Seasonal boundary dynamics of a groundwater/surface-water ecotone.

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Interstitial water, faunal samples, and hydrogeological data were collected beneath a riffle on the Speed River, southern Ontario, Canada. The purpose was to identify the location and seasonal fluctuation of the hyporheic/groundwater interface and to examine several aspects of water mass chemical signatures and the dynamics of the interstitial fauna. Concentration discontinuities in several water chemistry parameters delineated the chemical boundary between the true groundwater and hyporheic habitats. The groundwater mass was characterized as having higher levels of ammonium, alkalinity, and conductivity, and lower nitrate levels. Differences in water chemistry between the hyporheic and groundwater zones persisted throughout the year, though no single variable differed quantitatively between these two zones on all occasions. The location of the chemical discontinuity varied seasonally. Whereas hyporheic and groundwater faunal subunits of the interstitial community were identified and the location of the subunits coincided with the chemical breaklines, response to shifts in the position of the hyporheic/groundwater interface was taxon rather than subunit based. Fauna therefore provided poor spatial resolution in terms of pinpointing the location of the interface. Boundary fluctuation coincided with extremes in seasonal discharge patterns and was regulated by the relative strength of the upward force of baseflow and the downward force of advecting surface water. Identifying patterns of fluctuation of the hyporheic/groundwater interface, and consequently hyporheic habitat volume, may have important consequences for the storage, retention, and cycling of nutrients in lotic ecosystems.

Key words: ecotone; freshwater invertebrates; groundwater; hyporheic zone; hyporheic/groundwater interface; water chemistry.

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INTRODUCTION

Through initiatives cosponsored by the International Unions' Scientific Committee on Problems of the Environment (SCOPE) and UNESCO's Man and the Biosphere Programme (MAB), the characterization of landscape boundaries, or ecotones (*sensu* Holland 1988), has become an important research objective. It is now widely recognized that ecotones function as regulatory sites in the movement of nutrients (e.g., Lowrance et al. 1984), organic materials (e.g., McArthur and Marzolf 1986), and biotas (e.g., Ward and Palmer 1994) across landscapes. Concomitantly, there has developed a body of literature concerning the importance of ecotone management (see review in Di Castri et al. 1988, Naiman and Decamps 1990, Holland et al. 1991). While ecosystem boundaries often are defined by conspicuous changes in ecosystem characteristics (e.g., transition zone from forest to grassland), the ecotone between the surface and subsurface environments in lotic ecosystems, the hyporheic zone, is not precisely delineated as it cannot be reduced to a simple physical boundary (Gibert 1991).

Early attempts to describe the spatial extent of hyporheic zones were based largely on the vertical and lateral distributions of epigeal (derived from the surficial river bed environment) or hypogean (derived from the true groundwater environment) fauna. Where hypogean taxa were absent or poorly developed, studies focused on the depth of penetration of epigeal fauna. Both Coleman and Hynes (1970) and Williams and Hynes (1974) suggested that the hyporheic zone extended deep into the substratum (30-70 cm) beneath a riffle on the Speed River, Ontario, Canada, as they collected high numbers of typical epigeal taxa there. Where hypogean taxa were more populous, others have attempted to demarcate hyporheic limits based on epigeal-hypogean associations (e.g., Danielopol 1989, Ward 1989, Bretschko 1991). In these studies, the distinction between the hyporheic zone and the true groundwater zone was less clear, however, as hypogean-epigeal associations were often more spatially complex.

More recently, a few studies have heeded Hynes' (1983) plea to more actively integrate the principles of groundwater science into studies of river ecology and have attempted to delineate hyporheic zones using hydrogeological and chemical measures. based on work with conservative tracer injections, Triska et al. (1989) suggested a functional means by which the spatial extent of the hyporheic zone could be identified. Their two-component hyporheic zone included the surface region (the area beneath the bed surface that was chemically indistinguishable from the channel water, containing [greater than]98% advected channel water) and the interactive zone (characterized by [less than]98% but [greater

