

Benthic algal response to hyporheic-surface water exchange in an alluvial river

Kevin H. Wyatt · F. Richard Hauer · George F. Pessoney

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Abstract We studied the response of benthic algae to points of hyporheic-surface water exchange in the main channel of the Middle Fork Flathead River within the Nyack Flood Plain, Montana. We examined hyporheic exchange at 120 sites using piezometers and measuring vertical hydraulic gradient (VHG), hydraulic conductivity, and vertical discharge. We removed benthic algae from a single cobble at each site, and we used VHG to group sampling sites for statistical analysis. Algal cell density and chlorophyll *a* concentration were significantly higher at sites with hyporheic discharge (+VHG, upwelling) compared to both sites with hyporheic recharge (−VHG, downwelling) and sites with no hyporheic-surface water exchange (=VHG, neutral) (ANOVA, $P < 0.05$). The assemblages of algae at upwelling sites were also significantly

different from downwelling and neutral exchange sites (ANOSIM, $P < 0.05$). Filamentous green algae *Stigeoclonium* sp. and *Zygnema* sp. and a chrysophyte, *Hydrurus foetidus* (Villars) Trevisan were abundant at upwelling sites, whereas an assemblage of diatoms *Achnanthes minutissimum* (Kützing) Czarnecki, *Cymbella excisa* Kützing, *Diatoma moniliformis* Kützing, and *Gomphonema olivaceoides* Hustedt, were the most abundant taxa at downwelling and neutral exchange sites, occurring attached to, or in close association with the stalks of *Didymosphenia geminata* (Lyngbye) Schmidt. These data show that benthic algal communities are structured differently depending on the direction of hyporheic flux in the main channel of a large alluvial river, suggesting that hyporheic-surface exchange may influence the spatial distribution of main-channel benthic algae in rivers with hyporheic-surface water connectivity.

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K. H. Wyatt · G. F. Pessoney
Department of Biological Sciences, The University of
Southern Mississippi, Hattiesburg, MS 39406, USA

K. H. Wyatt · F. R. Hauer
Flathead Lake Biological Station, Division of Biological
Sciences, The University of Montana, Polson, MT 59860,
USA

K. H. Wyatt (✉)
Department of Zoology, Michigan State University,
East Lansing, MI 48824, USA
e-mail: wyattkev@msu.edu

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Introduction

Rivers have traditionally been viewed as two-dimensional systems, with connectivity, resource gradients, and material fluxes influenced by lateral interactions

along a longitudinal continuum (Webster & Patten, 1979; Vannote et al., 1980). The physical structure and spatial variability in riverine ecosystems are now understood across all three spatial (longitudinal, lateral, and vertical) and temporal dimensions (Ward, 1989, 1997; Stanford et al., 2005). With the hyporheic corridor concept, Stanford & Ward (1993) describe the importance of processes occurring within the hyporheic zone in maintaining environmental heterogeneity and biological diversity on the surface of alluvial flood plains.

The hyporheic zone, as defined by White (1993) includes saturated interstitial areas beneath the stream bed that contain some portion of channel water or that have been altered by channel water infiltration. This definition separates the hyporheic zone from ground waters that have not been influenced by channel processes (see Freeze & Cherry, 1979). Waters in the hyporheic zone have a complex set of physical (Amoros & Roux, 1988; Gilbert et al., 1990), chemical (Valett et al., 1990; Dahm et al., 1998), and biological variables (Stanford & Ward, 1988; Ward et al., 1998) that are different from surface waters.

In alluvial flood plains with porous substratum, rivers often follow a predictable pattern of vertical water movement between the hyporheic zone and surface flow (Stanford & Ward, 1993). At large spatial scales (i.e., entire flood plain-segment scale, *sensu* Frissell et al., 1986), hyporheic-surface water exchange is determined by the expansion and constriction of bedrock at the upstream and downstream ends of a flood plain, respectively. Negative pressure gradients resulting from porous gravel deposits allows surface water to move down into the hyporheic zone at the upstream region (i.e., downwelling) (Boulton, 1993). Hyporheic water flows parallel to the surface through interstitial pathways and discharges back onto the surface (i.e., upwelling) downstream, as the flood plain is confined by bedrock (Stanford & Ward, 1993). A portion of the hyporheic water is forced back into the main channel directly downstream in a general upwelling zone, while the remainder discharges onto lateral floodplain surfaces forming seasonal springbrooks, wetlands, and ponds (Brunke & Gonser, 1997; Stanford, 2006). At smaller spatial scales, hyporheic-surface water exchange is determined by localized geomorphic features such as pool-riffle sequences (Valett et al., 1994).

