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Complete List of Authors:	Yates, Adam; University of Western Ontario, Department of Geography and Canadian Rivers Institute Brua, Robert; Environment Canada, National Centre for Hydrologic Research Culp, Joseph; Environment Canada and Canada Rivers Institute, Department of Biology, University of New Brunswick Chambers, Patricia; Environment Canada, Canada Centre for Inland Waters Young, Roger; Cawthron Institute
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Variation in stream metabolism and benthic invertebrate composition along longitudinal profiles of two contrasting river systems

Yates, Adam G.^{1*}, Brua, Robert B.², Culp, Joseph M.³, Young, Roger G.⁴, Chambers, Patricia A.⁵,

¹Western University and Canadian Rivers Institute, Department of Geography, London, Ontario, Canada, adam.yates@uwo.ca

²Environment Canada, National Centre for Hydrologic Research, Saskatoon, Saskatchewan, Canada, bob.brua@canada.ca

³Environment Canada and Canadian Rivers Institute, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada, joseph.culp@canada.ca

⁴Cawthron Institute, Nelson, New Zealand, roger.young@cawthron.org.nz

⁵Environment Canada, Canada Centre for Inland Waters, Burlington, Ontario, Canada, patricia.chambers@canada.ca

* Corresponding Author Address:

Department of Geography, Western University,
1151 Richmond St.

London, Ontario N6A 5C2, Canada

phone: 519-661-2111 x85008

fax: 519-661-3750

Abstract

Our study aimed to determine drivers of longitudinal variation in stream metabolism and benthic macroinvertebrate (BMI) composition and assess concordance of these ecological measures for two Canadian rivers (Rat River and Tobacco Creek). Gross primary production was associated with longitudinal position in both rivers but also the percentage of the watershed used for agriculture and hydrogeomorphic zone. However, within and among zone differences in stream metabolism indicated longitudinal variation followed a staircase pattern rather than a clinal pattern. BMI composition was associated with network position in both rivers but hydrogeomorphic zones were only important in Tobacco Creek. Among zone differences in BMI communities in Tobacco Creek depended on season. Concordance between stream metabolism and BMI composition was not observed within either river despite metabolism and BMI composition being associated with longitudinal position. For these rivers, segment scale hydrogeomorphic conditions appear to be important modifiers of longitudinal patterns observed at the whole river scale. The lack of concordance between stream metabolism and BMI composition suggests reach scale processes are driving ecological differences within sampling sites.

Keywords: Benthic Macroinvertebrate Composition; Hydrogeomorphic Zones; Longitudinal Position; Rivers; Stream Metabolism

Introduction

Detecting patterns of ecological condition in lotic systems and then discerning the processes that regulate these patterns are critical steps towards effective management of aquatic resources. According to the River Continuum Concept (RCC; Vannote et al. 1980), ecological conditions in undisturbed river systems are predictably structured along longitudinal gradients driven by changes in the physical environment (e.g., light availability, channel width and velocity). However, the RCC has been strongly criticized as being overly simplistic in that it does not account for location-specific differences (i.e., “patchiness”) within a drainage basin (Statzner and Higler 1985; Townsend 1989; Thorp et al. 2006). Location-specific changes in ecological condition have been shown to arise as a result of tributary inflows (Benda et al. 2004; Wilson and McTammany 2014), changes in geomorphology (e.g., constricted channels vs floodplains) and hydrology (Montgomery 1999; Poole 2002), and local changes in stream hydraulics (Statzner and Higler 1986). This layering of location-specific changes onto broad longitudinal patterns means that a multi-scaled perspectives is required to discern patterns in ecological condition along river systems.

Many studies have quantified changes in ecological structure (Hawkins and Sedell 1981; Culp and Davies 1982; Statzner and Higler 1986; Grubaugh et al. 1996; Rice et al. 2001) and, to a lesser extent, ecological function (Bott et al. 1985; Meyer and Edwards 1990; Wiley et al. 1990; Young and Huryn 1996) along river profiles. Findings from several of these studies support the RCC hypothesis that ecological conditions mirror longitudinal zonation patterns (Hawkins and Sedell 1981; Culp and Davies 1982; Bott et al. 1985). However, other studies contend that

temporal and spatial discontinuities in hydrogeomorphology are more important in determining ecological condition than position along a stream's longitudinal gradient (see review by Thorp et al. 2008). For example, a meta-analysis of benthic invertebrate data showed that stream hydraulics, rather than longitudinal gradient, was the most important determinant of invertebrate distribution in 14 rivers spanning a variety of latitudes (Statzner and Higler 1986). Likewise, discharge associated with inter-annual variation in rainfall was found to be the primary determinant of gross primary production (GPP) along a 310 km longitudinal profile of the Taieri River, New Zealand (Young and Huryn 1996). Yet despite paradigm-related differences in the underlying drivers of ecological patterns, both the clinal and discontinuity based frameworks suggest that ecological structure (e.g., taxa richness) and function (e.g., stream metabolism) should vary concordantly. For example, the RCC predicts that environmentally driven changes in stream metabolism as measured as the balance of gross primary production and ecosystem respiration (ER) should be tracked by subsequent changes in benthic invertebrate composition in response to shifts in the availability of basal food resources (e.g., increases in periphyton biomass; Vannote et al. 1980). Assumptions of concordance in structure and function have led many common bioassessment frameworks to assume that compositional metrics can be used as surrogates of functional conditions (Bunn and Davies 2000). In response, recent studies have compared concordance between stream metabolism and benthic macroinvertebrate taxonomic metrics along land use gradients but found these two common bioassessment indicators are not always associated with the same environmental drivers (Young and Collier 2009; Yates et al. 2014).