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than]10% advected channel water). Williams (1989) identified several chemical discontinuities in two Canadian rivers, with break lines occurring from the river margin obliquely downwards under both the river bed and bank. He proposed that these discontinuities were indicators of the position of the hyporheic/groundwater interface. Using depth-to-groundwater temperature (i.e., the depth at which water temperature is isothermal with true groundwater) as an indicator of the location of the hyporheic/groundwater interface, White (1993) generated a three-dimensional model of the hyporheic zone beneath a 9 m long pool-riffle-pool sequence. These more recent studies are unique, as they represent the first explicit attempts to identify parameters that define the location of the hyporheic/groundwater interface. Yet, they provide no data to describe how the interface may shift in response to changes in relative inputs of the various sources contributing to flow in rivers. Temporal fluctuation in the volume of hyporheic interstices is likely to affect the retention and processing of material exchanged between the surface and subsurface environments. Accordingly, there is a need to identify patterns of hyporheic volume fluctuation in order that a more holistic interpretation of: (1) the nature and causes of the changes in water chemistry; and (2) the quantification of the import, export, and transformation of dissolved and particulate organic matter, which occur during exchange between contiguous groundwaters and streams, can be acquired (Williams 1993).

The goal of this study was to examine seasonal boundary fluctuation of the hyporheic/groundwater interface by quantitatively assessing the biotic and abiotic parameters beneath a stream riffle. Specifically, we were interested in the following aspects of hyporheic/groundwater dynamics: (1) do the hyporheic and groundwater zones have distinct and distinguishable chemical signatures and therefore could chemical discontinuities identified in the subsurface delineate the location of the hyporheic/groundwater interface?; (2) is the subsurface community divisible into a number of subunits whose relative positions identify the location of the hyporheic/groundwater interface?; (3) does faunal subunit distribution track seasonal shifts in the position of the hyporheic/groundwater interface?; and (4) is hyporheic/groundwater interface fluctuation related to the relative strengths of the upward force of baseflow and downward force of advected channel water?

MATERIALS AND METHODS

The study area

The study was conducted near the source of the Speed River, southern Ontario, Canada [ILLUSTRATION FOR FIGURE 1 OMITTED]. The Speed flows through gently undulating hills, drumlin fields, glacial spillways, and swampy depressions with an average gradient of 2 m/km (Ontario Department of Planning and Development 1953, Chapman and Putnam 1984). Bedrock in this region belongs to the Guelph dolomite horizon and soils are grey-brown podsols and humic glysols intermixed with outwash sand, gravels, and coarser glacial tills (Hoffman et al. 1964). Approximately 80% of the watershed is used for mixed farming, although floodplains of the upper course are largely wooded, reforested, or maintained as rough pastures (Bishop and Hynes 1969).

The main sampling area, the Rowan Farm study site (43 [degrees] 43 [minutes] 54 [seconds] N, 80 [degrees] 16 [minutes] 24 [seconds] W), consisted of a 40-m riffle and the adjacent riparian corridor. Along this reach, river width varied from 4 to 6 m and water depth ranged from 7 to 12 cm during baseflow conditions to 70 cm at the height of spring run-off. Typically, the seasonal discharge pattern along this portion of the Speed River is characterized by extended periods of high flow during the spring and fall and low flow during the summer and winter (unpublished data; Water Survey of Canada, Environment Canada, Guelph, Ontario, Canada).

To a depth of 30 cm, the substrate is composed primarily of gravels ([less than]10 cm diameter) intermixed with silts and sands together with a few larger dolomite slabs. Below 30 cm, substrate heterogeneity is low and substrate composition is dominated by medium and fine sands (*sensu* Cummins 1962). The subsurface sediment profile has been described in detail by Stocker and Williams (1972). Riparian vegetation is dominated by eastern white cedar (*Thuja occidentalis* L.) and paper birch (*Betula papyrifera*) mixed with willow (*Salix* sp.) along the north bank of the river and by goldenrod (*Solidago* sp.) and various grasses along the south bank.

Data collection

Sampling program. - As sampling effort was directed towards monitoring seasonal trends, biological, chemical, and hydrogeological data were collected during a single week-long sampling period per season from winter 1992-1993 through fall 1993. The exact time of sampling was based on seasonal river discharge extremes [ILLUSTRATION FOR

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FIGURE 2 OMITTED]. Spring and fall sampling commenced immediately following the peaks of seasonal discharge (29 April through 4 May and 27 October through 1 November, respectively). Summer and winter sampling occurred during the period when baseflow accounted for the greatest proportion of stream discharge (18 August through 23 August and 27 February through 4 March, respectively).