Much work has been done to explain the contrasting physiochemical and biotic conditions between hyporheic and lateral surface water in floodplain habitats (see review in Brunke & Gonser, 1997), but few studies have related the ecological significance of vertical connectivity and exchange on biological patterns in the main river channel (Boulton et al., 1998). Upwelling and downwelling zones at large spatial scales (i.e., upstream and downstream regions of a flood plain) are important in defining relationships between hyporheic exchange and biological patterns in the benthos of alluvial rivers (Baxter & Hauer, 2000). However, localized downwelling and upwelling sites (i.e., at the heads and tails of riffles) nested within large-scale zones of hyporheic exchange are important in refining these relationships.

Zones of hyporheic transport are thought to be responsible for the patchy distribution of algae in some rivers with hyporheic-surface water connectivity (Coleman & Dahm, 1990). Yet, few studies have evaluated main-channel benthic algae in response to hyporheic exchange at the fine spatial scale (i.e., cobble-scale) at which they respond to changes in benthic conditions (e.g., Henry & Fisher, 2003). Indices of hyporheic flux (i.e., vertical hydraulic gradient) are often averaged across points within a stratified study site (i.e., entire riffle) and mean algal biomass is calculated by pooling values of many cobbles within the site (Pepin & Hauer, 2002). Cobble-scale evaluations may more accurately reflect the level at which patchiness exists in upwelling zones because cobbles offer more spatial resolution. Given the importance of algae in biogeochemical cycling and primary production in rivers (Stevenson et al., 1996), understanding the response of benthic algae to hyporheic exchange is important in understanding the natural heterogeneity within riverine ecosystems (*sensu* Stanford et al., 2005).

We examined the response of benthic algae to hyporheic exchange in the main channel of the Middle Fork Flathead River within the (~10 km long) Nyack Flood Plain, Montana (Fig. 1). Based on known linkages between physical processes and biological patterns between surface and hyporheic habitats of the Middle Fork within the Nyack (Stanford et al., 1994; Case, 1995; Cavallo, 1997; Bansak, 1998; Ellis et al., 1998; Baxter & Hauer, 2000; Poole, 2000; Pepin & Hauer, 2002), we

hypothesized that main-channel sites of hyporheic upwelling support higher algal standing stock biomass with a different community composition than downwelling sites and sites without hyporheic-surface water exchange.

Methods

Study site

The Nyack Flood Plain ($\sim 30 \text{ km}^2$) is on the 5th-order Middle Fork of the Flathead River in north-western Montana (Fig. 1). The Middle Fork has a watershed area of about $3,000 \text{ km}^2$ and ranges in elevation from 1,000 to over 3,000 m asl. Riparian areas are dominated by various willows (*Salix* spp.), Englemann spruce (*Picea engelmanni* Parry ex Engelman), and black cottonwood (*Populus trichocarpa* Torrey and Gray) (Wondzell, 1992). Discharge

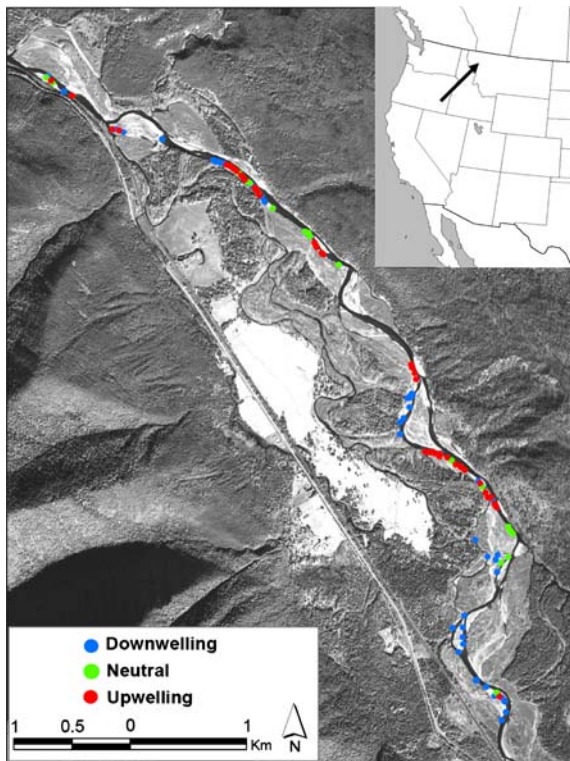


Fig. 1 Satellite image of the Nyack Flood Plain of the Middle Fork Flathead River, Montana USA. Symbols (○) show downwelling (blue), neutral (green), and upwelling (red) sites

