Developing environmental flow targets for benthic macroinvertebrates in large rivers using hydraulic habitat associations and taxa thresholds

Bernhard Wegscheider [a,e,f,*], Wendy A. Monk [b], Jennifer Lento [c], Katy Haralampides [d], Mouhamed Ndong [d], Tommi Linnansaari [a,c], R. Allen Curry [a,c]

[a] Canadian Rivers Institute, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB E3B 5A3, Canada
[b] Environment and Climate Change Canada @ Canadian Rivers Institute, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB E3B 5A3, Canada
[c] Canadian Rivers Institute, Department of Biology, University of New Brunswick, Fredericton, New Brunswick E3B 5A3, Canada
[d] Department of Civil Engineering, University of New Brunswick, Fredericton, New Brunswick E3B 5A3, Canada
[e] Institute of Ecology and Evolution and the Wyss Academy for Nature at the University of Bern, Bern, Switzerland
[f] Department of Fish Ecology and Evolution, Swiss Federal Institute of Science and Technology (EAWAG), Kastanienbaum, Switzerland

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ABSTRACT

Holistic environmental flows frameworks are built on our understanding of key flow-ecology relationships that support sensitive taxa and critical ecosystem functions under different flow and water level scenarios. Most research on flow-ecology relationships has typically focused on small systems, with less known about flow associations, indicator taxa, and environmental thresholds of assemblage change along hydraulic gradients of large non-wadeable rivers. We assessed benthic macroinvertebrate assemblage structure and applied Taxa Indicator Threshold ANalysis (TITAN) on biomonitoring data collected during a six-year period in the Wolastoq | Saint John River in Atlantic Canada. Flow velocity was strongly associated with the distribution and relative abundance of benthic macroinvertebrates in the river, and taxon associations reflected functional adaptations to flow. We identified 33 genus-level indicator taxa that were either positively or negatively associated with flow velocity. Weaker taxa responses were shown for the gradient in median substrate particle size where 22 negatively and positively responding taxa were identified. We predicted changes in indicator taxon abundance under different flow scenarios using a hydrodynamic model, and characterised the distribution and availability of suitable hydraulic habitat patches within a 20 km reach downstream of a large hydropower generating station. These observations set the stage for the development of ecologically-based flow targets to support holistic environmental flow management in large rivers.

1. Introduction

The magnitude, frequency, timing, variation, and duration of flows, particularly extreme high and low flows, act as key drivers in structuring biodiversity in riverine ecosystems (Mims and Olden 2013; Poff et al., 2007; Tickner et al., 2020). This natural flow regime supports key ecological processes (e.g., habitat structure, life history cues) and ecosystem services (e.g., nutrient processing) (Yarnell et al., 2015; Rideout et al., 2021). However, our understanding of these ecohydrological connections has been primarily focused on small- to medium-sized systems with limited examples for large non-wadeable rivers where large scale anthropogenic developments (e.g., hydropower dams) can drastically alter flow regimes.

Linking known flow-ecology relationships with flow scenarios can be used to define environmental flow needs in a management context to protect critical ecosystem functions (Yarnell et al., 2015; Tonkin et al., 2021). Benthic macroinvertebrates (BMI) form a species-rich and functionally-diverse biological group with a large range of preferences for habitats and flow types (Armanini et al., 2011; White et al., 2017), and thus, have the potential to be used to develop flow-ecology relationships. Large-scale BMI monitoring networks have facilitated the development of diagnostic indices of flow alteration that draw on the distribution of taxa along flow velocity gradients using either data-driven (e.g., Canadian Ecological Flow Index, CEFI, Armanini et al.,

2011) or knowledge- and literature-driven methods (e.g., the Lotic Invertebrate Index for Flow Evaluation, LIFE, Extence et al., 1999; Flow *T*-index, Laini et al., 2022). Monk et al. (2018) extended the detection of flow optima from individual species to an assemblage-level approach using a Taxa Indicator Threshold ANalysis (TITAN; Baker and King, 2010) based on taxonomic and trait information along an environmental gradient of flow velocity. Building on other studies, their results show clear directional responses of BMI assemblages to flow alteration in rivers in Canada (Armanini et al., 2011, 2014; Monk et al., 2018).

Within the literature, there is a systematic bias towards smaller, wadeable systems when developing flow-ecology relationships. However, large rivers have a higher diversity of hydraulic habitats than smaller systems (Buffagni et al., 2000), and BMI assemblages associated with these different functional habitat types differ from assemblages in wadeable streams (Vannote et al. 1980; Buffagni et al., 2000; Rempel et al., 2000) This suggests that indicator taxa derived from studies of wadeable streams may not be applicable in larger systems. This highlights a clear need for improved information on how BMI assemblages in larger systems reflect local flow conditions. Further, there is a need to improve our understanding of the response of ecological assemblages to changes in hydraulic habitat and altered flows in large rivers (Lancaster and Downes, 2010).

Here, we present a novel investigation of flow-ecology relationships within a large regulated river in Atlantic Canada. Our goal was to characterize habitat preferences of BMI taxa and identify indicator taxa for four major flow types along a hydraulic gradient: low, low-moderate, moderate, and high. Furthermore, we applied habitat preferences of BMI indicator taxa to a hydrodynamic model to predict areas of highest change in the BMI assemblage in response to potential flow alterations. The information and methods within this study will be useful for river managers as they develop and implement future environmental flow targets to support species diversity in large regulated rivers.

2. Methods

2.1. Study area

The study was conducted in the lower Wolastoq | Saint John River (W|SJR) watershed in central New Brunswick, Canada (Fig. 1). With a catchment area of over 55,000 km^2, the W|SJR is one of the largest rivers in northeastern North America (Linnansaari et al., 2017). The head of tide is ~ 130 km upstream from the river mouth, resulting in water levels in the study area rising ~ 20 cm at high tide, although salt water only mixes up to ~ 70 km upstream (Carter and Dadswell, 1983). Annual river discharge averages 1,100 m^{3}s^{-1}, with a dominant peak associated with the spring freshet and summer and winter low flows averaging 250 m^{3}s^{-1} (average width = 750 m and depth = 3 m; Curry and Munkittrick, 2005).

There are three hydropower generating stations along the mainstem of the W|SJR with additional barriers on some of the major tributaries. The Mactaquac Generating Station (MGS) is the largest dam in the catchment and is approaching a premature end of its service life (Curry et al., 2020). Operating as a run-of-the-river system at MGS, the downstream hydrograph mostly reflects the seasonal patterns in flow. However, differences from the natural hydrograph are seen through both within-day ramping operations required to meet societal energy demands that drive intra-daily water level variations downstream in addition to an artificially increased minimum low flow during summer months associated with attraction flows to support fish passage for Atlantic salmon, a regional species-at-risk (Monk et al., 2017).