Ecological conditions along a river are strongly influenced by the types and intensities of anthropogenic activities within the watershed. Agricultural activities have been particularly well demonstrated to affect ecological conditions in river systems (Allan 2004). For example, the combined effects of riparian vegetation removal and fertilizer application were linked to apparent homogenization of food resources and macroinvertebrate community composition along a river characterized by three distinct geomorphic zones (Delong and Brusven 1998). The presence of dams has also been widely demonstrated to disrupt ecological patterns as a result of effects on flow, temperature and water chemistry (Poff et al. 1997), presenting a clear example of how location-specific change can modify longitudinal pattern of downstream ecological condition (i.e. serial discontinuity concept or SDC; Ward and Stanford 1983; Ward and Stanford 1995). Finally, discharge of municipal wastewater and industrial effluents can alter patterns in ecological condition for 10-100 kilometres downstream of an outfall, including increasing primary production and shifting macroinvertebrate community structure (Boyle and Fraleigh Jr 2003; Gücker et al. 2006; Wassenaar et al. 2010). Despite the above examples, there is a lack of explicit analysis as to how the interactions between human activity, longitudinal position and hydrogeomorphology influence ecological conditions in river ecosystems (but see Villeneuve et al. 2015).

This study aimed to describe ecological patterns along longitudinal profiles of river systems and determine the environmental parameters driving this heterogeneity. Specifically, our hypotheses were: 1) stream metabolism and benthic macroinvertebrate community composition would vary with longitudinal position within each river system because of segment scale variations in land use and hydrogeomorphic conditions, and; 2) longitudinal patterns of benthic macroinvertebrate

composition and stream metabolism would be concordant as the taxonomic composition of benthic macroinvertebrate communities respond to changes in basal food resources, the latter also being the primary determinant of the balance of GPP and ER. These hypotheses were tested by measuring stream metabolism and benthic macroinvertebrate composition in the spring, summer and autumn seasons along the longitudinal profiles of two river systems in the Red River Valley. The contrasting land cover, hydrogeomorphology, and stream chemistry of the eastern and western tributaries of the Red River make this region ideal for investigating longitudinal variation of ecological patterns in aquatic systems and the drivers associated with these patterns. By making meaningful comparisons of these contrasting tributaries we will be able to further elucidate the importance of the interactions between network position, human activities and hydrogeomorphology to ecological patterns of river systems.

Methods

Study Area

This study was conducted in the Red River Valley of southern Manitoba, Canada (Fig. 1a). The valley comprises the historical bed of glacial Lake Agassiz and is characterized by a wide flat valley plain of fine glacio-lacustrine soils. Regional climatic conditions are humid continental with cold winters and warm summers. Annual precipitation is moderate (annual average = 416 mm/year) with most of the precipitation (>60%) falling as rain during intense, summer rainstorms (Environment Canada 2012). The valley is bounded on the east by the Canadian Shield and to the west by the Manitoba Escarpment. These geological patterns result in distinct

geomorphic differences between the eastern and western rivers flowing across the Red River Valley. Eastern rivers exhibit moderate gradient channels flowing from wetland areas in the headwaters before transitioning to low gradient, meandering rivers in the valley bottom that remain largely unmodified by human activities. In contrast, western rivers initiate in the steep gullies of the escarpment before rapidly transitioning into low gradient, meandering systems at the base of the escarpment. The lower reaches of the western rivers were historically a connected wetland complex, but have since been ditched and diked to generate a system of managed channels (Bossenmaier et al. 1974).

Two tributaries of the Red River, the Rat River (RR) and Tobacco Creek (TC), were selected to represent the eastern and western river systems, respectively (Fig. 1b). The two study rivers contrasted in terms of land use and physiography as well as hydrological and channel characteristics. For example, Tobacco Creek has a series of flow-over dams in the lower section of the river and can become intermittent in dry years (Glozier et al. 1996). In contrast, the Rat River has perennial flow and has experienced only minimal impacts to flow regimes for most of the river profile (see supplement for detail descriptions of each river system). Sampling stations were established at eight and ten sites along the Rat River and Tobacco Creek, respectively (Fig. 1c and 1d). Sites were located along the longitudinal profile to capture changes in channel form and land use.

Landscape Description

Catchment boundaries for each site were delineated from a 20 m digital elevation model (DEM) and a 1:50,000 stream network downloaded from Geobase Canada (available at: www.geobase.ca) using the ArcHydro 2.0 extension for ArcGIS 10 (ESRI, California, USA). The accuracy of the 1:50,000 stream networks were checked and adjusted as necessary using 2.5 m resolution SPOT images. The unique subcatchments associated with each site were then identified using the symmetrical difference function in ArcGIS 10 (ESRI, California, USA). Subcatchments for each site were defined as the area draining the section of river upstream of a site to the next most upstream site. For each of the identified subcatchments, the percentage of the areas classified as agricultural land use was calculated using data from a land cover layer for Manitoba (available at <https://mli2.gov.mb.ca>). The potential influence of wastewater treatment lagoon facilities in each sub-basin was estimated by calculating the minimum upstream channel distance to a lagoon outfall. Sites with no upstream outfall were given a value more than an order of magnitude greater than the longest upstream distance to a discharge point (i.e. 500 km). The influence of dams was calculated in the same manner. Distances to the stream source, defined as the initiation of the stream on the 1:50,000 stream networks, were measured as the in-channel upstream distance from each site to the stream source. The distance to source measure served as an indicator of each site's relative position along the longitudinal profile of each river system.

Stream segments for each site were defined as the channel section extending 1 km upstream of the sampling site on the river mainstem. In the few cases (4 segments) where this distance incorporated a minor tributary inflow, the tributary was ignored because flow additions to the mainstem were minimal. Segments were measured for each site using ArcGIS 10 (ESRI,

California, USA) and the 1:50,000 stream network. A 100 m buffer was generated on each side of a stream segment, and the percentage of the buffer area covered by natural vegetation (i.e., forest and grassland) was determined using the Manitoba land cover layer. Buffer width was based on having sufficient width to adequately capture the relatively coarsely resolved (30 m) land cover information. For each segment, we used four descriptors of hydrogeomorphology, channel width, gradient and sinuosity, as well as subcatchment soil texture, to delineate and describe hydrogeomorphic zones as recommended by Thorp et al. (2008; see supplement for full details).

