deeper sediments harbour species that are tolerant of low oxygen concentrations (Danielopol *et al.*, 1994; Plénet *et al.*, 1995).

Dissolved oxygen in many interstitial riparian habitats displays seasonal and/or diel fluctuations. For instance, the superficial riverbed sediments of Sycamore Creek have low oxygen concentrations during low summer discharge, when surface water no longer penetrates subsurface riparian habitats, whereas at other times of the year interstitial oxygen concentrations are high (Jones, 1995; Stanley & Boulton, 1995). The same thing occurs in the riparian zone of the Lobau wetland on the Danube (Mößlacher, 1994; Pospisil, 1994), where during the summer the dysaerobic conditions induce a sharp decline in metazoan diversity. Spatiotemporal patterns of redox gradients in sediments influence nutrient cycling and availability, thereby controlling energy flow through food webs.

Spatiotemporal dynamics

Appreciation of the interactive four-dimensional nature of lotic ecosystems has contributed to the development of stream ecology (Amoros *et al.*, 1987; Ward, 1989). Rivers and adjacent groundwaters interact along the vertical, lateral and longitudinal spatial dimensions and through time.

Space

Macroscale (longitudinal, lateral, vertical). At the catchment scale, from headwaters to the river mouth, interstitial communities change in composition and density over an extensive altitudinal gradient. Studies of the South Platte River, CO, U.S.A. (altitude 2000 m; 475 km long; Ward, Stanford & Voelz, 1994) and the Rhône River, France (2000 m and 500 km; Marmonier *et al.*, in press) yielded similar results: the longitudinal changes in the groundwater fauna reflecting local and regional geomorphic and hydrogeologic conditions that are to some extent decoupled from the altitudinal gradient. At the regional scale, the fluvial hydrosystem is composed of several alluvial sectors (see Fig. 6), each with its own physical characteristics and geomorphologic patterns, and each consisting of aquifers with distinctive hydrogeologic characteristics. According to the hyporheic corridor concept, however, similar patterns and processes occur sequentially along the river's course, resulting in a predictable zonation of the hyporheos (Stanford & Ward, 1993). Creuzé des Châtelliers (1991a), working on three distinct geomorphological sectors, demonstrated that the large scale heterogeneity of interstitial communities is linked to the regional environmental context of alluvial floodplain succession.

Migrating river channels create side arms and dead arms on floodplains, providing various contact zones between surface-and ground water. Along a cross-section through the Rhône River alluvial plain (Marmonier, Dole-Olivier & Creuzé des Châtelliers, 1992), as well as on the Kalispell Valley floodplain, Montana (Stanford, Ward & Ellis, 1994; Ward *et al.*, 1994) and in the Lobau Wetland in Vienna (Danielopol, 1984; Pospisil, 1994), distribution pat-

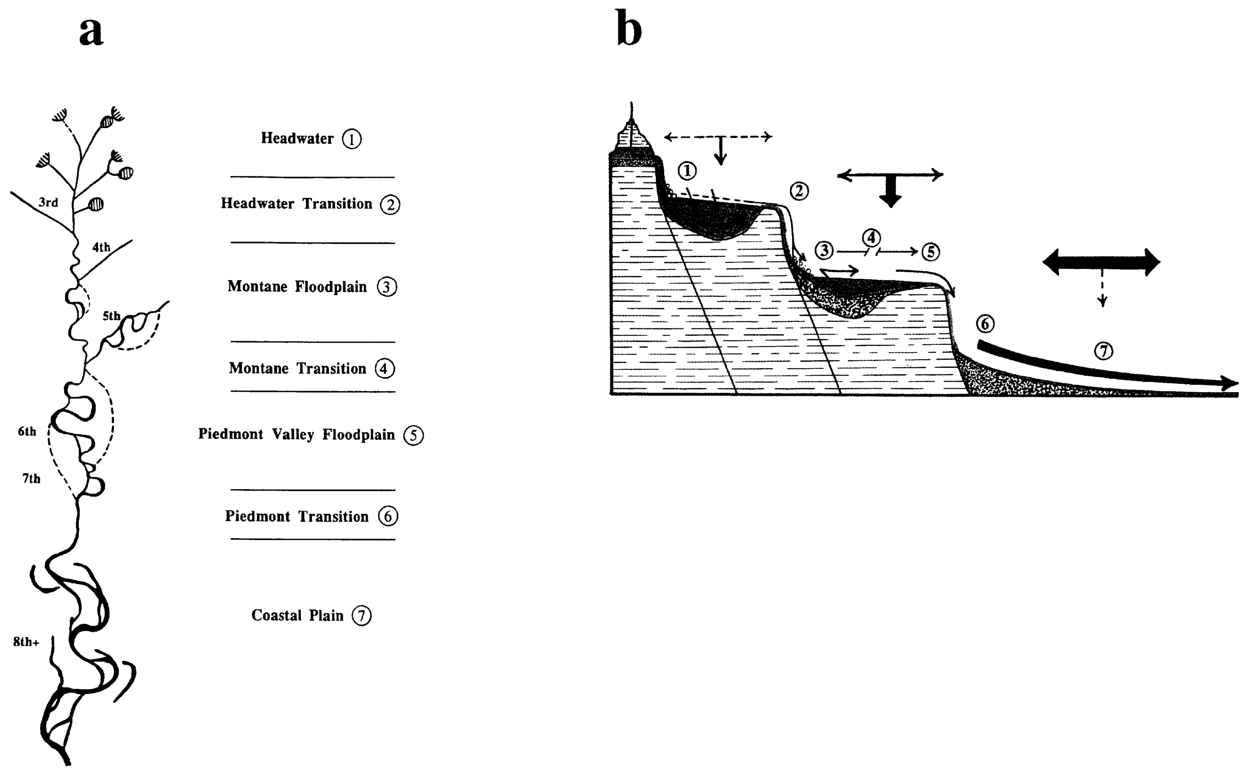

Fig. 6 A conceptual model illustrating the hyporheic corridor concept in plan view (a) and longitudinal vertical section (b). Strahler stream orders (3rd–8th) are shown in (a). Vectors above the floodplains in (b) represent the relative volume of annual overland (horizontal arrows) vs. interstitial flow (vertical arrows) at different locations along the longitudinal profile (from Stanford & Ward, 1993).

terns of the interstitial fauna were highly dynamic. For example, in the Rhône hypogean species such as *Fabaeformiscandona wegelini, Cryptocandona kieferi, Pseudocandona zschokkei* and *Niphargus rhenorhodanensis* were associated with the main channel, whilst *Troglochaetus beranecki, Niphargus renei* and *Microcharon reginae* were restricted to sites far from the main channel. In the hinterland of the Austrian wetland, the distribution of the fauna was less dependent on the circulation of the downwelling surface waters and the assemblage was dominated by stygobites (Mößlacher, 1994; Mößlacher *et al.*, 1996). Therefore, it appears that the lateral distribution of the interstitial dwelling fauna, at least in these examples, relates to geomorphic heterogeneity and hydrologic processes.

In a Rocky Mountain river, densities of interstitial animals increased markedly with depth (15, 30 and 50 cm) beneath the channel whereas, 2 m from the water's edge, density maxima occurred at 30 cm (Pennak & Ward, 1986). Densities 20 m from the water's edge were low and similar at all depths sampled. In a Rhône floodplain, Dole (1985) found marked differences in the vertical distribution (from 0.5 m to 3.0 m deep) of interstitial animals. Beneath the active channel, hypogean forms occurred deeper than at the floodplain margins, where the vertical zonation was not strictly defined. Dole-Olivier, Creuzé des Châtelliers & Marmonier (1993) observed repeated gradients in hypogean communities in the three spatial dimensions at the scale of the whole floodplain; laterally from abandoned channels to the main channel, vertically from deep to shallow sediments and longitudinally between areas of upwelling and downwelling. The temporal succession of organisms after a flood produced a similar gradient to that observed in space (Fig. 7). Such a repetition of the same gradient response pattern in four dimensions is exceptional and apparently reflects the response of hypogean species to environmental fluctuations, as addressed subsequently.

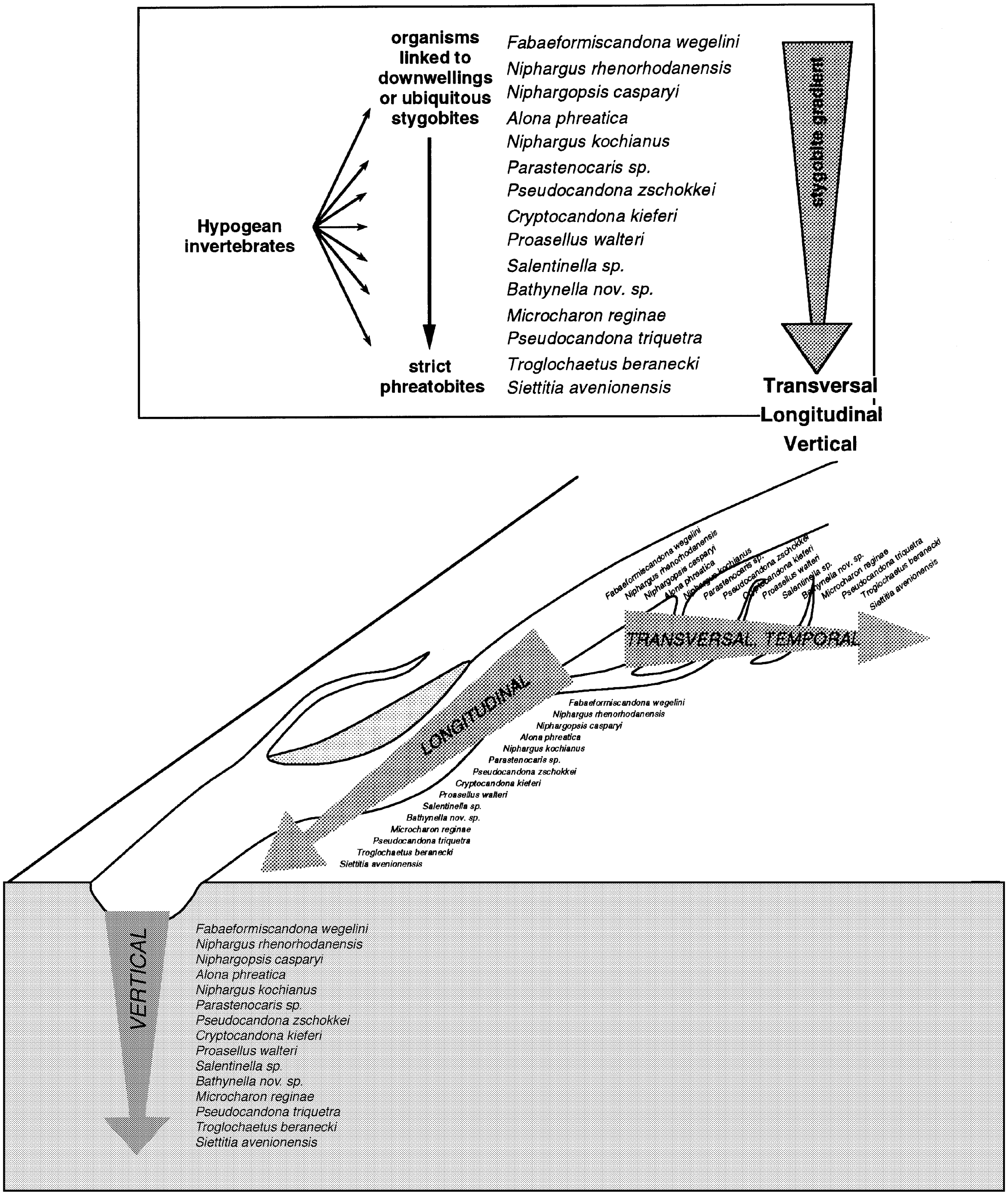

Fig. 7 The four-dimensional nature of the stygobite gradient on the Rhône River system. Stygobites are specialized subterranean (hypogean) forms, ranging from species widely distributed in various groundwater habitats (ubiquitous stygobites) to species restricted to phreatic ground water in alluvial aquifers (strict phreatobites). See Gibert *et al.* (1994) for detailed terminology. The stygobitic species shown here are ordinated according to their sensitivity to environmental fluctuations. All species are crustaceans, except *Troglochaetus beranecki* (Archiannelida) and *Siettitia avenionensis* (Coleoptera). This qualitative gradient was repeated in the three spatial dimensions, longitudinally in the main channel (several scales), transversally across the floodplain, and vertically through a depth of a few metres (from Dole-Olivier *et al.*, 1994).

Microscale-local patchiness. At the microscale, many investigations have emphasized the heterogeneous distribution of interstitial communities. Relationships between the origin and the circulation of the subsurface water within the sediments and the structure of interstitial invertebrate assemblages have been demonstrated (e.g. Godbout & Hynes, 1982; Hynes, 1983; Williams, 1984; Marmonier & Dole, 1986; Stanley & Boulton, 1993). A synthetic model was established for the River Rhône where the biological patchiness of these assemblages coincides with hydrological patchiness (Marmonier & Dole, 1986; 1991b; Creuzé des Châtelliers, 1991a; Dole-Olivier & Marmonier, 1992a,c; Dole-Olivier, Creuzé des Châtelliers & Marmonier, 1993; Plénet, Gibert & Marmonier, 1995). The model provides a simple qualitative prediction of the spatial distribution of invertebrates: in downwelling zones the interstitial community will be dominated by benthic organisms and in upwelling zones the community will be dominated by hypogean fauna. Moreover, the model defines the relationship between hydraulic conditions and hypogean invertebrates. For example, the isopod *Proasellus walteri* is not sensitive to water circulation patterns, whereas the amphipod *Niphargus rhenorhodanensis* is abundant in upwellings, regardless of depth, but rare in downwellings.

The hyporheic crustacean assemblage structure from 30 m^2 and 75 m^2 areas of Pyrenean brooks clearly documented the spatial heterogeneity linked to the subsurface flowpaths (Rouch, 1991, 1995). Kowarc (1990) noted that, at a microscale, patches of interstitial harpacticoid copepods were so dynamic that one could not perceive real patterns. Schmid (1991), who studied the chironomids within the same area, noted rapid vertical and horizontal movements over tens of cm, apparently in response to environmental disturbances, especially floods. At a somewhat larger, but still local, scale in a Rocky Mountain river, faunal densities progressively declined along a transect from hyporheic (underflow), to shore (2 m from channel), to phreatic (20 m from channel) habitats (Pennak & Ward, 1986). Each habitat had partially distinct interstitial communities. Similar distributions have been observed in the Sava River, Yugoslavia (Mestrov *et al.*, 1983; Rogulj *et al.*, 1994), a Canadian stream (Williams, 1989), a sandy Texan stream (Whitman & Clark, 1984) and a Sonoran Desert stream (Boulton, Valett & Fisher, 1992).

Temporal patterns

Multiannual. Few studies deal with long-term changes in interstitial habitats, though these must occur over the multiannual time scales at which floodplains and channels develop. While long-term natural changes in interstitial assemblages are poorly known, there are examples of long-term changes caused by human impacts. Herzog (1938) described a diverse interstitial fauna (more than twenty hypogean species) on a floodplain of the Rhine River. Now the metal-contaminated floodplain has only an impoverished fauna (Creuzé des Châtelliers *et al.*, 1992), in which epigean microcrustaceans are dominant, insects are rare, and strongly hypogean forms are absent.

Seasonal patterns. In an alluvial pond on the floodplain of the Adour River, France, Tabacchi (1992) reported passive and active movements by interstitial invertebrates in reponse to seasonal changes in water level. Some species passively followed the rise of water level, whereas others engaged in active movements to find refugia within the permanently inundated zone. Kowarc (1990), who studied the interstitial harpacticoid copepods of an Austrian mountain stream, noted that species like *Limnocamptus echinatus* displayed a strong peak in density during the spring and a weaker one during autumn. Schmid (1987, 1992) showed that, within the same stream, the first and second larval chironomid instars were most abundant during autumn. Some species (e.g. *Nilotanypus dubius*) were univoltine, with the fourth (prepupal) instars occurring during early summer, while other species (e.g. *Orthocladius rivulorum*) had two, overlapping annual generations. In an Austrian mountain stream, the first three instars of the chironomid *Orthocladius rivulorum* inhabitated the deeper sediment layers during autumn and winter, while the prepupae predominated in the surface sediment (Schmid, 1992). In a wetland of the Danube at Vienna, ostracods were most species rich during spring, when alluvial sediments were well oxygenated, whereas richness declined during summer and autumn when the subsurface water becomes hypoxic or even anoxic (Danielopol *et al.*, 1997).

