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Seasonal Effects of a Hydropeaking Dam on a Downstream Benthic Macroinvertebrate Community

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3 4	1	Seasonal Effects of a Hydropeaking Dam on a Downstream Benthic Macroinvertebrate
5 6	2	Community
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10	4	Running head: Hydropeaking effects on benthic macroinvertebrates
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42 43	18	Abstract
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45	19	As more hydroelectric dams regulate rivers to meet growing energy demands, there is
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47	20	ongoing concern about downstream effects, including impacts on downstream benthic
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49 50	21	macroinvertebrate (BMI) communities. Hydropeaking is a common hydroelectric practice where
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52	22	short-term variation in power production leads to large and often rapid fluctuations in discharge
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54	23	and water level. There are key knowledge gaps on the ecosystem impacts of hydropeaking in
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3 4	24	large rivers, the seasonality of these impacts, and whether dams can be managed to lessen
5 6	25	impacts. We assessed how patterns of hydropeaking affect abundance, taxonomic richness and
7 8	26	relative tolerance of BMIs in the Saskatchewan River (Saskatchewan, Canada). Reaches
9 10 11	27	immediately (<2km) downstream of the dam generally had high densities of BMIs and
12 13	28	comparable taxonomic diversity relative to upstream locations but were characterized by lower
14 15	29	ratios of sensitive (e.g. Ephemeroptera, Plecoptera, Trichoptera) to tolerant (e.g. Chironomidae)
16 17	30	taxa. The magnitude of effect varied with seasonal changes in discharge. Understanding the
18 19 20	31	effects of river regulation on BMI biodiversity and river health has implications for mitigating
21 22	32	the impacts of hydropeaking dams on downstream ecosystems. While we demonstrated that a
23 24	33	hydropeaking dam may contribute to a significantly different downstream BMI assemblage, we
25 26 27	34	emphasize that seasonality is a key consideration. The greatest differences between upstream and
27 28 29	35	downstream locations occurred in spring, suggesting standard methods of late summer and fall
30 31	36	sampling may underestimate ecosystem-scale impacts.
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34 35 26	38	Keywords: hydropower dam, benthos, large river, river health, seasonality, Northern Great
37 38	39	Plains, biotic index
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42 43	41	Introduction
44 45 46	42	At present, a large majority of the world's river systems have at least one dam
40 47 48	43	somewhere along their length (Nilsson et al., 2005), with more planned for the future (Zarfl et
49 50	44	al., 2015). The effects of dams on rivers have been well documented over the last several
51 52	45	decades, from changes in river thermal (Olden & Naiman 2010; Phillips et al., 2015) and flow
53 54 55 56 57 58	46	regimes (Poff et al., 2007) to altered biological assemblages (Poff & Zimmerman, 2010) and

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47	water quality (Phillips et al., 2016). While it is a clean, renewable energy source compared to oil,
48	gas, and coal burning, hydroelectric power generation also creates environmental impacts
49	(Rosenberg et al., 1997). Hydropeaking, where rapid changes in discharge are used by
50	hydroelectric facilities to produce power during daily peak demand, has recently become a focus
51	for understanding effects on instream benthic macroinvertebrate communities (Jones 2013a;
52	Jones 2013b; Armanini et al., 2014; Kennedy et al., 2016), but the impacts of hydropeaking
53	operations are generally less well known compared with the other dam impacts described above.
54	Benthic macroinvertebrates (BMIs) have been widely recognized as indicators of
55	ecosystem integrity due to their wide tolerance spectrum to a variety of environmental
56	disturbances (Bonada et al., 2006). Sensitive taxa such as most mayflies (Ephemeroptera),
57	stoneflies (Plecoptera), and caddisflies (Trichoptera) tend to decrease in abundance and diversity
58	in impacted rivers, while relatively tolerant taxa, including many chironomid species and
59	oligochaetes, remain. Several metrics have been developed that use BMIs to quantify aquatic
60	health, including the percentage of Ephemeroptera, Plecoptera, and Trichoptera (%EPT), the
61	ratio of EPT to Chironomidae (EPT/C), and the Modified Hilsenhoff's Biotic Index (BI; Plafkin
62	et al., 1989 in Mandaville, 2002). These metrics are often used in assessing the health of
63	wadeable streams and small rivers but are rarely applied to large river systems (Jackson et al.,
64	2010). The EPT/C metric has long been used for evaluating the effects of general environmental
65	disturbances (Karr, 1991; Hannaford & Resh, 1995). However, it is uncertain if the BI metric can
66	indicate physical stress from hydropeaking, as its calculation uses taxa tolerance values that were
67	developed for organic pollution. Studies are needed to test if BI can act as a general metric of
68	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 et al., 1999), studies that have examined the impact of hydropeaking dams on BMI communities (e.g. Jones, 2013a,b) 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 five 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).

