

Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange, sediment structure and physicochemistry

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SUMMARY

1. We studied the relative contributions of the magnitude and direction of vertical hydrological exchange, subsurface sediment composition and interstitial physicochemistry in determining the distribution of hyporheic invertebrates in the Kye Burn, a fourth order gravel-bed stream in New Zealand.
2. In winter 2000 and summer 2001, we measured vertical hydrological gradient (VHG), dissolved oxygen, water temperature and water chemistry using mini-piezometers, each installed in a different upwelling or downwelling zone. Next to every piezometer, a freeze core sample was taken to quantify the sediment, particulate organic matter and invertebrates.
3. Dissolved oxygen concentration at 25 cm was high on both occasions ($>9 \text{ mg L}^{-1}$) but was higher in winter than summer. Interstitial water temperature was higher in down than upwellings and was substantially higher in summer than winter. Other features of the subsurface sediments and interstitial nitrate–nitrite concentrations were similar on both occasions and in up and downwellings. Interstitial ammonium and soluble reactive phosphorous concentrations were higher in winter than summer and ammonium was higher in up than downwelling areas.
4. The proportion of fine sediment (63 μm –1 mm), sediment heterogeneity and VHG accounted for the greatest proportion of variance in invertebrate distributions in both summer and winter.
5. The hyporheos was numerically dominated by early instar leptophlebiid mayfly nymphs and asellotan isopods. Water mites were a taxonomically diverse group with 13 genera. Taxonomic diversity (Shannon–Weaver), but not taxon richness, was higher in upwelling areas, reflecting lower numerical dominance by a few taxa in these locations.
6. Sediment composition (particularly the amount of fine sediments) and vertical hydrological exchange determined the composition and distribution of the hyporheos. Patchiness in these factors is important in planning sampling regimes or field manipulations in the hyporheic zone.

Keywords: hyporheos, interstitial, invertebrates, streams

Introduction

A variety of physical and chemical factors interact to determine the three-dimensional distribution of

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invertebrates in the hyporheic zone. Among these, the vertical exchange of water is particularly influential, linking the surficial and interstitial systems of the streambed. Variations in the magnitude and direction of such exchanges influence the spatial and temporal extent of the hyporheic zone (Boulton, 1993; Fraser & Williams, 1998) and its fauna (Stanley & Boulton, 1993; Boulton & Foster, 1998; del Rosario & Resh,

2001). Factors that determine patterns in vertical hydrological exchange include local variations in bed gradient (Vaux, 1968; White, Elzinga & Hendricks, 1987; Mermilliod-Blondin *et al.*, 2000), in-stream obstacles diverting flow downwards (Williams, 1993) and sediment permeability (Vaux, 1968).

Sediments affect the nature of the hyporheic habitat directly (Brunke & Gonser, 1997). Sediment factors are of importance in determining the vertical distribution of the hyporheos including porosity (Maridet, Wasson & Phillippe, 1992) and the amount of fine material (Maridet *et al.*, 1992; Richards & Bacon, 1994). However, by interacting with vertical hydrological exchange (Vaux, 1968) sediment features may indirectly affect the hyporheic community by altering interstitial physicochemical conditions such as temperature, concentrations of oxygen and nutrients through changes in water residence time (Jones & Holmes, 1996; Sobczak & Findlay, 2002).

Community respiration in hyporheic sediments can represent a large proportion of the total respiration of the stream system (Grimm & Fisher, 1984; Naegeli & Uehlinger, 1997; Fellows, Valett & Dahm, 2001), resulting in a decrease in oxygen concentration with increasing contact time with heterotrophic biofilms in sediments (Cooling & Boulton, 1993; Findlay, 1995). The total abundance (Strommer & Smock, 1989; Boulton *et al.*, 1997; Franken, Storey & Williams, 2001), biomass (Strommer & Smock, 1989) and taxon richness of hyporheic invertebrates (Boulton *et al.*, 1997; Franken *et al.*, 2001) have been shown to be positively related to the interstitial oxygen concentration and, thus, may be affected by changes in the residence time of hyporheic water.

In this study, we consider the relative roles of vertical hydrological exchange, sediment parameters and physicochemical conditions in determining the small-scale distribution of hyporheic invertebrates in a gravel-bed stream. We took samples in mid-winter and mid-summer when differences in interstitial physicochemical conditions were expected to be greatest.

Methods

Study area

Samples were taken in a 200-m section of the Kye Burn, a fourth-order stream in the Otago Province in

the South Island of New Zealand ($44^{\circ}58'S$ $170^{\circ}18'E$). The Kye Burn catchment above the study reach (altitude 600–1600 m a.s.l.) comprises sparse matagouri scrub (*Discaria toumatou* Raoul) and tussock grassland (primarily *Chionochloa*), which is lightly grazed by sheep and subject to irregular burning.

This study was conducted in a section of stream constrained within a bedrock canyon (average ratio valley width: channel width approximately 2.7) that controls the channel path and limits the lateral extent of the bed sediments. Bedrock ridges dictate many of the pool-riffle sequences in the study section and are likely to affect vertical hydrological exchange and sub-surface flow patterns. The bed of the study reach is dominated by sediment from Timber Creek, a third order tributary 2 km upstream of the study site. Timber Creek contributes a large amount of fine sediment into the Kye Burn (Scarsbrook & Townsend, 1993). Discharge in the surface channel was low on both winter and summer sampling occasions (approximately 360 and 201 L s^{-1} , respectively) and did not vary appreciably during either sampling period. Mean annual flow in the Kye Burn is approximately 1100 L s^{-1} [National Institute of Water and Atmospheric Research (NIWA) Dunedin, unpublished data].

Sampling procedure and laboratory techniques

Samples were collected on two sampling occasions (winter, 4–7 August 2000; summer, 20–24 January 2000). On each sampling occasion, eight upwelling and eight downwelling areas were identified in the study reach from preliminary surveys using mini-piezometers. A piezometer was inserted at a random location within each area (up or downwelling) and a freeze core (details later) was taken within 40 cm of each piezometer. Adequate freeze cores could not be collected from two areas on each occasion, despite repeated attempts. These samples and the associated piezometer data were excluded from subsequent analyses. On the summer sampling occasion, nine upwellings and five downwellings were sampled as two freeze cores from downwellings failed and one area that was a downwelling in winter was found to be weakly upwelling in summer.

