River management alters ecosystem metabolism in a large oligotrophic river

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Abstract: Algae and aquatic plants support river food webs through in-situ primary production. However, gross primary production (GPP) and ecosystem respiration (ER) are rarely evaluated in the context of river management or habitat restoration. We estimated daily GPP and ER during 2 growing seasons for 7 reaches in the Kootenai River and 1 reach in the Elk River, spanning 290 river km across British Columbia, Canada, and Montana and Idaho, USA. We characterized responses of GPP and ER to river management, including reaches with unregulated flow, regulated flow, nutrient addition, and habitat restoration. Downstream GPP and ER generally increased after changes in river management, and higher management intensity led to greater increases. GPP and ER followed a seasonal pattern with low initial values in spring, elevated values in mid-summer, and a return to low values in late summer and autumn. Timing and duration of the elevated period for GPP and ER also differed among reaches following changes in river management. Our results suggest that river management affects GPP and ER, likely through reducing turbidity and the frequency and magnitude of extreme flow events, nutrient additions, and enhanced floodplain connectivity, thereby altering the timing and amount of autochthonous carbon available to the food web.

Key words: rivers, ecosystem metabolism, gross primary production, ecosystem respiration, nutrient addition, habitat restoration

Anthropogenic modification and management of river systems have altered hydrologic regimes (Vörösmarty and Sahagian 2000) and river ecosystems (Pringle 2000) worldwide (Naiman et al. 2005). On 60% of the largest rivers, dams, diversions, or other infrastructure exist (Revena et al. 2000), built for the purposes of producing hydropower, managing flood risk, providing navigation, and supplying water to agriculture, industry, and municipalities (Rosenberg et al. 2000, Vörösmarty and Sahagian 2000). Hydrologic alterations affect abiotic and biotic characteristics, including altered sediment transport, water chemistry, water temperature, flow regimes, and aquatic plant and animal communities (Jorde et al. 2007). Increasingly, the goal of river management is to ameliorate negative effects of prior anthropogenic modifications (Katz et al. 2007, Jähnig et al. 2010, Miller et al. 2010, Palmer et al. 2010).

Research investigating the biotic effects of dam and reservoir management have generally focused on organisms (e.g., fish, invertebrates, algae, macrophytes), rather than ecosystem processes (Olden et al. 2014). River ecosystem metabolism, gross primary production (GPP), and ecosystem respiration (ER) are processes that regulate carbon and nutrient cycling in river systems (Tank et al. 2010), linking abiotic factors, allochthonous inputs, and higher trophic levels. Advancements in automated sensors and statistical approaches allow for daily estimates of metabolism in rivers (Holtgrieve et al. 2010, Dodds et al. 2013, Demars et al. 2015, Appling et al. 2018). Improved and more numerous
metabolism estimates have furthered understanding of factors affecting river metabolism such as light, temperature, nutrients, organic matter, and flow regimes. However, measurements made over the course of a few days at a single reach are often used to characterize metabolism, even though multiple measurements, both temporally (Dodds et al. 2013) and spatially (Genzoli and Hall 2016), are necessary to accurately characterize metabolism across temporal and spatial gradients.

Stream size and landscape position influence river metabolism (Vannote et al. 1980), and GPP:ER ratios generally increase with stream order (Meyer and Edwards 1990, McTammany et al. 2003). Turbidity and light attenuation with depth may limit GPP and generally decrease GPP:ER in larger rivers (Vannote et al. 1980, Dodds et al. 2013). Most aquatic ecosystem metabolism work has focused on small streams, with limited work in larger rivers (Dodds et al. 2013, Hall et al. 2016). One difference between stream and river ecosystem metabolism is the location of primary producers, primarily benthos in smaller streams (Uehlinger et al. 2003), and a combination of benthos and plankton in larger rivers (Cole et al. 1992, Oliver and Merrick 2006, Ochs et al. 2013, Genzoli and Hall 2016). Also, although terrestrial invertebrates can account for around half of annual fish diets in small streams (Kawaguchi and Nakano 2001, Nakano and Murakami 2001, Kawaguchi et al. 2003, Baxter et al. 2007), food webs are largely dependent on in-situ primary production in large rivers (Thorp and Delong 2002, Cross et al. 2013).

Our understanding of river metabolism is improving (Dodds et al. 2013, Hall et al. 2016, Bernhardt et al. 2018), and many factors that affect river metabolism are influenced by river management. For example, reservoir operations alter relative rates of GPP and ER (Demars et al. 2011, Davis et al. 2012, Dodds et al. 2013, Hall et al. 2015, Bernhardt et al. 2018) by altering flow (Vörösmarty and Sahagian 2000) and temperature (Olden and Naiman 2010) regimes, impeding the flow of organic carbon, nutrients, and sediment (Jorde et al. 2007), and removing algal biomass (Poff et al. 1997). However, our knowledge is limited about how river management affects river metabolism (Slavik et al. 2004, Levi et al. 2013, Kupilas et al. 2017).

Case study

We used a case study of the Kootenai River (British Columbia, Canada, and Montana and Idaho, USA) and 1 of its tributaries to examine the effects of river management on ecosystem metabolism. The Kootenai River flows 781 km from the headwaters to its confluence with the Columbia River, draining ~50,000 km² in southeastern British Columbia, northwestern Montana, and northern Idaho (Fig. 1). For simplicity and clarity, we refer to this transnational river as Kootenai River, although it is spelled Kootenay in Canada. The Kootenai River originates in Canada’s Kootenay National Park north of Mt Assiniboine and flows south into transboundary Lake Koocanusa, a 135-km-long reservoir in British Columbia and Montana. After passing through Libby Dam, the river flows through northwestern Montana, west into Idaho, then north into British Columbia and through Kootenay Lake. It joins the Columbia River at Castlegar, 26 river km (Rkm) downstream of the lake. Major tributaries include the St Mary, Bull, and Elk rivers in Canada, and the Fisher, Yaak, and Moyie rivers in the USA. The St Mary and Bull rivers are upstream from Lake Koocanusa, the Elk River flows directly into Lake Koocanusa, and the remaining large tributaries flow into the Kootenai River downstream of Libby Dam.