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3 4	92	
5 6 7	93	Methods
7 8 9	94	The Saskatchewan River basin in Canada is one of North America's largest river basins
10 11	95	(405,864 km ²), spanning three provinces and includes one of the largest freshwater deltas in the
12 13	96	world (Partners for the Saskatchewan River Basin, 2009). This sand-dominated river begins in
14 15 16	97	the Rocky Mountains of Alberta and discharges into Lake Winnipeg in Manitoba. Two main
10 17 18	98	branches, the North Saskatchewan and South Saskatchewan rivers, merge to form the mainstem
19 20	99	Saskatchewan River (Fig. 1). Ice cover on the river typically lasts from late November to April,
21 22 22	100	although this can vary annually. Two large hydro dams were commissioned along the river
25 24 25	101	system: the Gardiner Dam in 1967 on the South Saskatchewan River and the E.B. Campbell
26 27	102	Dam in 1963 on the mainstem of the Saskatchewan River. Together, these dams alter the
28 29	103	seasonal and daily flow regime downstream (Gober & Wheater, 2014). The E.B. Campbell dam
30 31 32	104	formed the Tobin Lake reservoir, and from 1963 to 2004, this hydropeaking dam operated in
33 34	105	accordance with electricity demand, causing sudden changes in river depth downstream and
35 36	106	occasionally stranding fish. This prompted Fisheries and Oceans Canada to establish a minimum
37 38 39	107	flow requirement of 75 m ³ s ⁻¹ as a way to mitigate changes in water level. However, the river
40 41	108	downstream continues to experience daily changes in discharge and depth due to hydropeaking
42 43	109	practices (Fig. 2, Fig. A1); these changes attenuate downstream but are observable as far as 60
44 45 46	110	km from the dam (Euteneier, 2002).
40 47 48	111	A total of eight locations were sampled during the ice-free season of 2014: three
49 50	112	upstream locations were chosen as reference areas, while five downstream locations were
51 52	113	selected ranging from immediately below the dam (2 km) to \sim 50 km downstream (Fig. 1).
53 54 55 56 57 58 59	114	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 (Fig. 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 et al. 2018). 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. Samples were taken once per month from May-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 to the daily hydropeaking schedule followed later in the season (mid-July to September) (Fig. 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 labeled "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 (~1000 m³s⁻¹), at which point the spillway

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138	gates are opened and these pools fully connect and flow. During the months of May and June
139	2014, the channel had high flow as the dam was releasing water from the spring melt, whereas
140	the water returned to pools during the months of July, August, and September.

