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BENTHIC MACROINVERTEBRATE RESPONSE TO HYPORHEIC EXCHANGE ON TWO ALLUVIAL FLOOD PLAINS IN NORTHWEST MONTANA, U.S.A.

by
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Presented in partial fulfillment of the requirements
for the degree of
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Benthic macroinvertebrate response to hyporheic exchange on two alluvial flood plains in northwest Montana, U.S.A.

Director: F. Richard Hauer

Abstract

Contrasting hyporheic exchange regimes influenced the distributional patterns of benthic macroinvertebrates in the main channel of rivers flowing through two alluvial flood plains in northwestern Montana, U.S.A. I employed a random stratified design to sample macroinvertebrates, periphyton and seston seasonally between July 1999 and March 2000 from riffles affected by different groundwater-surface water exchange regimes. Sampling was stratified by bedform, current velocity and median substrate grain size in order to control for confounding explanatory variables. Study riffles were located in floodplain-scale regions of hyporheic recharge (downwelling) and discharge (upwelling) on two alluvial flood plains; one located on the fourth-order McDonald Creek and the other on the fifth-order Middle Fork Flathead River. I determined groundwater-surface water exchange patterns by installing mini-piezometers in riffles throughout the length of each flood plain and measuring vertical hydraulic gradients (VHG) and hydraulic conductivities. General patterns in groundwater-surface water exchange were demonstrated; downwelling occurred near the upper limit of each flood plain while downwelling occurred over the lower ½ of each flood plain. These patterns were confirmed by means of comparisons with previous studies conducted on flood plains in this region. There were no differences in the mean seston concentration between sites on either flood plain within any season. However, the Middle Fork transported more seston than McDonald Creek, reflecting differences in stream size and drainage area. Mean periphyton standing stock biomass varied with season and site on both flood plains. Although periphyton means were not significantly different in all seasons because of high within-site variation, maximum periphyton standing stock biomass was always 2-4 times greater in upwelling compared to downwelling sites. In addition, variation in algal standing stock biomass in upwelling zones was approximately twice what was measured in downwelling zones. These results support the findings of another study and suggest that primary production is greater, but spatially heterogeneous, in upwelling zones in response to the patchy discharge of nutrient-enriched hyporheic groundwater. Univariate statistical analyses of mean macroinvertebrate density and biomass measurements found no differences between upwelling and downwelling sites. However, multivariate analyses of species by site distance matrices revealed species-specific responses to differential hyporheic exchange. These differences between upwelling and downwelling zones were correlated with differences in algal biomass and hyporheic exchange regimes. The results of this study suggest that changes in the physical habitat structure of main channel riffles induced by hyporheic exchange patterns influences the distribution and abundance of macroinvertebrates utilizing those habitats. As such, these results underscore the functional importance of the hyporheic zone, and particularly of exchange processes between groundwater and surface water, in developing and maintaining the complex physical habitat mosaic and faunal associations evident in alluvial floodplain ecosystems.

Acknowledgements

The assistance of my major professor, Dr. F. Richard Hauer was indispensable and much appreciated throughout the course of this research. He provided perspective and guidance in the early stages, much needed assistance with fieldwork in the middle stages and yet more perspective and guidance during the latter stages of this project. The members of my graduate committee, Dr. Jack A. Stanford and Dr. Paul Alaback, provided many insightful suggestions at the beginning of this research that greatly improved the quality of the data I collected. They also provided comments on an earlier draft of this thesis that helped improve the final product. I wish to thank the staff and graduate students at the Flathead Lake Biological Station for the assistance they provided at many points throughout the course of this research. Stacey Clark, Eric Anderson and Craig Stafford all volunteered their help with fieldwork and for this I am grateful. Dr. Daniel B. Fagre facilitated access to Glacier National Park sites. Diane Whited assisted in constructing Figure 1. Finally, I would like to thank Stacey and Mica; I would not have been able to complete this work without Stacey's boundless encouragement and Mica's smiles. I was supported by a teaching assistantship from The University of Montana during 1998. Additional funding was provided by a grant from the USGS Global Climate Change Program.

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Introduction

Stream systems form dynamic drainage networks reflecting the geologic, geomorphic and climatic histories of the landscapes with which they are associated (Stanford 1996, Ward 1997, 1998a, 1998b). These influential factors interact across scales of space and time forming physically heterogeneous landscapes comprised of highly connected elements (Ward 1997, Tabacchi *et al.* 1998, Ward 1998a, 1998b). Because of their dynamic and highly interactive character, stream networks are not merely isolated, wet segments of a drainage basin, but essential components indivisible from the landscapes they drain.

Hynes (1975) formally recognized the importance of connectivity between a river and its valley with his assertion that the ultimate source of a stream's organic matter was the surrounding terrestrial environment. Since then, conceptual lotic ecosystem models have been developed in an effort to explain stream ecosystem dynamics from a catchment perspective (Vannote *et al.* 1980,Ward and Stanford 1983, Frissell *et al.* 1986, Minshall 1988, Junk *et al.* 1989, Ward 1989, Gregory *et al.* 1991, Stanford and Ward 1993, Ward and Stanford 1995). Early models, such as the River Continuum Concept (Vannote *et al.* 1980), focused on the longitudinal dimension of a riverine system and identified important energetic factors associated with observed patterns in biological diversity and faunal distribution along the continuum from headwaters to mouth (Vannote *et al.* 1980, Minshall 1988, Johnson *et al.* 1995). Lotic researchers now acknowledge that the structure and function of a river ecosystem are the direct results of the dynamic connectivity between a given river and its landscape in three spatial dimensions. That is, interactions among the lateral, vertical and longitudinal dimensions of a riverine ecosystem vary over multiple scales of time resulting in the high biological diversity and physical complexity evident in these systems (see Ward 1989, Gregory *et al.* 1991, Stanford and Ward 1992, 1993, Ward 1997, Tabacchi *et al.* 1998, Ward 1998a, 1998b).

Furthermore, contemporary lotic researchers recognize the importance of connectivity among stream, riparian and adjacent upland ecosystems within catchments and propose that pristine riverine landscapes are organized into geomorphic hierarchies of landscape features (see Frissell *et al.* 1986, Gregory *et al.* 1991, Stanford and Ward 1992, 1993, Giller *et al.* 1994, Ward 1997, Tabacchi *et al.* 1998, Ward 1998a, 1998b). A fundamental tenet of hierarchy theory is that patterns or processes at a given hierarchical level are constrained by processes occurring at higher levels (*cf.* O'Neill *et al.* 1986, Swanson *et al.* 1988, Kotliar and Weins 1990); this principle applies strongly to the organization of lotic ecosystems.

The catchment is the highest level of the stream geomorphic hierarchy; its boundaries define a given river's watershed and it is the most spatially extensive and temporally persistent landscape element. The remainder of the hierarchy is comprised of a series of nested elements, including the channel network, segment, reach and habitat. Spatial extent and temporal persistence decrease through this series (Frissell *et al.* 1986).

The geologic and geomorphic histories of its catchment define a stream network's drainage pattern. In northwest Montana, channel networks interact with catchments that have been heavily influenced by glaciation (Fagre *et al.* 1997). These channel networks are characterized by a predictable, repetitive sequence of segment types: bedrock confined segments alternate with unconfined alluvial segments, both of which contain reaches comprised of alternating riffle and pool habitat types.

Confined and alluvial segments differ in the relative sizes of their lateral and vertical dimensions. Bedrock confined segments typically flow through steep regions of a catchment and are characterized by straight, single thread channels with relatively high stream powers per unit stream length. Because of this, erosional features typically dominate confined segment types; very few depositional features occur along confined segments in this region (Hauer *et al.* 1997). Hence, the vertical dimension of confined reaches is often limited to shallow, spatially discrete channel bottom sediment deposits (Stanford and Ward 1992, 1993, Ward 1997, Hauer *et al.* 1997, Ward 1998a, 1998b). Additionally, the high level of bedrock control exerted on confined segments minimized any interaction in the lateral dimension between the stream and the terrestrial environment.

In contrast, alluvial segments flow through deep sediments deposited over broad, shallow valleys by long-term fluvial processes resulting in a vertical dimension which can extend tens of meters (Church 1992, Lewin 1992, Stanford and Ward 1992, 1993, Ward 1997, Huggenberger *et al.* 1998, Ward 1998a, 1998b). In northwest Montana, unconfined alluvial segments are distinctly defined on the landscape as spatially heterogeneous flood plains (see Amoros and Roux 1988, Stanford and Ward 1993, Hauer *et al.* 1997). Alluvial floodplain systems are physically dynamic across several scales of space and time. A topographically complex pattern of mixed age geomorphic surfaces is created as a river migrates across its flood plain through the processes of cut-and-fill alluviation and channel avulsion (Salo 1990, Gregory *et al.* 1991, Church 1992, Lewin 1992, Naiman and Décamps 1997). These surfaces are differentially colonized by macrophytes and influenced by large scale restructuring events, including sediment deposition and scouring by bedload transport or the movement of large woody debris during floods (Likens 1984, Naiman and Decamps 1997). In addition, interstitial surfaces with high hydrologic conductivities occur throughout the vertical dimension of alluvial flood plains forming preferential groundwater flow-paths. These zones, referred to as paleochannels, appear to be the beds of former river channels covered and filled with alluvium (Stanford and Ward 1993). This physical complexity, particularly in the vertical dimension, contributes to the development of hydrologic, thermal and biological complexity throughout the entire flood plain.

Extensive hydrologic exchange between ground water and surface water occurs in the vertical dimension of unconfined alluvial flood plains (see Boulton 1993, Stanford and Ward 1993, Brunke and Gonser 1997, Boulton *et al.* 1998, Malard *et al.* 1999). The processes of groundwater-surface water exchange operate within a hierarchy defined by floodplain geomorphology. Like other hierarchical systems, the broadest level is the most spatially extensive and temporally persistent, while subsequent levels are smaller and increasingly ephemeral.

At the largest scale ($10^{2\text{-}3}$ m, $10^{3\text{-}4}$ yr.) surface water flowing onto a flood plain at the upstream bedrock constriction point (knickpoint) penetrates the alluvium (downwells), recharging the aquifer as it enters the hyporheic zone. Hyporheic water moves through floodplain gravels along various interstitial pathways, including paleochannels, and erupts back to the surface (upwells) at various locations downslope (Boulton 1993, Stanford and Ward 1993, Brunke and Gonser 1997, Baxter and Hauer 2000). Not all of the hyporheic water returns directly to the main river channel in zones of generalized upwelling, a portion is discharged on lateral floodplain surfaces some distance from the channel forming ponds, wetlands and springbrooks.

Regardless of its location, upwelling hyporheic water confers a moderated and attenuated thermal regime to the surface water system resulting in summer cool and winter warm conditions relative to non-upwelling portions of the river channel. Several studies have demonstrated an increase in temperature of up to 4° C in upwelling zones compared to downwelling or neutral zones under cold winter conditions (see Valett *et al.* 1990, Case 1995, Cavallo 1997, Bansak 1998, Baxter and Hauer 2000). A moderated thermal regime such as this may confer an energetic subsidy to benthic invertebrate communities and contribute to physical habitat complexity by preventing the formation of anchor ice and surface ice in upwelling zones. Additionally, hyporheic discharge is enriched in both phosphorous and nitrogen (Ford and Naiman 1989, also see reviews in Brunke and Gonser 1997, Boulton *et al.* 1998, Dahm *et al.* 1998, Tabacchi *et al.* 1998) and has been shown to subsidize benthic primary production at both small (Valett *et al.* 1994) and large spatial scales (Bansak 1998).

Smaller scale patterns of upwelling and downwelling ($10^{0\text{-}1}$ m, $10^{0\text{-}1}$ yr.) also occur along unconfined alluvial segments. Ephemeral ponds and floodplain streams may only be present when the groundwater table is recharged after annual peak discharge or extremely large storm events (*cf.* White 1993). Localized downwelling and upwelling occur at the head and tail of each floodplain riffle (*cf.* White 1993, Valett *et al.* 1994). Thus, this spatially complex mosaic of floodplain habitats is constantly shifting in response to changes in hydrology and geomorphology over scales of time ranging from hours to millennia (White 1993).

Stanford and Ward (1993) proposed an expansive riverine ecosystem model that modified previous conceptual models (Vannote *et al.* 1980, Ward and Stanford 1983, Junk *et al.* 1989, Ward and Stanford 1995) by incorporating ecological interactions occurring between hydrologic subsystems (i.e., hyporheic - surface) in the vertical dimension. According to the hyporheic corridor concept (Stanford and Ward 1993), repetitive alluvial flood plains provide catchment-wide vertical connectivity in addition to the longitudinal connectivity proposed by the River Continuum Concept (Vannote *et al.* 1980) or the longitudinal and lateral connectivity proposed by the Serial Discontinuity Concept (Ward and Stanford 1995) and the Flood Pulse Concept (Junk *et al.* 1989). The Hyporheic Corridor Concept further hypothesized that repetitive floodplain elements would function as segment-scale (*sensu* Frissell *et al.* 1986) zones of hyporheic-surface water exchange, thereby increasing landscape heterogeneity and influencing, presumably enhancing, biological diversity patterns across the entire catchment.

For the past twenty years, the physical, chemical and biological environments of alluvial flood plains have been under extensive investigation worldwide. Most of the research has focused on the characteristics of the hyporheic zone and how interactions between ground and surface water environments may influence floodplain diversity patterns. Results have revealed speciose and unique interstitial invertebrate and microbial assemblages, complex thermal and hydrologic regimes, complex nutrient dynamics characterized by nutrient enriched hyporheic water and spatially diverse habitats partially controlled by variable hyporheic exchange (Amoros and Roux 1988, Stanford and Ward 1988, Triska *et al.* 1989, Gibert *et al.* 1990, Valett *et al.* 1990, Stanford *et al.* 1994, Valett *et al.* 1994, Ward *et al.* 1994, Case 1995, Cavallo 1997, Bansak 1998, Claret *et al.* 1998, Craft 1998, Dahm *et al.* 1998, Dole-Olivier 1998, Ellis *et al.* 1998, Ward *et al.* 1998, Baxter and Hauer 2000).