All data were collected from nine permanently installed sampling stations positioned at the head of the riffle in a transect across the river and into the adjacent banks [ILLUSTRATION FOR FIGURE 1B OMITTED]. The sampling device, the colonization corer, combines aspects of an artificial substrate sampler (after Panek 1991) and a bundle piezometer (Cherry 1983), which made it possible to collect faunal samples, interstitial water samples, and potentiometric head measurements at 0.2-m intervals between 0.1 and 1.1 m below the river bed surface. A detailed description of the colonization corer can be found in Fraser et al. (1996) and its performance, in comparison with other hyporheic samplers, is reported in Fraser and Williams (1997).

Macroinvertebrates. - Internal acrylic colonization sleeves, filled with sterilized Speed River sediment to specifications that mimicked the vertical sediment particle distribution of the river bed, were placed within the permanent standpipes. Following a minimum colonization period of 9 wk, the sleeves were removed from the corer with the aid of a tripod and winch. Both benthic (Mason et al. 1973, Lamberti and Resh 1985) and hyporheic (Coleman and Hynes 1970, Boulton et al. 1991) substrate colonization studies indicate that this is a sufficient time for levels of both organic matter and fauna to return to natural levels. As the sleeves were withdrawn they were wrapped in plastic film to prevent the loss of invertebrates. The sleeves were immediately cut into 20-cm sections (volume = 125 mL), and the sediment from each section was transferred to plastic sample jars. Samples corresponding to depths 20, 40, 60, 80, and 100 cm below the surface of the river bed thus were obtained from each station. These samples included sediment [+ or -] 10 cm from the depth indicated (e.g., 20-cm sample = 10-30 cm). In the field, all samples were preserved and stained using a mixture of 10% formalin and rose bengal. In the laboratory, each sample was floated with saturated calcium chloride to separate flocculent (organic) from nonflocculent material, washed through a 53-[[micro]meter] mesh net, and hand-sorted under 10-40x magnification with the aid of a dissecting microscope. The nonflocculent portions of the samples were visually inspected for cased caddisflies, bivalves, and other invertebrates not likely to be separated during floating.

Chemical measurements. - High-density polyethylene bottles were prepared according to a four-step protocol: (1) detergent wash; (2) 24-h 10% nitric acid soak; (3) distilled water rinse (7x); (4) de-ionized water rinse (5x). Each of the colonization corer water sampling tubes was cleared and allowed to refill prior to sampling. Triplicate water samples were pumped peristaltically through plastic tygon tubing from each of the 45 tubes as well as from the river itself. Each bottle was overfilled with at least two equivalent bottle volumes prior to sealing and storage at 4 [degrees] C until analysis could be performed. Cation and anion samples were filtered on site through 0.2-[[micro]meter] mesh cellulose filters with the aid of a hand-operated vacuum pump, and cation samples were acidified with ultrapure nitric acid (Ultrex II) to a pH of 2. Field and laboratory blanks and standards of known concentration were prepared in order to confirm the integrity of results derived from the analytical methods used.

Conductivity, temperature, pH, and dissolved oxygen were measured in the field using an ICM Water Analyzer, Series 51100 (Industrial and Chemical Measurement Incorporated, Hillsboro, Oregon, USA). Alkalinity (## and ## concentrations) was determined in the laboratory within 24 h of collection, using the color change standard method (APHA 1985). Biological oxygen demand was measured as the difference between the initial dissolved oxygen concentration (meter reading) and the dissolved oxygen level (modified Winkler method; APHA 1985) following 24 h of air incubation at 20 [degrees] C in the dark. Major ion concentrations were determined by high performance liquid chromatography using a Dionex 4000 Ion Chromatograph (Dionex Corporation, Sunnyvale, California, USA). All analyses were done in triplicate.

