Nutrient and flow vector dynamics at the hyporheic/groundwater interface and their effects on the interstitial fauna

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Abstract

Environmental conditions in the interstices beneath streams and rivers with porous beds are unlike those found either on the bed surface or in the true groundwater. For most of the year, in many streams, the bulk of the water in the hyporheic zone is provided by baseflow but, as it passes across the hyporheic/ groundwater interface, the physical and chemical nature of this groundwater changes, probably in response to mixing with surface water. Factors promoting the influx of surface water are associated with features of the bed and channel morphology. The upper and lower boundaries of the hyporheic zone are thought to vary in time, but at any instant they can be defined. As a habitat, the hyporheic zone fits the definition of an ecotone, although certain adverse features may result in reduced species diversity. There are limited, correlative, data available on the relationship of the fauna (hyporheos) to interstitial conditions and further study of the general biology of both species and populations is needed. In an attempt to stimulate future research on these systems, some preliminary models of hyporheic dynamics are proposed.

Introduction

The hyporheic zone beneath streams is an interstitial habitat bounded by surface water in the channel, above, and by true groundwater, below (Schwoerbel, 1961). The lower boundary, the hyporheic/groundwater interface, is thought to shift in response to changes in the pressure heads of different water masses, primarily baseflow (from the groundwater) and streamflow. However, in general, the movement of water through the hyporheic zone is poorly understood (Williams, 1989). The hyporheic fauna (termed 'hyporheos') is made up of species from the benthos found on the surface of the stream bed; species derived from hypogean environments such as the groundwater, subterranean waterbodies, and the

soil (Williams & Hynes, 1974); and a few forms that, although perhaps not endemic to this habitat, are more commonly found here (e.g. species belonging to the chironomid genera *Krenosmittia* and *Lopescladius*; Coffman & Ferrington, 1984). Although quantitative and qualitative studies have been made of hyporheic populations little is known of the physiology of species, their precise environmental requirements or their trophic relationships. Presumably the community is detritus based but how much of this rains down from the stream bed surface, how much is imported by groundwater, or how much is produced *in situ* is unknown. Some data on the concentrations of dissolved and particulate nutrients exist but these are patchy and temporally limited.

The purpose of this paper is (1) to attempt to

characterize the boundaries of the hyporheic zone; (2) to present data on the relationships of some of the species to interstitial water chemistry; and (3) to propose some models of hyporheic dynamics that, in testing, may stimulate future investigations.

Background

It would be wise to begin by defining some relevant terms. An *aquifer* is a geological formation, or group of formations, that not only contains water but, under ordinary field conditions, allows significant amounts of water to move through it (Bear, 1979). Aquifers may be 'confined' or 'unconfined' but discussion, here, is limited to the more common unconfined, or 'phreatic' aquifer, the upper boundary of which is marked by the water table. Above the water table is the capillary fringe, a zone often neglected in groundwater studies but one of considerable biological importance, particularly in streams that flow intermittently (Williams, 1987). Streams typically sit on top of aquifers, in valley bottoms, and exchange water with them. Of several different types of stream-aquifer interactions, the two most commonly encountered are: (1) effluent streams, in

which groundwater contained in the aquifer drains into the stream, as baseflow; and (2) influent streams, where the stream contributes to the groundwater flow (Fig. 1). The volume of water contributed to an aquifer by streamflow, or contributed to streamflow from an aquifer, is part of the regional water balance, which may vary seasonally. The rate at which water flows, in either direction, is governed by a number of factors, most important among which are the pressure heads generated by the respective water masses, and the permeability of the sediments forming the stream bed and surrounding aquifer. Crucial to the net direction of water flow is the level of the water table and this, in unconfined aquifers, is influenced by groundwater recharge, air entrapment during recharge, stream bank storage effects, evapotranspiration and uptake by riparian vegetation, and by atmospheric pressure (Freeze & Cherry, 1979).

Defining the hyporheic boundaries

For most of the year, in temperate streams with deep gravel beds, the bulk of the water in the hyporheic zone is provided through baseflow (see, for example, Wallis *et al.*, 1981). As it passes
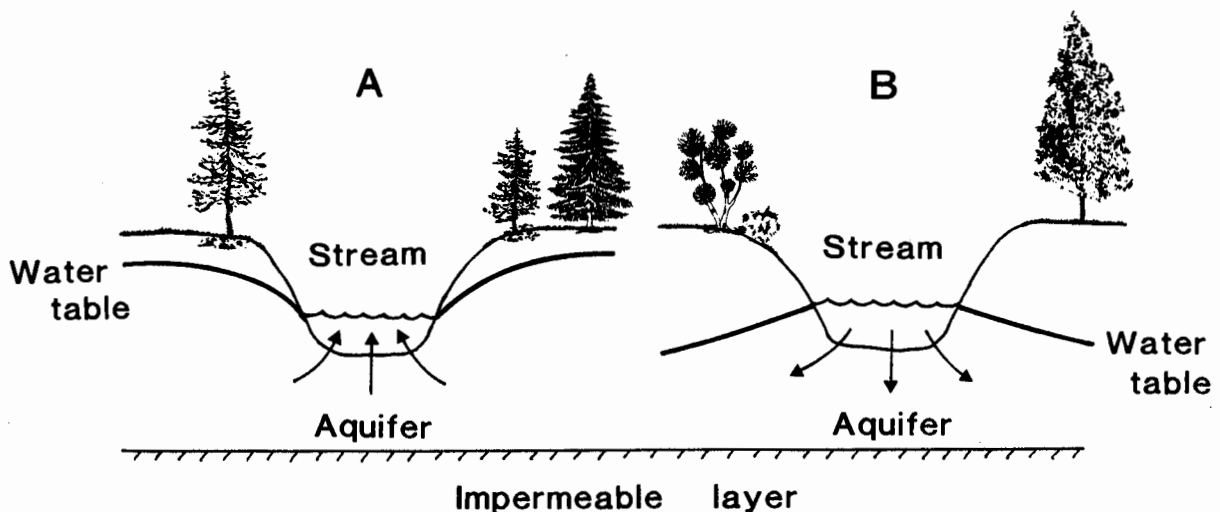

Fig. 1. The two most common stream-aquifer interrelationships: (A) an aquifer-fed, or 'effluent' stream; (B) a stream-fed aquifer ('influent' stream) (after Bear, 1979).

across the hyporheic/groundwater interface, some of its physical and chemical properties change, probably in response to contact with stream water, different sediment composition and configurations, dissolved oxygen, organic material raining down from the stream bed, and increased numbers and diversities of both micro- and macro-organisms. In certain types of stream (e.g. influent streams, such as are found in the Sonoran Desert, Arizona; Fisher *et al.,* 1982) much of the hyporheic water may be derived from streamflow, but the nature of this changes, too, as it penetrates the stream bed. Even in effluent streams, common bed features cause continuous, but more local, inputs of surface water into the hyporheic zone. These features include: gravel bars, rocks and debris (e.g. logs) that protrude above the general level of the stream bed, causing deflection of the current – some of it downwards; the concave sides of bends – where the momentum of the current forces water into the bank; and long riffles – where standing waves may develop which have a downward component (Fig. 2). Based on small, but measurable, differences between mean annual stream and groundwater temperatures, Whitman & Clark (1982) proposed that during winter, and at night in summer and autumn, cooler, denser stream water will displace underlying groundwater, leading to greater penetration of oxygen at these times. High velocity heads at the tail-ends of pools similarly are known to depress groundwater input in the downstream riffle (Bencala *et al.*, 1984). At certain times, however, (e.g. during spring and autumn spates) these inputs will be of greater magnitude and extent. There is some evidence (Rutherford & Hynes, 1987) to indicate that patterns of intermixing of streamflow and baseflow in the hyporheic zone may, at certain times of the year, change on a diel basis.