Pulses and events. In stream sediment, the distribution of the fauna is linked to short-term perturbations such as spates (Hynes, 1983). The impact upon the hyporheic biota is complex (Marmonier, 1991;

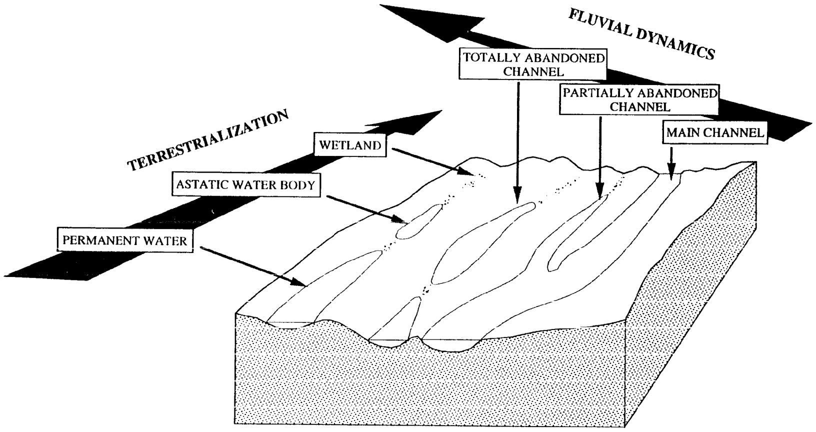

Fig. 8 Diagrammatic representation of the different aquatic habitats of the river channel in the floodplain, and the dynamic relation between flooding and encroachment of terrestrial conditions (from Dole-Olivier *et al.*, 1994).

Palmer, 1992; Dole-Olivier, Creuzé des Châtelliers & Marmonier, 1993; Boulton & Stanley, 1995) and appears not to be consistent at different sites. Marmonier & Creuzé des Châtelliers (1991) demonstrated that the effect of spates differs in downwelling and upwelling areas. In downwelling zones a spate displaced sediment and a wash-out effect was observed, reducing invertebrate density and diversity. The postspate period was characterized by a temporary enrichment of the interstitial habitat with epigean species (at 0.5 m depth). In zones fed by upwelling ground water (at low discharge), a trap effect was observed in the sediment during the spate. Here species richness was high immediately after the spate, with the sediment serving as a refuge for epigean invertebrates. About one month after the spate the interstitial fauna became impoverished, consisting only of hypogean forms.

Marmonier (1984) showed that disturbances in the Austrian Seebach, such as the deposition of new sediments on the old streambed, resulted in higher abundance and diversity of ostracods within the deeper layers. During a large spate on the Danube, Pospisil (1994) noted a 'flush' effect on the interstitial fauna, especially hypogean dwelling crustaceans like *Niphargus* sp., which were transported into the flooded wetland. The recovery of interstitial assemblages after floods can be very rapid (days to weeks in a Austrian mountain stream, Schmid-Araya, 1992; Schmid, 1993; or months in the case of the hypogean fauna of a Danube wetland, Danielopol *et al.*, 1992).

Moving through time and space

In the previous section we dealt separately with spatial and temporal dimensions. Spatial and temporal patterns are usually correlated, however, and in this section we consider space and time together.

On the spatial diversity and heterogeneity of interstitial habitats is superimposed a temporal pattern of disturbances of limited extent and duration. This results in a mosaic of patches, each having a particular faunal composition with peculiar origin and dynamics, size, shape, connectivity and age. This mosaic presents a higher physical and biological diversity than the underlying groundwater ecosystems.

Large scale spatiotemporal changes in interstitial fauna. Only a few studies have specifically examined long-term changes in interstital habitats at the scale of the floodplain. The major driving variables appear to be fluvial dynamics (which structures the physical habitat) and the process of terrestrialisation (hydrarch and riparian succession) (Fig. 8). Morphodynamics of the river causes the active channel to shift its position in the valley through transport and deposition processes; moving laterally, it abandons side arms and former meanders (Schumm, 1977; Bravard, Amoros & Pautou, 1986). A successional gradient is formed between the channel and the terrace. The dead arms closest to the active channel are connected with it and succession is controlled by allogenic factors (external, abiotic factors). Eventually, the dead arms are completely cut off and succession is controlled by

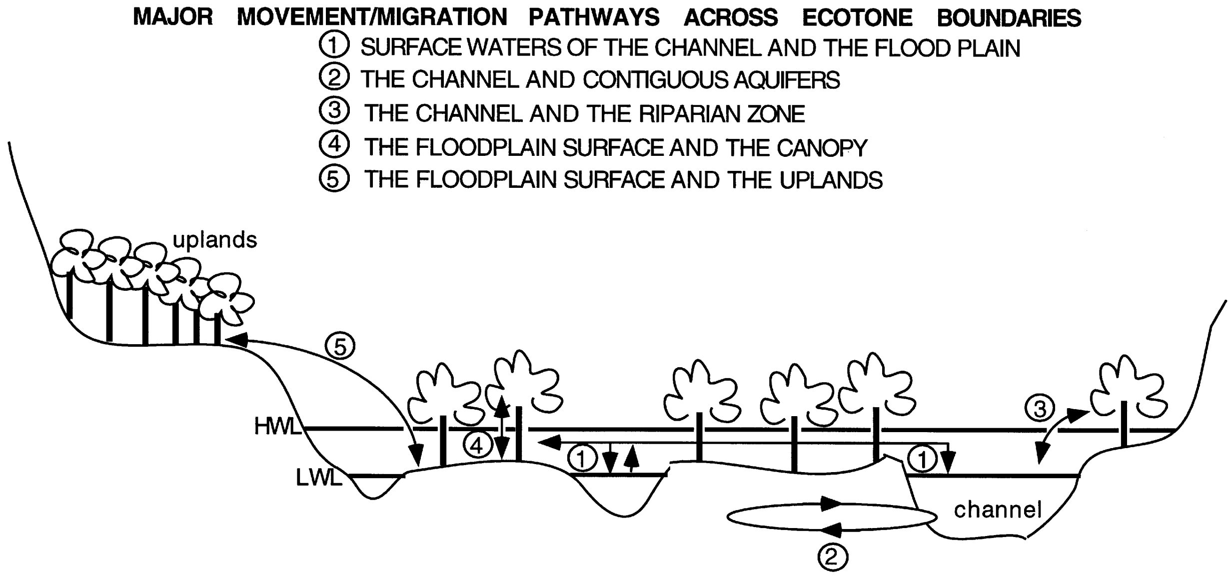

Fig. 9 Major movement/migration pathways across ecotone boundaries (see text). HWL and LWL refer to high and low water levels.

autogenic factors (internal, generally biotic factors). Aquatic communities are replaced by semiaquatic then terrestrial assemblages.

During the development of ecosystems at the surface, the water's connections with the underlying interstitial environment are also transformed. Succession of floodplain waterbodies may be illustrated by three stages: 'young' river segments that are part of the active channel network are characterized by rapid variations in discharge; 'intermediate' arms in the process of being abandoned that are connected to the channel only at the downstream end; and 'old' dead arms that are located outside of the zone that is regularly flooded (Dole & Chessel, 1986; Marmonier *et al.*, 1992; Dole-Olivier, Creuzé des Châtelliers & Marmonier, 1993; Dole-Olivier *et al.*, 1994). From the active channel to the old meander, the impact of floods decreases progressively and a gradient of physical stability linked to the hydrological regime of the river has been established (Fig. 4). The diversity of hypogean invertebrates and the percentage of hypogean species increased from the active channel to old meander. The 16 most abundant hypogean species were distributed along a transverse gradient across the floodplain, from those most tolerant to those most sensitive to hydrologic disturbance. For example, some species abundant in the main channel disappeared in the partially connected arm (e.g. *Fabaeformiscandona wegelini*, *Niphargus rhenorhodanensis*), while other, more strictly stygobite, species (*Troglochaetus beranecki, Niphargus renei, Microcharon reginae*) were restricted to places situated far from the present river channel. Some other ubiquitous and generalist species, such as *Niphargopsis casparyi,* were widely distributed across the floodplain. Moreover, the density and the biodiversity of interstitial assemblages were higher in the intermediate stage, fitting well with the intermediate disturbance hypothesis (Connell, 1978; Ward & Stanford, 1983).

In the alluvial floodplain of the Flathead River, Montana, Ward *et al.* (1994) showed that crustacean stygobites attained maximum relative abundance near the centre of the floodplain, whereas permanent hyporheos dominated near the river channel. They concluded that distribution and abundance are determined by hydrogeologic and geomorphic processes in the lattice-like alluvium. Subterranean palaeochannels constituted spatial discontinuities within the aquifer, producing a patchy distribution of the groundwater fauna.

Movements and migration. The active and passive displacement of aquatic and riparian species across ecotones is an important functional attribute of intact alluvial river systems (Junk *et al.*, 1989; Ward & Stanford, 1995), although few data are available for interstitial metazoans. Lateral migrations between the channel and the floodplain (pathway 1 in Fig. 9) are critical for flood-dependent fishes that exploit food and spawning sites on the inundated floodplain (Welcome, 1979; Goulding, 1980; Copp, 1989). Less is known regarding aquatic invertebrate movement/ migration between the channel and the floodplain. The best documented examples of active migration of aquatic invertebrates between the channel and floodplain are for mayflies (Ephemeroptera) in northern climes (Söderström, 1987; Gibbs & Siebenmann, 1996). During spring, nymphs migrate from the channel into floodplain habitats where the aquatic phase of the life cycle is completed. Such movements presumably avoid spate conditions in the channel during spring runoff and freezing or desiccation in the floodplain during autumn and winter. During the main period of nymphal growth in summer, predation pressure may be lower in floodplain waterbodies, whereas temperature and food availability are higher than in the channel. Experiments suggested that the nymphs use chemical cues to reach floodplain habitats, then use water temperature as the main cue for orientation (Söderström, 1988).

Little is known regarding subterranean migration between the channel and contiguous groundwater aquifers (pathway 2 in Fig. 9), though data from a grid of wells in the unconfined aquifer of the Flathead River, Montana, indicate its major importance in alluvial rivers (Stanford & Ward, 1988; Stanford *et al.*, 1994). Large numbers of stoneflies (Plecoptera) were collected from wells up to 2 km from the river channel. Unlike most stoneflies in the Flathead, the entire nymphal stage of several species occurs within the alluvial aquifer, mature nymphs returning to the river channel only to emerge, mate and oviposit. This new category of groundwater animals that reside in ground water as immatures but have a terrestrial adult stage, have been designated 'amphibites' (Gibert *et al.*, 1994). It is not known how the nymphs navigate in the subterranean realm, although they may follow thermal and/or chemical gradients.

A good deal is known of movements between the channel and the riparian zone (pathway 3 in Fig. 9), as discussed below in the section on 'whole river food webs'. Pathways 4 and 5 in Fig. 9 involve terrestrial species that actively migrate to other habitats during flooding. Other terrestrial forms have adaptations enabling them to remain *in situ*, such as plastron respiration or flood-resistant eggs (Adis, 1992). Some terrestrial animals, including species of Symphyla and Hymenoptera, migrate vertically, spending the flood phase in the alluvial forest canopy (pathway 4). Others move to the uplands during the flood phase (pathway 5), either by migrating horizontally ahead of the encroaching water (e.g. some species of Oligochaeta and staphylinid Coleoptera) or by flying (e.g. some species of carabid Coleoptera). Changes in edaphic and climatic conditions that precede floodplain inundation may initiate migratory behaviour (de Ribeiro & Adis, 1984).

Disturbance, patchiness and refugia. Recovery of lotic communities after disturbance is often very fast and this has been attributed to spatial and temporal heterogeneity in the habitat (Pickett & White, 1985; Turner, 1987; Hildrew & Giller, 1994; Hildrew, 1996; Palmer *et al.*, 1996; Lancaster & Belyea, 1997). Some habitat patches are less affected by disturbance and may act as 'refugia;' places or times where organisms have a greater chance of survival and from which they are subsequently available to recolonize the more severely affected areas. The spatial and temporal scales at which refugia may operate are best defined in terms of the generation time and individual life-range of the organism concerned (Hildrew & Giller, 1994; Lancaster & Belyea, 1997).

In ecological time, an important distinction is between mechanisms operating at scales greater or lesser than one generation time and/or one life-range, respectively. Lancaster & Belyea (1997) divide the former (more than one generation and/or one life range) into 'refugia through complex life cycles' and 'between-habitat refugia'. A common feature of both is that individuals may not survive the disturbance and persistence in any particular patch occurs through an external source of colonists. Many riverine organisms have complex life cycles involving movements between dissimilar habitats (e.g. floodplain pools and main channel) in the fluvial system (as in Fig. 9, see above). Absence of a fraction of individuals from a particular habitat type during disturbance therefore enables recolonization to take place subsequently. Some organisms persist by the long-storage of seed banks. This applies to aquatic macrophytes and has been proposed for stoneflies (Zwick, 1996). Alternatively, the population may be distributed among a number of habitat 'patches' of the same type, as in the several tributaries of a river. If these patches are disturbed differentially, survival occurs in the less disturbed examples only and these individuals are available to recolonize (between-habitat refugia).

At smaller ecological scales (less than one generation and/or one life range) there are mechanisms of refugium use that do depend on survival of individuals within a particular habitat patch. A good deal of empirical attention has been given to them and they involve changes in 'habitude' or the use of within-habitat refugia (Lancaster & Belyea, 1997). In 'changes in habitude' individuals survive in a habitat patch by a variety of mechanisms including dormancy or diapause, or by ontogenetic shifts in microhabitat use (as observed in the vertical distribution of larval chironomids in bed sediments, for example: Schmid, 1993). The use of within-habitat refugia is distinguished by the short-term exploitation, in response to a particular disturbance event, of the small-scale heterogeneity accessible to a single individual in its lifetime. Of course the spatial and time scales, defined by generation time and life range, that conceptually separate the various mechanisms of refugium use are less clear when we try to translate them into real spatiotemporal elements of the habitat of different organisms. Relatively large habitat features would constitute small scale patchiness for large, mobile and long-lived organisms, such as fish or birds, but not for short-lived, small organisms (Hildrew, 1996). Having outlined the very different concepts embedded in the inclusive term 'refugia,' we now turn to their application in the particular context of lotic communities and their groundwater and riparian boundaries.

At the small ecological scale of less than one generation time or life range, refugia may involve changes in habitude (see above). For some organisms interstitial habitats are occupied during part of their lives or by resistant stages. For example, the eggs of salmonid fishes develop within porous sediment. After hatching, fry disperse in the nursery habitat and the light gradient must be an important cue for vertical migration (Bardonnet & Gaudin, 1990). Salmonid juveniles can also take refuge in superficial interstitial habitats during low water periods. After return of high flow conditions, fish may move back to the riffles (Debowski & Beall, 1995). For some insects (Ephemeroptera, Trichoptera, Plecoptera, Coleoptera, Diptera) eggs may hatch and larvae reside in the hyporheic zone during their early development, while later life stages predominate in the benthos ('occasional hyporheos' Gray & Fisher, 1981; Williams, 1984; Pugsley & Hynes, 1985, 1986). While in the sediment, these stages are protected against the environmental variations characteristic of surface waters (e.g. high discharge, desiccation, extreme temperature, predators, etc.). For other insects the interstitial stage is predominant, with epigean life being restricted to emergence and an aerial adult stage (Berthelemy, 1968; Stanford & Ward, 1988).

In streams and rivers the most obvious sources of disturbance are fluctuations in flow (pulse disturbance in the form of spates and press disturbance such as drying; Boulton & Stanley, 1995). Spates, being short-term events, may occur unpredictably, modify the hydraulic characteristics of habitat patches differentially and cause high mortality for stream benthos (Resh *et al.*, 1988; Lancaster & Hildrew, 1993). Epigean organisms are trapped in sediment or migrate deeper, accumulate and/or survive differentially in debris, marginal and subsurface habitat patches, and then subsequently recolonize the entire habitat when conditions are more favourable (Power & Stewart, 1987; Sedell *et al.*, 1990). Refugia are available in natural stream channels in the form of flow dead zones and patches where hydraulic stress remains low even at peak flow (Lancaster & Hildrew, 1993). In a study of stream-dwelling microcrustaceans, Robertson, Lancaster & Hildrew (1995) showed that stream reaches that maintained low shear stress served as a refugium for surface-dwelling species of ostracods, cyclopoid copepods and cladocerans. For most meiofauna, however, more attention has been paid to the hypothesis that the hyporheic zone is a refugium.