Historically, the Kootenai River has been ultralotrophic (Snyder and Minshall 2005). However, mining activity has increased nitrogen loading to the Elk River, Lake Koocanusa, and the Kootenai River since 2005 (Dessouki and Ryan 2010, Teck et al. 2016), and the river is now considered oligotrophic (Ward et al. 2017). Phosphorus has been added to the Kootenai River at the Idaho—Montana border (276 Rkm) since 2006 to increase primary production and food resources available to declining fish populations (Hoyle 2012, Hoyle et al. 2014, Minshall et al. 2014). This whole-river nutrient addition altered algal communities in favor of more edible green algae and diatoms (Hoyle et al. 2014) and has increased macroinvertebrate richness and abundance (Minshall et al. 2014). Didymosphenia geminata cells in the Kootenai River were documented as early as 1866 (Lord 1866) and again following construction of Libby Dam (Perry and Huston 1983). Large mats of D. geminata were first noticed downstream of Libby Dam in the early 2000s (Hoffman and Marotz 2001).

Modifications to the Kootenai River include extensive levee construction and bank stabilization from 1920 to 1950 (Northcote 1973, Daley et al. 1981, Redwing Naturalists 1996) and construction of 7 dams to reduce flood risk and produce hydropower. Libby Dam, which was constructed in 1972 and formed Lake Koocanusa, reduced peak flow and increased base flow (Burke et al. 2009), increased fine sediment deposition despite a reduction in availability of fine sediment (Duke et al. 1999), reduced bed mobility (Burke et al. 2009), and altered nutrient levels (Woods 1982, Paragamian et al. 2002, Snyder and Minshall 2005, Dessouki and Ryan 2010). Biotic changes attributed to Kootenai River modifications include altered invertebrate population dynamics (Perry and Perry 1986), collapse of the Burbot (Lota lota) fishery (Paragamian 2000, Paragamian et al. 2000, Hardy and Paragamian 2013), a declining wild adult population of endangered Kootenai River White Sturgeon (Acipenser transmontanus) (Richards 1997, Duke et al. 1999, Paragamian et al. 2005), and reduced regeneration of black cottonwood (Populus trichocarpa) (Polzin and Rood 2000).

Libby Dam has a selective withdrawal system that provides dam operators some capacity to control the discharge of colder hypolimnetic water relative to warmer surface water, and by extension, the ability to influence downstream
water temperatures. River management strategies focused on recovery of Kootenai River White Sturgeon include increased spring dam discharge during spawning initiated in 1991 (Duke et al. 1999) and large-scale habitat restoration initiated in 2011 (Kootenai Tribe of Idaho 2016). Habitat restorations include increasing river depth, stabilizing banks, creating riparian buffers, creating and enhancing secondary channels and wetlands, creating eddy alcove habitat, creating and deepening pools, and installing large woody debris structures (Kootenai Tribe of Idaho 2016).

We estimated daily ecosystem metabolism for 2 growing seasons at 7 reaches of the Kootenai River and in 1 tributary to understand temporal and spatial patterns of ecosystem metabolism within the context of river management. Our 8 reaches had different river management including unregulated flow, regulated flow from dam operations, nutrient addition, and habitat restoration. In this study, habitat restoration refers to structural enhancements intended to improve fish and wildlife habitat. Our objectives were to: 1) characterize ecosystem metabolism across river management
in the Kootenai River watershed, 2) assess temporal and spatial patterns of ecosystem metabolism, and 3) examine potential influence of river management on observed patterns of GPP and ER. Characterizing ecosystem metabolism in the Kootenai River will provide resource managers another means to evaluate effectiveness of management strategies focused on increasing primary productivity and bottom-up controls on foodweb dynamics and on habitat restoration to enhance Kootenai River White Sturgeon and Burbot recovery. Previous ecosystem metabolism estimates in the Kootenai River (Snyder and Minshall 2005) indicated that primary production may be lower than pre-dam levels, and food and habitat limitations contributed to a declining Kootenai River White Sturgeon population (Snyder and Minshall 2005). However, ecosystem metabolism has not been characterized since 1995 (Snyder and Minshall 2005), and we use current approaches that are considered more reliable and representative (Demars et al. 2015).

METHODS

We collected data both in the field and from publicly-available datasets, estimated stream metabolism, and analyzed temporal and spatial patterns in metabolism to characterize how metabolism varied with river management. For field-collected data, we selected 8 sites, 7 of which are on the Kootenai River spanning 290 Rkm between Fort Steele, British Columbia, and Porthill, Idaho, USA (Fig. 1, Table 1). We included 1 site on the Elk River near Elko, British Columbia because this tributary has increased nitrogen loading and low phosphorus levels. Sites were grouped into 5 sections: unregulated Kootenai (UK), unregulated nitrogen (UN), regulated tailwater (RT), regulated phosphorus (RP), and regulated habitat restoration (RH) based on river characteristics and river management (Fig. 1). UK and UN sections are upstream of all impoundments and represent natural flow and temperature regimes with minimal riparian alteration or agricultural development. All other sections are downstream of Libby Dam and are subject to riparian alterations, agricultural development, regulated flows, and altered temperatures. Although we did not measure nitrogen or phosphorus concentrations, we assumed that concentrations during our study period were near the values reported in recent years (Table 2). From 2014 to 2016, nitrate levels ranged between 1.0 to 1.5 mg/L in the Elk River near UN (Teck et al. 2016). Downstream of Libby Dam, 2009 to 2011 summer nitrate concentrations ranged between 0.097 to 0.130 mg/L (Ward et al. 2017). For 2009 to 2011 summers, total dissolved phosphorus concentrations were 0.0024 mg/L upstream of the phosphorus addition site, 0.0048 mg/L downstream of the phosphorus addition site, and then decreased to upstream concentrations by Rkm 267 (Ward et al. 2017). RT and RP sections, between Libby Dam and the Moyie River confluence, are characterized by large cobble and gravel substrates, limited floodplain, and 2 to 3% macrophyte cover.