Sampling Approach

Stream physicochemical and ecological conditions were assessed during spring (May), summer (July) and autumn (October) 2010. Grab water samples for physicochemical determination were collected in the thalweg of each stream at approximately 60% depth. Water samples were analyzed for total nitrogen (TN), total phosphorus (TP) and total suspended solids (TSS) at Environment Canada's National Laboratory for Environmental Testing in Saskatoon, Saskatchewan, Canada. TN and TP samples were processed using a potassium persulphate digestion and concentrations (mg/l) were analyzed using colourmetric methods (APHA 2005a, 2005b), whereas TSS concentrations (mg/l) were determined using a gravimetric method. Conductivity, pH and temperature were measured at each site using a YSI 600QS Handheld Sampler. Canopy cover was measured with a densiometer as the proportion of stream shaded by tree canopy. Measurements were taken in the middle of the channel at three cross-sections representing the top, middle and bottom of the sampling reach. Percent canopy cover was

quantified by averaging measurements obtained facing the upstream, downstream, left bank and right bank positions for all three transects.

Ecological condition of each site was based on benthic macroinvertebrate (BMI) community composition and stream metabolism (i.e., GPP, ER and NEP). BMI assemblages were sampled using a single, three minute travelling kick and sweep with a D-frame net of 400 μm mesh size (Reynoldson et al. 2006). Sampling encompassed all available habitat types within the sampling reach in relative proportion to their occurrence based on a visual assessment. Collected samples were washed into a bucket and large debris scrubbed and removed. The remaining materials were preserved in 90% ethanol and transported to the lab. In the lab, a Marchant box (Marchant 1989) was used to subsample each sample by randomly selecting grid cells until a minimum of 300 organisms had been counted. All subsampled organisms were identified to family, except Chironomidae and water mites, which were identified to subfamily and class levels, respectively.

Stream metabolism was measured at each site using the open-system, single station method (Odum 1956; Owens 1974; Bott 1996) by measuring *in situ* diel changes in dissolved oxygen (DO) concentration using a sonde (YSI model 6600 EDS sonde equipped with a YSI model 6562 DO probe). Sondes were deployed in a well-mixed area at all sites from mid-May through mid-October; however, we focused data analysis on two-week periods in late May, late July and early October (i.e. periods concurrent with physicochemical and benthic invertebrate sampling). Concentrations of DO were measured at 30-minute intervals. Sonde failures at RR08 and at TC10 resulted in no data for these sites during spring and autumn, respectively. A light meter (HOBO® Temperature/Light Pendant Data Logger) was paired with each sonde and situated

approximately 1.25 m above the ground to identify day length at each site in light conditions representative of the reach upstream of the sonde. Average depth was estimated for each site by measuring the depth at 10 equally spaced points along 5 stream cross sections upstream of the sonde to account for local variation in stream morphology.

Reaeration coefficients (k) for each stream were estimated using the night-time regression method (Owens 1974). A spreadsheet regression model described by Young and Collier (2009) was used to generate k from oxygen depletion curves during the night-time period. Estimates of k were considered reliable if the resultant R^2 -value was greater than 0.4. Reliable estimates could not be generated for TC02 during summer and RR08 during autumn. The regression model then used the estimated k -values to calculate temperature corrected daily rates of ER and GPP ($\text{g O}_2/\text{m}^3/\text{d}$). Daily ER and GPP rates were converted from volumetric units ($\text{g O}_2/\text{m}^3/\text{d}$) to areal units ($\text{g O}_2/\text{m}^2/\text{d}$) by multiplying by the measured mean depth of the stream reach. Daily values were averaged by site for the sampled period. Net ecosystem production (NEP) was calculated as the difference between daily GPP and ER.

Analysis of Hydrogeomorphic Zones

Cluster analysis was conducted to identify and describe hydrogeomorphic zones for each study river. Four hydrogeomorphic variables measured at the segment scale (i.e., subcatchment soil texture category, mean channel gradient, channel sinuosity and mean channel width) upstream of each sample point were used in the cluster analysis. Soil texture categories were assigned a numerical rank of one (coarse) through five (very fine). All variables were normalized to

account for differences in measurement units prior to creating a resemblance matrix based on Euclidean distance. Cluster analysis was performed on the Euclidean distance matrices using the group-average method (Clarke 1993) in PRIMER (Clarke and Gorley 2006) (version 6.0, Primer-E Ltd, Plymouth, UK) to generate dendrograms.

Analysis of Drivers of Stream Metabolism

We used a General Linear Model (GLM) to determine if measures of stream metabolism (GPP, ER and NEP) differed among the hydrogeomorphic zones by season ($\alpha \leq 0.1$). We performed these analyses for each study river separately. Prior to analysis, we log transformed the stream metabolism measures and when overall models differed significantly performed pairwise comparisons using a Dunnett's T3 test ($\alpha \leq 0.1$).

Projections to Latent Structures (PLS), more commonly called PLS regression (Wold et al. 1984; Wold et al. 2001) were used to examine the relationship(s) between stream metabolism metrics (GPP, ER and NEP) and environmental variables associated with each site. PLS is ideal for these types of analyses as typically: 1) environmental data have many predictor variables relative to observations; 2) predictor variables are frequently, and often, highly correlated, i.e. multicollinearity; and 3) PLS can model several response variables simultaneously (Wold et al. 2001; Carrascal et al. 2009).

The calculated latent components in PLS regression maximize the covariance between the response and predictor variables (i.e., landscape, hydrogeomorphological and physicochemical descriptors) through the simultaneous decomposition of X and Y matrices or vectors. Prior to PLS analyses, predictor variables were centered and scaled to unit variance to give all variables

the same relative importance and response variables (GPP, ER and NEP) were log transformed to minimize deviations from normality. We used leave one out cross-validation to determine the minimum number of latent components needed to obtain the best PLS model. The cross-validated goodness of prediction (Q^2), percentage of variance explained for the response variables, and the cross-validated root mean squared error (RMSECV), which is the difference between the predicted and observed values of each individual pass, were also calculated. The importance of a predictor for both the independent and the dependent variables is given by the variable importance for the projection (VIP). The terms having large VIP values (>1.0) are the most relevant for explaining the dependent variable. Significance of the associations between the dependent (stream metabolism metrics) and independent (environmental descriptors) variables was assessed using a permutations test of cross-validated data ($\alpha \leq 0.1$). We used PLS_Toolbox (version 7.1, Eigenvector Research, Manson, WA, USA), an add-on for MATLAB (version 7.11, The MathWorks, Inc., Natick, MA, USA), to perform the PLS analyses.