In interstitial habitats, the 'hyporheic refuge hypothesis' has proved difficult to test. Along the Rhône River, Marmonier & Creuzé des Châtelliers (1991) showed that downwelling zones (upstream of gravel bars), receive a regular input of benthic animals during low discharge, but may contribute fauna to the stream during spates. In contrast, upwelling zones (downstream of gravel bar) may act as a refugium during spates. A strong relationship was demonstrated between spate intensity (amplitude and duration) and changes in the vertical distribution of fauna down to 2 m depth (Marmonier & Dole, 1986; Dole-Olivier & Marmonier, 1992b). Both hypogean and epigean organisms moved downwards during spates, resulting in an increase in the number of epigean organisms in interstitial layers just after spates. Post-spate recovery of interstitial fauna and their vertical distribution patterns consisted of a decrease of epigean and an increase of hypogean fauna in alluvia. Schmid-Araya (1995) showed that the density of a rotifer inhabiting superficial sediments of a mountain brook, *Proales theodora*, changed drastically after a flood (i.e. the density of surface animals decreased while that of interstitial populations at 10–30 cm depth increased). In contrast, in a sandy stream over a very shallow, poorly developed aquifer (about 50 cm depth), Palmer, Bely & Berg (1992) demonstrated that the hyporheic zone did not serve as a large source of meiofaunal colonists after disturbance. Even though small scale (cm) migrations of some copepods and chironomids into the streambed sediment were observed, downward movements were not adequate to prevent losses of meiofauna during spates. Subsequently, Palmer *et al*. (1995) and Schmid-Araya (1995) proposed that the utility of refugia to stream invertebrates is apparently quite species specific and the relationship between patch structure in streams and the impact of disturbance on fauna is complex.

The role of sediment as refugia during drying of the surface sediments was discussed by Gagneur & Chaoui-Boudghane (1991) and Boulton & Stanley (1995). They showed that animals survive in large number in the moist or saturated river bed sediments.

Refugia and evolution. Some have argued that the evolutionary origins of hypogean fauna involve the long-term use of refugia. In the 'refugium under constraints' model (Vandel, 1964; Botosaneanu & Holsinger, 1991) species escaped from unfavourable surface environmental conditions associated with climatic change (glaciation, regression, etc.). The 'active colonization' model (Rouch & Danielopol, 1987), however, focuses on the extension of species into new habitats, accompanied by changes in their ecological tolerance. It stresses the role of the steady periods that permit widespread species, or those in some way preadaped to hypogean life, to settle actively in the subterranean world. Boutin & Coineau (1990) propose a third alternative, incorporating some features of the first two, to explain the evolutionary invasion of inland interstitial waters by marine epigean animals. The first part of their 'two-step model' involves active colonization, and adaptation to, a marine interstitial environment (usually the sandy shore). The second part is an obligatory evolutionary adjustment to freshwater during periods of marine regression, involving a gradual 'freshening' of their environment. Hence, the zoogeography of groundwater biota involves the entire aquatic biosphere and the distribution of stygobites is a shifting mosaic of communities through the geological ages (Ward & Palmer, 1994). Hyporheic zones contribute to the persistence of the species involved over evolutionary time. This idea is well expressed by Boulton & Stanley (1995; p. 46), who noted that the deeper layers of riverbed sediments in subtropical areas form an 'environment (which) probably persisted as a stable refuge for millennia while major climate changes (e.g. increasing aridity) took place.'

Spatiotemporal theories and interstitial communities

In this section we develop the idea of interstitial habitats as spatiotemporally dynamic, with important environmental gradients along the three spatial dimensions and through time. Further, there is a nested hierarchy of physical variation at different scales along each of these dimensions. It is appropriate therefore to explore the possible consequences of this spatio-temporal complexity for the regulation of interstitial populations and the structuring of interstitial communities.

Speculatively, we can envisage assemblages of organisms inhabiting fluvial systems in a spatio-temporal 'paper chase' continually tracking suitable conditions whose distribution is driven by the dynamics of the river. There has been a great deal of recent interest in the possible role of spatial effects in ecology in general (Kareiva, 1994; Wu & Levin, 1994) and, particularly, how local instability and stochasticity in a patchy system with out-of-phase dynamics can produce regulation and stabilizing density-dependence at some larger scale. Our knowledge of the dynamics of the interstitial faunal is still rudimentary, yet consideration and subsequent tests of theoretical possibilities can guide new research.

Spatiotemporal theories in population and community ecology can conveniently be considered in relation to the generation time and life-time range of the organisms concerned (Hildrew & Giller, 1994; Hildrew, 1996). In this review we stress the obvious physical heterogeneity of groundwater and riparian habitats, although we have no clear view for most invertebrates of how heterogeneity is perceived at the scale of the organisms themselves (but see Hart *et al.*, 1996; for an exception to this for larval black flies). Nevertheless, the patchy distributions of interstitial organisms at spatial and temporal scales that have been measured suggests that we have identified parameters of ecological significance.

Landscape ecology is concerned with a mosaic of habitat patches at a spatial scale which lies mainly between the home range of an individual and the regional distribution of the species (Dunning *et al.*, 1992). This scale of patchiness impinges on the dynamics and distribution of species because, for example, patch quality varies such that some act as 'sources' and some as 'sinks' to the wider regional population. The total area, in addition to the distribution, shape and size of the individual patches, affect the organisms living there. Application of these ideas to the interstitial organisms of river floodplains seems obvious (see, for example, the differing habitat characteristics of various floodplain habitats depicted in Fig. 8 and the sequence of species inhabiting them). Each of these habitat patches has a 'lifetime' beyond that of the invertebrates living there and many individuals live out their lives in a single patch.

Metapopulation dynamics is an explicit model in which a regional population (a 'metapopulation') is fragmented into a series of local subpopulations which are occasionally linked by dispersal events (Hanski & Gilpin, 1997). Only a fraction of suitable habitat patches is used at any one instant. Regional persistence ('regulation') is possible in the face of local stochasticity and extinction because the intergenerational population dynamics in the different patches is 'out of phase.' Physical habitat patchiness may provide the basis for population fragmentation but this latter may also be achieved intrinsically, even in a uniform environment, by biological features such as limitation to the dispersal of progeny (see Tilman, 1994). Tilman's model seems potentially applicable to the slowly dispersing species of the groundwater (Strayer, 1994). In general, models incorporating large-scale (in relation to the individual organism) habitat fragmentation are important because they could explain species coexistence, without the need for local, stabilizing resource partitioning among potential competitors.

Whereas in metapopulation theory local populations may be scattered among habitat fragments, individuals *within* these local populations live in a theoretically uniform world. Other models of species coexistence, however, refer to patchiness at smaller spatial and temporal scales. These include the aggregation model (Atkinson & Shorrocks, 1981; Shorrocks & Rosewell, 1987; Ives, 1991; Sevenster, 1996) which refers to the independent aggregation of species within patches inhabitated for a single generation, at the end of which disperal occurs and populations are redistributed among a new set of patches. The model has been applied mainly to species using ephemeral and divided resources, such as dung, carrion and fallen fruit. Coexistence of species, which may be unlikely in a single patch, depends on the existence of refugia for the less competitive in the form of undiscovered patches. Again, one can see potential application for such a model in the small scale patchiness of interstitial habitats, and in which bouts of reproduction by potential competitiors could take place in neighbouring patches. Crucial here would be the microscale patchiness, for instance in the organic content of sediment, mentioned above.

The aggregation model, however, assumes that once the dispersion of individuals across the habitat patches is established in any generation then further dispersal does not occur. Tokeshi's (1994) stochastic patch dynamics model, on the other hand, envisages repeated bouts of dispersal, perhaps driven by abiotic events, during a single generation. This would produce stochastically a range of dispersion patterns from random to aggregated across the habitat patches. Aggregation would contribute to the coexistence of potential competitors but competition is in any case weak because repeated dispersal involves high density-independent mortality due to the risks of not finding a suitable patch. This model has been applied to chironomids of a gravel bed river with a prominent hyporheos (Schmid, 1992, 1993). Within the interstitial habitat, the zoobenthic community forms patches moving through the gravel sediments (Bretschko & Klemens, 1986; Panek, 1991a,b). Stochastic models therefore might successfully be applied to interstitial, epigean organisms subject to flow disturbances, and where competition may be weak. We might speculate that these kinds of mechanisms would be most prominent in the communities of superficial sediments. The theoretical possibility that spatiotemporal heterogeneity, so prominent in the environment, is crucial for interstitial communities through one or more of the mechanisms outlined above is thus alluring though unproven.

All these models are of interest because they suggest means to promote local species coexistence and high diversity in interstitial faunas. The overall biodiversity of interstitial faunas, including epigean and hypogean elements, is still a matter of controversy (Marmonier *et al.*, 1997), although there are grounds to expect it to be high indeed. These grounds are both at the level of evolutionary history and in contemporary ecological time. Many of the forms in groundwater are very ancient, dispersal is slow and there is a high degree of local endemism with marked regional 'hot-spots' (see Strayer, 1994). Ancient coastlines (where presumably marine forms invaded groundwater) are still visible by the endemic species found there, and the extent of ice during previous glaciations is marked by groundwater species. There is even evidence that some species could have persisted in groundwater beneath the ice at such times (Holsinger *et al.*, 1983).

Ecological features theoretically promoting high diversity have already been touched on. Productivity is often very low and species have long life cycles and few progeny, lessening the chances of competitive exclusion. There is a range of disturbance intensities across alluvial systems, and diversity may be high at points of intermediate disturbance. The interstitial milieu is a labyrinthine, finely divided habitat in which species exclusion by competition or predation is difficult yet in which speciation during spatial isolation is promoted. Uncovering the true biodiversity of groundwaters is an exciting challenge.

Metazoans in ecosystems

Organic matter

Organic matter provides the energy that drives nutrient cycles within ecosystems. Depending on the different mineralization rates of organic compounds and various transport mechanisms, production and processing sites differ in space and time. This separation is most conspicous in running water systems, where instream autotrophic production is generally less than the energy demand of the consumer community (Fisher & Likens, 1973; Minshall *et al.*, 1985). The 'River Continuum Concept' is in large part based on this dependence on allochthonous sources of organic matter (Vannote *et al.*, 1980). Throughfall or aerial drift account for 90% and bank run off for only about 10% of total annual imports of organic matter from the lateral riparian vegetation in low order streams. Coarse particulate organic matter (CPOM) is more abundant than fine (FPOM), and C/N ratios are generally lower in organic matter from bank runoff than direct inputs because of prior processing on the soil surface (Gessner, 1987; Moser, 1991, 1992; Dudgeon & Bretschko, 1996; Fig. 10). The streamwater distributes the imported organic matter in the channel (Bretschko, 1990). The food quality, indicated by C/N ratios, is generally poor, especially in CPOM, although leaching losses from freshly fallen leaves may not be as fast as previously thought (Gessner & Schwoerbel, 1989; Gessner, 1991). With increasing stream size the importance of lateral, above ground import pathways decreases in terms of $g\,cm^{-2}\,year^{-1}$ (Conners & Naiman, 1984; Weigelhofer & Waringer, 1994). Organic Carbon dissolved in rainwater amounts to about $2.5\,mg\,C\,L^{-1}$ (Meybeck, 1982); nevertheless, organic imports in rain water directly to streams are negligible, because of the restricted channel areas.

The most important above ground pathway, according to the River Continuum Concept, is the longitudinal one in medium to high order streams (carbon spiralling, Fig. 10). By far the most organic matter is transported in its dissolved state (DOM), followed by FPOM and CPOM. The concentration differences between dissolved and particulate forms are one to two orders of magnitude (Dudgeon & Bretschko, 1996). In spite of the dominance of DOM, large amounts of POM are transported downstream (Richardson, 1992), although most of it may become more or less refractory during transport. In unconstrained streams with floodplains the stream community relies on the production of the floodplain vegetation (both terrestrial and aquatic) according to the 'flood pulse concept' (Junk *et al.*, 1989). Also, the revised version of the 'serial discontinuity concept' (Ward & Stanford, 1995) stresses the importance of floodplains in the total functioning of river ecosystems.

The retention capacity of a river section is responsible for the proportion of the imported organic matter that is processed in the section. The most efficient above ground retention structures are debris dams,

Fig. 10 Organic Matter dynamics: 1, Throughfall or aerial drift. 2, Bank run-off. 3, Subsurface imports via soilwater percolating into the hyporheic zone. 4, Organic matter transfer from the channel surface into the hyporheic zone. 5, Debris dam, retaining organic matter of any kind. 6, Downstream spiralling of organic matter. 7, Exchange processes between the hyporheic zone and groundwater. The topmost layer of the hyporheic zone is dominated by stream water and stream fauna is therefore a part of the stream system. Insert: main energy pathways.

bank structures of various kinds and the periodically dry channel areas below the bankfull line (Bilby, 1981; Bretschko, 1990; Fig. 10). Of course, floodplains retain large amounts of organic matter over different periods of time (Smock, 1990). Biofilms, covering the surfaces of sediment grains, constitute a large proportion of the organic matter in the stream (Leichtfried, 1991, 1995) and immobilise large quantities of DOC (Findlay *et al.*, 1993). Most probably, biofilms provide the major food source for the hyporheic zone, mainly near the surface, where there are dense populations of epigean species (Bärlocher & Murdoch, 1989; Decho & Moriarty, 1990). Respired organic matter is replenished by imports with downwelling stream water, upwelling groundwater (Ford & Naiman, 1989; Fiebig & Lock, 1991) and laterally infiltrating soilwater (Fiebig *et al.*, 1990; Bishop *et al.*, 1994). Soil water is not only of quantitative but also of great qualitative importance, because it brings more or less preprocessed material directly to the biofilms of the hyporheic zone (Fig. 10).

Feeding

Cummins (1973) proposed using morpho-behavioural mechanisms of food acquisition to group aquatic invertebrates into functional feeding groups: shredders, scrapers, collectors and predators. Cummins & Klug (1979) recognized that some species are confined to a single functional feeding group (obligate feeders), whereas others (facultative feeders) are generalists that, while able to utilize a wide variety of food resources, are less efficient in harvesting a particular food type. Despite the major focus by lotic ecologists on the food and feeding of stream animals, few data are available that specifically deal with the trophic ecology of the interstitial fauna, especially true groundwater forms. Organic matter with a high content of proteins and carbohydrates, as occurs in fresh leaves, may be available in large quantities only in surficial sediments (Maridet *et al.*, 1996). Living algae are also confined to the upper sediment layers. Groundwater dwelling isopods, which live in habitats with low food quality and patchy food resources, invest more time in exploratory activities than in food acquisition (Danielopol *et al.*, 1994; Mößlacher & Creuzé des Châtelliers, 1996). Many groundwater animals from deep alluvial sediments collect food by ingesting fine sediment, bacteria and FPOM and by scraping detrital surfaces, thereby functioning both as browsers and deposit feeders (Danielopol, 1983, 1989; *unpublished*). The biofilm, consisting of bacteria, exopolymers and fungi that coat sediment surfaces, is eaten by copepods (O'Doherty, 1985; Decho & Moriarty, 1990; Perlmutter & Meyer, 1991), ostracods (Roca & Danielopol, 1991) and rotifers (Schmid-Araya & Schmid, 1995b). Biofilm probably constitutes the major food base for interstitial animals though many interstitial animals, including certain rotifers and nematodes, are predators (Schmid-Araya & Schmid, 1995b).

Metazoans and system linkages

Hydrological and biologic vectors. A stream ecosystem may be considered to consist of four 'building blocks', the channel and the floodplain each being divided vertically into above and below ground sections. The relative importance of these four building blocks is highly variable in various systems, and indeed one or two may be missing altogether, as are floodplains in constrained reaches.