2.2. Study design

The study was conducted along a 20-km portion of the W|SJR downstream of the MGS, representing a hydraulic gradient with decreasing slope, sediment particle size and flow velocity towards the downstream half of the study area (Fig. 1 and Table 1). There were 15 sites selected along the gradient in velocity and substrate size, chosen to characterize the range of flow velocity conditions found downstream of the MGS (Wallace and Monk 2015). Based on velocity data from 2014 to
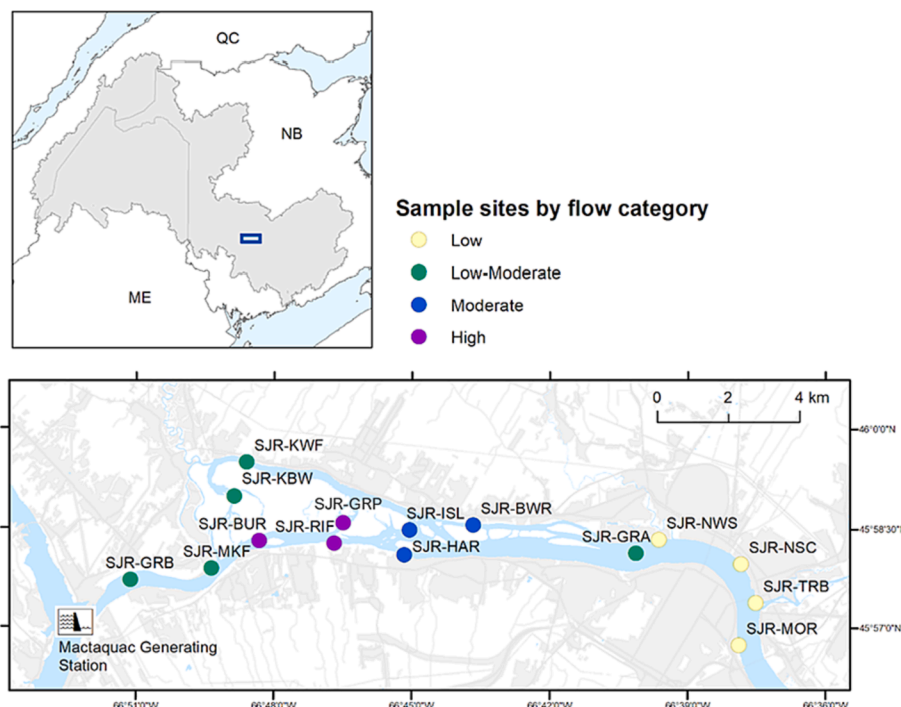

Fig. 1. Map of the Wolastoq | Saint John River watershed (top panel) and a detailed map of the study reach and sampling sites (bottom panel).

Table 1

Sample sites along the W|SJR with location coordinates (latitude and longitude in decimal degrees) and the flow category in which each site was classified for the purpose of characterizing the flow gradient.

Site Name	Latitude	Longitude	Flow category
SJR-MOR	45.94556	−66.63126	Low
SJR-NSC	45.96609	−66.63051	Low
SJR-NWS	45.97223	−66.66033	Low
SJR-TRB	45.95621	−66.62519	Low
SJR-GRA	45.96878	−66.66866	Low-Moderate
SJR-GRB	45.96179	−66.85193	Low-Moderate
SJR-KBW	45.98293	−66.81434	Low-Moderate
SJR-KWF	45.99136	−66.80995	Low-Moderate
SJR-MKF	45.96475	−66.82263	Low-Moderate
SJR-BWR	45.97583	−66.72768	Moderate
SJR-HAR	45.96820	−66.75268	Moderate
SJR-ISL	45.97453	−66.75076	Moderate
SJR-BUR	45.97171	−66.80534	High
SJR-GRP	45.97628	−66.77485	High
SJR-RIF	45.97108	−66.77806	High

2019, the sites sampled along the gradient were generally described as low flow (mean velocity = 0.012 m/s, SD = 0.0054 m/s), low-moderate flow (mean velocity = 0.077 m/s, SD = 0.092 m/s), moderate flow (mean velocity = 0.148 m/s, SD = 0.171 m/s), and high flow (mean velocity = 0.567 m/s, SD = 0.244 m/s; Table 2).

2.3. Data collection

BMI and environmental data were sampled once per year over a six-year period (2014 to 2019) at the 15 sites downstream the MGS (Fig. 1). In 2018, water levels on the river were too high to access sample sites, and sampling was not conducted. Sampling in each year took place in late August or early September. Data were collected by trained field personnel applying a standardized sampling protocol that adapted the national CABIN protocols (Environment and Climate Change Canada, 2012) for use in large river sampling (Wallace and Monk 2015). The greater depth and bankfull width of large rivers necessitates specialized sampling protocols for BMI assemblages in these systems (Flotemersch et al., 2006; Blocksom and Flotemersch, 2005). Within large rivers, nearshore wadeable areas have been found to have the highest diversity of BMI, and modified kick-sampling protocols within these habitats have been developed and applied elsewhere (Flotemersch et al., 2006; Culp et al., 2018). In our adapted protocol, benthic macroinvertebrates were collected along the shoreline of the river (i.e., not crossing the entire channel) (Wallace and Monk 2015). At a sample site, a travelling 3-minute kick net procedure (mesh size: 400 μm) was used, with the net held downstream of the operator as the operator disturbed the substrate and moved in a zig-zag direction upstream through the wadeable portion of the channel. For sites with minimum flow or high macrophyte coverage, a kick and sweep protocol was used, where the net was actively swept back and forth in the area where the operator was disturbing the substrate (Wallace and Monk 2015). Samples were preserved in 95 % ethanol and were sent to a Society for Freshwater Science-certified taxonomist (EcoAnalysts, ltd) for processing. Following the standard CABIN protocols (Environment and Climate Change Canada, 2014), random sub-sampling was completed using a Marchant box until at least

300 individuals were identified (the full subsample was sorted and identified if more than 50 % of the sample was required to reach a count of 300 individuals), and identification was to the genus level where possible, but many individuals were too small to identify to genus. Fixed counts from subsampling were scaled based on the percentage of the sample that was sorted in order to calculate an estimated abundance for each taxon that approximated the total abundance in the sample.

Aquatic habitat variables included substrate particle size (measured using a 100-pebble count method), standard water quality and hydraulic habitat parameters (Table 2). For the pebble count, 100 substrate particles were selected at random from within the sampling area and the intermediate axis (b-axis) of each particle was measured (to the nearest mm) and used to calculate the Wolman D_{50} (median diameter) and the % of substrate in each size class following Wolman particle size classes (Environment and Climate Change Canada, 2012). Water quality point measurements of dissolved oxygen saturation (%), conductivity (μS/cm^3), water temperature (°C) and pH were recorded at each site using a multiparameter water quality meter (YSI, Yellow Springs, OH, USA). As the cross section at the sample site was not wadeable, flow velocity and depth were recorded at 10 random locations within the sampling area, with velocity measured at 0.6 * depth (or the average of 0.2 * depth and 0.8 * depth) using a SonTek FlowTracker velocity flow meter. Velocity was used to examine the assemblage and taxon-specific responses to environmental gradients (described below). For indicator taxon modelling, flow velocity and water depth were converted to Froude number (Fr), which is a dimensionless hydraulic characteristic of the flow. Froude number was calculated as a function of water velocity, gravity acceleration and the hydraulic depth as:

$$Fr = \frac{v}{(gD)^{\frac{1}{2}}} \tag{1}$$

where v = velocity (m s^{-1}), g = gravitational acceleration constant (9.81 m s^{-2}), and D = depth (m).

2.4. Statistical analysis

2.4.1. Characterizing the flow gradient

Biotic metrics were used to characterize the BMI assemblage across the gradient in flow conditions. Total abundance, relative abundance of EPT taxa (Ephemeroptera, Plecoptera and Trichoptera, or mayflies, stoneflies, and caddisflies) and taxa richness were calculated at each site for each year of sampling. Additionally, species diversity, defined here as Shannon's index (H), was calculated using the *vegan* package (version 2.5–7, Oksanen et al 2020) in R (version 4.1.2, R Core Team, 2021). Abundance metrics were calculated using all taxonomic data, whereas richness and diversity were calculated using the number of unique taxa (at genus or coarser level) identified in a sample. Metric values were summarized by flow type (low, low-moderate, moderate-high, and high) to visually assess variability along the velocity gradient.

2.4.2. Assemblage response to environmental gradients

Multivariate analysis was used to assess variability in BMI assemblage composition (as relative abundance) among sites and among years, and to relate composition to environmental variables. Because there was mixed-level taxonomy in the data (due to individuals that

Table 2

Environmental conditions summarized for the five categories of flow conditions sampled in the W|SJR, including mean and standard deviation (SD) of flow velocity, depth, particle size (D_{50} or median), Froude number, and conductivity. Means and standard deviations are calculated based on five years of data for each flow category.