Four studies are of particular relevance to the research summarized in this thesis. All focused on interactions between groundwater and surface water habitats and helped identify the need for further investigation into the functional significance of hyporheic exchange in flood plain-river ecosystems. Three of the studies focused on the Nyack flood plain of the Middle Fork Flathead River and were extensions of an initial investigation conducted by Stanford, Ellis, Craft and Hanson (unpublished). This investigation demonstrated floodplain-scale downwelling and upwelling using water mass balance data, thermal subsidy in upwelling zones and a spatiotemporally dynamic shifting habitat mosaic on the Nyack flood plain in an effort to provide a scientific rationale for a Federal Reserve Water Right on the Middle Fork.

Case (1995) compared the composition of benthic macroinvertebrate assemblages from surface water habitats (springbrook and main channel) with hyporheic invertebrate assemblages on the Nyack flood plain. Her results suggested that hyporheic habitats contained unique invertebrate fauna and that benthic assemblages were more similar to each other than those occupying the adjacent hyporheic zone regardless of habitat type. She also demonstrated distinctly different thermal and chemical conditions among the three habitat types. Of particular interest, sites characterized by hyporheic discharge were thermally enhanced; they accrued up to 400 more annual degree-days than recharge habitats.

Cavallo (1997) investigated how thermal heterogeneity among various floodplain habitats influenced fish and amphibian diversity. Like Case (1995), his results showed that habitats associated with upwelling zones were characterized by moderated thermal regimes and distinctly different physical characteristics than downwelling habitats. He demonstrated that floodplain habitats contained vertebrate fauna distinct from river habitats and that this difference was a function of the moderated thermal regime and different physical conditions that characterized floodplain habitat types.

Bansak (1998) demonstrated that benthic algal assemblages responded to physical and chemical differences between areas of segment-scale generalized upwelling and downwelling on a flood plain. Cobbles in generalized upwelling zones supported higher periphyton biomass than cobbles in downwelling zones in response to phosphorous enrichment conferred from hyporheic discharge. Phosphorous concentrations were up to three times greater in hyporheic water compared to surface water. Like Case (1995) and Cavallo (1997), he also demonstrated a significantly moderated and attenuated thermal regime for surface water habitats in upwelling zones.

Baxter and Hauer (2000) studied several alluvial segments in the Swan River drainage of northwest Montana. They demonstrated that the discharge of ground water into main channel riffle habitats occurs across a hierarchy of spatial scales that affects thermal and physical habitat conditions. Their results indicated that bull trout (*Salvelinus confluentus*) responded to upwelling hyporheic water at both the reach- and habitat-scale (*sensu* Frissell *et al.* 1986) when choosing spawning locations. They suggested that this choice was related to the moderated thermal regime evident in upwelling reaches. They also demonstrated that alluvial flood plains are repetitive elements in riverine landscapes with surface-hyporheic exchange patterns very well predicted by segment-scale geomorphology. Specifically, at the floodplain scale, surface water downwelling is concentrated at locations near the upstream knickpoint, while a majority of the hyporheic upwelling occurs near the downstream knickpoint.

Within the river ecology literature, many experimental studies have documented complex energy flow through food webs that involve interactions among nutrients, periphyton and invertebrate consumers (see reviews by Feminella and Hawkins 1995, Borchardt 1996, Lamberti 1996). However, few studies have investigated whether changes induced in the *in situ* benthic environment, either in the physical habitat or at the primary producer trophic level, could lead to similar results (Ward 1989, Boulton 1993). Likewise, catchment-scale thermal regimes have long been recognized as influential to aquatic insect distribution and abundance along the longitudinal river continuum (see Ward and Stanford 1982, Stanford *et al.* 1988, Vinson and Hawkins 1998, Lowe and Hauer 1999). In spite of this, studies on a possible macroinvertebrate response to variation in segment-scale thermal conditions resulting from differential groundwater-surface water exchange on large alluvial flood plains are virtually nonexistent (but see Boulton *et al.* 1998 for a further perspective).

The objective of this study was to investigate the relationship between segment-scale surface water–groundwater exchange and patterns in the distribution and abundance of main channel benthic macroinvertebrates. I was specifically interested in determining if, within similar riffle habitats, the composition and structure of benthic macroinvertebrate assemblages differed between zones of segment-scale upwelling and downwelling on alluvial flood plains. Since large- (10^3-m) and small-scale (10^{-2}-m) patterns in the distribution and abundance of benthic macroinvertebrates have been linked to physical habitat conditions (see Reice 1980, Sheldon 1980, Resh and Rosenberg 1984, Culp and Davies 1985, Clements 1987, Parker 1989, Quinn and Hickey 1990, Ward 1992, Wohl *et al.* 1995, Vinson and Hawkins 1998, Lowe and Hauer 1999), I employed a stratified design to identify and sample riffles with similar seston dynamics, current velocities and substrate grain sizes in an effort to isolate the effects of hyporheic exchange. I addressed this question at both the stream segment (floodplain) and channel network (across stream order) scales (*sensu* Frissell *et al.* 1986).

I developed four working hypotheses: 1) riffles in upwelling zones would have higher algal standing stock biomass than similar riffles in downwelling zones; 2) riffles in upwelling zones would support higher densities of macroinvertebrates than similar riffles in downwelling zones; 3) macroinvertebrates collected from riffles in upwelling zones would be larger than those collected from similar riffles in downwelling zones; and 4) the composition and structure of macroinvertebrate assemblages would vary with river, but assemblages associated with riffles in upwelling zones would consistently contain more and larger individuals than assemblages associated with similar riffles in downwelling zones. The corresponding null hypothesis for each working hypothesis was that there would be no measurable differences between upwelling and downwelling zones on either flood plain.

Methods

Field Sites

I conducted fieldwork in main channel riffle habitats on two alluvial flood plains in northwestern Montana, U.S.A. (Fig. 1). I selected flood plains based on total area and river size to facilitate an across-scale investigation. The 4th order Moose Country and 5th order Nyack flood plains cover approximately 3-km^2 and 30-km^2, respectively (Table 1). Both flood plains are within the 24,241-km^2 Flathead River drainage basin. The Flathead Basin's underlying geology is sedimentary bedrock from the late Paleocene to the Proterozoic; its mountain ranges are part of the Rocky Mountain Belt Supergroup and its geomorphology reflects the recent glacial history of the region (Alt and Hyndman 1973, Hauer *et al.* 1999). Rivers within the Flathead Basin show a repetitive sequence of

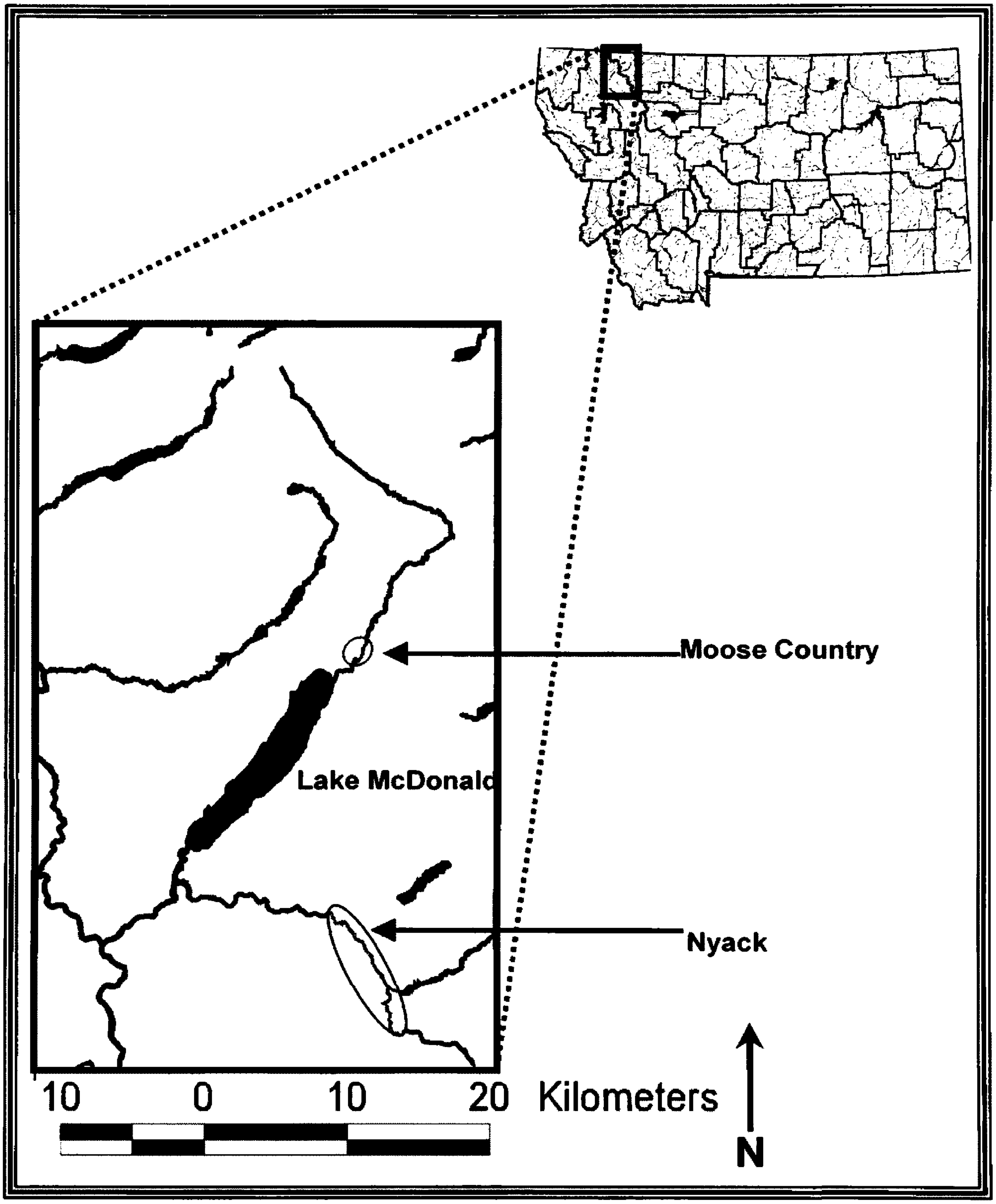

Figure 1: Location map of study sites in northwest Montana, U.S.A. Inset

Table 1. Study site description and results of site suitability assessments. One sample t-test on H_0: The true mean VHG is zero. Mann-Whitney test on H_0: There is no difference in the mean VHG values between sites on a flood plain.

Flood plain	**River**	**Order**	**Area (km^2)**	**Site**	**VHG (mean ± 1 SE)**	**Significance**	
						t-test	**Mann-Whitney**
Moose Country	McDonald Creek	4	~ 3	UW	0.029 ± 0.006	< 0.0005	< 0.0005
				DW	- 0.332 ± 0.083	< 0.0005	
Nyack	Middle Fork Flathead River	5	~ 30	UW	0.008 ± 0.003	0.042	< 0.0005
				DW	- 0.525 ± 0.189	0.027	

bedrock-confined segments alternating with unconfined alluvial segments. Alluvial segments are often characterized by the presence of flood plains containing unconfined aquifers in which connectivity between hyporheic groundwater and surface water is maximized, resulting in physically, spatially and biologically complex ecosystems.

Large-scale patterns of upwelling and downwelling are well understood on the Nyack flood plain. Stanford *et al.* (1994) and Poole (2000) discuss detailed descriptions of and mechanisms for these patterns; I will only provide a summary here. Downwelling occurs at the flood plain's upper knickpoint and continues for approximately 2-km, by which point 30% of the river flow has recharged the Nyack alluvial aquifer (Stanford *et al.* 1994, Poole 2000). Return flow to the river channel begins approximately 8-km from the upper knickpoint and all of the recharged water is returned to the Middle Fork's channel before it enters the confined segment 10-km downstream from the upper knickpoint (Stanford *et al.* 1994, Poole 2000).

Baxter and Hauer (2000) provided support for the generality of this pattern; they observed similar groundwater-surface water exchange patterns on flood plains in four separate watersheds in northwest Montana. On all of the flood plains in their study, strong downwelling zones were found at the upper knickpoints while upwelling zones occurred near the lower knickpoints. During the early phase of my research, I conducted an exploratory investigation with a stratified random design to identify large-scale zones of downwelling and upwelling on the Moose Country flood plain and confirm patterns described for the Nyack flood plain within similar riffle habitats.

Groundwater-Surface Water Exchange

I quantified groundwater-surface water exchange on these flood plains with mini-piezometers constructed of 5/8" internal diameter PVC pipe. I installed an array of mini-piezometers (n = 8 to 25) in randomly selected locations in riffles near the upper and lower knickpoints of each flood plain using a piezometer driver and methods outlined by Baxter (1997). All piezometers were finished to depths of 50-cm to 75-cm below the river bottom, bailed to ensure that they were free of blockages and left to equilibrate for up to 15 minutes. I then calculated the vertical hydraulic gradient (VHG) at each piezometer from the equation:

$$\mathrm{VHG} = \mathrm{d}h/\mathrm{d}l$$

where $\mathrm{d}h$ is the difference measured between the hydraulic head inside and outside the piezometer and $\mathrm{d}l$ is the piezometer's depth of penetration into the stream bottom (see Lee and Cherry 1978, Dahm and Valett 1996). Vertical hydraulic gradient is a unitless ratio in which negative values indicate downwelling, or groundwater recharge, while positive values indicate upwelling, or groundwater discharge.

