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RESEARCH ARTICLE

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Seasonal effects of a hydropeaking dam on a downstream benthic macroinvertebrate community

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Abstract

As more hydroelectric dams regulate rivers to meet growing energy demands, there is ongoing concern about downstream effects, including impacts on downstream benthic macroinvertebrate (BMI) communities. Hydropeaking is a common hydroelectric practice where short-term variation in power production leads to large and often rapid fluctuations in discharge and water level. There are key knowledge gaps on the ecosystem impacts of hydropeaking in large rivers, the seasonality of these impacts, and whether dams can be managed to lessen impacts. We assessed how patterns of hydropeaking affect abundance, taxonomic richness, and relative tolerance of BMIs in the Saskatchewan River (Saskatchewan, Canada). Reaches immediately (<2 km) downstream of the dam generally had high densities of BMIs and comparable taxonomic diversity relative to upstream locations but were characterized by lower ratios of sensitive (e.g., Ephemeroptera, Plecoptera, and Trichoptera) to tolerant (e.g., Chironomidae) taxa. The magnitude of effect varied with seasonal changes in discharge. Understanding the effects of river regulation on BMI biodiversity and river health has implications for mitigating the impacts of hydropeaking dams on downstream ecosystems. Although we demonstrated that a hydropeaking dam may contribute to a significantly different downstream BMI assemblage, we emphasize that seasonality is a key consideration. The greatest differences between upstream and downstream locations occurred in spring, suggesting standard methods of late summer and fall sampling may underestimate ecosystem-scale impacts.

KEYWORDS

benthos, biotic index, hydropower dam, large river, Northern Great Plains, river health, seasonality

1 | INTRODUCTION

At present, a large majority of the world's river systems have at least one dam somewhere along their length (Nilsson, Reidy, Dynesius, & Revenga, 2005), with more planned for the future (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). The effects of dams on rivers have been well documented over the last several decades, from changes in river thermal (Olden & Naiman, 2010; Phillips, Pollock, Bowman, McMaster, & Chivers, 2015) and flow regimes (Poff, Olden, Merritt, & Pepin, 2007) to altered biological assemblages (Poff & Zimmerman, 2010) and water quality (Phillips, Davies, Bowman, & Chivers, 2016). Although it is a clean, renewable energy source compared with oil, gas, and coal burning, hydroelectric power generation also creates environmental impacts (Rosenberg et al., 1997). Hydropeaking, where rapid changes in discharge are used by hydroelectric facilities to produce power during daily peak demand, has recently become a focus for understanding effects on instream benthic macroinvertebrate (BMI) communities (Armanini et al., 2014;

Jones, 2013a; Jones, 2013b; Kennedy et al., 2016), but the impacts of hydropeaking operations are generally less well-known compared with the other dam impacts described above.

BMIs have been widely recognized as indicators of ecosystem integrity due to their wide tolerance spectrum to a variety of environmental disturbances (Bonada, Prat, Resh, & Statzner, 2006). Sensitive taxa such as most mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) tend to decrease in abundance and diversity in impacted rivers, whereas relatively tolerant taxa, including many chironomid species and oligochaetes, remain. Several metrics have been developed that use BMIs to quantify aquatic health, including the percentage of Ephemeroptera, Plecoptera, and Trichoptera (%EPT), the ratio of EPT to Chironomidae (EPT/C), and the modified Hilsenhoff's biotic index (BI; Plafkin et al., 1989; Mandaville, 2002). These metrics are often used in assessing the health of wadeable streams and small rivers but are rarely applied to large river systems (Jackson, Battle, & Sweeney, 2010). The EPT/C metric has long been used for evaluating the effects of general environmental disturbances (Hannaford & Resh, 1995; Karr, 1991). However, it is uncertain if the BI metric can indicate physical stress from hydropeaking, as its calculation uses taxa tolerance values that were developed for organic pollution. Studies are needed to test if BI can act as a general metric of disturbance.

Large rivers in the North American Great Plains naturally experience predictable fluctuations in discharge and depth throughout the year, rising with snowmelt and mountain runoff in the late spring and returning to baseflow by late summer (Poff, 1996). Dams regulate these fluctuations, often attenuating flood conditions by discharging less water over a longer period than the natural spring meltwater surge. Despite knowledge that patterns in BMI diversity and abundance are seasonally dependent (Linke, Bailey, & Schwindt, 1999), studies that have examined the impact of hydropeaking dams on BMI communities (e.g., Jones, 2013a, 2013b) are often conducted during the late summer, presumably to capture the highest diversity and later life stages of BMIs. This sample design does not capture the univoltine BMIs that develop and emerge in the spring and early summer, such as winter stoneflies and many mayfly species. How seasonal variations in flow overlaid by hydropeaking affect BMI life histories is poorly characterized.

Here, we assessed the potential effects of a daily hydropeaking dam on downstream BMI communities by comparing five downstream locations with three upstream reference locations sampled monthly during the ice-free season in 2014. We hypothesized that the BMI assemblages immediately downstream of the dam are affected by the hydropeaking operations and that river health, as calculated using BMI metrics such as EPT/C and BI, is compromised at these locations through a combination of abrupt changes in flow, considerable fluctuations in water level, and repeated wetting and drying of the riverbed (Kennedy et al., 2016). We also examined the potential for seasonal variation in effects by evaluating BMI assemblages across 5 months that varied considerably in flow conditions. Given the large number of extant dams, the common use of hydropeaking, and ongoing dam construction in many regions (Zarfl et al., 2015), understanding the effects of hydropeaking is a key step towards better understanding the costs and benefits of alternative flow management regimes (Jones, 2014).