Sample quality was assessed by determining "correctness." Correctness was evaluated based on the assumption that water is a neutral substance and therefore the cation milliequivalent sum should equal the anion milliequivalent sum. The following formula was used to calculate the charge-balance error (E):

$$E (\%) = \frac{([\Sigma][zm.sub.c] - [\Sigma][zm.sub.a])}{([\Sigma][zm.sub.c] + [\Sigma][zm.sub.a])} \times 100 \quad (1)$$

where [zm.sub.c] is the molality of cation species and [zm.sub.a] is the molality of anion species (WATSPEC; Wigley 1977). Samples with E [greater than] 10% suggested that the chemical analyses likely contained inaccuracies (Freeze and Cherry 1979, Hem 1989) and therefore were not included in further data analyses. In cases where a sample was

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eliminated from further data analyses the mean value was based on the values of the remaining samples. Less than 3% of the total number of samples collected were eliminated and in no instance was it necessary to discard more than one in three samples from a triplicate.

Hydrogeology. - Water-level measurements were made in each water-sampling tube using an electric water-level indicator. Measurements were repeated 6 times over the duration of each week-long seasonal sampling period. The head data were contoured to depict potential groundwater flow for a vertical cross section of the study site, [approximately]12 m across by 1.5 m deep. Equipotential lines join points of equal hydraulic head and, assuming isotropicity of the medium through which flow occurs, flow is perpendicular to these lines. The velocity of flow is proportional to the hydraulic gradient (i), the change in water-level elevation between two points over the distance through which the change takes place (Freeze and Cherry 1979).

Data analysis

Ordination and classification techniques were used to identify potentially important environmental variables and taxa, and to assess the degree of similarity among sampling sites (Furse et al. 1984, Wright et al. 1984). Species assemblages were ordinated using Correspondence Analysis (CA) and the program CANOCO (ter Braak 1986, 1988) applied to a single, combined-seasons invertebrate data set. This allowed analysis of the spatial and temporal data simultaneously. In CA, sites are arranged into an objective order, those with similar taxonomic composition occurring most closely together. The relative strengths of the ordination axes are given by eigenvalues and the relative importance of each axis, in explaining variance in the data set, is expressed as the ratio of an eigenvalue to the sum of the eigenvalues for all axes combined. Axes are measured in standard deviations and are a measure of taxon turnover. A complete turnover in taxa can be expected in 4 SD (Hill 1979). A sizeable proportion of the specimens collected were first- or early-instar larvae that were difficult to identify to the genus or species level. Consequently, so as not to complicate the data set with multilevel taxonomic identifications, the family level was used for ordination. We acknowledge that patterns in hyporheic faunal distribution have been shown to occur at fine taxonomic levels (e.g., Williams 1989, Vervier and Gibert 1991); however, in this study identification to these levels proved impractical. CA axes were related to measured environmental variables using multiple linear regression (SPSS 6.1.3; Norusis 1995). Although linear tests may not recognize cyclical or seasonal patterns, this methodology has been used successfully in previous studies with similar objectives (e.g., Omerod and Edwards 1987, Grown and Davis 1994).

Classification of sites was made by two-way indicator species analysis (TWINSpan, Hill 1979) following conversion of quantitative taxon abundance data into a qualitative format. Conversion was accomplished by categorizing each taxon and its abundance level into individual units termed pseudospecies. In the analysis, taxa with high abundance, for example, are included not only at the appropriate pseudospecies abundance level, but also at all lower levels. As a result any given taxon may be present in a data set numerous times (Furse et al. 1984). Further details pertaining to this and advantages associated with TWINSpan are given by Furse et al. (1984) and Wright et al. (1984). based on cursory examination of our invertebrate density data, we applied three logarithmic abundance categories (each with a corresponding pseudospecies) to family-level identifications. Abundance categories 1 and 2 correspond to pseudospecies for which 1-9 and 10-99 individuals, respectively, were collected. Abundance category 3 corresponds to pseudospecies for which [greater than]100 individuals were collected. We elected to use three pseudospecies per taxon as we thought this adequately reflected the difference between rare and abundant families. The analysis was arrested following three dichotomies as beyond this level groupings were likely to be too small to be meaningful.