Mini-piezometers (Lee & Cherry, 1978) were made from 1 m lengths of 30 mm polyvinyl chloride (PVC) pipe. Piezometers were inserted to a depth of 25 cm,

using a T-bar and sledgehammer, to measure the magnitude and direction of vertical hydrological gradient (VHG) at each sampling location. Each piezometer was pumped out using a hand-operated bilge pump and allowed to recharge before any measurements were taken. VHG was measured on several occasions before sampling as outlined by Dahm & Valett (1996). Interstitial temperature and dissolved oxygen concentration of the interstitial water were measured using a YSI 85 handheld field probe (Yellow Springs Instruments incorporated, Yellow Springs, OH, USA). Water samples for chemical analyses were taken using acid-washed 60-mL syringes, filtered (using acid-washed Whatman GF/F filters) into sterile containers, transported to the laboratory in an ice-filled container, and frozen until analysis. A Skalar San^{PLUS} autoanalyser (Skalar Analytical BV, Breda, the Netherlands) was used to measure the concentration of nitrate-N ($\text{NO}_3\text{-N}$ by cadmium reduction; Wood, Armstrong & Richards, 1967), ammonium ($\text{NH}_4\text{-N}$: phenol-hypochlorite method; Solorzano, 1969) and soluble reactive phosphorous (SRP; molybdate-antimony method; Murphy & Riley, 1963). Ideally, several piezometers would have been inserted to a range of depths at each location to provide depth-specific data. However, given the time required to install each piezometer and extract water samples, it would not have been possible to take freeze-core samples and several piezometer samples simultaneously, particularly during the short days of winter.

Invertebrate and sediment samples were taken using liquid nitrogen following the freeze core technique of Pugsley & Hynes (1983). A metal standpipe was driven into the bed to a depth of 50 cm within 40 cm of each piezometer. Loose surface particles were ignored and the sediment surface was taken to be the upper limit of consolidated sediment. Freeze core samples were taken after a 2-day settling period to allow invertebrates to recover after the insertion of the standpipe (Olsen, Matthaei & Townsend, 2002). After 15–20 min of freezing, the core was extracted from the sediment using a tripod and winch. Each core was divided into 10 cm depth layers, which were placed in separate preweighed resealable plastic bags and stored in ice for up to 12 h until processed in the laboratory. In the laboratory, the wet weight of each depth layer was determined (to the nearest gram) and each sample was preserved in 5% formalin before storage. Before processing, samples were elutriated to separate coarse sediment (>1 mm) from fine sediment (<1 mm), particulate organic matter (POM) and invertebrates. The separated fine sediment, POM and invertebrates were washed through a series of sieves (250, 125 and 63 μm). Macroinvertebrates and POM retained in the 250 μm sieve were stored in 5% formalin and stained with Rose Bengal for at least 48 h before processing.

After elutriation, the coarse gravels (>1 mm) from each depth layer were dry-sieved through a sieve tower (1, 2, 4, 8 and 16 mm) using a sieve shaker (Endercots EFL Mk 3 Test sieve shaker, Endecotts Ltd, London, UK), each size fraction oven-dried (70 °C) in preweighed aluminium trays for 24 h and weighed to the nearest gram. Particles over 32 mm (secondary axis) were measured with a ruler and split into further size classes (32, 64 and 128 mm). Fine gravels (63 μm –1 mm) were wet-sieved into size classes (63–125, 125–250, 250–500 μm , and 500 μm –1 mm), oven-dried (70 °C) in preweighed aluminium trays for 48 h and weighed to the nearest 0.1 g. Median particle size (D_{50}) and substratum heterogeneity (H; ratio of D_{60} to D_{10} – Schwoerbel, 1961) were estimated by linear interpolation. The size class distribution of surface sediment was estimated by measuring the secondary axes of 378 random particles within the study reach (Wolman, 1954).

Porosity was measured as the water content of each depth layer in proportion to the total volume of the depth layer. The volume of water in each depth layer was estimated by subtracting the dry sediment weight (>63 μm) from the wet weight of the sample and converting the resultant water mass to a volume using the approximate density of water as 1 g mL^{-1} . The sediment volume of each depth layer was defined as the volume displaced by the sediment upon complete immersion in a 5-L plastic container.

Macroinvertebrates (>250 μm) were sorted under a dissecting microscope (at 7–40 \times magnification) and identified to the lowest practical taxonomic level. Insects were identified using the keys provided in Winterbourn, Gregson & Dolphin (2000). The predominance of early instars prevented the identification of genus or species of many taxa (e.g. leptophlebiidae). Water mites were individually mounted whole on slides in Hoyer's solution (Harvey, 1998), examined using a compound microscope and identified to genus where possible, using published keys and species descriptions (Cook, 1983; Schwoerbel, 1984; Cook,

1992). Invertebrate density estimates in each depth layer were standardised to a sediment volume of 1000 cm³. Mean sediment volume was variable, as would be expected from a heterogeneous substratum such as that in the Kye Burn. Depth layers with a sediment volume of <100 cm³ were excluded.

The amount of POM in each depth layer was estimated by drying samples at approximately 70 °C (after invertebrates were removed) for at least 48 h and obtaining dry weights of the POM and any associated fine sediment. These samples were then ashed at 500 °C for 2 h and the ash-free dry mass (AFDM) of POM in the depth layer calculated (standardised to 1000 cm³).

Statistical analysis

The relationships between physicochemical variables and the abundance of invertebrate taxa were explored using partial canonical correspondence analysis (CCA; ter Braak & Verdonschot, 1995) in CANOCO version 4.0. The first of these analyses included environmental variables that were measured in each depth layer together with VHG, as the direction and relative magnitude of vertical hydrological exchange is unlikely to vary appreciably with depth in a porous bed such as the Kye Burn. Variables included in these analyses were: VHG, D₅₀, H, percentage of sediment: 63–250 µm, 250 µm–1 mm, 1–4 mm, 4–16 and 16–64, porosity, AFDM POM. These CCAs were carried out on log₁₀(x + 1) transformed invertebrate data (to down-weight abundant taxa) with depth as a covariate and permutations restricted for a split-plot design. Whole plots (whole cores) were permuted completely at random while depth layers were not permuted.

A second set of partial CCAs was carried out on measurements taken from water collected from the piezometers (at 25 cm depth) and equivalent data collected from the 20–30 cm depth layer of the cores. The proportion of sediment 63–250 µm was specified as a covariate in the second analysis. Variables included in this analysis were: VHG, dissolved oxygen concentration, temperature, nitrate/nitrite concentration (NO_x), ammonium concentration (NH₄), SRP, and AFDM of POM. Invertebrate data was log₁₀ (x + 1) transformed and permutations were unrestricted.