2 | METHODS

The Saskatchewan River basin in Canada is one of North America's largest river basins (405,864 km^2), spanning three provinces and includes one of the largest freshwater deltas in the world (Partners for the Saskatchewan River Basin, 2009). This sand-dominated river begins in the Rocky Mountains of Alberta and discharges into Lake Winnipeg in Manitoba. Two main branches, the North Saskatchewan and South Saskatchewan rivers, merge to form the mainstem Saskatchewan River (Figure 1). Ice cover on the river typically lasts from late November to April, although this can vary annually. Two large hydro dams were commissioned along the river system: the Gardiner Dam in 1967 on the South Saskatchewan River and the E.B. Campbell Dam in 1963 on the mainstem of the Saskatchewan River. Together, these dams alter the seasonal and daily flow regime downstream (Gober & Wheater, 2014). The E.B. Campbell dam formed the Tobin Lake reservoir, and from 1963 to 2004, this hydropeaking dam operated in accordance with electricity demand, causing sudden changes in river depth downstream and occasionally stranding fish. This prompted Fisheries and Oceans Canada to establish a minimum flow requirement of 75 m^3 s^{-1} as a way to mitigate changes in water level. However, the river downstream continues to experience daily changes in discharge and depth due to hydropeaking practices (Figure 2, Figure A1); these changes attenuate downstream but are observable as far as 60 km from the dam (Euteneier, 2002).

A total of eight locations were sampled during the ice-free season of 2014: three upstream locations were chosen as reference areas, whereas five downstream locations were selected ranging from immediately below the dam (2 km) to ~50 km downstream (Figure 1). During the study, the ratio of daily maximum to daily minimum flows released from the dam was 1.2 ± 0.2 in June, 1.8 ± 0.9 in July, 3.0 ± 0.9 in August, and 4.6 ± 1.5 in September (Figure 2). Locations were chosen knowing that hydrological impacts of hydropeaking attenuate with increasing distance from the dam (e.g., Moog, 1993), but the two downstream sites most affected by hydropeaking are DS2 and DS3 because they are wider with shallower pitched shorelines compared with DS1 where the channel is narrower (Table A1, Watkinson, Ghamry, & Enders, 2019). The furthest site downstream, DS4, experiences lessened water level variability because of attenuation, but here, the river still rises and falls approximately 1 m during summer hydropeaking (T. Jardine, unpublished data). Below the dam, low water levels occur in early morning after reduced power generation overnight, so sites DS1 to DS3 were typically sampled in order starting early in the day to limit sampling in the varial zone and maximize sampling in the permanently wetted zone. In August and September, site DS4 was sampled at both high and low water to test for differences in communities in the varial and permanently wetted zone at this location.

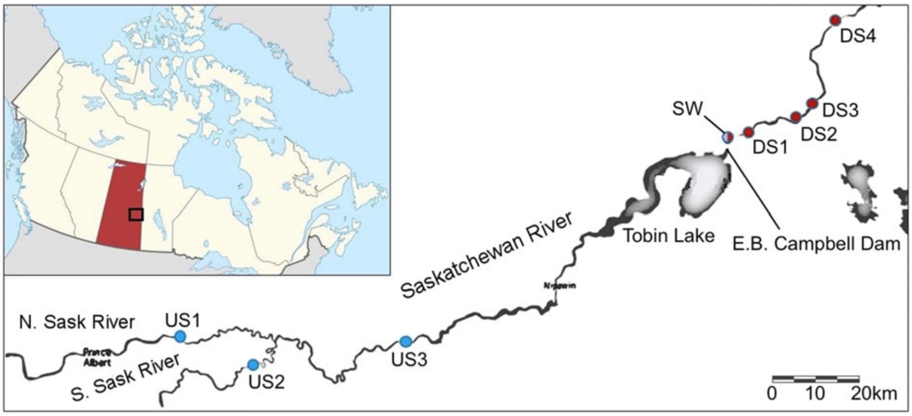

FIGURE 1 The portion of the Saskatchewan River system sampled in this study. Blue dots indicate upstream (reference) reaches, red dots are downstream (test) locations, and the split dot indicates the sampling location immediately downstream of E.B. Campbell Dam. The inset illustrates the sample area's location in Saskatchewan, Canada [Colour figure can be viewed at wileyonlinelibrary.com]

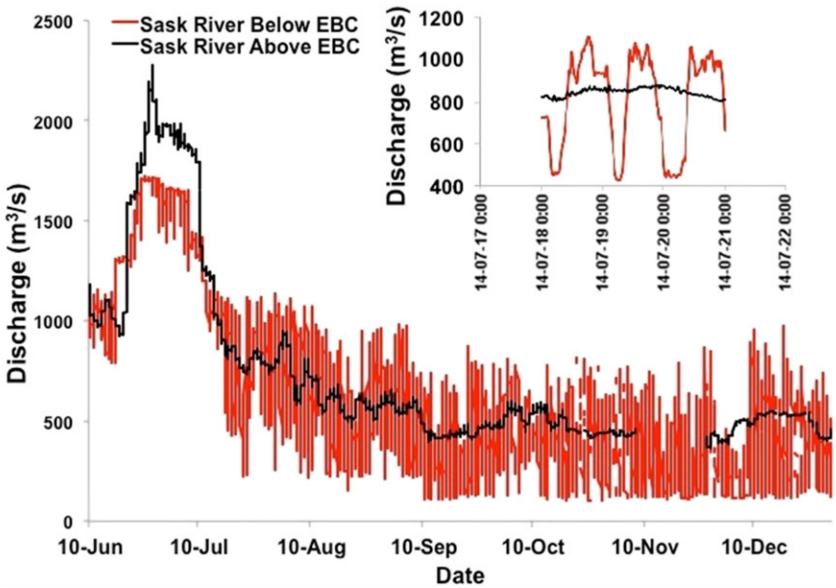

FIGURE 2 Discharge data for the Saskatchewan River above and below E.B. Campbell Dam for June–December of 2014 (Environment Canada gauges 05KD007 and 05KD003). The erratic changes in discharge downstream of the dam are the result of hydropeaking. Data from 12:00 am on July 18 to 12:00 am on July 21, 2014 illustrate the daily peaks and troughs in discharge experienced by the river downstream due to hydropeaking (inset). Data were not available for the upstream gauge prior to June 10 [Colour figure can be viewed at wileyonlinelibrary.com]