At mean discharge and below, only parts of river channels contain flowing water and some areas of the sediment surface are dry. At low discharge, the wetted channel is confined to the 'Thalweg.' The aquatic fauna is not restricted to the wetted channel areas, however, and they continue to live in the water-filled, and even moist, interstices below the dry sediment surface, especially if there is sufficient oxygen and even slight current. In the strongly regulated Austrian Danube, gravel banks are stabilized by groynes and suitable conditions for lotic fauna beneath dry areas are restricted to a few small and topographically defined locations (G. Bretschko, unpublished data). The flow of water through the sediment governs the distribution of epigean animals because it is the link to the surface (the source of oxygen) and to organic matter (the energy source of the sediment community) (Fig. 5). The intensity and distribution of downwelling and upwelling depends on the hydraulic conductivity of the sediment and on the hydraulic head (Stanford *et al.*, 1996; Huggenberger *et al.*, 1998).

Organic matter is transported into the hyporheic zone in both its dissolved (Findlay *et al.*, 1993; Jones *et al.*, 1995) and particulate forms, although the latter is less often studied. Moser (1992) measured the POM imports into the sediments of the Austrian mountain brook using tube traps (diameter: 25 mm, length 200 mm). He found an average import of nearly 2 g TOC $\text{day}^{-1}\,\text{m}^{-2}$, which is about six times the channel imports (throughfall and bank runoff). This discrepancy is explained by the fact that POM is frequently washed in and out of the hyporheal in a gravel stream, as is DOM. This explanation is supported by the C/N ratio of the trapped material, which is much lower than the C/N ratio of the channel imports.

Transport of organic matter increases with increasing discharge. Some is washed downstream and lost from the site under consideration and part is redistributed, horizontally as well as vertically. The downstream losses depend on the retention capacity, and hyporheic biofilms become progressively more important as retention structures with increasing discharge. When discharge exceeds the capacity of the channel, organic matter is exported, as well as imported, laterally over the bankfull line. Drifting POM and terrestrial insects increased exponentially as bankfull discharge was exceeded (Tockner, 1990).

Precipitation that has passed through the soil to the ground water and, finally, upwells through the hyporheic zone may play an important role that has only recently been recognized (see Squillace, 1996; Dahm *et al.*, 1998). Dissolved organic matter is imported via this pathway and is brought into direct contact with the hyporheic biofilm, some being retained and available to animal consumers (Pusch *et al.*, 1998; Schmid-Araya, 1994, 1995).

Imports and exports of organic matter by 'biological vectors' occur via surface and subsurface pathways as described above (Fig. 9 and associated text). The spatial extent of subterranean migration between the channel and contiguous aquifer is largely dependent on sediment characteristics and exchange properties.

Generally, hydraulic conductivity is low in soils and sediments outside the main channel, limiting the distribution of lotic species to within a few metres of the channel margins (Schwoerbel, 1961a; Bretschko, 1981; Harvey & Bencala, 1993). More extended distributions of lotic and hyporheic species occur in young floodplains with a lattice work of alluvial-filled palaeochannels of high hydraulic conductivity (Stanford & Ward, 1988; Stanford *et al.*, 1994). Studies of organic drift have focused on the downstream transport of organisms in surface waters (Brittain & Eikeland, 1988) and compensatory upstream movements, especially by the winged adult stage of aquatic insects (Müller, 1982). More studies on the drift of interstitial animals in surface and subsurface waters and their active movements within the sediment (e.g. Panek, 1991a,b; Palmer, 1992) are needed.

Depletion of interstitial animals. Little attention has been paid to the fate of metazoans lost from the hyporheic zone. Losses at groundwater upwelling zones could have major ecological importance over a broad spectrum of functions and spatial scales (Brunke & Gonser, 1997). However, during low water the drift of hyporheic fauna is probably minor. In a dead-arm of the Rhône River, hand-net samples and artificial substrata were collected from a fluvial spring, consisting of a large funnel 2 m deep and 7 m in diameter in the middle of the channel (Plénet, Marmonier & Gibert, 1995). The hypogean fauna constituted 83% of the total fauna 1.5 m beneath the bed, 70% at 1 m, 70% at 0.5 m, 21% at 0.2 m, 5% at the physical boundary of the spring and 0% in the channel itself. Upwellings such as fluvial springs (aquifer-fed streams) seem to limit the net loss of metazoans by low biological permeability at the groundwater/surface water ecotone.

During high water following major floods in a sand bottomed stream, Palmer (1990a) observed a marked decline in hyporheic meiofaunal abundance, with losses primarily from the top sediment layer creating a peak in the downstream drift of meiofauna. Marmonier (1988) and Marmonier & Creuzé des Châtelliers (1991) demonstrated that the numerial abundance and the number of species were strongly reduced in downwelling zones during spates. Upwellings were subjected to the infiltration of surface water during spates (a reversal of the usual piezometric gradient) and suffered an impoverishment of interstitial fauna immediately after the spate. The surface/interstitial ecotones of streams are very difficult to study, however, due to the mobility of stream bed forms on the scale of flood events, altered patch composition of the hyporheos and the reduced river-aquifer exchanges by sedimentation (Marmonier, 1991). Moreover, the dewatering of saturated banks after floods can cause substantial bank erosion and increase the hyporheos drift.

Another metazoan loss is due to the incision of streams (lowering of the bed surface) and the loss by erosion of the upper layer of sediments. In the European Alps, for example, the compound effects of various human activities have produced a general narrowing and incision that may lower the bed 10–15 m in extreme cases (Bravard *et al.*, *unpublished*). Incision leads to increased drainage and lowering of the piezometric levels throughout the alluvial plain. Former channels gradually dry up, and the hydraulic connection between surface and groundwater disappears. If the hydraulic connection is disrupted, there is impoverishment of the interface zone and its biological role in preserving the quality of the water is impaired (Marmonier *et al.*, 1992).

We need to know much more, especially quantitatively, about the loss of metazoans from the hyporheic zone. The goal in this research should be to enhance our general understanding of the 'elasticity' of the ecotone (*sensu* Gibert *et al.*, 1990), the limits of hyporheic zone resistance and resilience, and to learn how specific types of disturbance alter the system and affect its capacity for recovery.

Whole-river food webs. The depiction and conceptualisation of trophic interactions in an ecological community as a 'food web' is a familiar idea, yet the meaning of food webs remains elusive and their practical study is among the most problematic challenges in ecology (Hildrew, 1992; Polis & Winemiller, 1996). Surveys of published food webs have revealed consistent patterns and generated considerable debate among community ecologists because they might reveal the decisive forces shaping natural communities (e.g. Lawton, 1989; Sugihara *et al.*, 1989).

Two particular challenges arise in the study of 'whole river' food webs. The first is the problem of taxonomic resolution. Paine (1996) exhorts us 'not to exclude the taxonomically awkward meiofaunal organisms, picoplankton, fungi and other decomposers and their little known interactions.' Yet such organisms have been largely ignored in food webs and, since most energy passes through small rather than large organisms (e.g. Perlmutter & Meyer, 1991), we might be studying food web 'patterns' by looking at organisms that, in terms of carbon and nutrients, are insignificant.

From the metazoan perspective we should note that startlingly high biodiversity has recently been revealed in the benthos and interstitial sediments of some stony rivers and streams. More than a thousand species of metazoans have been identified from the Breitenbach, a small stream in central Germany (Zwick, 1992) and Schmid-Araya & Schmid (1995a) reported 569 animal species from just 100 m of the Oberer Seebach, a gravel stream in Austria. Many of the species in Oberer Seebach are meiofaunal groups (animals not large enough to be macroinvertebrates or small enough to be microorganisms) almost never included in food web studies of streams and rivers, including 101 species of rotifers, thirty-four microcrustaceans, forty-five nematodes, plus a variety of groups not fully assessed. Gut content analysis of small predators in the Oberer Seebach revealed rotifers to be the dominant prey of early instar stoneflies and tanypod chironomids, as well as less well known meiofaunal predators such as microturbellarians and nematodes (Schmid-Araya & Schmid, 1995b). It seems premature to talk of food web patterns in streams and rivers until such links have been explored more fully.

A second challenge to the analysis of whole river food webs arises form the spatio-temporal heterogeneity of river systems, including their floodplains and riparian zones plus superficial and subsurface interstitial habitats. The history of fluvial ecology has largely been marked by the gradual appreciation of the openess and temporal dynamism of lotic systems (Hynes, 1975, 1983; Junk *et al.*, 1989; Ward, 1989a). Lotic food webs are truly embedded in those of the landscape and groundwater around them, at least partly through the movement and migrations across habitat boundaries depicted in Fig. 9.

Winemiller (1996) has recently considered temporal and spatial variation in food webs on freshwater floodplains, including aquatic terrestrial linkages. There has been less attention paid, however, to vertical linkages between benthic and subsurface systems. Here, the problems of taxonomic resolution of 'small' metazoa and the spatial heterogeneity of river systems are linked, since small-bodied, poorly studied forms are progressively more important as we move down from the sediment surface. Food web linkages between the benthos, hyporheos and groundwater faunas, moreover, are driven by hydraulic exchange and partly by vertical movements of temporarily interstitial forms, such as some insects, during their larval lives.

We present a conceptual model of the connections of stream food webs with groundwater and riparian systems in Fig. 11 and of the feeding linkages of the superficial benthos along vertical and lateral spatial dimensions in Fig. 12. River ecosystems are characterised by external linkages and by subsidies of allochthonous detritus (and are thus generally 'donor-controlled, i.e. the ultimate consumers do not effect the renewal rate of the resource) and by movements and migrations of prey and predators (see Polis *et al.*, 1996). Some quantitative data are available for movements between the channel and the riparian zone.

In streams with well-developed riparian canopies, large numbers of terrestrial arthropods fall into the water and can constitute up to 90% of the summer food of salmonid fishes (Hunt, 1975). During summer, terrestrial invertebrates contributed from 11 to 36 $g\,m^{-2}$ dry weight to a British trout stream (Mason & Macdonald, 1982). The input of terrestrial invertebrate biomass beneath sycamore (*Acer pseudoplatanus*) trees was more than three times greater than beneath ash (*Fraxinus excelsior*), indicating the importance of riparian community structure. The most abundant taxa were three insect orders (Coleoptera, Diptera and Homoptera) and arachnids. Biomass is also transferred to the riparian zone as aquatic insects emerge from the stream. The adults of aquatic insects may, at times, constitute appreciable portions of total arthropods in streamside vegetation. Based on a study of a Californian stream, Jackson & Resh (1989) concluded that terrestrial adults of aquatic species play an important role in transporting energy and nutrients from aquatic to riparian systems. The contribution of adult aquatic insects to total arthropod biomass decreased with distance from the channel, but was still 11% 150 m from the stream. Most published estimates of total emergence range between 3 and 7 $g\,m^{-2}\,year^{-1}$ dry mass, with highest values exceeding

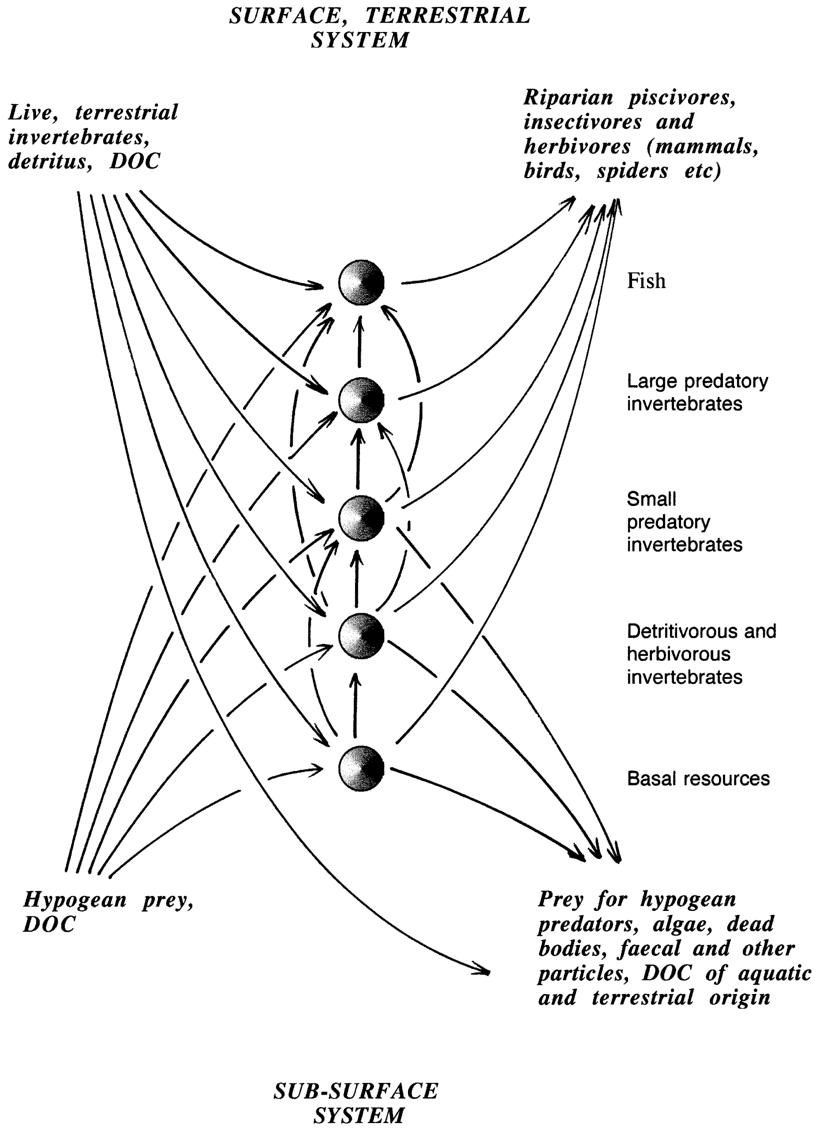

Fig. 11 A summary of the external linkages between a stream benthic food web and its neighboring terrestrial and subsurface (interstitial) sytems. At the centre of the figure is a simplified food web for the surface benthos, consisiting of five elements (shown by circles): fish, large and small predatory invertebrates, herbivorous/detritivorous invertebrates and basal resources (algae, detritus, macrophytes). Trophic linkages within this web (arrows passing between circles) indicate extensive omnivory (species feeding at more then one level: see Hildrew, 1992). Energy subsidies to the web (from the surface terrestrial system and from hypogean sources) are shown via linkages denoted by arrows from the left, while exported energy is shown by arrows to the right.

$20\,g\,m^{-2}\,year^{-1}$ (Jackson & Fisher, 1986). In a desert stream with an open canopy 97% of the emerging insect biomass was transferred to the riparian food web (Jackson & Fisher, 1986). Although this may not represent a typical situation, the rather scant data from other streams suggest that net losses from the stream may exceed 50% of the emerging insect biomass.

Subsidies of nutrients and detritus, from riparian vegetation and floodplains, can have important community level impacts producing 'bottom-up' effects in river food webs and increasing their productivity (Vannote *et al.*, 1980; Junk *et al.*, 1989; Stanford *et al.*, 1996). Subsidies of prey to consumers (as in terrestrial prey to aquatic predators such as fish) can raise predator populations above the level sustainable on the basis of *in situ* (aquatic) resources alone and produce apparent top-down trophic cascades in the aquatic system (Polis *et al.*, 1996).