Table 1. General site characteristics including river km (Rkm), slope, and mean annual discharge (Q, m$^3$/s). Characteristics specific to the study period include mean (minimum–maximum) Q, mean river depth ($\bar{z}$, m), mean river width ($\bar{w}$, m), mean river velocity ($\bar{v}$, m/s), mean standardized air–water gas exchange rate ($\kappa_{CO2}$, ± standard error), and mean daily reach length (based on 1.6$\nu/k$). UK = unregulated Kootenai, UN = unregulated nitrogen, RT1 = regulated tailwater 1, RT2 = regulated tailwater 2, RP1 = regulated phosphorus 1, RP2 = regulated phosphorus 2, and RP3 = regulated phosphorus 3, RH = regulated habitat.

| Site | Rkm | Slope (%) | Mean annual Q | Year | $Q$ (m$^3$/s) | $\bar{z}$ | $\bar{w}$ | $\bar{v}$ | $\kappa_{CO2}$ (d) | Reach length (km) |
|------|-----|-----------|---------------|------|--------------|---------|------|------|----------------|-----------------|
| UK   | 519 | 0.07      | 171           | 2016 | 234 (85–662) | 2.5     | 109  | 1.13 | 5.8 ± 0.7 | 53              |
| UN   | 32  | 0.18      | 48            | 2016 | 52 (22–153)  | 0.9     | 70   | 0.96 | 6.6 ± 0.4 | 28              |
| RT1  | 348 | 0.07      | 327           | 2016 | 253 (116–792) | 2.2     | 136  | 0.96 | 5.8 ± 0.4 | 37              |
| RT2  | 333 | 0.08      | 327           | 2017 | 313 (119–735) | 2.3     | 137  | 1.07 | 4.7 ± 0.2 | 45              |
| RP1  | 274 | 0.09      | 391           | 2017 | 313 (119–735) | 2.3     | 137  | 1.07 | 4.7 ± 0.2 | 45              |
| RP2  | 267 | 0.08      | 391           | 2016 | 300 (128–1093) | 2.6     | 123  | 1.15 | 6.3 ± 1.1 | 35              |
| RP3  | 259 | 0.07      | 391           | 2017 | 382 (135–946) | 2.7     | 126  | 1.25 | 2.5 ± 0.2 | 77              |
| RH   | 229 | 0.03      | 412           | 2017 | 425 (141–1102)| 5.4     | 116  | 0.42 | 0.7 ± 0.2 | 55              |

* UN is at Rkm 32 on the Elk River, which flows into Lake Koocanusa at Kootenai River Rkm 457.
(Snyder and Minshall 2005). Extensive *D. geminata* mats were present in the RT section upstream of the nutrient addition site. RT sites are 4.8 and 20.5 km downstream of Fisher River inflow, and there is no tributary input between RT sites. Similarly, RP sites are 12.3 to 26.8 km downstream of Yaak River inflow, and there is no tributary input between RP sites. RP sites are situated downstream of the nutrient addition site and upstream of Moyie River inflow. The RH section is characterized by compacted lacustrine clay and fine sediment substrate with a meandering channel and 37% macrophyte cover between Bonners Ferry and Kootenay Lake (Snyder and Minshall 2005), and RH is downstream of habitat restoration and 30.3 km downstream of Moyie River inflow.

### Data collection

To estimate ecosystem metabolism, we used a miniDOT oxygen logger (Precision Measurement Engineering, Vista, California) to measure dissolved oxygen and water temperature at each site every 10 min from May through October 2016 and 2017. We calibrated dissolved oxygen and temperature measurements at the beginning and end of each season by placing all loggers in the same bucket of water and aerating at room temperature and 0°C following manufacturer instructions. We took measurements from May through October because high winter river discharge from Libby Dam limited river access from November through April. We periodically cleaned sensors in 2016, but periodic biofilm accumulation on the sensors interfered with oxygen measurements, and data were compromised. Therefore, we consistently cleaned and checked loggers every 2 wk in 2017. We qualitatively evaluated the oxygen data for evidence of biofilm accumulation. Distinct decreases in dissolved oxygen values following cleaning, along with increasing daily range of dissolved oxygen values, indicated biofilm accumulation on probes, and we removed affected data from analysis.

Additional data needed to estimate daily reach-scale metabolism (following Van de Bogert et al. 2007) include: river discharge (*Q*, m³/s), river depth and velocity, barometric pressure, air–water gas exchange rate (*k*), and solar insolation data. We obtained *Q* data from Water Survey of Canada and United States Geological Survey gaging stations within 30 km upstream of sites (Table S1). We estimated river depth and velocity as linear functions of discharge for each reach. We measured river width (*w*, m) and river depth (*z*, m) along transects perpendicular to river flow for each reach, repeating transect measurements on 5 to 8 d at different *Q*. We calculated velocity (*v*, m/s) as 

\[
 v = \frac{Q}{zw}
\]

(Table S2). The range of *Q* encountered during transect measurements encompassed 64 to 93% of the range of *Q* reported during our study period for Kootenai River reaches and 47% for the Elk River reach (Figs S1, S2). To estimate oxygen saturation in water, we used barometric pressure data reported by MesoWest for Cranbrook, British Columbia (UK and UN sites), Bonners Ferry, Idaho (all other sites), or Kalispell, Montana (if unavailable for Cranbrook or Bonners Ferry) in combination with dissolved oxygen and water temperature measurements (Garcia and Gordon 1992). Subsequently, we estimated *k* as the slope of the linear relationship between the dissolved oxygen rate of change and the difference between 100% oxygen saturation and estimated oxygen saturation from the time of darkness until dissolved oxygen reached equilibrium, following a nighttime regression approach (Hornberger and Kelly 1975). We used Schmidt number scaling to convert *k* to *k*₆₀₀, which standardizes *k* across variable water temperatures (Jähne and Haußecker 1998). We aggregated daily *k*₆₀₀ estimates to monthly mean *k*₆₀₀, seasonal mean *k*₆₀₀ and 7-d rolling mean *k*₆₀₀ for each site. We calculated reach length, the length of river contributing to our metabolism estimate, as reach length (km) = 1.6*v* / *k*₆₀₀, where *v* is the mean daily river velocity in units of km/d (Chapra and Di Toro 1991, Hall et al. 2012). Reach length represents the distance in which 80% of the dissolved oxygen has turned over in the water, and it varies daily in response to changes in *k*₆₀₀ and velocity mediated by *Q*. Finally, we estimated solar insolation for each site based on latitude and longitude (Yard et al. 2005).