Samples were taken once per month from May to September and corresponded to seasonal changes in flows and associated hydropeaking, as higher discharges occur associated with the spring freshet (May to mid-July) compared with the daily hydropeaking schedule followed later in the season (mid-July to September; Figure 2). This period constitutes the bulk of the ice-free season (typically from April to November) and covers the period where water temperatures exceeded 12°C, above which most BMI taxa can grow and complete their life cycles. The location immediately below the dam is in a spillway channel (hereafter labelled “SW”), a part of the original river channel that was bypassed during construction. This channel normally consists of a series of small, isolated pools with little or no flow, except when discharges from the reservoir exceed the capacity of the power station (~1,000 m^3 s^{-1}), at which point, the spillway gates are opened, and these pools fully connect and flow. During the months of May and June 2014, the channel had high flow as the dam was releasing water from the spring melt, whereas the water returned to pools during the months of July, August, and September.

The sampling methods in this study followed a modified kick and sweep protocol for large rivers as described in the Saskatchewan Northern Great Plains Ecosystem Health Assessment Manual (Ministry of Environment (MoE) & Saskatchewan Watershed Authority (SWA), 2012). BMIs were collected using a standard D-frame kicknet with a 500 μm mesh and 0.3 m opening. Each sampled location was divided into three sublocations, each 100 m apart. The first sublocation was chosen haphazardly, and the remaining two were selected 100 m upstream from the previous. Samples were taken from shore to the deepest wadeable depth (one transect per sublocation) or until 1 min of sampling time elapsed. The entire contents of each sweep were preserved using 95% ethanol. Macroinvertebrates were identified to genus or, when practical, to species. Saskatchewan-specific keys were used to identify Ephemeroptera (Webb, 2002), Plecoptera (Dosdall, 1976), Trichoptera (Smith, 1984), and Hemiptera (Brooks & Kelton, 1967). All other taxa were identified using Merritt, Cummins, and Berg (2008). Sample area was estimated using the size of the net (0.3 m) and the total length of each sampling transect, which was then used to estimate BMI densities.

River health was estimated using taxa tolerance values summarized in Mandaville (2002) to calculate an overall BI using the following formula:

$$BI = \frac{\sum x_i t_i}{n}, \quad \text{(Eq.1)}$$

where x_i is the number of individuals of a species, t_i is the tolerance value of a species, and n is the total number of individuals. A low BI score indicates low levels of environmental stress (typically pollution) as there are more sensitive taxa present, whereas a high BI score is indicative of a stressed environment with a high proportion of tolerant taxa. The tolerance values for macroinvertebrates were originally based on their resistance to organic pollution (Plafkin et al., 1989; Mandaville, 2002). In contrast, the use of EPT/C is known for its applicability to a variety of environmental disturbances beyond pollution (Mandaville, 2002). An EPT/C score was also calculated for each location, using the ratio of sensitive taxa (Ephemeroptera, Plecoptera, and Trichoptera) to Chironomidae (a relatively tolerant group) plus one (EPT/C + 1) to account for areas without chironomids. To assess community diversity, a Shannon's diversity score was calculated for each location. BI, EPT/C, and Shannon's diversity scores were calculated for all three sublocations before calculating mean scores for the site. A series of habitat variables, including water quality (pH, conductivity, turbidity, total suspended solids, total nitrogen and phosphorus, benthic and suspended chlorophyll *a*, and dissolved organic carbon) and substrate, was collected at each site on each visit (Supplementary material).

To compare upstream versus downstream communities, we used canonical correspondence analysis (CCA), analysis of similarities (ANOSIM), and similarity percentages (SIMPER). CCA was done using R (version 3.4.2; R Project for Statistical Computing, Vienna, Austria) with the *vegan* and *lmom* packages. The ANOSIM and SIMPER analyses were done using PRIMER Version 6.1.13 (PRIMER-E software, Plymouth, United Kingdom; Clarke & Warwick, 2001). Prior to performing these analyses, we chose to adjust the community matrix by removing rare taxa that had a total abundance of ≤5 and had an occurrence of ≤4 in the matrix. Though removal can negatively impact otherwise significant differences in a dataset (Cao, Larsen, & Thorne, 2001), rare taxa can create "noise" that might obscure otherwise clear patterns (e.g., Reece, Reynoldson, Richardson, & Rosenberg, 2001). Nonbenthic taxa were completely removed from the dataset. Using this subset, the data were $\log_{(n+1)}$ transformed and used to calculate a taxa-by-taxa dissimilarity matrix using the Bray–Curtis dissimilarity metric that is commonly used for analysing BMI assemblages (Clarke & Warwick, 2001; Phillips et al., 2015). ANOSIM was used to compare average rank similarities of the benthic communities upstream and downstream of E.B. Campbell Dam. To evaluate which taxa were most responsible for any dissimilarity between upstream and downstream locations, a family-level SIMPER analysis was performed. All tests were done separately for each month of analysis. As our main purpose was to identify whether hydropeaking affects the BMI assemblage downstream, the site SW was omitted from the CCA, ANOSIM, and SIMPER analyses as it was not affected by hydropeaking.