Opposed to these downward, surface inputs is baseflow. It is clear that groundwater does not exert a uniform upward force under the entire stream bed (Godbout & Hynes, 1982) but, rather, an uneven upward flow (not unlike the inputs from the surface) resulting from the mixed nature of stream substrates. The picture of the hyporheic

zone that emerges, therefore, is one of a somewhat ragged-edged, middle zone (Fig. 2) in which environmental conditions are neither the same as in the top few centimetres of stream bed (the 'benthic zone', in the strict sense) nor the same as in the groundwater proper. The hyporheic habitat therefore fits the definition of an 'ecotone' (Allaby, 1988) quite well, although certain environmental adversities (e.g. limited dissolved oxygen levels) may result in a lower species diversity compared with the surface of the stream bed.

Despite, the probable non-linear nature of the hyporheic/groundwater boundary, a recent attempt was made to locate it through examination of discontinuities in the properties of interstitial water samples taken beneath the beds of two Canadian streams (Williams, 1989). In the Rouge River, which has a porous bed some 40 cm deep underlain by clay, changes in the levels of a number of chemical parameters occurred from a point near the bank/surface water margin obliquely down under the river (examples are shown in Fig. 3). Levels of alkalinity, measured as mg l^{-1} of $CaCO_3$, in July, were very similar in both the river water and in the interstitial water immediately beneath the channel however, on the bank side of the breakline, levels were considerably higher. A similar pattern was evident for dissolved carbon dioxide, although surface water levels were lower. Nitrate-N levels were, conversely, very much lower under the bank (Fig. 3A). There was no obvious breakline shown in the levels of orthophosphate across the transect, and amounts were quite variable although they were generally much greater in the interstices (Fig. 3B).

In August in nearby Duffin Creek, which has a deeper bed, two breaklines were evident. The first, typified by dissolved oxygen, the amount of organic matter (Fig. 4C, D), alkalinity, suspended solids, B.O.D. and carbon dioxide, ran from about the river margin obliquely down under the bank. The second ran from near the margin obliquely down under the river bed, and was the pattern seen in nitrate-N (Fig. 4A) and sulphide levels. There was no pattern to the distribution of orthophosphate levels apart from a tendency to be higher in the interstices (Fig. 4B). Levels of both
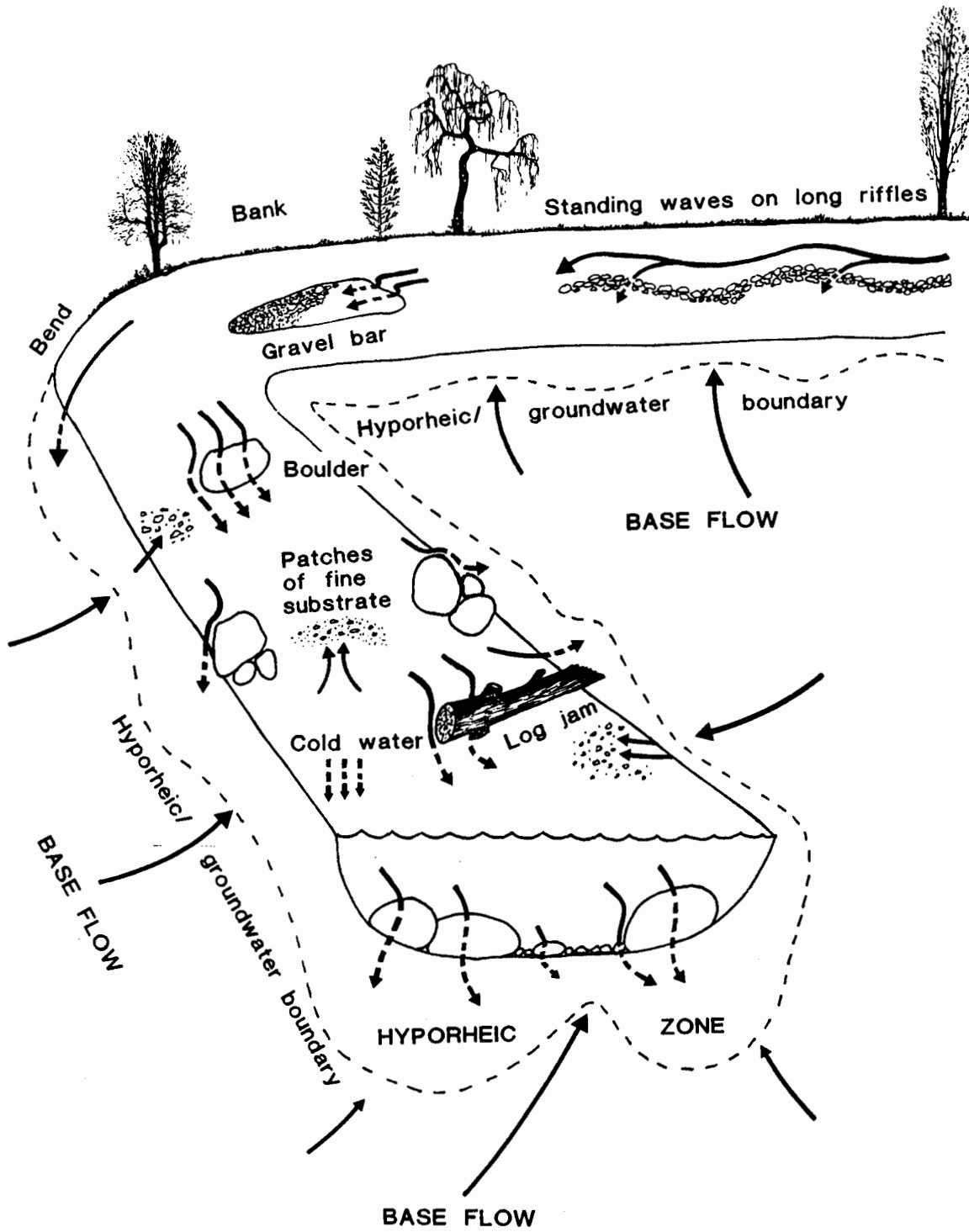
Fig. 2. Examples of the means by which water is believed to flow through the hyporheic zone (———→ indicates movement from the groundwater; – – –→ indicates movement from the surface water).
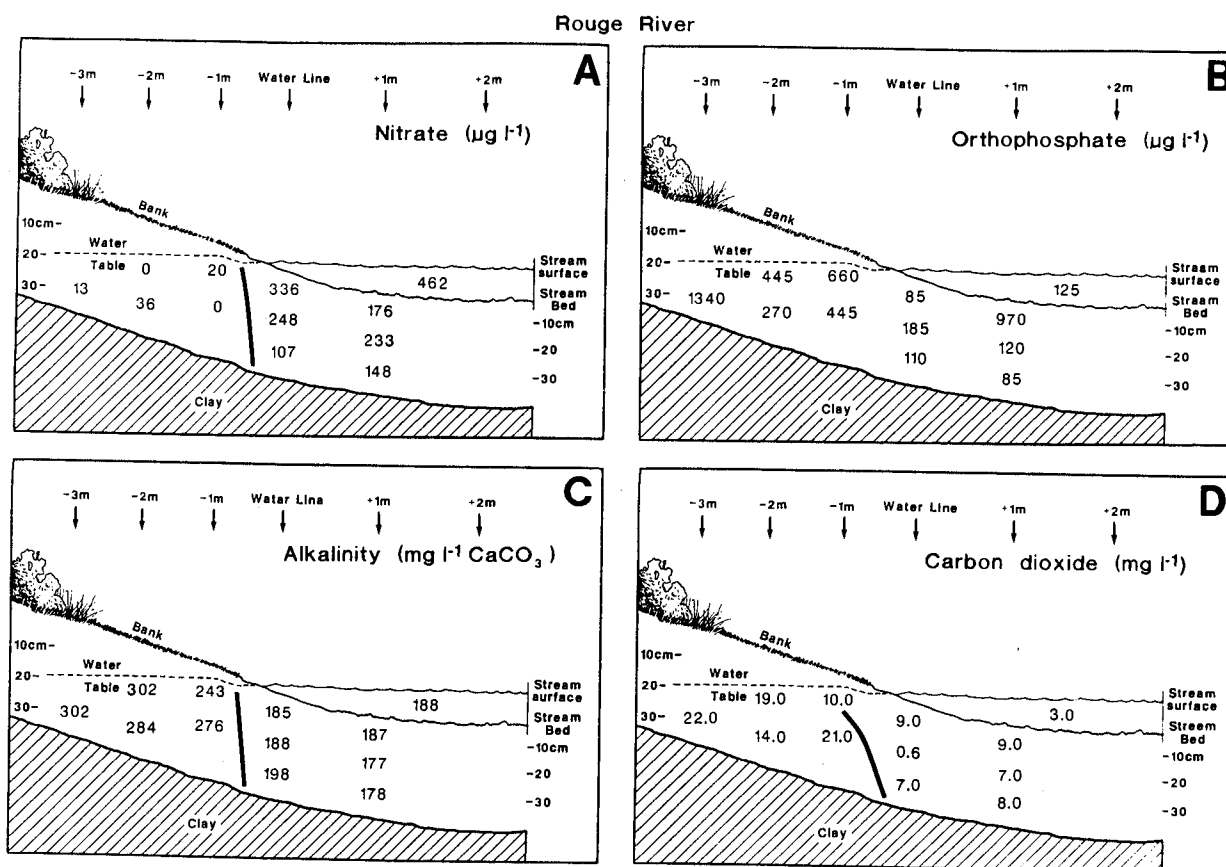
Rouge River