### River metabolism

We estimated daily metabolism following van de Bogert et al. (2007):

\[
 mO_{2(t)} = mO_{2(t-\Delta t)} + \left( \frac{GPP}{z} \right) \left( \frac{PPFD_t}{PPFD_d} \right) + \left( \frac{ER}{z} \right) \Delta t + \left( k_{600} \left( O_{2sat(t)} - mO_{2(t-\Delta t)} \right) \right) \Delta t
\]

Table 2. Nutrient concentrations reported for the Kootenai and Elk rivers.

| Nutrient   | Location                                                                 | Date      | Concentration (mg/L) | Reference            |
|------------|--------------------------------------------------------------------------|-----------|----------------------|----------------------|
| Nitrate    | Elk River near our unregulated nitrogen site                             | 2014–2016 | 1.0–1.5              | Teck et al. 2016     |
| Nitrate    | Kootenai River downstream of Libby Dam                                  | 2009–2011 | 0.097–0.130          | Ward et al. 2017     |
| Phosphorus | Kootenai River upstream of phosphorus addition site                      | 2009–2011 | 0.0024               | Ward et al. 2017     |
| Phosphorus | Kootenai River downstream of phosphorus addition site                    | 2009–2011 | 0.0048               | Ward et al. 2017     |

**Note:** Additional data included: *Q*, m³/s; river depth and velocity; barometric pressure; air–water gas exchange rate; solar insolation.
where $mO_2(t)$ is modeled $O_2$ at time step $t$, $O_{2s(a)}(t)$ is measured $O_2$ saturation concentration at time step $t$, GPP and ER units are $g$ $O_2$ $m^{-2}$ $d^{-1}$, $z$ is mean hourly river depth, $PPFD(t)$ is solar insolation at time step $t$, $PPFD(d)$ is total daily solar insolation, $\Delta t$ is the length of the time step (10 min). We used an extended day length of 32 h, which included the 24 h for the day being calculated, the final 2 h of the preceding day, and the first 6 h of the following day. We fit the above equation to our measured oxygen data, estimating the parameters for GPP and ER that minimized the log-likelihood of a normal distribution (Genzoli and Hall 2016). We estimated river metabolism for sites UK, UN, RT1, RT2, RP1, and RP2 in 2016 and for all 8 sites in 2017.

At each site, we estimated metabolism based on the monthly, seasonal, and 7-d rolling mean $k_{600}$ estimates. To examine how $k$-aggregation methods affected model output, we used simple linear regression to relate metabolism estimates between $k$-aggregation methods. We used the 7-d rolling mean $k$ estimate for all GPP, ER, and GPP:ER estimates because there was little difference between $k$-aggregation methods. Linear relationships between GPP and ER estimates with different $k$-aggregation methods had slopes near 1 and y-intercepts near 0 (Fig. S3). Although $k$ and GPP as well as $k$ and ER were linearly related for most sites, the relationships have low $r^2$ values, indicating that our metabolism model is not overfitting with respect to $k$ except at the UK site (Fig. S4).

**Statistical analysis**

To examine temporal and spatial patterns in metabolism, we used 2 techniques: 1) changepoint detection of mean and variance, and 2) comparison of within and between sites based on analysis of variance and Tukey honest significant difference tests. We conducted all data processing and analysis in R (version 3.4.4; R Project for Statistical Computing, Vienna, Austria). To identify within-site temporal changes in metabolism, we used the cplyeanvar function from package changepoint (Killick et al. 2016), which identifies single and multiple changepoints within data (Killick and Eckley 2014). We used an asymptotic penalty and segmented-neighbor methods to look for $\sim$5 changepoints (Killick and Eckley 2014).

Based on these changepoints, we identified distinct temporal periods and evaluated differences in period characteristics including period start date, period duration, and mean metabolism. We described spatial differences in period start and period duration, which were both statistically derived based on occurrences of changes in mean and variance. We examined differences in mean metabolism temporally among periods for each individual site and spatially among sites for each period.

**RESULTS**

Daily metabolism ranged from 0 to 25.2 $g$ $O_2$ $m^{-2}$ $d^{-1}$ for GPP and from 0 to $-36.7$ $g$ $O_2$ $m^{-2}$ $d^{-1}$ for ER (Fig. 2).

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**Figure 2.** Daily ecosystem metabolism estimates, gross primary production (positive values), and ecosystem respiration (negative values) from May through October 2016 (black) and 2017 (gray). Panel labels indicate reach name arranged from upstream (upper left) to downstream (lower right): UK = unregulated Kootenai, UN = unregulated nitrogen, RT = regulated tailwater (2 sites), RP = regulated phosphorus (3 sites), and RH = regulated habitat.
The number of daily ecosystem metabolism estimates differed between temporal periods, sites, and years (Table 3). We estimated GPP and ER for the fewest number of days at the UK reach and at the RH reach (Table 3). In 2017, we estimated GPP and ER for more than 100 d at UN, RT1, RT2, RP1, RP2, and RP3 sites. Mean reach length ranged from 28 to 82 km and was longer in 2017 for all reaches with estimates in both years (Table 1).

**Temporal and spatial patterns**

Ecosystem metabolism varied temporally along the Kootenai River, roughly following the seasons with low initial values during spring, elevated values during summer, and reduced values during autumn. Timing and duration of elevated summer values differed among reaches and was asynchronous for GPP and ER in multiple reaches. Therefore, we classified these 3 distinct periods as initial, elevated, and reduced (Fig. 3A–C). Although these periods follow a seasonal pattern, use of terminology suggestive of time, such as spring, summer, or autumn, may obscure the differences in timing and duration we observed in 2017 among the 6 reaches with all periods identified (Figs 3A–C, 4). Few estimates at some reaches did not allow for identification of all periods within those reaches (Fig. 2).

Timing of the elevated period for GPP and ER differed among and within reaches in 2017. The elevated period for GPP and ER occurred latest at the UN reach (June 30). The elevated period for GPP started 9 to 11 d earlier (June 19–21) at reaches RT1, RT2, RP1, RP2, and RP3. The timing of the elevated period occurred asynchronously for GPP and ER at RT reaches where the start of elevated-period ER preceded that of GPP by 8 d at RT1 and 19 d at RT2 (Fig. 3A–C). In contrast, the start of elevated period occurred simultaneously for GPP and ER at UN, RP2, and RP3.

Duration of the elevated period differed among reaches. The elevated period was shortest at the UN reach (GPP: 25 d, ER: 26 d), intermediate at RT reaches (GPP: 50–53 d, ER: 38–68 d), and longest at RP reaches (GPP: 75–114 d, ER: 112–115 d). ER at RP3 (53 d) was an exception and was similar to RT sites (Fig. 3A–C). Elevated period duration for ER at RP1 included the initial period duration because values were similar between initial and elevated periods as described below. Similarly, elevated period duration for GPP at RP2 included the reduced period duration.