River systems provide important subsidies to surrounding landscapes in addition to insect emergence. For instance many animals feed preferentially in the stream but spend resting periods in neighbouring terrestrial systems. Consequently, they export organic matter and nutrients out of the stream systems. These animals comprise snakes, fish eating birds, waterfowl, wading birds, a few passerine species (e.g. the dipper *Cinclus cinclus*) and shrew mice (Niethammer *et al.*, 1990; Owen & Black, 1990; Omerod & Tyler, 1991). Other animals feed on

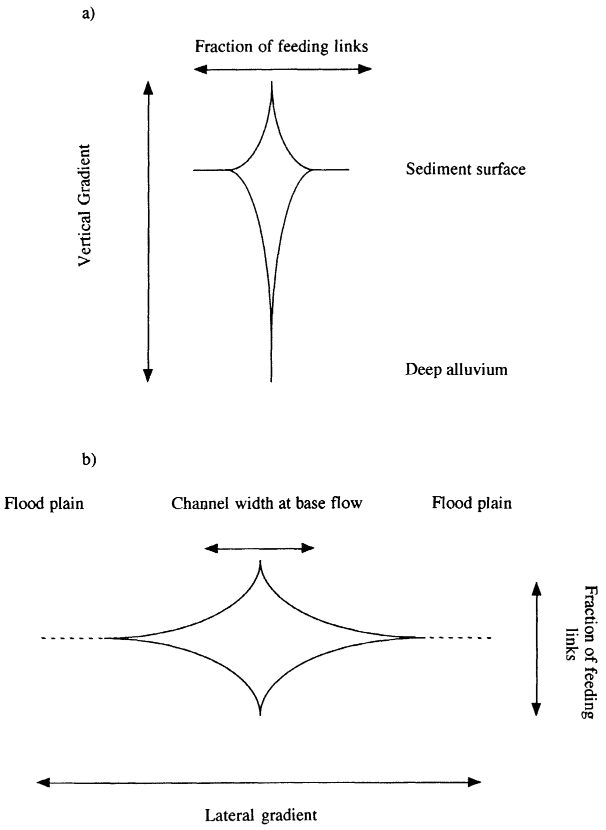

Fig. 12 A conceptual model of the 'spatial connectance' of benthic food webs (a) vertically and (b) laterally. In each case 'fraction of links' refers to the mean fraction of trophic links, of those species characteristic of the superficial benthos in mid-channel, that involve eating or being eaten by species whose modal distribution lies (a) along the vertical gradient from the riparian canopy to the deep interstitial or (b) along the lateral gradient into the riparian and floodplain. Most linkages involve species that share the same distribution along the gradient, others involve species partially separated along the gradient, and thus must involve biotic or abiotic transport mechanisms that may occur in 'pulses.'

terrestrial plants, but repeatedly visit the river for drinking and bathing. Because they also defecate there, organic matter is transported from the land to the stream. This is a major source of allochthonous organic matter in areas with high densities of herbivorous mammals, e.g. in tropical Africa (Sheppe & Osborne, 1971). Beaver (*Castor canadensis*) in the temperate and subarctic climatic zone and hippopotamus (*Hippopotamus amphibius*) in the old world tropics transport large amounts of allochthonous matter into the stream system.

While such food web linkages with the surface system of the floodplain are fairly well appreciated, we know very little of the subsurface linkages although they may be extensive, as depicted in Figs 11 and 12. Thus, food webs in and around river systems fully reflect the spatiotemporal complexity of the physical system and connectedness of its different components. Seasonal and stochastic physical and biotic events in rivers systems, such as floods and migrations, produce pulses of new 'spatial connectance' (see Fig. 12) in food webs, and these need theoretical and empirical investigation.

Metazoans as ecosystem engineers

Jones *et al.* (1994) introduced the concept of ecosystem engineers for 'organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials.' The concept is useful when one tries to understand better the roles of species in ecosystems (Lawton, 1994).

Ecosystem engineering processes are visible at various spatial and temporal scales under natural conditions; they are also amenable to study under laboratory conditions (see below). Many metazoans within lotic and associated riparian systems are such potential 'engineers.' We present here two environmental processes, bioturbation and comminution, within which metazoans act as 'ecosystem engineers.'

Bioturbation. Benthic metazoans modify the sediment by burrowing and feeding activities and by pelletization or compaction of the egested sediment (Lazim & Learner, 1987). As a consequence, bacteria associated with sediment particles are either stripped out by metazoans or their biological activity increases following gut passage (Levinton, 1995).

In the British chalkstreams examined by Ladle & Griffiths (1980), tubificid worms alone rework up to 0.5% of the fine sediments per day during summer. The grain size of the sediment changes through the production of large faecal pellets. For instance, the diameter of faecal particles of the amphipod *Gammarus* and the isopod *Asellus* vary between 0.2 and 0.5 mm, similar in size to the medium sand fraction. Hargrave (1976) showed that the pelletization of fine silt by the amphipod *Hyalella azteca* increased markedly the microbial activity of the sediment (more than 400 times expressed as oxygen uptake). Similar effects are expected for other metazoans with high ingestion and gut passage rates, such as *Gammarus pulex*, *Baetis rhodani and Simulium* sp. which have gut clearance times of 20–40 min (Berrie, 1976).

Slow sand and/or trickling filters provide useful analogues to some natural aquatic environments. Metazoans, especially oligochaetes and nematodes, feeding on the biofilm which develops on the surface of mineral particles and within the interstitial spaces, improve the water filtration and change the filtrate quality (Husmann, 1974; Solbé, 1975; Eder, 1980). Metazoans grazing either on the superficial exopolymer layers or ingesting senescent bacteria, allow the proliferation of new generations of metabolically active bacteria within the biofilm (Cullimore, 1993). *Plectus palustris*, a freshwater interstitial nematode can ingest up to 650% of its body weight in bacterial biomass per day (Duncan *et al*., 1974). This species therefore has the potential to stimulate the growth of bacterial biofilms by maintaining populations in a logarithmic growth phase (Eder, 1983). A similar effect was observed (i.e. either the increase of bacterial numbers, Andriati, 1994; or bacterial activity, Griebler, 1996) in laboratory microcosms (slow sand filters) perfused with water containing high concentration of nitrate, where tubificids (*Tubifex tubifex, Limnodrilus hoffmeisteri* and *L. udekemianus*) were added at densities comparable to those occurring in the Danube wetlands in Austria. Denitrification of the perfused water into the sediments started earlier and proceeded at higher intensities in the columns where tubificids bioturbated the superficial sediment layers than in the control filters without worms (Merle, 1994).

Comminution. Particle size reduction or comminution is an important process in aquatic ecosystems. Shredders, which feed on CPOM, produce FPOM mechanically, through their feeding activities, and by egesting faecal pellets within that size range.

An ecosystem model developed by Webster (1983) predicted an important role for shredders in making FPOM available to consumers in streams. Mayfly nymphs of the genus *Stenonema,* which feed on FPOM, displayed more than twelve times higher growth rates when reared in aquaria with insect shredders (*Tipula* and *Pycnopsyche*) (Cummins *et al*., 1973). Similar effects were found in the experiments of Short & Maslin (1977), who fed radiophosphorous-labeled alder leaves to the shredder *Pteronarcys californica* (Plecoptera). In the presence of the shredder, the uptake of labeled leaf material was significantly greater for two collector species, the caddisfly *Hydropsyche* and the black fly *Simulium*, than when the shredder was absent. Microbial activity during leaf decomposition also increases when shredders are present (Petersen & Cummins, 1974).

The total surface of small detritus particles produced by shredders is greatly increased, offering new microhabitats for bacterial proliferation. Feeding activities by isopods, both epigean and hypogean species, on leaves of *Carpinus betulus* allowed bacteria and fungi to penetrate deeper in the leaf tissue (Mößlacher, 1994; Mößlacher & Creuzé des Châtelliers, 1996).

Do metazoans make any difference in ecosystem functioning? It appears that the impact that 'engineering' organisms have on ecosystem functioning depends on the spatial and temporal scale of their actions. Lawton & Jones (1995) emphasize several factors, including population density, spatial distribution patterns, the length of time organisms act as 'ecosystem engineers,' and the number and types of resources that are modulated, that determine the impacts of ecosystem engineers. Application of insecticides to an Appalachian stream eliminated 90% of the secondary producers, including the shredders (Wallace & Webster, 1996). This resulted in a major reduction in leaf litter breakdown and the export of the FPOM, compared to untreated streams. Restoration of the shredder functional group after insecticide application ceased was accompanied by a return to normal rates of leaf-litter processing. In other manipulations of ecosystems, however, such effects were not apparent. When shredders were removed from decaying plant litter in wetlands, the decomposition rates remained unaltered, suggesting that processing of the litter was mainly accomplished through microbial pathways (Batzer & Wissinger, 1996).

Danielopol (1989) discussed the impressive pelletization process of groundwater dwelling crustaceans like *Asellus* and *Proasellus* (Isopoda) and *Niphargus* (Amphipoda). It was suggested that such metazoans could increase the local permeability of the substratum through their feeding activities. Additional field evidence in a wetland did not, however, corroborate this expectation (Danielopol *et al*., 1997). The densities of these microcrustaceans occurring in the ground-

Table 1 Some research needs directly related to groundwater metazoans of alluvial river-riparian systems

Topics	Questions/problems
Autecology	
Hypogean/epigean affinity	Constraints to penetration (vertical, lateral) of surface/subterranean species into hypogean/epigean habitats
Interactions: hypogean/epigean species	Role of biotic interactions in shaping distribution patterns across boundaries.
Basic environmental requirements	Responses to gradients of oxygen, temperature, substratum variables, toxins, etc.
Life history traits	Adaptations to the subterranean milieu. Environmental cues.
Sensory perception	Adaptations to the subterranean milieu. Role of allelochemicals. Cues used to navigate within subterranean interstices.
Community Ecology	
Biodiversity of groundwater metazoa	Local/regional biodiversity. Levels of endemism. Estimates of global biodiversity. Factors structuring biodiversity across scales Species/area curves. Rate of species turnover.
Patchy distribution	Role of biotic/abiotic variables in structuring assemblages across scales.
Species saturation	Differences between hypogean habitat patches and between epigean and hypogean habitats.
Temporal stability of assemblage structure	Differences between hypogean habitat patches and between epigean and hypogean habitats.
Ecosystem Processes	
Productivity/energy flow	Relative productivity of different compartments of the river–riparian system. Energy flux between epigean/hypogean compartments.
Food webs	Trophic linkages between compartments of the river–riparian system. Role of alluvial aquifers in whole system food web structure.
Restoration efforts	Role of groundwater fauna in total ecosystem function and recovery.
Disturbance	Role of distrubance in ecosystem processes mediated through metazoans.
Methodological Aspects	
Sampling	Accurate quantitative sampling of groundwater fauna.
Experimentation	Conducting field experiments in alluvial aquifers.
Molecular techniques	Metapopulation structure across scales. Habitat fragmentation. Gene flow.

water habitats below the riparian forest were apparently too low to produce any large-scale (metre scale) effect on the subsurface water flow.

Research prospect and management

Research on alluvial river–riparian systems has rarely been conducted from an integrated holistic perspective and groundwater metazoans are typically excluded even from otherwise comprehensive research projects. There is clearly a general need to include groundwater animals as integral components of research programs at all levels of organization (Table 1). The topics in Table 1 and the following text are intended as examples rather than an all-inclusive catalogue of research needs.

At the autecological level we lack basic understanding regarding factors that constrain some organisms, but not others, to one side of the surface water-ground water ecotone. The data are insufficient even to speculate upon the roles of predation, competition and parasitism in structuring distribution patterns across boundaries, and the basic environmental requirements of the vast majority of groundwater metazoans are unknown. Studies in chemical ecology may provide insight into the behavioural repertoire of groundwater fauna.

At the community level many interesting questions related to biodiversity and community structure, major topics in contemporary ecological research, remain virtually uninvestigated in alluvial aquifer systems. Basic estimates of the number of species of groundwater metazoans are available in very few places (Marmonier *et al*., 1997; Rouch & Danielopol, 1997; Ward, 1998). The situation appears analogous to that of the deep sea benthic environment, which was formerly thought to be a biological desert because the inhabitants were small and sparse, sampling was inadequate and the habitat was mistakenly believed to be homogeneous (Nybakken, 1993). Results from more intensive, quantitative sampling, however, now suggest that the biodiversity of deep sea benthos is similar to that of terrestrial tropical communities (Grassle & Maciolek, 1992). When progressively larger areas of the deep sea were sampled, the species richness increased continuously, without a reduction in the proportion of rare species. Will this same pattern be found for metazoans of alluvial aquifers? For the deep sea benthos, a positive relationship between sediment particle size diversity and species diversity has been demonstrated (Etter & Grassle, 1992). One would expect a similar relationship in alluvial aquifers.

At the ecosystem level we know even less regarding the roles of metazoans in processes such as production and energy flow. Because ground water constitutes about two-thirds of the earth's nonoceanic water, such knowledge is essential for a basic understanding of carbon flow and material cycling in freshwaters. Better knowledge on the role of groundwater animals may provide insight into restoration processes in alluvial river systems. Preliminary findings suggest that disturbance is a major structuring agent that operates over a range of spatiotemporal scales in ground waters (Gibert *et al*., 1994), but few definitive data are available.

Lack of critical knowledge on the ecology of groundwater metazoans at all levels of organization relates to the difficulties of designing a valid sampling programme (Rouch & Danielopol, 1997) and conducting field experiments in subterranean habitats (Palmer, 1993). These problems relate to the fact that the fauna is distributed in dynamic patches within a complex, three-dimensional matrix. Molecular techniques offer an alternative avenue of investigation that have the potential partially to compensate for these difficulties (Ward & Palmer, 1994).

Effective ecosystem management requires a strong conceptual understanding of the structural and functional attributes of natural river systems (Stanford & Ward, 1992; Sparks, 1995). For alluvial rivers this means recognising that it is the *absence* of floods that constitutes 'disturbance' (Ward & Stanford, 1995; Stanford *et al*., 1996). River protection and restoration therefore must maintain or re-establish a 'natural' disturbance regime (i.e. fluvial dynamics) in order to ensure a wide range of successional stages, see also Tabacchi *et al*. (1998) (riparian and hydrarch seres), habitat heterogeneity, and connectivity (including hydraulic connectivity between ground waters, surface waters and riparian systems). For example, biodiversity across riverine landscapes is purportedly structured by the interactions between natural disturbance and environmental gradients, resulting in positive feedback between connectivity and spatiotemporal heterogeneity (Ward *et al*., in press). Our basic premise is that a 'connected' riparian–ground water system provides protection from pollutants, clogging of interstices, reductions in habitat heterogeneity and reductions in successional stage diversity, thereby maintaining suitable habitat conditions for diverse biotic assemblages in ground water, riparian and surface water environments (see also Wissmar & Beschta, 1998). The implications of this perspective for aquatic conservation are obvious. Biomonitoring programs should include riparian and groundwater faunas as integral components of sampling and analysis. Restoration of alluvial rivers must not only address connectivity between the river channel and the floodplain, but also between surface and ground waters (Schiemer, 1995; Ward & Stanford, 1995). Rigorous investigation of groundwater metazoans, as integrators of environmental conditions at the river–riparian interface, provide opportunities to achieve a truly holistic synthesis of alluvial river ecosystems.

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References

Adis J. (1992) How to survive six months in a flooded soil: strategies in Chilopoda and Symphyla from central Amazonian floodplains. *Studies on Neutropical Fauna and Environment*, **27**, 117–129.

Amoros C. & Roux A.L. (1988) Interactions between water bodies within the floodplains of large rivers. Function and development of connectivity. *Connectivity in Landscape Ecology. Münstersche geographische Arbeiten*, **31**, 125–130.

Amoros C., Roux A.L., Reygrobellet J.L., Bravard J.P. & Pautou G. (1987) A method for applied ecological studies of fluvial hydrosystems. *Regulated Rivers*, **1**, 17–36.

Andrassay J. (1962) Nematoden aus dem Ufergrundwasser der Donau von Bratislava bis Budapest. *Archiv für Hydrobiologie Supplement*, **27**, 91–117.

Andriati E. (1994) The role of oligochaetes on the microbial activity in a slow filtration column using groundwater with high nitrogen concentration. 19th Post-graduate Training Course in Limnology. Research Report, p. 21. Institute of Limnology, Mondsee.

Angelier E. (1953) Recherches écologiques et biogéographiques sur la faune des sables submergés. *Archives de Zoologie Expérimentale et Générale*, **90**, 37–161.

Atkinson W.D. & Shorrocks B. (1981) Competition on a divided and ephemeral resource. *Journal of Animal Ecology*, **50**, 461–471.

Bardonnet A. & Gaudin P. (1990) Pénétration de la lumière à l'intérieur des graviers des frayères à salmonidés: incidences possibles sur le comportement des alevins. *Bulletin of the Français de la Pêche et de la Pisciculture*, **318**, 145–152.

Bärlocher F. & Murdoch J.H. (1989) Hyporheic biofilms – a potential food source for interstitial animals. *Hydrobiologia*, **184**, 61–67.

Barr T.C. & Holsinger J.R. (1985) Speciation in cave faunas. *Annual Review of Ecology and Systematics*, **16**, 313–337.

Batzer D.P. & Wissinger S.A. (1996) Ecology of insect communities in nontidal wetlands. *Annual Reviews in Entomology*, **41**, 75–100.

Berrie A.D. (1976) Detritus, Microorganisms and Animals in Fresh Water *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes* (eds J. M. Andersen & A. MacFadyen). Blackwell Scinetific Publications, Oxford.