Fig. 3. Diagram of the Rouge River, Ontario showing the levels of water chemistry parameters measured, in July, at a variety of depths across a transect from mid-river to beneath the bank: (A) nitrate-N [μg l^{-1}]; (B) orthophosphate [μg l^{-1}]; (C) alkalinity [mg l^{-1} CaCO$_3$]; (D) dissolved CO$_2$ [mg l^{-1}]. Water samples were taken using a standpipe (see Williams & Hynes, 1974). Areas of discontinuity are indicated by a thick black line.

nitrate-N and orthophosphate were considerably lower in Duffin Creek than in the Rouge River.

It was proposed that these breaklines represented the approximate positions of the hyporheic/groundwater boundary in these two small rivers, at these two moments in time, respectively. Variation in the position of the lower end of the breakline in Duffin Creek, together with the apparent randomness of the levels of orthophosphate in the interstices of both rivers, may reflect local reactions within pockets of substrate having different physical and/or chemical characteristics. In the case of phosphorus, the complex nature of its various forms with their ability to be adsorbed onto sediment surfaces and subsequently regenerated into solution by biotic

processes (Mortimer, 1971; Stevenson, 1986), makes interpretation difficult. Other studies (e.g. Grimm *et al.*, 1981; Triska *et al.*, 1989) have reported high levels of phosphorus in hyporheic waters. Processes by which phosphorus and other nutrients are retained and transformed within the hyporheic zone clearly require more detailed investigation.