Both sets of analyses contained some missing depth layers (winter: one missing 40–50 cm depth layer; summer: one missing 10–20 cm depth layer and one

missing 40–50 cm depth layer). Analyses using split-plot designs in CANOCO cannot be performed on datasets with missing sub-plots (depth layers). If the remaining depth layers within that core showed a clear trend with depth (for example, leptophlebiidae often showed a marked decline with depth) the missing value was replaced with a value extrapolated from the remaining depth layers in the core. If no trend was apparent in the remaining depth layers within that core, the missing value was entered as an average of the remaining values.

Comparisons of season and zone (up versus downwelling) effects on the composition of the community were conducted using a two-way crossed analysis of similarities (ANOSIM) in Primer version 5 on a Bray-Curtis similarity matrix obtained from log₁₀(x + 1) transformed invertebrate data. Separate univariate ANOVAs were carried out to compare the effect of season and zone on taxon richness, diversity (Shannon-Weaver) and equitability (Simpson's index) (Begon, Harper & Townsend, 1996) in the 14 cores sampled on each occasion. Total invertebrate abundance and the abundance of the 16 most common taxa were analysed in more detail (including analysis of depth effects) using a univariate split-plot design. The error term for the season effect was Core (season). Core (VHG) was the error for the VHG effect. The season-area interaction was tested against Core (season × VHG). Other effects were tested against the residual mean square. For each test, data were tested for normality and equality of variance. If either assumption was violated, comparisons were made using a rank-sum test or Kruskal-Wallis test (Sokal & Rohlf, 1995).

Results

Physicochemical conditions

The magnitude of VHG ranged from -0.12 (downwelling) to 0.12 cm cm⁻¹ (upwelling) in winter and from -0.07 to 0.09 cm cm⁻¹ in summer. Winter interstitial water was colder and contained greater concentrations of dissolved oxygen, ammonium and SRP than water collected in summer (Table 1). Concentrations of dissolved oxygen, SRP and nitrate-nitrite did not differ between up and downwellings but upwelling water was colder than downwelling water on both occasions (Table 1).

Table 1 Physicochemical conditions (at 25 cm below sediment surface) and sediment characteristics of freeze core samples from the hyporheic zone (10–50 cm) of the Kye Burn in up and downwelling areas in winter 2000 and summer 2001. Values in brackets (V^*) are the unbiased coefficients of variation for each mean estimate

	Winter		Summer		ANOVA		
	Upwell	Downwell	Upwell	Downwell	S	Z	$S \times Z$
Temperature (°C)	3.7 (27.4)	4.3 (9.8)	14.1 (4.7)	14.6 (2.3)	***	*	
DO (mg L ⁻¹)	12.1 (6.1)	12.2 (5.1)	9.8 (3.4)	10.3 (2.0)	***		
Nitrate/nitrite (µg L ⁻¹)	18.2 (58.4)	10.0 (56.2)	12.9 (77.2)	15.4 (36.3)			
SRP (µg L ⁻¹)†	20.1 (66.6)	10.6 (33.6)	7.2 (64.1)	3.7 (20.6)	***		
Ammonium (µg L ⁻¹)†	7.8 (60.7)	4.9 (55.3)	2.9 (41.2)	3.6 (35.0)	***	*	
Median particle size (mm)	27.9 (73.5)	21.1 (99.3)	19.3 (80.3)	16.5 (43.3)			
Heterogeneity ($D_{60} : D_{10}$)	31.1 (47.8)	20.6 (53.1)	24.6 (38.7)	18.1 (48.5)			
Porosity (%)	18.9 (45.8)	16.4 (18.0)	19.4 (16.7)	17.1 (17.1)			
Fine sediment (>1 mm; %)	11.0 (51.5)	7.2 (57.4)	11.2 (60.4)	7.9 (16.4)			
POM (g AFDM 5000 cm ⁻³)	0.49 (35.6)	0.33 (28.3)	0.59 (23.5)	0.52 (19.4)			
Sample size (<i>n</i>)	7	7	9	5			

† ANOVA carried out on log₁₀-transformed data.

S, season effect; Z, upwelling versus downwelling; S × Z, season–zone interaction effect. *** = $P > 0.005$, * = $P > 0.05$, otherwise $P < 0.1$.

The volume of depth layers in the freeze cores ranged from 100 to 4050 cm³ and did not vary between seasons ($P = 0.53$), up and downwellings ($P = 0.18$) or with depth ($P = 0.32$). The nature of the subsurface sediments was variable in both up and downwelling zones on both sampling occasions, as indicated by large coefficients of variation (V^*) for the sediment characteristics (Table 1). No differences were apparent between the sampling occasions (seasons), zones (upwellings versus downwellings) or for the season–zone interaction. Bed porosity varied with depth, with the 10–20 cm depth layer having a lower porosity than the deeper depth layers ($P = 0.032$). Surface sediments were coarser and more homogeneous ($D_{50} = 32$ mm, H = 4.3, *n* = 378) than hyporheic sediments, but statistical comparison of these values is not appropriate given the difference in sampling methods used to obtain the data.

Composition and distribution of the hyporheos

Taxon richness did not differ between up and downwellings ($F_{1,24} = 0.12$, $P = 0.73$) or sampling occasions ($F_{1,24} = 0.21$, $P = 0.65$). The interaction between season and VHG was almost significant ($F_{1,24} = 3.78$, $P = 0.06$) reflected in higher taxon richness in upwellings than in downwellings in winter, whilst in summer richness was similar between zones. Taxonomic diversity (as measured by the Shannon–Weaver diversity index) and equitability (Simpson's

index) were higher in up than in downwellings (Shannon–Weaver (*H*): $F_{1,24} = 20.01$, $P < 0.001$; Simpson's (*E*): $F_{1,24} = 4.91$, $P = 0.04$) but did not differ between sampling occasions ($HF_{1,24} = 0.84$, $P = 0.37$; *E*: $F_{1,24} = 0.11$, $P = 0.75$). No interaction between zone and season was apparent for diversity ($F_{1,24} = 0.63$, $P = 0.44$) but equitability was similar in up and downwellings in winter but higher in upwellings than in downwellings in summer (the season–VHG interaction was almost significant: $F_{1,24} = 3.40$, $P = 0.08$).