141 The sampling methods in this study followed a modified kick and sweep protocol for 142 large rivers as described in the Saskatchewan Northern Great Plains Ecosystem Health 143 Assessment Manual (MoE & SWA, 2012). Benthic macroinvertebrates were collected using a 144 standard D-frame kicknet with a 500 µm mesh and 0.3 m opening. Each sampled location was 145 divided into 3 sub-locations, each 100 m apart. The first sub-location was chosen haphazardly 146 and the remaining two were selected 100 m upstream from the previous. Samples were taken 147 from shore to the deepest wadeable depth (1 transect per sub-location) or until 1 minute of 148 sampling time elapsed. The entire contents of each sweep were preserved using 95% ethanol. 149 Macroinvertebrates were identified to genus or, when practical, to species. Saskatchewan-150 specific keys were used to identify Ephemeroptera (Webb, 2002), Plecoptera (Dosdall, 1976), 151 Trichoptera (Smith, 1984), and Hemiptera (Brooks & Kelton, 1967). All other taxa were 152 identified using Merritt et al. (2008). Sample area was estimated using the size of the net (0.3 m) 153 and the total length of each sampling transect, which was then used to estimate BMI densities. 154 River health was estimated using taxa tolerance values summarized in Mandaville (2002) 155 to calculate an overall BI using the following formula:

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

157 where x_i is the number of individuals of a species, t_i is the tolerance value of a species, and n is 158 the total number of individuals. A low BI score indicates low levels of environmental stress 159 (typically pollution) as there are more sensitive taxa present, whereas a high BI score is 160 indicative of a stressed environment with a high proportion of tolerant taxa. The tolerance values

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161	for macroinvertebrates were originally based on their resistance to organic pollution (Plafkin et
162	al., 1989, in Mandaville, 2002). In contrast, the use of EPT/C is known for its applicability to a
163	variety of environmental disturbances beyond pollution (Mandaville, 2002). An EPT/C score
164	was also calculated for each location, using the ratio of sensitive taxa (Ephemeroptera,
165	Plecoptera, and Trichoptera) to Chironomidae (a relatively tolerant group) plus one (EPT/C+1)
166	to account for areas without chironomids. To assess community diversity, a Shannon's diversity
167	score was calculated for each location. BI, EPT/C and Shannon's diversity scores were
168	calculated for all 3 sub-locations before calculating mean scores for the site. A series of habitat
169	variables, including water quality (pH, conductivity, turbidity, total suspended solids, total
170	nitrogen and phosphorus, benthic and suspended chlorophyll a, dissolved organic carbon) and
171	substrate, was collected at each site on each visit (Supplementary material).
172	To compare upstream versus downstream communities, we used canonical
173	correspondence analysis (CCA), analysis of similarities (ANOSIM), and similarity percentages
174	(SIMPER). CCA was done using R (version 3.4.2; R Project for Statistical Computing, Vienna,
175	Austria) with the vegan and lmom packages. The ANOSIM and SIMPER analyses were done
176	using PRIMER Version 6.1.13 (PRIMER-E software, Plymouth, United Kingdom; Clarke &
177	Warwick, 2001). Prior to performing these analyses, we chose to adjust the community matrix by
178	removing rare taxa that had a total abundance of ≤ 5 and had an occurrence of ≤ 4 in the matrix.
179	Though removal can negatively impact otherwise significant differences in a dataset (Cao et al.,
180	2001), rare taxa can create 'noise' that might obscure otherwise clear patterns (e.g. Reece et al.,
181	2001). Non-benthic taxa were completely removed from the dataset. Using this subset, the data
182	were $log_{(n+1)}$ transformed and used to calculate a taxa-by-taxa dissimilarity matrix using the
183	Bray-Curtis dissimilarity metric, which is commonly used for analyzing 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 similarity percentages (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. **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 (Fig. 3, Table A2). Mayflies were the most common taxa, with 17 families overall (Fig. 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 (Fig. 3). Further downstream (8-30km from dam), richness was generally lower

relative to sites US1 to US3 and SW. In contrast, DS4 (+53 km) was comparable to upstreamlocations.