The position of the upper boundary likely varies less than the lower one and is thought to be within 5 to 10 cm of the stream bed surface (Williams, 1984). Significant changes in environmental conditions, particularly water chemistry, are known to occur over very small vertical distances in the finer sediments of lentic systems (e.g. Brundin, 1951) but these have been little studied in the
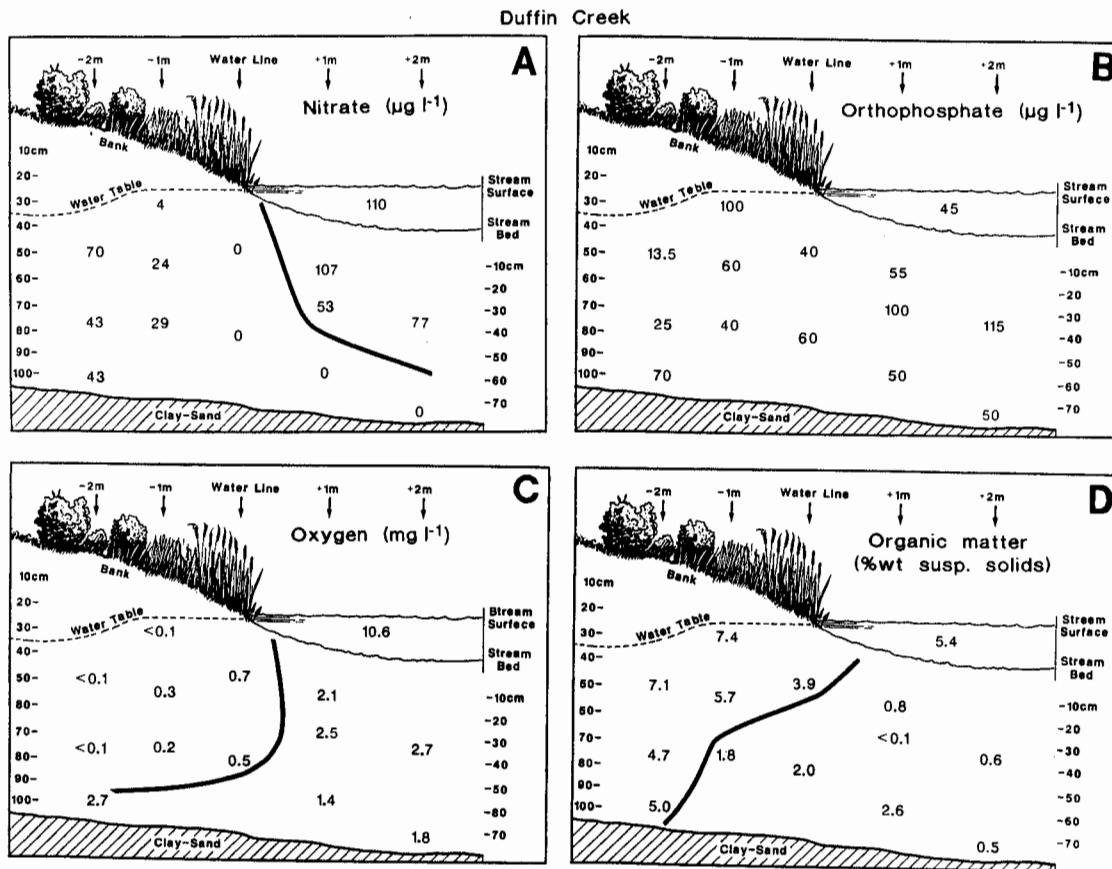
Duffin Creek

Fig. 4. Diagram of Duffin Creek, Ontario showing the levels of water chemistry parameters measured, in August, at a variety of depths across a transect from mid-river to beneath the bank: (A) nitrate-N [μg l^{-1}]; (B) orthophosphate [μg l^{-1}]; (C) dissolved oxygen [mg l^{-1}]; (D) interstitial particulate organic matter [% wt of suspended solids]. Water samples were taken using a standpipe (see Williams & Hynes, 1974). Areas of discontinuity are indicated by a thick black line.

coarser substrates of stream beds. It is interesting to note, however, that in both rivers the levels of most parameters differed between the surface water and adjacent interstitial water, a distance of between 10 and 15 cm (Figs 3 and 4).

Confirmation of the positions of the hyporheic boundaries, proposed on the basis of chemical discontinuities, in the two Canadian rivers came from an analysis of the distribution patterns of the faunas (Williams, 1989). Ordination (DECORA-NA) and community classification (TWIN-SPAN) techniques indicated that, in both rivers, the factor most associated with community structure was linear distance from mid-river. In each system, a river community was distinguished from

a community under the bank, and these were separated by a community characteristic of the river margin, the latter corresponding to the approximate position of the chemical breakline (the hyporheic/ groundwater boundary). Additionally, in Duffin Creek, the analysis distinguished between a surface (benthic) and a hyporheic community, indicative of the predicted upper boundary.

Relationship of the fauna to interstitial water chemistry

Again, there has been little research done on this in streams. Many of the taxa in the Canadian
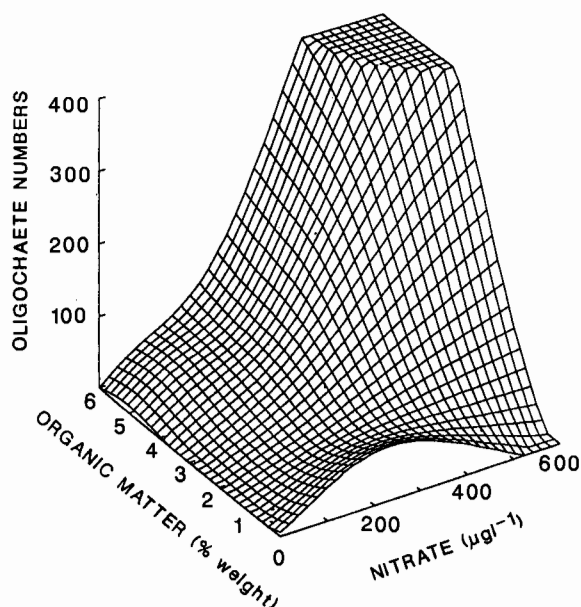
Fig. 5. The interrelationship between oligochaete density (expressed as numbers in 75 cm³ of gravel) and the levels of nitrate-N and particulate organic matter in the interstices beneath the Rouge River, in July.

Fig. 6. The interrelationship between oligochaete density (expressed as numbers in 75 cm³ of gravel) and the levels of nitrate-N and sulphide in the interstices beneath Duffin Creek, in August (the upper plateau indicated is probably not real and due to extrapolation by the computer programme because of the few data points available at this end of the scale).

study showed no correlation with the suite of parameters measured (Williams, 1989). Nevertheless, in the Rouge River, the overall density of invertebrates was negatively correlated with both the conductivity and the alkalinity of the interstitial water (not surprising since these two parameters tend to be highly correlated themselves; $r = 0.98$, in this case). The density of oligochaetes was positively correlated with both the amount of nitrate-N and organic matter in the interstices ($r = 0.62$ and 0.65, respectively; the interrelationship is summarized in Fig. 5). Nematode numbers were positively correlated with levels of sulphide in the Rouge River interstices ($r = 0.60$). In Duffin Creek, oligochaete numbers were positively correlated ($r = 0.71$) with nitrate-N levels, but not organic matter, and were negatively correlated ($r = -0.54$) with sulphide (interrelationship shown in Fig. 6).

It is difficult to judge the biological significance of some of the correlations obtained between environmental water chemistry and fau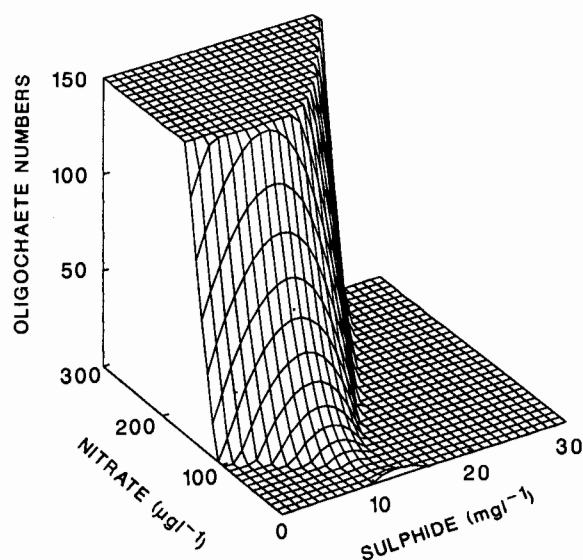nal density in these two rivers. It has been shown, for example, that benthic density increases with calcium levels over the range 7.4 to 167.0 mg l^{-1} (Egglishaw, 1968). The negative correlation found between the amount of $CaCO_3$ and density in the Rouge River may be a consequence of the very high levels of the former found in groundwater (243 to 302 mg l^{-1}; Fig. 3C) in this region of highly calcareous soils. Why no relationship between faunal density and calcium level was detected in Duffin Creek (interstitial range 192 to 356 mg l^{-1}) is puzzling. A positive correlation between the density of oligochaetes and the amount of organic matter present is understandable, as the latter forms the bulk of their diet. The relationship with nitrate-N may be an indirect one through the amount of organic matter generated – high nitrate levels resulting in increased plant growth, on the stream bed, culminating, upon decomposition, in increased organic matter much of which will settle into the interstices. An interesting pattern evident in the distribution of nitrate-N across both river transects (Figs 3A & 4A) is that the highest levels occurred in the surface water,

