

Distribution Patterns of Hyporheic Fauna in a Riparian Floodplain  
Terrace, Queets River, Washington

by

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Abstract

Distribution Patterns of Hyporheic Fauna in a Riparian Floodplain  
Terrace, Queets River Washington

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Hydrologic linkages between rivers and their floodplains are essential for maintaining ecological structure and function in these dynamic ecosystems. In particular, hyporheic zones can regulate the transfer of nutrients from productive floodplains to oligotrophic surface habitats and provide habitat for aquatic insects, an important food source for resident fishes. Recently, attention has focused on the potential influences of invertebrates on the functional significance of hyporheic zones. Studies investigating hyporheic invertebrates have focused on communities within the active channel, either beneath the wetted channel or channel gravel bars. The floodplain hyporheic zone has received little attention in the literature but may be important in rivers with extensive floodplains. The objectives of this study were to describe hyporheic invertebrate community structure in the floodplain hyporheic zone and to relate spatial and temporal patterns in community structure to hydrology, organic matter and microbial biomass, and

physico-chemical parameters. Piezometers in a floodplain riparian terrace on the Queets River were sampled during early summer 1999, late summer 1999, fall 1999, winter 2000, spring 2000, and later summer 2000. The invertebrate assemblage was consistent with cyclopoid copepods, copepod nauplii and rotifers dominating numerically throughout the study. Archiannelids, hydrachnidia and harpacticoid copepods were common but did not contribute substantially to overall invertebrate abundance. Aquatic insects such as chironomids, ceratopogonids, and plecoptera were surprisingly rare across sample dates. Overall invertebrate distribution across the terrace was characterized by high spatial and low temporal heterogeneity. At the terrace scale, spatial heterogeneity was related to wood, with high-wood piezometers representing temporally stable 'hotspots' of total invertebrate abundance. Within the terrace, along individual flowpaths, spatial heterogeneity appeared to be driven by a mosaic of overlying vegetation patch-types. Hyporheic invertebrate communities can provide unique insights into the linkage between rivers and their adjacent floodplains, and may ultimately play an important role as indicators of water quality and ecosystem health.

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## **Dedication**

For my parents  
Maureen and Jonathan Coe

## INTRODUCTION

Connectivity between rivers and their floodplains is essential for maintaining proper ecological function in these dynamic ecosystems (Ward & Stanford 1995, Ward 1998, Ward *et al.* 1999). Alteration of natural disturbance regimes through river regulation has resulted in a loss of habitat heterogeneity, productivity and biodiversity in these 'flood-dependent' environments (Ward & Stanford 1995, Ward 1998). Similarly, removal of trees from adjacent riparian areas has led to a reduction in inputs of large wood debris (LWD) which influences pool frequency, channel morphology and retention of organic matter (Sedell *et al.* 1988, Bilby & Ward 1991, Fetherston *et al.* 1995). In the Pacific Northwest, the legacy of these anthropogenic modifications is the recent endangered species listing of Pacific salmon (*Oncorhynchus* spp.), which highlights the inability of our rivers to maintain healthy fish populations. In addition to surface connectivity, river ecologists are increasingly acknowledging the importance of subsurface linkages in maintaining structure and function of river ecosystems. In particular, the hyporheic zone has recently been recognized as a fundamental link between the active channel and floodplain areas (Stanford *et al.* 1994, Edwards 1998). The hyporheic zone is an area of saturated sediments located beneath and adjacent to streams and rivers (Triska *et al.* 1989).

Intense microbially-mediated biogeochemical processing within the hyporheic zone regulates nutrient transformations and fluxes to surface aquatic ecosystems (Findlay 1995, Triska *et al.* 1993). Nutrient-rich hyporheic subsidies enhance surface water productivity (Valett *et al.* 1994), particularly in oligotrophic river ecosystems of the

Pacific Northwest (Fevold 1998). For instance, on the Queets River, Washington, algal production in floodplain back channel habitats was 3.8 to 6.5 times higher at hyporheic upwelling sites than at sites without hyporheic subsidies (Fevold 1998).

The hyporheic zone also functions as a rearing habitat and refuge for aquatic macroinvertebrates. Adult stoneflies (Plecoptera) emerging from the hyporheic zone on the Flathead River, Montana, provide an important food source for resident fishes (Stanford *et al.* 1994). In low-gradient rivers, hyporheic zones with high interstitial volume contribute significantly to total system invertebrate production (Smock *et al.* 1992). For instance, on the Flathead River, invertebrate biomass in the hyporheic habitat could potentially exceed estimates in the active channel habitat (Stanford & Ward 1988). The hyporheic zone can also serve as refuge from disturbance and as a post-disturbance colonization source, with obvious implications for invertebrate community resilience to disturbance. Studies in intermittent streams suggest that hyporheic zones provide refuge for epigeal (surface) invertebrates during the dry season (Cooling & Boulton 1993, Clinton *et al.* 1996). Similarly, fauna migrate deeper into the interstitial spaces during floods (Palmer *et al.* 1992, Dole-Oliver & Marmonier 1992). Although there is vertical migration by some taxa during high flows, it may not be enough to prevent substantial losses during floods (Palmer *et al.* 1992). Dole-Olivier *et al.* (1997) concluded that the 'refugium effect' is dependent on the amplitude of the flood disturbance, the stability of the substratum and hydraulic heterogeneity.

Biogeochemical processing within the hyporheic zone can be influenced by the activity of invertebrates inhabiting the interstices. The functional importance of

invertebrates is well established in marine systems (Gerlach 1978, Findlay & Tenore 1982, Traunspurger *et al.* 1997) suggesting that hyporheic invertebrates (hyporheos) might be as functionally significant. Invertebrates act as ecosystem engineers, maintaining hydraulically conductive subsurface environments through burrowing activities (Gerlach 1978). In alluvial backwater sediments where disturbance is minimal, invertebrates maintain 'open' pores through the pelletization of fine particles (Danielopol 1984, Danielopol 1989). Invertebrate bioturbation influences nutrient cycling by increasing nutrient flux and oxygen availability (Gerlach 1978, Findlay & Tenore 1982). Microbial biomass and activity are also indirectly influenced by invertebrate activity through the breakdown of particulate organic matter to dissolved forms for microbial consumption (Findlay & Tenore 1982). Further, direct grazing can be important in stimulating bacterial growth and activity (Traunspurger *et al.* 1997).

The role of microbes as an important food source for hyporheic invertebrates has been addressed in only a few studies (Barlocher & Murdoch 1989, Brunk & Fischer 1999). In general, research has focused on the influence of hydrology and physico-chemical parameters (references herein), with efforts directed on reach-scale (meters) distribution patterns of hyporheic invertebrate communities residing within the active channel hyporheic zone, either beneath the wetted channel or beneath channel gravel bars. Hyporheic invertebrate communities typically exhibit high spatial and temporal heterogeneity. Vertically, invertebrate densities and taxonomic richness decrease with depth in response to reductions in porosity and dissolved oxygen with depth (Williams & Hynes 1974, Maridet *et al.* 1992, Maridet & Phillippe 1995, Maridet *et al.* 1996, Adkins

& Winterbourn 1999). Longitudinally, hyporheic communities vary along flowpaths, from upwelling to downwelling zones (Dole-Olivier & Marmonier 1992, Cooling & Boulton 1993, Boulton & Stanley 1995). In general, oxygen-rich, downwelling zones are characterized by epigean (surface) fauna whereas upwelling hypoxic zones are dominated by hypogean (subsurface) fauna. Longitudinal patterns in community structure appear to correspond to oxygen availability which varies as a function of stream hydrology, permeability of bed sediments and residence time of hyporheic water (Cooling and Boulton 1993).

Invertebrate communities in floodplain hyporheic zones, lateral to the active channel, have received considerably less attention. Research on the Flathead River, Montana and large alluvial rivers in Europe have focused on large-scale (kilometers) patterns of hyporheos across the floodplain environment. In general, the spatial distribution of hyporheic fauna depends on groundwater infiltration and floodplain position, or proximity to the active channel (Chafiq *et al.* 1992, Marmonier *et al.* 1992, Ward *et al.* 1994). On the Rhone River, sites on the margin of the floodplain were characterized by high hypogean diversity while those along the river were characterized by high epigean and low hypogean diversity (Marmonier *et al.* 1992). Hypogean taxa 'appear to be highly sensitive to hydrologic perturbations in the surface water' (Marmonier 1991, Marmonier & Creuze des Chatelliers 1991). At the floodplain scale, patterns in invertebrate distribution appear to be 'more gradual than patchy' (Ward & Palmer 1994).

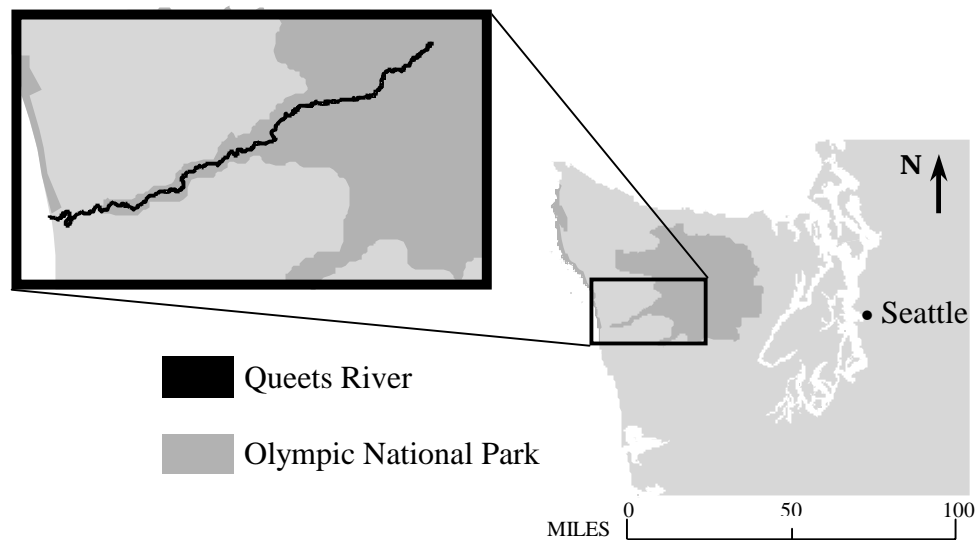
In addition to hydrologic influences, some studies have shown strong correlations between community structure and physico-chemical parameters (Williams 1989, Palmer 1990, Boulton & Stanley 1995) whereas others have not (Strayer 1994b, Strayer *et al.* 1997). Overall, no single variable or suite of variables seems to explain observed patterns in hyporheic invertebrate distribution across all studies and all scales. Since hyporheic zones are by nature detritus-based, it has been suggested that microbial biomass and associated biofilms may be an important food source for hyporheic invertebrates and therefore important in determining invertebrate distribution (Barlocher & Murdoch 1989, Storey *et al.* 1999).

This research uses an integrated approach to investigate hyporheic invertebrate community structure. Specifically, the objectives are to describe spatial and temporal patterns in invertebrate community structure and distribution in a floodplain and to relate those patterns to hydrology, organic matter, microbial biomass and activity, and physico-chemical parameters. Although the microbial component will not be addressed in this thesis, the relationship between the invertebrates and the microbial community within this hyporheic zone will be explored when the results of an ongoing study on microbial community structure are available (Clinton 2001b). This research is intended to address the gap between our knowledge of small-scale (meters) trends in active channel and large-scale (kilometers) trends in floodplain hyporheic invertebrate communities.

## METHODS

### *Study Area*

This study was conducted on the Queets River, a coastal floodplain river draining a 1157 km<sup>2</sup> watershed on the Olympic Peninsula in western Washington (Figure 1).

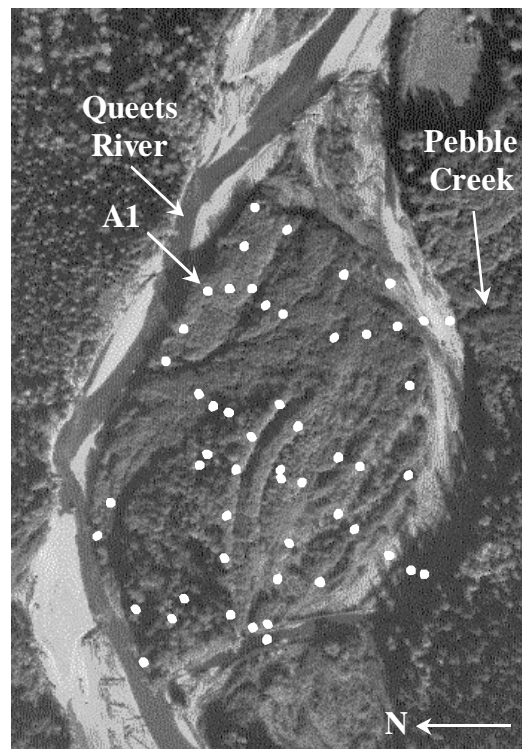


**Figure 1.** Queets River, Olympic Peninsula, Washington State. Figure modified from Coe (2001).

The Queets flows 83 km from the western slopes of the Olympic Mountains to the Pacific Ocean. Over 90% of the length of the mainstem lies within the boundaries of the Olympic National Park. Rain-on-snow events create rapid increases in discharge resulting in large floods (two over 2800 m<sup>3</sup>/s during the last 5 years) that recede within a few days. Precipitation in the Queets valley averages 301 cm annually (1931-2000) and air temperatures range from 9.3°C in summer to 4.2°C in winter (WWRC 2001, Clearwater). During the study, mean monthly discharge varied from 23 m<sup>3</sup>/s in September 1999 (summer low-flow) to 383 m<sup>3</sup>/s in December 1999 (USGS, Queets Near

Clearwater). The highest daily discharge was recorded during a flood ( $2,197\text{m}^3/\text{s}$ ) in December 1999.