on the Nyack is driven by a spring snowmelt event in May–June (June monthly average $284.87 \text{ m}^3 \text{ s}^{-1}$, Fig. 2), then decreasing thereafter, with a minimum monthly average of $19.85 \text{ m}^3 \text{ s}^{-1}$ in January (USGS gauge # 12358500 located 11 km downstream of the Nyack). The active channel follows a braided pattern with alternating riffle-pool sequences. Detailed land survey shows that the gradient is approximately 1.2 m km^{-1} over the length of the flood plain (FLBS, unpublished data). Alluvial fill of the flood plain consists of gravel and cobble deposits about 10 m thick, which overlie a layer of low permeable Tertiary clay (Stanford et al., 1994). The highly permeable surficial substratum material allows for large water volume interaction between hyporheic and surface waters, with the Middle Fork losing as much as 30% of its volume at baseflow to the hyporheic zone in the first two km of the flood plain (Stanford et al., 2005). Hyporheic water is highly aerobic and nitrogen and phosphorus are in higher concentrations than in water entering the flood plain from the main channel of the Middle Fork (Stanford et al., 1994; Bansak, 1998). Hyporheic water discharges onto lateral floodplain surfaces, forming spring brooks and ponds or follows long interstitial flow paths and returns directly to the main channel downstream as the flood plain is confined by bedrock (Stanford et al., 1994).

Sampling design

We selected sampling sites randomly by superimposing numbered gridlines onto a map of the Middle Fork within the Nyack Flood Plain. We then used a random numbers table to select points representing sampling reaches (200 m-long section of the main

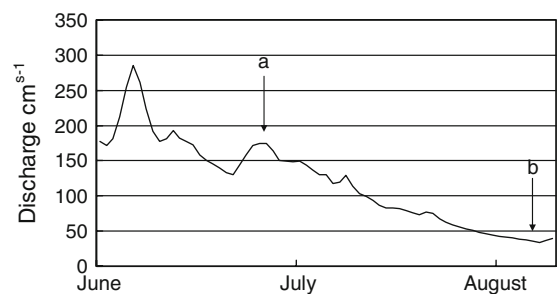


Fig. 2 Hydrograph of the Middle Fork (USGS gauge # 12358500 located 11 km downstream of the Nyack Flood Plain) and time line for study, beginning on June 25, 2004 (a) and ending on August 4, 2004 (b)

channel) along the numbered gridlines. We divided each reach into 10 evenly spaced transects extending across the channel or in a few cases transects were limited to the wadable shore. Along each transect, we established three sampling points of $\frac{1}{4}$, $\frac{1}{2}$, or $\frac{3}{4}$ width of wetted channel from the river bank. We collected one sample per transect at either the $\frac{1}{4}$, $\frac{1}{2}$, or $\frac{3}{4}$ position across the stream width, beginning with $\frac{1}{4}$ on transect 1, then $\frac{1}{2}$ at transect 2, and $\frac{3}{4}$ at transect 3, continuing for all transects at each reach. We continued this process for 41 days, sampling a total of 120 sites beginning on June 25 and ending on August 4 2004.

Measuring hyporheic-surface water exchange

We measured hyporheic-surface water exchange at each site by installing a piezometer into the sediments and calculating vertical hydraulic gradient (VHG), hydraulic conductivity (K , cm s^{-1}), and vertical discharge (Q , $\text{cm}^3 \text{s}^{-1}$). Each piezometer consisted of a 3 cm internal diameter metal pipe with 20 evenly spaced 7/10 cm holes over the bottom 16 cm of its length. We installed piezometers to depths of 28–57 cm, checked to make sure they were free of obstructions, and then we left each piezometer to equilibrate for ~ 15 min before calculating VHG using the equation described in Dahm et al. (2006):

$$\text{VHG} = \frac{h_s - h_p}{L} \quad (1)$$

where h_s represents the height of the top of the piezometer above stream surface; h_p , the height from the top of the piezometer to the water level inside the piezometer; and L , depth the piezometer was driven into sediments from the substratum surface (Baxter & Hauer, 2000). VHG is a unitless ratio that estimates pressure differentials between hyporheic and surface waters. VHG is a positive number in conditions of hyporheic discharge (+VHG, upwelling sites), negative in conditions of hyporheic recharge (–VHG, downwelling), and 0 where pressure differentials are equal and there is no hyporheic-surface water exchange (=VHG, neutral).