reduced levels occurred in the hyporheic zone, and the lowest levels occurred on the groundwater side of the lower boundary. Fiebig (1988) showed, similarly, that whereas water in both the channel and the interstices of the bank of the Afon Hafren, Wales, was high in nitrate-N but low in ammonium-N, the situation was reversed in the soilwater under the adjacent forest. It is conceivable that if, in the Canadian study, most of the nitrogen present in the true groundwater was in the form of ammonium, conversion to nitrate by nitrifying bacteria would not be possible until it came in contact with water containing oxygen. This would account for the marked increase in nitrate levels seen on the hyporheic side of the breaklines, in both rivers. In Duffin Creek, there was a significant positive correlation ($r = 0.61$; $p < 0.05$) between the levels of dissolved oxygen and nitrate. In Little Lost Man Creek in northwestern California, the presence of dissolved oxygen on the stream side of the hyporheic/groundwater interface was coincident with a switch from ammonium-N to predominantly nitrate-N (Triska *et al.*, 1989).

The positive correlation between nematode density and sulphide levels in the Rouge may relect the ability of this group to thrive under anaerobic conditions (Wharton, 1986); sulphide and oxygen levels were strongly negatively correlated in both rivers ($r = -0.75$ in the Rouge, and $r = -0.81$ in Duffin Creek).

Hyporheic models

Even though information on the hyporheic zone and its fauna is still sparse, and hard data on environmental processes within the interstices rare, construction of preliminary models of the dynamics of the system may be useful. This is best done pictorially. The models apply primarily to the rhithronic portions of streams or small rivers with deep, porous beds in temperate regions of the Northern Hemisphere, where most of the data have been gathered.

During springtime in these streams, baseflow predominates (left-hand side of Fig. 7A) except during snowmelt, in colder regions, when surface runoff causes high streamflow. In the latter case, meltwater is prevented from penetrating to the groundwater (and thus increasing baseflow) by a layer of frozen soil; under such conditions, the extent of the hyporheic zone may increase temporarily (right-hand side of Fig. 7A). In terms of major nutrient inputs to the system, total organic carbon (TOC) entry is moderate, with dissolved organic carbon (DOC) and particulate organic carbon (POM) coming from the stream, but some DOC also coming from the groundwater. Total organic nitrogen (TON) is likely to be low (Leichtfried, 1988) and derived from both the stream and groundwater. Dissolved oxygen levels are variable, with deeper penetration accompanying periods of increased streamflow (Williams & Hynes, 1974); groundwater may contain oxygen under certain circumstances (Krogius & Krokhin, 1948; Winograd & Robertson, 1982). Hyporheic densities are typically low at this time of year as insects make their way to the surface of the stream bed prior to emergence. Biomass and diversity are, correspondingly low (Williams & Hynes, 1974).

During reduced surface flow, in open streams, in summer, baseflow may again supply most of the water in the channel, with the possible raising of the hyporheic/groundwater interface (Fig. 7B, right-hand side). In heavily-wooded streams, however, uptake of groundwater and subsequent transpiration by riparian vegetation may result in a lowered water table (Lee & Hynes, 1978) and greater penetration of streamflow into the interstices (Fig. 7B, left-hand side). Moderate inputs of DOC might be expected from the groundwater (Ford & Naiman, 1989), while inputs of POM, in the form of sloughed-off algal cells from the stream bed surface, settle down into the interstices (Williams *et al.*, 1983). POM derived from bank erosion may be forced into the interstices during summer spates (Leichtfried, 1988). Inputs of nitrogen, during summer, have been recorded as high (~ 15 mg l^{-1} N in an alpine stream; Leichtfried, 1988) and seem to come primarily from ammonium in the groundwater (Wetzel, 1983). Dissolved oxygen in the hyporheic zone is
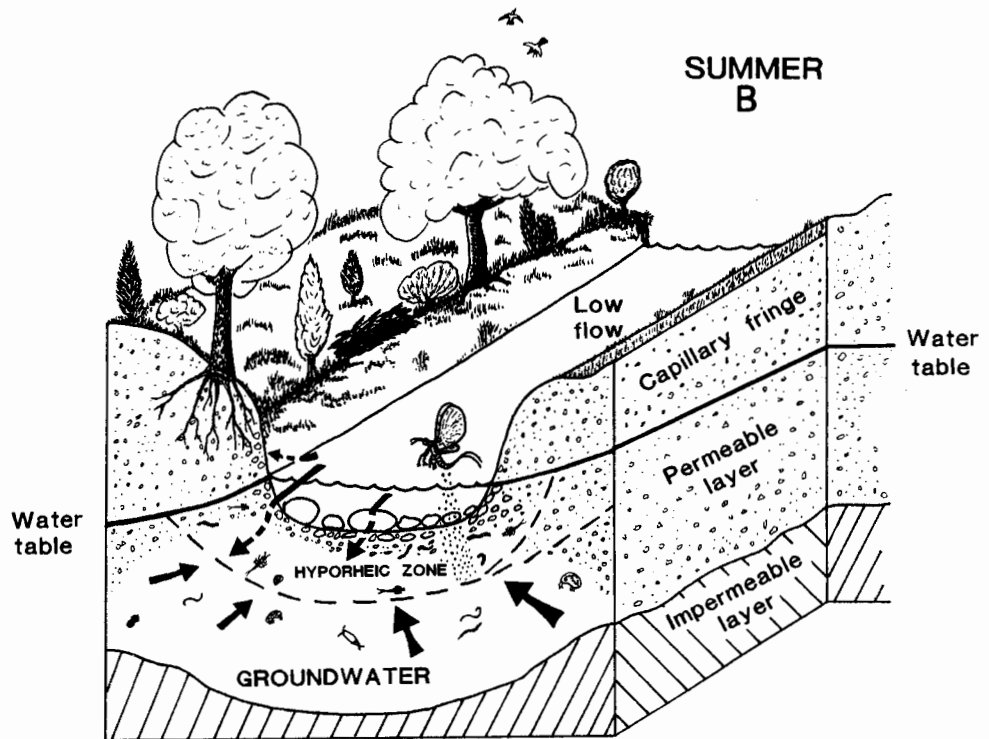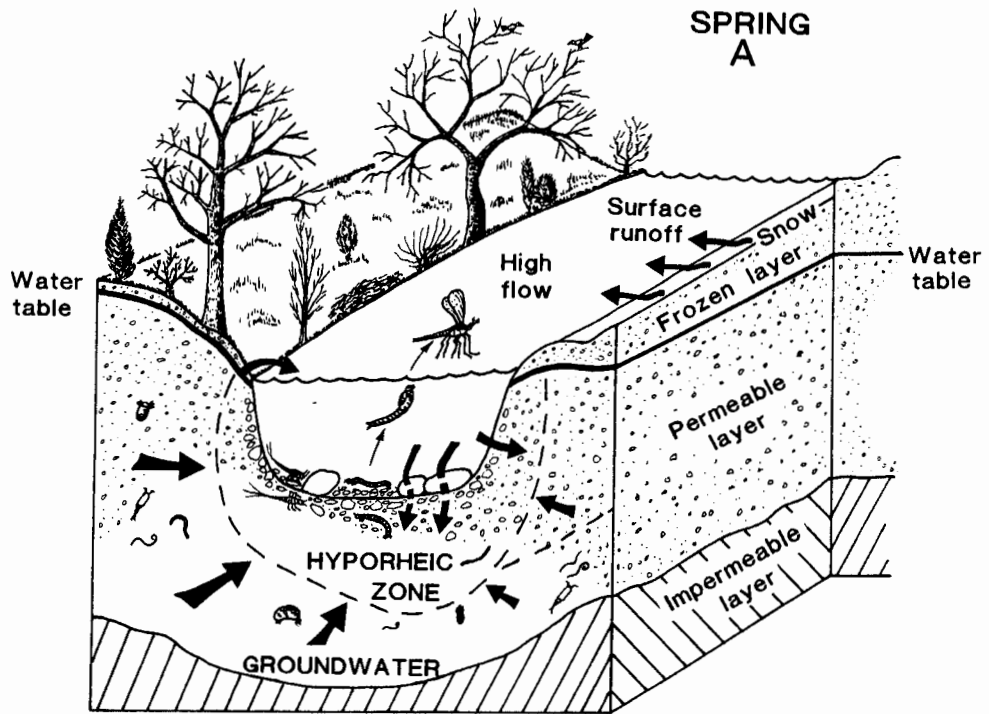
generally low, due to warmer temperatures and increased biological activity, but would be expected to be higher after summer spates in open watersheds, and in streams in which the water table is low and streamflow penetrates deeply. In terms of the fauna, density is moderate and increasing as eggs hatch and small larvae colonize the interstices. Biomass is low at first, but increases as these animals grow, and diversity steadily increases.