Berthelemy C. (1968) Contribution à la connaissance des Leuctridae (Plécoptères). *Annales de Limnologie*, **4**, 175–198.

Bilby R.E. (1981) Role of organic debris dams in regulating the export of dissolved and particulate organic matter from a forested watershed. *Ecology*, **62**, 1234–1243.

Bishop K., Petterson C., Allard B. & Ying-Hua L. (1994) Identification of the riparian sources of aquatic dissolved organic carbon. *Environment International*, **20**, 11–19.

Botosaneanu L. & Holsinger J.R. (1991) Some aspects concerning colonization of the subterranean realm – especially of subterranean waters: a response to Rouch & Danielopol, 1987. *Stygologia*, **6**, 11–39.

Boulton A.J. & Stanley E.H. (1995) Hyporheic processes during flooding and drying in a Sonoran Desert stream. *Archiv für Hydrobiologie*, **134**, 27–52.

Boulton A.J., Valett H.M. & Fischer S.G. (1992) Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. *Archiv für Hydrobiologie*, **125**, 37–61.

Boutin C. & Coineau N. (1990) 'Regression model evolution,' 'two-step model evolution' and the origin of continental stygobiontic interstitial microfauna. *Revue de Micropaléontologie*, **33**, 303–322.

Bravard J.P., Amoros C., Bornette G., Bournaud M., Creuzé des Châtelliers M., Gibert J., Peiry J.L. & Tachet H. (1997) River incision in southeast France: morphological phenomena and ecological impacts. *Regulated Rivers*, **13**, 75–90.

Bravard J.-P., Amoros C. & Pautou G. (1986) Impact of civil engineering works on the successions of communities in a fluvial system. A methodological and predictive approach applied to a section of the Upper Rhône River, France. *Oïkos*, **47**, 92–111.

Bretschko G. (1981) Vertical distribution of zoobenthos in an alpine brook of the Ritrodat-Lunz study area. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **21**, 873–876.

Bretschko G. (1990) The dynamic aspect of coarse particulate organic matter (CPOM) on the sediment surface of a second order stream free of debris dams (Ritrodat-Lunz study area). *Hydrobiologia*, **203**, 15–28.

Bretschko G. (1991) Bedsediments, groundwater and stream limnology. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **24**, 1957–1960.

Bretschko G. (1992) Differentiation between epigeic and hypogeic fauna in gravel streams. *Regulated Rivers*, **7**, 17–22.

Bretschko G. (1994) Bedsediment extension and grain shape and size distribution. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **25**, 1631–1635.

Bretschko G. (1995) The ecological importance of stream bedsediments, regardless of wether or not they are inundated. *Folia Facultatis Scientarium Naturalium Universitatis Masarykianae Brunensis, Biologia*, **91**, 5–17.

Bretschko G. & Christian E. (1989) Collembola in the bed sediments of an Alpine gravel stream (Ritrodat-Lunz study area, Austria). *International Revue der Gesamte Hydrobiologie*, **74**, 491–498.

Bretschko G. & Klemens W.E. (1986) Quantitative methods and aspects in the study of the interstitial fauna of running waters. *Stygologia*, **2**, 279–316.

Brittain J.E. & Eikeland T.J. (1988) Invertebrate drift – a review. *Hydrobiologia*, **166**, 77–93.

Brown K.E. (1991) Mollusca: Gastropoda. *Ecology and Classification of North American Freshwater Invertebrates* (eds J. H. Thorp & A. P. Covich), pp. 285–314. Academic Press, San Diego.

Brunke M. & Gonser T. (1997) The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology*, **37**, 1–33.

Camacho A.I., ed. (1992) *The Natural History of Biospeleology.* Monografias, Museo Nacional de Sciencias Naturales, Madrid.

Castella E., Richardot-Coulet M., Roux C. & Richoux P. (1991) Aquatic macroinvertebrates assemblage of two contrastingfloodplains: The Rhône and Ain Rivers, France. *Regulated Rivers*, **6**, 289–300.

Chapelle F.H. (1993) *Groundwwater Microbiology and Geochemistry*. J. Wiley, New York.

Chappuis P.A. (1942) Eine neue Methode zur Untersuchung der Grundwasserfauna. *Acta Scientiarum Mathematicarum Naturalium Kolozsvar*, **6**, 3–7.

Connell J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Conners M.E. & Naiman R.J. (1984) Particulate allochthonous inputs: Relationships with stream size in an undisturbed watershed. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1473–1484.

Copp G.H. (1989) The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes*, **26**, 1–27.

Creuzé des Châtelliers M. (1991a). Dynamique de Répartition des Biocénoses Interstitielles du Rhône en Relation Avec des Caractéristiques Géomorphologiques (Secteurs de Brégnier-Cordon, Miribel-Jonage et Donzère-Mondragon). PhD thesis, University of Lyon, France.

Creuzé des Châtelliers M. (1991b) Geomorphologic processes and discontinuities in the macrodistribution of the interstitial fauna. A working hypothesis. *Verhandlungen der Internationale Vereinigung für Theor Etische und Angewandte Limnologie*, **24**, 1609–1612.

Creuzé des Châtelliers M., Marmonier P., Dole-Olivier M.-J. & Castella E. (1992) Structure of interstitial assemblages in a regulated channel of the River Rhône ʻ(France). *Regulated Rivers*, **7**, 23–30.

Cullimore R.D. (1993) *Practical Manual of Groundwater Microbiology*. Lewis Publ., Chelsea.

Cummins K.W. (1973) Trophic relations of aquatic insects. *Annual Review of Entomology*, **18**, 183–206.

Cummins K.W. & Klug M.J. (1979) Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, **10**, 147–172.

Cummins K.W., Petersen R.C., Howard F.O., Wuycheck J.C. & Holt V.I. (1973) The utilization of leaf by stream detritivores. *Ecology*, **54**, 336–345.

Dahm C.N., Grimm N.B., Marmonier P., Valett H.M. & Vervier P. (1998) Nutrient Dynamics at the interface between surface waters and ground waters. *Freshwater Biology*, **40**, 427–451.

Danielopol D.L. (1976) The distribution of the fauna in the interstitial habitats of riverine sediments of the Danube and the Piesting (Austria). *International Journal of Speleology*, **8**, 322–329.

Danielopol D.L. (1983) Der Einfluss organischer Verschmutzung auf das Grundwasser-Ökosystem der Donau im Raum Wien und Nieder-Österreich. *Bundesministerium für Gesundheit und Umweltschutz, Forschungsberichte*, **5**/**83**, 5–160.

Danielopol D.L. (1984) Ecological investigations on the alluvial sediments on the Danube in the Vienna area – a phreatobiological project. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, **22**, 1755–1761.

Danielopol D.L. (1989) Groundwater fauna associated with riverine aquifers. *Journal of the North Americain Benthological Society*, **8**, 18–35.

Danielopol D.L. (1991) Spatial distribution and dispersal of interstitial Crustacea in alluvial sediments of a backwater of the Danube at Vienna. *Stygologia*, **6**, 97–110.

Danielopol D.L., Creuzé des Châtelliers M., Mösslacher F., Pospisil P. & Popa R. (1994) Adaptation of Crustacea to interstitial habitats: A practical agenda for ecological studies. *Groundwater Ecology* (eds J. Gibert D. L. Danielopol & J. A. Stanford), pp. 217–243. Academic Press, San Diego.

Danielopol D.L., Dreher J., Gunatilaka A., Kaiser M., Niederreiter R., Pospisil P., Creuzé des Chatelliers M. & Richter A. (1992) Ecology of organisms living in a hypoxic groundwater environment at Vienna (Austria); methodological questions and preliminary results. *Proceedings of the 1st International Conference of Ground Water Ecology* (eds J. Simons & J. Stanford), U.S. Environmental Protection Agency, AWRA, Washington, DC.

Danielopol D.L., Rouch R., Pospisil P., Torreiter P. &

Mößlacher F. (1997) Ecotonal animal assemblages; their interest for groundwater studies. *Groundwater/Surface Water Ecotones* (eds J. Gibert, J. Mathieu & F. Fournier), pp. 11–20. Cambidge University Press, Cambridge.

Debowski P. & Beall E. (1995) Influence de fortes variations de niveau en étiage sur les mouvements et la distribution de saumons atlantiques juvéniles (*Salmo salar* L) en fonction de l'habitat dans un ruisseau expérimental. *Bulletin of the Français de la Pêche et de Lapisciculture*, **337**, 338, 339, 267–338, 339, 275.

Decho A.W. & Moriarty D.J. (1990) Bacterial exopolymer utilization by a harpacticoid copepod: a methodology and results. *Limnology and Oceanography*, **35**, 1039–1049.

Dole M.J. (1985) Le domaine aquatique souterrain de la plaine alluviale du Rhône à l'est de Lyon, 2. Structure verticale des peuplements des niveaux supérieurs de la nappe. *Stygologia*, **1**, 270–291.

Dole M.-J. & Chessel D. (1986) Stabilité physique et biologique des milieux interstitiels. Cas de deux stations du Haut Rhône. *Annales de Limnologie*, **22**, 69–81.

Dole-Olivier M.-J., Creuzé des Châtelliers M. & Marmonier P. (1993) Repeated gradients in subterranean landscape – example of the stygofauna in the alluvial floodplain of the Rhône River (France). *Archiv für Hydrobiologie*, **127**, 451–471.

Dole-Olivier M.-J. & Marmonier P. (1992a) Patch distribution of interstitial communities: prevailing factors. *Freshwater Biology*, **27**, 177–191.

Dole-Olivier M.-J. & Marmonier P. (1992b) Effects of spates on interstitial assemblages structure. Disturbance–perturbation relationship, rate of recovery. *Hydrobiologia*, **230**, 49–61.

Dole-Olivier M.-J. & Marmonier P. (1992c) Ecological requirements of stygofauna in an active channel of the Rhône River. *Stygologia*, **7**, 65–75.

Dole-Olivier M.-J., Marmonier P., Creuzé des Châtelliers M. & Martin D. (1994) Interstitial fauna associated with the alluvial floodplains of the Rhône River (France). In. *Groundwater Ecology* (eds Gibert J. Danielopol D. & Stanford J.), pp. 313–346. Academic Press, San Diego.

Dudgeon D. & Bretschko G. (1996) Allochthonous inputs and land–water interactions in seasonal streams: tropical Asia and temperate Europe. *Perspectives in Tropical Limnology* (eds F. Schiemer & K. T. Boland). Academic Publishing bv, Amsterdam, the Netherlands.

Duncan A., Schiemer F. & Klekowski R.Z. (1974) A preliminary study of feeding rates on bacterial food adult females of a benthic nematode *Plectus palustris* DeMann, 1880. *Polish Archives of Hydrobiology*, **21**, 249–258.

Dunning J.B., Danielson B.J. & Pulheim H.R. (1992) Ecological processes that effect populations in complex landscapes. *Oikos*, **65**, 169–175.

Eder R. (1980) Beiträge zur Kenntnis der interstitiellen Nematoden-fauna am Beispiel eines Schotterkörpres der Donau bei Fischamend. PhD Thesis, University of Wien.

Eder R. (1983) Nematoden aus dem Interstitial der Donau bei Fischamend (Niederösterreich). *Archiv für Hydrobiologie*, (Suppl. 68), 100–113.

Etter R.J. & Grassle J.F. (1992) Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature*, **360**, 576–578.

Fenchel T. & Finlay B.J. (1995) *Ecology and Evolution in Anoxic Worlds*. Oxford University Press, Oxford.

Ferrington L.C. (1987) Chironomidae in the capillary fringe of the Cimarron River bed. *Journal of Kansas Enthomological Society*, **60**, 153–156.

Fiebig D.M. & Lock M.A. (1991) Immobilization of dissolved organic matter from groundwater discharging through the stream bed. *Freshwater Biology*, **26**, 45–55.

Fiebig D.M., Lock M.A. & Neal C. (1990) Soil water in the riparian zone as a source of carbon for a headwater stream. *Journal of Hydrobiology*, **116**, 217–237.

Findlay S., Strayer D., Goumbala C. & Gould K. (1993) Metabolism of Streamwater dissolved organic carbon in the shallow hyporheic zone. *Limnology and Oceanography*, **38**, 1493–1499.

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, **43**, 421–439.

Ford T.E. & Naiman R.J. (1989) Groundwater-surface water relationship in boreal forest watersheds: Dissolved organic carbon and inorganic nutrient dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 41–49.

Gagneur J. & Chaoui-Boudghane C. (1991) Sur le rôle du milieu hyporhéique pendant l'assèchement des oueds de l'ouest algérien. *Stygologia*, **6**, 77–89.

Gessner M. (1987) Eintrag von partikulärem organischen material und fallaubabbau in einem mittelgebirgsbach. Dipl. Arbeit, Universität Konstanz.

Gessner M.O. (1991) Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. *Freshwater Biology*, **26**, 387–398.

Gessner M.O. & Schwoerbel J. (1989) Leaching kinetics of fresh leaf-litter with implications for the current concept of leaf-processing in streams. *Archiv für Hydrobiologie*, **115**, 81–90.

Gibbs K.E. & Siebenmann M. (1996) Life history attributes of the rare mayfly *Siphlonisca aerodromia*

Needham (Ephemeroptera: Siphlonuridae). *Journal of the North American Benthological Society*, **15**, 95–105.

Gibert J., Dole-Olivier M.-J., Marmonier P. & Vervier P. (1990) Surface Water–Groundwater Ecotones. *The Ecology and Management of Aquatic-Terrestrial Ecotones.* Man and the Biosphere Series, Vol 4 (eds R. J. Naiman & H. Decamps), pp. 199–225. Parthenon Publ. Group, Paris.

Gibert J., Stanford J.A., Dole-Olivier M.-J. & Ward J.V. (1994) Basic attributes of groundwater ecosystems and prospects for research. *Groundwater Ecology* (eds J. Gibert D. L. Danielopol & J. A. Stanford), pp. 7–40. Academic Press, San Diego.

Ginet R. & Decou V. (1977) *Initiation à la Biologie et à l'Écologie Souterraines*. J.P. Delarge, Paris.

Godbout L. & Hynes H.B.N. (1982) The three dimensional distribution of the fauna in a single riffle in a stream in Ontario. *Hydrobiologia*, **97**, 87–96.

Goldhammer D.S. & Ferrington L.C. (1992) Emergence of aquatic insects from epirheic zones of capillary fringe habitats in the Cimarron River, Kansas. *Proceedings of theeedings of the First International Conference on Ground-Water Ecology* (eds J. Simons & J. A. Stanford), pp. 155–164. U.S. Environmental Protection Agency, AWRA, Washington, DC.

Goulding M. (1980) *The Fishes and the Forest*. University of California Press, Berkeley.

Grassle J.F. & Maciolek N.J. (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist*, **139**, 313–341.

Gray L.J. & Fisher S.G. (1981) Postflood recolonization pathways of macroinvertebrates in a lowland sonoran desert stream. *The American Midland Naturalist*, **106**, 249–257.

Griebler C. (1996) Dimethylsulfoxide (DMSO) reduction. A new method to determine in situ microbial activities in aquatic sediments, with special applications for groundwater systems. MA Thesis, University of Wien.

Hall C.A.S., Stanford J.A. & Hauer F.R. (1992) The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos*, **65**, 377–390.

Hanski I. & Gilpin M.E., eds. (1997) Metapopulation Biology. *Ecology, Genetics and Evolution,* Academic Press, San Diego.

Hargrave T.B. (1976) The central role of invertebrate faeces in sediment decomposition. *The Role of Terrestrial and Aquatic Organisms in Decompostiton Processes*. (eds J. M. Anderson & A. Macfadyen), pp. 301–322. Blackwell Science, Oxford.

Hart D.D., Clark B.D. & Jasentuliyana A. (1996) Fine scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography*, **41**, 297–308.

Harvey J.W. & Bencala K.E. (1993) The effect of streambed topography on surface-subsurface water exchanges in mountain catchments. *Water Resource Research*, **29**, 89–98.

Hervant F. & Mathieu J. (1995) Ventilatory and locomotory activities in anoxia and subsequent recovery of epigean and hypogean curstaceans. *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Vie,* **318**, 585–592.

Herzig A., Bretschko G., Gaviria E.A., Stipanits B. & Zoufal H. (1987) Quantitative Zoobenthosuntersuchungen im Stauraum Altenwörth. Arbeitsgemeinschaft Donauforschung. *26 Arbeitstagung IAD, Wissenschaftliche Kurzreferate,* 127–132.