We measured hydraulic conductivity (K , cm s^{-1}) of the sediments for each piezometer using falling head tests (Fetter, 1994) and calculated using the modified Hvorslev (1951) equation described in Baxter et al. (2003) and Dahm et al. (2006):

$$K = \frac{(0.2501)(D)}{(d_t)} \left| \ln \frac{h_0}{h} \right| \quad (2)$$

where D is the inside diameter (cm) of the piezometer and d_t is the time it takes for the head level to drop from h_0 to h . We calculated water flux (Q , $\text{cm}^3 \text{s}^{-1}$) between hyporheic and surface waters as vertical discharge according to Darcy's equation:

$$Q = - (K)(A)(\text{VHG}) \quad (3)$$

where A is the cross-sectional area of the piezometer, and VHG and K were calculated from Eqs. 1 and 2, respectively (Fetter, 1994). We used VHG as an index of hyporheic flux and Q as the magnitude of vertical discharge at each site.

Sampling benthic algae

We used cobble-scale evaluations of benthic algae to reflect the spatial scale at which hyporheic-surface water interactions occur in the main channel. At each sampling site, we selected and removed a single cobble from the most immediate point downstream from where we inserted the piezometer into the sediments. We collected algae by removing a defined area (8 cm^2) from the top surface of each cobble with a toothbrush, and then we rinsed materials from the toothbrush into a labeled sample bottle (Steinman & Lamberti, 2006). We homogenized each sample in a 100 ml volume of water, and then preserved a 50 ml subsample in a 4% formaldehyde solution for community analysis (American Public Health Association, 1998). We filtered a separate 50 ml subsample of homogenate onto a glass fiber filter (Whatman type GF/F 47 mm diameter) for spectrophotometric chlorophyll a analysis following methanol extraction (Tett et al., 1975). We analyzed algae by counting at least 300 cells or colonies per sample in a Palmer-Maloney nanoplankton counter chamber and identified algae to the lowest taxonomic level possible at $400\times$ magnification following Prescott (1962), Bold & Wynne (1985), and Wehr & Sheath (2003). For diatom compositional analysis, we acid-cleaned an aliquot of each sample, and mounted cleaned diatoms to a microslide using NAPHRAX[®] mounting medium (Patrick & Reimer, 1966). We identified and enumerated diatom valves at $1,000\times$ magnification following Kramer & Lange-Bertalot (1986, 1988, 1991a, b) and Patrick & Reimer (1966, 1975). We

quantified benthic algal abundance as cells cm^{-2} of cobble substrate using the formula provided in Lowe & Laliberte (2006).

Data analysis

We used VHG as an indicator of hyporheic exchange to group sites into categories for statistical analysis. We constructed three groups consisting of a random sample of ($n = 49$) upwelling sites, ($n = 52$) downwelling sites, and ($n = 19$) neutral exchange sites, with the randomness of our sampling design reflected in the unequal number of sites pooled into each respective group (Fig. 3). Prior to analysis, we log-transformed K values, chlorophyll a measurements, and algal cell abundance data to meet statistical requirements of normality and homogeneity of variance.

We evaluated differences in K values, chlorophyll a measurements, and absolute cell abundance data among upwelling, downwelling, and neutral exchange sites with a 1-factor analysis of variance (ANOVA), and then we made multiple comparisons among groups of sites with a Tukey's post hoc test using JMP (Release 5.0.1a, SAS Institute, Inc.,

2002). We expected algal biomass to increase with time, so we used linear regression analysis to evaluate the effect of seasonality on chlorophyll a concentration.

We evaluated differences in the composition of benthic algae among downwelling, neutral, and upwelling sites using an Analysis of Similarities (ANOSIM) analysis and pairwise post-hoc tests (Clark, 1993) using PC-ORD for Windows version 4.25 (MjM Software, Gleneden Beach, Oregon). ANOSIM operates directly on a dissimilarity matrix and tests statistically, whether there is a significant difference between two or more groups of sampling units. We only included algal genera in the ANOSIM that were found occurring at $>5\%$ relative abundance. If algal communities are different at upwelling, downwelling, and neutral exchange sites, then compositional dissimilarities between sites will be greater than those within sites. We examined the responses of taxa to hyporheic exchange by calculating the relative abundance and absolute cell abundance of individual taxa or taxonomic groups. We examined differences in the absolute cell abundance of taxa occurring at $>5\%$ relative abundance among groups of downwelling, neutral, and upwelling sites with a 1-factor ANOVA, and then we made multiple comparisons among groups of sites with a Tukey's post hoc test using JMP (Release 5.0.1a, SAS Institute, Inc., 2002). The alpha level for all tests was set at $\alpha = 0.05$.