The composition of the hyporheos differed between sampling occasions (ANOSIM; Global *R* = 0.25, $P = 0.003$) and between up and downwellings (ANOSIM; Global *R* = 0.18, $P = 0.04$). These differences are apparent in a non-metric multidimensional scaling (MDS) ordination with downwellings generally having lower scores on dimension 1 than upwelling zones, whilst summer cores tended to have lower scores on dimension 2 than winter cores (Fig. 1). Samples with low scores on dimension 1 were characterised by greater numbers of leptophlebiids, orthoclad chironomids and isopods, and low numbers of *Hydora* and oligochaetes. Samples with low scores on dimension 2 have high densities of leptophlebiids and orthoclad chironomids, and low densities of *Polyplectropus*, *Hydora*, Cladocera (Chydoridae) and oligochaetes. Total invertebrate densities in the hyporheos were higher in winter than summer ($F_{1,14} = 4.88$, $P = 0.04$) and the distribution of total

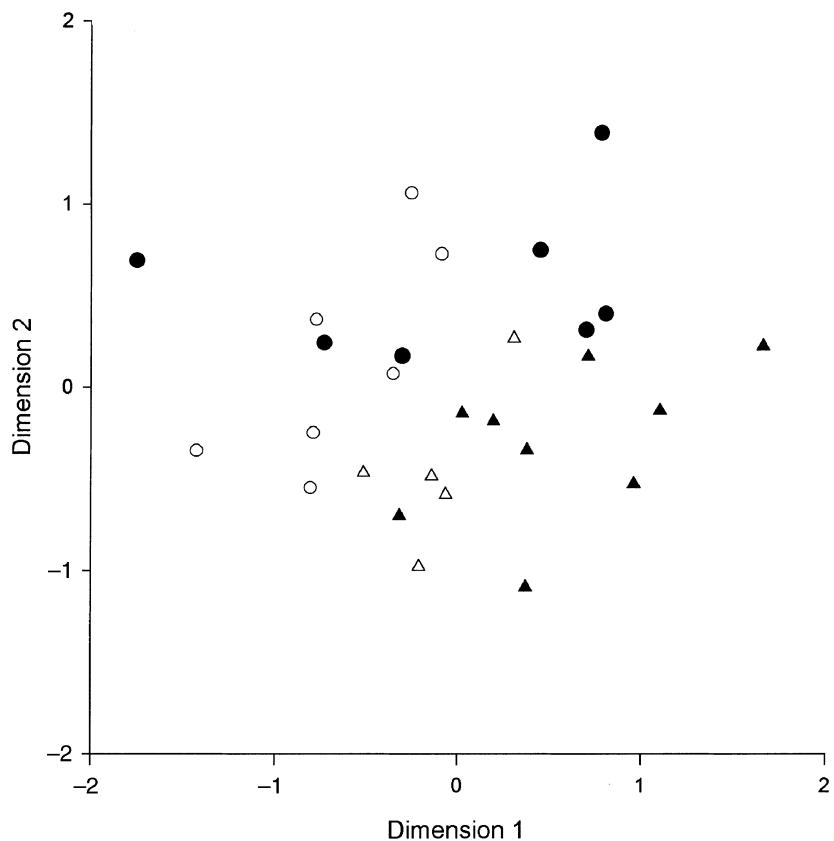


Fig. 1 Two-dimensional non-metric multidimensional scaling ordination (stress = 0.20) of composition of the hyporheos in summer (triangles) and winter (circles). Open symbols represent samples taken from downwellings and solid symbols represent samples taken from upwellings.

abundance with depth differed between the two sampling occasions (Fig. 2a; date–depth interaction: $F_{3,72} = 4.03, P = 0.01$). The depth distribution of total invertebrate abundance did not differ between up and downwelling zones (Fig. 2a; $F_{1,6} = 0.44, P = 0.53$).

The abundance of leptophlebiid mayflies (Ephemeroptera – primarily early instars of *Deleatidium* spp.) was similar on the two occasions ($F_{1,14} = 1.57, P = 0.23$) and in both up and downwelling zones ($F_{1,6} = 0.25, P = 0.64$). Leptophlebiids were most abundant in the upper layers of the sediment (Fig. 2b; $F_{3,72} = 35.34, P < 0.001$). The abundance of larval *Hydora* was similar on both occasions ($F_{1,14} = 0.49, P = 0.53$) and in both zones ($F_{1,6} = 0.24, P = 0.64$) but *Hydora* larvae were not found in significantly higher densities deeper in cores in winter than in summer (Fig. 2c; season–depth interaction not significant: $F_{3,72} = 2.53, P = 0.06$). Although more isopods were collected in winter, the difference was not significant ($F_{1,14} = 3.49, P = 0.08$). They were abundant deep in the sediment (>20 cm) in downwellings but were more uniformly distributed in upwellings (Fig. 2d; VHG–depth interaction: $F_{3,72} = 3.81, P = 0.01$). These

isopods included the genus *Heterias* (Asellota: Janiridae) and at least one other unnamed taxon (Buz Wilson, personal communication).

Amphipods were more abundant in downwellings than upwellings in winter, whilst summer densities were similar in the two zones (season–VHG interaction was not significant: $F_{1,4} = 5.84, P = 0.07$). All amphipods collected were blind and unpigmented, and included species of *Paraleptamphopus* (Eusiridae) and *Paracrangonyx* (Gammaridae). Copepods were collected in greater densities in winter than summer (Rank-sum test; $T = 278.5, P < 0.001$). Oribatid mites were scarce in both up and downwelling zones on both sampling occasions and one species of trombidoid mite was occasionally found in both zones in summer (Table 2). Thirteen genera of water mites from nine families were identified (Table 2). Two most abundant mite genera were *Pseudotryssatus* and *Paratryssatus* (Aturidae: Notoaturinae). *Pseudotryssatus* was the most common [including at least two species; *P. dapsilus* Cook and *P. indentatus* (Hopkins)]. *Paratryssatus minutus* (Hopkins) was not collected below 30 cm into the bed (depth:

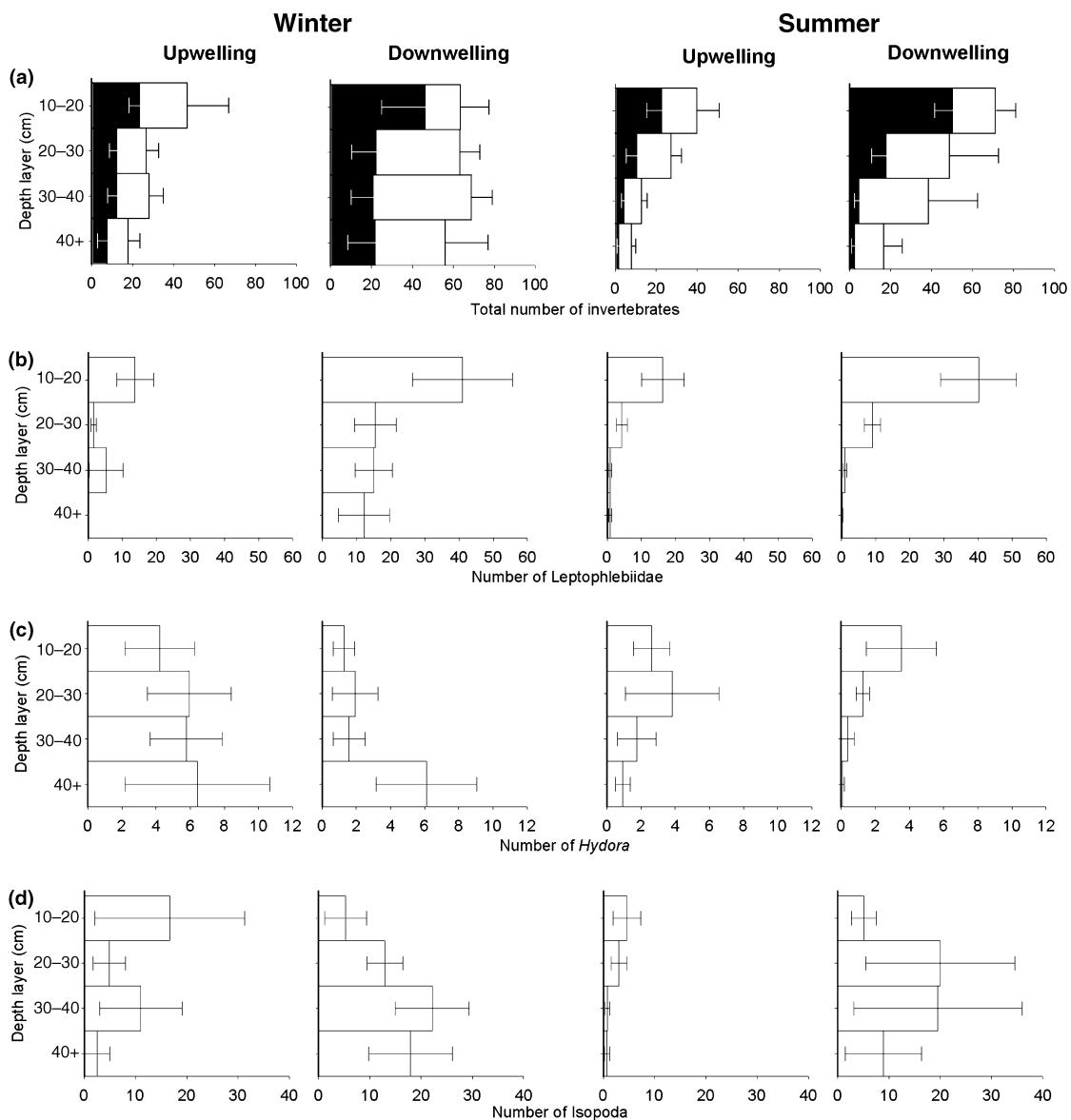


Fig. 2 Mean density \pm SE (per 1000 cm³) of major invertebrate taxa between 10–50 cm in the sediments of up and downwellings in the Kye Burn in winter (August 2001) and summer (January 2001). (a) Total invertebrate (dark = insect, light = non-insect), white error bars are standard errors for insect densities whilst black error bars are standard errors for the total invertebrate abundance. (b) Leptophlebiidae. (c) *Hydora* larvae. (d) Isopoda (Asellota).

$F_{3,72} = 5.85, P = 0.001$ and was most abundant in the 20–30 cm depth layer. Most other mite taxa were rare (Table 2).

Invertebrate–sediment relationships

The winter CCA accounts for 32.4% of the total variance of the species data (trace = 0.924, $F = 2.33$, $P = 0.006$). The first CCA axis is primarily a gradient of increasing proportion of fine sands (63–250 μ m)

and accounts for 38.4% of the species–environment relationship (Fig. 3a; $\lambda = 0.36$, $F = 6.66$, $P = 0.01$). Other variables that weight strongly on this axis include medium-coarse sand (250 μ m–1 mm), POM and sediment heterogeneity. Leptophlebiid mayflies, *Olinga*, and orthoclad chironomids have low scores on this axis indicating that they tended to be found in areas with low amounts of sand (Fig. 3a). Meanwhile, a number of taxa have high scores on this axis, including *Polyplectropus*, the water mite *Pseudotryss-*

Table 2 Summary of the mean invertebrate densities of taxa (individuals per 4000 cm³) in the hyporheic sediments (10–50 cm) in up and downwelling zones in winter and summer with standard errors in brackets

Taxon	Winter		Summer	
	Upwell	Downwell	Upwell	Downwell
Ephemeroptera				
Ameletopsidae				
<i>Ameletopsis perscitus</i>		*		
Leptophlebiidae	15.4 (5.6)		81.7 (25.7)	
Nesameletidae				
<i>Nesameletus</i>	*		*	*
Plecoptera				
Gripopterygidae			*	*
Eustheniidae				
<i>Stenoperla prasina</i>			*	
Trichoptera				
Conoesucidae				
<i>Olinga feredayi</i>	*		1.5 (0.9)	
<i>Pycnocentrodes</i>				*
Hydrobiosidae				
<i>Psilochorema</i>	*			*
Other Hydrobiosidae			*	*
Hydropsychidae				
<i>Aoteapsyche</i>				*
Hydroptilidae			*	*
Polycentropodidae				
<i>Polyplectropus</i>	*		*	
Coleoptera				
Elmidae				
<i>Hydora</i> (larvae)	25.0 (7.2)		9.4 (4.8)	
Gyrinidae	*			
Scirtidae		*		
Megaloptera				
Corydalidae				
<i>Archichauliodes diversus</i>	*		*	1.8 (0.5)
Diptera				
Ceratopogonidae	*			*
Chironomidae				
Chironominiae	*	*		
Orthocladinae	*		3.1 (1.2)	
Podonominae	*	*		*
Tanytropinae	1.5 (1.4)	*		*
Simuliidae				
<i>Austrosimilium</i>	*	*	*	*
Tipulidae				
Eriopterini	3.2 (1.1)		1.0 (0.5)	
Collembola	1.4 (1.4)	*		*
Amphipoda	2.7 (1.4)		15.7 (6.3)	
Ostracoda	2.3 (1.4)		3.5 (2.4)	
Isopoda (Asellota)				
Janiridae	28.3 (21.7)		60.4 (9.4)	
Cladocera				
Chydoridae	1.6 (0.7)		6.6 (4.9)	
Syncarida	*	*		
Copepoda	7.0 (4.1)		32.4 (19.9)	
Acari				
Oribatida	*	*	*	*
Trombidioidea				
Trombidioidea indet.			*	*

Table 2 (Continued)