Herzog L. (1938) Crustaceen aus unterirdischen Biotopen des Rheintales bei Strassburg. III. Mitteilung, *Zoologischer Anzeiger*, **123**, 45–47.

Hildrew A.G. (1992) Food webs and species interactions. *The Rivers Handbook* (eds P. Calow & G. E. Petts), Vol 1, pp. 309–330. Blackwell Science, Oxford.

Hildrew A.G. (1996) Whole river ecology: special scale and heterogeneity in the ecology of running waters. *Archiv für Hydrobiologie*, **113** (Suppl. 10), 25–43.

Hildrew A.G. & Giller P.S. (1994) Patchiness, species interactions and disturbance in the stream benthos. *Aquatic Ecology. Scale, Pattern and Process* (eds P. S. Giller, A. G. Hildrew & D. G. Raffaelli), pp. 21–62. Symposium of the British Ecological Society, Blackwell Science, Oxford.

Holsinger J.R., Mort J.S. & Recklies A.D. (1983) The subterranean curstacean fauna of castleguard cave, Columbia Icefields, Alberta, Canada, and its zoogeographic significance. *Arctic and Alpine Research*, **15**, 543–549.

Huggenberger P., Hoehn E., Beschta R. & Woessner W. (1998) Groundwater control on riparian/fluvial systems. *Freshwater Biology*, **40**, 407–425.

Hunt R.L. (1975) Food relations and behaviour of salmonid fishes. *Coupling of Land Water Systems* (ed. A. D. Hasler), pp. 137–151. Springer-Verlag, New York.

Husmann S. (1974) Die ökologische Bedeutung der Mehrzellfauna bei der naturlichen und künstlichen Sandfiltration. *Berichte Untersuchungen und Planungen der Stadtwerke Wiesbaden AG*, **2**, 173–183.

Hynes H.B.N. (1975) The Stream and Its Valley, *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*, **19**, 1–15.

Hynes H.B.N. (1983) Ground water and Stream Ecology. *Hydrobiologia*, **100**, 93–99.

Ives A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecological Monographs*, **61**, 75–94.

Jackson J.K. & Fisher S.G. (1986) Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology*, **67**, 629–638.

Jackson J.K. & Resh V.H. (1989) Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. *Environmental Entomology*, **18**, 278–283.

Jones J.B. (1995) Factors controlling hyporheic respiration in a desert stream. *Freshwater Biology*, **34**, 91–99.

Jones J.R., Fisher S.G. & Grimm N.B. (1995) Vertical hydrologic exchange and ecosystem metabolism in a Sonoran desert stream. *Ecology*, **76**, 942–952.

Jones C.G., Lawton J.H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Special Publications of Fisheries and Aquatic Sciences*, **106**, 110–127.

Karaman S. (1935) Die Fauna unterirdischen Gewässer Jugoslawiens. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **7**, 46–73.

Kareiva P. (1994) Space: the final frontier for ecological theory *Ecology*, **75**, 1.

Klausnitzer B. & Pospisil P. (1991) Larvae of *Cyphon* sp. (Coleoptera, Helodidae) in groundwater. *Aquatic Insects*, **13**, 161–165.

Klemens W.E. (1991) Quantitative sampling of bedsediments (Ritrodat-Lunz study area, Austria). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **24**, 1926–1929.

Kowarc V.A. (1990) Zeitlich Räumliche Verteilungsmuster und Produktionsbiologie der Harpacticiden (Copepoda, Crustacea) in einem Gebirgsbach. PhD Thesis, University of Wien.

Ladle M. & Griffiths B.S. (1980) A study on the faeces of some chalk stream invertebrates. *Hydrobiologia*, **74**, 161–171.

Lancaster J. & Belyea L.R. (1997) Nested hierarchies and scale dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society*, **16**, 221–238.

Lancaster J. & Hildrew A.G. (1993) Characterising instream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1663–1675.

Lawton J.H. (1989) Food webs. *Ecological Concepts* (ed. J. M. Cherrett), pp. 43–78. Symposia of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Lawton J.H. (1994) What do species do in ecosystems? *Oikos*, **71**, 367–374.

Lawton J.H. & Jones C.G. (1995) Linking species and ecosystems: organisms as ecosystem engineers. *Linking Species and Ecosystems* (eds C. G. Jones & J. H.Lawton), pp. 141–150. Chapman & Hall, New York.

Lazim M.N. & Learner M.A. (1987) The influence of sediment composition and leaf litter on the distribution of tubificid worms (Oligochaeta). *Oecologia*, **72**, 131–136.

Leichtfried M. (1985) Organic matter in gravel streams (Project Ritrodat-Lunz).- *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **22**, 2058–2062.

Leichtfried M. (1988) Bacterial substrates in gravel beds of a second order alpine stream (Project Ritrodat-Lunz, Austria). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **23**, 1325–1332.

Leichtfried M. (1991) POM in bedsediments of a gravel stream (RITRODAT-Lunz study area, Austria). *Verhandlungen der Internationalen Vereinigung für teoretische und angewandte Limnologie*, **24**, 1921–1925.

Leichtfried M. (1995) Organic matter in bedsediments – an energy source for lotic ecosystems (a compilation of a long term study). *Folia Facultatis Scientiarium Naturalium Universitatis Masarykianae Brunensis, Biologia*, **91**, 77–93.

Levinton J. (1995) Bioturbators as ecosystems engineers: control of the sedimentary fabric, inter-individual interactions and material fluxes. *Linking Species and Ecosystems* (eds C. G. Jones & J. H.Lawton), pp. 29–36. Chapman & Hall, New York.

Maridet L., Philippe M., Wasson J.G. & Mathieu J. (1996) Spatial and temporal distribution of macroinvertebrates and trophic variables within the bed sediment of three streams differing by their morphology and riparian vegetation. *Archiv für Hydrobiologie*, **136**, 41–64.

Marmonier P. (1984) Vertical distribution and temporal evolution of the ostracod assemblages of the Seebach sediments (Lunz-Austria). *Jahresbericht Biologische Station Lunz*, **7**, 49–82.

Marmonier P. (1988) Biocenoses Interstitielles et Circulation Des Eaux Dans le Sous-Ecoulement D'un Chenal Amenage Du Haut-Rhône Francais. PhD Thesis, Universität Claude Bernard, Lyon.

Marmonier P. (1991) Effect of alluvial shift on the spatial distribution of interstitial fauna. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, **24**, 1613–1616.

Marmonier P. & Creuzé des Châtelliers M. (1991) Effects of spates on interstitial assemblages of the Upper Rhône River. Importance of spatial heterogeneity. *Hydrobiologia*, **210**, 243–251.

Marmonier P., Creuzé des Châtelliers M., Dole-Olivier M.-J., Plénet S. & Gibert J. (*in press*) Rhône groundwater systems. In: *Ecosystems of the World 30*. (eds H.

Wilkens D. Culver & J. Humphreys). Elsevier, Amsterdam.

Marmonier P. & Dole M.J. (1986) Interstitial amphipods of a by-passed section of the Rhône river: distribution patterns and reaction to spates. *Science de L'eau*, **5**, 461–486.

Marmonier P., Dole-Olivier M.-J. & Creuzé des Châtelliers M. (1992) Spatial distribution of interstitial assemblages in the floodplain of the Rhône River. *Regulated Rivers*, **7**, 75–82.

Marmonier P., Ward J.V. & Danielopol D.L. (1997) Biodiversity in groundwater/surface water ecotones: central questions. *Groundwater/Surface Water Ecotones: Biological and Hydrological Interactions and Management Options* (eds J. Gibert, J. Mathieu & F. Fournier), pp. 231–235. Cambridge University Press, Cambridge.

Mason C.F. & Macdonald S.M. (1982) The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology*, **12**, 305–311.

Mathieu J. (1983) Le metabolisme réspiratoire de *Niphargus* (Amphipode hypogé). Déterminisme de sa variabilité par la comparaison de deux populations de *N. rhenorhodanensis.* Doct. Thesis Etat, University of Claude Bernard, Lyon.

Merle C. (1994) Etude experimental de l'activité des Oligochaetes Tubificidae sur les écoulements d'eau et les flux d'oxygène et de nitrate au niveau de l'interface eau × sédiment. Ma Thesis, University of Lyon.

Mestrov M., Stilinovic B., Habdija I., Lattinger R., Maloseja Z., Kerovec M., Cicin-s. & ain L. (1983) The ecological characteristics of interstitial groundwaters in relation to the water of the River Sava. *Acta Biologica Knj*, **9**, 5–33.

Meybeck M. (1982) Carbon, nitrogen, and phosphorus transported by world rivers. *American Journal of Sciences*, **282**, 401–450.

Minshall G.W. (1984) Aquatic Insect-Substratum Relationships, 358–400. *The Ecology of Aquatic Insects* (eds V. H. Resh & D. M.Rosenberg), Praeger, New York.

Minshall G.W., Cummins K.W., Petersen R.C., Cushing C.E., Urns D.A., Sedell J.R. & Vannote R.L. (1985) Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 1045–1055.

Moser H. (1991) Input of organic matter (OM) in a low order stream (Ritrodat-Lunz study area, Austria). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **24**, 1913–1916.

Moser H. (1992) Oberflächeneintrag und Verfrachtung organischer Substanz bei einem Gebirgsbach. PhD Dissertation, University of Wien.

Mosley M.P. (1982) New Zealand river temperature regimes. *Water and Soil Miscellaneous Publication* 36. Wellington, N.Z.

Möβlacher F. (1994) Beobachtungen eines Grundwasserökosystems in Freiland (Lobau, Wien) und experimentelle Untersuchungen über die Respirometrie, Freß- und Bewegungsaktivität einiger Süβwasserisopoden (Crustacea,. Asellidae*)*. Diplomarbeit, University of Wien.

Möβlacher F. & Creuzé des Châtelliers M. (1996) Physiological and behavioural adaptations of an epigean and a hypogean population of *Asellus aquaticus* (L.) Crustacea, Isopoda). *Archiv für Hydrobiologie*, **138**, 187–198.

Möβlacher F., Pospisil P. & Dreher J. (1996) A groundwater ecosystem study in tho wetland Lobau (Vicnna) reflecting the interactions between surface water and groundwater. *Archiv für Hydrobiologie* (Suppl. 113), 451–455.

Müller K. (1982) The colonisations cycle of freshwater insects. *Oecologia (Berlin)*, **52**, 202–207.

Naiman R.J. & Décamps H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621–658.

Niethammer J., Krapp F. & Genoud M. (1990) Handbuch der Säugetiere Europas. Bd.3. Insektenfresser – Insectivora; Herrentiere – Primates. AULA-Verlag GmbH, Wiesbaden.

Notenboom J. (1991) Marine regressions and the evolution of groundwater dwelling amphipods (Crustacea). *Journal of Biogeography*, **18**, 437–454.

Nybakken J.W. (1993) *Marine Biology*, 3rd edn. Harper Collins, New York.

O'Doherty E.C. (1985) Stream-dwelling copepods: their life history and ecological significance. *Limnology and Oceanography*, **30**, 554–564.

Omerod S.J. & Tyler S.J. (1991) Predatory exploitation by a river bird, the dipper *Cinclus cinclus* (L.), along acidic and circumneutral streams in upland Wales. *Freshwater Biology*, **25**, 105–116.

Orghidan T. (1959) Ein neuer Lebensraum des unterirdischen Wassers, der hyporeische Biotop. *Archiv für Hydrobiologie*, **55**, 392–414.

Owen M. & Black J.M. (1990) *Waterfowl Ecology*. Blackie, Glasgow & London.

Paine R.T. (1996) Preface. *Food Webs: Integration of Patterns and Dynamics* (eds G. N. Pollis & K. O. Winemiller). Chapman & Hall, London.

Palmer M.A. (1990a) Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creck, Virginia. *Journal of the North American Benthological Society*, **9**, 17–25.

Palmer M. (1990b) Understanding the movement dynamics of a stream-dwelling meiofauna community using marine analogs. *Stygologia*, **5**, 67–74.

Palmer M.A. (1992) Incorporating lotic meiofauna into our understanding of faunal transport processes. *Limnology and Oceanography*, **37**, 329–341.

Palmer M.A. (1993) Experimentation in the hyporheic zone: challenges and prospectus. *Journal of the North American Benthological Society*, **12**, 84–93.

Palmer M.A., Arensburger P., Botts P.S., Hakenkamp C. & Reid J.W. (1995) Disturbance and the community structure of stream invertebrates: patch-specific effects and the role of refugia. *Freshwater Biology*, **34**, 343–356.

Palmer M.A., Arensburger P., Martin A.P. & Denman D.W. (1996) Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates. *Oecologia*, **105**, 247–257.

Palmer M.A., Bely A.E. & Berg K.E. (1992) Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia*, **89**, 182–194.

Panek K.L.J. (1991a) Migrations of the macrozoobenthos within the bedsediments of a gravel stream. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **24**, 1944–1947.

Panek K.L.J. (1991b) Dispersionsdynamik Des Zoobenthos in Den Bettsedimenten Eines Gebirgsbaches. PhD Dissertation, Universität Wien.

Pennak R.W. & Ward J.V. (1986) Interstitial faunal communities of the hyporheic and adjacent groundwater biotops of a Colorado mountain stream. *Archiv für Hydrobiologie*, (Suppl. 74), 356–396.

Perlmutter D.G. & Meyer J.L. (1991) The impact of a stream-dwelling harpacticoid copepod upon detritally associated bacteria. *Ecology*, **72**, 2170–2180.

Petersen R.C. & Cummins K.W. (1974) Leaf litter processing in a woodland stream. *Freshwater Biology*, **4**, 343–368.

Pickett S.T.A. & White P.S. (1985) Patch dynamics: a synthesis. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett & P. S. White), pp. 371–384. Academic Press, Inc., San Diego.

Plénet S., Gibert J. & Marmonier P. (1995) Biotic and abiotic interactions between surface and interstitial systems in rivers. *Ecography*, **18**, 296–309.

Polis G.A., Holt R.D., Menge B.A. & Winemiller K.O. (1996) Time, space and life history: influences on food webs. In: *Food Webs: Integration of Patterns and Dynamics* (eds G. A. Polis & K. O. Winemiller), pp. 435–460. Chapman & Hall, London.

Polis G.A. & Winemiller K.O., eds. (1996) *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, London.

Pospisil P. (1994) Die Grundwassercyclopiden (Crustacea, Copepoda) der Lobau in Wien (Osterreich); Faunistische, Taxonomische und Ökologische Untersuchungen. PhD Thesis, University of Wien.

Pospisil P. (1994) The groundwater fauna of a danube aquifer in the 'Lobau' wetland in Vienna, Austria. *Groundwater Ecology* (eds J. Gibert, D. L. Danielopol & J. Stanford), pp. 347–366. Academic Press, San Diego.

Power M.A. & Stewart A.J. (1987) Disturbance and recovery of an algual assemblage following flooding in an Oklahoma stream. *American Midland Naturalist*, **117**, 333–345.

Pugsley C.W. & Hynes H.B.N. (1985) Summer diapause and nymphal development in *Allocapnia pygmaea* (Burmeister) (Plecoptera: Capniidae) in the Speed River, Southern Ontario. *Aquatic Insects*, **7**, 53–63.

Pugsley C.W. & Hynes H.B.N. (1986) Three-dimensional distribution of winter stonefly nymphs, *Allocapnia pygmaea,* within the substrate of a southern Ontario river. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1812–1817.

Pusch M., Fiebig D.M., Brettar I., Eisenmann H., Ellis B., Kaplan L., Lock M., Naegeli M. & Traunspurger W. (1998) The role of micro-organisms in the ecological connectivity of running waters. *Freshwater Biology*, **40**, 453–495.

Reid J.W. (1984) Semiterrestrial meiofauna inhabiting a wet campo in central Brazil, with special reference to the Copepoda (Crustacea). *Hydrobiologia*, **118**, 95–111.

Resh V.H., Brown A.V., Covich A.P., Gurte M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **8**, 433–455.

de Ribeiro M., N.G. & Adis J. (1984) Local rainfall variability – a potential bias for bioecological studies in the Central Amazon. *Acta Amazonica*, **14**, 159–174.

Richardson J.S. (1992) Coarse particulate detritus dynamics in small, montane streams of south-western British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 337–346.