Flow category	n	Flow velocity (m/s)		Depth (cm)		D_{50} (cm)		Froude number		Conductivity (μS/cm)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Low	4	0.012	0.005	44.0	13.6	0.195	0.427	0.006	0.003	116.6	20.4
Low-Moderate	5	0.076	0.092	38.6	14.2	3.111	1.308	0.037	0.038	96.8	25.0
Moderate	3	0.148	0.172	45.5	10.5	3.474	1.355	0.074	0.090	109.3	10.2
High	3	0.567	0.244	29.2	10.4	3.931	1.198	0.345	0.130	109.7	9.17

were too small to be identified to genus level), we combined all BMI data at the subfamily level for Chironomidae and at the level of family for insects and order or higher for non-insects for the multivariate analysis. Analysis at this taxonomic level allowed us to retain all data for a more accurate representation of assemblage differences, and the family and genus levels have been shown to provide similar distinction among BMI assemblages in multivariate analysis (Bowman and Bailey, 1997). Prior to analysis, rare taxa (those present in <5 % of samples) were removed to focus the analysis on dominant assemblage patterns. Our goal with multivariate analysis was to assess assemblage response to environmental gradients with a focus on characterizing taxonomic associations with flow types, and we therefore chose to use Canonical Correspondence Analysis (CCA), which is based on maximizing correlations of taxa and environmental variables to identify species optima (Legendre and Legendre, 2012). The set of abiotic habitat variables considered for the CCA model was examined by using a threshold correlation of $|r| = 0.7$ (Pearson correlation coefficient) between variables to indicate high collinearity and remove redundant variables. The final set of environmental variables selected for analysis included velocity, depth, water temperature, dissolved oxygen, pH, conductivity, and substrate D_{50}. Environmental predictor variables were centered and scaled to account for differences in measurement scale across variables, and relative abundances of taxa were $\log 10 (x + 1)$ transformed. Significance of CCA axes and significance of marginal effects of environmental variables were tested with permutation tests with 999 permutations. CCA was conducted using the vegan package in R.

2.4.3. Taxon-specific response to environmental gradients

To quantify the relationship between the relative abundance of BMI taxa and environmental variables describing flow and habitat conditions, the TITAN2 method (Baker and King, 2010) was applied using the TITAN2 package (Baker et al., 2020) in R. This method computes — for each taxon — change points that maximize the association of both occurrence and relative abundance on one side of an environmental gradient (Baker and King, 2010). For our analysis, we chose to assess a gradient in flow velocity (velocity in m/s) and a gradient in substrate size (median sediment diameter in cm). Because there is variability in flow preference within insect families (Monk et al., 2018), this analysis was completed with genus-level data (excluding individuals identified to family or coarser level) to more accurately reflect BMI associations with flow and substrate. To reduce the effect of rare species in the calculation of scores, we only included genus-level taxa that were detected at a minimum of five sites (n = 90 taxa). Following Dufrene and Legendre (1997), indicator value (IV) scores were the product of the percentage of sampling units in which a taxon modality occurs and the percentage of the number of individuals captured by each partition. Each individual taxon modality was classified as responding positively or negatively to the environmental gradient and further assigned as both pure (change in occurrence and relative abundance of the taxon is in the same direction for ≥ 95 % of the 999 bootstrapped runs) and reliable (≥95 % of 999 bootstrapped runs are significantly different from a random distribution at p < 0.05). IV z-scores standardize the original IV scores relative to the mean and SD of permuted samples along the environmental gradient (Baker and King, 2010). The sum of IV z-scores was used as an indicator of assemblage-level thresholds by identifying peaks in sums of all taxon modality z-scores along the gradient associated with the maximum decline in all negative indicator taxa ($z-$) or increase in occurrence and relative abundance of all positive indicator taxa ($z+$). Peaks in the values indicate points along the environmental gradient that produce large amounts of change in assemblage composition and/or structure. Plateaus denote regions of similar change.

2.4.4. Modeling indicator taxon response to flow scenarios

Flow-ecology relationships of selected indicator taxa were applied to a 2D hydrodynamic model (Delft3D-FLOW 4.01.00; Deltares 2013) that was developed for a 20 km stretch of the W|SJR from the MGS downriver

to the City of Fredericton, NB. Delft3D-Flow solves unsteady continuity and Reynolds-averaged Navier-Stokes equations (NATECH Environmental Services Inc., 2015) and was applied in two-dimensional hydrostatic mode, simulating depth-averaged velocity and water levels for eight discrete flow values, ranging from historic summer low flow (35 $m^3 s^{-1}$; i.e., pre-MGS) to bankfull discharge (i.e., 4390 $m^3 s^{-1}$). Calibration and validation of the hydrodynamic model is described in detail in Wegscheider et al (2021) and NATECH Environmental Services Inc. (2015). Briefly, the numerical model was calibrated by adjusting the resistance of the flow to the bed roughness, input as a spatially specific Manning's n, until predicted and measured water levels matched using data for the entire flow record in 2008 (an extreme flood year). To validate the model's overall performance, current velocity and discharge data were collected using a mobile acoustic Doppler current profiler (ADCP) at 14 transects in the main channel and between the islands for three representative flow ranges; these events were coordinated with the owner-operator of the MGS, NB Power, and the flow rate was held at a constant value, corresponding to predetermined levels during the collection of the validation data (low flows 6 and 14 Sept 2017 at 68–210 $m^3 s^{-1}$; medium flows, 16 Nov 2017 at 405–531 $m^3 s^{-1}$; high flows, 3 Nov 2017 at 1145–1790 $m^3 s^{-1}$). Overall, predictions of flow had an estimated relative deviation from observed values at high, medium and low flows within 9, 10 and 18 % respectively (Ndong et al. unpublished).

Three taxa were selected to model the response to changes in flow scenarios, based on their occurrence and dominance in samples, as well as their classification and IV z-scores in TITAN2: a z + indicator taxa (Ephemeroptera: *Ephemerella*), a z- indicator taxa (Gastropoda: *Valvata*), and a common, widely distributed genus (Amphipoda: *Gammarus*). The spatial distributions of the selected taxa were assessed in relation to Froude number, as a more integrated measure of hydraulic habitat, using Generalized Additive Models (GAMs). GAMs were used to fit relative abundance of selected indicator taxa, using the model:

$$g(E(y)) = \beta_0 + s_1(x_1) + \cdots + s_i(x_i)$$

where g is the link function, E is the expected value, β_0 is the intercept, x_1 corresponds to the input variables (Froude Nr) and s_i are the cubic spline smoothing functions. To measure the accuracy of the resulting GAMs, the goodness of fit index "total deviance explained" was used, which represents the relative difference between the residual and the null deviances. The *mgcv* package (version 1.8; Wood 2011) in R was used to construct GAM-models with the *gaussian* –option selected as the link function.

For the purpose of visualizing responses to different flow conditions, we modeled the relative abundance and spatial distribution of the three indicator taxa across three simulated discharge scenarios. Discharge scenarios of 175, 425 and 990 $m^3 s^{-1}$ were chosen to represent the range of typical flow conditions during sampling events. Modeled flow velocity and water depth were converted to Froude numbers for each scenario across the model element (175,204 grid cells) using Eq. (1). These modeled Froude numbers were applied to the hydraulic habitat GAMs to predict relative abundance of each chosen taxon under the three scenarios.

3. Results

3.1. Characterizing the flow gradient

Habitat conditions were generally consistent across years and varied in a predictable manner along the length of the flow gradient. Mean depth was similar in the low, low-moderate, and moderate flow categories, but was most shallow in the high velocity site category (Table 2). Expectedly, faster flows were associated with a larger median particle size and the sites in the low flow category were characterized by a small mean D_{50}, consistent with a sand-dominated site (Table 2). However,

variability in median particle size was generally low among all sites (particularly higher-flow sites), and reflected typical conditions in a large river. Froude number increased on average from low flow to high flow sites, but remained below 1, indicating subcritical flow. Other environmental variables were relatively similar across the sites and years; for example, the range of average conductivity was between 96.8 and 116.6 μS/cm across the different flow types (Table 2).