In the autumn, baseflow predominates (Fig. 7C) although there may be brief periods when streamflow input increases, especially after heavy rainfall but before the water table rises increasing baseflow. Conditions like this may cause the hyporheic/groundwater boundary to oscillate. TOC input may not be as great as in summer (Leichtfried, 1988), although the source now switches to the breakdown products of autumn-shed leaves. DOC input from the groundwater continues. Input of nitrogen has been recorded as less than in summer (Leichtfried, 1988) and is probably derived from both the groundwater (as ammonium) and from the start of breakdown of riparian leaves (initially as organic nitrogen). Dissolved oxygen levels in the hyporheic zone in the autumn are probably not much different from those seen in the summer and, again, may be expected to rise after heavy rainfall when streamflow input to the interstices increases. Hyporheic density is high at this time, with increasing diversity as more species hatch from summer-laid eggs, and increasing biomass as the animals grow (Williams, 1984).

Winter is the time of maximum density, diversity and biomass of the hyporheos. Baseflow predominates and the volume of the hyporheic zone remains relatively constant apart from minor oscillations in the position of the hyporheic/groundwater interface caused by local changes in input from streamflow (Fig. 7D). Where anchor ice forms on the bed surface, in cold climates, input of streamflow is reduced. Ice forming on the stream surface may also diminish streamflow. This is the time of peak breakdown of allochthonous CPOM to FPOM, some of which either settles or is carried into the interstices. DOC is derived both from this breakdown process (Crocker & Meyer, 1987) and from the groundwater. Organic nitrogen originating from leaves, other allochthonous inputs, stream macrophytes and algae, and from dead animal tissues is at its highest level in the stream in winter (Leichtfried, 1988) and becomes mineralized in the sediment by the activity of heterotrophic bacteria. The ammonium produced is rapidly changed, in the presence of oxygen, to nitrate. Some of this nitrate, through microbial activity at low redox potential, will be converted to N_2O or N_2, both of which will be subsequently lost to the atmosphere (Kaushik et al. 1981). Oxygen levels in the interstices may be moderately high because of decreased water temperatures, and may increase after heavy rain. However, consumption by the fauna is also high.

These models have been built primarily around effluent streams, as studies on the hyporheic zone of influent systems are rare. However, one such system, Sycamore Creek, Arizona is currently receiving considerable attention. It is known, for example, that high levels of dissolved oxygen and inorganic nitrogen occur in the interstices of this desert stream (Grimm & Fisher, 1984) and that the size of the hyporheic zone is dependent on discharge, which varies according to season and storm intensity. Surface flow is typically low for much of the year, with the consequence that the hyporheic zone in this and, presumably, other influent systems represents a major portion of the available aquatic environment (Valett et al., 1990) – indeed, during dry periods, the only water present is hyporheic. Hyporheic processes must, necessarily, play a fundamental role in the functioning of such aquatic ecosystems particularly as, for example, the interstices of Sycamore Creek are known to contain more than three times the amount of organic matter found on the stream bed surface (Grimm & Fisher, 1989). The evidence available so far indicates that hyporheic conditions in influent streams are strongly influenced by patterns of surface flow (Valett et al., 1990), perhaps more so than in baseflow-dominated effluent streams?