Robertson A.L., Lancaster J. & Hildrew A.G. (1995) Stream hydraulics and the distribution of microcrustacea: a role for refugia? *Freshwater Biology*, **33**, 469–484.

Roca J.R. & Danielopol D.L. (1991) Exploration of interstitial habitats by the phytophilous ostracod Cypridopsis vidua (O.F. Müller). *Annales de Limnologie*, **27**, 243–252.

Rogulj B., Marmonier P., Lattinger R. & Danielopol D.L. (1994) Fine-scale distribution of hypgean Ostracoda in the interstitial habitats of the river Sava and Rhône. *Hydrobiologia*, **287**, 19.28.

Rouch R. (1991) Structure du peuplement des Harpacticides dans le milieu hyporhéique d'un ruisseau des Pyrénées. *Annales de Limnologie*, **27**, 227–241.

Rouch R. (1995) Peuplement des Crustacés dans la zone hyporhéique d'un ruisseau des Pyrénées. *Annales de Limnologie*, **31**, 9–28.

Rouch R. & Danielopol D.L. (1987) L'origine de la faune aquatique souterraine, entre le paradigme du refuge et le modèle de la colonisation active. *Stygologia*, **3/4**, 345–372.

Rouch R. & Danielopol D.L. (1997) Species richness of microcrustacea in subterranean freshwater habitats. Comparative analysis and approximate evaluations. *Internationale Revue der Gesamten Hydrobiologie*, **82**, 121–145.

Schiemer F. (1995) Revitalisierungsmassnahmen für Augewässer-Möglichkeiten und Grenzen. *Archiv für Hydrobiologie Supplementband*, **101**, 383–398.

Schlieper C., ed. (1972) *Research Methods in Marine Biology.* Sidgrvick & Jackson, London.

Schmid P. (1987) Die Zeitliche und Räumliche Dynamik der Chironomiden in Einem Gebirgsbach. PhD Thesis, University of Wien, pp. 396.

Schmid P.E. (1991) Spatial and temporal population dynamics of larval Chironomidae in a mountain brook (Ritrodat-Lunz experimental area, Austria). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **24**, 1934–1940.

Schmid P.E. (1992) Habitat preferences as patch selection of larval and emerging chironomids (Diptera) in a gravel brook. *Netherlands Journal of Aquatic Ecology*, **26**, 419–429.

Schmid P.E. (1993) Random patch dynamics of larval Chironomidae (Diptera) in the bed sediments of a gravel stream. *Freshwater Biology*, **30**, 239–255.

Schmid-Araya J.M. (1992) Spatial and temporal distribution of micro-meiofaunal groups in an alpine gravel stream. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **25**, 1649–1655.

Schmid-Araya J.M. (1993) Spatial distribution and population dynamics of a benthic rotifer, Embata laticeps (Murrray) (Rotifera, Bdelloidea) in the bed sediments of a gravel brook. *Freshwater Biology*, **30**, 395–408.

Schmid-Araya J.M. (1994a) Spatial and temporal distribution of micro-meiofaunal groups in an alpine gravel stream. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, **25**, 1649–1655.

Schmid-Araya J.M. (1994b) Temporal and spatial distribution of benthic Microfauna in sediments of a gravel streambed. *Limnology and Oceanography*, **38**, 1813–1821.

Schmid-Araya J.M. (1995) Disturbance and population dynamics of rotifers in bed sediments. *Hydrobiologia*, **313/314**, 279–290.

Schmid-Araya J.M. (1995) New records of rare Bdelloidea and Monogononta rotifers in gravel streams. *Archiv für Hydrobiologie*, **135**, 129–143.

Schmid-Araya J.M. & Schmid P.E. (1995a) The invertebrate species of a gravel stream. *Jahresbericht der Biologischen Station Lunz*, **15**, 11–21.

Schmid-Araya J.M. & Schmid P.E. (1995b) Preliminary results on diet of stream invertebrate species: the meiofaunal assemblages. *Jahresbericht der Biologischen Station Lunz*, **15**, 23–31.

Schumm J.A. (1977) *The Fluvial System*. Wiley Interscience, New York.

Schwoerbel J. (1961a) Subterrane Wassermilben (Acari: Hydrachnellae, Porohalacaridae und Stygothrombiidae), ihre Ökologie und Bedeutung für die Abgrenzung eines aquatischen Lebensraumes zwischen Oberfläche und Grundwasser. *Archiv für Hydrobiologie*, (Suppl. 25), 242–306.

Schwoerbel J. (1961b) Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. *Archiv für Hydrobiologie*, (Suppl. 25), 182–214.

Schwoerbel J. (1964) Die Bedeutung des Hyporheals für die benthische Lebensgemeinschaft der Fliessgewässer. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie*, **15**, 215–226.

Schwoerbel J. (1967) Die stromnahe phreatische Fauna der Donau (hyporheische Fauna). *Limnologie der Donau, Lieferung*, **3**, 284–294.

Sedell J.R., Reeves G.H., Hauer F.R., Stanford J.A. & Hawkins C.P. (1990) Role of refugia in recovery from disturbance: modern fragmented and disconnected river systems. *Environmental Management*, **14**, 711–724.

Sevenster J.G. (1996) Aggregation and coexistence I. Theory and analysis. *Journal of Animal Ecology*, **65**, 297–307.

Shepherd B.G., Hartman G.F. & Wilson W.J. (1986) Relationships between stream and intragravel temperatures in coastal drainages, and some implications for fisheries workers. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1818–1822.

Sheppe W. & Osborne T. (1971) Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs*, **41**, 179–205.

Shorrocks B. & Rosewell J. (1987) Spatial patchiness and community structure: coexistence and guild size of drosopholids on ephemeral resources. In. *Organization of Communities: Past and Present* (eds J. H. R. Gee & P. S. Giller). Symposia of the British Ecological Society, *Blackwell Scientific Publications*, Oxford, pp. 347–371.

Short R.A. & Maslin P.E. (1977) Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. *Ecology*, **58**, 935–938.

Smith I.M. & Cook D.A. (1991) Water Mites. *Ecology and Classification of North American Freshwater Invertebrates* (eds J. H. Thorp & A. P. Covich), pp. 523–592. Academic Press, San Diego.

Smock L.A. (1990) Spatial and temporal variation in organic matter storage in low-gradient, headwater streams. *Archiv für Hydrobiologie*, **118**, 169–184.

Söderström O. (1987) Upstream movements of invertebrates in running waters – a review. *Archiv für Hydrobiologie*, **111**, 197–208.

Söderström O. (1988) Environmental cues used in upstream orientation by *Parameletus chelifera* and *P. minor* (Ephemeroptera) nymphs; an experimental study. *Hydrobiologia*, **162**, 235–241.

Solbé J.F. (1975) Annelida. *Ecological Aspects of Used-Water Treatement* (eds C. R. Curds & H. A. Hawkes), pp. 305–336. Academic Press, London.

Sparks R.E. (1995) Need for ecosystem management of large rivers and their floodplains. *Bioscience*, **45**, 168–182.

Squillace P.J. (1996) Observed and simulated movement of bank-storage water. *Ground Water*, **34**, 121–134.

Stanford J.A. & Ward J.V. (1988) The hyporheic habitat of river ecosystems. *Nature*, **335**, 64–66.

Stanford J.A. & Ward J.V. (1992) Management of aquatic resources in large catchments: recognizing interactions between ecosystem connectivity and environmental disturbance. *Watershed Management* (ed. R. J. Naiman), pp. 91–123. Springer-Verlag, New York.

Stanford J.A. & Ward J.V. (1993) An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society*, **12**, 48–60.

Stanford J.A., Ward J.V. & Ellis B. (1994) Ecology of the alluvial aquifers of the Flathead River, Montana. *Groundwater Ecology* (eds J. Gibert, D. L. Danielopol & J. Stanford), pp. 36–390. Academic Press, San Diego.

Stanford J.A., Ward J.V., Liss W.J., Frissell C.A., Williams R.N., Lichatowich J.A. & Coutant C.C. (1996) A general protocol for restoration of regulated rivers. *Regulated Rivers*, **12**, 391–413.

Stanley E.H. & Boulton A.J. (1993) Hydrology and the distribution of hyporheos: perspectives from a mesic river and a desert stream. *Journal of the North American Benthological Society*, **12**, 79–83.

Stanley E.H. & Boulton A.J. (1995) Hyporheic processes during flooding and drying in a Sonoran Desert stream. I Hydrologic and chemical dynamics. *Archiv für Hydrobiologie*, **134**, 1–26.

Strayer D.L. (1994) Limits to biological distributions in groundwater. *Groundwater Ecology* (eds J. Gibert, D. L. Danielopol & J. A. Stanford), pp. 287–310. Academic Press, San Diego.

Sugihara G., Schoenly K. & Trombla N. (1989) Scale invariance in food web properties. *Science*, **245**, 48–52.

Tabacchi E. (1992) Colonization of periodically inundated interstitial habitats of an alluvial pond by invertebrates. *Regulated Rivers*, **7**, 153–164.

Tabacchi E., Correll D.L., Hauer R., Pinay G., Planty-Tabacchi A.-M. & Wissmar R.C. (1998) Development, maintenance and role of riparian vegetation in the landscape. *Freshwater Biology*, **40**, 497–516.

Tilman D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Tockner K. (1990) Auswirkungen eines Hochwassers auf die Drift im Oberen Seebach. *Jahresbericht Biologische Station Lunz*, **12**, 123–135.

Tokeshi M. (1994) Community ecology and patchy freshwater habitats. *Aquatic Ecology: Scale, Patterns and Process* (eds P. S. Giller, A. G. Hildrew & D. G. Raffaelli), pp. 63–91. Symposia of the British Ecological Society, Blackwell Science, Oxford.

Triska F.J., Kennedy V.C., Avanzino R.J., Zellweger G.W. & Bencala K.E. (1989) Retention and transport of nutrients in a third-order stream in northwestern California: Hyporheic processes. *Ecology*, **70**, 1893–1905.

Turner M.G. (1987) *Landscape Heterogenity and Disturbance*. Springer, New York.

Vandel A. (1964) Biospéologie. *La Biologie des Animaux Cavernicoles*. Gauthier-Villars Ed, Paris.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Vannote R.L. & Sweeney B.W. (1980) Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, **115**, 667–695.

Wallace J.B. & Webster J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of in Entomology*, **41**, 115–139.

Ward J.V. (1985) Thermal charactreistics of running waters. *Hydrobiologia*, **125**, 31–46.

Ward J.V. (1989a) Riverine–Wetland Interactions. *Freshwater Wetlands and Wildlife* (eds R. R. Sharitz & J. W. Gibbons). DOE Symposium Series, 61, pp. 385–400 U.S. Department of the Eenvironemt, Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Ward J.V. (1989b) The four dimentional nature of lotic ecosystems. *Journal of the North American Benthological Society*, **8**, 2–8.

Ward J.V. (1992) *Aquatic Insect Ecology*, Vol I. Wiley, New York.

Ward J.V. (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, **83**, 269–278.

Ward J.V. & Palmer M.A. (1994) Distribution patterns of interstitial freshwater meiofauna over a range of spatial scales, with emphasis on alluvial river-aquifer systems. *Hydrobiologia*, **287**, 147–156.

Ward J.V. & Stanford J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, **27**, 97–117.

Ward J.V. & Stanford J.A. (1983) The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. *Dynamics of Lotic Eecosystems* (eds T. D. Fontaine & S. M. Bartell), pp. 347–356. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Ward J.V. & Stanford J.A. (1983) The serial discontinuity concept of lotic ecosystems. *Dynamics of Lotic Ecosystems* (eds T. D. Fontaine & S. M. Bartell). Ann Arbor Science Publications, Ann Arbor, MI.

Ward J.V. & Stanford J.A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers*, **11**, 105–119.

Ward J.V., Stanford J.A. & Voelz N.J. (1994) Spatial distribution patterns of crustacea in the floodplain aquifer of an alluvial river. *Hydrobiologia*, **287**, 11–17.

Ward J.V., Tockner K. & Schiemer F. (in press) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers.*

Ward J.V. & Voelz N.J. (1994) Groundwater fauna of the south platte river system, Colorado. *Groundwater Ecology* (eds J. Gibert, D. L. Danielopol & J. A. Stanford), pp. 391–423. Academic Press, San Diego.

Ward J.V. & Wiens J.A. (in press) Ecotones of riverine ecosystems: role and typology, spatio-temporal dynamics, and river regulation. *Fish and Land/Water Ecotones* (eds M. Zalewski, F. Schiemer & J. Thorpe). Parthenon Publ., Carnforth, UK.

Webster J.R. (1983) The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. *Ecological Monographs*, **53**, 383–404.

Weigelhofer G. & Waringer J.A. (1994) Allochthonous input of Coarse Particulate Organic matter (CPOM) in a First to Fourth Order Austrian Forest Stream. *Internationale Revue der Gesamten Hydrobiologie*, **79**, 461–471.

Welcome R.L. (1979) *Fisheries Ecology of Floodplain Rivers.* Longman, London.

Whitman R.L. & Clark W.J. (1984) Ecological studies of the sand-dwelling community of an east Texas stream. *Freshwater Invertebrate Biology*, **3**, 59–79.

Williams D.D. (1984) The hyporheic zone as a habitat for aquatic insects and associated arthropods. *The Ecology of Aquatic Insects* (eds V. H. Resh & D. M. Rosenberg), pp. 430–455. Praeger Publishers, New York.

Williams D.D. (1989) Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. *Freshwater Biology*, **22**, 189–208.

Winemiller K.O. (1996) Factors during temporal and spatial variation in aquatic floodplain food webs (R. T. Paine), pp. 298–312.

Wissmar R. & Beschta R.L. (1998) Restoration and management of riparian ecosystems: a catchment perspective. *Freshwater Biology*, **40**, 571–585.

Wu J. & Levin S.A. (1994) A spatial patch dynamic modelling approach to pattern and process in an annual grassland. *Ecological Monographs*, **64**, 447–464.

Zingg T. (1935) Beitrag zur Schotteranalyse. Die Schotteranalysr und ihre Anwendung auf die Glattalschotter. *Schweizerische Mineralogische und Petrographische Mittel*, **15**, 39–140.

Zwick P. (1992) Stream habitat fragmentation – a threat to biodiverstiy. *Biodiversity and Conservation*, **1**, 80–97.

Zwick P. (1996) Variable egg development of *Dinocras* spp. (Plecoptera, Perlidae) and the stonefly seed bank theory. *Freshwater Biology*, **35**, 81–100.

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Appendix

Species referred-to in this paper

Plants
- *Acer pseudoplantanus* L.
- *Carpinus betulus* L.
- *Fraxinus excelsior* L.

Animals
- Archiannelida
- *Troglochaetus beranecki* Delachaux Rotatoria
- *Proales theodora* (Gosse)

Oligochaeta
- *Limnodrilus hoffmeisteri* Claparède
- *Limnodrilus udekemianus* Claparède
- *Tubifex tubifex* Müller

Nematoda
- *Plectus palustris* DeMan
- *Tobrilus gracilis* (Bastian)

Cladocera
- *Alona phreatica* Dumont

Copepoda:
- *Limnocamptus echinatus* (Mrazek)
- *Parastenocaris dianae* Chappuis

Ostracoda
- *Cryptocandona kieferi* (Klie)
- *Fabaeformiscandona wegelini* (Petkovski)
- *Pseudocandona triquetra* (Klie)
- *Pseudocandona zschokkei* (Wolf)

Syncarida
- *Bathynella* nov. sp.

Isopoda
- *Microcharon reginae* Dole & Coineau
- *Proasellus walteri* Chappuis

Amphipoda
- *Gammarus pulex* (L.)
- *Hyalella azteca* Saussure
- *Niphargopsis casparyi* Pratz
- *Niphargus kochianus* Bate
- *Niphargus renei* Karaman
- *Niphargus rhenorhodanensis* Schellenberg

Insecta
- *Baetis rhodani* Pictet
- *Cyphon palustris* Thomson
- *Nilotanypus dubius* (Meigen)
- *Orthocladius rivulorum* Kieffer
- *Pteronarcys californica* Newport
- *Siettitia avenionensis* Guignot

Pisces
- *Salmo trutta* L.

Aves
- *Cinclus cinclus* (Bechst.)

Mammalia
- *Castor canadensis* Kuhl
- *Hippopotamus amphibius* L.