Taxon	Winter		Summer	
	Upwell	Downwell	Upwell	Downwell
Anisitsiellidae				*
<i>Anisitsiellides partitus</i>				*
Aturidae				
<i>Kritaturus jacundus</i>	*	*	*	*
<i>Paratryssaturus minutus</i>	*	2.0 (0.8)	*	1.6 (1.0)
<i>Planaturus setipalpis</i>	*			*
<i>Pseudotryssaturus</i> spp.	2.4 (0.9)	*	8.9 (3.4)	4.3 (1.2)
<i>Notoaturninae deutonymph</i>	2.3 (1.2)	*	*	*
Hydryphantidae				
<i>Euwandesia tenebrio</i>				*
Hygrobatidae				
<i>Zelandobates crinitus</i>	*	*		
Limnesiidae				
<i>Limnesia</i> spp.	*	*	1.2 (0.4)	2.0 (0.5)
Momoniidae				
<i>Neomomonnia</i>	*	1.1 (0.7)	1.9 (0.7)	1.5 (1.0)
<i>Momonnia hopkinsi</i>				*
Oxidae				
<i>Flabellifrontipoda smithi</i>			*	*
Pionidae				
<i>Schminkea pacifica</i>	*		*	
Mideopsidae				
<i>Guineaxonopsis confusus</i>			*	
Other				
Unidentified	*		*	*
Oligochaeta	2.8 (1.7)	1.3 (0.6)	*	2.7 (2.1)
Nematoda	7.1 (3.9)	17.0 (15.4)	4.7 (1.2)	14.2 (13.4)
Mollusca				
<i>Potamopyrgus antipodarum</i>	*	*	*	
Total Invertebrate	113.2 (26.7)	243.6 (34.2)	82.6 (16.6)	170.8 (49.5)
Taxon richness	16.4 (1.4)	12.9 (1.4)	14.1 (1.3)	16.6 (1.7)
Shannon–Weaver diversity index (<i>H</i>)	0.81 (0.04)	0.66 (0.04)	0.88 (0.04)	0.67 (0.05)
Simpson's index (<i>E</i>)	0.30 (0.05)	0.28 (0.05)	0.41 (0.05)	0.19 (0.06)

* indicates the presence of a taxon at a mean density of less than 1 individual per 4000 cm³.

saturus, *Hydora* and Nematoda, suggesting these taxa occurred in areas with a high proportion of sand (Fig. 3a). The second axis is primarily a gradient of increasing VHG (from downwelling to upwelling) and accounts for an additional 22.8% of the species–environment relationship (Fig. 3a). Chironomids of the subfamilies Chironominae and Podonominae, as well as *Pseudotryssaturus*, have high scores on this axis suggesting they were found mainly in upwellings. On the other hand, leptophlebiids, orthoclad chironomids, isopods and nematodes have lower scores on this axis indicating they were generally found in downwellings (Fig. 3a).

The summer CCA accounts for a total of 30.7% of the total variation in the invertebrate ordination

(trace = 0.76, *F* = 1.86, *P* = 0.005). The first axis of this CCA represents a gradient of increasing sediment heterogeneity and VHG and decreasing proportion of gravels (4–16 mm) and coarse sand/fine gravels (1–4 mm). This axis accounts for 46.6% of the variance in the species–environment relationship (Fig. 3b; λ = 0.353, *F* = 7.01, *P* = 0.001). The centroids of early instar gripopterygid stonefly nymphs (mainly immature *Zelandobius*) and *Pseudotryssaturus* both have high scores on this axis, indicating that they occurred in upwellings and areas with heterogeneous sediments. Meanwhile, taxa that have low scores on this axis, including asellotan isopods, orthoclad chironomids and amphipods, occurred in downwellings with lower proportions of fine sediment. The second axis