In total, 65 macroinvertebrate families including 172 genera were recorded across the 15 sites and 5 years of sampling ($n = 72$ samples). At a coarse level, samples from low, low-moderate, and moderate sites were dominated by amphipods, with an average relative abundance of amphipods of 33.9, 38.4, and 57.2 % across years, respectively. Families of Amphipoda included Crangonyctidae, Gammaridae, Hyalellidae. The most dominant taxonomic groups in low flow sites were typical of low velocity conditions, and included gastropods (families Ancylidae, Hydrobiidae, Lymnaeidae, Physidae, Planorbidae, Valvatidae, and Viviparidae; average relative abundance summed across all families = 27.4 %) and non-biting midges (*Cladotanytarsus*, 9.3 %) in addition to amphipods (Gammaridae). Many of these taxa were also dominant in low-moderate and moderate flow sites, but were found at lower relative abundances on average (e.g., gastropods relative abundance of 8.9 and 18.1 %, respectively; worms/leeches 10.4 and 6.3 %, respectively) than were observed in low flow sites. Gastropoda in these sites were from Ancylidae, Hydrobiidae, Lymnaeidae, Physidae, Planorbidae, and Valvatidae. The mayfly family Caenidae (*Caenis*) was the second-most abundant taxon in low-moderate sites, at 12.6 % on average across years. In contrast, high flow sites were dominated by some taxa that are more typical of higher velocities, including the mayfly family Ephemerellidae (*Ephemerella, Eurylophella, Teloganopsis*; 17.5 % on average) and the caddisfly family Hydropsychidae (*Ceratopsyche, Cheumatopsyche, Hydropsyche, Macrostemum*; 10.5 % on average), though taxa associated with lower flows were also very abundant, including midges (subfamily Orthocladiinae, 12.5 %), gastropods (taxa from Ancylidae, Hydrobiidae, Lymnaeidae, Physidae, and Planorbidae; 33.1 %), and amphipods (taxa from Crangonyctidae and Gammaridae; 10.8 %). Calculated BMI metrics for richness and diversity were generally similar among flow categories (Table 3). A large difference among flow categories was observed for % EPT, which was higher on average in high flow sites (mean = 47 %) than in other flow categories (mean ranging from 2.6 to 11.2 %), although there was a great deal of variability in this metric (Table 3).

3.2. Assemblage association with environmental gradients

The CCA of the BMI assemblage constrained to flow, substrate, and water quality variables resulted in a separation of samples in multivariate space that was largely consistent with flow categories. The dominant gradient was a separation of high flow samples from all other flow categories along the first axis (which explained 13.7 % of unconstrained variance in the BMI assemblage), with high flow samples positively associated with flow velocity and median substrate diameter (Fig. 2A). On the other end of the gradient, most low flow samples were separated from low-moderate and moderate flow samples along the second axis (which explained 3.6 % of unconstrained variance; Fig. 2A). Most low

flow sites were negatively associated with median substrate diameter and positively associated with pH and depth, whereas many low-moderate and moderate flow sites were positively associated with DO and median substrate diameter along this gradient. In the CCA, marginal effects were statistically significant for velocity ($F = 6.10$; $p = 0.001$), substrate diameter ($F = 1.96$; $p = 0.018$), DO ($F = 2.32$; $p = 0.012$), and temperature ($F = 2.13$; $p = 0.031$), but did not indicate a significant effect of depth, pH, or conductivity. High flow samples represented optima for a number of EPT taxa with adaptations for fast flows (including filter feeders and clingers such as Hydropsychidae, Perlidae, Baetidae). In contrast, the taxa most strongly associated with low, low-moderate, and moderate flow samples included swimmers and burrowers such as beetles, true bugs, alderflies, bivalves, and families of mayflies (Ephemeridae).

3.3. Taxon-specific association with environmental gradients

The TITAN analysis indicated clear assemblage change points for flow velocity, but there was more variability and a less clear response to the gradient in substrate size. There was a narrow range of optimal flow velocities for negatively responding taxa (assemblage threshold = 0.02, 5th quantile = 0.01, 95th quantile = 0.04; Fig. 3), whereas positively responding taxa were distributed across a wider range of flow velocities (assemblage change point = 0.32, 5th quantile = 0.11, 95th quantile = 0.41; Fig. 3). Similarly, taxa that decreased in frequency and abundance with median substrate particle size (D50) had a narrower optima range (assemblage threshold = 1.5, 5th quantile = 0.6, 95th quantile = 1.9; Fig. 3) compared with positively responding taxa (assemblage threshold = 3.3 cm, 5th quantile = 1.3 cm, 95th quantile = 4.2 cm; Fig. 3), though there was more variability in both negatively and positively responding taxa than was observed along the velocity gradient. The 95th percentiles for filtered sum $z+$ and filtered sum $z-$ overlapped for median substrate diameter, whereas there was a stronger distinction between these responses for flow velocity, with no overlap (Fig. 3).

Overall, we identified 33 indicator taxa (18 $z+$ and 15 $z-$ indicator taxa) out of the possible 90 taxa that consistently responded in frequency and abundance to sampled gradients of flow velocity (Fig. 4a). The $z-$ indicator taxa included sedentary and/or burrowing taxa such as the molluscs *Amnicola, Gyraulus, Lyogyrus, Pisidium*, and *Valvata*, alderfly *Sialis*, and the tubificid worms *Aulodrilus* and *Spirosperma*, all of which had taxa changepoints at velocities near zero, and a narrow probability density function. Some highly mobile taxa (swimmers) were also $z-$ indicator taxa, including the amphipod *Gammarus*, which had a much higher change point and wider probability density function, reflecting its high abundances across most sites. The $z+$ indicator taxa had change points across a wide range of flow velocities, and generally had wider probability density functions than $z-$ indicator taxa (Fig. 4a). Caddisflies and mayflies dominated the $z+$ indicator taxa, including the caddisflies *Glossosoma, Macrostemum*, and *Chimarra* and the mayflies *Teloganopsis* and *Baetis*, which were associated with the highest flow velocities.

Fewer taxa had consistent associations with the substrate gradient, with 22 indicator taxa (8 $z+$ and 14 $z-$) identified (Fig. 4b). The $z-$ indicator taxa included many sedentary and burrowing taxa, whereas $z+$

Table 3
Summary of biotic metrics calculated for BMI assemblages in sites in each flow category, including the mean and standard deviation (SD) of the percent Ephemeroptera, Plecoptera, and Trichoptera (EPT), taxonomic richness, Shannon diversity, and total abundance. Means and standard deviations are calculated based on 5 years of data for each flow category.