SPRING
A

Water table

Surface runoff

Snow

Frozen layer

Water table

High flow

Permeable layer

HYPORHEIC ZONE

Impermeable layer

GROUNDWATER

SUMMER
B

Water table

Low flow

Capillary fringe

Water table

Permeable layer

HYPORHEIC ZONE

Impermeable layer
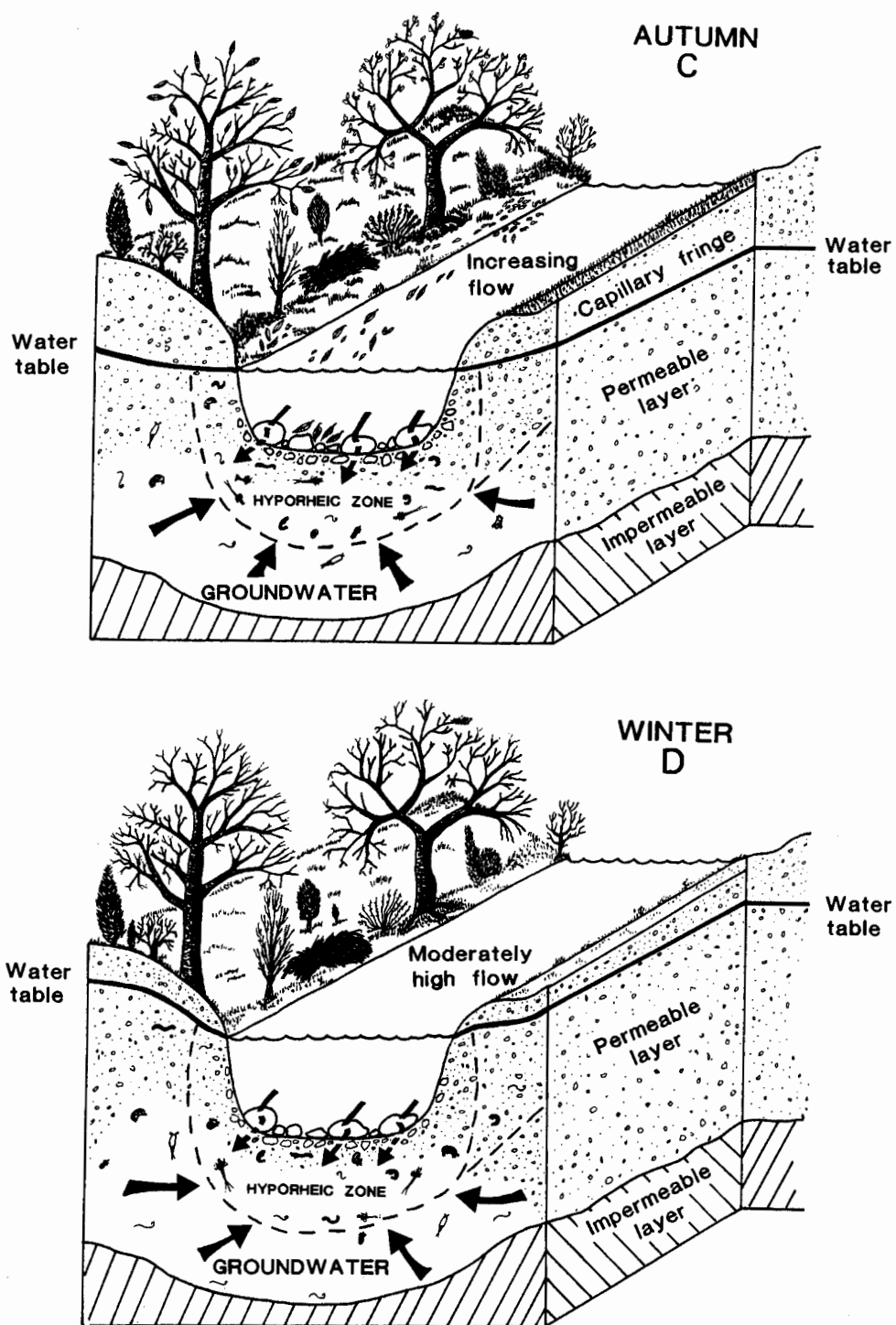
Water table

GROUNDWATER

Fig. 7. Descriptive models of the dynamics of the hyporheic zone and surrounding surface- and groundwater. Direction of water movement is indicated by arrows, and their size estimates the relative magnitude of flow. Stages in the life cycle, location and size of representative invertebrates are also shown, as are features of riparian vegetation: (A) spring; (B) summer; (C) autumn; (D) winter (adapted from Williams, 1981).

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Discussion

Research on the hyporheic zone and its fauna is still largely descriptive and even this stage is not well advanced. Early scepticism of the magnitude and widespread nature of these interstitial populations had a retarding effect, but this has largely been overcome. A second problem has been development of suitable hyporheic samplers robust enough to penetrate mineral substrates while, at the same time, having sufficient sophistication and speed to capture organisms *in situ*. No hyporheic sampling technique is as easy to use as most benthic samplers, but this is an inevitable consequence of the rigorous nature of the habitat. However, a variety of corers and artificial substrate samplers is now available. Perhaps those with most promise are: (1) the standpipe corer (Williams & Hynes, 1974) which enables discrete, though small, samples of substrate to be removed quickly; (2) the frozen core sampler (Stocker & Williams, 1972) which, with the important advance of a presampling electrical shock to immobilize organisms (Bretschko, 1985), enables bigger and undisturbed volumes of substrate to be removed; and (3) the cage-pipe sampler (Panek, 1991) – a slim form of artificial substrate sampler.

Information on the flow vector dynamics within the hyporheic zone is still patchy, known only from a few short-term measurements in a handful of locations. Groundwater hydrologists have provided freshwater ecologists with a framework within which we can be guided, but the scale upon which most hydrologists work is too large to provide much insight into flow patterns in the top 1 m or so of stream beds. It seems that in effluent streams, the net movement of water through the hyporheic zone is upwards, with groundwater as the source. Near the surface of the stream bed, this water becomes mixed with stream water that has been deflected downwards by a variety of surface features. Penetration of oxygen and organic material allows the immature stages of many benthic species to colonize the interstices. Through the biological processes of these invertebrates, those of microorganisms on the surfaces of the sediment particles ('biofilm' *sensu* Lock

et al., 1984), and purely chemical reactions resulting from the contact of two water types, the nature of the water changes so as to produce environmental conditions that are neither those of pure groundwater or pure stream water. In influent streams, and, under certain circumstances, in effluent streams, the net movement of water through the hyporheic zone is downwards, with stream water as the source. With less 'resistance' from baseflow, penetration of oxygen and organic materials is likely to extend further thus pushing the hyporheic/groundwater boundary deeper and creating a larger hyporheic zone.

Future research needs

What are urgently needed now are studies to locate the upper and lower hyporheic boundaries in a variety of running water systems, together with temporal tracking of boundary flux. There should be detailed examination of the nature and causes of the changes that occur in the chemistry of water as it crosses these boundaries and, especially, of the transformation among the various chemical states of nitrogen and phosphorus. Quantification of the import, export and transformation of both dissolved and particulate organic matter is crucial to any understanding of the productivity of the hyporheic zone. Alongside research on the physical and chemical environment must be more sophisticated studies on the environmental requirements and general biology of the hyporheos. Foremost among the latter should be examination of the physiology of interstitial organisms, particularly their tolerance of low oxygen levels and their relationship to water chemistry. Implications of the three-dimensional nature of benthic populations to estimates of lotic invertebrate production (Williams, 1984) have still to be quantified.