The study site was a 600 m wide by 1,000 m long riparian terrace located in a lower alluvial floodplain reach, 25 km from the coast (Figure 2). The Queets River flowed along the north side of the terrace and surface water from a floodplain tributary, Pebble Creek, flowed along the south side of the terrace, entering the Queets River at the western end of the terrace.



**Figure 2.** The floodplain riparian terrace study site, adjacent to the Queets River, showing the distribution of the 54 piezometers.

Forest riparian vegetation on the study site ranged in successional stage from bare cobble to mixed old-growth conifer. The younger, upstream portion of the terrace was

dominated by young and mature (> 20 years old) red alder (*Alnus rubra* Bong.), whereas sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) co-dominated the older, downstream part of the terrace (Estelle Balian, University of Washington, personal communication). Black cottonwood (*Populus trichocarpa* Torr. & Gray) and willow (*Salix* spp.) were also present. Although common in the Queets Valley, western red cedar (*Thuja plicata* Donn) was absent on the terrace. Major understory shrub species included blackberry (*Rubus ursinus* Cham. & Schlecht.), salmonberry (*Rubus spectabilis* Pursh) and huckleberry (*Vaccinium ovalifolium* Smith). The soils on the terrace were characterized by entisols consisting of moderately drained fine sand and A and C horizons which are weakly developed (Bechtold 2000). Uplifted marine sediments containing mudstone, sandstone and shales-siltstone comprised the parent material of the Queets River valley (Bechtold 2000).

### ***Field and Laboratory Procedures***

#### **Piezometer Installation**

In 1998 and 1999, 54 open-ended 2.5 cm PVC piezometers were installed 30 – 60 cm into the water table during summer low-flow (Figure 2). Water depths below the soil surface varied from < 1 m in young cobble areas to > 4 m in the old growth areas.

Piezometers were surveyed for lateral position using a Trimble differentially corrected global positioning system, accurate to less than a meter horizontally. Elevation relative to an arbitrary datum point was determined using a level (TopCon AT-F6 autolevel) and stadia rod.

## **Hyporheic Invertebrates**

Invertebrate samples were collected from each piezometer on 15 JUL 1999, 25 SEP 1999, 20 NOV 1999, 1 MAR 2000, 14 JUN 2000 and 19 SEP 2000 using a self-priming manual bilge pump (Guzzler, Bosworth Company). Four liters of water were withdrawn from each piezometer and filtered through a 63  $\mu\text{m}$  mesh. Material retained on the mesh was preserved in the field using 3.7% formaldehyde solution (10% formalin). Rose Bengal (Acid Red 94) was added to the samples to allow for ease of sorting. All samples collected were sorted for September 1999 (n = 44), March 2000 (n = 46), June 2000 (n = 48) and September 2000 (n = 43) to maximize comparisons between summer low-flow and winter and spring high-flow conditions. A subset of 30 piezometers was sorted for July 1999 (n = 25) and November 1999 (n = 31). These samples were chosen to include both perimeter piezometers and piezometers distributed across the terrace. Samples containing large amounts of gravel were elutriated 15 x to remove lighter particles, including invertebrates. The remaining substrates from each sample were randomly sorted under a microscope to determine whether elutriation successfully removed invertebrates. After elutriation, samples were transferred to 70% ethanol and sorted. Invertebrates were identified to the lowest taxonomic level and enumerated using an Olympus zoom stereo dissecting microscope (SZ-1145, 18 – 110 X magnification). Large ciliates, gastrotrichs and rotifers were collectively classified as rotifers.

## **Organic Matter**

Total organic matter samples were collected from each piezometer on 10 OCT 1999, 30 NOV 1999, 14 MAR 2000, 27 JUN 2000 and 27 SEP 2000. Samples were not collected in July 1999. Total organic matter included both woody and nonwoody organic matter, and invertebrates. Samples were collected 1 - 2 weeks after invertebrates to allow for recovery from the prior sampling. One liter of water was withdrawn using a self-priming manual bilge pump. Three 1L replicate samples were collected from the Queets River near piezometer 'A1' (Figure 2). Samples with low turbidity were processed in the field by filtering 1L onto 0.7  $\mu\text{m}$ , 47 mm Whatman GF/F filters (ashed @ 500°C and preweighed). Three subsamples, ranging from 15 ml to 180 ml, were filtered for those samples with high turbidities. Dry weights were obtained after drying the filters at 60°C for a minimum of 2 days. Filters were ashed for 3 hours at 500°C to obtain ash-free dry mass.

The woody component of organic matter was determined by picking wood particles, > 1 mm in size, from the invertebrate samples. The wood was preserved in 70% ethanol before being filtered onto 0.7  $\mu\text{m}$ , 47 mm Whatman GF/F filters (ashed @ 500°C and preweighed). Ash-free dry mass was not determined as it was assumed that the wood removed from the sample was free of inorganic particles.

## **Physico-chemical Measurements**

Physicochemical data were collected from each piezometer prior to invertebrate collection. Dissolved oxygen and temperature were measured with a Y.S.I. Model 30 oxygen meter calibrated in water-saturated air at stream temperature. Water was pumped

through a manifold containing probes for the meters. The data were recorded, within 1 to 2 minutes, when oxygen values stabilized. Specific electrical conductance was measured with a Y.S.I. Model 55. Water levels were determined by dipping a metal measuring tape down each piezometer until a 'plunking' noise indicated that the tape had contacted water. Depth to water was used to calculate hydraulic head from the surveyed piezometer-top elevations. Hydraulic conductivities were measured once during the course of the study using the falling head test (Bouwer 1989).

### **Data Analysis**

A balanced design approach was used to compare invertebrate community structure and distribution among sample dates. Although a minimum of 30 piezometers was sampled for each date, only 20 of those piezometers were sampled on all six dates. Therefore, cumulative abundance (individuals/terrace) and mean densities (individuals/4L) were determined from those 20 piezometers sampled on all dates. Similarly, mean densities for the 20 individual piezometers (individuals/4L) were calculated by averaging densities for the six dates. Mean total invertebrate and individual taxa densities for the terrace and individual piezometers were compared across sample dates using a one-way ANOVA ( $\alpha = 0.05$ ). The coefficient of variation was used to compare variation across dates (Zar 1996).

Total invertebrate and individual taxa densities were regressed ( $\alpha = 0.05$ ) against organic matter and physicochemical parameters (SPSS, v.8S). All samples for each season were considered for regression analysis. Where necessary, data were transformed ( $\log(x+1)$ ) to meet the assumptions of normality. Since organic samples included

invertebrates, the number of individuals in each taxonomic group was multiplied by the average of meiofaunal weight estimates for major taxa from Goose Creek, Virginia (Poff *et al.* 1993) and Mirror Lake, New Hampshire (Strayer 1994a). The contribution of invertebrates to total organic matter was represented as a percentage of total organic matter concentration.

Longitudinal distance along a flowpath and lateral distance from river were also calculated for inclusion in regression analysis. Longitudinal distance from river was determined by estimating distance of each piezometer from a point upstream of the terrace where hydraulic head contour maps indicated that surface water entered the terrace. Lateral distance from river was determined by calculating the distance of each piezometer from the Queets River at 90° to its direction of flow.

Total invertebrate densities along three individual flowpaths were also regressed ( $\alpha = 0.05$ ) against organic matter and physicochemical parameters. Hydraulic head, a combination of water elevation and water pressure, was used to make inferences about the direction of subsurface flow within the terrace. Three virtual flowpaths were delineated by krigging (Surfer, v.7) hydraulic head data and superimposing the flowpaths onto the flow net at right angles to the field of flow (Clinton 2001a, in review). The piezometers along each flowpath were assumed to be hydrologically connected. In addition, the effects of patch-type and date on total invertebrates across the terrace were analyzed using a 2-way ANOVA ( $\alpha = 0.05$ ).

## RESULTS

### ***Overall Community Composition***

Twenty-three major taxa were collected from 54 piezometers (n=237) between July 1999 and September 2000 (Table 1 & Appendix A). Cyclopoid and harpacticoid copepods, juvenile copepods (nauplii), archiannelids, rotifers, and hydrachnidia were the 'most common' taxa, occurring in greater than 70% of the piezometers (Table 1). Parastenocaridid copepods were identified as being present in the harpacticoid group (Janet Reid, Smithsonian Institution, personal communication). Collembola, oligochaetes, nematodes, tardigrades, ostracods, isopods and amphipods were considered to be 'relatively' common occurring in 25 – 50% of piezometers. Analysis of 12 of 68 amphipods collected from the terrace throughout the study revealed 3 or 4, undescribed species of *Stygobromous* sp. (John Holsinger, Old Dominion University, personal communication). Epigeal taxa including chironomids, ceratopogonidae, and plecoptera were considered 'rare,' occurring in less than 20% of piezometers sampled. Bathynellaceans were also considered to be rare. Twenty-four bathynellaceans from samples collected in September 1999 and March 2000 were identified as *Pacificabathynella sequoiae*, a species first described at Mt. Tamalpais State Park, California, in 1973 (Schminke & Noodt, 1988).

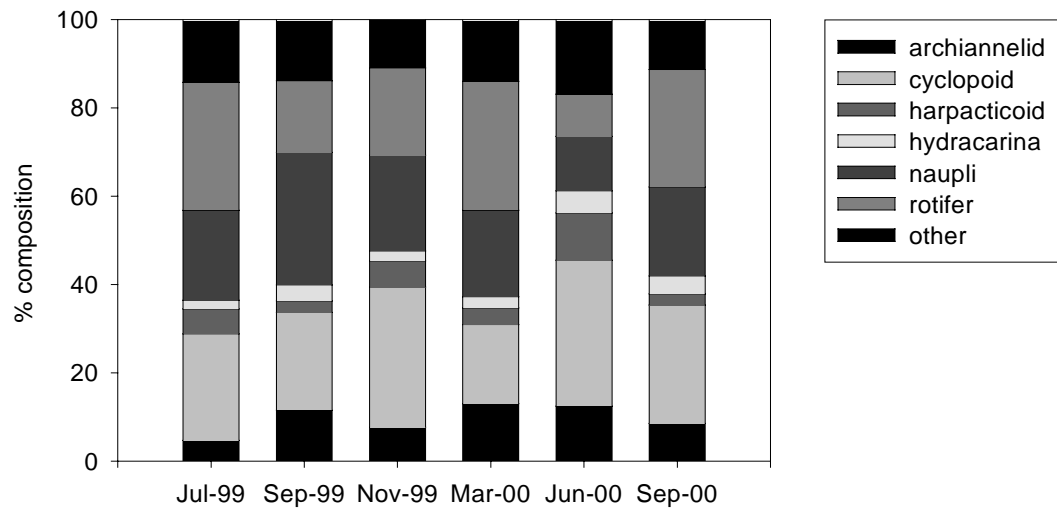
Cumulative total invertebrate abundance across the terrace ranged from 1088 individuals in June 2000 to 3734 individuals in July 1999 (Table 2). Cyclopoid copepods dominated numerically in November 1999 (32%), June 2000 (33%) and September 2000 (27%) whereas copepod nauplii dominated in September 1999 (27%) and rotifers

dominated in July 1999 (29%) and March 1999 (29%). Community composition was similar among sample dates with cyclopoid copepods, juvenile copepods (nauplii) and rotifers together comprising from 55% to 74% of total invertebrate abundance (Figure 3).

**Table 1.** Percentage occurrence of taxa collected from 55 piezometers (n = 237) between July 1999 to September 2000.

Taxon	Occurrence (%)
Crustacea: Copepoda: Cyclopoida	94.9
Archiannelida	87.8
Rotifera	85.2
Crustacea: Copepoda: Juvenile Copepod (Naupli) <sup>†</sup>	84.0
Arachnida: Hydrachnidia	72.6
Crustacea: Copepoda: Harpacticoida	70.5
Insecta: Collembola	44.7
Annelida: Oligochaeta	40.5
Nematoda	38.4
Tardigrada	32.1
Crustacea: Ostracoda	32.1
Crustacea: Isopoda	30.8
Crustacea: Amphipoda	28.7
Crustacea: Bathynellacea	16.0
Insecta: Diptera: Chironomidae	10.1
Platyhelminthes: Microturbellaria	8.9
Crustacea: Chydoridae	5.9
Insecta: Hemiptera	3.8
Insecta: Plecoptera	3.4
Insecta: Coleoptera	3.0
Mollusca: Gastropoda	2.5
Crustacea: Bosminidae	2.1
Insecta: Diptera: Ceratopogonidae	1.3
Insecta: Diptera: Tipulidae	0.4

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.



**Figure 3.** Percent composition of ‘most common’ taxa across terrace. Based on 20 piezometers sampled consistently across sample dates. ‘Other’ category includes 18 major taxa.

**Table 2.** Cumulative total invertebrate abundance (individuals) from 20 piezometers sampled between July 1999 and September 2000.

Taxon	Date					
	Jul-99	Sep-99	Nov-99	Mar-00	Jun-00	Sep-00
Archiannelida	174	279	119	362	135	233
Cyclopoida	902	537	495	497	360	735
Harpacticoida	210	64	92	104	117	70
Hydrachnidia	74	88	35	71	54	111
Nauplii <sup>†</sup>	760	727	309	545	134	553
Rotifera	1085	393	338	813	104	729
Other <sup>††</sup>	529	336	170	388	184	311
<b>Total</b>	<b>3734</b>	<b>2424</b>	<b>1558</b>	<b>2780</b>	<b>1088</b>	<b>2742</b>

<sup>†</sup> Nauplii are not considered as separate taxa.