3 | RESULTS

A total of 67,506 individuals from 237 different invertebrate taxa were collected. The number of taxa at each location ranged from 13 to 53 (Figure 3, Table A2). Mayflies were the most common taxa, with 17 families overall (Figure 3, Table A2) and ranged in abundance from 2 to 8,816 individuals m^{-2}. On the whole, taxonomic richness tended to increase throughout the sampling season, with the greatest change shown at SW, 2 km downstream of the dam in the spillway channel (Figure 3). Further downstream (8–30 km from dam), richness was

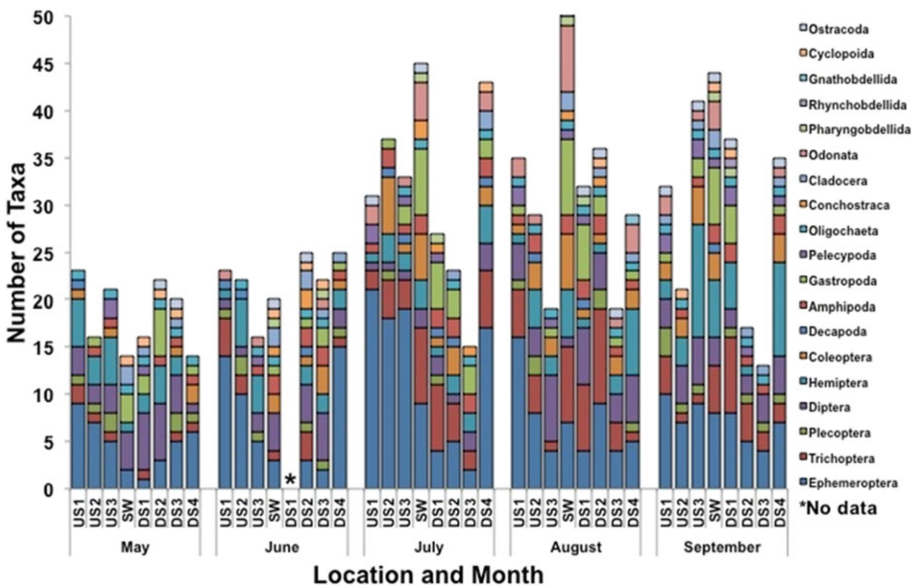

FIGURE 3 Benthic macroinvertebrate orders present at each location (labels as in Figure 1) in the Saskatchewan River across the months of May to September 2014 [Colour figure can be viewed at wileyonlinelibrary.com]

generally lower relative to sites US1 to US3 and SW. In contrast, DS4 (+53 km) was comparable with upstream locations.

In addition to changes in flow regime, the biophysical environment differed below the dam. In the river upstream of the dam, higher turbidity, TSS, and suspended chlorophyll *a* concentrations were typically observed relative to downstream (Table A2). In contrast, the downstream reaches appeared to have more benthic chlorophyll *a* and marginally higher DOC values compared with upstream. Higher concentrations of benthic chlorophyll immediately below the dam were observed between July and September (Table A3). Total phosphorus was marginally higher at upstream locations, whereas pH, conductivity, and total nitrogen were similar among locations both upstream and downstream. Mean daily temperature appeared to fluctuate more at upstream locations compared with the regulated regime observed downstream (Figure A2). Additionally, warmer and cooler temperatures were recorded upstream from May–July to August–September, respectively, relative to downstream locations (Figure A2).

Average BMI density ranged from 39 to 2,477 individuals m^{-2} (Figure 4). Densities at upstream locations were relatively similar throughout the sampling season, whereas taxa had sharply increased densities at locations immediately below the dam (SW and DS1; +2 and +8 km) from July to September (Figure 4), largely due to an increase in tolerant taxa. Further downstream (+21 to +53 km), densities were similar to those found upstream (Figure 4).

Three indices of river health showed impairment at sites immediately below the dam. BI values were generally higher at SW (+2 km) and DS1 to DS3 (+8 to +28 km) (Figure 5). Mean BI values ranged from 3.40 to 5.64 upstream of the dam across seasons and were higher below the dam (range 4.45–7.65), especially from May to July, but this varied by location. The furthest site from the dam, DS4 (+53 km), had BI values that were within the range (95% confidence interval) of those observed at the upstream reaches in all months except July. Samples at this site taken at low and high water levels had similar BI values in August (low water = 5.21, high water = 4.92) but different BI values in September (low water = 7.00, high water = 5.74) because the latter low water sample contained only chironomids. Taxonomic richness at locations below the dam was comparable with those upstream (Figure 3), but Shannon's diversity scores