Analysis of Drivers of BMI composition

Fourth root transformed abundances of benthic macroinvertebrates were used to assess differences in assemblages among seasons and hydrogeomorphic zones for each study river. From these transformed abundances, we calculated Bray-Curtis similarities followed by ordination of the assemblages using nonmetric multidimensional scaling (NMDS). Analysis of similarities (ANOSIM) (Clarke 1993) randomization tests were performed ($\alpha \leq 0.10$) to assess differences in assemblage structure among season and hydrogeomorphic zones. ANOSIM compares similarities among replicates within a treatment level with similarities from all pairs of

replicates between treatment levels. The R test statistic produced by the ANOSIM procedure ranges from 0 (Bray-Curtis similarities between and within sites are similar) to 1 (all replicates within sites are more similar to each other than to any replicate from another treatment level). The SIMPER (similarity percentages) routine was used to determine the contribution of each species to the overall change in assemblage structure identified by the ANOSIM test. This SIMPER procedure compares the percentage composition that each species makes to the average dissimilarity between two treatment levels. Thus, the most important species in terms of ability to discriminate between the assemblages of two treatment levels could be determined. To assess if certain environmental variables were correlated with the benthic macroinvertebrate assemblage, a BIOENV (matching of biotic and environmental patterns) procedure was performed (Clarke and Warwick 1994). The BIOENV procedure calculates the degree of association between two similarity matrices. We generated the biotic matrices using Bray-Curtis abundance similarities and the abiotic matrices using normalized, Euclidean distance (Clarke and Warwick 1994). Abiotic matrices included data for stream water variables (TN, TP, pH, TSS, conductivity and temperature) and segment scale variables (percent canopy cover, agriculture and natural riparian vegetation, distance to source, wastewater treatment and dams). The matching of biotic and abiotic (environmental) data matrices is founded on the assertion that pairs of samples that are mostly similar in their values for a set of abiotic (environmental) data would be expected to have rather similar species composition. This BIOENV calculation is done by rank correlating the matching elements in the two similarity matrices using Spearman rank correlation. These multivariate analyses were performed using the PRIMER software package (version 6.0, Primer-E Ltd, Plymouth, UK, Clarke and Gorley 2006).

Analysis of Concordance

The concordance between the metrics of stream metabolism and BMI community composition was assessed within each river system using the RELATE procedure test in PRIMER (Clarke and Ainsworth 1993) for each individual season and for all seasons combined. RELATE, which is a non-parametric test of the pairwise association of two resemblance matrices, was conducted by first generating individual resemblance matrices for each set of stream metabolism metrics and BMI assemblage. The set of functional variables included GPP, ER and NEP. Bray-Curtis distance was used to generate the resemblance matrix for BMI assemblage data. Strength of resulting pairwise tests was assessed using Spearman Rank correlation coefficients and statistical significance was assessed using a permutation procedure with 999 permutations ($\alpha \leq 0.1$).

Results

Environmental Descriptors and Hydrogeomorphic Zones

Analysis of environmental descriptors of the Rat River showed a general increase in agricultural land cover at the catchment scale from the uppermost site (RR01) to the lowermost site (RR08, Table 1). There was only one dam and one wastewater treatment facility on the Rat River and consequently only site RR07 and RR08 were influenced by these human activities. At the segment scale, % natural cover in the riparian zone was generally greatest in the headwater sites (but see also RR07) and lowest at RR04 where the river flowed through an agricultural area. Gradient generally declined throughout the river system with the exception of the segment

upstream of RR06 where the gradient increased as the stream passed through the transition to the Red River Valley bottom. This location was also marked by a change from coarser subcatchment soils that dominated the upper two thirds of the river system to the very fine soils of the valley. Sinuosity was greatest at site RR08, however, the degree of meandering was similar to that at RR04. Channel width peaked at RR06 before narrowing at sites RR07 and RR08 in the valley bottom. Means of all stream water chemistry variables, but pH, generally increased from site RR01 to site RR08, although TN, TP and TSS all showed a local maximum at sites RR04 or RR05.

Most sites in Tobacco Creek were exposed to substantial amounts of human activity at the catchment scale (Table 2). TC03 had the lowest %agriculture at 60%. All sites were within 40km of a dam and only TC01, TC02 and TC03 were not influenced by effluent from wastewater treatment lagoons. %Natural cover in the segment riparian zone was lowest at site TC10 and highest at site TC01. Width followed the opposite trend with average channel width increasing 4 fold between TC07 and TC08. Stream gradient was greatest in the headwater sites and declined by 40 fold by the lowest site. Sinuosity was greatest in the middle section of the river and subcatchment soil texture was characterized as very fine in the four lowest sites and generally medium fine in all other sites but TC03. TN and TP concentrations were high throughout the river system ($\text{TN} > 850 \mu\text{g/l}$ and $\text{TP} > 95 \mu\text{g/l}$), but were greatest at sites TC08 or TC10. Conductivity reached a maximum at TC06 and TSS was greatest at TC09.

Hydrogeomorphic analysis resulted in the identification of 3 distinct zones in each river system (see supplement for full details). From upstream to downstream Rat River zones were defined

as: 1) Wetland Zone (RR01, RR02 and RR03); 2) River-run Zone (RR04, RR05 and RR06), and;
3) Lowland Zone (RR07 and RR08). Tobacco Creek zones were defined as: 1) Escarpment Zone
(TC01, TC02 and TC03); 2) Meandering Zone (TC04, TC05 and TC06); and, 3) Channelized
Zone (TC07, TC08, TC09 and TC10).

Environmental Drivers of Stream Metabolism

Stream metabolism metrics differed among the three hydrogeomorphic zones in the Rat River for
all parameters and all seasons except ER in autumn and NEP in spring and autumn (Fig. 2).

Spring GPP ($F = 27.4$, $p < 0.001$) and ER ($F = 7.8$, $p = 0.001$) differed among all three zones. In
contrast, summer GPP showed differences only between the Wetland and Lowland sites with the
Lowland having greater rates of GPP ($F = 7.2$, $p = 0.002$). The Lowland zone sites also had greater
ER in summer ($F = 7.5$, $p < 0.001$) than the Wetland zone ($p < 0.001$) and the River-run zone (p
 < 0.005). Summer NEP ($F = 9.5$, $p < 0.001$) showed the same pattern of differences among
zones as ER. The Lowland zone also had greater GPP ($F = 8.9$, $p = 0.001$) than both the Wetland
and River-run zones in autumn.