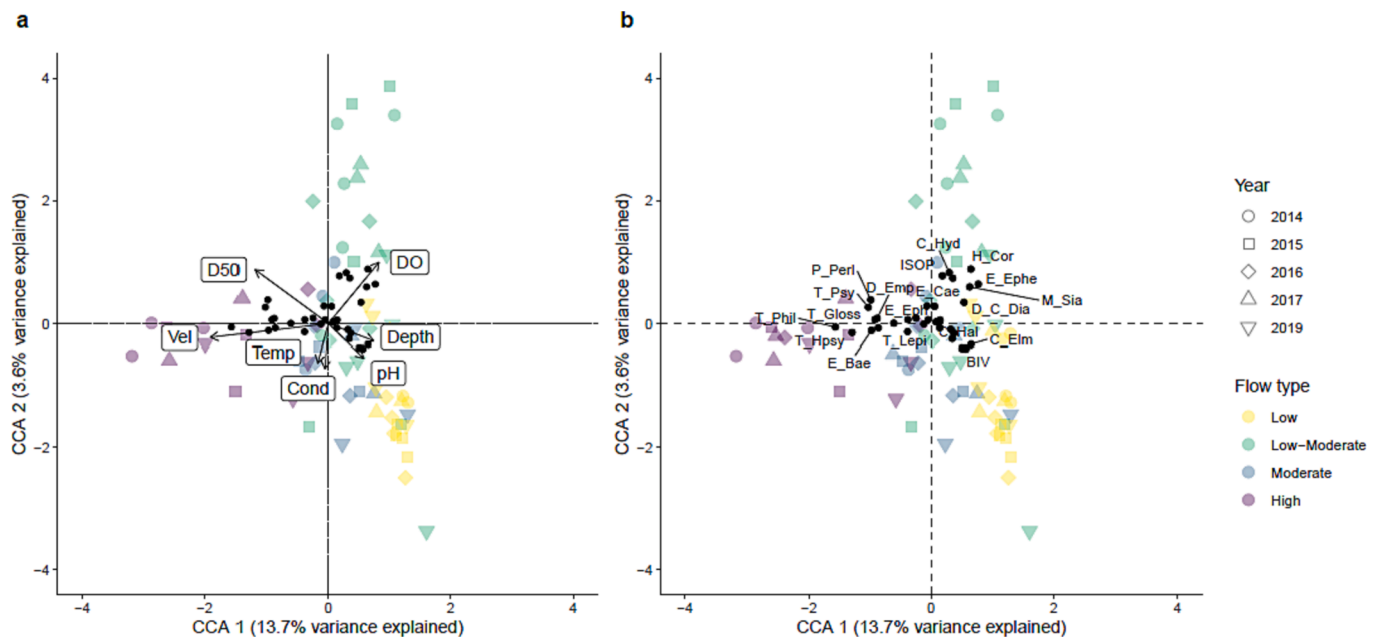| Flow category	% EPT		Richness		Shannon diversity		Total abundance	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Low	2.6	2.0	28.7	9.5	2.0	0.46	7205.7	12841.1
Low-Moderate	10.2	11.3	25.3	11.7	1.8	0.70	7134.3	12585.2
Moderate	11.2	9.2	24.8	10.5	1.5	0.69	4487.4	3866.3
High	47.0	34.0	24.1	8.3	2.0	0.72	4635.7	4265.6

Fig. 2. Canonical Correspondence Analysis (CCA) ordination of A) environmental variables and B) benthic macroinvertebrate abundance data for 72 samples collected along the main stem of the W|SJR, with the colour of points indicating the flow category and the shape indicating the year. Arrows denote habitat variables included in the CCA. Axis labels indicate the percent unconstrained variance in the BMI assemblage that is explained by each axis. To facilitate the interpretation of the figure, only a subset of taxa are labelled.

taxa included several clingers. Several of the taxa associated with lower flow velocities were also associated with smaller substrate size with 11 taxa (e.g., *Hygrobates*, *Cladotanytarsus*, and *Pisidium*) consistently identified as $z-$ taxa across both gradients. There were an additional 7 $z+$ taxa (e.g., *Hydropsyche*, *Ephemerella*, *Lepidostoma*, and *Tvetenia*) that were consistently associated with both higher flow velocities and larger median substrate size. Probability density functions for substrate size were generally wide across all $z+$ and $z-$ indicator taxa, and taxa change points covered a wide range of substrate sizes (Fig. 4b).

3.4. Modeling indicator taxon response to flow scenarios

The hydraulic habitat GAMs explained 9.35 to 34 % of the total deviance in relative abundance for the selected taxa (Table 4). Relationships with Froude number were quite variable for all three genera. The GAM curve for *Ephemerella* was variable across the Froude gradient while *Gammarus* and *Valvata* both showed generally lower relative abundance at higher Froude values (Fig. 5).

Modeled relative abundance using the hydraulic habitat GAMs indicated habitats within the river where increased relative abundance of $z+$ and $z-$ indicator taxa might be expected under the three flow scenarios (Fig. 6). With increasing flow scenarios, the preferable habitat increased by 8 % for $z+$ taxa, and decreased by 16 % for $z-$ taxa at moderate flows. Preferable habitat for $z-$ taxa increased by 33 % at high flows, but this may have reflected uncertainty around the GAM at higher flows. Preferable habitat for the dominant taxon *Gammarus* only changed by 1 % among the flow scenarios (Fig. 6). The models highlighted the spatial distribution and variability of suitable flow habitat patches for the different taxa types, indicating how changes to flow might alter composition of the BMI assemblage as the size and location of suitable habitats changes (Fig. 6).

4. Discussion

Large rivers are often under-represented in flow-ecology studies despite their significant taxonomic and functional diversity and heterogeneity of flow habitats (Cogerino et al. 1995; Beechie et al. 2005;

Knehtl et al. 2021). Furthermore, many large rivers are affected by multiple pressures and stressors (Leitner et al. 2021), yet long-term monitoring programs are still focused on small- to medium-sized rivers (Blocksom and Flotemersch 2005; Floury et al. 2013), likely because of the relative ease of monitoring them, compared with the logistical difficulties of monitoring large rivers. However, effective management of large rivers requires routine monitoring of ecological conditions and an understanding of natural variability that can be expected in these systems, particularly across different flow habitats. Here, we evaluated individual taxa and benthic assemblage associations along a flow gradient to characterize ecological baselines within a large river habitat. We successfully identified taxa that were consistently associated with low or high flow habitats, and characterized assemblage changepoints in relation to flow. Through predictive modeling of relative abundance for key taxa along a hydraulic gradient, we were able to quantify changes in composition that would be expected under different flow scenarios, which can support effective monitoring and flow management of large rivers.