For TWINSpan site groups (first TWINSpan dichotomy only), mean values of individual chemical parameters that were significantly correlated with CA axes 1 or 2 (and therefore presumably related to differences in macroinvertebrate assemblage) were calculated. Means were compared using t tests (SPSS 6.1.3; Norusis 1995) following appropriate transformations to fulfil the assumptions of normality (Wilk-Shapiro) and homoscedasticity ([F.sub.max]).

TABLE 1. Mean hydraulic gradient (i, cm/cm) between the surface of the river bed and a depth of 1 m below the bed surface in the Speed River, February 1993 through October 1993. River cross section is divided into two sections - midriver to Station 1 and midriver to Station 9.

Sampling	Midriver to	Midriver to
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period	Station 1	Station 9
Spring	0.08	0.04
Summer	0.16	0.07
Fall	0.10	0.06
Winter	0.12	0.08

For the multiple regression, an [Alpha] level of P [less than] 0.05 was used as the critical value for statistical significance. For the comparisons of TWINSPAN site group means, [Alpha] was corrected for multiple tests using the Bonferroni method ($P \text{ [less than] } [\text{Alpha}]/n$, where n is the number of null hypotheses tested; Sokal and Rohlf 1981). We deemed it appropriate to use $P \text{ [less than] } 0.05$ in the regression analysis, as this was employed purely as an exploratory tool to identify potentially important environmental variables. A more rigorous level of significance was adopted for the subsequent comparison of TWINSPAN site group means, which validated only those variables, identified by the regression analysis, likely to be of biological significance.

RESULTS

Macroinvertebrates

In total, 28 different taxa were identified (the majority to family) from samples obtained at the Speed River. These included representatives of both the "occasional" (the larvae of benthos that occupy the hyporheic habitat for a portion of their life cycle) and "permanent" (animals that complete their entire life cycle in the hyporheic habitat) hyporheos (sensu Williams and Hynes 1974), though the former were far more numerous than the latter. Total density was highest during the fall and winter ([greater than]100 animals per liter of sediment) and lowest during the summer ([less than]50 animals per liter sediment). Total density decreased with depth below the river bed and was lower also outside the active river channel. Of the aquatic insect larvae identified, chironomids were most abundant and were found regularly to depths of 60 cm below the river bed, though specimens were found to 80 and 100 cm below the bed during the spring and fall. Larvae of other aquatic insects (e.g., Ephemeroptera, Trichoptera, Plecoptera) typically penetrated to only 20 cm below the bed surface though they, like the chironomids, were found deeper during spring and fall. Lumbricid oligochaetes and hyalellid amphipods were the only taxa that seemed particularly limited in terms of their spatial distribution. Lumbriculidae were found only outside the limits of the active river channel and Hyalellidae were found only deep (60-100 cm) below the bed surface.

Water chemistry

Interstitial water was characterized as calcium-bicarbonate, which is typical for both this river system (e.g., Williams and Hynes 1974) and this region (e.g., Hill 1990). Over the study period, water temperature ranged from 22-24 [degrees] C to 2-0 [degrees] C in the interstices near the surface of the river bed and changed in near-uniform increments to 6-8 [degrees] C deep below the bed and under the river banks. Not surprisingly, dissolved oxygen decreased with depth below the river bed, although there were differences among seasons in terms of the depth of detectable levels of oxygen. During spring and fall oxygen was detectable regularly to 80 cm below the bed surface, but it was rarely detectable below 60 cm during summer and winter.

Severe spatial concentration gradients were evident for three water chemistry parameters (alkalinity, conductivity and nitrate), and these data are summarized in Fig. 3. At all sampling times, near-surface interstitial water had lower levels of both alkalinity [ILLUSTRATION FOR FIGURE 3, A-D OMITTED] and conductivity [ILLUSTRATION FOR FIGURE 3, E-H OMITTED] than the groundwater. Although alkalinity and conductivity levels generally decreased with depth, this trend was not uniform. Chemical discontinuities occurred landwards from each of the river margins down beneath the channel. In summer and winter these breaklines occurred near the river margins and at shallow depths under the river bed; they extended farther landwards and deep beneath the bed in the spring and fall. Similar spatial and temporal patterns were observed for nitrate [ILLUSTRATION FOR FIGURE 3, I-L OMITTED]. Nitrate levels peaked in the shallow interstices directly beneath the river bed in the summer and winter with this area extending deeper and landward in the fall but, unlike the latter two parameters, not during the spring.