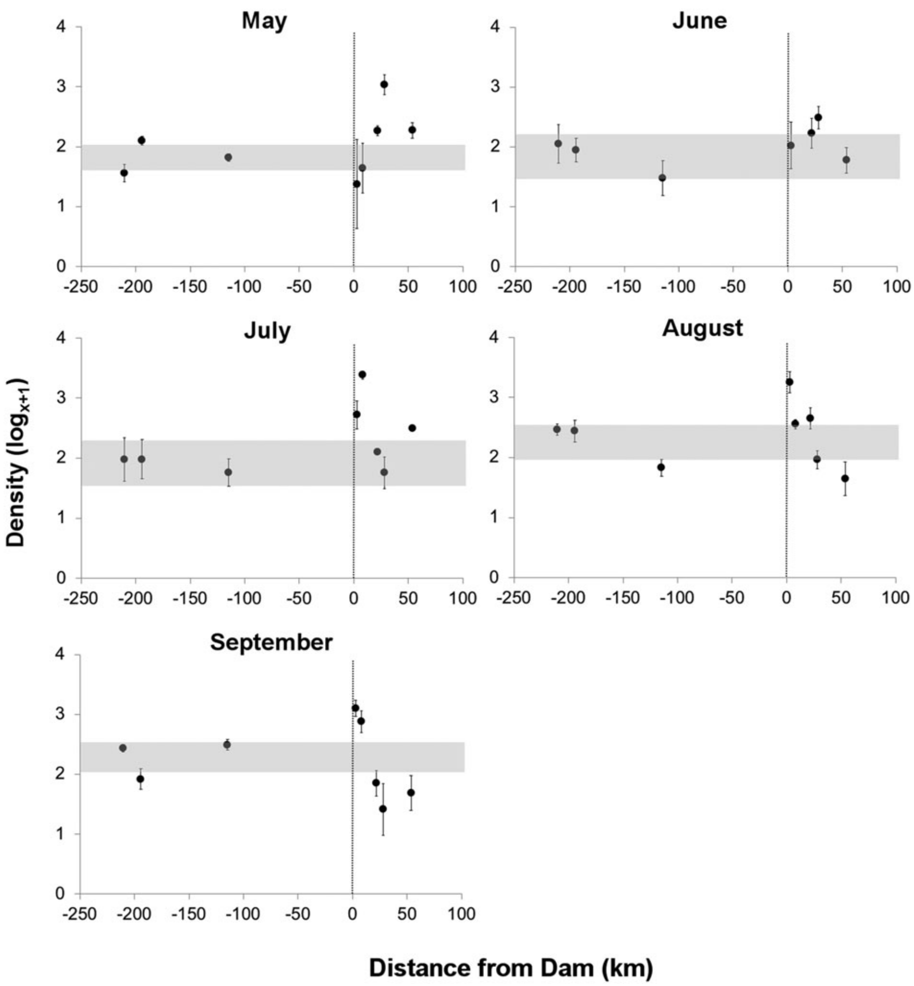

FIGURE 4 Benthic macroinvertebrate density ($\log_{x+1}$) across the sampling area versus the distance of each location from E.B. Campbell Dam, shown as a vertical dotted line, in kilometres. Distances upstream/downstream of the dam are depicted as negative/positive numbers, respectively. Grey boxes indicate the 95% CI for the upstream locations. Distances from the dam for each location are as follows: US1 (−210 km), US2 (−194 km), US3 (−114 km), SW (+2 km), DS1 (+8 km), DS2 (+21 km), DS3 (+28 km), and DS4 (+53 km)

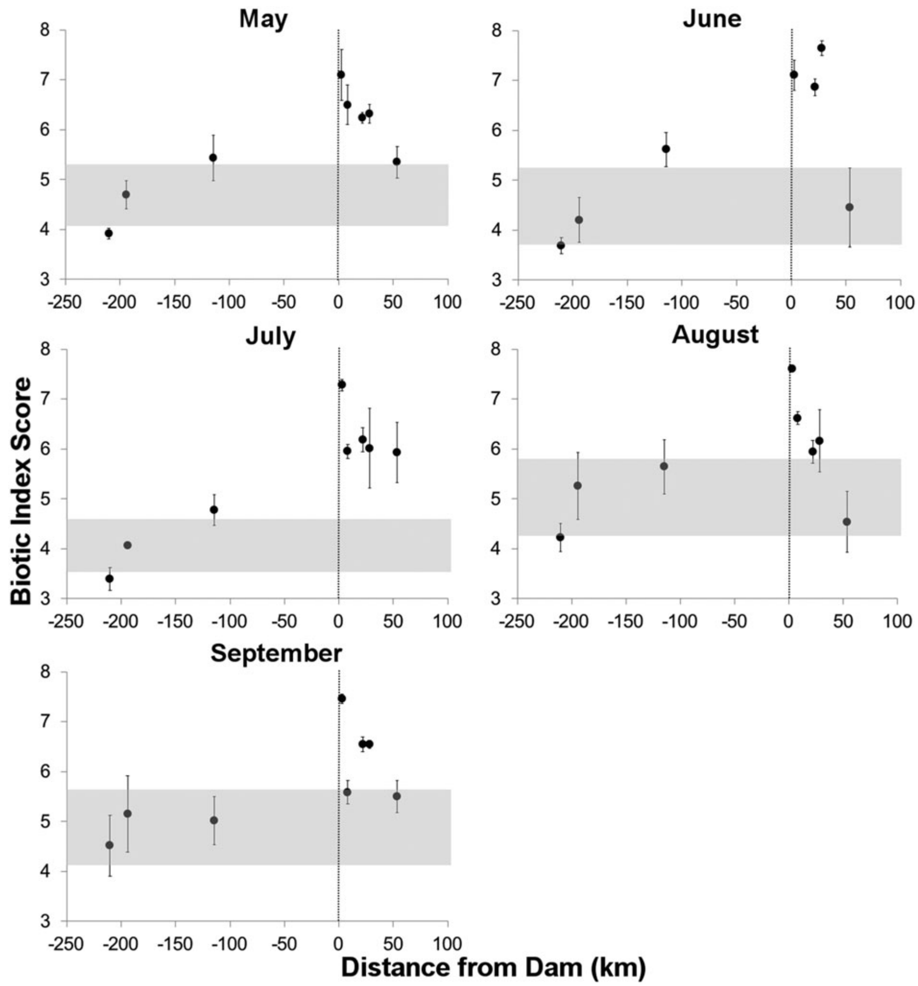

FIGURE 5 Biotic index scores for each location from May to September 2014 versus distance from E.B. Campbell Dam. Labels as in Figure 4

were generally higher at upstream locations compared with those immediately downstream of the dam, with only DS4 (+53 km) having values consistently comparable with those upstream (Figure 6). Mean EPT/C + 1 values were highest upstream of the dam (0.16 to 43.42 versus 0.03 to 7.39 downstream) and, like the BI, had values comparable with the upstream reference locations at the location furthest from the dam (Figure A3). In a comparison of monthly BI to EPT/C + 1 scores, a general negative correlation was observed in the first 3 months of sampling but not August and September (Figure A3).