PLS analyses of the Rat River stream metabolism and environmental driver data identified one
latent vector that described 34% of the variation in the environmental descriptors and 28% of the
variation in the stream metabolism metrics. The first latent vector (LV1) organized the sites
predominantly along the longitudinal profile of the river, although there was some overlap of the
sites in the middle to upper reaches. Environmental descriptors most associated with LV1 were
hydrogeomorphic zones, increases in distance to source, % agriculture, TN, pH and conductivity
going downstream along the longitudinal profile of the river. Rates of ER and NEP in the Rat

River were not strongly loaded to the latent vector, whereas GPP was strongly loaded with the longitudinal pattern associated with LV1. Cross-validated significance tests confirmed the lack of association between ER and NEP concentrations and the environmental descriptors ($p \geq 0.14$). GPP was significantly associated with hydrogeomorphic zone, % agriculture and % natural riparian, distance to source, pH and conductivity ($p < 0.05$). Sites generally grouped by zone on LV1 with the Lowland sites clearly separated from the River-run and Wetland sites. Longitudinal order was, however, only conserved within the River-run site. Furthermore, sites in the upper two zones sometimes overlapped with the transition sites RR03 (Wetland zone) and RR04 (River-run) grouping tightly together. RR02 only grouped with the wetland sites in spring and was situated with the River-run group in the other two seasons.

Stream metabolism in Tobacco Creek showed differences among zones for all parameters and seasons, except NEP during autumn (Fig. 2). In spring, all three zones were different in GPP ($F = 36.0$, $p < 0.001$) with the Channelized zone having the greatest GPP and the Escarpment zone having the least. The Channelized zone also had greater ER ($F = 11.9$, $p < 0.001$) and NEP ($F = 17.8$, $p < 0.001$) than Meandering and Escarpment zones, however, no differences were observed between Meandering and Escarpment. Differences among zones were small in summer and although all models were significant (GPP: $F = 11.0$, $p < 0.001$; ER: $F = 3.7$, $p = 0.034$; NEP: $F = 3.6$; $p = 0.039$), the only pairwise differences identified were for GPP where both the upper and mid zones were different with the Channelized zone, which again showed the greatest mean rate. The lack of pairwise differences among zones for summer ER and NEP suggest insufficient statistical power to detect differences. Autumn GPP ($F = 3.6$, $p = 0.035$) showed a different pattern than that observed in spring and summer as no difference was observed between the

Meandering and Channelized zones. Both zones had greater mean rates than the Escarpment zone. This pattern was also observed for ER in autumn ($F = 3.0$, $p = 0.059$).

PLS analysis of stream metabolism and environmental drivers in Tobacco Creek showed a pattern of the environmental descriptors along one latent vector. The Escarpment sites (TC01 to TC03) were tightly grouped at one end of LV1, whereas the sites in the Channelized lower reaches (TC07 to TC10) were grouped at the other end and the Meandering zone sites represented a transition area with TC04 on the boundary of the Escarpment group, TC05 in the middle and TC06 bordering the Channelized group. The longitudinal position within each hydrogeomorphic zones was not conserved, except for the Meandering zone, in which longitudinal position from TC04 to TC06 was maintained. Environmental variables associated with the longitudinal profile were hydrogeomorphic zone, increases in distance to source and % agriculture, and decreases in distance to wastewater treatment outflows and % canopy cover, together explaining 41% of the total variation in the environment. Latent vector 1 explained 27% of the variation in the metrics of stream metabolism in Tobacco Creek. Only GPP was significantly associated with LV1 ($p < 0.1$). Significant predictors of GPP in Tobacco Creek were hydrogeomorphic zone, increases in % agriculture and distance to source, and decreases in % canopy cover ($VIP > 1$).

Environmental Drivers of Benthic Macroinvertebrate Composition

Ordination of the benthic macroinvertebrate assemblage in the Rat River (Fig. 3a) revealed that the Lowland zone differed from the Wetland zone ($R = 0.50$, $P = 0.04$) and the River-run zone (R

= 0.25, $P = 0.08$) with more Elmidae, Sphaeriidae, Simuliidae, and Oligochaetes, but fewer Corixidae, Leptohyphidae, Hydrobiidae and Physidae in the upper two zones (i.e., Wetland and River-run). No significant differences were observed in community composition between the Wetland and River-run zones ($R = 0.05$, $P = 0.33$) nor were any significant differences observed among seasons for the Rat River ($R = 0.01$, $P = 0.45$).

The BIOENV analysis for the Rat River revealed that % canopy cover, % agriculture and distance to source were best correlated ($r = 0.47$) with the benthic macroinvertebrate assemblage. More specifically, changes in benthic assemblages were correlated with increases in % agriculture and distance to source, and sites RR01, RR05 and RR07 having the greatest % canopy cover.

Shifts in BMI composition in Tobacco Creek were evident among seasons and hydrogeomorphic zones (Fig. 3b). Spring differed from summer ($R = 0.60$, $P = 0.002$) and autumn ($R = 0.47$, $P = 0.006$), while summer and autumn were similar ($R = 0.14$, $P = 0.16$). Regardless of season, the BMI assemblage from the Escarpment and Meandering zones did not differ ($R = 0.16$, $P = 0.22$), while the Channelized zone was different from the Escarpment ($R = 0.53$, $P = 0.001$) and Meandering ($R = 0.33$, $P = 0.006$) zones. SIMPER analysis revealed that Simuliidae, Leptophlebiidae and Limnephilidae were more common in spring, whereas Caenidae, Baetidae, Corixidae, Physidae and Sphaeriidae were more common in summer and autumn. Macroinvertebrate taxa characteristic of wetlands, such as Hyalellidae, Coenagrionidae, Hydrocarini and Corixidae, were more common in the Channelized zone, while Simuliidae and

Orthocladiinae were less common in the Channelized zone when compared to the upper two zones.