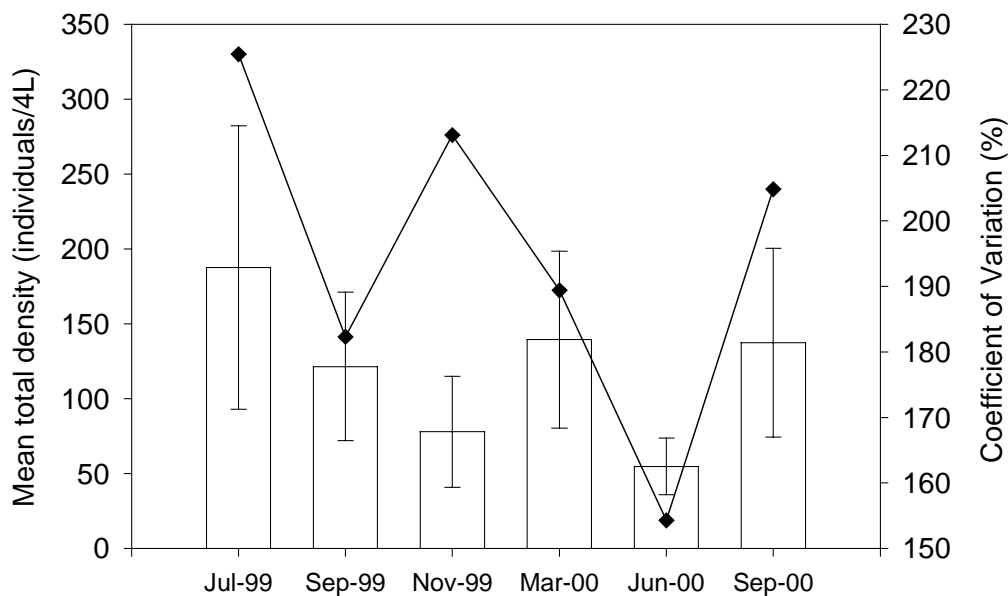
<sup>††</sup> Category includes 18 major taxa.

Whereas archiannelids, hydrachnidia and harpacticoids occurred in > 70 % of all samples, these taxa each comprised < 15% of total abundance. Throughout the study, contribution to total abundance averaged 10% for archiannelids, 6% for harpacticoid copepods and 3% for hydrachnidia. Eighteen major taxa were included in the 'other' category and contributed 11-17% to total abundance (Table 2). Isopods, nematodes and oligochaetes contributed from 43% (September 1999) to 75% (July 1999) to the 'other' category totals.

### ***Total Invertebrate Spatio-Temporal Dynamics***

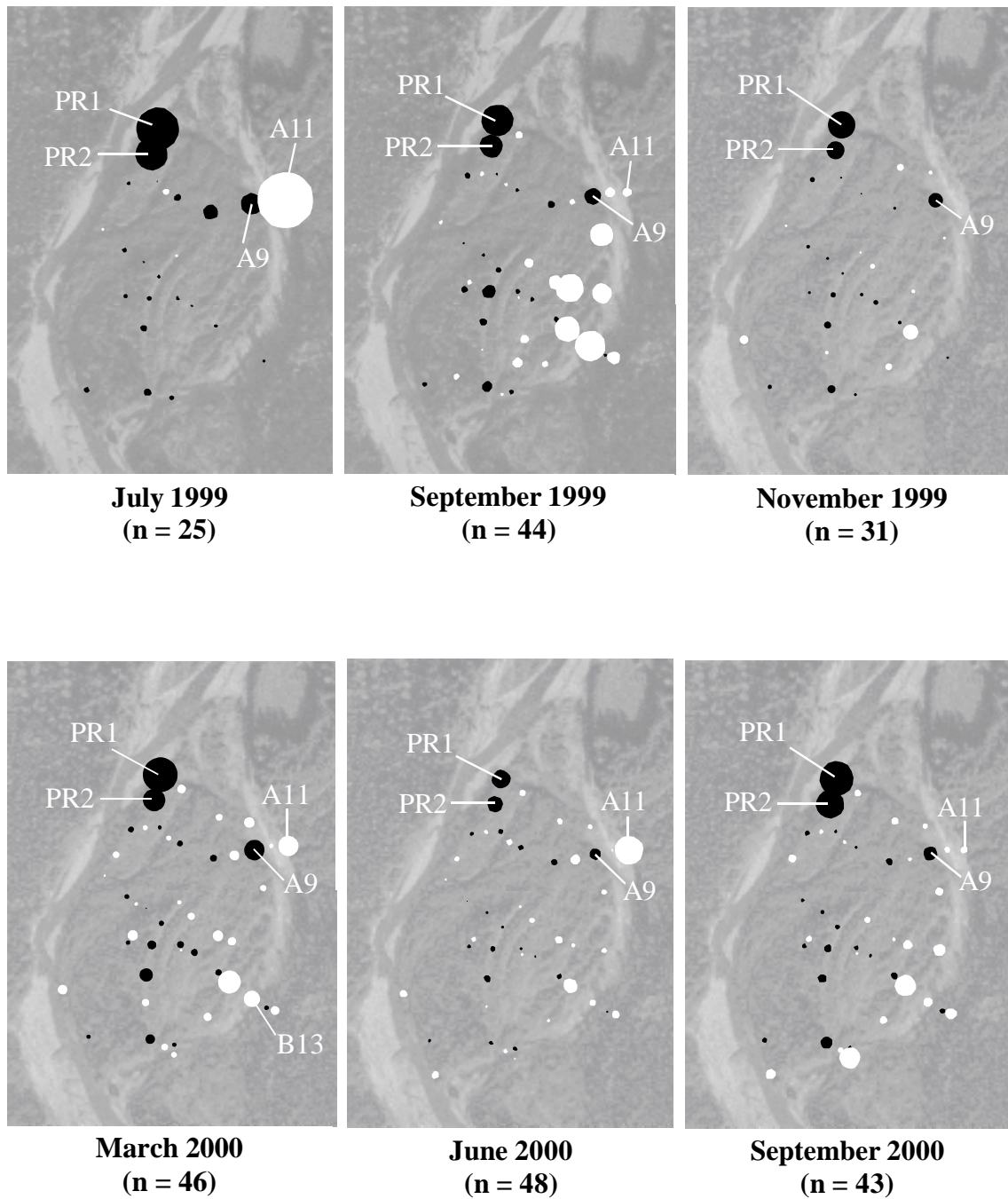
Mean densities were not significantly different among sample dates (ANOVA,  $p > 0.05$ ,  $n = 20$ ) (Figure 4). However, densities were highest in July 1999 ( $188 \pm 95$  (S.E.) individuals/4L) and lowest in June 2000 ( $55 \pm 19$  (S.E.) individuals/4L). Variance (coefficient of variation) was lowest in June 2000 and highest in July 1999 (Figure 4). Invertebrate distributions across the floodplain riparian terrace exhibited seasonal consistency, with highest densities along the perimeter of the terrace, adjacent to the Queets River and Pebble Creek, and lowest densities in the middle of the terrace (Figure 5). In July 1999, there was pronounced disparity between high-density piezometers along the perimeter of the terrace and low-density piezometers in the middle of the terrace. In contrast, differences between perimeter and middle terrace piezometers were less obvious in June 2000. Within the 20 piezometers sampled consistently across seasons, individual piezometer densities ranged from 3-323 individuals/4L in June 2000 to 4-1707 individuals/4L in July 1999 (Figure 5, black bubbles). Of these 20

piezometers, PR1 exhibited highest densities during all 6 sample dates, contributing 29% to 46% to total terrace abundance. Consideration of all piezometers confirmed highest



**Figure 4.** Mean total invertebrate densities (bars) and coefficient of variation across sample dates (line). Means  $\pm$  S.E. were calculated from 20 piezometers sampled on all dates.

densities in PR1 in September 1999 (926 individuals/4L), November 1999 (705 individuals/4L), March 2000 (1129 individuals/4L) and September 2000 (1093 individuals/4L). However, A11, the only piezometer within the wetted channel (Figure 5), exhibited the highest densities in July 1999 (2976 individuals/4L) and June 2000 (765 individuals/4L). A11 was submerged in November 1999 and, therefore, could not be



**Figure 5.** Temporal trends in total invertebrate densities. Bubbles are centered on the piezometers. Consistently high invertebrate density piezometers are designated with labels. Black bubbles represent 20 piezometers sampled on all 6 dates. White bubbles represent additional piezometers sampled.

sampled at that time. In addition to piezometers PR1 and A11, A9 and PR2 were also important contributors to overall terrace abundance across sample dates (Figure 5).

In conclusion, spatial variance seemed to be higher than temporal variance (Figure 5). A two-way analysis of variance substantiated this conclusion. The mean sum of squares was higher for the piezometer factor (339,069) than for the seasonal factor (45,095).

### ***Individual Taxa Spatio-Temporal Dynamics***

Most individual taxa showed no significant differences in mean densities among sample dates (ANOVA,  $p > 0.05$ ,  $n = 20$ ). Taxa previously described as ‘most common’ and numerically dominant (cyclopoid and juvenile copepods (nauplii) and rotifers) exhibited trends similar to total invertebrates with highest densities along the perimeter of the terrace and lowest densities in the middle of the terrace. Although there were no significant differences in terrace densities among seasons, mean densities were highest in July 1999 and lowest in June for cyclopoid copepods (and copepod nauplii) and rotifers (Table 3). In general, cyclopoid copepods, copepod naupli and rotifers showed similar trends in variation to total invertebrates (Figure 6). However, rotifer variation was noticeably higher in September 2000 than any other date.

Taxa described as ‘most common,’ but not numerically dominant also exhibited spatial trends similar to the community as a whole. However, the differences between high invertebrate density piezometers along the perimeter of the terrace and low invertebrate density piezometers, in the middle of the terrace, were less pronounced in these taxa (Appendices C – H). Archiannelida was one of the only taxa that exhibited a

significant difference in density with date (ANOVA,  $p = 0.039$ ,  $n = 20$ ). Mean archiannelid density was significantly higher in March 2000 than in November 1999 (Table 3). These two sample dates also represented the highest and lowest invertebrate densities, respectively. There were no significant differences in mean harpacticoid

**Table 3.** Mean  $\pm$  S.E. densities (individuals/4L) for ‘most common’ taxa across all dates. Means  $\pm$  S.E. were determined from 20 piezometers sampled on all dates.

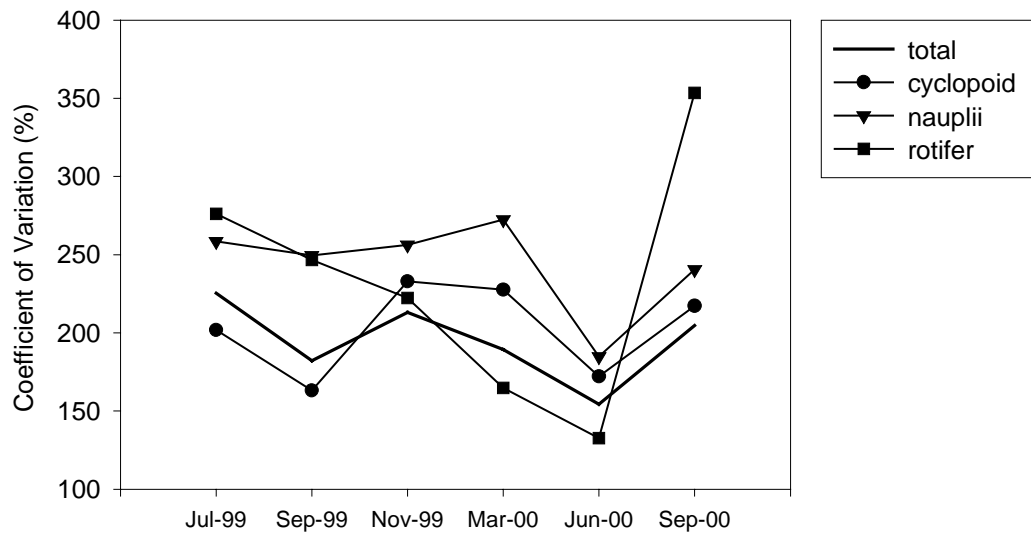
Taxon	Date					
	Jul 99	Sep 99	Nov 99	Mar 00	Jun 00	Sep 00
Archiannelida	8 $\pm$ 2	14 $\pm$ 3	6 $\pm$ 2	18 $\pm$ 5	7 $\pm$ 2	12 $\pm$ 3
Cyclopoida	45 $\pm$ 20	27 $\pm$ 10	25 $\pm$ 13	25 $\pm$ 13	18 $\pm$ 7	37 $\pm$ 18
Nauplii	38 $\pm$ 22	36 $\pm$ 20	15 $\pm$ 9	27 $\pm$ 17	7 $\pm$ 3	28 $\pm$ 15
Harpacticoida	11 $\pm$ 6	3 $\pm$ 2	5 $\pm$ 2	5 $\pm$ 2	6 $\pm$ 2	4 $\pm$ 1
Hydrachnidia	4 $\pm$ 1	4 $\pm$ 2	2 $\pm$ 1	4 $\pm$ 2	3 $\pm$ 1	6 $\pm$ 2
Rotifera	54 $\pm$ 34	20 $\pm$ 11	17 $\pm$ 8	41 $\pm$ 15	5 $\pm$ 2	36 $\pm$ 29

and hydrachnidia densities between dates. However, mean harpacticoid density was highest in July 1999 and lowest in September 1999, whereas mean hydrachnidia density was highest in September 2000 and lowest in November 1999 (Table 3).

With the exception of isopods, nematodes and oligochaetes, taxa considered to be ‘relatively’ common were not concentrated in piezometers A9, PR1, PR2 (Figure 5), but distributed throughout the terrace (Appendices C – H). Of this group, only tardigrades showed significant differences among sample dates (ANOVA,  $p = 0.005$ ,  $n = 20$ ). Mean

tardigrade densities were significantly greater in March 2000 ( $1.7 \pm 0.5$  (S.E.)

individuals/4L) than in September 1999 ( $0.4 \pm 0.2$  (S.E.) individuals/4L), November



**Figure 6.** Coefficient of variation across sample dates for total invertebrates and two dominant taxa. Juvenile copepods, or nauplii, include both harpacticoid and cyclopoid copepods and are not considered as separate taxon.