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 to upstream. Higher concentrations of benthic chlorophyll immediately below the dam were observed between July and September (Table A3). Total phosphorus was

•	207	marginally higher at upstream locations, whereas pH, conductivity, and total nitrogen were
	208	similar among locations both upstream and downstream. Mean daily temperature appeared to
	209	fluctuate more at upstream locations compared to the regulated regime observed downstream
0 1	210	(Fig. A2). Additionally, warmer and cooler temperatures were recorded upstream from May-July
2 3	211	and August-September, respectively, relative to downstream locations (Fig. A2).
4 5 6	212	Average BMI density ranged from 39 to 2,477 individuals m ⁻² (Fig. 4). Densities at
6 7 8	213	upstream locations were relatively similar throughout the sampling season, whereas taxa had
9	214	sharply increased densities at locations immediately below the dam (SW and DS1; +2 and +8
1	215	km) from July-September (Fig. 4), largely due to an increase in tolerant taxa. Further
3 4 5	216	downstream (+21 to +53 km), densities were similar to those found upstream (Fig. 4).
6 7	217	Three indices of river health showed impairment at sites immediately below the dam.
8 9	218	Biotic index (BI) values were generally higher at SW (+2 km) and DS1 to DS3 (+8 to +28 km)
0 1	219	(Fig. 5). Mean BI values ranged from 3.40 to 5.64 upstream of the dam across seasons and were
2 3 4	220	higher below the dam (range 4.45 to 7.65), especially from May to July but this varied by
5 6	221	location. The furthest site from the dam, DS4 (+53 km), had BI values that were within the range
7 8	222	(95% confidence interval) of those observed at the upstream reaches in all months except July.
9 0 1	223	Samples at this site taken at low and high water levels had similar BI values in August (low
2	224	water = 5.21 , high water = 4.92) but different BI values in September (low water = 7.00 , high
4 5	225	water = 5.74) because the latter low water sample contained only chironomids. Taxonomic
6 7	226	richness at locations below the dam was comparable to those upstream (Fig. 3) but Shannon's
8 9 0	227	diversity scores were generally higher at upstream locations compared to those immediately
1 2	228	downstream of the dam, with only DS4 (+53 km) having values consistently comparable to those
3 4 5 6	229	upstream (Fig. 6). Mean EPT/C+1 values were highest upstream of the dam (0.16 to 43.42 versus

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3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20	230	0.03 to 7.39 downstream) and, like the BI, had values comparable to the upstream reference
	231	locations at the location furthest from the dam (Fig. A3). In a comparison of monthly BI to
	232	EPT/C+1 scores, a general negative correlation was observed in the first three months of
	233	sampling, but not August and September (Fig. A3).
	234	The benthic assemblage at SW (+2 km) and DS1 (+8 km) varied from other locations,
	235	with high densities of tolerant taxa including amphipods and Caenis mayfly larvae from July-
	236	September. As these taxa are typically associated with lentic environments, the reach of the river
	237	downstream where these species were in high abundance was deemed the 'lentic impact zone.'
21 22	238	This zone extended at least 8 km downstream, and lentic taxa abundance generally decreased
23 24 25	239	with distance from the dam. To assess whether high amphipod densities at downstream locations
25 26 27	240	were the main influence for increased BI scores, the scores for all locations were calculated in
28 29 30 31 32 33 34 35 36	241	the absence of amphipods. This had little effect on BI scores across all locations, indicating that
	242	although they were present in high densities, amphipods were not the primary driver of BI
	243	scores.
	244	Upstream and downstream locations had significantly different assemblages throughout
37 38	245	all months even when including the furthest downstream location (ANOSIM, Table A3).
39 40 41	246	Corixidae (Hemiptera), Baetidae (Ephemeroptera), Chironomidae (Diptera), and Hydropsychidae
41 42 43	247	(Trichoptera) were among the families that contributed the most to differentiating upstream
44 45	248	locations from those downstream (SIMPER, Table A3). Assemblages at upstream locations
46 47 48 49 50 51 52 53 54 55 56	249	separated from those sampled downstream, and those found immediately below the dam formed
	250	distinct clusters, whereas further locations (DS4; >50 km) become more similar to upstream
	251	communities (Fig. 7).