In Tobacco Creek, the benthic macroinvertebrate assemblage best matched ($r = 0.56$) an environmental pattern that included hydrogeomorphic zone, % canopy cover, % natural riparian, distance to source, concentrations of TN and water temperature. Many of these variables showed the greatest increase in the channelized zone, such as distance to source, TN concentrations and water temperature, but low percent canopy cover. % natural riparian tended to be highest in the escarpment zone, but was similar for the meandering and channelized zones.

Concordance Assessment

Analysis of the degree of concordance between indicators of stream metabolism and BMI composition revealed no significant associations ($p > 0.1$) between longitudinal patterns of stream metabolism and BMI composition for either river system for any season. Likewise, correlations between stream metabolism and BMI composition were not significant ($p > 0.1$) for either river when all seasons were combined.

Discussion

Our assessment of longitudinal patterns of stream metabolism and BMI composition in two contrasting river systems in southern Manitoba supported our hypothesis that ecological condition would vary with hydrogeomorphic conditions and land cover at the segment scale,

although land use was entangled with longitudinal position. We conclude that hydrogeomorphic characteristics are key modifiers of the larger scale template set by longitudinal position. Yet, despite stream metabolism and benthic macroinvertebrates being associated with similar large scale drivers our results did not support our hypothesis of concordance between stream metabolism and benthic invertebrate community composition. Our finding provides further evidence that measures of ecological function, such as stream metabolism are not necessarily captured by measures of community composition.

Drivers of Longitudinal Patterns of Ecological Condition

Longitudinal study of two rivers in southern Manitoba showed that patterns of stream metabolism were associated with river profile position when considered at the whole river scale. For both rivers, GPP and ER increased with distance downstream, with variation in stream metabolism largely consistent among seasons. The general patterns of increasing GPP and ER with downstream distance are in agreement with past studies of forested river systems (Minshall et al. 1983; Meyer and Edwards 1990; McTammany et al. 2003) and were associated with riparian vegetation patterns of both Tobacco Creek and the Rat River (i.e., shaded headwaters and more open middle and lower reaches). Moreover, as predicted by the RCC (Vannote et al. 1980), both systems exhibited a more autochthonous driven metabolism in the middle to lower sections of the river with NEP values reaching or nearing 0. Observations in Tobacco Creek fit predictions of the RCC particularly well as NEP peaked over 0 in the upper sites of the channelized zone before declining in the deeper and more turbid lower-most sites. However, our findings indicate that human activities and associated stressors were confounded with the

longitudinal profile making interpretation of the importance of longitudinal position difficult. In particular, increasing % agriculture was associated with longitudinal patterns of GPP in both river systems. Agriculture has been routinely identified as a driver of GPP in streams through changes in light and nutrient availability (Bernot et al. 2010; Frankforter et al. 2010; Yates et al. 2013). The lack of association of TN, TP and TSS with GPP in this study suggests that the association with agriculture may have occurred because the percentage of agriculture was positively associated with distance to source in the catchments of both rivers. Thus, while there is some uncertainty in the role of human activity as a driver, it appears that longitudinal position and hydrogeomorphic characters are the primary drivers of stream metabolism in the studied rivers.

The relationships we observed between the defined hydrogeomorphic zones and stream metabolism suggest that while network position is important at the whole river scale, it did not account for among site variations observed at the segment scale. Rather, our findings indicated that stream metabolism in both the Rat River and Tobacco Creek exhibited discontinuities (sensu Poole 2002; Thorp et al. 2008) along the river profile rather than the clinal pattern purported by the RCC (Vannote et al. 1980). These discontinuities manifested in two ways. First, we observed that longitudinal ordering of sites was not conserved within all hydrogeomorphic zones. Rather it appears that local characteristics, such as canopy cover, result in greater dissimilarity in adjacent sites than network position would predict. For example, in Tobacco Creek, GPP at TC01 was more similar to TC04 than TC03, a scenario likely explained by the closed canopy at TC03 compared to the more open canopy at the other two sites. Second, the frequently strong among-zone differences in metrics of stream metabolism indicate that

metabolism did not follow a gradual clinal pattern as would be predicted by the RCC. Rather, metabolism varied such that rates exhibited minimal differences for the length of a single zone prior to a comparatively abrupt change associated with a discontinuity in hydrogeomorphology. The role of hydrogeomorphic discontinuities at the segment scale is best exemplified by the difference in GPP between the Meandering and Channelized zones of Tobacco Creek where sudden change in channel form and gradient as a result of channel modification and a series of dams corresponded with a significant increase in GPP. The scale of observation is thus critical when examining the relative roles of network position and hydrogeomorphology, with network position explaining general patterns at the whole river scale and hydrogeomorphic discontinuities explaining ecological changes at the segment scale. Our findings thus support hypotheses put forth by Thorp et al. (2008) that acknowledge the role of network position as a driver of patterns of ecological function and structure over the river continuum, but predict that local scale conditions will be more important when the river is assessed at smaller scales.

Studies of stream metabolism that incorporate both spatial and seasonal variation are not widely reported in the literature (but see Minshall et al. 1983; Bott et al. 1985; Wiley et al. 1990). Our study provides new knowledge regarding the interactive effects of space and time on stream metabolism. First, our findings show that longitudinal patterns of stream metabolism are consistent among seasons for both of the studied rivers. However, the magnitude of stream metabolism varied seasonally throughout the river profile. Specifically, we observed an increase in stream metabolism from spring to summer followed by a decline from summer to autumn. This seasonal pattern is consistent with observations from a study by Wiley et al. (1990) in the Vermillion River. The observed seasonal patterns combined with the association between rates

of ER and GPP at nearly all sites, in all seasons, suggests that temporal variations in stream metabolism in the two study rivers are primarily associated with seasonal changes in primary production that occur in cold, northern climates. These results contrast with studies examining stream metabolism in forested streams (e.g., Minshall et al. 1983; Bott et al. 1985) that found patterns of stream metabolism were inconsistent among seasons and peak production did not always occur during summer. The differences between studies in shaded forest streams versus our more open prairie streams suggests a strong dichotomy (i.e., light versus temperature) in the overriding environment control of seasonal variation of stream metabolism and spatial variation along river profiles.