The benthic assemblage at SW (+2 km) and DS1 (+8 km) varied from other locations, with high densities of tolerant taxa including amphipods and *Caenis* mayfly larvae from July to September. As these taxa are typically associated with lentic environments, the reach of the river downstream where these species were in high abundance was deemed the "lentic impact zone." This zone extended at least 8 km downstream, and lentic taxa abundance generally decreased with distance from the dam. To assess whether high amphipod densities at downstream locations were the main influence for increased BI scores, the scores for all locations were calculated in the absence of amphipods. This had little effect on BI scores across all locations, indicating that although they were present in high densities, amphipods were not the primary driver of BI scores.

Upstream and downstream locations had significantly different assemblages throughout all months even when including the furthest downstream location (ANOSIM, Table A3). Corixidae (Hemiptera), Baetidae (Ephemeroptera), Chironomidae (Diptera), and Hydropsychidae (Trichoptera) were among the families that contributed the most to differentiating upstream locations from those downstream (SIMPER, Table A3). Assemblages at upstream locations separated from those sampled downstream and those found immediately below the dam formed distinct clusters, whereas further locations (DS4; >50 km) become more similar to upstream communities (Figure 7).

4 | DISCUSSION

Large rivers are among the most impacted freshwater ecosystems in the world (Nilsson et al., 2005; Poff et al., 2007). Hydroelectric dams are common along these systems, and the effects of hydropeaking operations on downstream ecosystems have only recently been fully addressed, despite the large number of dams that practice hydropeaking (e.g., Jones, 2013a; Kennedy et al., 2016). The scale and scarcity of large rivers like the Saskatchewan have made it difficult

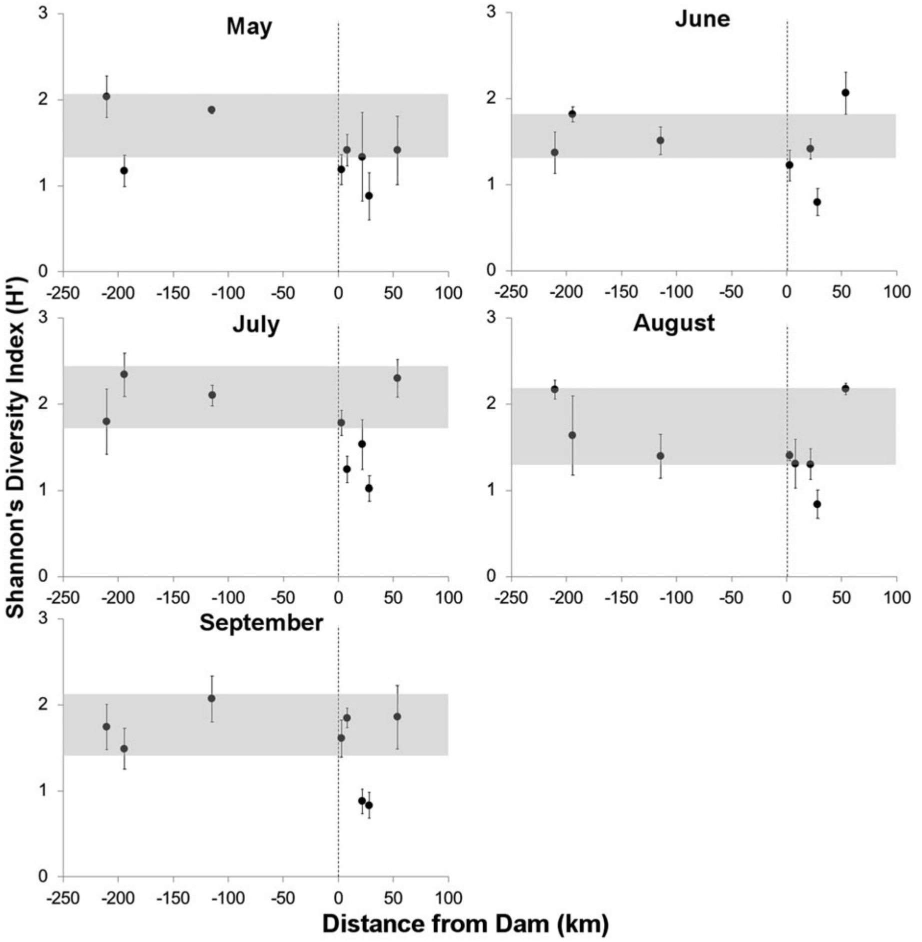

FIGURE 6 Shannon Diversity Index scores for each location from May to September 2014 versus distance from E.B. Campbell Dam. Labels as in Figure 4