Both GPP and ER differed between temporal periods as evaluated for each reach and year individually. For example, at RT2 in 2017, GPP and ER differed between periods (GPP: F(2,132) = 208.8, p < 0.001; ER: F(2,115) = 102.8, p < 0.001). Post-hoc Tukey tests showed that GPP and ER for the elevated period were higher than for initial and reduced periods (Table 3). The one exception was RP2 in 2017, where ER during the reduced period was higher than the elevated period (Table 3). Reduced values were similar to initial values at all sites except RP1 and RP2 (both downstream of phosphorus additions). At RP1, ER at the initial stage was much higher than the reduced stage (Fig. 4, Table 3). The opposite pattern occurred at RP2, where GPP in the reduced stage was higher than GPP in the initial stage (Fig. 4, Table 3).

Ecosystem metabolism varied spatially for each period and year, generally increasing downstream (Fig. 3D–F, Table 3). GPP and ER values were lowest furthest upstream at UN for all temporal periods, and post-hoc Tukey tests

| Site     | Year | Gross primary production | Ecosystem respiration |
|----------|------|--------------------------|-----------------------|
|          |      | Initial | Elevated | Reduced | Initial | Elevated | Reduced |
| UN       | 2016 | 2.9 ± 0.2 (12) | 5.2 ± 0.1 (58) | – | – | – | – |
| RT1      | 2016 | 1.5 ± 0.3 (6)  | 7.1 ± 0.3 (35) | – | – | – | – |
| RT2      | 2016 | – | 13 ± 2.3 (11) | 5.8 ± 0.1 (36) | – | – | – | – |
| RP1      | 2016 | – | 8.3 ± 0.3 (12) | – | – | – | – |
| RP2      | 2016 | 5.3 ± 0.4 (10) | 14.4 ± 1.7 (5) | 7.3 ± 0.2 (49) | – | – | – | – |
| UN       | 2017 | 1.3 ± 0.2 (16) | 5.5 ± 0.2 (25) | 2.3 ± 0.1 (59) | – | – | – | – |
| RT1      | 2017 | 2.2 ± 0.1 (34) | 8.8 ± 0.4 (36) | 3.6 ± 0.1 (65) | – | – | – | – |
| RT2      | 2017 | 4.6 ± 0.2 (36) | 11.7 ± 0.4 (46) | 4.8 ± 0.1 (60) | – | – | – | – |
| RP1      | 2017 | 3.7 ± 0.5 (34) | 8 ± 0.2 (75) | 2.7 ± 0.1 (33) | – | – | – | – |
| RP2      | 2017 | 3.9 ± 0.1 (35) | 11.2 ± 0.3 (39) | 8.7 ± 0.2 (57) | – | – | – | – |
| RP3      | 2017 | 4.4 ± 0.1 (17) | 9.4 ± 0.3 (49) | 5.3 ± 0.5 (14) | – | – | – | – |
showed that GPP and ER at UN differed from all other sites in both years except for the initial 2016 GPP at RT1, which was similar to initial 2016 GPP at UN. Between the 2 RT reaches, metabolism values were higher further downstream for all periods. In contrast, ecosystem metabolism did not consistently increase moving downstream between the 3 RP reaches for all periods.

Although we were not able to classify temporal periods for UK or RH, these sites also showed a general increase in ecosystem metabolism moving downstream. GPP and ER at UK in 2016 (1.1 ± 0.2, n = 26; –3.3 ± 0.4, n = 26) and 2017 (0.4 ± 0.1, n = 20; –0.6 ± 0.1, n = 20) were similar to initial UN values. Post-hoc Tukey tests showed that GPP and ER at UK were lower than all other sites in both years regardless of temporal period, except for the initial GPP and reduced ER at RT1 in 2016. Similarly at RH, GPP values (12.5 ± 0.9, n = 23) were similar to elevated values at RT2 and RP2, whereas ER values (–15.6 ± 1.8, n = 23) were near elevated values at RP1. Post-hoc Tukey tests showed that during September and October of 2017, GPP and ER were highest at RH compared to all other sites.

The GPP:ER ratio was temporally and spatially variable along the Kootenai River between different management sections (Fig. 5). In 2017, GPP:ER ratios followed the same temporal pattern as GPP and ER at the UN reach and was lowest during the asynchrony in timing of elevated period GPP and ER at reaches RT1 and RT2. However, there were no similarities between temporal characteristics of GPP:ER ratios and GPP or ER at reaches RP1, RP2, and RP3. In 2017, the number of days with GPP:ER ≥1 was greatest at UN (99), RP3 (77), and RP2 (71), whereas the number of days with GPP:ER <1 was greatest at RP1 (130), RT2 (118), and RT1 (89).

**Water temperature and Q**

Water temperatures increased moving downstream, but daily differences in water temperature between sites were small. Daily mean water temperature ranged from 6.0 to 21.5°C (Fig. S5), and the daily difference in daily mean water temperature between UK, the furthest upstream site, and all other sites ranged between –2.18 to 3.81°C between May and October of 2017. Water temperatures during the
1st half of July were ∼1°C colder at RT sites compared to UK and ∼1°C warmer at RP sites compared to UK. For all sites, water temperature increased during the initial and elevated periods and decreased during the reduced period. For the UN, RT1, and RT2 sites, water temperatures increased throughout the elevated period, whereas water temperatures had started to decrease during the elevated period at sites RP1, RP2, and RP3 (Fig. S5). Linear regression showed that GPP changed very little (slope near 0) across a range of water temperatures (Fig. S6). There were negative relationships between ER and water temperature during the initial (p < 0.001, $r^2 = 0.098$), elevated (p = 0.0054, $r^2 = 0.023$), and reduced (p = 0.014, $r^2 = 0.021$) periods. However, $r^2 < 0.1$ for all relationships indicated that very little of the variation in GPP or ER was explained by water temperature.