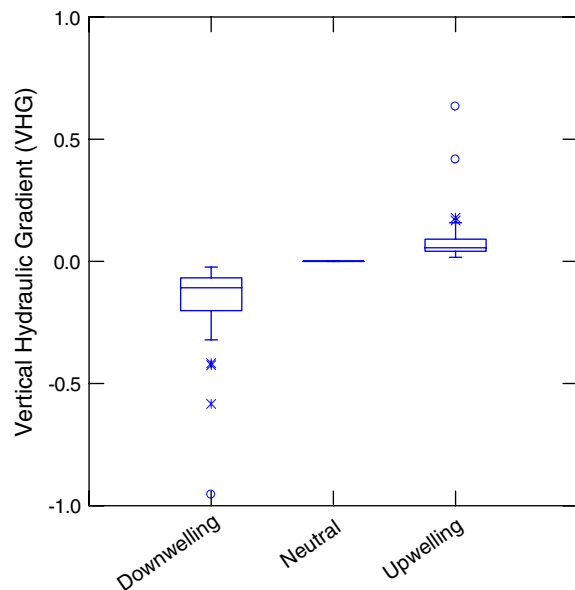


Fig. 3 Box and whisker plot of vertical hydraulic gradient (VHG) corresponding to 120 sites sampled in the Middle Fork within the Nyack Flood Plain, grouped into categories of Downwelling ($n = 52$), Neutral ($n = 19$), and Upwelling ($n = 49$) sites

Results

Hyporheic-surface water exchange

The distribution of upwelling and downwelling sites were spatially dynamic within the flood plain, with upwelling sites embedded within general zones of downwelling and downwelling sites embedded within general upwelling zones in the upper and lower 25% of the flood plain, respectively (Fig. 1). The average magnitude of VHG at downwelling sites was greater ($\sim 100\%$ higher) than upwelling sites (Fig. 3). The results of falling head tests indicated that the substratum was highly permeable throughout the Nyack, resulting in high K and Q values. As K values were similar among groups (ANOVA, $F_{2, 117} = 0.66$,

$P = 0.5173$), we were able to use VHG as an index for hyporheic flux (Q) in Eq. 3. Vertical discharge was high at both downwelling and upwelling exchange sites, with Q values as high as $4.10 \times 10^{-7} \text{ m}^3 \text{ s}^{-1} \text{ m}^{-2}$ at upwelling sites and $9.58 \times 10^{-7} \text{ m}^3 \text{ s}^{-1} \text{ m}^{-2}$ at downwelling sites. We found no trend among the distribution of upwelling, downwelling, and neutral exchange sites sampled in relation to sampling date.

Algal responses to hyporheic-surface water exchange

Chlorophyll a concentrations were relatively low at all sites ($<1.2 \mu\text{g cm}^{-2}$), but mean chlorophyll a concentration was more than double at upwelling sites ($0.51 \mu\text{g cm}^{-2}$) than that of downwelling ($0.24 \mu\text{g cm}^{-2}$) or neutral ($0.18 \mu\text{g cm}^{-2}$) exchange sites, and this amount was statistically significant (ANOVA, $F_{2, 117} = 29.33$, $P < 0.001$, Tukey's test, $P < 0.05$, Fig. 4). There was not a significant difference in chlorophyll a concentration between downwelling and neutral exchange sites. A bed-load transport event resulting from the spring snowmelt

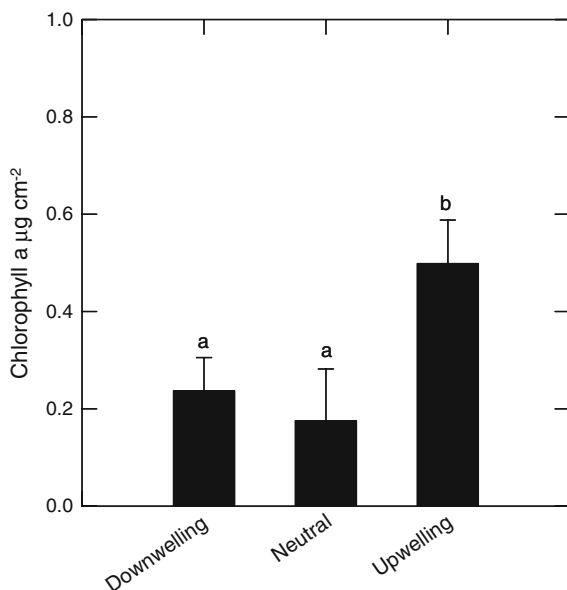


Fig. 4 Mean (± 1 standard error) chlorophyll a concentration ($\mu\text{g cm}^{-2}$ of substratum) from cobbles collected at points of Downwelling ($n = 52$), Neutral ($n = 19$), and Upwelling ($n = 49$) in the Middle Fork Flathead River within the Nyack Flood Plain. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$)