1999 ( $0.3 \pm 0.2$  (S.E.) individuals/4L) and September 2000 ( $0.2 \pm 0.1$  (S.E.)

individuals/4L). Mean ostracod densities ranged from  $0.4 \pm 0.2$  (S.E.) individuals/4L

(June 2000) to  $1.1 \pm 0.4$  (S.E.) individuals/4L (March 2000). Mean amphipod densities

ranged from  $0.5 \pm 0.2$  (S.E.) individuals/4L (June 2000) to  $1.1 \pm 0.3$  (S.E.) individuals/4L

(March 2000). Throughout the study, piezometers A9, PR1 and PR2 comprised an

average of 83% of the oligochaetes, 74% of the nematodes, and 80% of the isopods found

on the terrace (n=20). Mean oligochaete densities ranged from  $1.5 \pm 0.7$  (S.E.)

individuals/4L (June 2000) to  $14 \pm 8$  (S.E.) individuals/4L (July 1999). Mean nematode densities ranged from  $1.2 \pm 0.5$  (S.E.) individuals/4L (November 1999) to  $4 \pm 2$  (S.E.) individuals/4L (July 1999). Mean isopod densities ranged from  $1.5 \pm 0.6$  (S.E.) individuals/4L (September 1999) to  $7 \pm 5$  (S.E.) individuals/4L (March 2000).

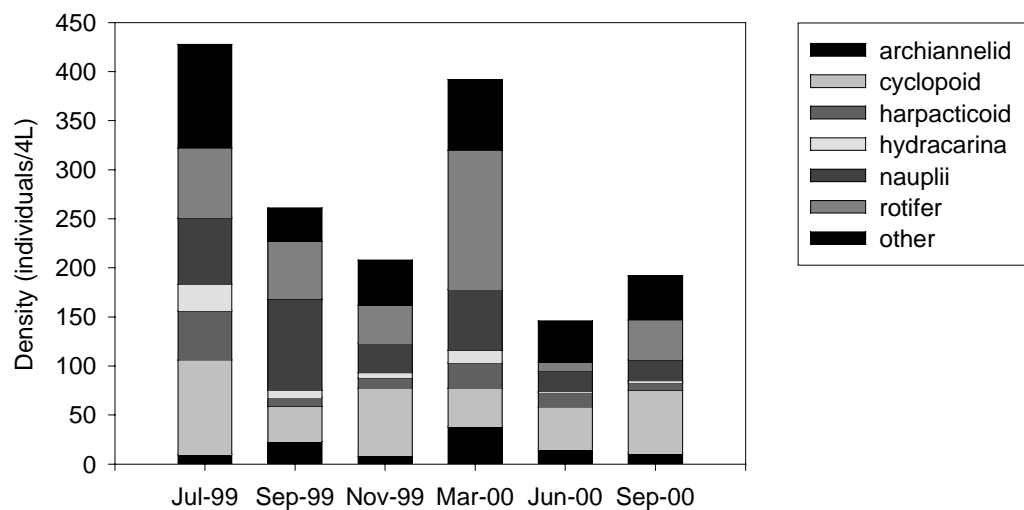
Aquatic insect taxa were noticeably scarce throughout the study. Chironomidae larvae were the most common and abundant insect taxa with a majority of the individuals occurring in piezometer A11 across sample dates. Chironomid densities in A11 were highest in July 1999 (2928 individuals/4L), followed by June 2000 (675 individuals/4L) and then by March 2000 (347 individuals/4L). The lowest densities occurred in September 1999 (8 individuals/4L) and September 2000 (32 individuals/4L). Flooding prevented A11 sample collection in November 1999. Overall, piezometer A11 represented from 57.1% (September 1999) to 99.9% (July 1999) of chironomid abundance across the terrace. Other dipterans such as ceratopogonidae and tipulidae were less common. Ceratopogonidae occurred only once in A11 in June 2000 (6 individuals/4L) and tipulidae occurred only once in the middle of the terrace in September 2000 (1 individual/4L). Plecoptera were similarly infrequent. Of the 237 samples collected, stoneflies were found in only five samples (totaling 6 individuals) in March 2000 and three samples (totaling 3 individuals) in September 2000. Unlike the dipterans and plecopterans, collembola were distributed throughout the terrace during all sample dates (Appendices C - H). Collembola was the only insect taxa that had significant differences in density across dates (ANOVA,  $p = 0.046$ ,  $n = 20$ ). Mean collembola density was significantly higher in September 2000 ( $1.3 \pm 0.3$  (S.E.)

individuals/4L) than in November 1999 ( $0.20 \pm 0.01$  (S.E.) individuals/4L). Individual piezometer densities generally ranged from 1 to 4 individuals/4L but a maximum density of 22 individuals/4L was observed in the middle of the terrace in September 1999. Throughout the study, only 9 coleopterans and 12 hemipterans were collected. With the exception of bathynellaceans and microturbellarians, rare non-insect taxa such as bosmina, chydoridae and gastropoda exhibited no regular patterns in distribution. Bathynellaceans occurred consistently in piezometer PR2 throughout the study with densities ranging from 5 individuals/4L in November 1999 to 26 individuals/4L in July 1999. PR2 contributed from 57% (June 2000) to 81% (September 1999) to cumulative bathynellacean abundance across the terrace ( $n = 20$ ). Similarly, with the exception of March 2000, microturbellarians were consistently found in piezometers PR1 and PR2. This taxon was most abundant in September 1999 with 100% of cumulative microturbellarian abundance occurring in PR1 and PR2. The lowest cumulative abundance was found in November 1999, with only 3 individuals occurring in piezometers PR1 and PR2. Throughout the study, only 4 chydoridae, 4 bosmina and 4 gastropoda were collected from the 20 piezometers.

### ***Piezometer Temporal Dynamics***

Consistent with mean densities, piezometers A9, PR1 and PR2 exhibited highest total densities in July 1999 and lowest total densities in June 2000 (Figures 7-9). In A9, densities ranged from 146 individuals/4L to 428 individuals/4L. Cyclopid copepods dominated numerically in November 1999 (33%), June 2000 (30%) and September 2000 (33%) while copepod nauplii dominated in September 1999 (48%) and rotifers dominated

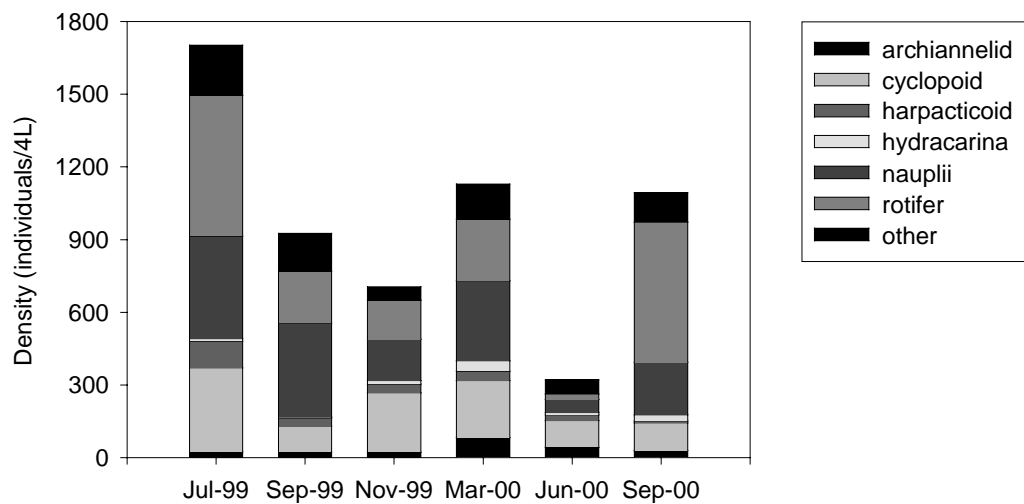
in March 2000 (36%) (Figure 7). The ‘other’ category dominated numerically in July 1999 (25%). Nematodes, isopods and oligochaetes together comprised 92% of the ‘other’ category in July 1999. Of the most common taxa (> 70% samples), hydrachnidia contributed the least to total density (1- 4%) in piezometer A9 for all sample dates except July 1999 in which archiannelida contributed the least (2%) to total density.



**Figure 7.** Taxa contribution to seasonal densities (individuals/4L) for piezometer A9.

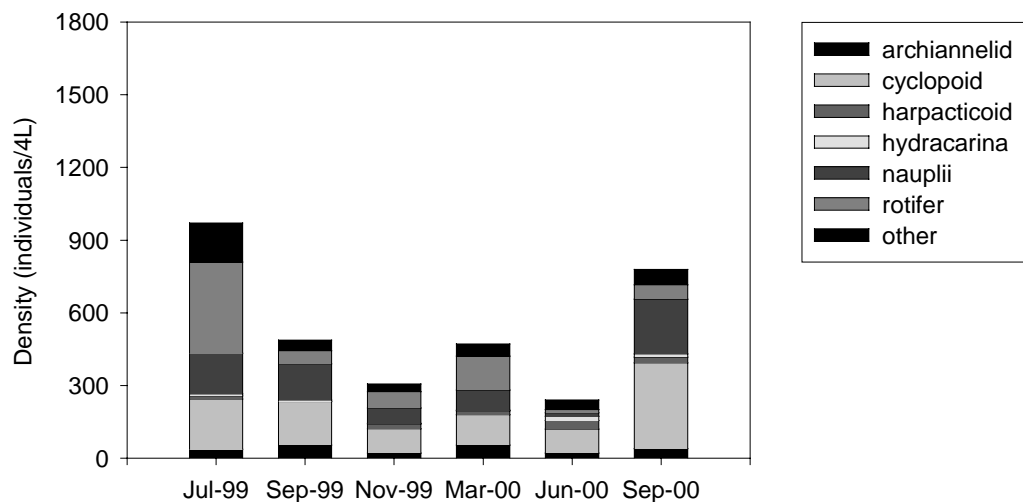
In PR1, densities ranged from 321 individuals/4L in June 2000 to 1703 individuals/4L in July 1999. Similar to A9, cyclopid copepods, nauplii and rotifers were numerically the most important groups in PR1 (Figure 8). Rotifers dominated in July 1999 (34%) and in September 2000 (53%), cyclopid copepods dominated in November 1999 (35%) and June 2000 (34%), and nauplii dominated in September 1999 (42%) and March 2000 (29%). Of the ‘most common’ taxa, hydrachnidia were the least important

numerically in July 1999 (1%), September 1999 (0.4%), November 1999 (2%) and June 2000 (3%). Harpacticoid copepods contributed the least in March 2000 (3%) and September 2000 (1%).



**Figure 8.** Taxa contribution to seasonal densities (individuals/4L) for piezometer PR1.

Densities in PR2 ranged from 240 individuals/4L in June 2000 to 970 individuals/4L in July 1999. Cyclopoid copepods dominated in September 1999 (37%), November 1999 (33%), June 2000 (41%) and September 2000 (45%) whereas rotifers dominated numerically in July 1999 (39%) and March 2000 (30%) (Figure 9). Consistent with both A9 and PR1, either hydrachnidia or harpacticoid copepods contributed the least to totals (0.4 – 5%) for all sample dates except June 2000. Rotifers contributed the least to totals in June 2000 (5%).



**Figure 9.** Taxa contribution to seasonal densities (individuals/4L) for piezometer PR2.

### ***Parameters Influencing Total Invertebrate Distribution***

Average values for organic matter and physico-chemical parameters are presented in Tables 4 and 5, respectively. Total, woody and non-woody organic matter concentrations were all lowest in September 1999 (Table 4). However, the highest concentrations for both total organic matter ( $5.3 \pm 1.8$  (S.E.) mg/L) and non-woody organic matter ( $4.8 \pm 1.7$  (S.E.) mg/L) were observed in March 2000. Woody organic matter concentration was highest in July 1999 ( $1.5 \pm 1.0$  (S.E.) mg/L). In all piezometers where organic matter was collected, the estimated contribution of invertebrates (see Methods) to total organic matter concentration (mg/L) did not exceed 11%. The exception was piezometer A11 in June 2000, when invertebrates contributed 44% to total

**Table 4.** Mean values  $\pm$  S.E. for organic matter (n = 20). Organic matter was not collected in July 1999.

Sample Date	Parameter		
	Total Organic Matter (mg/L)	Woody Organic Matter (mg/L)	Non-Woody Organic Matter (mg/L)
Jul-99	-	1.47 $\pm$ 1.03	-
Sep-99	1.51 $\pm$ 0.42	0.09 $\pm$ 0.04	1.41 $\pm$ 0.40
Nov-99	3.09 $\pm$ 0.89	1.09 $\pm$ 0.68	1.87 $\pm$ 0.90
Mar-00	5.30 $\pm$ 1.80	0.52 $\pm$ 0.38	4.78 $\pm$ 1.69
Jun-00	3.38 $\pm$ 1.00	0.42 $\pm$ 0.32	2.95 $\pm$ 0.76
Sep-00	2.55 $\pm$ 0.60	0.13 $\pm$ 0.08	2.42 $\pm$ 0.56

organic matter. Total, woody and non-woody organic matter concentrations for 20 piezometers sampled across seasons are presented in Appendix B.

Mean dissolved oxygen concentrations ranged from  $2.5 \pm 0.4$  (S.E.) mg/L in September 1999 (summer low-flow) to  $6.6 \pm 0.4$  (S.E.) mg/L in February 2000 (winter). Similarly, percent saturation was lowest in September 1999 ( $23.6 \pm 3.9$  (S.E.) %) and highest in February 2000 ( $53.1 \pm 3.4$  (S.E.) %). Mean hydraulic head ranged from  $97.2 \pm 0.1$  (S.E.) m (September 1999) to  $97.9 \pm 0.1$  (S.E.) m (June 2000). Mean temperatures were lowest in February 2000 ( $6.9 \pm 0.2$  (S.E.) °C) and highest in September 2000, during summer low-flow ( $12.9 \pm 0.1$  (S.E.) °C). Mean electrical conductivity ranged from  $66.0 \pm 1.8$  (S.E.)  $\mu$ S in July 1999 to  $75.8 \pm 1.5$  (S.E.)  $\mu$ S in June 2000. The lack of variation in

the electrical conductivity of the hyporheic water throughout the grid and the similarity to surface water values indicated that the hyporheic water was entirely surface water derived

**Table 5.** Mean values  $\pm$  S.E. for physico-chemical parameters (n = 20). Dissolved oxygen data were not available for September 2000.