Hydraulic conductivities (k, in cm/s) of the floodplain sediments were determined with falling head tests (Fetter 1994). A falling head test was performed on each piezometer and hydraulic conductivity was estimated using the modified Hvorslev equation described in Baxter and Hauer (2000):

$$k = [(0.2501)\,(D)\,(\ln\,(h_0/h))]\;/\;(dt)$$

where D is the inside diameter of the piezometer and dt is the interval of time required for the head level to drop from h_0 to h. After calculating VHG and k for each piezometer, I used Darcy's Law to quantify the flux (Q, in cm^3s^{-1}) of water between the groundwater and surface water compartments of the floodplain gravels:

$$Q = -(k)(A)(VHG)$$

where A is the cross sectional area of the piezometer and *k* and VHG are calculated from the above equations (Fetter 1994). Mean values of VHG, *k* and Q were used in all subsequent analyses. If the mean hydraulic conductivities were equal at two locations then flux was simply a function of VHG. After identifying and confirming generalized upwelling and downwelling zones, I randomly selected a study riffle on each flood plain within each upwelling and downwelling zone (Table 1, Figure 2).

Benthic Macroinvertebrates

I employed a stratified random design (stratified by habitat type = similar riffles) to quantitatively sample benthic macroinvertebrates seasonally from six randomly selected 0.25-m^2 plots in each riffle with a modified kicknet using methods described by Hauer and Stanford (1981) and Hauer and Resh (1996). I collected a total of 48 samples per flood plain (six samples at two sites on four collection dates). I sampled seasonally during 1999 and 2000 (July, October, December and March). These dates represented summer, fall, early winter before ice formation and early spring after ice out yet before warm overnight temperatures initiated annual snowmelt runoff. Each sample was preserved in the field with 70-% EtOH and returned to the Flathead Lake Biological Station where it was rinsed and sorted. Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa were identified to species when possible using available keys and an existing reference collection (Jensen 1966, Gaufin *et al.* 1972, Edmunds *et al.* 1976, Wiggins

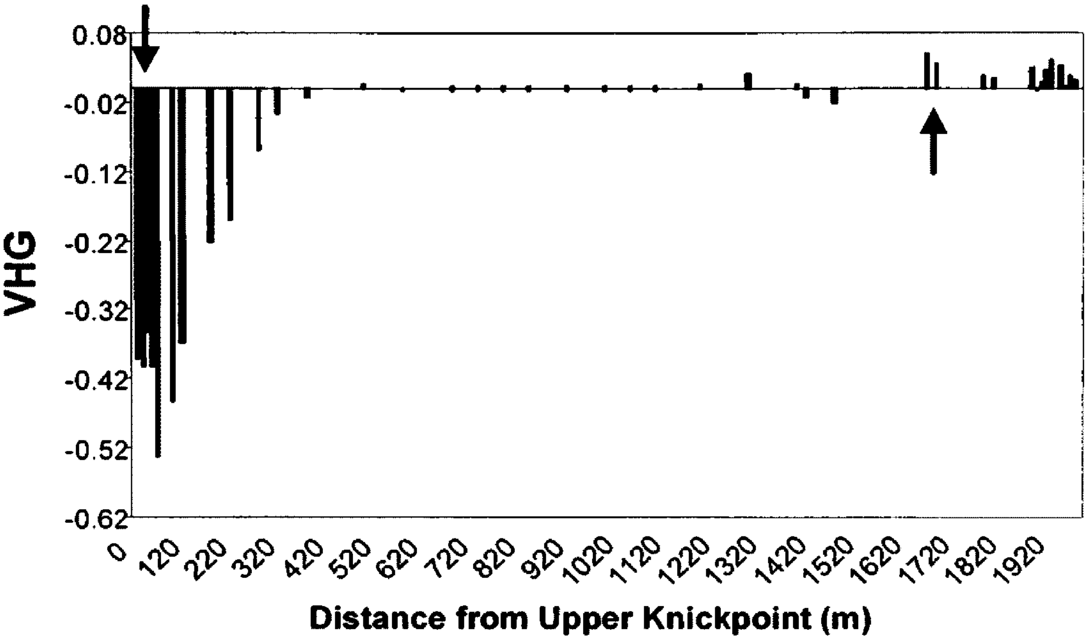

Figure 2: Plot of Vertical Hydraulic Gradient as a function of distance from the upper knickpoint on the Moose Country flood plain. Arrows denote the locations of study riffles.↓ indicates downwelling and ↑ indicates upwelling.

1977, Stewart and Stark 1988, Merritt and Cummins 1996, FLBS reference collection) and to genus in early instars. I quantified macroinvertebrate abundance from these data by calculating community level densities and biomass. I also quantified individual condition by measuring the size of common taxa.

Taxon biomass was determined by first spinning individual taxa from each sample at 650 RPM for three minutes in an International Equipment Co. Model HN centrifuge to remove residual preservative and then weighing to the nearest 0.0005-g on an AND Company electronic balance Type ER-182A (Stanford 1973). I determined mean individual size of common taxa by measuring either the interocular distance (Trichoptera and Plecoptera) or head capsule width (Ephemeroptera) of a randomly selected subsample of approximately 50 individuals. I defined common taxa operationally as those taxa that had more than approximately 25 late instar individuals in each sample on a flood plain. These taxa were not chosen *a-priori*, but were selected after a preliminary inspection of the samples. Common taxa often varied between flood plains and among seasons, but were always common to both sites within a given flood plain and season. Voucher specimens were preserved, labeled and archived at the Flathead Lake Biological Station.

Periphyton

I scraped a 4-cm^2 area of periphyton from the surfaces of five randomly selected rocks at each riffle on each sampling date. The scraped area was then scrubbed with a bristle brush to dislodge any remaining cells. I rinsed the scraped surface, blade and brush onto a glass fiber filter (Gelman type AE) and froze each filter on dry ice in the field (Steinman and Lamberti 1996). Chlorophyll *a* concentration, a surrogate of algal standing stock biomass, was quantified by acetone extraction followed by spectrophotometric analysis (American Public Health Association 1998). I conducted all periphyton analyses within 30 days from the collection date.

Seston, Substrate, and Current Velocity

At each sampling date, I collected seston (1-µm < suspended particulate matter < 1000-µm) by straining three 100-L grab samples of water collected from the river thalweg at each site through two sieves (1-mm and 64-µm mesh). The seston accumulated on the 64–µm sieve was transferred into a rinsed 125-mL HDPE container. A 25-L aliquot of the flow-through from the sieves was collected in a DI rinsed container. This aliquot of flow-through represented the < 64-µm size fraction of seston. Samples were placed on ice and returned to the Flathead Lake Biological Station for AFDW analysis. I filtered seston through pre-ashed Gelman type AE glass fiber filters (1-µm pore diameter), dried and ashed all samples within 24-h according to standard analysis procedures (Wallace and Grubaugh 1996, American Public Health Association 1998).

I quantified the dominant substrate grain size of each riffle with a modified Wolman pebble count on the first visit to each riffle. I pooled all particles in each riffle and constructed frequency distributions. The median diameter of each distribution was categorized according to the Wentworth Classification scheme ($-\log_2(d_{50})$) for comparison between riffles (Minshall 1984). Near substrate current velocity was measured at approximately 3-cm above the river bottom at each sample plot on each collection date with a Scientific Instruments Inc. Model 1215 type AA magnetic head current meter.

Statistical Analyses

I assessed site suitability by first comparing the mean hydraulic conductivity values (*k*) of each pair of sites on a flood plain to verify that they were equal. Since the hydraulic conductivities were equal between sites on a flood plain (see Results) I was able to use VHG alone as an index of groundwater flux (see flux equation in VHG section above). I compared the mean VHG values of each pair of sites on a flood plain with a Mann-Whitney test of H_0: the mean VHGs of the riffles are equal. I then performed a one-sample t-test on the mean VHG of each riffle to confirm that each was different from zero, i.e., each riffle's mean VHG was significantly positive or negative. I defined suitable riffles as those with mean VHG values both different from each other and different from zero at $p \leq 0.05$. Using those criteria, riffles with significant positive or negative mean VHG values were receiving water from or losing water to the hyporheic zone, respectively. Suitable sites were thus located in regions of the flood plain under the influence of contrasting groundwater-surface water exchange regimes.

Differences in macroinvertebrate assemblage composition and structure were analyzed with both multivariate and univariate techniques. Since species composition was highly variable among seasons and between flood plains I performed all tests seasonally within flood plains. In all cases, I considered p-values of 0.10 or less significant.

I conducted three multivariate analyses with PC-ORD for Windows Version 3.2 (McCune and Mefford 1997): Multi-Response Permutation Procedures (MRPP), Mantel tests of association and Indicator Species Analysis. For the multivariate tests, species by site matrices were constructed based on raw EPT abundance data and then coded by habitat type (i.e., upwelling or downwelling).

I used nonparametric MRPP to determine if species composition differed between habitat types on a flood plain. My MRPP tested the null hypothesis that there was no site effect on species composition. I converted the species by site matrices to distance matrices using Sorenson's distance:

$$S = 1 - (2w / (a+b))$$

where w is the sum of the smaller abundance values of taxa common to both upwelling and downwelling sites and a and b are the sum of all taxa abundances in upwelling and downwelling sites. Each MRPP produced an R-statistic, which described the level of observed compared to expected within group homogeneity based on the distance matrices. R-statistics can assume values of -1 to 1. Positive values suggested that there was more within group homogeneity than expected and, thus, differences in species composition between sites; negative values suggested less within-group homogeneity and, thus, no site differences. MRPP associated a p-value with each R-statistic, providing a statistical interpretation of significance.

I used the nonparametric Mantel test to determine whether differences in macroinvertebrate assemblages were significantly associated with environmental parameters (chlorophyll-*a* and VHG). As in MRPP, I used Sorenson's distance to convert both species by site and environmental conditions by site matrices to distance matrices. Specifically, the Mantel test evaluated the null hypothesis that no relationship existed between site-specific differences in species composition and environmental conditions. A p-value was obtained by performing 2000 iterations of a Monte Carlo randomization procedure.

I used Indicator Species Analysis on seasonal species abundance by site matrices of each flood plain to identify taxa indicative of upwelling or downwelling habitats, i.e., to determine the drivers of differences uncovered with MRPP. In PC-ORD, the relative abundance and relative occurrence of each taxon was used to calculate an indicator value for that taxon. Indicator values ranged from 0 to 100 and were indices of whether the presence of a given taxon was indicative of a specific habitat type (no indication to perfect indication). I used a Monte Carlo randomization procedure with 2000 iterations to test the null that a taxon's observed indicator value was no different from what could be expected by chance.

In addition to multivariate analyses, I compared mean values of macroinvertebrate abundance measured as density, biomass and relative abundance. Very obvious differences in aquatic insect assemblages may be demonstrated with comparisons of mean community-level values. In fact, this approach has been used to show the effect of catastrophic disturbance events on insect communities and to illustrate regional differences in the composition of macroinvertebrate communities (Reice 1984). I used Mann-Whitney U tests to compare total EPT density and biomass and EPT relative abundance and biomass seasonally within flood plains to determine if there were gross differences in macroinvertebrate assemblages correlated with groundwater-surface water exchange patterns.

Macroinvertebrate assemblage structure is also often examined from a trophic perspective. Aggregating species into functional feeding groups often helps describe differences in assemblage composition between locations or treatments by highlighting differences in the relative abundances of different food type specialists (Cummins and Merritt 1996). Functional feeding group (FFG) composition has proven useful in describing changes in the longitudinal distribution patterns of macroinvertebrates related to the availability of specific energetic resources such as CPOM, FPOM, plant material and prey species (Vannote *et al.* 1980, Minshall and Petersen 1985). FFG analysis has also been successful as a descriptor of changes in community structure related to river impoundment and other types of flow regulation (Stanford *et al.* 1988). I aggregated EPT taxa collected in upwelling and downwelling zones into five functional feeding groups based on each taxon's primary mode of feeding: collector-filterer, collector-gatherer, predator, scraper/grazer and shredder (*sensu* Cummins and Merritt 1996). Taxa were further categorized as specialists or generalists depending on whether they utilized more than one type of food resource, e.g., a generalist obtains energy and nutrients from both detritus and live plant material while a specialist only eats living plants. Differences in the relative abundance of FFG's were analyzed with Mann-Whitney U tests to determine if there were gross changes in the assemblage structure from a food availability perspective.

I also used Mann-Whitney U tests to compare the mean individual sizes and biomass of several common taxa and to test for seasonal between-site differences in chlorophyll-*a*, seston concentration and current velocity within flood plains. I converted the median particle diameter of each riffle's substrate distribution to a categorical value on the Wentworth scale and considered the substrate composition to be different between sites on a flood plain if the median particle diameter fell into different Wentworth categories (Minshall 1984).

Results

Seston, Current Velocity and Substrate

Despite strong seasonal trends, there were no significant differences between seston AFDW concentrations at upwelling versus downwelling sites on either flood plain within any season ($p > 0.05$ between sites within season and flood plain). I measured annual maximum mean seston concentrations in the summer samples, which were collected shortly after annual peak discharges. Nyack sites transported more seston (mean ± 1 SE, 0.553-mg/L ± 0.04-mg/L) than the Moose Country sites (0.225 mg/L ± 0.05-mg/L) in this season. I measured annual minimum mean seston concentrations in the winter samples, which were collected during a period corresponding to extended baseflow conditions. As with the maxima, Nyack sites carried larger minimum seston loads (0.130-mg/L ± 0.01-mg/L) than the Moose Country sites (0.098-mg/L ± 0.01-mg/L).

There were no differences in mean near-substrate current velocities between sites on either flood plain in any season (Nyack $p > 0.10$, Moose Country $p > 0.10$ in all seasons). Overall mean values varied with season but no trends were evident. However, mean current velocities were generally higher at the Nyack sites than the Moose Country sites. I measured ranges in current velocity from 0.50-mps to 0.86-mps at the Nyack sites and 0.44-mps to 0.65-mps at the Moose Country sites.