4.1. Large river BMI assemblages

Large river benthic communities have not been as well studied as those in smaller streams and tributaries, in part due to the difficulties in sampling non-wadeable systems (Flotemersch et al. 2006; Blocksom and Johnson 2009; Jackson et al. 2010). Furthermore, large river sampling methods that focus on collecting soft sediment samples in the mid-channel may not be representative of the full range of diversity observed across edge habitats (Blocksom and Flotemersch 2005; Flotemersch et al. 2006). Although a large percentage of the benthic habitat in large rivers is soft-bottom substrate in the deeper mid-channel regions, it has been demonstrated that most of the diversity in benthic assemblages is found in shoreline habitats that contain a number of microhabitats that vary with respect to substrate composition and hydraulic habitat (see Cogerino et al. 1995 and references therein). For example, Cogerino et al. (1995) described 18 different habitat types along the banks of the Upper Rhône River and noted higher densities and diversity of BMI in shoreline habitats than in deeper profundal zones of
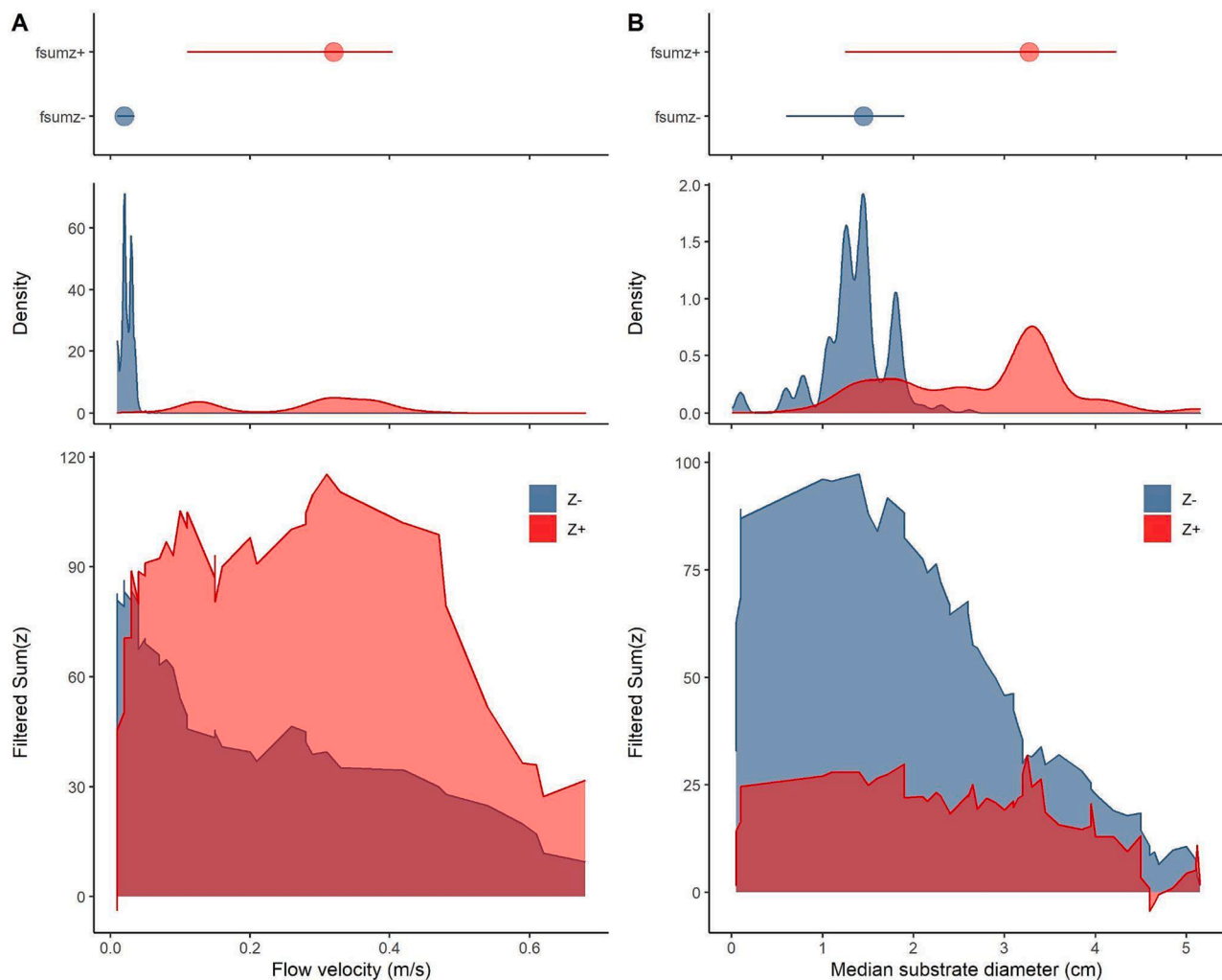
Fig. 3. Assemblage response plots from Threshold Indicator Taxa ANalysis (TITAN2) comparing the response taxa modalities to changes in flow velocity (m/s) and median substrate diameter (cm). Taxa that responded positively to the gradient are shown in red, while negative indicator taxa are shown in blue. The bottom panel shows the magnitude of change among negative indicator taxa ($z-$) and positive indicator taxa ($z+$) along the gradient. Taxa change points (across 999 bootstrapped replicates) are plotted as a probability density function in the middle panel. The top panel shows the observed filtered sum ($z-$) and filtered sum ($z+$) maxima as circles with the 95th percentile of their distributions as horizontal lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the river. Sampling across these habitat types can better allow us to identify biotic-abiotic associations within the system, which can lead to a greater understanding of the ecology of large river communities. Our study in the W|SJR provides an opportunity to describe and characterize shoreline assemblages across flow habitat types in a large river, adding to our knowledge of spatial variation within these under-studied systems.

The strongest differences in BMI assemblage composition in the W|SJR were between high-flow sites and lower-flow sites, with high-flow sites characterized by a higher abundance of EPT taxa that are filter-feeders or have morphological adaptations for faster flow conditions. At lower flows, taxa that are characterized as swimmers, crawlers, or burrowers predominated, including beetles, true bugs, molluscs, midges, fishflies, and isopods. These patterns highlighted functional linkages between habitat conditions and assemblage structure across sample sites, consistent with flow-ecology studies in smaller systems and low-land rivers that have noted compositional differences among flow habitat types (e.g., Guareschi et al., 2014; Monk et al., 2018; Mathers et al., 2019; White et al., 2017). Despite these patterns, diversity metrics were similar among flow habitats. Similarly, in their large-scale study of long-term data from 543 streams in the United States,

Chinnayakanahalli et al. (2011) found that richness measures did not respond to differences in flow, but composition did vary in association with streamflow. Benthic assemblages of different flow types may have replacement of species with different traits that are better suited to the particular habitat conditions, which might not affect values of classical diversity metrics such as the Shannon Index (Pander et al., 2018). Other diversity metrics may reflect the dominance of an individual taxon across all sites, such as *Gammarus* in our samples, which is a pattern that is broadly typical of large river samples (Jackson et al., 2010).

The biotic associations with flow habitat in our study speak to the importance of different habitat types and habitat patches in the shore-line regions of the main channel in large rivers. Differences in flow and substrate composition contribute to variability in benthic habitats in large rivers, which can lead to spatial differences in the assemblage composition of benthic macroinvertebrates longitudinally (Cogerino et al., 1995; Jowett 2003; White et al., 2019) and overall high diversity across large river ecosystems. In our study, flow velocity was the strongest environmental correlate of BMI composition, and lower variability in substrate composition contributed to a weaker and less consistent effect of this variable. Despite differences in flow, median substrate size was similar among sites and representative of small
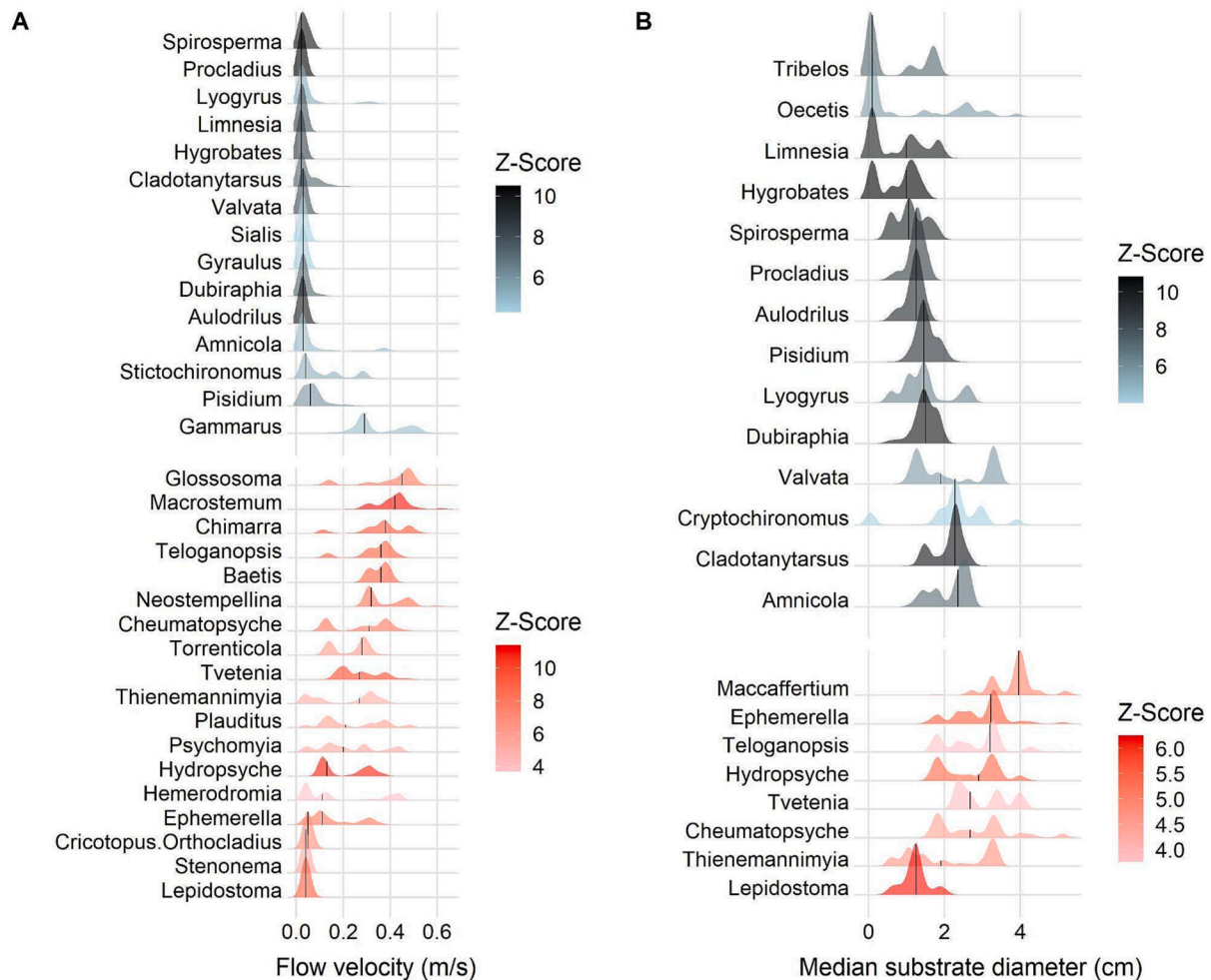
Fig. 4. Individual response plots from Threshold Indicator Taxa ANalysis (TITAN2) comparing the response taxa modalities to changes in flow velocity (m/s) and median substrate diameter (cm). Taxa that responded positively to the gradient are shown in red, while negative indicator taxa are shown with blue. Taxa change points (across 999 bootstrapped replicates) are visualized as a probability density function with colour intensity scaled according to the magnitude of the response (i. e., its standardized *z*-score). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Generalized additive models (GAMS) that relate abundance of selected indicator taxa in the W|SJR with Froude number (Fr). *z*+ taxon: *Ephemerella*; *z*− taxon: *Valvata*; common taxon: *Gammarus*; df = degree of freedom, SE = standard error, % TD explained = percent of total deviation explained.