Sample Date	Parameter				
	Dissolved Oxygen (mg/L)	% Saturation	Electrical Conductivity ( $\mu$ S)	Temperature ( $^{\circ}$ C)	Hydraulic Head (m)
Jul-99	3.29 $\pm$ 0.43	30.68 $\pm$ 3.91	65.99 $\pm$ 1.75	12.54 $\pm$ 0.39	97.45 $\pm$ 0.14
Sep-99	2.47 $\pm$ 0.41	23.61 $\pm$ 3.94	70.07 $\pm$ 1.36	12.07 $\pm$ 0.17	97.17 $\pm$ 0.13
Nov-99	2.68 $\pm$ 0.43	23.85 $\pm$ 3.80	88.64 $\pm$ 2.83	10.31 $\pm$ 0.18	97.75 $\pm$ 0.15
Mar-00	6.57 $\pm$ 0.43	53.07 $\pm$ 3.35	67.83 $\pm$ 1.34	6.94 $\pm$ 0.15	97.44 $\pm$ 0.12
Jun-00	4.76 $\pm$ 0.44	42.18 $\pm$ 3.78	75.78 $\pm$ 1.48	10.10 $\pm$ 0.15	97.89 $\pm$ 0.14
Sep-00	-	-	72.17 $\pm$ 1.25	12.94 $\pm$ 0.13	97.22 $\pm$ 0.13

(Clinton, 2001a, in review). Hydraulic conductivity measurement was measured once in each piezometer and ranged from  $8.1 \times 10^{-7} \text{ m s}^{-1}$  to  $>1.8 \times 10^{-3} \text{ m s}^{-1}$ .

Significant positive relationships were found between total invertebrate densities and organic matter concentration for all sample dates (Tables 6-10). Total organic matter and its components wood ( $> 1\text{mm}$ ) and non-wood organic matter, explained more variation than any other parameter. In July 1999, wood, alone, explained 37.2% of the variation in totals. However, organic matter was not collected during this time. Total invertebrates were positively correlated with wood in piezometers with high dissolved

oxygen concentrations ( $> 6$  mg/L) in November 1999 ( $r^2 = 0.33$ ). Total organic matter (wood included) explained more variation than any other variable in September 1999, March 2000, September 2000 (Tables 7, 9, 11). In November 1999, total invertebrates were positively correlated with total organic matter at high dissolved oxygen concentrations ( $r^2 = 0.22$ ). Taxa richness was similarly correlated with either total organic matter or wood across all dates (Tables 6-11).

**Table 6.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for July 1999 ( $n = 24$ ). Total organic matter was not collected in July 1999.

Taxon	$r^2$	Significance	Relationship	Parameter
Archiannelida	0.582	0.000	+	Wood @ Medium DO
Log Cyclopoida	0.432	0.000	+	Log Wood
Log Copepod Nauplii	0.474	0.002	+	Log Wood
Log Harpacticoida	0.384	0.001	+	Temperature @ Medium DO
Hydrachnidia	0.207	0.025	+	Temperature
Log Rotifera	0.696	0.000	+	Log Wood @ High Hydraulic Head <sup>††</sup>
Log Total	0.372	0.002	+	Log Wood
Log Taxa	0.305	0.005	+	Log Wood @ Medium DO

<sup>†</sup> Medium dissolved oxygen concentrations ranged from 2 – 6 mg/L.

<sup>††</sup> High hydraulic head measurements were  $> 97.00$ m.

**Table 7.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for September 1999 (n = 42).

Taxon	r <sup>2</sup>	Significance	Relationship	Parameter
Archiannelida	0.181	0.005	+	Temperature
Log Copepod Nauplii	0.312	0.000	+	Temperature
Log Cyclopoida	0.272	0.000	+	Log Wood @ 0-200m along Flowpath
Log Harpacticoida	0.202	0.003	+	Non-wood OM @ 0-200m along Flowpath
Log Hydrachnidia	0.212	0.002	+	Wood @ 400-700m along Flowpath
Log Rotifera	0.181	0.005	+	Distance from River
Log Total	0.193	0.004	+	Log Total Organic Matter
Taxa	0.209	0.002	+	Total OM @ 0-200 m along Flowpath

**Table 8.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for November 1999 (n = 27).

Taxon	r <sup>2</sup>	Significance	Relationship	Parameter
Archiannelida	0.229	0.011	+	Hydraulic Conductivity @ High DO <sup>†</sup>
Log Copepod Nauplii	0.361	0.001	+	Hydraulic Conductivity @ High DO
Log Cyclopoida	0.299	0.003	+	Wood @ High DO
Log Harpacticoida	0.191	0.023	+	Wood
Hydrachnidia	0.446	0.000	+	Wood @ High DO
Log Rotifera	0.443	0.000	+	Log Total Organic Matter
Log Total	0.326	0.002	+	Wood @ High DO
Log Taxa	0.355	0.001	+	Wood @ High DO

<sup>†</sup>High dissolved oxygen concentrations were > 6 mg/L.

**Table 9.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for March 2000 (n = 43).

Taxon	r <sup>2</sup>	Significance	Relationship	Parameter
Archiannelida	0.201	0.003	+	Log Total Organic Matter
Log Copepod Nauplii	0.300	0.000	+	Log Wood @ High Head <sup>†</sup>
Log Cyclopoida	0.306	0.000	+	Log Wood @ High Head
Log Harpacticoida	0.294	0.000	+	Log Wood @ High Head
Log Hydrachnidia	0.256	0.001	+	Total Organic Matter @ High DO <sup>††</sup>
Log Rotifera	0.418	0.000	+	Log Total Organic Matter
Log Total	0.358	0.000	+	Log Total Organic Matter
Taxa	0.439	0.000	+	Log Wood

<sup>†</sup> High hydraulic head measurements were > 97.00m.

<sup>††</sup> High dissolved oxygen concentrations were > 6 mg/L.

**Table 10.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for June 2000 (n = 45).

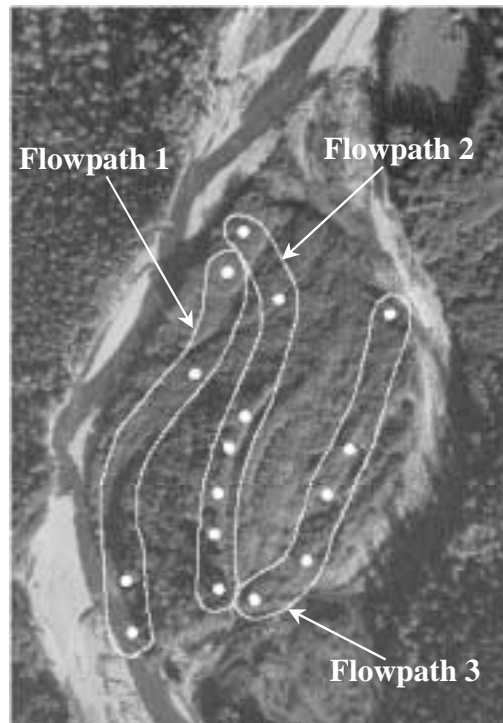
Taxon	r <sup>2</sup>	Significance	Relationship	Parameter
Log Archiannelida	0.180	0.004	+	Log Wood @ High DO <sup>†</sup>
Log Copepod Nauplii	0.283	0.000	+	Total Organic Matter @ High DO
Log Cyclopoida	0.239	0.001	+	Total Organic Matter @ High DO
Harpacticoida	0.455	0.000	+	Log Wood
Log Hydrachnidia	0.274	0.000	+	Non-Wood @ High DO
Log Rotifera	0.302	0.000	+	Distance along Flowpath
Log Total	0.222	0.001	+	Total Organic Matter @ High DO
Log Taxa	0.213	0.001	+	Log Total Organic Matter

<sup>†</sup> High dissolved oxygen concentrations were > 4 mg/L.

**Table 11.** Single most important variables generated by regression analysis of invertebrate densities on physico-chemical parameters for September 2000 (n = 41). Dissolved oxygen data were not available.

Taxon	r <sup>2</sup>	Significance	Relationship	Parameter
Log Archiannelida	0.491	0.004	+	Total Organic Matter
Log Copepod Nauplii	0.694	0.000	+	Log Wood
Log Cyclopoida	0.625	0.000	+	Total Organic Matter
Log Harpacticoida	0.650	0.000	+	Total Organic Matter
Hydrachnidia	0.935	0.000	+	Log Wood
Log Rotifera	0.861	0.000	+	Total Organic Matter
Log Total	0.823	0.000	+	Total Organic Matter
Taxa	0.929	0.000	+	Non-Wood

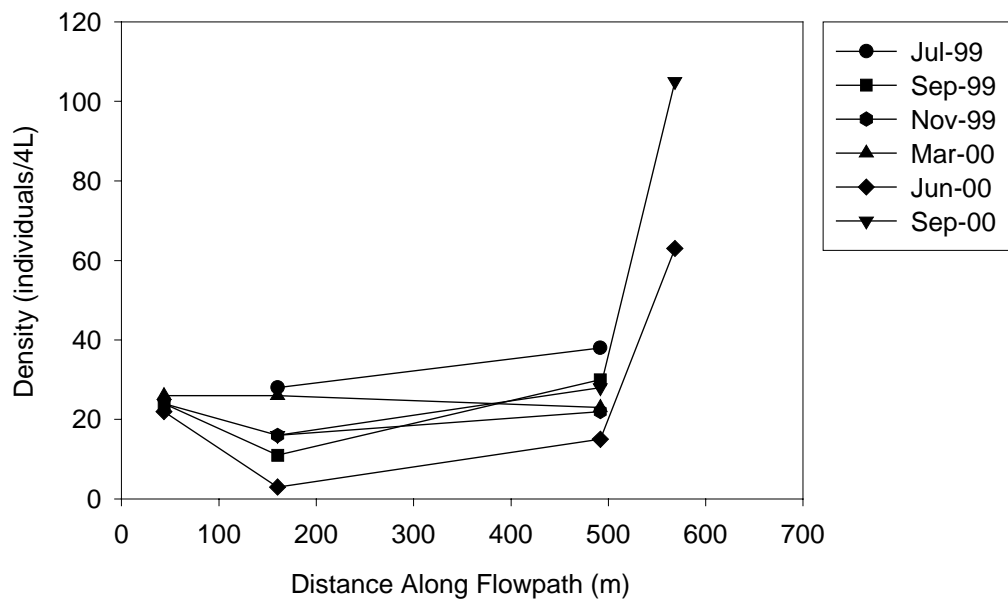
Although totals were not directly correlated with longitudinal distance from the river, analysis of individual flowpaths (see Methods) revealed some interesting trends. Flowpath 1 extended almost 600 m along the northern side of the terrace, from the Queets River to the old-growth portion of the terrace (Figure 10). Densities showed seasonal consistency with slight decreases from the piezometer near the Queets River to the piezometer located 160 m along the flowpath, after which there were noticeable increases in density (Figure 11) in piezometers located in the old-growth patch-type.



**Figure 10.** Location of 3 individual virtual flowpaths across floodplain terrace.

There were no statistically significant relationships between total invertebrates and any of the parameters measured when individual dates were considered. This was likely due to the low number of piezometers in flowpath 1 (Figure 11). However, consideration of all dates revealed a positive relationship between total invertebrates and total organic matter ( $p = 0.036$ ,  $r^2 = 0.37$ ,  $n = 12$ ).

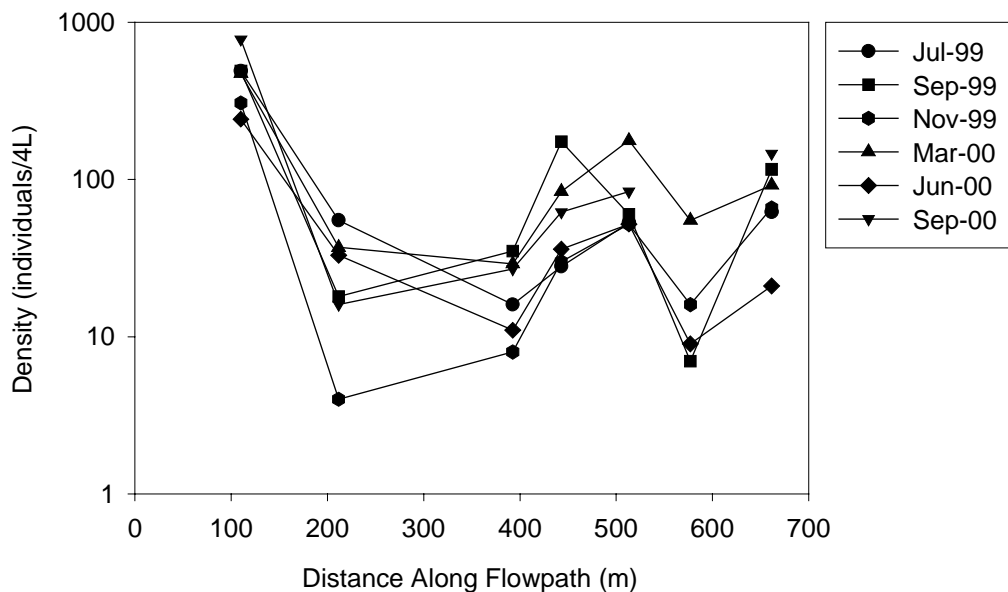
Flowpath 2 extended from the Queets River through the middle of the terrace along a paleochannel, or preferential flowpath, located ~ 400 m from the beginning of the flowpath (Figure 10). Densities again showed seasonal consistency with decreases from > 250 individuals/4L to < 55 individuals/4L within the first 200 m (Figure 12). However, densities increased in the paleochannel where water flowed beneath mature alder (> 20



**Figure 11.** Total invertebrate density along flowpath 1 at different sampling dates.

years old) patch-types.