TABLE 2. Correspondence analysis summary for the ordination of the

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combined, all-seasons data set. Only the values for the first four ordination axes are given.

Axis	Eigenvalue	Cumulative % variance explained	Length (SD)
1	0.287	35.2	2.28
2	0.103	47.8	1.16
3	0.048	48.4	0.94
4	0.037	48.9	1.01

Note: Variance explained by each axis is the ratio of its eigenvalue to that of the total inertia (i.e., all ordination axes combined).

Hydrogeology

Interstitial water flow within the component of the flow system sampled appeared to be typical of an effluent river (*sensu* Williams 1989) [ILLUSTRATION FOR FIGURE 4 OMITTED]. Measured hydraulic potential, or head, beneath the river was greater than that of the water level of the river, indicating that net water movement was generally upwards into the channel. In only one instance was this not the case: during the spring sampling period, the river head was greater than the head 20 cm below the bed surface at midriver, indicating the potential for net water flow into the interstices [ILLUSTRATION FOR FIGURE 4 OMITTED].

From spring through fall, between 60 and 100 cm below the surface of the river bed, at sampling stations 7, 8, and 9, the head data indicated that flow was virtually horizontal across the river rather than vertical into the river. The head data also indicated that the relative upward force of baseflow varied among seasons and within seasons across the transect. There was substantial seasonal variation in the hydraulic gradient (*i*) between the river and the subsurface (Table 1), *i* was greatest for the summer and winter sampling periods. Periods of high *i* were coincident with times of the year when discharge in the river was dominated by baseflow. For individual seasons, the head distribution was asymmetrical across the river (Table 1). For all seasons, *i* was greater from midriver to the south bank than from midriver to the north bank.

TABLE 3. Results of the multiple linear regression (correlation coefficients) between CA axes 1 and 2 and measured environmental parameters for which there was one significant correlation (*P* [less than] 0.05).

Variable	Axis 1	Axis 2
Alkalinity	0.364(***)	...
Conductivity	0.323(***)	...
Dissolved oxygen	-0.195(*)	...
Nitrate	-0.163(*)	-0.181(*)
Sodium	...	0.161(*)

* *P* [less than] 0.05, ** *P* [less than] 0.01, *** *P* [less than] 0.001. Ellipses indicate that the correlation was not significant.

Ordination and relationship with measured environmental parameters

The primary and secondary ordination axes, which together explained nearly 50% of the variance in the data set, were 2.28 and 1.16 SD in length and represented changes in taxonomic composition of [approximately]85 and 55%, respectively (Table 2). Grouping of sampling sites was readily evident [ILLUSTRATION FOR FIGURE 5 OMITTED] and corresponded well with the distinction between groundwater and hyporheic sites generated by the level-1 TWINSpan dichotomy. The ordination displayed a much stronger distinction between hyporheic and groundwater community subunits vs. seasonal changes in faunal composition. This is likely the result of the level of taxonomic identification used, as seasonal changes in the major taxa are more conspicuous at the genus level (Williams and Hynes 1974).

Water chemistry parameters significantly correlated with either CA Axis 1 or 2 scores are listed in Table 3. Alkalinity and

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conductivity were the most highly correlated with Axis 1. Other variables significantly correlated with Axis 1 included dissolved oxygen and nitrate (Table 3). Variables significantly correlated with Axis 2 included nitrate and sodium (Table 3).