We examined the relationships between GPP and Q and between ER and Q for each period individually with all sites combined (Figs S7, S8). GPP increased with Q during the initial (p = 0.0018, $r^2 = 0.049$), elevated (p < 0.001, $r^2 = 0.034$), and reduced (p < 0.001, $r^2 = 0.079$) periods. Similarly, ER increased with Q during the elevated (p < 0.001, $r^2 = 0.05$) and reduced (p < 0.001, $r^2 = 0.049$) periods. Although ecosystem metabolism increased with Q, $r^2 < 0.1$ indicated that Q explained very little of the variability in GPP and ER.

**DISCUSSION**

Time series GPP and ER data in large rivers offer opportunities to evaluate ecosystem metabolism response to river management. Ecosystem metabolism may be influenced by dams (Munn and Brusven 2004, Davis et al. 2012, Aristi et al. 2014), discharge, turbidity, light, temperature (Dodds et al. 2013, Hall et al. 2015), and nutrients (Levi et al. 2013), but identifying correlations between ecosystem metabolism and river management can be challenging. Additionally, there is limited research describing metabolism response to unregulated vs regulated flow (Munn and Brusven 2004, Aristi et al. 2014), nutrient additions (Slavik et al. 2004), or habitat restoration (Kupilas et al. 2017). We found that river management within the Kootenai River watershed contributes to temporal and spatial differences in GPP, ER, and GPP:ER ratios.

Our ecosystem metabolism estimates in the Kootenai River were within the range reported for earlier estimates on the Kootenai River (Snyder and Minshall 2005) and other streams and rivers (Hall et al. 2016) (Fig. 6), whereas our GPP:ER estimates in the Kootenai River are generally higher. Kootenai River GPP and ER followed a temporal pattern reported in other large rivers (Dodds et al. 2013, Genzoli and Hall 2016) with higher mid-summer rates. However, the number of high daily GPP and ER estimates in the Kootenai River appear to be fewer than reported for the Klamath River in Oregon and California, USA (Genzoli and Hall 2016), the Mississippi River (Minnesota in the north to Louisiana in the south, USA), or the Chattahoochee River (Alabama, Georgia, and Florida, USA) (Dodds et al. 2013). The spatial pattern we found of increasing
GPP and ER downstream was similar to that reported on small rivers (Q < 20 m³/s) with increasing stream order in the Ogeechee River Basin in Georgia, USA (Meyer and Edwards 1990) and GPP along the Little Tennessee River in North Carolina, USA (McTammany et al. 2003) but contrary to trends along the Klamath River (Genzoli and Hall 2016) with discharge similar to the study site. Creation of a reservoir, regulated flow, nutrient addition, and habitat modification likely contribute to temporal and spatial differences in ecosystem metabolism in the Kootenai River.

**Unregulated flow vs regulated flow**

Earlier timing of the elevated period and consistently-higher GPP and ER downstream of Libby Dam may have been in response to flow regulation and associated decreases in sediment, suspended particulate matter, bed mobility, and associated turbidity. Large reservoirs trap sediment and suspended particles (Williams and Wolman 1984), which reduces downstream turbidity and thereby increases light availability to the benthos. At sites downstream of dams, this increased light availability can elevate GPP (Davis et al. 2012). Turbidity, which decreases light availability and thereby decreases GPP and contributes to temporal and spatial variability (Dodds et al. 2013, Hall et al. 2015), could partially explain temporal and spatial differences in GPP that we observed. For example, the elevated period started latest at the UN site for both GPP and ER and started earlier in regulated reaches. Elevated turbidity from tributary inputs (Munn and Brusven 2004, Hall et al. 2015) or increased flow (Dodds et al. 2013) may contribute to decreased GPP reported at downstream reaches (Munn and Brusven 2004, Genzoli and Hall 2016), but turbidity would be expected to be relatively constant in regulated reaches. High GPP and ER estimates at regulated reaches downstream of Lake Koocanusa compared with unregulated reaches upstream of Libby Dam, as well as differences in the timing of elevated period may, then, be indicative of an effect of the lower turbidity associated with regulated flow. We did not measure turbidity, and we suggest future studies include turbidity as a potential mechanism by which flow regulation alters the timing and amount of autochthonous carbon contributions into river systems.

Flow regulation may also have elevated river metabolism and altered the timing of elevated-period GPP through other mechanisms, such as differences in bed mobility and scouring. Regulated flow from dam operations reduces hydrologic variability, including the magnitude and frequency of extreme flow events (Jorde et al. 2007, Aristi et al. 2014). Flow regulation contributes to elevated GPP and ER downstream of reservoirs (Aristi et al. 2014) by reducing bed mobility and enhancing algal proliferation (Morley et al. 2008) or enhancing accumulation of dissolved organic carbon, suspended particulate organic matter, and benthic organic matter including plankton from the reservoir (Aristi et al. 2014).

Downstream of Libby Dam, extensive *D. geminata* mats persist during high flows, suggesting low bed mobility and limited scouring even during high flows. Unregulated flow at UN and UK reaches may have lowered metabolism and delayed timing of the elevated period compared to regulated sites because scouring and bed mobility may have limited biofilm development. Future analyses of these dynamics would benefit from simultaneous measurements of bed mobility, biofilm biomass, and ecosystem metabolism.

An additional regulated-flow-associated mechanism for increased river metabolism in sites downstream of Libby Dam is the presence and proliferation of large *D. geminata* mats, which are common downstream of large dams (Kirkwood et al. 2009). These mats alter structure and diversity of diatom assemblages (Gillis and Lavoie 2014), provide habitat for bacteria, epiphytes, or other periphyton (Spaulding and Elwell 2007, Whitton et al. 2009), and may increase GPP and ER. Elevated invertebrate abundance in areas affected by *D. geminata* (Gillis and Chalifour 2010) suggests that *D. geminata* proliferation increases GPP and shifts available resources for primary consumers. In the Kootenai River, onset of *D. geminata* mat development that may directly contribute to GPP often begins in late winter, prior