For all dates considered, electrical conductivity explained more variation in log transformed totals along flowpath 2 than any other variable ( $p = 0.000$ ,  $r^2 = 0.44$ ,  $n = 26$ ). However, totals were positively correlated with dissolved oxygen concentrations in September 1999 ( $p = 0.016$ ,  $r^2 = 0.80$ ,  $n = 6$ ) and November 1999 ( $p = 0.026$ ,  $r^2 = 0.75$ ,  $n = 6$ ). Totals were positively correlated with wood in July 1999 and March 2000 but piezometer PR2, at the beginning of the flowpath, was driving these relationships. Organic matter explained more variation in totals than any other variable in June 2000 ( $p = 0.018$ ,  $r^2 = 0.70$ ,  $n = 6$ ) and in September 2000 ( $p = 0.006$ ,  $r^2 = 0.88$ ,  $n = 6$ ).

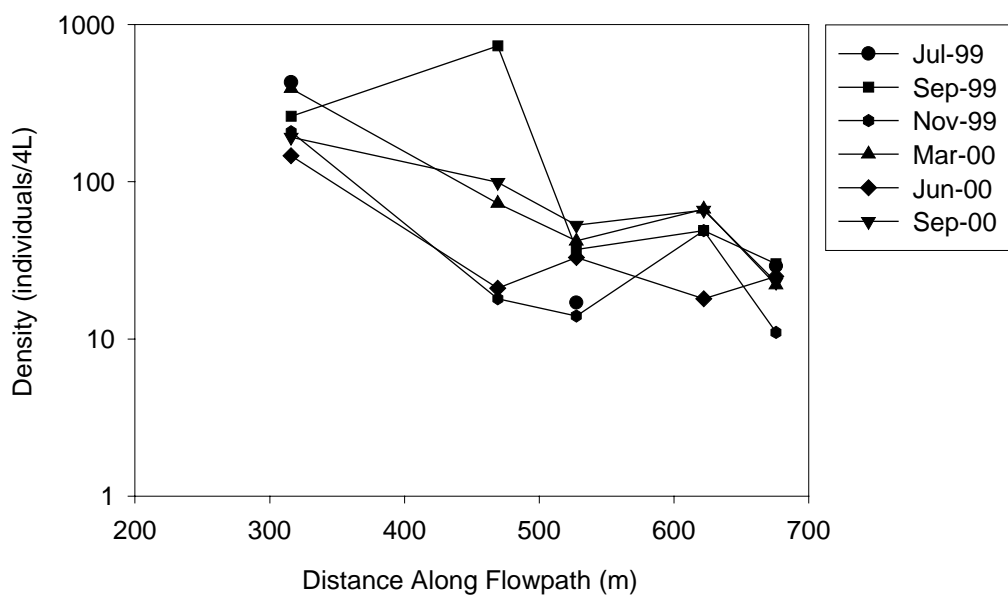


**Figure 12.** Total invertebrate density along flowpath 2 across sample dates.

Flowpath 3 extended from the Pebble Creek side of the terrace from ~300 m along the flowpath through gravel patch-types to the terrace drain (almost 700 m) (Figure 10). With the exception of a large increase in rotifers in one piezometer in September 1999, densities again were seasonally consistent decreasing from over 200 individuals/4L to less than 100 individuals/4L (Figure 13). Densities appeared to be less variable than densities along flowpath 1 and 2, exhibiting a log-linear decrease with distance along flowpath.

In flowpath 3, log totals were positively correlated with organic matter in September 1999 ( $p = 0.004$ ,  $r^2 = 0.96$ ,  $n = 5$ ) and March 2000 ( $p = 0.017$ ,  $r^2 = 0.89$ ,  $n =$

5). No relationships were found in July 1999 due to the low number of piezometers in regression analysis ( $n = 3$ ). Wood explained more variation than any other variable in November 1999 and June 2000 but these relationships were driven by piezometer A9 at the beginning of the flowpath. Hydraulic head was the single most important variable in September 2000 ( $p = 0.018$ ,  $r^2 = 0.88$ ,  $n = 5$ ). Similarly, head was important when all dates were considered, explaining 23% of the variation in log totals ( $p = 0.030$ ,  $n = 20$ ).



**Figure 13.** Total invertebrate density along flowpath 3 across sample dates.

Within the three flowpaths considered, the variation in densities along the flowpaths indicated that there was a relationship between patch-type and invertebrate

densities. However, across the terrace, total invertebrate densities did not vary significantly with patch or date (2-way ANOVA,  $\alpha > 0.05$ ).

### ***Parameters Influencing Individual Taxa Distributions***

Similar to total invertebrates, total organic matter and wood explained more variation than any other variable for the 'most common' taxa (Tables 6 – 11). In general, organic matter and wood explained less of the variation in September 1999 and June 2000 than the other dates (Tables 7 and 10). Indirectly, dissolved oxygen was important in November 1999 and June 2000 when taxa were correlated with wood and, in some cases, other variables in piezometers with high dissolved oxygen concentrations ( $> 4$  mg/L) (Tables 8 and 10). A few taxa were not correlated with either organic matter or wood. Temperature was important for explaining variation in harpacticoid copepod and hydrachnid densities in July 1999 and archiannelid and copepod nauplii densities in September 1999. Rotifers were positively correlated with distance from river and distance along flowpath in September 1999 and June 2000, respectively (Tables 7 and 10).

## DISCUSSION

### *Community Composition*

The invertebrate community in this floodplain terrace was characterized by high spatial and low temporal heterogeneity with highest densities consistently found in a few piezometers. In contrast, invertebrates residing in the active channel hyporheic zones are highly variable both spatially and temporally in response to extreme environmental fluctuations (Marmonier 1991, Kowarc 1992). In addition, similarity in community composition across piezometers and sample dates suggests a high degree of assemblage persistence. However, the taxonomic resolution of this study was relatively coarse. If identification had been to genus, for example, I may have seen greater variation in temporal composition.

Quantitative comparisons with hyporheic invertebrate communities from other floodplain hyporheic zones are difficult due to inconsistencies in sampling the hyporheic zone (Palmer 1993). Except for research on the Flathead River, Montana, most researchers have used of the Bou-Rouch pump which is comparable to the pump used in our study. However, even within a study area, different volumes (3L, 4L, 5L, 10L) are collected and variable mesh sizes (60  $\mu\text{m}$ , 100  $\mu\text{m}$ , 150  $\mu\text{m}$  and 300  $\mu\text{m}$ ) are used. Quantitative data in the literature are often expressed as percent composition rather than absolute densities. Therefore, the following discussion will not address quantitative invertebrate comparisons but will qualitatively compare the findings of this study with other floodplain hyporheic research.

Consistent with most floodplain hyporheic studies (Pennak & Ward 1986, Ward 1986, Ward *et al.* 1994, Canton & Chadwick 2000, Dole-Olivier *et al.* 1994), crustaceans were both most common and numerically dominant in this floodplain terrace. At this site cyclopoid copepods dominated the crustacean group confirming that cyclopoid copepods are both ubiquitous and numerically important in floodplain hyporheic habitats (Danielopol 1976, Pennak & Ward 1986, Ward & Stanford 1994, Marmonier *et al.* 1992). Harpacticoid copepods were not abundant, relative to cyclopoid copepods, although they were abundant in other studies (Pennak & Ward 1986, Marmonier *et al.* 1992). Harpacticoids, especially parastenocaridid harpacticoids, can be important scavengers of fine organic matter and bacteria due to their small and appressed mouthparts (Janet Reid, Smithsonian Institution, personal communication). Copepod nauplii have received little attention in the hyporheic literature. Individual species of lake zooplankton undergo seasonal peaks in abundance (Kurki *et al.* 1999, Tallberg *et al.* 1999). Similarly, identification of both adult and juvenile hyporheic copepods, to a higher taxonomic resolution, may help to explain seasonal trends in individual species of hyporheic copepods.

Rotifers were also important numerically despite the fact that they were probably underestimated throughout this study. Rotifers and associated groups adhere to sediment particles and require chemical extraction using  $MgCl_2$  (Ricci & Balsamo 2000). Total rotifer abundance, per unit area, is high in interstitial habitats, exceeding abundances in the surface environment (Schmid-Araya 1998). The presence of rotifers is often not reported (Strayer *et al.* 1997) because they pass through mesh sizes larger than 100  $\mu m$

(Hummon 1981). Rotifers are an important link between microbial and meio- and macro-invertebrates in lotic food webs (Schmid-Araya 1998). Rotifers feed on particles 'not efficiently grazed by larger invertebrates' (Schmid-Araya & Schmid 2000). In turn, rotifers are consumed by larval aquatic insects, predatory nematodes, microturbellarians and other rotifers (Schmid & Schmid-Araya 1997). Likewise, microturbellarians represent an important link between microbial and meiofaunal communities but were probably underestimated in this study. Quantitative analysis requires identification of this taxon within hours of sampling as preservation often results in complete destruction of individuals or distorts body shapes making them indistinguishable from sediments (Kolasa 2000).

The presence of archiannelids in > 70% of the samples was unexpected as several floodplain studies have found this taxon to be uncommon or absent (Danielopol 1976, Danielopol 1984, Marmonier *et al.* 1992). The use of larger mesh-sizes (> 100  $\mu\text{m}$ ) differentially excludes small hyporheic invertebrates such as archiannelids (Dole Olivier *et al.* 1993) suggesting that they may be more common and abundant than previously thought. My findings are consistent with those on the South Platte River where archiannelids (*Troglochaetus* sp.) were common when collected using a 48  $\mu\text{m}$  mesh (Pennak & Ward 1986). Similarly, although there are few published reports of the presence of archiannelids on the Flathead River (Stanford *et al.* 1994), this taxon is also common at most sites (Eric Snyder, University of Montana, personal communication).

Aquatic insects were noticeably scarce in this floodplain hyporheic zone. Other studies have found insects to be uncommon with plecoptera, collembola (semi-aquatic),

coleoptera, tipulidae, ceratopogonidae comprising < 4% of total population (Danielopol 1976, Pennak & Ward 1986). Generally, chironomids comprise a majority of the insects found (Williams 1984, Pennak & Ward 1986). This is consistent with my findings although a majority of the chironomids were concentrated in the single active-channel piezometer. Increased chironomid densities in piezometers A11 during July 1999, June 2000 and March 2000 suggests that these insects may be moving into the hyporheic zone during high flows.

The lack of stoneflies in this study, however, is not consistent with findings on the Flathead River where plecopterans such as *Paraperla* and *Isocapnia* are common and numerically dominant in most wells within the hyporheic zone (Stanford & Gaufin 1974, Stanford & Ward 1988). The dearth of stoneflies at this study site is likely due to differences in pump types and piezometer size and installation depth (Jack Stanford, University of Montana, personal communication). Samples on the Flathead River were collected from larger wells (5-10 cm diameter, slotted on all sides) installed at greater depths (3-7.6 m) and sampled using a more powerful pump (gas-powered diaphragm pump) (Ellis & Stanford 1998). Our samples were taken within the upper layer of the hyporheic zone (30 cm into the water table at low-flow), suggesting that if present in this system, subterranean stoneflies may be utilizing deeper parts of the hyporheic zone. The Flathead River floodplain sediments have higher hydraulic conductivities (up to 10 cm/sec) (Ward *et al.* 1994) than those measured on the Queets River floodplain (0.000001 to 0.002 cm s<sup>-1</sup>) suggesting that pore spaces may be large on the Flathead River.

Therefore larvae in the Queets River may be limited by the size of the interstitial spaces (Brunke & Gonser 1997).

Amphipods were rare in comparison to findings on the Flathead River where the subterranean amphipod *Stygobromous* was the most common crustacean, occurring in all but the channel well (Ward *et al.* 1994). In contrast, the low frequency and abundance of amphipods on the Rhone River (Marmonier *et al.* 1992), Danube (Danielopol 1976) and South Platte (Pennak & Ward 1986) rivers were comparable to this study. Analysis of 12 of the 68 amphipods revealed 3-4 new species, suggesting that the Queets River represents a 'hotspot' of amphipod biodiversity despite the low densities (John Holsinger, Old Dominion University, personal communication). A well in Montana is the only other site in western North America to yield three different species of *Stygobromous* (John Holsinger, Old Dominion University, personal communication). In the eastern United States where *Stygobromous* distribution is limited to springs and caves, it is rare to see two or more species of *Stygobromous* in the same location (Canton & Chadwick 2000). In hyporheic habitats in the western United States, it is unusual to see less than two species of *Stygobromous* in the same location (Canton & Chadwick 2000).

Oligochaetes and nematodes have been found to be either dominant or co-dominant in other floodplain studies (Danielopol 1976, Marmonier *et al.* 1992). However, they constituted a small portion to overall abundance in this study. Our findings are more consistent with those on the South Platte River where nematodes and oligochaetes comprised 1% and 6%, respectively, of the hyporheic fauna (Pennak & Ward 1986). Similarly, ostracods did not contribute substantially to overall invertebrate

abundance at this study, findings corroborated by research on the South Platte River (Pennak & Ward 1996) and on the Danube (Danielopol 1976). Ostracods may appear to be less abundant at this site and others because they tend to exhibit aggregated distributions (Danielopol 1991). My scale of sampling may be too coarse to fully capture hyporheic ostracod abundance and distribution (Pennak & Ward 1986).