Small cobble particles (64-mm to 128-mm diameter) dominated the substrate of all study riffles. There were no significant between-site differences in the substrate grain size composition, although downwelling sites tended to have larger substrate particles than upwelling sites. Across all sites, the median particle diameter expressed on the

Wentworth Classification scale was -6. However, the Nyack flood plain contained larger particles than the Moose Country flood plain (117-mm *vs*. 87-mm), reflecting differences in conveyance between the two rivers.

VHG and Site Suitability

Moose Country

I identified suitable riffles in generalized downwelling and upwelling zones of the Moose Country flood plain approximately 30-m and 1750-m downstream from the upper bedrock knickpoint (Figure 2). Since both sites contained sediments with hydraulic conductivities of approximately 0.05-cm/s, values within the range expected for unconsolidated, well-sorted gravels (Fetter 1994), I used VHG as an index of groundwater flux. Both riffles had mean VHG values highly significantly different from zero ($p < 0.0005$ in both upwelling and downwelling zones) and each other ($p< 0.0005$), permitting me to assign them as suitable study sites (Table 1, Figure 3). However, the relative strengths of groundwater-surface water exchange were not equal at the upwelling and downwelling sites. The mean VHG in the upwelling zone was approximately 12 times less than in the downwelling zone (Table 1). In addition, the distribution of VHG's was highly variable in the upwelling zone but constant in the downwelling zone. Approximately 14% of the mini-piezometers I installed in the upwelling zone had negative VHG measurements while all of the mini-piezometers in the downwelling zone had negative VHG measurements (Figure 3). Such a difference in VHG between upwelling and downwelling zones indicated a patchy, non-uniform discharge of hyporheic water in upwelling reaches of the floodplain river channel but strong homogeneous surface water recharge in downwelling zones.

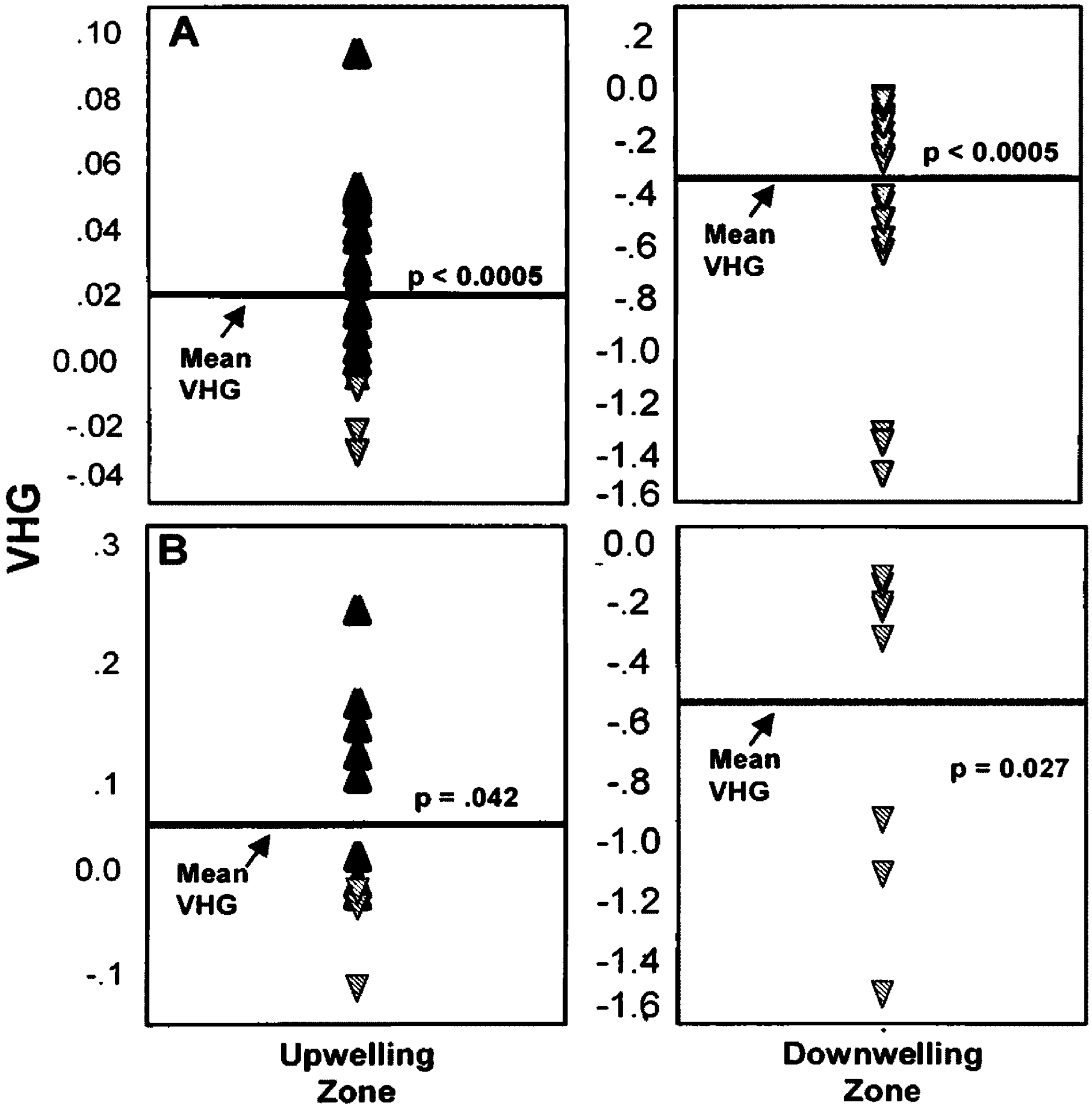

Figure 3: Scatterplots of VHG values at **A**: Moose Country sites and **B**: Nyack sites. Figure should be read across the panels. Solid upward facing arrows indicate piezometers with positive VHG values, Open downward facing arrows indicate piezometers with negative VHG values.

Nyack

I identified two suitable study riffles in previously described generalized downwelling and upwelling zones (J. A. Stanford, unpublished data) of the Nyack flood plain approximately 1500-m and 7500-m below the flood plain's upper constriction point. Like the Moose Country sites, both Nyack sites contained sediments with similar hydraulic conductivities of approximately 0.09-cm/s, values within the range expected for unconsolidated, well-sorted gravels (Fetter 1994). Therefore, I used VHG as an index of groundwater flux. Mann-Whitney U test results suggested that these riffles were under the influence of significantly different ($p < 0.0005$) groundwater-surface water exchange regimes (Table 1). One-sample t-test results showed that the true mean VHG values did not equal zero in either the downwelling (VHG = -0.525, $p = 0.027$) or upwelling (VHG = 0.008, $p = 0.042$) zones (Table 1, Figure 3). Therefore, the riffles were under the influence of contrasting groundwater-surface water exchange regimes. However, the strength of this exchange was not the same at upwelling and downwelling sites. The magnitude of VHG in the upwelling zone was approximately 100 times less than in the downwelling zone (Table 1) and its distribution was patchy; approximately 29% of the mini-piezometers that I installed in the upwelling zone had negative VHG's (Figure 3). All of the piezometers I installed in the downwelling zone, on the other hand, had negative VHG's (Figure 3). Like at the Moose Country sites, this difference in VHG data suggests a non-uniform discharge of hyporheic groundwater across riffles in the upwelling zone and a strong uniform recharge of surface water into the alluvium of downwelling zones.

Periphyton Standing Stock Biomass

Moose Country

Chlorophyll *a* concentration, an index of periphyton standing stock biomass, differed between upwelling and downwelling sites in every season and exhibited a strong seasonal trend (Figure 4). Minimum chlorophyll *a* concentrations (Mean ± 1 SE), which I obtained from the summer samples, were surprisingly similar between sites (0.101-μg/cm^2 ± 0.008-μg/cm^2). I calculated maximum periphyton standing stock biomass in the winter samples from the upwelling zone (2.279-μg/cm^2 ± 0.400-μg/cm^2) and spring samples from the downwelling zone (1.102-μg/cm^2 ± 0.182-μg/cm^2) (Figure 3). Although I only demonstrated a statistically significant difference in mean chlorophyll-*a* concentrations for the winter samples ($p = 0.016$), I always measured maximum chlorophyll-*a* concentrations from the upwelling site. Furthermore, the average range of chlorophyll-*a* concentrations was approximately 78% larger in samples taken from the upwelling zone compared with those taken from the downwelling zone.

Nyack

Periphyton standing stock biomass at the Nyack sites followed a pattern similar to that at Moose Country where I observed differences in chlorophyll-*a* concentrations between upwelling and downwelling sites both within and among seasons (Figure 4). Chlorophyll *a* concentration (Mean ± 1 SE) was lowest at both sites in the summer samples (0.213-μg/cm^2 ± 0.088-μg/cm^2 UW, 0.218-μg/cm^2 ± 0.286-μg/cm^2 DW) and highest in the fall samples (8.172-μg/cm^2 ± 2.511-μg/cm^2 UW, 2.724-μg/cm^2 ± 2.424-μg/cm^2 DW) (Figure 4). I demonstrated significantly different mean chlorophyll-*a* values

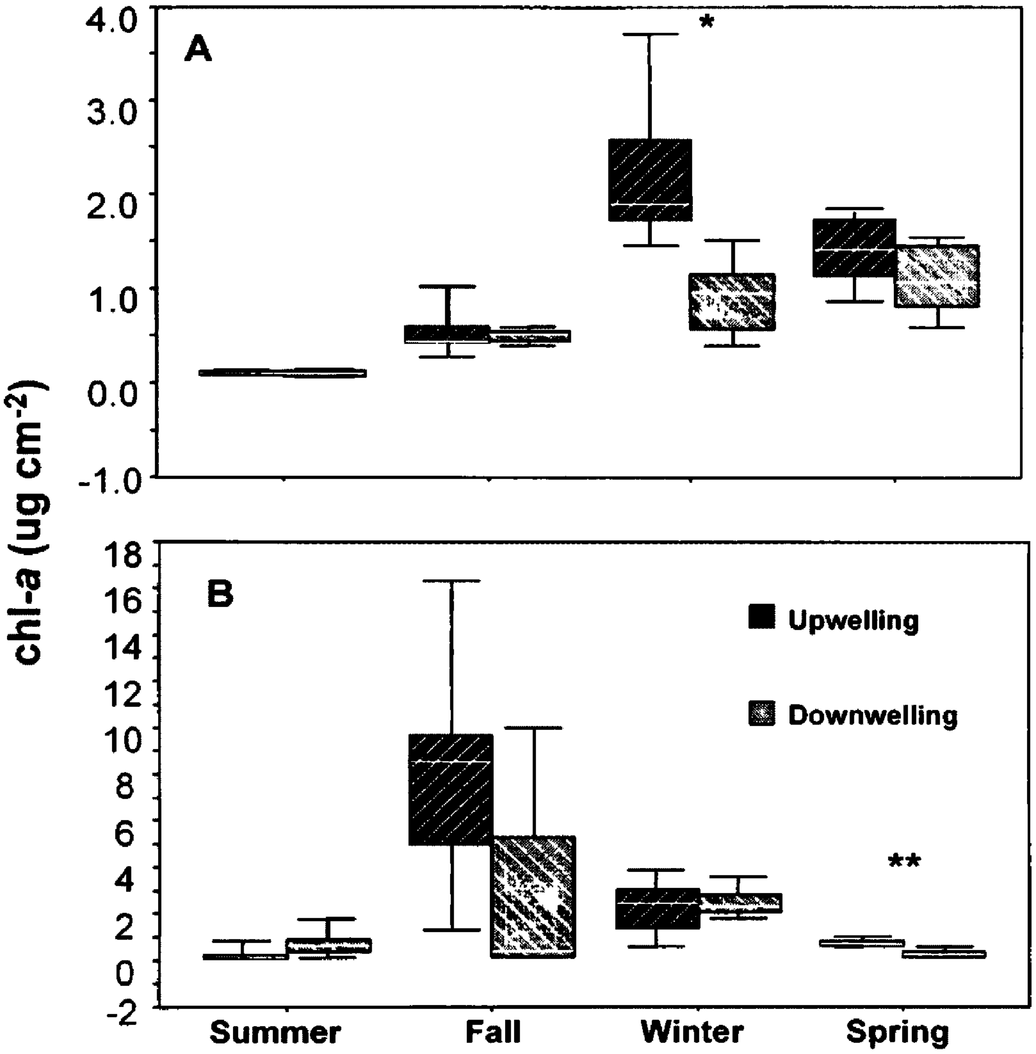

Figure 4: Seasonal distribution of chl-*a* at Moose Country (A) and Nyack (B) sites. Boxes represent the interquartile range of values measured at that date, whiskers indicate minimum and maximum values. * = $p < 0.05$, ** = $p < 0.01$.

in the spring samples only ($p = 0.008$). However, like at the Moose Country sites, maximum chlorophyll-*a* concentrations were always measured in samples collected from the upwelling zone. The average range of chlorophyll-*a* values was approximately 85% larger in samples taken from the upwelling zone when compared with those collected from the downwelling zone.

Benthic Macroinvertebrates

Moose Country Univariate Analyses

Univariate analyses on community-level measurements of macroinvertebrate abundance did not demonstrate differences between floodplain-scale zones of upwelling and downwelling zones in the main channel riffle habitats that I sampled. Community structure and composition varied seasonally, reflecting the variety of life history strategies evolved by aquatic macroinvertebrates. However, there were no differences ($p > 0.10$ in all seasons) in mean total EPT density or biomass between upwelling and downwelling habitats within any season. I measured maximum mean annual density in the spring and minimum mean annual density in the fall. Densities ranged from1178-individuals/m^2 to 6357-individuals/m^2 in the upwelling zone and 2876-individuals/m^2 to 3982-individuals/m^2 in the downwelling zone. Biomass measurements reflected this same seasonal pattern with values ranging from 1.09-g/m^2 to 13.82-g/m^2 in the upwelling zone and 1.01-g/m^2 to 16.52-g/m^2 in the downwelling zone. Variation in seasonal abundance and biomass was comparable between habitat types and never exceeded 32% of the mean value.