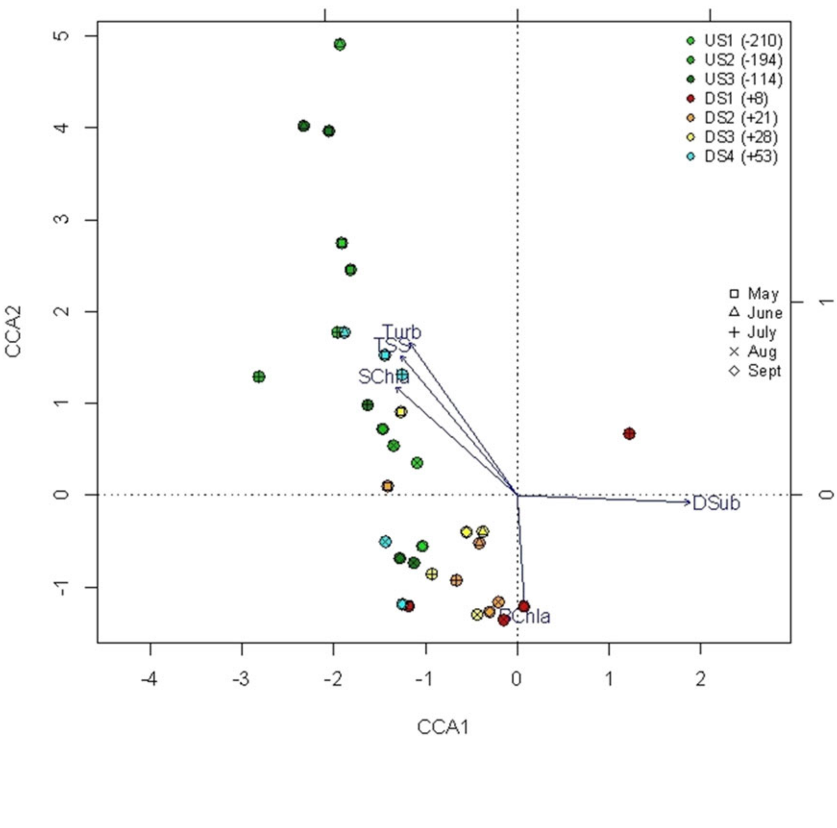

FIGURE 7 Canonical correspondence analysis illustrating the differences in benthic macroinvertebrate community structure at seven locations along the Saskatchewan River. Locations upstream of E.B. Campbell dam are green; downstream are red, orange, yellow, and light blue. Numbers in brackets represent distance upstream (negative) and downstream (positive) from E.B. Campbell Dam in kilometres. Turb = turbidity, TSS = total suspended solids; SChla = suspended chlorophyll *a*; BChla = benthic chlorophyll *a*; DSub = dominant substrate [Colour figure can be viewed at wileyonlinelibrary.com]

to quantify the effects of anthropological disturbances, and traditional reference condition approaches often cannot be applied to these systems (Phillips et al., 2015). Additionally, the majority of hydropeaking studies have not considered the possible effects of seasonality on benthic communities as most of them are conducted in the late summer months (August–September) when the extent of flow variation can be high and the mean daily flows relatively low. Our key findings included altered benthic assemblages below the dam along with increased BI and decreased EPT/C scores compared with upstream locations, indicative of deteriorated river health. Seasonality in hydropeaking was reflected in the changes to downstream BMI community tolerance, density, and diversity.

Immediately downstream of the dam in the spillway channel (SW; +2 km), the benthic assemblage consisted mainly of tolerant taxa usually found in lentic environments (e.g., amphipods, *Caenis* mayfly larvae). These taxa were found in very high abundance from July to September after flow through this reach had ceased but were absent from May to June samples when this channel was used as a spillway to accommodate high flows. Unlike the other downstream reaches, SW was not subjected to daily hydropeaking from July to September, resulting in little to no flow and much higher abundances of lentic taxa. Although it does not reflect daily hydropeaking, SW is still subjected to seasonal changes in flow and more likely reflects changes that would occur when large reservoirs are used primarily for extraction (e.g., irrigation supply) and only release water during extreme high flow events.

Because amphipods have relatively high tolerance to environmental disturbances and were found in high densities immediately below the dam, these areas had correspondingly high BI values. Surprisingly, the removal of amphipods did little to change the BI scores across all locations, even when their numbers were in the thousands. Therefore, downstream benthic communities changed in composition in terms of their tolerance to disturbance, and the dominant taxon was not solely responsible for that change. Chironomidae were also found in very high densities below the dam, a taxon that is highly tolerant to environmental disturbance. Amphipods are a mainly lentic taxon that helped define the lentic impact zone found downstream. We assume they were flushed downstream from the reservoir and previously isolated spillway pools during high flows in May and June. It is recommended that the lentic impact zone be accounted for in future projects and sampling designs that assess the effects of impoundments on river health, as its size may vary annually and seasonally. Doing so would require classifying taxa as lentic or lotic according to available guides (e.g., Merritt et al., 2008), determining if there are spatial gradients in the proportion of lentic taxa, and removing those taxa from analysis as appropriate. The macroinvertebrate community at the first riverine site downstream, DS1 (+8 km), also consisted of high densities of taxa in the filter-feeding functional group (e.g., Hydropsychidae) from mid to late summer, similar to findings in the regulated Magpie River system (Jones, 2013a). As proposed by Richardson and Mackay (1991), these filter-feeding communities are probably sustained by plankton that originated in the reservoir.

Further downstream (>20 km from the dam), BMI abundance and diversity were much lower. At DS2 (+21 km) and DS3 (+28 km) in August and September, daily hydropeaking was most severe because of a low-pitched shoreline that results in large changes in water level. Our CCA shows that these two sites tend to be similar to each other yet distinct from other downstream sites (Figure 7). Macrophytes that often harbour high BMI abundance relative to bare substrate in deeper parts of the channel (Needham, 1934) were absent at sites between 21 and 53 km downstream, likely due to the change in substrate (cobble and coarse gravel to sand) and the rapid fluctuations in water level resulting from daily hydropeaking (J. Mihalicz, pers. obs.). Bejarano, Jansson, and Nilsson (2018) reviewed the effects of hydropeaking on riverine plants and concluded that abrupt changes in water level and flow have a marked effect on vegetation in the riparian zone. This suggests that the absence of macrophyte growth at our downstream locations is likely due to hydropeaking.