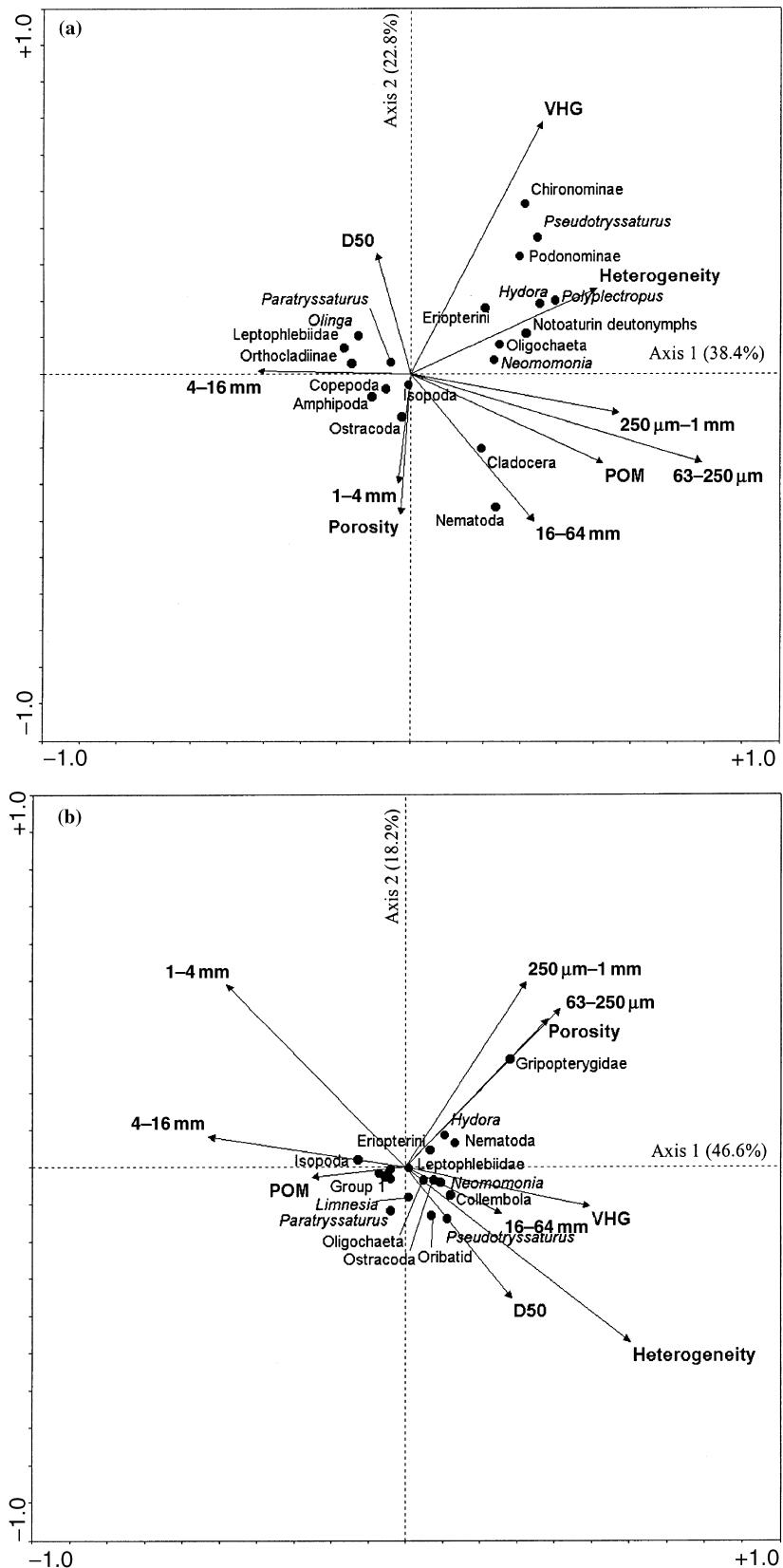


Fig. 3 Whole core canonical correspondence analysis (CCA) biplots of invertebrate taxa relative to sediment factors and vertical hydrological gradient (VHG) for (a) winter (b) summer (group 1 = *Archicranchialoides diversus*, Orthocladiinae, Podonominae, Tanypodinae, Amphipoda). The percentage of the variance explained by each axis is the percentage of the species–environment relationship.

is primarily a gradient of decreasing sediment heterogeneity and increasing amounts of fine sediments (63–250 µm, 250 µm–1 mm and 1–4 mm) and accounts for a further 18.2% of the variance in the species–environment relationship (Fig. 3b). *Hydora*, nematodes and Eriopterini have high centroid scores suggesting that these taxa were found in homogeneous sediments with a high proportion of fine sediments, whereas *Pseudotryssatus*, *Paratryssatus* and *Limnesia* tended to be associated with more heterogeneous sediments with few fine sediments.

Some consistent relationships were present in both summer and winter CCAs and in univariate analyses (see Table 2). Orthoclad chironomids were more abundant in downwellings and in areas with a high proportion of fine sediments (63–250 µm). *Hydora* and nematodes were found in areas with a high proportion of fine sediments (both 63–250 µm) in both seasons. On both occasions, *Pseudotryssatus* was generally found in upwellings whilst asellotan isopods and *Paratryssatus* were most abundant in downwellings. Amphipods and *Paratryssatus* were negatively associated with proportions of fine sediments (both 63–250 µm and 250 µm–1 mm) on both occasions.

Invertebrate–physicochemistry relationships

Partial CCAs were carried out on data from the 20–30 cm depth layer, consider the amount of variance accounted by physicochemical variables after accounting the effects of fine sediments (63–250 µm). The first axis of the winter 20–30 cm partial CCA did not account for a significant proportion (36.6%) of the variance in invertebrate distributions ($\lambda = 0.32$, $F = 1.68$, $P = 0.29$). Given the high P -value associated with this axis, interpretation from this, or any subsequent axis, is not appropriate. However, all the CCA axes in total account for 68.6% of the remaining variation in the invertebrate data (trace = 0.61, $F = 1.63$, $P = 0.04$) suggesting that, although no axis alone accounts for a significant proportion of the remaining variance, the combination of all CCA axes (incorporating all factors) accounts for a significant proportion of the remaining variance.

In summer, the first axis of the 20–30 cm CCA accounts for 41.5% of the remaining variance in the invertebrate data ($\lambda = 0.32$, $F = 1.77$, $P = 0.07$). This axis represents a gradient in the amount of POM and

interstitial water temperature. All CCA axes together account for 68.0% of the total variation but this value is not significant (trace = 0.77, $F = 1.21$, $P = 0.18$).

Discussion

Vertical hydrological exchange, sediments, physicochemistry and invertebrate distributions

The amount of fine sediment (63–250 µm and <1 mm) and sediment heterogeneity ($D_{60} : D_{10}$) were identified on both sampling occasions as being among the factors accounting for the greatest amount of variance in the invertebrate data. Sediment factors (including the proportion of fine sediments) have been suggested to be important determinants of the distribution of hyporheic invertebrates in other studies (Maridet *et al.*, 1992; Richards & Bacon, 1994). Sediment may have direct effects on invertebrates in our study by altering habitat characteristics (such as pore size) or by restricting their ability to feed, respire or move. Alternatively, sediment effects may be mediated via one or more variables that are themselves influenced by sediment characteristics. For example, a change in sediment composition may alter permeability and hydrological exchange (Vaux, 1968), indirectly affecting interstitial physicochemical conditions via changes to hyporheic residence times (Jones & Holmes, 1996; Sobczak & Findlay, 2002).

The VHG was also among the factors most closely associated with invertebrate distribution. This accords with previous reports that VHG is a major determinant of hyporheic community composition (Stanley & Boulton, 1993; Boulton & Foster, 1998; del Rosario & Resh, 2001). Upwelling interstitial water is often colder and lower in dissolved oxygen than surface or downwelling water (Sterba *et al.*, 1992; Boulton & Foster, 1998; Franken *et al.*, 2001) but may be warmer than surface water in winter (Williams & Hynes, 1974; Claret, Marmonier & Bravard, 1998). In this study, however, interstitial water was colder in upwellings than in downwellings on both sampling occasions. Upwelling hyporheic water may be important in some systems by supplying surface producers with limiting nutrients (Coleman & Dahm, 1990), but this was not apparent for any of the measured nutrients in our study.

The amount of POM was also represented on the first CCA axis in winter, when it was closely correlated with the proportion of fine sediments.

It is not clear whether the relationship between invertebrates and POM apparent in the CCA is real or a consequence of the correlation between POM and fine sediments. In summer, POM accounted for little variance in invertebrate distributions and POM was not correlated with fine sediments on this occasion. Previous studies of relationships between interstitial organic matter and hyporheic density have also produced mixed results, with some reporting significant relationships (Schwoerbel, 1961; Williams & Hynes, 1974; Strayer *et al.*, 1997), some reporting no relationships (Godbout & Hynes, 1982; Cooling & Boulton, 1993) and others with ambiguous results (Maridet *et al.*, 1992). Brunke & Gonser (1999) found that, while the amount of particulate organic carbon and the proportion of fine sediments were not significantly related to the abundance of the hyporheos, the ratio of these two was strongly correlated with the density of the hyporheos. In an experiment in which coarse POM was buried in the hyporheic zone of a gravel-bed river, Boulton & Foster (1998) found that neither hyporheic chemistry nor fauna were affected in upwelling or downwelling zones.

Interstitial dissolved oxygen concentration is often strongly related to the abundance, biomass and taxon richness of hyporheic invertebrates. However, this was not the case in our study. Because interstitial water in the Kye Burn was highly oxygenated in all samples ($>9\text{ mg L}^{-1}$), it was unlikely to reach a concentration limiting for hyporheos of the Kye Burn. Significant relationships between dissolved oxygen and invertebrates may only occur in systems in which strong gradients in dissolved oxygen are present (Strommer & Smock, 1989; Franken *et al.*, 2001).