A statistical analysis of functional feeding group composition showed no significant differences between upwelling and downwelling habitats ($p > 0.10$ in all seasons). The collector-gatherer FFG dominated all samples, comprising an average of 45% of the upwelling zone community and 40% of the downwelling zone community in all seasons. The predator and collector-filterer FFGs contributed few individuals to either habitat type and did not show any temporal trends. In every season, filter feeders and predators each comprised an average of 3% to 5% of the community. The scraper/grazer FFG achieved its maximum relative abundance in the winter samples, contributing 59% of the total individuals to the upwelling zone and 46% to the downwelling zone. In all other seasons, scraper/grazers comprised approximately 15% to 20% of the community. Shredder relative abundance reached a spring maximum in the upwelling zone (37%) and a fall maximum in the downwelling zone (40%). In all other seasons, shredder abundance was variable and comprised between 1% and 19% of the community on average. Variation in seasonal FFG relative abundance often exceeded 100% of the mean value, resulting in nonsignificant differences between sites even when the mean values appeared widely separated.

I compared the mean individual size, mean individual biomass and total density of four common taxa from upwelling and downwelling sites. *Drunella doddsi* (Ephemeroptera: Ephemerellidae) and *Drunella coloradensis* (Ephemeroptera: Ephemerellidae) are ubiquitous generalist scraper/grazer/facultative predator mayflies. Both are univoltine and occur across a broad range of environments from headwaters to large river habitats (Edmunds *et al.* 1976).

D. coloradensis was sampled in high enough densities to be considered common in the summer samples only, when its size, measured as head capsule width, was approximately 1.75-mm ± 0.02-mm (mean ± 1 SE) at both sites. I calculated densities of 33-individuals/m^2 ± 12-individuals/m^2 in the upwelling zone samples and 25-

individuals/m^2 ± 8-individuals/m^2 in the downwelling zone samples. Mean individual biomass was likewise similar between upwelling (0.35-g/ind. ± 0.09-g/ind.) and downwelling (0.36-g/ind ± 0.12-g/ind.) zones.

D. doddsi was common in all samples and showed a distinct temporal trend in size, measured as head capsule width. I collected the largest individuals (3-mm ± 0.036-mm) in the summer samples and the smallest (1.7-mm ± 0.04-mm) in the winter samples. Both fall and spring samples contained individuals of approximately the same size at both sites (2.5-mm ± 0.025-mm). Patterns in mean individual biomass, total abundance and total biomass reflected the pattern evident in size. Although there were no differences within any season, all measured parameters attained their highest values in the summer samples and their lowest in the winter.

Arctopsyche grandis (Trichoptera: Hydropsychidae) is a generalist filter feeding caddisfly common to northwestern Montana rivers. *A. grandis* is abundant in riffles of 4th and 5th order rivers in this region (Hauer and Stanford 1981). Its distributional patterns have been linked to catchment-scale patterns in water temperature (Lowe and Hauer 1999). *A. grandis* is semivoltine, requiring two years to complete its life cycle. Adults emerge during June and July. I first collected *A. grandis* in the fall samples at densities of approximately 60-individuals/m^2. Subsequent samples contained *A. grandis* at the same approximate densities and no between-site differences in either individual size ($p = 0.537$) or biomass ($p = 0.550$) were demonstrated on any sampling date.

Glossosoma sp. (Trichoptera: Glossosomatidae) is a specialist grazer caddisfly. Approximately 25 species have been described in North America and all but three species are restricted to Western mountain regions (Wiggins 1977). In northwest Montana, *Glossosoma alascense* feeds exclusively on live periphyton material (Hauer 1980) and always occurs on the surfaces of cobbles. *Glossosoma alascense* is univoltine; adults emerge from June through August (Hauer 1980). I collected *Glossosoma* in all seasons but only considered it abundant in the fall samples, where I calculated densities of 30-individuals/m^2 to 35-individuals/m^2 (Figure 5). Although there was no significant difference between upwelling and downwelling *Glossosoma* density, individuals living in the upwelling zone were significantly larger with respect to both mean interocular distance ($p < 0.0005$) and mean individual biomass ($p = 0.05$, Figure 6). *Glossosoma* total biomass was also larger in upwelling zones, reflecting the larger individual size ($p = 0.05$, Figure 5).

Moose Country Multivariate Analyses

Mantel test results indicated that between-site differences in species composition were significantly associated with chlorophyll-*a* and VHG in all seasons except for spring (Table 2). The strongest associations were calculated for the fall samples ($r = 0.374$, $p = 0.005$ and $p = 0.006$) although associations in the winter samples were also highly significant ($r = 0.201$, $p = 0.026$ and $p = 0.035$) (Table 2). The chlorophyll-*a* association strength could not be assessed for the summer samples due to similar mean chlorophyll-*a* concentrations of 0.102-µg/cm^2 at the upwelling and downwelling sites (Table 2). Differences in spring macroinvertebrate samples were marginally correlated with chlorophyll-*a* ($r = 0.068$, $p = 0.121$) and VHG ($r = 0.068$, $p = 0.130$), but this association was not statistically significant (Table 2).

Multi-response permutation probability analysis of the Moose Country data demonstrated strong differences between macroinvertebrate assemblage composition and structure in upwelling versus downwelling sites in all seasons (Table 3). The differences

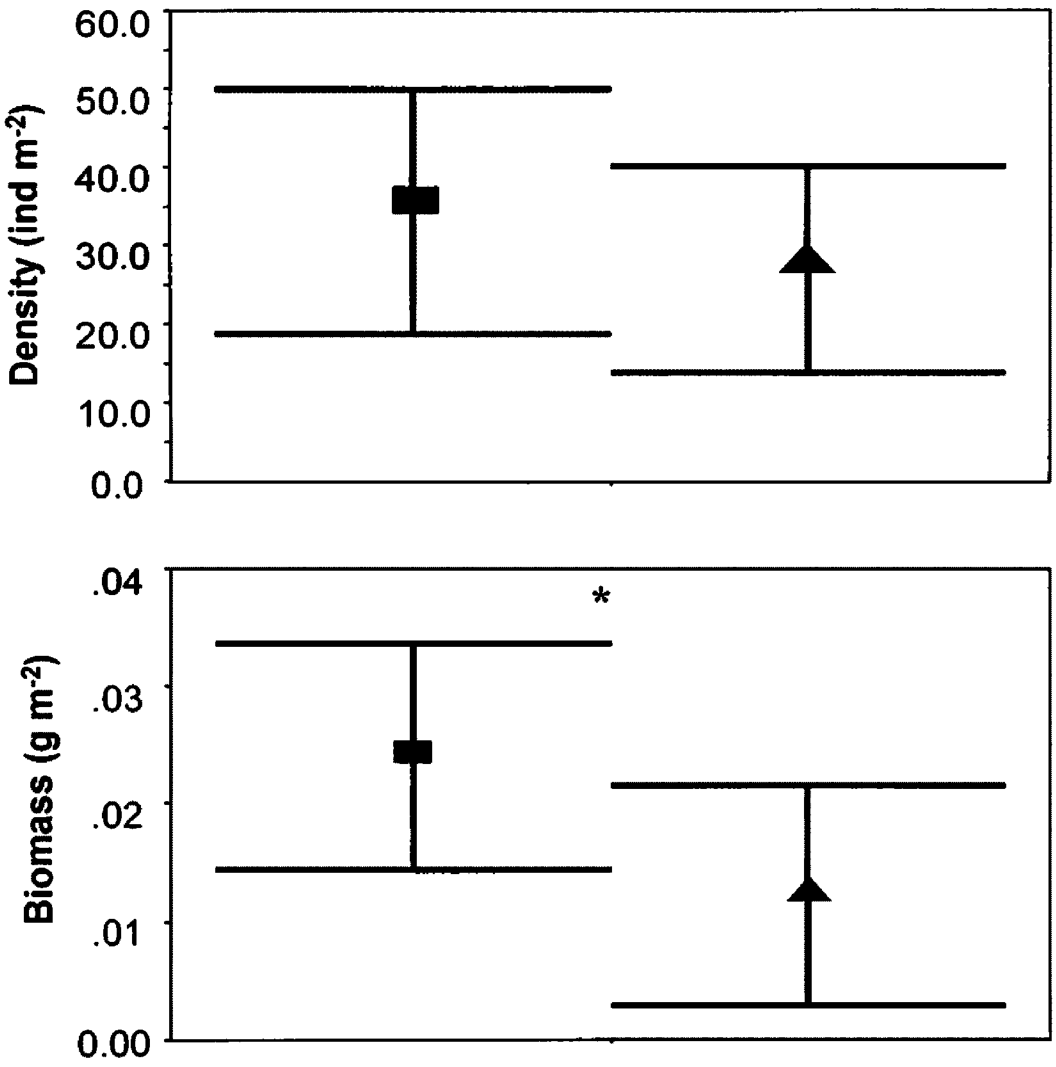

Figure 5: *Glossosoma* density and biomass at Moose Country sites on the fall 1999 collection date. Error bars represent 95% confidence intervals on the means. * = $p < 0.05$. Closed squares represent the upwelling zone, closed triangles represent the downwelling zone

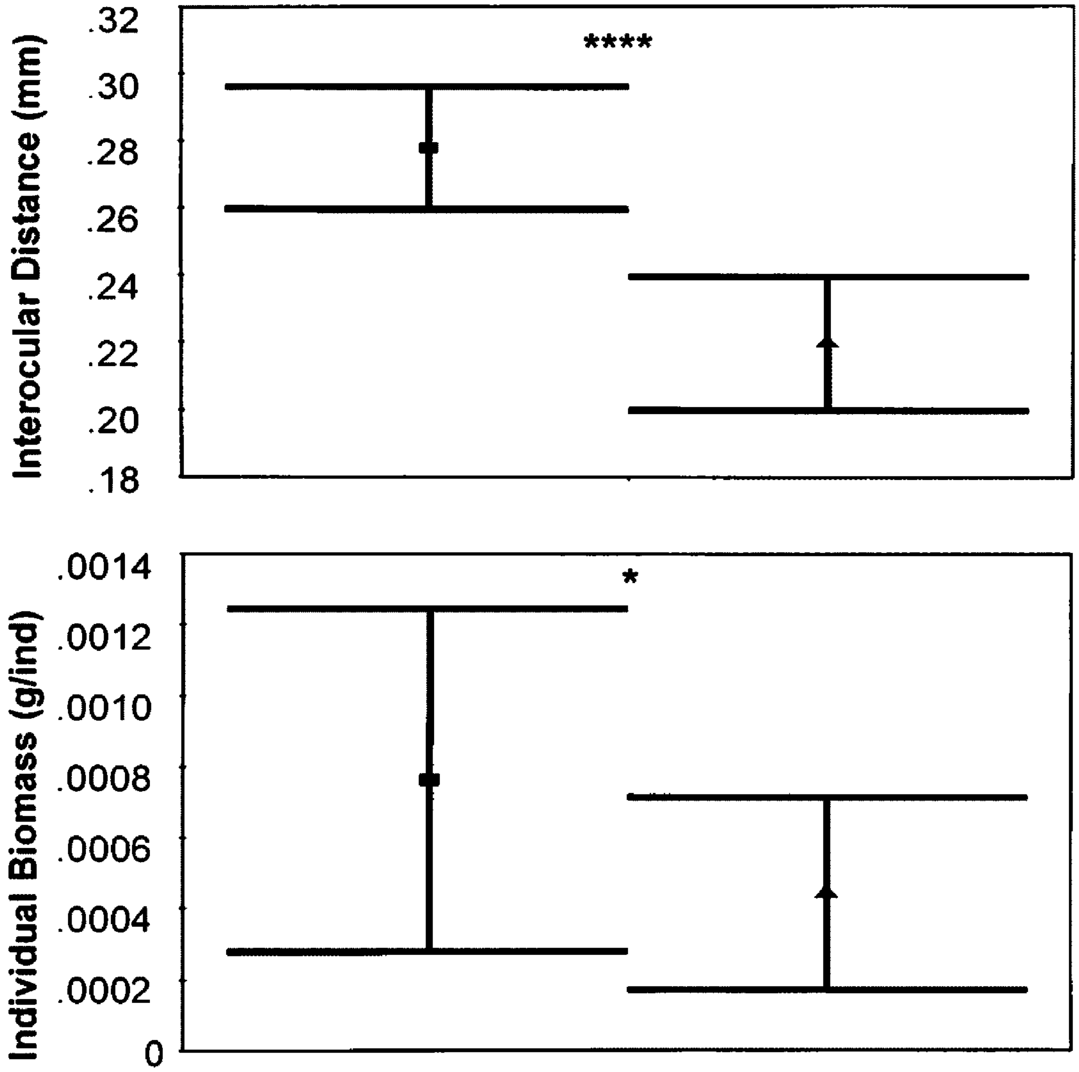

Figure 6: *Glossosoma* individual size and biomass at Moose Country sites on the fall 1999 collection date. Error bars represent 95% confidence intervals on the means. * = $p < 0.05$, **** = $p < 0.0005$ Closed squares represent upwelling zones, closed triangles represent downwelling zones.

Table 2. Mantel test of association among assemblage structure and environmental variables between riffles located in UW zones and riffles located in DW zones on two alluvial flood plains. Monte Carlo randomization procedures with 2000 iterations were employed to obtain p-values.