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4 5 6	253	Discussion
7 8 0	254	Large rivers are among the most impacted freshwater ecosystems in the world (Nilsson et
9 10 11	255	al., 2005; Poff et al., 2007). Hydroelectric dams are common along these systems and the
12 13	256	concerns of hydropeaking operations have only recently been fully addressed, despite the large
14 15 16	257	number of dams that practice hydropeaking (e.g. Jones, 2013a; Kennedy et al., 2016). The scale
17 18	258	and scarcity of large rivers like the Saskatchewan have made it difficult to quantify the effects of
19 20	259	anthropological disturbances, and traditional reference condition approaches often cannot be
21 22 22	260	applied to these systems (Phillips et al., 2015). Additionally, the majority of hydropeaking
25 24 25	261	studies have not considered the possible effects of seasonality on benthic communities as most of
26 27	262	them are conducted in the late summer months (August-September) when the extent of flow
28 29	263	variation can be high and the mean daily flows relatively low. Our key findings included altered
30 31 32	264	benthic assemblages below the dam along with increased BI and decreased EPT/C scores
33 34	265	compared to upstream locations, indicative of deteriorated river health. Seasonality in
35 36	266	hydropeaking was reflected in the changes to downstream BMI community tolerance, density,
37 38 30	267	and diversity.
39 40 41	268	Immediately downstream of the dam in the spillway channel (SW; +2 km), the benthic
42 43	269	assemblage consisted mainly of tolerant taxa usually found in lentic environments (e.g.
44 45	270	amphipods, Caenis mayfly larvae). These taxa were found in very high abundance from July-
46 47 48	271	September after flow through this reach had ceased, but were absent from May-June samples
49 50	272	when this channel was used as a spillway to accommodate high flows. Unlike the other
51 52	273	downstream reaches, SW was not subjected to daily hydropeaking from July-September,
53 54 55 56	274	resulting in little to no flow and much higher abundances of lentic taxa. Although it does not
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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.

278 Because amphipods have relatively high tolerance to environmental disturbances and 279 were found in high densities immediately below the dam, these areas had correspondingly high 280 BI values. Surprisingly, the removal of amphipods did little to change the BI scores across all 281 locations, even when their numbers were in the thousands. Therefore, downstream benthic 282 communities changed in composition in terms of their tolerance to disturbance and the dominant 283 taxon was not solely responsible for that change. Chironomidae were also found in very high 284 densities below the dam, a taxon that is highly tolerant to environmental disturbance. Amphipods 285 are a mainly lentic taxon that helped define the lentic impact zone found downstream. We 286 assume they were flushed downstream from the reservoir and previously isolated spillway pools 287 during high flows in May and June. It is recommended that the lentic impact zone be accounted 288 for in future projects and sampling designs that assess the effects of impoundments on river 289 health, as its size may vary annually and seasonally. Doing so would require classifying taxa as 290 lentic or lotic according to available guides (e.g. Merritt et al. 2008), determining if there are 291 spatial gradients in the proportion of lentic taxa, and removing those taxa from analysis as 292 appropriate. The macroinvertebrate community at the first riverine site downstream, DS1 (+8 293 km), also consisted of high densities of taxa in the filter-feeding functional group (e.g. 294 Hydropsychidae) from mid- to late summer, similar to findings in the regulated Magpie River 295 system (Jones, 2013a). As proposed by Richardson and Mackay (1991), these filter-feeding 296 communities are probably sustained by plankton that originated in the reservoir.

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297 Further downstream (>20 km from the dam), BMI abundance and diversity were much 298 lower. At DS2 (+21 km) and DS3 (+28 km) in August and September, daily hydropeaking was 299 most severe because of a low-pitched shoreline that results in large changes in water level. Our 300 CCA shows that these two sites tend to be similar to each other yet distinct from other 301 downstream sites (Fig. 7). Macrophytes, which often harbor high BMI abundance relative to bare 302 substrate in deeper parts of the channel (Needham, 1934), were absent at sites between 21 and 53 303 km downstream, likely due to the change in substrate (cobble and coarse gravel to sand) and the 304 rapid fluctuations in water level resulting from daily hydropeaking (J. Mihalicz, pers. obs.). 305 Bejarano et al. (2018) reviewed the effects of hydropeaking on riverine plants and concluded that 306 abrupt changes in water level and flow have a marked effect on vegetation in the riparian zone. 307 This suggests that the absence of macrophyte growth at our downstream locations is likely due to 308 hydropeaking.