scoured cobbles within the main channel just prior to the initiation of this study (Fig. 2), resulting in low chlorophyll a values early in the sampling season, and then increasing thereafter (Fig. 5). Chlorophyll a concentrations increased more rapidly with time since peak discharge at upwelling sites ($r^2 = 0.3577$, $P < 0.0001$) than downwelling ($r^2 = 0.0049$, $P = 0.8019$) and neutral ($r^2 = 0.2524$, $P = 0.0163$) exchange sites (Fig. 5). The abundance of algal cells cm^{-2} of cobble substrate was also greater at upwelling sites compared to downwelling and neutral exchange sites (ANOVA, $F_{2, 117} = 12.17$, $P < 0.0001$, Tukey's test, $P < 0.05$, Fig. 6), and there was not a significant difference in algal cell abundance between downwelling and neutral exchange sites.

The composition of benthic algae at upwelling sites was statistically different from downwelling (ANOSIM, Global $R = 0.310$, $P < 0.001$) and neutral exchange sites (ANOSIM, Global $R = 0.256$, $P < 0.001$), and downwelling and neutral exchange sites were similar in composition (Global $R = 0.004$, $P = 0.414$). The most common taxa or taxonomic groups at upwelling sites were, in order of their relative abundance: filamentous green algae, $\sim 60\%$; diatoms, $\sim 25\%$; and a single chrysophyte, *Hydrurus foetidus* (Villars) Trevisan $\sim 12\%$ (Table 1). *Stigeoclonium* sp. and *Zygnema* sp. were the most abundant filamentous green algae, occurring at $\sim 54\%$ and $\sim 5\%$ relative abundance, respectively. An

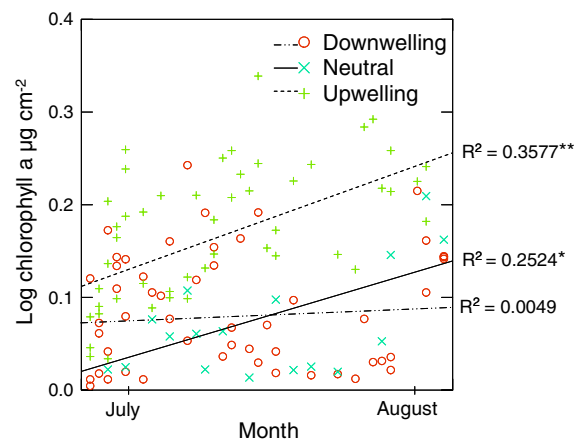


Fig. 5 Standing crop biomass of algae on cobbles at Downwelling, Neutral, and Upwelling sites in relation to sampling date in the Middle Fork Flathead River within the Nyack Flood Plain. Asterisks indicate significance at $P < 0.05$ (*), $P < 0.001$ (**)

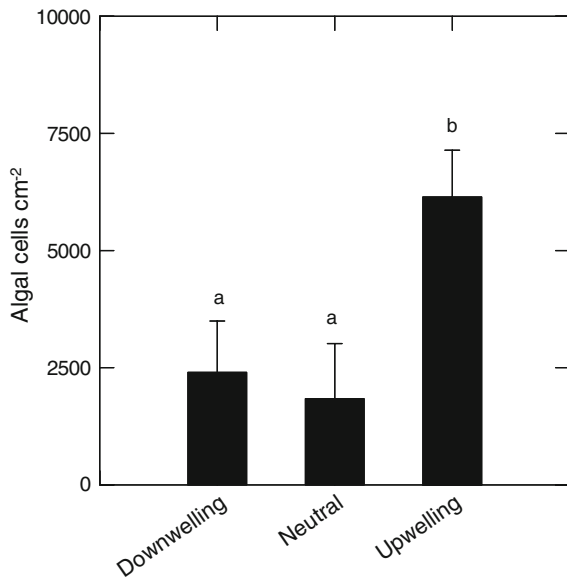


Fig. 6 Total abundance (± 1 standard error) in cells cm^{-2} of substratum from cobbles at points of Downwelling ($n = 52$), Neutral ($n = 19$), and Upwelling ($n = 49$) in the Middle Fork Flathead River within the Nyack Flood Plain. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$)

assemblage of diatoms, *Achnanthydium minutissimum* (Kützing) Czarnecki, *Cymbella excisa* Kützing, *Gomphonema olivaceoides* Hustedt, and *Diatoma moniliformis* Kützing occurred at $\sim 90\%$ relative abundance at downwelling and neutral exchange sites, where they were found growing attached to, or in close association with the stalks of *Didymosphenia geminata* (Lyngbye) Schmidt. *Didymosphenia geminata* was numerically much less common than other diatoms ($< 2\%$ relative abundance at all sites), but its stalks often formed massive growths at upstream downwelling zones.