		Moose Country		Nyack	
Season	Variable	r	p-value	r	p-value
Summer	chl-*a*	†	†	.25030	0.1835
	VHG	.37641	0.0965	.25030	0.1840
Fall	chl-*a*	.37415	0.0055	.36030	0.0015
	VHG		0.0060		0.0030
Winter	chl-*a*	.20069	0.0255	.43424	0.0100
	VHG		0.0345		0.0115
Spring	chl-*a*	.06799	0.1205	.44017	0.0020
	VHG		0.1300		0.0025

† Mean chlorophyll-*a* concentrations were identical at upwelling and downwelling Moose Country sites on the Summer 1999 collection date.

were highly significant in the summer, fall and winter samples and marginally significant in the spring (Table 3). I found the greatest difference between sites in the fall samples (R-statistic = 0.115, p = 0.004) and the smallest in the spring (R-statistic = 0.036, p = 0.094) (Table 3).

Seasonal Indicator Species Analysis of upwelling and downwelling Moose Country sites allowed me to define two general categories of indicator species (Table 4). Species membership in any given category varied, but each general category of indicator operated identically across every season except for summer, when I was unable to demonstrate any significant habitat indicators (Table 4). Obligate scraper/grazers and taxa with hyporheic habitat affinities were always indicators of upwelling zones regardless of season (e.g., *Glossosoma* (Trichoptera: Glossosomatidae), *Paraperla frontalis* (Plecoptera: Chloroperlidae) and Capniidae spp. (Insecta: Plecoptera)). Generalist feeders, on the other hand, were indicators of either upwelling or downwelling in every season (e.g., *Zapada* spp. (Plecoptera: Nemouridae), *Drunella doddsi* (Ephemeroptera: Ephemerellidae), *Rhithrogena robusta* (Ephemeroptera: Heptageniidae) (Table 4, Figure 7).

Nyack Univariate Analyses

Similar to the Moose Country sites, univariate analyses on community level abundance measurements were unable to demonstrate differences between large-scale upwelling and downwelling zones in the main channel riffle habitats sampled. As expected, community composition and structure varied seasonally but there were no significant differences in mean total EPT density or biomass between samples collected in upwelling versus downwelling zones in any given season ($p > 0.10$ in all seasons). Samples taken from the Nyack sites showed the same temporal patterns in density and

Table 3. MRPP analysis on differences between macroinvertebrate communities associated with upwelling zones and those associated with downwelling zones. Positive values of R indicate more within-habitat homogeneity than expected and, hence, differences between upwelling and downwelling habitats. Monte Carlo procedures with 2000 iterations generated the reported p-values.

	Nyack		Moose Country	
Season	R-statistic	p-value	R-statistic	p-value
Summer	0.087	0.084	0.100	0.051
Fall	0.100	0.002	0.115	0.004
Winter	0.101	.0004	0.065	0.021
Spring	0.117	0.002	0.036	0.094

Table 4. Macroinvertebrate taxa indicative of upwelling or downwelling habitat types at Moose Country and Nyack flood plains. Monte Carlo randomization procedures with 2000 iterations were used to calculate significance of each taxon's indicator value. GF denotes generalist feeder taxa, HHA denotes taxa with hyporheic habitat affinities, OS/G denotes obligate scraper/grazer taxa.

		Nyack		
Season	Site Indicated	Taxon	Group	Sig.
Fall	UW	*Rhithrogena* spp	GF	0.052
	UW	*Pteronarcella badia*	GF	0.003
	UW	*Glossosoma* sp	OS/G	0.066
	UW	*Arctopsyche grandis*	GF	0.012
	DW	*Isogenoides colubrinus*	GF	0.003
Winter	UW	*Drunella doddsi*	GF	0.012
	UW	*Taenionema* sp	GF	0.024
	UW	*Paraperla frontalis*	HHA	0.012
	UW	*Glossosoma* sp	OS/G	0.008
	DW	*Rhithrogena robusta*	GF	0.003
	DW	*Baetis* spp	GF	0.012
	DW	*Hydropsyche cockerelli*	GF	0.035
Spring	UW	*Ephemerellidae*	GF	0.023
	UW	*Capniidae*	HHA	0.006
	UW	*Paraperla frontalis*	HHA	0.003
	UW	*Glossosoma* sp	OS/G	0.005
	DW	*Ephemerella inermis*	GF	0.016
	DW	*Rhithrogena robusta*	GF	0.042
	DW	*Paraleptophlebia* sp	GF	0.034
	DW	*Arctopsyche grandis*	GF	0.004
		Moose Country		
Fall	UW	*Epeorus grandis*	GF	0.047
	UW	*Zapada cinctipes*	GF	0.038
	UW	*Zapada columbiana*	GF	0.008
	UW	*Paraperla frontalis*	HHA	0.024
	UW	*Glossosoma* sp	OS/G	0.055
Winter	UW	*Ephemerellidae*	GF	0.027
	UW	*Capniidae*	HHA	0.056
	DW	*Rhithrogena robusta*	GF	0.005
	DW	*Drunella doddsi*	GF	0.001
	DW	*Zapada oregonensis*	GF	0.037
Spring	UW	*Leuctridae*	GF	0.045
	UW	*Prostoia besametsa*	GF	0.002
	UW	*Paraperla frontalis*	HHA	0.015
	DW	*Drunella doddsi*	GF	0.062

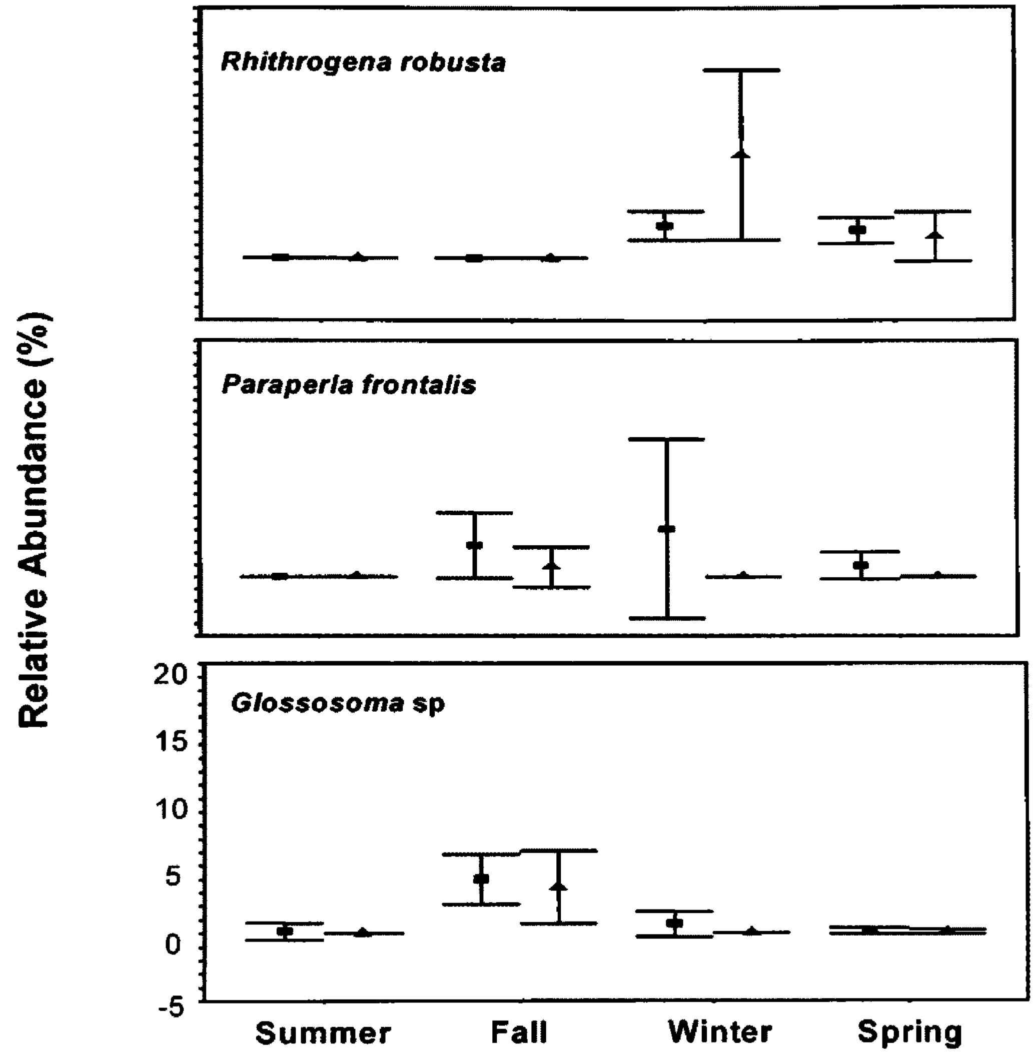

Figure 7: Seasonal relative abundance of representative indicator species at Moose Country sites from Table 4. Error bars are 95% confidence intervals on the means. Closed squares represent upwelling zones, closed triangles represent downwelling zones.

biomass as the Moose Country samples but contained more individuals. Annual maximum mean total density and biomass, measured in the spring samples, were not significantly different (5083-ind/m^2 and 16.09-g/m^2 UW; 5230-ind/m^2 and 22.29-g/m^2 DW) nor were the minima, which were measured in the summer samples (1560-ind/m^2 and 4.33-g/m^2 UW; 1677-ind/m^2 and 2.47-g/m^2 DW). Variation about the mean values was similar between sites and among seasons and never exceeded 35% of the mean.

Results of analyses performed on aggregated functional feeding group data did not demonstrate any differences within any season between the relative abundance of FFGs in main channel upwelling versus downwelling zones ($p > 0.10$ in all seasons). Patterns in the relative abundance of the five FFGs were identical to those seen at the Moose Country sites, with the exception of the collector-filterer group, which occurred in higher densities in the Nyack samples. Collector-gatherer organisms dominated the community in all seasons, comprising an average of 44% of the community sampled in upwelling zone and 41% of the community sampled in the downwelling zone. The relative abundances of predators (6%) and shredders (16%) were stable across the period sampled. Scrapers comprised approximately 25% of the summer, winter and spring community but only 9% of the fall community. The collector-filterer FFG was virtually unrepresented in the summer samples, comprising only 0.3% of the community, but by the fall collection date its relative abundance had grown to 25%. A seasonal decrease in collector-filterer relative abundance was seen in the winter (15%) and spring (11%) samples. As was the case with the Moose Country data, the variation associated with FFG mean relative abundance at the Nyack sites was often close to 100% of the mean.

I compared the mean individual size, mean individual biomass, mean sample density and mean sample biomass of four taxa common to the upwelling and downwelling Nyack sites. *D. doddsi* was common in fall, winter and spring samples and temporal trends were evident. While not common in the summer samples, *D. doddsi* was present in large enough numbers to allow us to estimate individual size for that season. Nyack samples showed the same general pattern in head capsule width as the Moose Country samples; *D. doddsi* individuals were largest on the summer and smallest on the winter collection date. Mean individual biomass peaked in winter for the upwelling zone (4.39-g/m^2) and in spring for the downwelling zone (2.73-g/m^2). I measured maximum abundance in the winter upwelling samples (385-ind/m^2) and the fall downwelling samples (195-ind/m^2). Like at the Moose Country sites, although head capsule width, individual mass, total abundance and individual biomass showed strong temporal trends, there was no evidence of a within-season site effect with respect to any of these characteristics.

Arctopsyche grandis was common at both Nyack sites. I first collected *A. grandis* on the fall sampling date. Samples taken from upwelling sites in this season contained significantly higher densities of *A. grandis* than downwelling samples (664-ind/m^2 ± 256-ind/m^2 *vs.* 145-ind/m^2 ± 56-ind/m^2). Fall total biomass was similarly higher in upwelling samples. Winter and spring samples contained *A. grandis* at similar densities (100-ind/m^2 to 150-ind/m^2) and no differences in either individual size or biomass was demonstrated for any sampling date ($p > 0.10$ in all seasons).

Pteronarcella badia (Plecoptera: Pteronarcyidae) is a generalist, detritus shredding stonefly indigenous to the Middle Fork Flathead River (Stanford 1975). Intensive studies of *P. badia* life history and ecology conducted by Stanford (1975) indicated a feeding preference for allochthonous leaf litter. *P. badia* is univoltine in northwestern Montana; adults emerge from the river's edge in June (Stanford 1975). I collected *P. badia* from my upwelling and downwelling sites on the Nyack flood plain in every season (Figures 8 and 9).

Interactions between *P. badia* populations and hyporheic exchange on the Nyack flood plain were complex. I did not see any temporal trends in total abundance or total biomass. These values remained relatively constant within a habitat type across seasons, ranging from 75-ind/m^2 to 150-ind/m^2 in the upwelling zone and 12-ind/m^2 to 57-ind/m^2 in the downwelling zone (Figure 8). Samples taken from upwelling sites always contained a significantly larger number of organisms than those taken from downwelling sites ($p < 0.05$ in all seasons) and were more variable with respect to total *P. badia* density (Figure 8). However, there were never any differences in total sample biomass between upwelling and downwelling zones (Figure 8).

Within each season, the riffle located in the downwelling zone tended to support larger individuals than the similar riffle in the upwelling zone (Figure 9). The differences in mean individual size were not significant in the summer or fall samples, but downwelling sites supported significantly larger *P. badia* individuals on the winter ($p = 0.001$) and spring ($p = 0.011$) collection dates. Mean individual biomass data reflected this general pattern of larger individuals in the downwelling site. However, individual biomass was significantly higher ($p < 0.10$) in the downwelling *P. badia* samples in every season (Figure 9).