Indicator	df	logLik	Intercept (±SE)	deviance	% TD explained	F ratio	p
Ephemerella	3.99	−244.765	3.04 (±0.88)	3781.368	34.0	9.561	<0.001
Valvata	8.82	−176.421	1.27 (±0.35)	566.441	23.0	2.160	0.044
Gammarus	2.00	−349.115	33.00 (±3.69)	68626.390	9.35	7.220	0.009

particle size. Other studies of BMI assemblage variation in relation to hydraulic habitat have described a stronger influence of substrate composition (e.g., White et al., 2019; Vázquez et al., 2020), but these studies have generally covered a wider range of substrate types. While both flow velocity and substrate composition were significant predictors in the CCA, pH and conductivity were not significant due to the relative invariability of water chemistry among sites and years.

4.2. Flow associations of BMI in large rivers

TITAN identified optimal ranges and change points of flow velocity and substrate size for BMI assemblages and individual indicator genera in the W|SJR, thus expanding the availability of ecological association and tolerance data for BMI in large rivers. Patterns in relation to flow velocity were more clear than those for substrate, with a narrower optimal range and less variability around change points. Moreover,

there was less variability around estimates for *z*− taxa for flows. The results suggested that taxa associated with slow flows, such as *Spirosperma*, *Procladius*, *Limnesia*, *Valvata*, and *Aulodrilus* were optimally found over a narrow range of flow velocities close to minimal flow, whereas taxa associated with faster flows, such as *Glossosoma*, *Macrostemum*, *Hydropsyche*, *Tvetenia*, and *Cheumatopsyche* were tolerant of a wider range of flow velocities. This information is critical for understanding spatial and temporal variability in BMI assemblages in large river habitats, and in particular for predicting the anticipated response of BMI assemblage composition to changes in habitat conditions due to river regulation and climate change (Wang et al., 2020; Lawrence et al., 2010).

The analysis of flow associations was additionally beneficial because we were able to quantify large-river flow-ecology relationships at the genus level. Ecological preferences can show greater variability at lower taxonomic resolutions, particularly within families with a greater
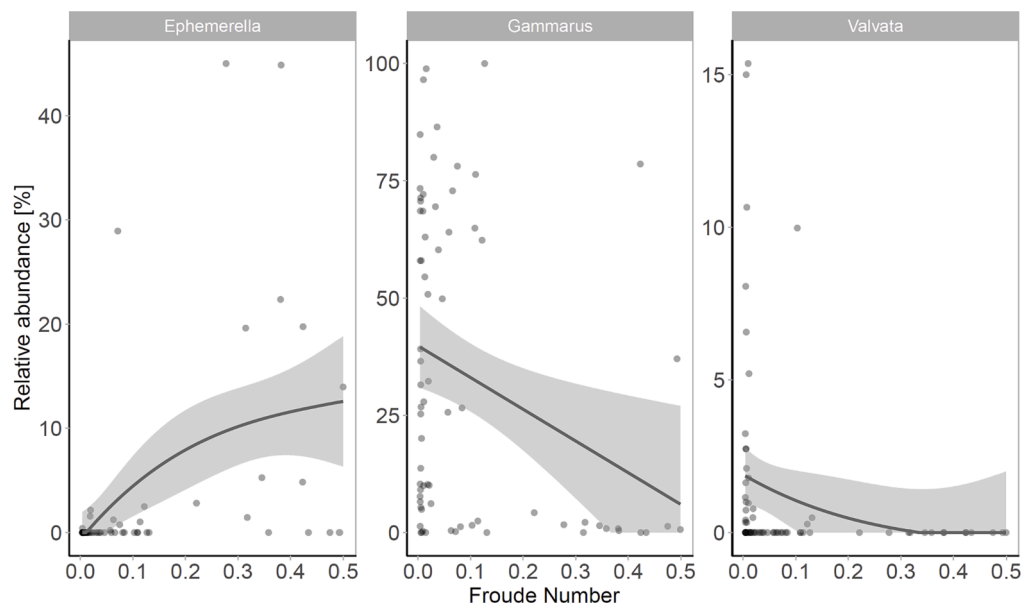
Fig. 5. Relative abundance of selected $z+$ taxa (*Ephemerella*), $z-$ taxa (*Valvata*) and dominant taxa (*Gammarus*) as a function of Froude number, and 95 % confidence region using Generalized Additive Models (GAM).
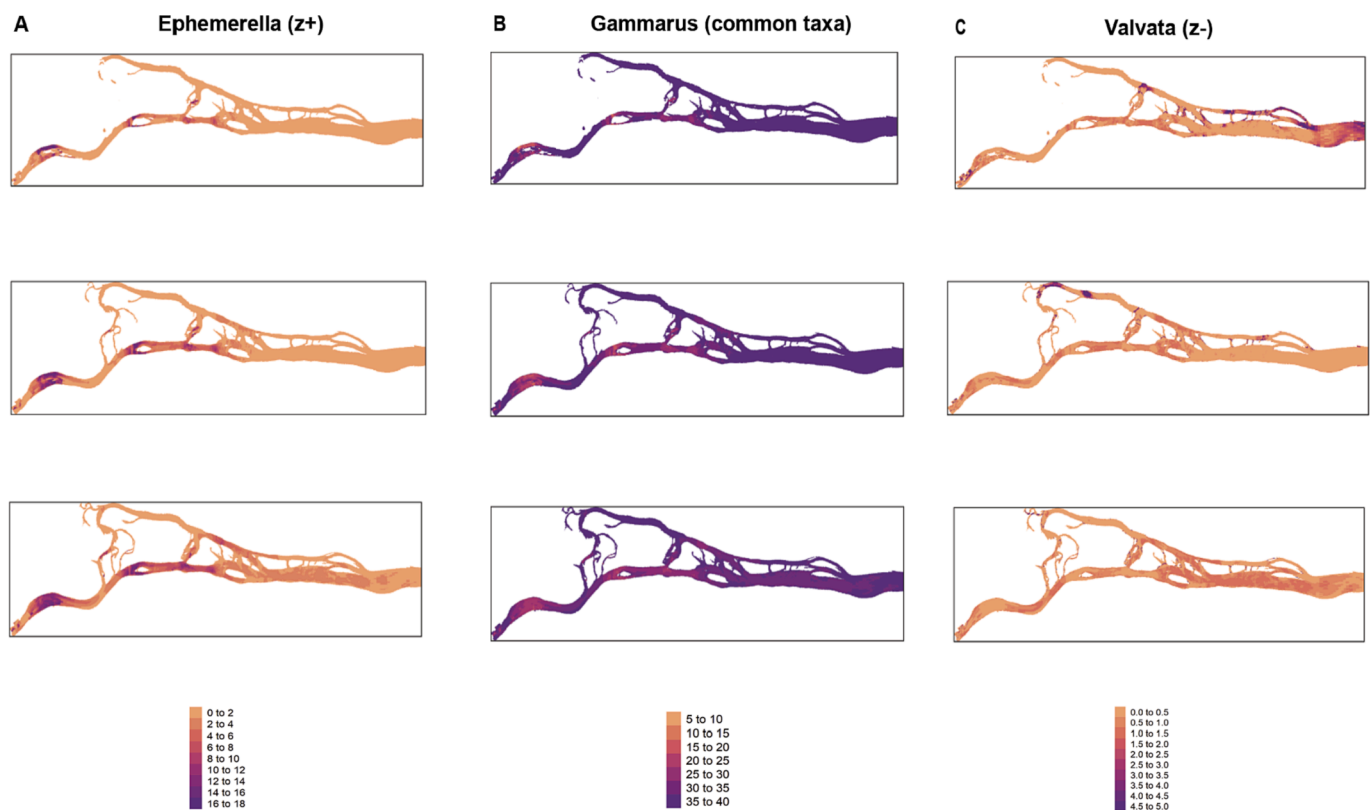