Bathynellaceans were rarely found (< 20% samples) and were concentrated in 1-2 piezometers. This was consistent with findings on the South Platte River where occurrence was 'highly irregular' (Pennak & Ward 1986) and on the Flathead River where bathynellaceans were absent in hyporheic habitats and present in 10% of the sites in phreatic, or true groundwater, habitats (Stanford & Ward 1988). Densities at phreatic sites on the South Platte River were considerably higher (up to 440 individuals/5L) than those found in this study suggesting that bathynellaceans are more associated with groundwater than hyporheic water (Pennak & Ward 1986). The species identified in our study, *Pacificabathynella sequoiae*, has only been found in a gravelly bank pit, about 3 m from the surface water (Schminke & Noodt 1988). Although only a few specimens were identified, it is unusual to find more than one species of bathynellacean together in the same location (Janet Reid, Smithsonian Institution, personal communication). The presence of 'true groundwater' fauna such as bathynellaceans, isopods and archiannelids in this surface water derived hyporheic zone raises interesting questions regarding the use of invertebrates for delineating hyporheic and groundwater environments (Gibert *et al.* 1994). Clearly, the perception of affinity for groundwater and hyporheic habitats is

imperfect and requires a better understanding of both the ecological requirements of these invertebrates as well as the biogeochemical properties of the environment.

### ***Parameters Influencing Invertebrate Distribution***

It is not surprising that wood is present within the hyporheic zone and that it explained more variation, in both individual taxa and total densities, than any other variable. Retention of sediment by large wood debris (LWD) jams is the primary process forming riparian floodplain terraces in this river (Fetherston *et al.* 1995). LWD buried by sediment can remain in the system for up to 1,400 years (Hyatt & Naiman 2001). If LWD is buried within the hyporheic zone, the amount of wood fragments collected was likely dependent on the degree of decomposition of that wood, and was probably a tiny fraction of what is buried within the floodplain. Therefore, some of the residual variation in the regression analysis, using wood as an independent variable, may have been caused by my inability to adequately quantify the amount of wood available to these invertebrates. Regardless, at the scale of this floodplain terrace, wood seems to be important for creating ‘hotspots’ of invertebrate abundance.

Whereas other studies have found positive relationships between organic matter and invertebrate densities (Strayer *et al.* 1997, Brunke & Gonser 1999), no study, to date, has reported a link between wood and invertebrates in the hyporheic zone. The importance of wood for invertebrates in the surface environment is well established (Sedell *et al.* 1988, Tank & Winterbourn 1996, Hoffman & Hering 2000, Braccia & Batzer 2001). Coarse woody debris provides refugia from high flows, and a stable substrate for retention of organic matter, biofilm development, oviposition and pupation

(Hoffman & Hering 2000 & references therein). As the hyporheic zone experiences stable flows and is detritally-based, it is likely that wood functions either as a direct or indirect food source. For example, some marine isopods are facultative xylophagites consuming wood through chewing, gouging and mining activities (Gonor *et al.* 1988). Alternatively, wood can trap organic matter (Sedell *et al.* 1988, Bilby & Ward 1991, Fetherston *et al.* 1995) and act as an important substrate for the development of 'extensive' biofilms (Golladay & Sinsabaugh 1991). Clearly, a lack of knowledge of the functional roles of individual taxa impedes any determination of the wood-use strategies utilized by the invertebrates in this study.

Although most freshwater organisms are 'obligate aerobes' (Strayer *et al.* 1997), I found no direct relationships between the Queets hyporheic invertebrate community and dissolved oxygen concentration at the terrace scale. Hydrology, organic matter and the activity and abundance of microorganisms collectively contribute to the heterogeneous nature of dissolved oxygen in subsurface environments (Malard & Hervant 1999) suggesting that the integrative nature of our sampling technique may not be adequately capturing this heterogeneity. If hyporheic invertebrates are exploiting small-scale microhabitats where dissolved oxygen is adequate to maintain metabolic activity, sampling 4 liters from an undetermined volume may obscure relationships between invertebrates and dissolved oxygen (Strayer *et al.* 1997). Hyporheic fauna are found in environments characterized by spatially heterogeneous dissolved oxygen concentrations because they are adapted to survive suboxic (< 0.3 mg/L) and dyoxic (0.3-3.0 mg/L) conditions and recover from 'severe hypoxia' rapidly (Malard & Hervant 1999).

Whether these invertebrates possess adaptations or are utilizing microzones of high dissolved oxygen has yet to be determined (Strayer 1994b). Similarly knowledge of whether individual taxa are considered to be temporary or permanently residents in the hyporheic zone is important for determining oxygen thresholds in this subsurface environment.

Although there was no direct relationship between dissolved oxygen concentration and hyporheic invertebrate distribution, there seemed to an interaction between dissolved oxygen concentration and the amount of wood and total organic matter available. Similarly, Strayer *et al.* (1997) found that sediment organic matter was important at sites where ‘ample’ dissolved oxygen was present. In hypoxic conditions, hyporheic invertebrates can compensate for energy lost via high ventilation rates by reducing activity, including feeding and/or search for food (Malard & Hervant 1999). Hyporheic invertebrates may actively feed under higher dissolved oxygen concentrations but employ a ‘sit and wait’ strategy when oxygen is limiting.

In contrast to other floodplain hyporheic studies (Marmonier *et al.* 1992, Ward *et al.* 1994), this community showed no relationship to lateral distance from river. Similar to my results, on the Flathead River lateral distance from river was not ‘a good predictor of faunal similarity’ when invertebrates were considered in individual wells (Ward *et al.* 1994). However, lateral distance from the river became important when community structure was compared among habitats (channel wells, near-floodplain wells, far-floodplain wells) (Ward *et al.* 1994). The importance of scale must be considered in any comparisons between floodplain hyporheic zones (Hakenkamp *et al.* 1993). My study

suggests that the presence of wood is important for explaining variability on a scale of hundreds of meters whereas changes in ‘physical habitat stability’ (Marmonier *et al.* 1992) and ‘geomorphic and hydrogeologic features’ reflected by distance from river are important on a scale of a floodplain (kilometers). At this scale, however, it is difficult to characterize the hydrology of the study area. If the supply of oxygen and food is important, and it is related to the proximity of advecting surface water, as many studies have shown (Williams 1989, Marmonier 1991, Dole-Olivier & Marmonier 1992), analysis of the role of lateral distance from the channel cannot be made without a good understanding of the hydrology of the study area.

It is surprising that no direct relationships were found between total invertebrates or individual taxa, and hydraulic conductivity. Hydraulic conductivity can influence the supply of dissolved oxygen and organic matter supply, and temperature (Findlay 1995, Brunke & Gonser 1997). However, water flow rates will be controlled by the pattern of hydraulic conductivities throughout the upstream flowpath, which may not be fully described with point measurements at the relatively low density of these piezometers. In addition, hydraulic conductivities in 44% of the piezometers within the terrace were too high to measure with a falling head test, so we set them equal to the highest measurable values. The combination of low spatial resolution and hydraulic conductivities outside the measurement range make any conclusions about the effects of hydraulic conductivities speculative. Temperature did not change dramatically among piezometers and therefore was not an important influence on distribution across the terrace. However,

changes in temperature across sample dates were more dramatic suggesting that this variable may be important at a given site.

Total invertebrate densities did not decrease consistently along the three individual flowpaths. Other studies have shown that dissolved oxygen and organic carbon decrease steadily along flowpaths as these resources are consumed by the microbial community and invertebrates (Findlay 1995, Findlay & Sobczak 1996). If the only surface inputs of labile carbon were advecting surface water, invertebrates would also be expected to decrease along a flowpath as labile carbon was rapidly metabolized and their microbial food resources diminished. However, there were no consistent decreases in total invertebrate density with distance along each flowpath, rather densities within two flowpaths actually increased down the flowpaths. Although there was no effect of patch-type on total densities across the entire terrace, the seasonally consistent patterns within individual flowpaths suggest that there was another source of labile carbon creating food for invertebrates at certain locations. I interpret this as evidence for the input of carbon from forest soils overlying the hyporheic flowpaths. Overlying patch-type explained 20-47% of the variability in dissolved organic carbon (DOC) concentrations in spring and summer on this floodplain terrace (Clinton 2001a, in review). Clinton (2001b) found that forest soil leachates contained sufficient labile carbon to support growth by bacteria taken from the hyporheic zone, confirming that forest soil leachates could stimulate hyporheic bacterial growth and create additional food sources for grazing invertebrates. These findings indicate that the hyporheic zone within

forested floodplains is influenced not only by advecting surface water but also by interactions with overlying floodplain soils (Bechtold 2000).

### ***Management Implications***

Relative to dynamic surface environments, floodplain hyporheic zones harbor stable and persistent invertebrate communities. Although surface invertebrates have been used as indicators of ecosystem health (Karr 2000), they are adapted to living in dynamic environments that are characterized by extreme physical fluctuations. In contrast, hyporheic communities may be more suitable indicators of environmental change because they are subjected to less extreme physical fluctuations and therefore may be more sensitive to changes in their environment. The use of hyporheic invertebrates as indicators of hyporheic health (Boulton 2000) is promising. Studies in areas impacted by forestry (Trayler & David 1998) and agriculture (Boulton *et al.* 1997) have found that biodiversity decreases in response to these activities. Currently, however, there are limitations to the use of hyporheic invertebrates as indicators of ecosystem health. Many of the species are undescribed and data on the ecological requirements of these invertebrates are lacking (Boulton 2000). In addition, sampling methods would need to be standardized to ensure comparative results (Palmer 1993).

This study has highlighted the importance of maintaining connection between rivers and their adjacent floodplains. Similar to the surface environment, wood appears to be an important source of stability for the invertebrate community in this floodplain hyporheic zone. Riparian area deforestation reduces the supply of wood into surface and subsurface environments. Similarly, management practices preventing channel migration

reduce the ability of rivers to bury wood and create depositional surfaces for the establishment of early successional species. A reduction of wood inputs to the hyporheic zone over long time scales, and the loss of habitat heterogeneity and food source would impair hyporheic invertebrate communities. Perhaps more importantly, however, the ‘plugging’ of interstitial spaces via siltation and removal of sediments through channel incision can ultimately result in a reduction in habitat available to these communities.

Ultimately, the importance of hyporheic zones to overall system structure and function depends on both activity within the hyporheic zone (nutrient transformations, for example) and connection with the surface environment (Boulton *et al.* 1998, Boulton 2000). Similarly, invertebrates within the hyporheic zone might only be deemed important, from a management prospective, if they 1) directly or indirectly affect hyporheic microbial activity through grazing or movement through the sediments, or 2) are transferred to the surface environment where they become a food source for important commodities such as fish. Our knowledge of hyporheic invertebrate communities is expanding but clearly more research is needed to determine the functional roles of invertebrates residing within the hyporheic zone.

## CONCLUSIONS

The invertebrate community in this floodplain hyporheic zone was characterized by high assemblage persistence at this relatively coarse level of taxonomic resolution. Consistent with other floodplain hyporheic studies, crustaceans represented the most prevalent group with dominance by cyclopoid copepods. Rotifers were also important numerically despite being underestimated in this study. Insect taxa were noticeably rare compared with research on the Flathead River where stoneflies are dominant. This disparity may have been a consequence of different sampling equipment and protocols, highlighting the need to standardize sampling techniques. In addition, differences in the systems and goals of the researchers may have also contributed to these discrepancies. In a hyporheic zone that it is entirely surface water derived, the presence of fauna commonly accepted to be obligate groundwater fauna highlights the need for a better understanding of both the ecological requirements of these invertebrates as well as the biogeochemical properties of the environment.

Overall invertebrate distribution across the terrace was characterized by high spatial and low temporal heterogeneity. The seasonal stability of high density piezometers suggests that floodplain hyporheic zones can contribute to total system invertebrate production over time. At the terrace scale, spatial heterogeneity was related to wood, with high-wood piezometers representing temporally stable 'hotspots' of invertebrate abundance. The source of wood within the hyporheic zone is unknown but is likely LWD buried by sediment through channel migration. As the hyporheic zone experiences stable flows and is detritally-based, wood probably functions as either a

direct or indirect food source. Within the terrace, along individual flowpaths, spatial heterogeneity appears to be driven by a mosaic of overlying patch-types. Invertebrate densities did not decrease, as predicted, with distance from carbon and energy source at the head of the flowpaths. However, this finding could not be substantiated because there were too few data to run the appropriate statistical tests. Clearly, more work is needed to determine the relationship between wood and patch-type and invertebrate distribution.

This study has highlighted the importance of maintaining connectivity between surface and subsurface systems. No study to date has demonstrated a link between hyporheic invertebrates and wood although the importance of wood in the surface environment is well established. The interaction between rivers and adjacent riparian areas, provide stable inputs of wood and other forms of organic matter which are essential for maintaining heterogeneous invertebrate distributions within floodplain hyporheic zones. Channel migration serves to bury LWD, supplying wood to the hyporheic zone over long periods of time. Hyporheic zones are also important integrators of inputs from advecting surface water and floodplain soils. Flooding maintains a heterogeneous environment through the creation of depositional surfaces for the establishment of early successional species. The resulting mosaic of successional stages can affect carbon inputs to subsurface environments, ultimately influencing hyporheic invertebrate distribution.

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**Appendix A.** Checklist of taxa collected from Queets River between July 1999 and September 2000. Invertebrates were identified to the lowest taxonomic resolution.

Phylum	Class	Order	Family	
Annelida	Oligochaeta			
	Archiannelida			
Arthropoda	Arachnida			
	Insecta	Coleoptera		
		Collembola		
		Diptera		Ceratopogonidae
				Chironomidae
				Tipulidae
Hemiptera				
Plecoptera				
Malacostraca	Amphipoda	Crangonyctidae		
	Isopoda			
Bathynellaceae				
Branchiopoda	Cladocera	Bosminidae		
		Chydoridae		
Maxillopoda	Cyclopoida			
	Harpacticoida			
Ostracoda				
Mollusca	Gastropoda			
Nematoda				
Platyhelminthes		Microturbellaria		
Rotifera				
Tardigrada				

**Appendix B.** Total organic matter and wood concentrations for 20 piezometers sampled between July 1999 and September 2000. Total organic matter was not collected in July 1999.