Our assessment of benthic macroinvertebrate community composition in the Rat River and Tobacco Creek indicates that community structure is associated with longitudinal position. Yet, similarly to stream metabolism, agricultural activity was also an important predictor of community composition although the area of influence was the catchment scale for the Rat River whereas agriculture in the riparian area was important for Tobacco Creek. Delong and Brusven (1998) also found that agricultural activities could influence longitudinal patterns in benthic macroinvertebrate composition in a river in Idaho, USA. However, unlike the Delong and Brusven (1998) study, we found no evidence that the widespread agriculture in the Tobacco Creek watershed was homogenizing community composition. Rather, hydrogeomorphic conditions in Tobacco Creek appear to disrupt the clinal pattern along the longitudinal gradient. Indeed, BMI composition exhibited distinct differences among hydrogeomorphic zones, although sites within each zone had similar communities. The importance of local hydrologic and geomorphic conditions is consistent with past studies of longitudinal patterns in benthic

macroinvertebrate composition (e.g., Statzner and Higler 1986; Rice et al. 2001). In contrast, hydrogeomorphic zone was not a predictor of community composition in the Rat River. Furthermore, only the communities in the Lowland zone could be differentiated as distinct and within zone variance in BMI composition was similar to among zone variance. The limited effect of hydrogeomorphic zone in the Rat River suggests that the distribution of our sampling sites may have been insufficient to capture important components of environmental heterogeneity. This is evident from the substantial within-zone variability displayed by many of the parameters used to generate the hydrogeomorphic clusters for the Wetland and River-run zones. We hypothesize that the addition of sites along the Rat River profile, as well as inclusion of additional environmental metrics, would produce a larger number of hydrogeomorphic groups and a more robust explanation of patterns in benthic macroinvertebrate community composition.

Of the two rivers examined, only Tobacco Creek exhibited significant seasonal variation in benthic macroinvertebrate community composition. The observed differences between the two rivers may be in part due to contrasting flow regimes. The Rat River is perennial throughout its length with little seasonal variation in flow rates and hydraulic habitats outside of the spring melt. In contrast, Tobacco Creek displays limited flow in the channelized zone during late summer and early autumn in all but the wettest years (Glozier et al. 1996). Furthermore, the presence of low head dams in the channelized zone creates a long sequence of deeper water with more lentic-like habitats for much of the summer and autumn. Indeed, although flow was continuous in our study year, flow can be intermittent in the channelized zone in years with minimal summer precipitation. Flow regime has been shown to be a key predictor of seasonality in stream communities with more stable flow regimes exhibiting reduced seasonality in

community composition and less stable regimes, particularly those with intermittent flow patterns, exhibiting increased seasonality (e.g., Bogan and Lytle 2007; Eady et al. 2014). These general associations between seasonal variability and flow regime fit our observations of limited seasonal variation in macroinvertebrate community composition in the Rat River and significant shifts in the dominant taxa groups from spring to summer in Tobacco Creek. Past studies have also found that taxa preferring lower flow conditions opportunistically take advantage of stagnant or slow flowing waters during drought periods and can become dominant in the community as high flow preferring taxa perish (Bogan and Lytle 2007). These findings are consistent with our observations of taxa preferring faster flowing waters being replaced by lentic taxa during the summer season. Further exploration of the associations between seasonal as well as interannual variations in flow conditions are likely to aid in understanding observed dynamics in the benthic macroinvertebrate communities of Tobacco Creek.

Assessment of Ecological Concordance

We predicted concordance between stream metabolism and BMI composition because changes in stream metabolism are a direct measure of a river's food base (Young et al. 2008). Furthermore, the expected among-site differences in GPP should be associated with concordant shifts in the primary consumer community (e.g., increased abundance of grazing taxa). Indeed, associations between stream metabolism and BMI composition are predicted in several prevailing riverine paradigms (e.g., Vannote et al. 1980; Thorp et al 2008). Yet, despite longitudinal position being identified as an important predictor of stream metabolism and BMI composition in both rivers, our analyses found no evidence of spatial concordance within the

longitudinal profiles of the Rat River and Tobacco Creek in any of the three sampling seasons. The lack of concordance between stream metabolism and BMI composition may have resulted from the fact that oxygen dynamics, which we used to estimate stream metabolism, can integrate environmental conditions, such as light availability, for substantial distances upstream depending on reaeration rates and velocity (Chapra and Di Toro 1991). Variation in upstream conditions could have led to over- or under-estimation of primary production in the sampling reach from which the BMI were collected. However, this explanation is unlikely to solely account for the lack of concordance observed because our study rivers were largely low-gradient systems with similar canopy and flow conditions for several kilometres upstream. Additional sources of variation may have resulted from reach and patch scale environmental variables such as substrate and water velocity driving BMI composition through habitat and resource availability (sensu Beisel et al. 2006; Straka et al. 2012). Divergence of structure and function in our rivers may also have resulted from differential responses to a multi-stressor environment. Differential response of structural and functional metrics to human activity has been observed in several recent studies (e.g., Izagirre et al. 2008; Young and Collier 2009; Silva-Junior and Moulton 2011), including one in southern Manitoba (Yates et al. 2014). Thus, if our results are representative of a universal discordant relationship between BMI composition and stream metabolism, they support past assertions that measures of structure cannot necessarily serve as surrogates of functional conditions in stream systems (Bunn 1995). Our study extends this growing body of literature by indicating that ecological structure and function can lack concordance throughout a river continuum and across seasons. Given concordance between function and structure is the theoretical construct for using patterns of ecological structure (e.g., taxa richness and abundance) as indicators of ecosystem condition (Bunn et al. 1999), our

finding is also further evidence that future bioassessment programs need to monitor both structure and function in order to accurately assess changes in river condition.

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Tables

Table 1. Values of environmental descriptors measured at 8 sites along the longitudinal profile of the Rat River in southern Manitoba Canada. Stream water parameters are presented as means (standard deviation) based on three samples collected in spring, summer and fall. WWT refers to wastewater treatment lagoon.