Nyack Multivariate Analyses

Mantel test results indicated that differences in species composition between sites on the Nyack flood plain were significantly associated with VHG and chlorophyll-*a* in all seasons except for summer (Table 2). Strongest associations were calculated for the

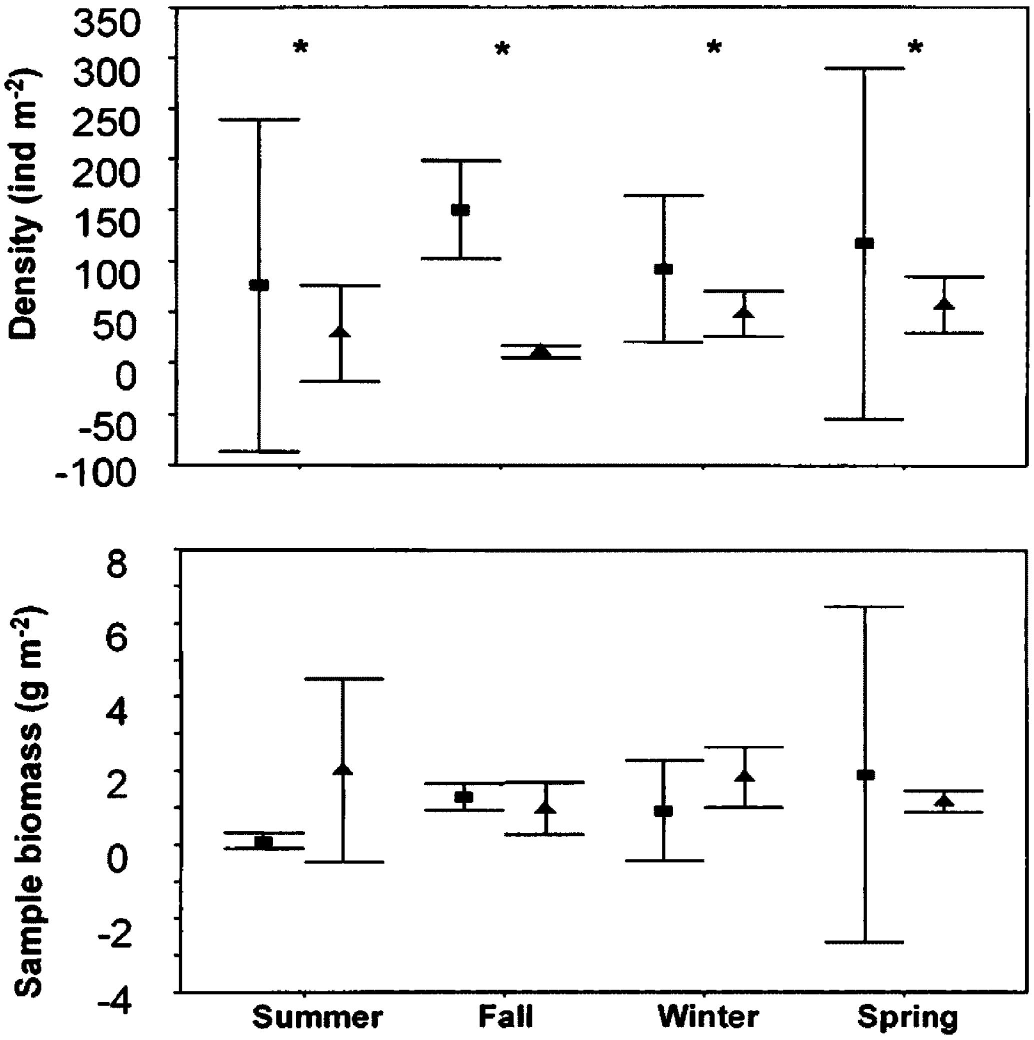

Figure 8: Seasonal *Pteronarcella badia* density and biomass at Nyack sites. Error bars represent 95% confidence intervals on the means. * = $p < 0.05$. Closed squares represent upwelling zones, closed triangles represent downwelling zones.

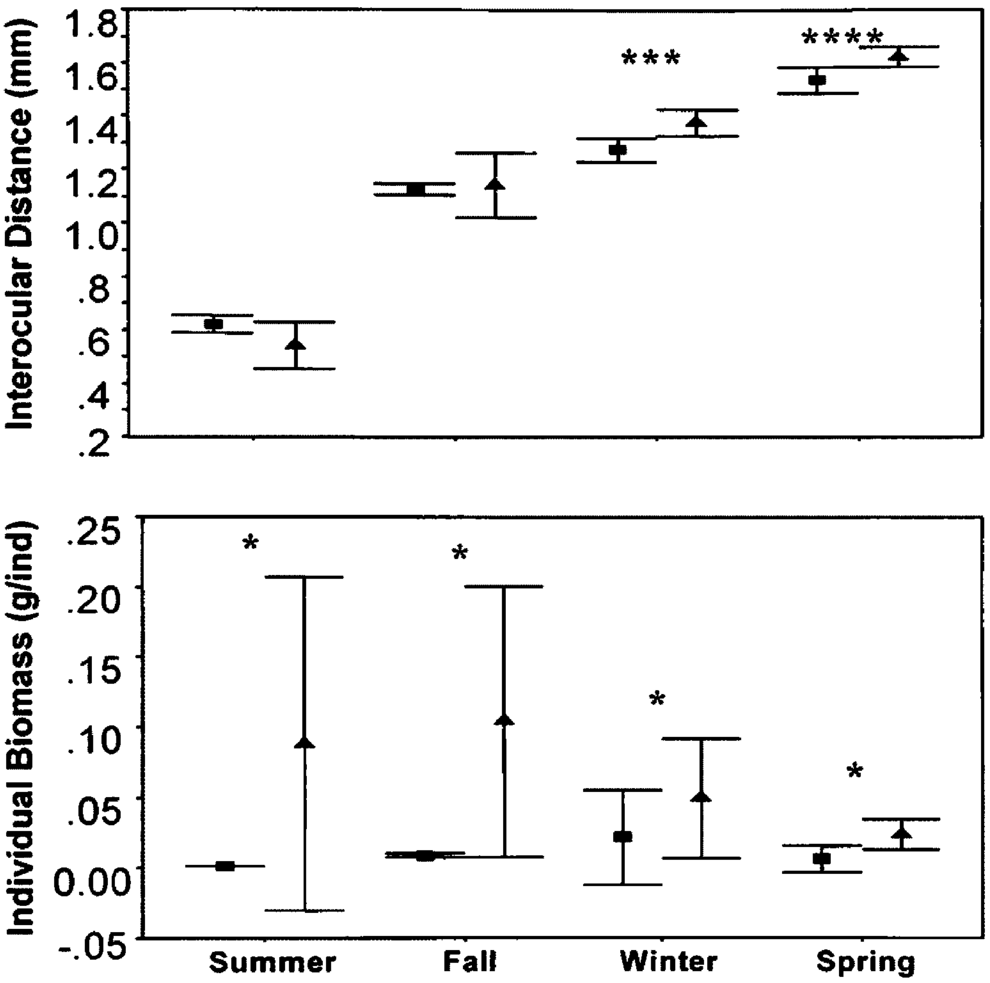

Figure 9: *Pteronarcella badia* mean individual size and biomass at Nyack sites on all collection dates. Error bars are 95% confidence intervals on the means. * = $p < 0.10$, ** = $p < 0.05$, *** = $p < 0.01$, **** = $p < 0.001$. Closed squares represent upwelling zones, closed triangles represent downwelling zones.

spring samples (r = 0.441, p = 0.003 and p = 0.002), although associations in the winter (r = 0.434, p = 0.012 and p = 0.010) and fall (r = 0.360, p = 0.003 and p = 0.002) were also highly significant (Table 2).

Multi-response permutation probability analysis on the Nyack sites suggested that strong differences existed between macroinvertebrate community composition and structure in upwelling versus downwelling sites in all seasons (Table 3). The differences were highly significant in the fall, winter and spring samples and marginally significant in the summer (Table 3). I found the greatest difference between upwelling and downwelling Nyack sites in the spring samples (R-statistic = 0.117, p = 0.002). Species composition and structure were most similar in upwelling and downwelling zones in the summer (R-statistic = 0.087, p = 0.084) (Table 3).

Seasonal Indicator Species Analysis on upwelling and downwelling Nyack sites resulted in the identification of the same two general categories of indicator species as at the Moose Country sites (Table 4). Similarly, species membership in any one category varied, but each general category of indicator operated identically across every season except for summer, when I was unable to demonstrate any significant habitat indicators (Table 4). Obligate scraper/grazers and taxa with hyporheic habitat affinities were always indicators of upwelling regardless of season, while generalist feeders indicated both upwelling and downwelling in every season (Table 4, Figure 10).

Discussion

I anticipated three distinct responses to contrasting groundwater-surface water exchange within similar riffles on alluvial flood plains. The predictions were based on previous research conducted in similar systems and included a periphyton response (*sensu*

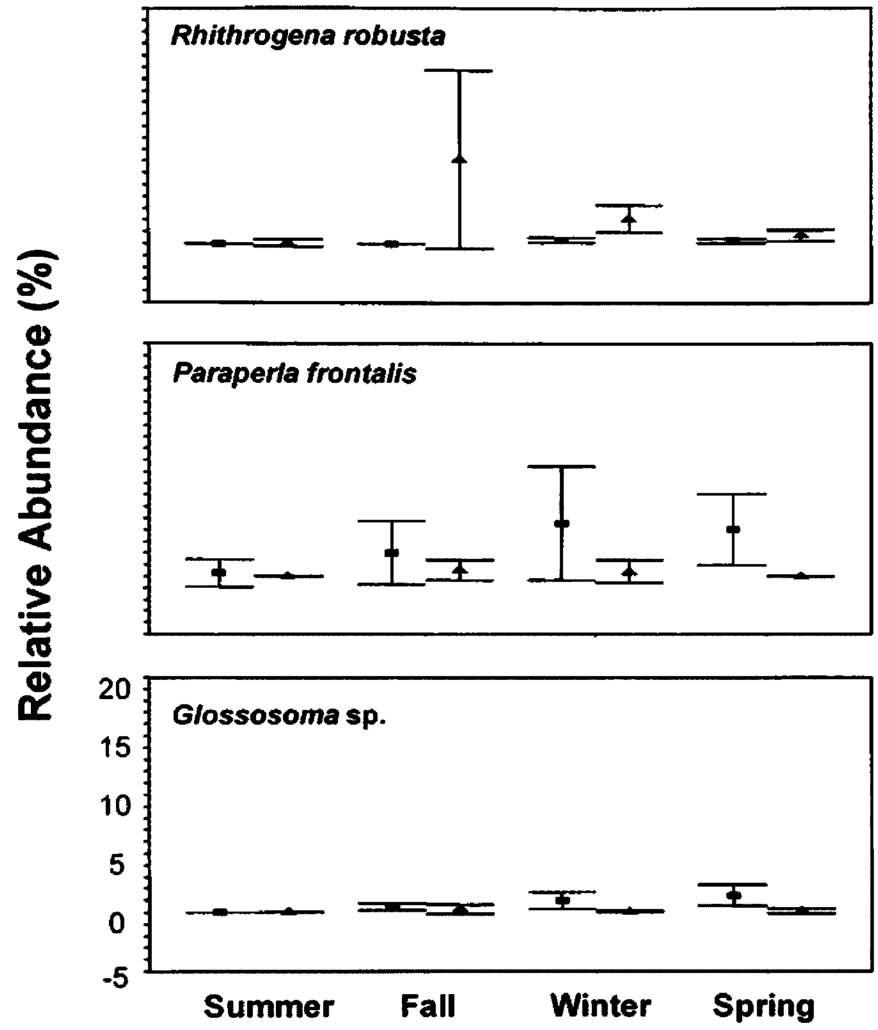

Figure 10: Seasonal relative abundance of representative indicator species at Nyack sites from Table 4. Error bars are 95% confidence intervals on the means. Closed squares represent upwelling zones, closed triangles represent downwelling zones.

Bansak 1998), a community-level macroinvertebrate response (*sensu* Case 1995) and an organism-level macroinvertebrate response to hyporheic discharge (as suggested by Stanford *et al.* 1994, Cavallo 1997, Baxter and Hauer 2000) in upwelling zones. Furthermore, I predicted that these responses would not be restricted to a single flood plain but would occur across scales of floodplain area and river size as suggested by Stanford and Ward (1993).

Habitat Variables and VHG

My results indicated that despite large between-floodplain differences reflecting differences in river size and catchment area, there were no within-floodplain differences in seston concentrations, current velocities or substrate grain sizes between riffles on either of the flood plains I studied. I anticipated this, and in fact attempted to control for differences in these variables with the stratified sampling design. However, the magnitude and variability of groundwater - surface water exchange varied both between and within flood plains.

Although the relative difference in VHG between upwelling and downwelling sites was greater at Nyack (DW ≈ 100 X UW) than at Moose Country (DW ≈ 12 X UW), a pattern of strong uniform downwelling and weak variable upwelling on both flood plains emerged (Table 1, Figure 3). These patterns in groundwater-surface water exchange were not surprising when viewed in the context of hydrogeomorphically complex floodplain ecosystems.

Surface water interacts dynamically with floodplain geomorphology in three spatial dimensions. The strongest interaction occurs in the vertical dimension at the geomorphically, well-defined upper floodplain knickpoint. At this location, strong, uniform, floodplain-scale downwelling occurs as a function of the change in slope associated with the transition from confined to alluvial segment type and the depressed piezometric gradient of the floodplain gravels. Upwelling, on the other hand, occurs across the entire area of the flood plain as hyporheic groundwater discharges to the surface at multiple locations downslope from the upper knickpoint (Stanford and Ward 1993, Stanford *et al.* unpublished). Upwelling hyporheic water contributes directly to the formation and maintenance of a complex mosaic of floodplain habitats by forming lotic and lentic water bodies and influencing the production of floodplain vegetation. Springbrooks and wetlands account for an unknown, but expectedly large, proportion of the total aquifer discharge and are formed on lateral floodplain surfaces when high volume interstitial flow-paths with high hydraulic conductivities (saturated paleochannels) intersect the surface.