![Graph](image-url)
to our study period. However, *D. geminata* mats may have indirectly contributed to GPP during our study period by providing habitat for other primary producers (Spaulding and Elwell 2007, Whitton et al. 2009). The earlier timing of the elevated period for ER relative to GPP at the RT sites may indicate respiration of senescing *D. geminata* and bacteria within the mat material, which was produced prior to the start of our metabolism measurements. Furthermore, these *D. geminata* mats may enhance retention of dissolved and suspended organic matter, thereby contributing to the elevated metabolism we observed at RT reaches. In contrast, *D. geminata* was not prolific or abundant upstream of any other reaches where increasing GPP preceded or was concurrent with increasing ER. Although the earlier timing of the elevated period for ER at RT sites may indicate respiration of senescing *D. geminata* and bacteria within the mat material, which was produced prior to the start of our metabolism measurements. Furthermore, these *D. geminata* mats may enhance retention of dissolved and suspended organic matter, thereby contributing to the elevated metabolism we observed at RT reaches. In contrast, *D. geminata* was not prolific or abundant upstream of any other reaches where increasing GPP preceded or was concurrent with increasing ER. Although the earlier timing of the elevated period for ER at RT sites could be from other upstream carbon sources, we would expect to see altered timing at the downstream RP sites as well. However, we did not observe similar asynchrony in elevated-period timing at RP reaches. The timing of *D. geminata* contributions to GPP prior to our study period combined with the earlier shift in timing of elevated ER likely contributed to RT reaches having generally-lower GPP:ER ratios compared to other reaches. Although *D. geminata* mats are often considered a nuisance, they likely directly and indirectly increase GPP and shift timing of elevated ER, thus altering the timing of the release of carbon to the Kootenai River food web.

**Nutrient addition**

Nutrient addition can elevate ecosystem metabolism in rivers whether added as phosphorus fertilizer (Slavik et al. 2004) or from anadromous spawning salmon (Levi et al. 2013). For example, nutrient additions in the Kuparuk River in Alaska, USA (Q = 2–5 m³/s) increased GPP and ER, although the effects declined after 8 y of additions (Slavik et al. 2004). Nutrient availability and metabolism are not always correlated (Hall et al. 2016). However, in our study area it appears that there is an association between them. Our daily GPP and GPP:ER ratio estimates at RP sites were higher than pre-phosphorus addition estimates from the same area reported by Snyder and Minshall (2005), suggesting that phosphorus addition might have increased GPP and GPP:ER ratios. The substantially-longer duration of the elevated-period GPP and ER and higher GPP:ER ratios at RP sites with phosphorus addition, compared to all other sites, suggests that phosphorus addition may promote GPP and ER for a longer period and shift the river toward autotrophy. Similarly, higher phosphorus availability in the Klamath River coincided with higher GPP and net ecosystem production (Genzoli and Hall 2016) and an apparent increase in

Fig. 6. Comparison of gross primary production (GPP) and ecosystem respiration (ER) metabolism estimates for the Kootenai River in this study (A) to other estimates for the Kootenai River (Snyder and Minshall 2005) and other rivers (Hall et al. 2016) (B). Most reported metabolism estimates are from rivers with mean annual discharge <10 m³/s (gray points), which is less than 1/20th of the mean annual discharge on the Kootenai River. Black points indicate rivers with mean annual discharge >10 m³/s. Points in panel A are daily estimates for all reaches in both 2016 and 2017. Points in panel B are reported means and frequently represent measurements made over a few days. The 29 Kootenai River data points from Snyder and Minshall (2005) shown in panel B are mean values reported for each of several months in 1993, 1994, and 1995 and are based on measurements made over the course of a few days at 4 locations near our regulated phosphorus reaches and our regulated habitat reach. Axes are log₁₀ scaled.
Habitat restoration

Habitat restoration in the Kootenai River may increase ecosystem metabolism through a variety of mechanisms. Restorations that slow current velocity and increase water residence time could promote increased macrophyte density (Jähnig et al. 2010), which substantially contributes to GPP (Fisher and Carpenter 1976). For example, elevated GPP and ER in a restored reach of the Ruhr River (Q = 21.3 m$^3$/s) in western Germany have been attributed to increased abundance of macrophytes (Kupilas et al. 2017). Habitat restorations that increased macrophyte abundance in other rivers (Kail et al. 2015), including remeandering and installing large woody debris structures, have been implemented in the Kootenai River, offering a potential mechanism for the higher GPP and ER we observed at RH compared to other sites in September and October of 2017. Habitat restoration in the Kootenai River has led to increased floodplain connectivity, which would be expected to increase allochthonous nutrient inputs (Aspetsberger et al. 2002) and stimulate productivity. These increased nutrients may be a 2nd potential mechanism for the high GPP and ER at RH. Although it appears that there may be an effect of habitat restoration on river metabolism, additional work is needed to improve understanding of how habitat restoration affects carbon availability and quality and subsequent foodweb dynamics.

Implications for future research

Our study found that river management, including unregulated and regulated flows, nutrient addition, and habitat restoration, may be related to spatial and temporal changes in ecosystem metabolism in the Kootenai River. We characterized temporal and spatial differences in GPP and ER and identified associations between those differences and river management practices, but we did not measure additional parameters, such as turbidity, nutrient concentrations, and bed mobility. Including measurements of these additional parameters in future work would allow for a quantitative assessment of mechanistic drivers of river metabolism. The location of tributaries, Libby Dam, the nutrient addition site, and habitat restoration projects confined placement of the sites and limited replication for some management practices. Additionally, few ecosystem metabolism estimates at the UK and RH sites limited our characterization of temporal patterns in these reaches. Future work to estimate ecosystem metabolism in large rivers may benefit from inclusion of additional tributary sites and sites in unregulated reaches, as well as additional habitat restoration reaches, to improve understanding of autochthonous carbon contributions to the food web by tributaries and restored reaches. Our results imply that river management likely increased autochthonous carbon, but the quantity, quality, and timing of the release of the carbon may limit potential benefits to the food web. Additional research is needed to increase our understanding of the causal relationships between river management practices and ecosystem metabolism. Food resources are limited in the Kootenai River, highlighting the importance of management decisions that may increase autochthonous carbon inputs to support food web dynamics and recovery of threatened and endangered fisheries.

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LITERATURE CITED

Appling, A. P., R. O. Hall, C. B. Yackulic, and M. Arroita. 2018. Overcoming equifinality: Leveraging long time series for stream metabolism estimation. Journal of Geophysical Research: Biogeosciences 123:624–645.

Aristi, I., M. Arroita, A. Larrañaga, L. Ponsati, S. Sabater, D. von Schiller, A. Elosegi, and V. Acuña. 2014. Flow regulation by dams affects ecosystem metabolism in Mediterranean rivers. Freshwater Biology 59:1816–1829.