Acknowledgements

References

Allaby, M., 1988. Dictionary of the environment (3rd edn). Macmillan Reference Books, London, 423 pp.

Bear, J. 1979. Hydraulics of groundwater. McGraw-Hill, London, 569 pp.

Bencala, K. E., V. C. Kennedy, G. W. Zellweger, A. P. Jackman & R. J. Avanzino, 1984. Interactions of solutes and streambed sediments: 1. An experimental analysis of cation and anion transport in a mountain stream. Wat. Resourc. Res. 20: 1797–1803.

Bretschko, G., 1985. Quantitative sampling of the fauna of gravel streams (Project Ritrodat-Lunz). Verh. int. Ver. Limnol. 22: 2049–2052.

Brundin, L. 1951. The relation of oxygen microstratification at the mud surface to the ecology of the profundal bottom fauna. Rep. Freshw. Res. Drottningholm 32: 32–43.

Coffman, W. P. & L. C. Ferrington, 1984. Chironomidae. In R. W. Merritt & K. W. Cummins (eds), An introduction to the aquatic insects of North America, Kendall/Hunt Pub. Co., Dubuque, Iowa, 722 pp.

Crocker, M. T. & J. L. Meyers, 1987. Interstitial dissolved organic carbon in sediments of a southern Appalachian headwater stream. J. N. Am. Benthol. Soc. 6: 159–167.

Egglishaw. H. J., 1968. The quantitative relationship between fauna and plant detritus in streams of different concentrations. J. appl. Ecol. 5: 731–740.

Fiebig, D. M., 1988. A study of riparian zone and stream water chemistries, and organic matter immobilization at the stream-bed interface. Ph. D. Thesis, Univ. Wales, 311 pp.

Fisher, S. G., L. J. Gray, N. B. Grimm & D. E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecol. Monogr. 52: 93–110.

Ford, T. E. & R. J. Naiman, 1989. Groundwater-surface water relationships in boreal forest watersheds: dissolved organic carbon and inorganic nutrient dynamics. Can. J. Fish. aquat. Sci. 46: 41–49.

Freeze, R. A. & J. A. Cherry, 1979. Groundwater. Prentice-Hall, New Jersey, 604 pp.

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

Grimm, N. B. & S. G. Fisher, 1984. Exchange between surface and interstitial water: implications for stream metabolism and nutrient cycling. Hydrobiologia 111: 219–228.

Grimm, N. B. & S. G. Fisher, 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. J. N. Am. Benthol. Soc. 8: 293–307.

Grimm, N. B., S. G. Fisher & W. L. Minckley, 1981. Nitrogen and phosphorus dynamics in hot desert streams of southwestern U.S.A. Hydrobiologia 83: 303–312.

Kaushik, N. K., J. B. Robinson, W. N. Stammers & H. R. Whiteley, 1981. Aspects of nitrogen transport and transformation in headwater streams. In M. A. Lock & D. D. Williams (eds), Perspectives in running water ecology, Plenum Press, New York, 430 pp.

Krogius, F. V. & E. M. Krokhin, 1948. On the production of young sockeye salmon (*Oncorhynchus nerka* Walb.) Izvestiia Tikhookeanskovo Nauchno-Issledovatelskovo. Instituta Rybnovo Koziasitva i Okeanografii 28: 3–27. (Fisheries Research Bd of Canada Transl. Ser. No. 109).

Leen D. R. & H. B. N. Hynes, 1978. Identification of groundwater discharge zones in a reach of Hillman Creek in southern Ontario. Wat. Pollut. Res. Can. 13: 121–133.

Leichtfried, M., 1988. Bacterial substrates in gravel beds of a second order alpine stream (Project Ritrodat-Lunz. Austria). Verh. int. Ver. Limnol. 23: 1325–1332.

Lock, M. A., R. R. Wallace, J. W. Costerton, R. M. Ventullo & S. E. Charlton, 1984. River epilithon: towards a structural-functional model. Oikos 42: 10–22.

Mortimer, C. H., 1971. Chemical exchanges between sediments and water in the Great Lakes – speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16: 387–404.

Panek, K. L. J., 1991. Migrations of the macrozoobenthos within the bed sediments of a gravel stream (Ritrodat-Lung study area, Austria). Verh. Internat. Verein. Limnol. 24: 1944–1947.

Rutherford, J. E. & H. B. N. Hynes, 1987. Dissolved organic carbon in streams and groundwater. Hydrobiologia 154: 33–48.

Schwoerbel, J., 1961. Uber die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. Arch. Hydrobiol. Suppl. 25: 182–214.

Stevenson, F. J., 1986. Cycles of soil: carbon, nitrogen, phosphorus, sulphur, micronutrients. Wiley-Interscience, New York, 380 pp.

Stocker, Z. S. J. & D. D. Williams, 1972. A freezing core method for describing the vertical distribution of sediments in a stream bed. Limnol. Oceanogr. 17: 136–138.

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

Valett, H. M., S. G. Fisher & E. H. Stanley, 1990. Physical and chemical characteristics of the hyporheic zone of a Sonoran Desert stream. J. N. Am. Benthol. Soc. 9: 201–215.

Wallis, P. M., H. B. N. Hynes & S. A. Telang, 1981. The importance of groundwater in the transportation of allochthonous dissolved organic matter to the streams draining small mountain basins. Hydrobiologia 79: 77–90.

Wetzel, R. G. 1983. Limnology. W. B. Saunders Co., Philadelphia, PA., 767 pp.

Wharton, D. A., 1986. A functional biology of nematodes. Croom Helm, London, 192 pp.

Whitman, R. L. & W. J. Clark, 1982. Availability of dissolved oxygen in interstitial waters of a sandy creek. Hydrobiologia 92: 651–658.

Williams, D. D., 1981. Migrations and distributions of stream benthos. In M. A. Lock & D. D. Williams (eds), Perspectives in running water ecology, Plenum Press, New York, 430 pp.

Williams, D. D., 1984. The hyporheic zone as a habitat for aquatic insects and associated arthropods. In V. H. Resh & D. M. Rosenberg (eds), The ecology of aquatic insects, Praeger Scientific, New York, 625 pp.

Williams, D. D., 1987. The ecology of temporary waters. Croom Helm, London, 205 pp.

Williams, D. D., 1989. Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. Freshwat. Biol. 22 189–208.

Williams, D. D. & H. B. N. Hynes, 1974. The occurrence of benthos deep in the substratum of a stream. Freshwat. Biol. 4: 233–256.

Williams, D. D., A. T. Read & K. A. Moore, 1983. The biology and zoogeography of *Helicopsyche borealis* (Trichoptera: Helicopsychidae): a Nearctic representative of a tropical genus. Can. J. Zool. 61: 2288–2299.

Winograd, I. J. & F. N. Robertson, 1982. Deep oxygenated groundwater: an anomaly or common occurrence? Science 216: 1227–1230.