Fig. 6. Predicted relative abundance from GAMs of A) *Ephemerella*, B) *Gammarus*, and C) *Valvata*, with taxa grouped according to TITAN2 into increasers ($z+$), dominant taxa and decreasers ($z-$) along an environmental gradient of Froude number at a range of typical summer flow conditions (175 m³s⁻¹ top panels, 425 m³s⁻¹ middle panels, 990 m³s⁻¹ bottom panels). Low relative abundance sites are shown in orange, whereas, areas with highest predicted relative abundance are shown in purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

number of genera (e.g., Limnephilidae). Although spatial and taxonomic coverage of species distribution, dispersal and habitat preferences in public databases is improving considerably with the advent of large-scale environmental monitoring (Sarremejane et al., 2020; Schmidt-Kloiber and Hering, 2015; Vieira et al., 2006; Tachet et al., 2010; Laini et al., 2022), ecological preference data of numerous taxa at lower taxonomic levels is uncertain or often not available. Our study identified 33 indicator genera for flow velocity, providing important ecological information for large river BMI assemblages, and potentially contributing to trait records for these taxa.

4.3. Modeling assemblage change under flow scenarios

Development and management linked to human water needs alter the natural flow regime of rivers and these impacts are exacerbated by climate change (Dyer et al. 2014; Poff and Ward 1990; Tickner et al. 2020). Globally, altered flows and habitat fragmentation are having a severe impact on biodiversity within river ecosystems (Barbarossa et al., 2020; Reid et al., 2019; Wang et al., 2020). Flow releases from hydropower reservoirs are targeted to meet societal energy demands, consequently homogenizing river flows (Poff et al., 2007; Tonkin et al., 2018), dampening seasonal floods (Acreman et al., 2014; Yarnell et al., 2015), and interrupting sediment transport as well as migration pathways for biota (Baldan et al., 2020; Wohl et al., 2015). In Europe alone, over a million barriers are impacting the structure and function of streams and rivers (Belletti et al., 2020), which highlights the importance of implementing monitoring programs and tools to guide the protection of these systems. Wang et al. (2021) identified differences in taxonomic richness and beta diversity between regulated and unregulated rivers, with changes to flow, connectivity, temperature, and water chemistry contributing to changes in composition downstream of dams. These flow alterations drive changes in structure and function of aquatic and riparian assemblages, for example shifting assemblage structure to a greater dominance of more disturbance-tolerant taxa. Recovery of assemblages downriver of dams may not be evident for several km, depending on the severity of impacts from hydrologic alteration (Mellado-Díaz et al. 2019).

The distribution and availability of suitable hydraulic habitat patches is highly dependent on discharge conditions, as exemplified by three modelled flow scenarios covering the range of field sampling conditions. $z+$ taxa showed the highest change points in frequency and abundance in riffle sections with coarse substrates in the upstream half of the study area, particularly at the upper flow range of 990 m^3/s, while negative indicator taxa ($z-$) showed the highest magnitude of change in slow flowing study reaches at the side and main channel. However, estimates of aquatic habitat in hydropower regulated rivers have been shown to be sensitive to the type of calibration and friction law applied in shallow habitats (Cassan et al. 2022), resulting in the lower model performance at low flows. There are inherent inaccuracies associated with field measurements of flow in large rivers (e.g., blanking distance at the riverbed, estimations made at the edges of the transects, transect line track) that are most pronounced at the lowest flows, and calibration with additional transect measurements at the lower flow range may be necessary to reduce uncertainty in environmental flow recommendations.

Climate-induced changes in future flow regimes need to be considered when setting environmental flow objectives. While our study utilised a steady-state flow model, dynamic models that consider changes to the timing, duration, and frequency of flow events would provide a more accurate representation of flow conditions that is more strongly linked to ecological response. For example, an increased frequency and duration of low flow periods could result in altered local shear stress conditions and a reduction in the sediment transport capacity of rivers. As a result, sensitive species such as freshwater pearl mussels may be threatened through increased fine sediment deposition in benthic habitats (Baldan et al., 2021; Baldan et al., 2020). Wegscheider et al. (2022) modelled future flows in a changing climate in the W|SJR, and predicted prolonged duration of low flow events during the summer months, with potential negative implications for habitat quality of rheophilic fish species. Similar responses can be expected for rheophilic BMI that were mostly constrained to riffle sections in the upstream half of the study area, highlighting the need to set ecologically based environmental flow targets in the W|SJR.

4.4. Management implications

Assemblage responses to river flows could be used to develop environmental flow targets to maintain and support habitats of a diverse set of taxa with often contrasting ecological preferences. In our study, we estimated the assemblage change point along a flow gradient, which indicates the flow conditions at which the BMI assemblage changes from one dominated by taxa associated with low flows to one dominated by taxa associated with high flows. Such information could be used in a management context to set flow targets and understand how flow alteration could lead to large-scale shifts in assemblage composition, particularly if such information is coupled with modelling of future flows across large river habitats. Furthermore, we identified individual taxa that responded negatively or positively to flow, and quantified abundance-flow relationships for those taxa to predict their response to different flow conditions. By establishing and pairing these relationships with spatial hydrodynamic models, we provided an example of how managers could use estimates of flow habitat availability to understand the implications of different flow operations and how high or low flows could result in loss or gain of habitat for indicator taxa. Linking response curves of BMI assemblages to hydrodynamic models offers a new tool to develop and test environmental flow objectives, considering a wide range of habitat requirements of species. The findings and methods of this study can be transferred to other large rivers with multi-pressure environments, and represent useful tools to support biomonitoring and environmental flow programs in Canada and across the world.

CRediT authorship contribution statement

Bernhard Wegscheider: Conceptualization, Developing methods, Data analysis, Preparation of figures and tables, Conducting the research, data interpretation, writing. **Wendy A. Monk:** Conceptualization, Developing methods, Data analysis, Preparation of figures and tables, Conducting the research, data interpretation, writing. **Jennifer Lento:** Conceptualization, Developing methods, Data analysis, Preparation of figures and tables, Conducting the research, data interpretation, writing. **Katy Haralampides:** Developing methods, Data analysis. **Mouhamed Ndong:** Developing methods, Data analysis. **Tommi Linnansaari:** Conducting the research, data interpretation, writing. **R. Allen Curry:** Conceptualization, Conducting the research, data interpretation, writing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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