We found significantly higher cell densities at upwelling sites of filamentous green algae (ANOVA, $P = 0.0001$) and the species *Stigeoclonium* sp. (ANOVA, $P = 0.0001$), *Zygnema* sp. (ANOVA, $P = 0.0255$), and a lower cell density of the species *Gomphonema olivaceoides* (ANOVA, $P = 0.0001$). There was significantly higher absolute cell abundance at downwelling sites of diatoms (ANOVA, $P = 0.0061$) and the species *Achnanthydium minutissimum* (ANOVA, $P = 0.0225$), *Cymbella excisa* (ANOVA, $P = 0.0273$), and *Diatoma moniliformis* (ANOVA, $P = 0.0001$, Table 2).

Table 1 Relative abundance of taxa and taxonomic groups with $> 5\%$ relative abundance

Taxon and taxonomic groups	Relative abundance		
	Downwelling	Neutral	Upwelling
<i>Hydrurus foetidus</i>	3.62	3.07	12.21
<i>Filamentous greens</i>	5.83	6.34	59.87
<i>Stigeoclonium</i> sp.	5.83	6.34	54.17
<i>Zygnema</i> sp.	0	0	5.25
<i>Diatoms</i>	89.84	89.65	25.40
<i>Achnanthydium minutissimum</i>	58.34	67.64	20.27
<i>Cymbella excisa</i>	7.03	4.01	1.43
<i>Gomphonema olivaceoides</i>	5.89	10.31	1.37
<i>Diatoma moniliformis</i>	8.94	5.67	1.53

Discussion

Response of benthic algae to hyporheic-surface water exchange

The large-scale pattern of vertical water movement documented in this study is a predictable response to the natural geology of this region and has been observed in previous studies of the Middle Fork within the Nyack Flood Plain (e.g., Stanford et al., 1994, 2005). Our sampling design allowed us to capture environmental heterogeneity associated with small-scale hyporheic exchange embedded within large-scale downwelling and upwelling zones located in the extreme upstream and downstream regions of the flood plain, respectively (Fig. 1). Since we grouped sites for statistical comparisons based on VHG, and then compared algal biomass and community composition among groups of sites, we were able to eliminate variability that is often associated with averaging VHG and algal biomass across a stream reach. Our observations show that algae respond to hyporheic upwelling at the cobble scale as predicted by Pepin & Hauer (2002), offering an empirical explanation for the patchy distribution of algal biomass that workers have visually observed on the Nyack for years. Since there was an even distribution of upwelling, downwelling, and neutral exchange sites sampled with time since peak discharge, the increase in biomass at upwelling sites with seasonality should not have skewed our results.

Table 2 *F* values (df = 2,117) from ANOVA of average cell density in cells cm⁻² of taxa and taxonomic groups with >5% relative abundance at Downwelling, Neutral, and Upwelling sites

Taxon and taxonomic groups	Cells cm ⁻²			
	<i>F</i>	Downwelling	Neutral	Upwelling
<i>Hydrurus foetidus</i>	n.s.	237 (204) ^a	55 (29) ^a	1005 (361) ^a
Filamentous greens	48.77****	381 (142) ^a	114 (37) ^a	4895 (537) ^b
<i>Stigeoclonium</i> sp.	41.11****	381 (142) ^a	114 (37) ^a	4462 (529) ^b
<i>Zygnema</i> sp.	2.05*	0 (0) ^a	0 (0) ^a	433 (257) ^b
Diatoms	9.32**	5246 (950) ^a	1580 (364) ^b	2026 (241) ^b
<i>Achnanthydium minutissimum</i>	6.85*	3816 (662) ^a	1220 (329) ^b	1670 (228) ^b
<i>Cymbella excisa</i>	6.27*	460 (111) ^a	72 (18) ^b	118 (28) ^b
<i>Gomphonema olivaceoides</i>	6.63****	385 (72) ^a	186 (38) ^b	112 (35) ^b
<i>Diatoma moniliformis</i>	8.16****	585 (126) ^a	102 (46) ^b	126 (37) ^b

Values are (±1 SE)

Values having the same letter are not significantly different (Tukey's test, $P < 0.05$)

* $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$

If anything, we may have underestimated the influence of upwelling on algal biomass by including sites that were scoured early in the season. These results do, however, show that upwelling sites recover from the spring bed-load transport event more rapidly than downwelling sites, which maintained relatively low chlorophyll *a* values throughout the sampling season. Since algae are the primary food source for many stream macroinvertebrates and linkages have been made between the distribution of benthic algae and Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa in the Middle Fork within the Nyack (Pepin & Hauer, 2002), differences in algal biomass at upwelling and downwelling sites during the summer growing season may have implications that cascade up through the entire benthic food web.