309 Water quality parameters differed substantially between upstream and downstream 310 locations, especially chlorophyll a (benthic and suspended) and turbidity (Table A1). These 311 differences may contribute to the change in benthic assemblage composition observed below the 312 dam (Fig. 7). Higher benthic chlorophyll a concentrations at locations immediately below the 313 dam, likely owing to greater light penetration in clearer waters, translate to greater food source 314 availability for BMIs, which may explain the dense populations of tolerant taxa found there 315 including gastropods and Caenid mayflies. Lower turbidity values downstream of the dam are 316 likely due to the loss of suspended load in the reservoir. These changes highlight how additional 317 physical alterations to river habitat resulting from hydropeaking can consequently affect water 318 quality and, ultimately, the biotic community (Melcher et al., 2017).

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River Research and Applications

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 one year to the next, but seasonally as well (Peterson et al., 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 three 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 to 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,

341 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, 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 et al., 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 were 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 (DFO 2018). 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 (Fig. 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 (Fig. A3). Our study, in conjunction with others (e.g. Borisko et al., 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.

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River Research and Applications

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, 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 (Fig. 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.

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505 Figure legends

Fig. 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.

Fig. 2: Discharge data for the Saskatchewan River above and below E.B. Campbell Dam for

511 June-December of 2014 (Environment Canada gauges 05KD007 and 05KD003). The erratic

512 changes in discharge downstream of the dam are the result of hydropeaking. Data from 12:00 am

513 on July 18 to 12:00 am on July 21, 2014 illustrates the daily peaks and troughs in discharge

5 514 experienced by the river downstream due to hydropeaking (inset). Data were not available for the

515 upstream gauge prior to June 10th.

516 Fig. 3: Benthic macroinvertebrate orders present at each location (labels as in Figure 1) in the
517 Saskatchewan River across the months of May to September 2014.

Fig. 4: Benthic macroinvertebrate density (\log_{x+1}) across the sampling area versus the distance of

519 each location from E.B. Campbell Dam, shown as a vertical dotted line, in kilometers. Distances

520 upstream/downstream of the dam are depicted as negative/positive numbers, respectively. Grey

521 boxes indicate the 95% CI for the upstream locations. Distances from the dam for each location

³ 522 are as follows: US1 (-210 km), US2 (-194 km), US3 (-114 km), SW (+2 km), DS1 (+8 km), DS2

523 (+21 km), DS3 (+28 km), and DS4 (+53 km).

Fig. 5: Biotic index scores for each location from May-September 2014 versus distance from
 525 E.B. Campbell Dam. Labels as in Figure 4.

Fig. 6: Shannon Diversity Index scores for each location from May-September 2014 versus

527 distance from E.B. Campbell Dam. Labels as in Figure 4.

Fig. 7: Canonical correspondence analysis illustrating the differences in benthic macroinvertebrate community structure at 7 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 kilometers. Turb = turbidity, TSS = total suspended solids; SChla = suspended chlorophyll a; BChla = benthic chlorophyll a; DSub = dominant substrate



Figure 1





Fig. 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 illustrates the daily peaks and troughs in discharge experienced by the river downstream due to hydropeaking (inset).





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Fig. 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.



Fig. 4: Benthic macroinvertebrate density (logx+1) across the sampling area versus the distance of each location from E.B. Campbell Dam, shown as a vertical dotted line, in kilometers. 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).

529x564mm (72 x 72 DPI)











Fig. 7: Canonical correspondence analysis illustrating the differences in benthic macroinvertebrate community structure at 7 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 kilometers. Turb = turbidity, TSS = total suspended solids; SChla = suspended chlorophyll a; BChla = benthic chlorophyll a; DSub = dominant substrate

190x254mm (96 x 96 DPI)