While both summer and winter CCAs identified significant relationships between invertebrates and environmental factors, neither ordination accounted for more than a third of the total variance in the invertebrate dataset. In part, this probably reflects high variability in the distribution of the hyporheos. It is also probable that unmeasured sediment (e.g. pore size), physicochemical and biotic factors influence distributions of hyporheic invertebrates. Dissolved oxygen concentration and other physicochemical variables are likely to vary with depth (Williams & Hynes, 1974; Brunke & Gonser, 1999) and such patterns vary between cores depending on the direction and magnitude of VHG (Claret *et al.*, 1998; Brunke & Gonser, 1999). Variation with depth in these

factors may account for some of the unexplained variance in the whole-core CCAs. Finally, the ability to account for invertebrate patterns in the cores using data from piezometers may be restricted because of environmental heterogeneity at the scale of the distance (<40 cm) between the two sampling devices. Despite these potential limitations, our results lend further support to the hypotheses that amount of fine sediment and VHG determine, in large part, the distribution of hyporheic invertebrates in gravel-bed streams.

As with any observational study it is impossible to attribute characteristics of the hyporheic community to direct causal effects of measured variables. Experimental manipulation of such variables would help to resolve relationships but are technically very difficult (Palmer, 1993). Given our current state of knowledge, further observational, phenomenological studies are needed as well as laboratory (e.g. dissolved oxygen, as reviewed in Malard & Hervant, 1999) and field-based experimental manipulations (e.g. Boulton & Foster, 1998).

Community composition

The composition of the hyporheos differed on the two sampling occasions, as did total invertebrate abundance and abundance of certain taxa (e.g. copepods). Shannon–Weaver scores revealed higher diversity in upwelling zones on both occasions. This was because of a higher equitability in the distribution of individuals among taxa in upwelling zones (higher Simpson's index) and not to a greater number of taxa.

A large number of macroinvertebrate taxa were collected on both occasions, but the hyporheos was numerically dominated by a few taxa, particularly leptophlebiidae and asellotan isopods. This dominance was particularly strong in downwellings and in summer (lowest equitability scores). Leptophlebiid mayfly nymphs, especially *Deleatidium*, have previously been reported to be a major component of the hyporheos of New Zealand streams (Scarsbrook, 1995; Adkins & Winterbourn, 1999; Fowler & Death, 2001) and are generally most abundant near the sediment surface (Scarsbrook, 1995; Adkins & Winterbourn, 1999; Burrell, 2001). Whilst predominantly epigean, some individuals (particularly early instars) penetrate deeper into the sediments, possibly to avoid competition, predation or disturbance (Williams, 1984).

Larval elmid beetles are often common in hyporheic zones (Poole & Stewart, 1976; Marchant, 1988; Boulton & Foster, 1998). Larval *Hydora* were more abundant deep in our cores in winter compared with summer. In an Australian river, Marchant (1995) reported that in June (austral winter) most coleoptera (composed mainly of elmid larvae) occurred below 10 cm compared with other sampling occasions when at least 70% were present in the surface layers. He speculated that this may have been in response to high surface flow at the time. In our study, the winter sampling was conducted at low discharge after a prolonged period of near baseflow conditions, so it is unlikely that the observed difference between winter and summer was a response to changes in surface discharge. Other factors, such as the availability or distribution of food within the sediments, may account for the observed differences in distributions between the seasons.

Asellotan isopods have also been reported in New Zealand from the hyporheic zones of four rivers in Canterbury (Burrell, 2001), but at much lower densities than obtained here (or by Olsen, Matthaei & Townsend, 2001, where they were incorrectly identified as Anthuridea). Interstitial isopoda (particularly Asellota) are also known from the hyporheic zones of streams in Europe (Creuzé des Châtelliers & Reygrobelle, 1990; Plénet, Gibert & Marmonier, 1995) and North America (Stanford & Ward, 1988; Strommer & Smock, 1989; Boulton, Valett & Fisher, 1992; del Rosario & Resh, 2001), but Pennak & Ward (1986) noted the absence of micro-isopods from the hyporheic zone of the South Platte River.

Insects generally accounted for about half the total hyporheic density in both upwelling and downwelling zones, but because of the mesh size used (250 µm) many meiofauna may not have been retained in the sieve. Densities of meiofauna may be high in the hyporheic zone of streams and is likely to be numerically dominated by non-insect taxa (Pennak & Ward, 1986; Palmer, 1990; Schmid-Araya, 2000). Thus, the proportion of the hyporheos that are insects given here is likely to be an over-estimate if only the macrofauna are considered. Hyporheic communities dominated by epigean taxa (especially insects) may be characteristic of unstable streams, compared with more stable streams, which tend to be dominated by hypogean taxa, particularly crustaceans (Fowler & Death, 2001). The Kye Burn is unstable because of a

high sediment supply and periodic high discharge events. Flood events move a large proportion of surface particles (Matthaei, Peacock & Townsend, 1999a) and produce a mosaic of sediment patches with an average depth of 10–15 cm of bed disturbance, although scour patches as deep as 60 cm and as much as 22 cm of fill have been recorded (Matthaei, Peacock & Townsend, 1999b). Such instability is consistent with the numerical dominance of epigean taxa in the hyporheos of the Kye Burn.

Thirteen genera of water mites were collected in this study. In most previous studies in New Zealand and other countries, these have been generally lumped into the uninformative grouping 'Hydracarina' but in the Kye Burn, this is clearly a diverse assemblage, both taxonomically and ecologically. It is apparent that we are only beginning to understand the diversity and biology of the hyporheos in New Zealand, as has been suggested for Australia (Boulton, 2001). Greater taxonomic effort is required before the true diversity of New Zealand hyporheic systems becomes apparent.

Sediment characteristics (particularly the amount of fine sediments) and the pattern of vertical hydrological exchange account for some of the small-scale patchiness in the distribution of the hyporheos in the Kye Burn identified by Olsen *et al.* (2001). The mechanisms underlying variability in the distribution of fine sediments are poorly understood, but may involve the heterogeneous effects of bed-moving spates or the redistribution of fine sediments at low flow. Patchiness in these factors, and the consequent variability in abundance and composition of the hyporheos, need to be taken into account when planning sampling regimes or field manipulations in the hyporheic zone. Field manipulations of hyporheic physicochemical conditions (as in Richards & Bacon, 1994; Boulton & Foster, 1998) provide a valuable step to establish the role of these variables in determining the diversity and structure of the hyporheos in gravel-bed streams.

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