Classification

The two site groups generated at TWINSpan level 1 were characterized as either groundwater or hyporheic sites for each seasonal invertebrate data set [ILLUSTRATION FOR FIGURE 6 OMITTED]. Comparison of the TWINSpan classification scheme and the CA axes suggested that site group membership was strongly related to water conductivity and alkalinity. During all seasons, groundwater sites were characterized by higher conductivity and alkalinity levels, though statistical differences between mean levels of conductivity and alkalinity were found only for spring and fall and spring, respectively (Table 4). Nitrate concentration was also a strong indicator of group membership. The mean nitrate concentration of hyporheic sites was significantly greater than that of groundwater sites during summer, fall, and winter (Table 4). A small degree of seasonal variation in site group membership was evident. For the fall, and especially the spring, sampling periods, the boundary between the hyporheic and groundwater site groups was located deeper beneath the river bed and farther into the banks. Density and diversity were generally higher in the hyporheic zone, although many of the numerically dominant taxa were found also in groundwater sites. Taxa that were particularly diagnostic of hyporheic sites included the Ephemeroptera (Caenidae, Ephemerellidae), Plecoptera, and Trichoptera (Helicopsychidae, Hydropsychidae) [ILLUSTRATION FOR FIGURE 7 OMITTED]. Taxa that were diagnostic of groundwater sites included the Amphipoda (Hyalellidae) and Oligochaeta (Lumbriculidae) [ILLUSTRATION FOR FIGURE 7 OMITTED].

At TWINSpan level 2, the division of hyporheic sites seemed depth related - generally shallow sites separated from sites deeper under the river bed [ILLUSTRATION FOR FIGURE 6 OMITTED]. The division between shallow and deep sites was closer to the surface of the river bed during the summer and winter and deeper beneath the bed during spring and fall. In each of the seasons the division was based on the abundance of the diagnostic taxa. For each season, differential taxa of the shallow hyporheic sites included pseudospecies 2 taxa (i.e., high abundance), while deeper hyporheic sites included pseudospecies 1 taxa (low abundance). The division of groundwater sites generally separated riparian groups from those directly beneath the active river channel [ILLUSTRATION FOR FIGURE 6 OMITTED]. Lumbriculidae were found exclusively outside the active channel, whereas Hyalellidae were found in greater abundance beneath, but within the lateral limits of, the river.

TWINSpan level-3 divisions failed to produce any discernible patterns. Group membership often was limited to too few sites (one or two samples) to prove meaningful.

DISCUSSION

One strategy previously employed to locate the hyporheic/groundwater interface has been to separate the interstitial community into its epigeal, hypogean, and hyporhean (fauna derived from the hyporheic zone) subunits. Williams (1989) used community classification (TWINSpan) to make a distinction between three faunal subunits: bank, river, and one that was unique [TABULAR DATA FOR TABLE 4 OMITTED] to the margin between the two. The position of this margin faunal group was coincident with breaklines in several water chemistry parameters, and it was proposed that this faunal component of the interstitial community was an indicator of the hyporheic/groundwater interface. In a similar fashion, Ward and Voelz (1994) used frequency of occurrence data to characterize the hyporhean and hypogean elements of the invertebrate community at the South Platte River, Colorado. Whereas both studies identified taxa that were particularly diagnostic, it is not clear whether the distinction between the biotic subunits is truly representative of a spatial distinction between the hyporheic and groundwater habitats. The same concern can be raised with regard to the invertebrate data collected in this study. Although some taxa were found exclusively in either the groundwater or hyporheic habitat, it is difficult to make a clear distinction between what the TWINSpan analysis divided into the two interstitial faunal subunits. This is perhaps not surprising when we consider that the concentration range of individual water chemistry parameters measured was likely well within the tolerance range of the interstitial taxa collected. It is possible that various abiotic (e.g., sediment features, interstitial flow patterns) or, alternatively, biotic factors (e.g., competition, predation, reproduction, food resources) that were not measured may more adequately explain the distribution of, and distinction between, hyporhean and hypogean taxa. These factors are likely of varying importance, but to date few definitive data are available to assess their importance, especially in field situations (Ward and Palmer 1994). Further, acquiring these data may still be some time away as the required background information regarding the physiological status and ecological requirements of the vast majority of interstitial organisms is presently lacking. Therefore, while the invertebrate data may provide a useful

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measure of probable habitat location, it likely provides poor spatial resolution in terms of pinpointing the location of the hyporheic/groundwater interface.