Piezometer	July 1999		September 1999		November 1999	
	Total Organic Matter	Wood	Total Organic Matter	Wood	Total Organic Matter	Wood
A-1	-	0.018	0.200	0.048	0.573	0.000
A-4	-	0.000	0.403	0.012	1.844	0.000
A-6	-	0.074	0.203	0.063	0.703	0.000
A-7	-	0.242	0.359	0.018	1.633	0.344
A-9	-	0.248	1.908	0.017	2.489	0.986
B-2	-	0.039	0.149	0.009	0.453	0.029
B-4	-	0.021	0.113	0.008	0.220	0.006
B-6	-	0.009	1.007	0.010	1.174	0.000
B-7	-	0.032	0.739	0.081	3.000	0.000
B-9	-	0.058	5.133	0.007	15.200	0.046
B-10	-	0.031	0.521	0.000	0.380	0.020
B-12	-	0.005	0.302	0.000	0.413	0.000
C-1	-	0.129	0.637	0.021	3.978	0.162
C-4	-	0.088	0.697	0.006	3.244	0.180
C-7	-	0.065	0.195	0.008	3.244	0.089
P-2	-	0.099	3.350	0.023	1.917	0.112
P-3	-	0.734	2.467	0.667	2.796	0.666
P-4	-	0.057	1.081	0.021	1.274	0.098
PR-1	-	7.631	6.478	0.269	12.978	6.920
PR-2	-	19.727	4.172	0.583	4.289	12.177

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**Appendix B (cont).**

Piezometer	March 2000		June 2000		September 2000	
	Total Organic Matter	Wood	Total Organic Matter	Wood	Total Organic Matter	Wood
A-1	0.467	0.018	0.598	0.000	0.357	0.000
A-4	0.623	0.008	0.436	0.006	0.178	0.007
A-6	0.725	0.000	0.609	0.008	0.523	0.000
A-7	1.393	0.039	0.787	0.106	0.520	0.007
A-9	5.240	0.157	4.956	0.120	7.339	0.076
B-2	0.418	0.041	0.283	0.000	0.297	0.000
B-4	0.268	0.083	0.209	0.000	0.376	0.049
B-6	1.325	0.045	-	0.018	1.909	0.072
B-7	3.711	0.108	4.261	0.000	1.378	0.057
B-9	12.711	0.049	8.833	0.045	6.122	0.000
B-10	0.428	0.040	0.461	0.020	0.272	0.034
B-12	0.351	0.019	0.357	0.000	0.098	0.000
C-1	3.730	0.011	2.400	0.013	2.274	0.000
C-4	7.278	0.016	2.839	0.042	5.772	0.017
C-7	0.686	0.000	0.205	0.000	0.436	0.022
P-2	4.559	0.010	2.256	0.000	1.659	0.024
P-3	6.248	0.561	3.208	0.132	3.989	0.062
P-4	8.785	0.103	4.161	0.055	3.461	0.075
PR-1	35.089	1.629	16.222	6.348	7.733	1.493
PR-2	12.089	7.498	11.250	1.397	6.361	0.604

**Appendix C.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in July 1999.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	10	2	5	0	0	1
A-4	0	0	2	1	1	0
A-6	8	12	12	8	5	5
A-7	0	27	156	0	0	25
A-9	10	68	96	50	27	71
B-2	2	9	11	2	0	3
B-4	7	3	0	1	0	0
B-6	3	3	6	2	0	5
B-7	8	0	1	1	1	1
B-9	1	1	2	1	1	3
B-10	7	4	5	0	1	0
B-12	5	0	2	2	0	0
C-1	9	0	14	2	5	1
C-4	24	16	9	6	1	2
C-7	2	7	9	1	3	2
P-2	5	0	2	2	5	2
P-3	8	1	3	1	4	4
P-4	4	18	12	7	1	2
PR-1	24	422	347	110	11	581
PR-2	37	167	208	13	8	377

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix C (cont).**

Piezometer	Relatively Common Taxa						
	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	0	0	0	0	0	2	0
A-4	0	0	0	0	0	0	0
A-6	1	2	0	0	0	1	0
A-7	0	0	1	2	0	0	4
A-9	0	52	27	2	2	18	2
B-2	1	0	0	0	0	0	0
B-4	0	0	0	0	0	0	0
B-6	0	0	0	0	1	0	0
B-7	1	0	0	0	1	0	0
B-9	0	0	0	0	0	0	1
B-10	0	0	0	0	0	0	0
B-12	0	0	0	0	0	0	0
C-1	0	1	0	3	2	0	0
C-4	0	1	0	0	0	1	2
C-7	0	1	0	0	3	1	0
P-2	0	0	0	0	0	0	0
P-3	3	2	0	0	0	0	1
P-4	2	4	0	0	3	0	0
PR-1	1	125	38	7	3	11	9
PR-2	0	84	16	1	4	6	1

**Appendix D.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in September 1999.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	23	5	7	0	0	4
A-4	2	2	4	0	0	2
A-6	4	0	8	0	0	3
A-7	0	3	44	0	3	3
A-9	23	93	36	9	7	59
B-2	1	3	4	0	1	2
B-4	5	2	2	1	4	0
B-6	4	6	17	0	2	7
B-7	12	0	7	0	1	5
B-9	5	4	7	3	1	3
B-10	17	8	4	1	1	0
B-12	3	3	2	0	2	4
C-1	6	0	7	1	6	4
C-4	21	21	54	2	2	6
C-7	11	6	8	1	1	1
P-2	10	1	14	1	4	0
P-3	39	14	9	9	42	20
P-4	15	19	17	0	2	3
PR-1	24	388	107	33	4	213
PR-2	54	149	179	3	5	54

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix D (cont).**

Piezometer	Relatively Common Taxa						
	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	1	0	0	0	0	1	0
A-4	1	0	0	0	0	0	0
A-6	0	0	0	0	0	2	1
A-7	1	0	0	0	0	1	1
A-9	1	7	7	4	3	6	3
B-2	0	0	0	0	0	0	0
B-4	0	0	1	0	0	0	0
B-6	7	1	2	0	0	0	2
B-7	0	0	2	0	0	2	0
B-9	0	0	0	0	0	1	0
B-10	0	0	1	0	3	1	1
B-12	0	0	0	0	0	0	0
C-1	1	2	2	0	0	0	0
C-4	2	0	0	0	2	0	6
C-7	2	0	0	0	0	0	0
P-2	4	0	0	0	1	0	0
P-3	22	3	2	0	5	1	4
P-4	1	0	0	0	1	1	0
PR-1	0	37	45	2	1	3	1
PR-2	0	2	1	1	3	11	3

**Appendix E.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in November 1999.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	20	2	3	1	0	1
A-4	1	0	0	0	1	4
A-6	0	1	2	0	0	1
A-7	0	1	4	1	0	3
A-9	8	30	69	11	5	39
B-2	2	6	6	0	1	0
B-4	1	2	4	2	0	1
B-6	0	0	7	0	0	4
B-7	0	0	4	3	1	6
B-9	1	0	2	3	2	13
B-10	4	2	7	1	0	0
B-12	1	1	2	2	1	1
C-1	4	0	4	0	2	9
C-4	14	13	14	7	0	13
C-7	0	3	5	0	0	2
P-2	1	0	0	0	2	1
P-3	1	3	11	3	1	4
P-4	16	10	6	3	2	8
PR-1	23	171	245	36	14	161
PR-2	22	64	100	19	3	67

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix E (cont).**

Piezometer	Relatively Common Taxa						
	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	0	0	0	0	0	0	0
A-4	0	0	0	0	0	0	0
A-6	0	0	0	0	0	0	0
A-7	0	0	2	0	0	0	0
A-9	1	16	3	0	2	16	5
B-2	0	0	0	0	1	0	0
B-4	0	1	0	0	0	0	0
B-6	0	0	0	0	0	0	0
B-7	0	1	0	0	0	0	0
B-9	0	0	3	2	0	0	0
B-10	0	0	0	0	0	0	0
B-12	0	0	0	0	0	0	0
C-1	0	1	0	0	2	0	0
C-4	1	3	0	0	0	0	1
C-7	1	0	0	0	0	0	0
P-2	0	0	3	0	0	0	0
P-3	0	3	0	0	2	1	1
P-4	0	5	1	0	0	1	0
PR-1	0	7	10	2	1	25	8
PR-2	1	9	1	1	7	7	0

**Appendix F.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in March 2000.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	18	0	12	0	0	2
A-4	9	1	1	0	0	4
A-6	6	10	2	0	2	7
A-7	0	0	10	0	0	31
A-9	38	62	39	26	13	142
B-2	4	0	7	3	1	9
B-4	0	0	2	1	0	0
B-6	9	0	5	0	0	1
B-7	24	2	0	1	1	11
B-9	8	1	2	2	1	29
B-10	11	7	13	2	0	7
B-12	6	5	1	1	1	5
C-1	7	1	1	0	0	8
C-4	44	13	12	1	0	13
C-7	5	4	5	1	0	3
P-2	5	2	1	0	2	17
P-3	10	10	13	9	0	27
P-4	20	16	12	2	2	102
PR-1	83	329	235	38	45	254
PR-2	55	82	124	17	3	141

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix F (cont).**

Piezometer	Relatively Common Taxa						
	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	0	2	0	0	0	0	2
A-4	0	0	0	0	2	0	0
A-6	1	1	2	4	0	1	0
A-7	1	0	1	7	0	0	0
A-9	0	24	14	4	1	22	1
B-2	0	0	1	0	0	0	0
B-4	0	1	0	0	0	0	0
B-6	2	1	1	0	1	2	0
B-7	0	1	3	2	3	0	2
B-9	1	0	2	3	0	0	0
B-10	0	1	0	0	0	0	0
B-12	0	0	1	0	0	0	0
C-1	0	1	1	2	1	1	0
C-4	1	1	2	0	0	2	2
C-7	2	0	0	1	0	0	0
P-2	0	0	1	0	0	0	1
P-3	0	2	1	0	8	0	4
P-4	0	0	15	6	2	0	0
PR-1	0	19	11	3	3	99	8
PR-2	1	23	2	1	1	11	2

**Appendix G.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in June 2000.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	6	2	5	0	0	5
A-4	1	3	11	2	2	7
A-6	0	1	7	8	1	12
A-7	0	4	6	0	3	20
A-9	15	21	43	15	1	9
B-2	1	0	2	0	0	0
B-4	5	1	3	0	1	2
B-6	4	0	7	3	1	1
B-7	8	1	3	1	0	0
B-9	1	1	1	0	0	4
B-10	9	6	7	5	3	1
B-12	1	4	0	1	1	1
C-1	0	0	10	0	1	0
C-4	3	7	6	2	1	0
C-7	4	3	9	2	6	1
P-2	3	0	3	1	2	0
P-3	2	2	12	9	1	0
P-4	8	9	16	8	4	5
PR-1	43	54	110	24	9	23
PR-2	21	15	99	36	17	13

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix G (cont).**

Piezometer	Relatively Common Taxa						
	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	1	0	0	0	0	0	0
A-4	2	0	1	0	0	1	0
A-6	0	3	0	0	1	0	0
A-7	2	0	3	1	0	0	0
A-9	1	9	6	0	0	23	1
B-2	0	0	0	0	0	0	0
B-4	0	1	0	0	0	0	0
B-6	0	1	0	1	0	0	0
B-7	0	0	0	0	0	0	0
B-9	0	0	0	1	0	0	0
B-10	0	0	1	0	0	1	0
B-12	0	0	0	0	0	0	0
C-1	1	0	0	2	0	0	0
C-4	1	0	0	0	0	0	1
C-7	0	0	0	0	0	0	0
P-2	0	0	0	0	0	1	1
P-3	0	0	0	2	4	3	0
P-4	1	0	0	1	0	0	0
PR-1	0	11	14	0	0	14	4
PR-2	0	4	1	2	2	6	2

**Appendix H.** Invertebrate densities (individuals/4L) for 20 piezometers sampled in September 2000.

Piezometer	Most Common Taxa					
	Archiannelida	Copepod Nauplii <sup>†</sup>	Cyclopoida	Harpacticoida	Hydrachnidia	Rotifera
A-1	18	1	7	1	0	1
A-4	2	1	3	2	0	1
A-6	0	1	7	1	1	2
A-7	0	9	34	1	0	5
A-9	11	21	64	8	2	41
B-2	6	3	3	0	3	1
B-4	8	2	5	1	0	3
B-6	4	2	11	1	1	8
B-7	12	3	3	2	2	2
B-9	1	1	4	0	2	0
B-10	3	9	21	4	6	5
B-12	4	4	4	0	18	1
C-1	10	2	7	2	3	3
C-4	43	25	55	2	2	1
C-7	7	2	9	0	2	1
P-2	4	1	3	0	6	8
P-3	8	7	13	6	19	3
P-4	23	17	13	7	6	4
PR-1	29	216	115	8	25	580
PR-2	40	226	354	24	13	59

<sup>†</sup> Juvenile cyclopoids and harpacticoids are included in nauplii category and not considered as separate taxa.

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**Appendix H (cont).**


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Relatively Common Taxa							
Piezometer	Collembola	Oligochaeta	Nematoda	Tardigrada	Ostracoda	Isopoda	Amphipoda
A-1	2	0	0	0	0	0	1
A-4	0	6	0	0	0	0	0
A-6	1	0	0	0	0	1	0
A-7	1	0	0	1	1	0	0
A-9	1	12	14	0	3	7	3
B-2	0	0	0	0	0	0	0
B-4	0	0	0	0	0	0	2
B-6	1	0	0	0	1	0	0
B-7	2	0	0	1	0	0	1
B-9	1	1	2	0	0	0	1
B-10	1	0	0	0	2	1	0
B-12	3	0	0	0	0	0	0
C-1	0	0	0	0	1	0	0
C-4	2	7	0	0	3	3	3
C-7	1	1	0	0	0	0	0
P-2	0	0	2	0	0	0	0
P-3	0	1	0	0	1	2	1
P-4	2	2	4	0	4	0	0
PR-1	5	20	36	1	0	54	2
PR-2	2	34	6	1	2	3	2

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