However, a portion of the aquifer is discharged directly into the main river channel near the lower end of the flood plain as the encroaching downslope confined segment causes an elevation of the piezometric gradient. The unconsolidated alluvium surrounding the main channel in these upwelling zones contains poorly sorted sediments, probably as a legacy of past discharge events with variable magnitudes, temporally variable cut-and-fill alluviation and discrete channel avulsion events. Micro-scale heterogeneity in sediment conductivity causes non-uniform groundwater discharge within upwelling reaches (see Darcy's Law in Methods section), resulting in a highly variable distribution of VHG measurements. This is clearly illustrated in Figure 3. Moreover, since Stanford *et al.* (1994) were unable to demonstrate any significant phreatic sources for the Nyack aquifer, it is likely that a significantly large proportion of the total aquifer discharge occurs in springbrooks, wetlands and ponds. Hence, the magnitude of upwelling is much smaller than the magnitude of downwelling in the main channel as a function of this difference between the total volume of water recharging the aquifer at the upper knickpoint and the total volume of water discharging into the main channel.

Although both of the study riffles in my designated upwelling zones were receiving significant groundwater discharge (i.e., significantly positive mean VHG), approximately 15% to 30% of the piezometers I installed in those riffles displayed negative VHG measurements. This was probably a function of spatial heterogeneity in the vertical dimension of the sediments and associated variation in the piezometric gradient downslope from the upper knickpoint. It is likely that some piezometers were intersecting regions of high hydraulic conductivity relative to the surrounding alluvium (subsurface interbars) or discrete locations where clasts with diameters much greater than the surrounding alluvium were buried; at these locations advection of the surface water or high velocity interstitial flow was recharging these flow pathways (*sensu* White 1990, see Baxter 1997 for similar results). This highly variable discharge of hyporheic water explains the spatially variable periphyton response evident in the upwelling zones of both flood plains and will be discussed in more detail below.

Periphyton

Periphyton standing stock biomass responded to upwelling as anticipated; upwelling zones supported higher levels of primary production than downwelling zones. Although I was only able to demonstrate significant differences in mean chlorophyll-*a* concentrations on one collection date at each flood plain, maximum values were always obtained from particles collected in upwelling zones. Furthermore, algal standing stock biomass was more variable in upwelling zones with ranges approximately 80% larger than those measured in downwelling zones.

This pattern suggested that the distribution of periphyton was spatially heterogeneous (patchy) in upwelling zones. Field observations confirmed this conclusion; in upwelling zones some clasts were covered with visibly abundant periphyton and others appeared almost bare, while in downwelling zones there were no visibly discernible periphyton accumulations on any streambottom cobbles.

Nitrogen and phosphorous enrichment in hyporheic water has been demonstrated in a wide variety of locations and across spatial scales ranging from gravel bars to river segments (Ford and Naiman 1989, Triska *et al.* 1989, Valett *et al.* 1990, Stanford *et al.* 1994, Valett *et al.* 1994, Bansak 1998, Dahm *et al.* 1998, Dole-Olivier 1998, Ellis *et al.* 1998). In the Middle Fork, nitrogen and phosphorous are in significantly higher concentrations (up to 300% greater) in hyporheic water (see Stanford *et al.* 1994, Bansak 1998, Ellis *et al.* 1998).

It was this supply of limiting nutrients conferred from discharging hyporheic water that elicited the algal response in the generalized upwelling zones of both flood plains in every season (see Bansak 1998 for similar results), but the response was not uniform across the riffles due to the microhabitat patchiness evident in the distributions of VHG's in these upwelling zones. Instead, the algal response occurred at the scale of individual cobbles (microhabitat scale *sensu* Frissell *et al.* 1986), and not across the entire riffle (habitat scale *sensu* Frissell *et al.* 1986). As such, cobbles located near microhabitat-scale (10^{-1}m) localized upwelling zones within a riffle supported higher periphyton standing stock biomass than particles from other zones of the same riffle. It follows that those clasts that supported the maximum algal biomass on each date were sampled from patches within the generalized upwelling zone characterized by large positive VHG's.

Because of this hierarchical and patchy nature of upwelling – even within a single riffle - mean values may not be the most ecologically significant measurement of algal production in alluvial river-flood plain ecosystems. Maximum values that reflect the inherent spatial heterogeneity (patchiness) of upwelling may be more important because most obligate grazers (e.g., *Glossosoma*) identified in this research were mobile. Mobile grazers can move among resource patches utilizing those patches that contain the highest algal biomass. Hence, macroinvertebrate distributional patterns responded to a localized increase in primary production within riffles in generalized upwelling zones despite there being no demonstrable difference in mean values calculated across the entire riffle.

Benthic Macroinvertebrates

As with the physical variables, community-level measurements of macroinvertebrate density, biomass and species composition varied predictably between the two flood plains investigated in this study. Nyack sites supported macroinvertebrates at higher densities and biomass per m^2 of river bottom than Moose Country sites and distinct invertebrate taxa were present in different proportions on each flood plain (Figures 7 and 10). However, univariate statistical analyses of mean community-level measurements of macroinvertebrate density and biomass did not show significant differences between samples collected from upwelling zones compared with those collected from downwelling zones. On the surface, these results suggested that there was no macroinvertebrate response to variable groundwater-surface water exchange; i.e., the composition and structure of benthic macroinvertebrate assemblages vary with flood plain but not as a function of VHG within a flood plain.

However, the variance associated with the density and biomass measurements in this study was large (25% to > 100% of the mean) and was probably a function of the inherent spatial heterogeneity of riffle habitats in spite of the stratified sampling design. Downes *et al.* (1993) demonstrated how naturally existing spatial heterogeneity within similar riffle habitats could effectively mask any ecologically significant difference between sites due to the wide confidence limits associated with estimates of density or biomass. In a review of how the patch dynamic concept applies to lotic systems, Pringle *et al.* (1988) suggested that the scale at which much aquatic sampling is done might not be the scale at which the organisms of interest perceive their environment (i.e., 0.25 m^2 incorporates many cobbles, but benthic macroinvertebrates might respond to between-cobble differences).

Hence, randomly sampling a biophysically complex riffle, even with a stratified design, may capture too many microhabitat variants to be useful when attempting to uncover patterns in the distribution and abundance of macroinvertebrates due to the small-scale habitat selection behavior of many taxa (see Cudney and Wallace 1980, Hauer and Stanford 1981). This may be especially true when community-wide measurements of macroinvertebrate density are used as indices. I concluded that, given the highly variable nature of the macroinvertebrate data and the high degree of similarity between sites, multivariate analyses and investigations of species-specific responses would provide more insight into possible community differences than standard univariate statistical approaches. Analyses based on sample-level measurements of density or biomass should not be used when assessing complex and subtle ecological processes.

Indeed, although univariate statistics were unable to differentiate between upwelling and downwelling habitats, multivariate analyses (MRPP, Mantel tests and Indicator Species Analysis) on the macroinvertebrate assemblage data revealed highly significant differences between sites. These differences were significantly correlated with differences in VHG and chlorophyll-*a*. Furthermore, multivariate analyses suggested that these differences were driven by subtle species-specific responses to hyporheic groundwater discharge.

Species-specific responses identified by the multivariate analyses may be explained by two types of modifications to the physical habitat template resulting from the discharge of hyporheic groundwater to riffles in upwelling zones: (1) nutrient enriched hyporheic discharge in upwelling zones indirectly affected the specialist-herbivore component of the main channel macroinvertebrate community by subsidizing periphyton production, and (2) the presence of upwelling hyporheic flow-paths directly altered the species composition of macroinvertebrate assemblages with the addition of taxa with hyporheic habitat affinities.

Glossosoma

There was a species-specific response to upwelling-induced periphyton production demonstrated by *Glossosoma*. On the Nyack flood plain, *Glossosoma* sp. was a significant indicator of upwelling in every season, except summer, when communities were very similar. At the Moose Country sites *Glossosoma* indicated upwelling in the fall only; abundances were too low to be significantly indicative of any habitat type in any other season.

I attribute the differences in *Glossosoma* numbers between flood plains to differences in the availability and abundance of food. As an obligate grazer, *Glossosoma* relies exclusively on periphyton as a food resource (*cf.* Hauer 1980). While periphyton production was indeed higher in the upwelling zones at both flood plains, the absolute concentrations of chlorophyll-*a* were much higher at the Nyack sites, which could explain the higher numbers of *Glossosoma* at those sites in every season. On both flood plains, *Glossosoma* was collected almost exclusively from upwelling zones and in significantly greater relative abundances despite the small proportion of the community it represented. I believe the greater abundance of *Glossosoma* in upwelling zones was a function of increased periphyton production.

Glossosoma individuals were in high enough numbers to be considered common at the Moose Country sites on the fall collection date. At that time, organisms collected from upwelling zones were significantly larger compared to those taken from downwelling zones. However, there were no differences in total *Glossosoma* densities between sites. These results are similar to those reported from an experimental study on algal-grazer interactions (Hart and Robinson 1990) in which the individual size and densities of two grazing caddisflies were up to two times greater in enriched laboratory streams than in control streams. My results indicate a bioenergetic subsidy (*sensu* Hall *et al.* 1992) to *Glossosoma* indirectly conferred by groundwater discharge and mediated through periphyton primary production.

Pteronarcella badia

Another species-specific response was not attributable to upwelling-induced increases in periphyton production. *Pteronarcella badia* was common in all samples collected on the Nyack flood plain in every season. A pattern in *P. badia* abundance, size and individual mass emerged that was plainly different from the pattern exhibited by *Glossosoma*; upwelling zones supported larger numbers of smaller individuals than downwelling zones in every season. This was an unexpected result and did not support my hypothesis that upwelling zone populations would consistently be comprised of more and larger individuals. It was, however, a response to a change induced in the physical habitat by differential groundwater-surface water exchange. In particular, *P. badia*'s increased size in the downwelling zone was most likely the result of an excess in food at that site.

Although not explicitly measured in this study, field observations indicated more coarse leaf detritus entrained between cobbles in the downwelling zone of the Nyack flood plain. This difference in food availability could potentially provide *P. badia* communities inhabiting downwelling habitats with an energetic advantage over those inhabiting upwelling habitats. Alternatively, between-site size differences could have resulted from differences in the sex ratios of the respective populations. *P. badia* is strongly sexually dimorphic; females are larger than males (Stanford 1975). These explanations remain untested and certainly merit further investigation.

Paraperla frontalis and the Capniidae

A final type of species-specific response to upwelling was demonstrated by *Paraperla frontalis* (Plecoptera: Chloroperlidae) and members of the Plecopteran family Capniidae, taxa with known hyporheic habitat affinities. These taxa were rarely collected in my benthic samples. However, when present, they were highly significant indicators of upwelling. In fact, they were not present in samples taken from downwelling zones.

Both of these taxa spend their entire larval stages in the hyporheic zone, only returning to surface water habitats to emerge (Stanford and Ward 1988, Stanford *et al.* 1994). *P. frontalis* preferentially selects emergence locations in the main river channel, final instar nymphs and adults are rarely associated with springbrook habitats (Stanford *et al.* 1994, Case 1995). Adults of both taxa are commonly collected in streamside vegetation sweeps and pitfall traps. The exact mechanisms by which these taxa navigate through the alluvium back to the main river channel pre-emergence are unknown, but studies on the Kalispell flood plain of the mainstem Flathead River (Montana, U.S.A.) suggest that *P. frontalis* nymphs may follow temperature gradients to emergence locations (Stanford *et al.* 1994). The fact that I collected these amphibitic Plecopteran taxa almost exclusively from upwelling zones suggests that they follow hyporheic discharge flow-paths directly to upwelling reaches in the main river channel as opposed to moving up some sort of interstitial surface water gradient to emerge from downwelling reaches.

Conclusions

Segment-scale groundwater-surface water exchange patterns of rivers flowing through alluvial flood plains in northwest Montana occurred predictably across scales of flood plain area and river size. Strong, uniform downwelling was concentrated near the upper floodplain knickpoint. Upwelling occurred throughout the lower half of these flood plains but was variable due to interaction between segment-scale and habitat- or microhabitat-scale flow paths.

This segment-scale hyporheic exchange directly augmented primary productivity in upwelling zones of flood plains, regardless of their sizes. As a result, algal biomass was maximized in the upwelling zones of these flood plains. The algal response was likely attributable to an energetic subsidy gained by access to nutrient enriched hyporheic discharge in upwelling zones. Furthermore, periphyton appeared to respond to variable upwelling at the scale of individual cobbles and not across an entire riffle.

Benthic macroinvertebrates also responded to differences in groundwater-surface water exchange in the main channels of rivers flowing through these alluvial flood plains. As with the periphyton, the macroinvertebrate response was not isolated to a particular flood plain or river but occurred across scales of both floodplain area and river size. The response, while generalizable, was species-specific. Hence, univariate analyses of total densities and biomasses were unable to detect these differences. Ecologically-significant responses to complex and subtle environmental differences may have been hidden within habitat- or sample-scale data due to its inherently high variability. Therefore, conclusions drawn from univariate statistical analysis of these types of data would not have accurately reflected real differences.

Benthic macroinvertebrates responded to their environment in species-specific manners. Therefore, multivariate analyses performed on species by site dissimilarity matrices were able to isolate and demonstrate highly significant differences between upwelling and downwelling habitats. Species-specific differences were the result of changes in the physical habitat of upwelling zones induced both directly and indirectly by hyporheic groundwater discharge. Indirect obligate scraper/grazer responses to hyporheic discharge were mediated through increased periphyton production, while taxa with hyporheic habitat affinities responded directly to the presence of hyporheic discharge flow paths.

The results of this study underscore the functional importance of the hyporheic zone to alluvial river ecosystems. Exchange processes between ground water and surface water are important in providing physical-biological linkages in these systems. As such, the biological complexity that characterizes alluvial flood plains is inseparable from the physical complexity derived from the large-scale exchange between ground water and surface water.

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