In contrast to faunal distribution, the water chemistry data proved more definitive in distinguishing between the hyporheic and groundwater habitats. Concentration discontinuities in a number of the chemical parameters measured, with breaklines typically occurring from a meter or two landwards of the river margins down under the channel, were recorded. Concentration discontinuities of this sort were first reported by Williams (1989) at both the Rouge River and Duffin Creek, in southern Ontario. Since the latter study, others also have reported chemical discontinuities or steep concentration gradients over small spatial scales extending vertically beneath and laterally outside the wetted channel (e.g., Triska et al. 1989, 1993a, Holmes et al. 1994, McClain et al. 1994). We suggest that these discontinuities represent the nonphysical boundary between the hyporheic and groundwater environments. Groundwater was characterized by higher levels of alkalinity, conductivity, and ammonium, and lower levels of nitrate. Differences in alkalinity and conductivity between the two water masses probably can be attributed to site-specific local and, to a lesser extent, regional geomorphological features. However the nitrate-ammonium relationship is one that has been observed in several other systems. For example, Valett et al. (1990) found high levels of $\text{N}[\text{O.sub.3}]\text{-N}$ in the hyporheic zone of a Sonoran Desert stream, and Triska and his group have repeatedly recorded high levels of hyporheic nitrate alongside low levels of ammonium in the groundwater at Little Lost Man Creek in northwestern California (e.g., Triska et al. 1993). This phenomenon was reported also by McClain et al. (1994) at the Barro Branco Stream in the Central Amazon Basin.

Water chemistry data also provided a more reliable spatial measure of hyporheic/groundwater interface seasonal fluctuation. Faunal data indicated that changes in macroinvertebrate distribution were taxon rather than community based as taxa turnover between the two faunal subunits was not complete. In this sense, therefore, it may be somewhat erroneous to describe boundary fluctuation as indicated by the distribution of the hyporhean and hypogean faunal subunits when it appears that only a number of individual taxa seem to be affected. The occurrence of these indicator taxa may be of use in identifying general spatial trends but would not be appropriate markers of the interface itself. Conversely, differences between the hyporheic and groundwater masses persisted throughout the year, yet the location of the concentration discontinuity varied. Williams (1993) suggested that boundary fluctuation of the hyporheic/groundwater interface was probably the direct result of variation in the upward force of base flow and the downward force of advecting channel water. Our hydrogeological data support this hypothesis. During the spring and fall sampling periods, the interface was deeper beneath the active channel and farther out laterally under the banks. These same sampling periods coincided with the times at which the hydraulic gradient between the surface and interstitial environments was the least and surface discharge was the greatest. This, along with the fact that our sample transect was located at the head of a riffle (a convex stream bed surface), could account for a high degree of convective flow of river water into the stream bed (Vaux 1968, Boulton 1993). With this reasoning it is plausible that the relative forces of downwelling river water and upwelling groundwater regulate the location and fluctuation of the hyporheic/groundwater interface. In actuality, therefore, it is likely that we have recorded boundary fluctuation as a result of variable channel discharge patterns rather than the effects of seasonality. This implies that in ecosystems where isolated discharge events rather than seasonal discharge patterns regulate surface-subsurface hydraulic exchange the hyporheic zone, or more precisely the hyporheic habitat volume, would fluctuate according to the timing of these events. This suggestion is supported by a recent study (Stanley and Boulton 1995) that reported fluctuations in the boundaries of hyporheic subsystems in response to flooding and drying of a Sonoran Desert stream.

Recent studies have quantified the inorganic nitrogen storage and retention capacity of hyporheic sediments (e.g., Triska et al. 1990, 1994, Kim et al. 1992, Holmes et al. 1994), along with the implications of the potential availability of the hyporheic inorganic nitrogen pool to lotic environments (e.g., Hendricks and White 1988, Ward 1989). Our study adds a further dimension. A central premise of a model depicting nitrogen cycling between contiguous groundwater and stream water, presented by Triska et al. (1993), was the transient storage of ammonium in hyporheic sediments. We have shown that the hyporheic volume, and therefore the quantity of hyporheic sediments available for ammonium adsorption, varies according to surface discharge patterns. Although the effect this may have on the hyporheic inorganic nitrogen pool has yet to be quantified it warrants inclusion in models that predict solute flow between groundwaters and surface ecosystems. Further studies also will have to: (1) quantify the broader significance of hyporheic volume variation in many biological and geochemical processes, including, for example, nitrification, denitrification, phosphorus cycling, and metabolism; and (2) determine the impact(s) of hyporheic habitat size fluctuation on resident interstitial biota.

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