Descriptor	RR01	RR02	RR03	RR04	RR05	RR06	RR07	RR08
Catchment Scale								
%Agriculture	0	4.7	1.8	1.3	2.6	1.6	19	38
Distance to Dam (km)	N/A	N/A	N/A	N/A	N/A	N/A	4.6	17.4
Distance to WWT (km)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	10.5
Distance to Source (km)	3.83	9.14	15.7	39.2	85.9	113.4	135.1	147.9
Segment Scale								
%Natural	93	96	88	19	85	67	95	73
Gradient (m/km)	3.7	1.7	0.67	0.75	0.56	1.6	0.51	0.37
Sinuosity	1.25	1.16	1.44	2.52	1.81	1.84	1.94	2.63
Soil Texture	Coarse	Coarse	Coarse	Coarse	Coarse	Coarse	Very Fine	Very Fine
Width (m)	1.15	4.06	6.07	10.72	10.23	17.62	15.43	9.51
Stream Water								
Conductivity ($\mu\text{S}/\text{cm}$)	218 (20)	284 (38)	281 (24)	278 (18)	309 (36)	311 (43)	317 (48)	333 (62)
pH	7.9 (0.2)	8.0 (0.1)	7.9 (0.1)	8.0 (0.1)	7.9 (0.1)	8.1 (0.1)	8.2 (0.1)	8.2 (0.1)
Temperature ($^{\circ}\text{C}$)	12.2 (5.7)	13.6 (6.7)	14.7 (6.7)	15.1 (6.3)	14.4 (6.5)	13.2 (6.6)	15.7 (6.9)	15.6 (7.3)
TN ($\mu\text{g}/\text{l}$)	430 (167)	610 (114)	740 (88)	740 (107)	790 (77)	750 (85)	770 (99)	790 (72)
TP ($\mu\text{g}/\text{l}$)	28 (4.5)	22 (14)	17 (3.6)	25 (9.1)	27 (9.8)	14 (3.8)	19 (3.5)	33 (2.1)
TSS (mg/l)	3.4 (2.6)	1.7 (0.9)	3.5 (2.3)	4.5 (4.0)	4.8 (1.4)	2.7 (1.5)	2.7 (0.8)	10.9 (1.7)

Table 2. Values of environmental descriptors measured at 10 sites along the longitudinal profile of Tobacco Creek in southern Manitoba Canada. Stream water parameters are presented as mean (standard deviation) based on three samples collected in spring, summer and fall. WWT refers to wastewater treatment lagoon.

Descriptor	TC01	TC02	TC03	TC04	TC05	TC06	TC07	TC08	TC09	TC10
Catchment Scale										
%Agriculture	66	69	60	72	72	91	92	86	92	93
Distance to Dam (km)	4.0	4.3	14.4	9.3	19.6	39.3	0.8	8.2	15.8	24.0
Distance to WWT (km)	N/A	N/A	N/A	8.5	18.7	38.4	47.7	26.8	34.5	42.7
Distance to Source (km)	7.8	8.1	18.1	27.7	38.0	57.7	66.9	88.9	96.6	104.7
Segment Scale										
%Natural	100	94	63	33	55	47	58	82	54	13
Gradient (m/km)	8.5	18.2	4.5	2.2	0.91	0.79	0.99	0.99	0.56	0.50
Sinuosity	1.28	1.04	1.11	1.82	2.17	2.45	1.00	1.00	1.08	1.97
Soil Texture	Med-Fine	Med-Fine	Medium	Med-Fine	Med-Fine	Med-Fine	Very Fine	Very Fine	Very Fine	Very Fine
Width (m)	1.86	2.4	5.98	4.34	3.05	5.29	4.28	16.73	10.63	12.12
Stream Water										
Conductivity (µS/cm)	538 (31)	526 (26)	655 (62)	785 (113)	895 (135)	941 (112)	895 (97)	820 (37)	792 (35)	738 (70)
pH	8.2 (0.2)	8.2 (0.2)	8.1 (0.1)	8.1 (0.1)	8.1 (0.1)	8.1 (0.1)	8.1 (0.2)	8.2 (0.2)	8.2 (0.4)	7.9 (0.1)
Temperature (°C)	11.2 (5.6)	10.6 (6.1)	11.3 (7.0)	12.7 (6.8)	14.0 (6.8)	15.1 (9.2)	14.0 (7.5)	15.2 (9.0)	14.4 (8.8)	14.5 (7.4)
TN (µg/l)	859 (345)	907 (505)	896 (488)	934 (498)	1225 (669)	1833 (674)	1810 (1068)	2093 (1558)	2037 (1295)	1937 (1249)
TP (µg/l)	171 (22)	143 (38)	131 (44)	99 (54)	96 (25)	196 (59)	175 (19)	288 (29)	277 (74)	314 (47)
TSS (mg/l)	21.0 (12)	21.8 (18)	23.5 (18)	21.0 (25)	19.8 (17)	23.7 (11)	14.4 (15)	19.2 (9.2)	27.1 (13)	26.1 (24)

Figure Captions

Fig. 1. Maps indicating location of (a) study area in Canada and (b) the two study basins (Tobacco Creek and Rat River) location in the Red River Valley south of Winnipeg, Manitoba. Sampling sites (shaded circle symbols) were located in a longitudinal pattern along the wadeable portions of each river system, c) Rat River and d) Tobacco Creek, at distances that captured tributary inflows, changes in basin geomorphology, land use (grey shading) and the presence of dams (chevron symbols).

Fig. 2. Mean and standard deviations of gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP) for hydrogeomorphic zones in the Rat River and Tobacco Creek during the spring, summer and autumn seasons. Letters (a, b, c) denote among zone differences for each individual metric of stream metabolism ($\alpha = 0.1$).

Fig. 3. Non-metric multidimensional scaling (Bray-Curtis distance) ordinations indicating similarity between benthic invertebrate assemblage composition for Rat River (a) and Tobacco Creek (b), Manitoba, Canada samples collected at 8 and 10 sites, respectively, in the spring (May), summer (July) and autumn (October).

254x309mm (300 x 300 DPI)

Fig. 3. Non-metric multidimensional scaling (Bray-Curtis distance) ordinations indicating similarity between benthic invertebrate assemblage composition for Rat River (a) and Tobacco Creek (b), Manitoba, Canada samples collected at 8 and 10 sites, respectively, in the spring (May), summer (July) and autumn (October).

140x171mm (150 x 150 DPI)