Water quality parameters differed substantially between upstream and downstream locations, especially chlorophyll *a* (benthic and suspended) and turbidity (Table A1). These differences may contribute to the change in benthic assemblage composition observed below the dam (Figure 7). Higher benthic chlorophyll *a* concentrations at locations immediately below the dam, likely owing to greater light penetration in clearer waters, translate to greater food source availability for BMIs, which may explain the dense populations of tolerant taxa found there including gastropods and caenid mayflies. Lower turbidity values downstream of the dam are likely due to the loss of suspended load in the reservoir. These changes highlight how additional physical alterations to river habitat resulting from hydropeaking can consequently affect water quality and, ultimately, the biotic community (Melcher et al., 2017).

Although literature on the effects of hydropeaking on river biota is becoming more common (e.g., Jones, 2014; Kennedy et al., 2016; Melcher et al., 2017), the macroinvertebrates in many studies are collected in late summer or early autumn. In doing so, it is probable that many emergent insect species are not accounted for and thus any effects of hydropeaking on these taxa remain unknown. Benthic assemblages vary not only from 1 year to the next but seasonally as well (Peterson, Hunt, Marineau, & Resh, 2017). For example, in our data set, univoltine *Isoperla* sp. stoneflies were relatively common at upstream sites in May and June but were effectively absent in the remaining 3 months. Warmer waters upstream in May could also have accelerated development and emergence of this taxa. As the composition of the downstream macroinvertebrate communities changed from one month to the next with the emergence of some taxa, the overall tolerance of the community remained relatively high compared with upstream reaches. Yet differences were greatest in the months May to July, with all four nearest downstream sites falling outside the 95% confidence intervals defined by the upstream reference sites. This suggests that late summer/autumn sampling of BMI communities may underestimate the general effects of hydropeaking. However, the high water levels that we encountered during May and June meant that our sampling largely occurred in recently wetted areas at all locations, perhaps misrepresenting resident biota throughout the study system. The interplay between mean flow conditions, changes in extent of hydropeaking, and biotic sensitivity should be considered in individual rivers when considering sampling design.

Despite our best efforts, studying large rivers presents a unique set of challenges. Their size can make it difficult to quantify the effects of impacts both longitudinally and laterally. In the present study, macroinvertebrates were sampled from one side of the river in the near shore, varial zone but not from deeper parts of the channel. Many species would not have been collected with our methods, and the use of other techniques and instruments would be required to sample them (e.g., Peterson grab sampler and Hess sampler). Taxa that are sensitive to regular wetting and drying are more likely to be found in deeper areas of the channel below hydropeaking facilities, whereas tolerant species tend to inhabit the edge habitat (Jones, 2013b; Kjaerstad, Arnekleiv, Speed, & Herland, 2018). This speaks to key questions regarding sampling design to understand impact. Our methods may be overly sensitive, showing a greater proportion of tolerant taxa than if the whole channel was sampled. This can be beneficial in assessing impacts but may overestimate them at the ecosystem scale. In the case of the Saskatchewan River below E.B. Campbell, the varial zone can constitute up to one third the wetted width (Watkinson et al. 2019). As such, changes to the BMI community in this zone only would still constitute a considerable change to the overall community, even if the assemblage in the permanently wetted zone remains unchanged.

Determining river health often requires the use of several metrics to assign a score to the reach in question. In our assessment, BI scores for reaches in the Saskatchewan River system were negatively correlated with their EPT/C (Figure A3). However, an important drawback of using EPT/C values is the use of specific taxa. The high densities of tolerant *Caenis* mayflies in August and September at downstream sites indicated healthy river conditions according to EPT/C, despite the BI metric suggesting otherwise (Figure A3). Our study, in conjunction with others (e.g., Borisko, Kilgour, Stanfield, & Jones, 2007), suggests that the tolerance values for organic pollution compiled by Mandaville (2002) for use with the Modified Hilsenhoff BI may be applicable to environmental disturbances more generally in aquatic systems and that metrics considering the entire benthic community may be preferred when determining ecosystem integrity. One such metric, the Canadian Ecological Flow Index, would be useful in hydropeaking contexts because it considers flow tolerances of taxa in a given sample (Armanini et al., 2014).

The present study has illustrated that the hydropeaking E.B. Campbell Dam supports a downstream BMI assemblage that has high densities and comparable species richness relative to upstream, but this assemblage is shifted to one characterized by tolerant, lentic-associated taxa. A key piece of environmental legislation in Canada, the Fisheries Act, currently assesses impacts of industrial operations on aquatic environments based on their effects on fishes, namely, through their habitat including provision of food (Fisheries act. RSC, 1985). As a result, this legislation would view the increased abundances of BMIs downstream of the dam as a positive effect while ignoring the change in the assemblage and, more importantly, overall tolerance to disturbance. Despite the establishment of a minimum flow requirement in 2004, discharge and water depth continue to change on a daily basis with effects apparent as far as 53 km downstream (Figure A1). Hydropeaking is an important means of matching power production to power requirements; however, we have found evidence that hydropeaking may contribute to the alteration of downstream biotic communities. Minimum flow requirements have many benefits, but more work is required to understand how to best manage dams to better mimic the natural flow regime, especially in systems dominated by multiple control structures that have competing demands for water. Integrated systems approaches that allow trade-offs among industrial and ecological uses will help mitigate current impacts of hydropower and hydropeaking and maintain its importance as part of the renewable energy portfolio.

DATA AVAILABILITY STATEMENT

Raw data at the genus level are available in the supporting information associated with this article (Table A2).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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