This is the first study to show differences in a main-channel benthic algal community at sites with different hyporheic exchange in a large alluvial river. The community of benthic algae represented in this study was similar to previous reports by Prescott & Dillard (1979). Results of algal community analysis suggests that higher amounts of biomass as chlorophyll *a* may be due to the increases in some of the filamentous green algae that were abundant at upwelling sites, particularly *Stigeoclonium* sp. and *Zygnema* sp. *Stigeoclonium* sp. is often found in high abundance in waters with a high concentration of dissolved nutrients and ubiquitous in low abundances across a range of habitats including nutrient poor

waters (Kingston, 2003). We found *Stigeoclonium* sp. present at sites throughout the flood plain, but it occurred at relatively low absolute and relative abundances at downwelling and neutral exchange sites (Tables 1, 2), suggesting that conditions at these sites were less preferred by the taxon than upwelling sites. *Hydrurus foetidus*, the second most abundant filamentous taxon at sites with hyporheic upwelling, is common in fast-flowing, cold, unregulated rivers of mountainous regions (Graham & Wilcox, 2000), but it is often eliminated from, or reduced to a low abundance in the benthos with warm thermal effluent (Squires et al., 1979). Following this autecological profile, we would expect to find *H. foetidus* across all sites within the Middle Fork, which is cool and unregulated, but we would expect it to occur at a higher relative abundance at upwelling sites which are often cooler in the summer and warmer in the winter than similar downwelling sites (Ward, 1985; Case, 1995).

The assemblage of small epilithic diatoms, which were found in high relative abundance at downwelling and neutral exchange sites, were structured in part by *Didymosphenia geminata*. Since much of the biomass associated with *D. geminata* occurs within its stalk and it is a relatively large diatom, it rarely accounts for much more than 1% of the cells in a benthic assemblage (Bahls, 2004), even when it is observed growing in large masses as it was in the Middle Fork. The stalks of *D. geminata* are made

primarily of polysaccharides and protein, forming complex, multi-layered structures that are resistant to degradation, making it a relatively stable substrate in the stream benthos even after the chloroplasts are not present within the cell (Spaulding & Elwell, 2007). We believe that *D. geminata* is particularly important to our study of the Middle Fork because its stalk provides substrate for *Achnanthydium minutissimum* and other diatoms to attach and in doing so, built an assemblage that we found to be statistically different from upwelling sites. A high relative abundance of *D. geminata* and *A. minutissimum* are indicative of low nutrient waters (Biggs, 1996; Kociolek & Spaulding, 2003), and the secretion of a mucilage stalk in these taxa is thought to be an evolutionary adaptation to counter nutrient limitation in the stream benthos (Kingston, 2003).

High concentrations of nutrients in hyporheic waters have been documented across a range of locations and spatial scales from gravel bars to floodplain segments (Ford & Naiman, 1989; Valett et al., 1994; Dahm et al., 1998). On the Nyack Flood Plain, water in the hyporheic zone contains higher concentrations of both N and P (up to 300%) compared to surface water in the main channel of the Middle Fork upstream of the Nyack (see Stanford et al., 1994; Bansak, 1998). Since algae require elements in fixed proportion to grow and reproduce (Steinman & Mulholland, 2006), an increase in available nutrients can result in a significant increase in algal biomass (Freeman, 1986; Lowe & Pan, 1996) and changes in algal assemblage composition (Stevenson & Rollins, 2006). Based on results from this earlier research, we believe that higher amounts of algal biomass and the corresponding algal community indicative of nutrient-rich waters at upwelling sites are the result of nutrient enrichment from hyporheic waters during hyporheic discharge.

This research highlights the need to incorporate a vertical component into longitudinal stream paradigms and may be useful to consider when developing algal monitoring programs. A better understanding of the processes along the hyporheic corridor-surface-water interface is needed in order to protect river ecosystems from human disturbance and rehabilitate river systems that have been impaired. By incorporating a vertical dimension into future studies coupled with airborne hyperspectral technology and modeling of ecological data (i.e., Whited et al., 2003), the natural processes

that shape floodplain biocomplexity and productivity will be better understood.

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