Aspetsberger, F., F. Huber, S. Kargl, B. Scharinger, P. Peduzzi, and T. Hein. 2002. Particulate organic matter dynamics in a river floodplain system: Impact of hydrological connectivity. Archiv für Hydrobiologie 156:23–42.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading Rainbow Trout usurp a terrestrial prey subsidy from native char and reduce their growth and abundance. Oecologia 153:461–470.

Bernhardt, E. S., J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. Harvey, M. Arroita, A. Appling, M. Cohen, W. H. McDowell, and R. Hall. 2018. The metabolic regimes of flowing waters. Linnology and Oceanography 63:S99–S118.
Burke, M., K. Jorde, and J. M. Buffington. 2009. Application of a hierarchical framework for assessing environmental impacts of dam operation: Changes in streamflow, bed mobility and recruitment of riparian trees in a western North American river. Journal of Environmental Management 90:S224–S236.

Chapra, S. C., and D. M. Di Toro. 1991. Delta method for estimating primary production, respiration, and reaeration in streams. Journal of Environmental Engineering 117:640–655.

Cole, J. J., N. F. Caraco, and B. L. Peierls. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? Limnology and Oceanography 37:1608–1617.

Cross, W. F., C. V. Baxter, E. J. Rosi-Marshall, R. O. Hall, T. A. Kennedy, K. C. Donner, W. Kelly, A. Holly, S. E. Seegert, and K. E. Behn. 2013. Food-web dynamics in a large river discontinuum. Ecological Monographs 83:311–337.

Daley, R., E. Carmack, C. Gray, C. Pharso, S. Jasper, and R. Weigand. 1981. The effects of upstream impoundments on Kootenay Lake, BC. Scientific Series No. 117. National Water Research Institute, Vancouver, Canada.

Davis, C., C. Frithsen, W. Wirthlin, and J. Memmott. 2012. High rates of primary productivity in a semi-arid tailwater: Implications for self-regulated production. River Research and Applications 28:1820–1829.

Demars, B. O., J. R. Manson, J. S. Olafsson, G. M. Gislason, R. Gumundsdottir, G. Woodward, J. Reiss, D. E. Pichler, J. J. Rasmussen, and N. Friberg. 2011. Temperature and the metabolic balance of streams. Freshwater Biology 56:1106–1121.

Demars, B. O., J. Thompson, and J. R. Manson. 2015. Stream metabolism and the open diel oxygen method: Principles, practice, and perspectives. Limnology and Oceanography: Methods 13:356–374.

Dessouki, T. C. E., and A. Ryan. 2010. Canada–British Columbia water quality monitoring agreement (water quality assessment of the Kootenay, Elk and St Mary River). Environment Canada, Ottawa, Canada.

Dodds, W. K., A. M. Veach, C. M. Ruffing, D. M. Larson, J. L. Fischer, and K. H. Costigan. 2013. Abiotic controls and temporal variability of river metabolism: Multiyear analyses of Mississippi and Chatahoochee River data. Freshwater Science 32:1073–1087.

Duke, S. P., A. M. Ennis, R. Hallock, J. Hammond, S. Ireland, J. Laufle, R. Lauzier, L. Lockhard, and B. Marotz. 1999. Recovery plan for Kootenai River White sturgeon (Acipenser transmontanus). Journal of Applied Ichthyology 15:157–163.

Fisher, S. G., and S. R. Carpenter. 1976. Ecosystem and macrophyte primary production of the Fort River, Massachusetts. Hydrobiologia 49:175–187.

Garcia, H. E., and L. I. Gordon. 1992. Oxygen solubility in seawater: Better fitting equations. Limnology and Oceanography 37:1307–1312.

Gentzoli, L., and R. O. Hall. 2016. Shifts in Klamath River metabolism following a reservoir cyanobacterial bloom. Freshwater Science 35:795–809.

Gillis, C.-A., and M. Chalifour. 2010. Changes in the macrobenthic community structure following the introduction of the invasive alga Didymosphenia geminata in the Matapedia River (Québec, Canada). Hydrobiologia 647:63–70.

Gillis, C.-A., and I. Lavoie. 2014. A preliminary assessment of the effects of Didymosphenia geminata nuisance growths on the structure and diversity of diatom assemblages of the Restigouche River basin, Quebec, Canada. Diatom Research 29:281–292.

Hall, R. O., T. A. Kennedy, and E. J. Rosi-Marshall. 2012. Air–water oxygen exchange in a large whitewater river. Limnology and Oceanography: Fluids and Environments 2:1–11.

Hall, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19:73–86.

Hall, R. O., C. B. Yackulic, T. A. Kennedy, M. D. Yard, E. J. Rosi-Marshall, N. Voichick, and K. E. Behn. 2015. Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. Limnology and Oceanography 60:512–526.

Hardy, R., and V. L. Paragamian. 2013. A synthesis of Kootenai River Burbot stock history and future management goals. Transactions of the American Fisheries Society 142:1662–1670.

Hoffman, G. C., and B. Marotz. 2001. Summary of algae flush at Libby Dam, July 2001. Report to US Army Corps of Engineers, Portland, Oregon by Montana Fish, Wildlife and Parks, Kalispell, Montana. (Available by email request to author G. Hoffman at gregory.c.hoffman@usace.army.mil)

Holtgrieve, G. W., D. E. Schindler, T. A. Branch, and Z. T. A’mar. 2010. Simultaneous quantification of aquatic ecosystem metabolism and reaeration using a Bayesian statistical model of oxygen dynamics. Limnology and Oceanography 55:1047–1063.

Hornberger, G. M., and M. G. Kelly. 1975. Atmospheric reaeration in a river using productivity analysis. Journal of the Environmental Engineering Division 101:729–739.

Hoyle, G. 2012. Kootenai River Nutrient Addition Monitoring Program Bonneville Power Administration 2010 project summary. Responses of water chemistry, benthic periphyton, and algal taxonomic structure to experimental additions of phosphorous and nitrogen in the Kootenai River ecosystem. Project no. 1994-049-00.

Hoyle, G. M., C. Holderman, P. J. Anders, B. Shafii, and K. I. Ashley. 2014. Water quality, chlorophyll, and periphyton responses to nutrient addition in the Kootenai River, Idaho. Freshwater Science 33:1024–1029.

Jähne, B., and H. Haußecker. 1998. Air–water gas exchange. Annual Review of Fluid Mechanics 30:443–468.

Jähnig, S. C., K. Brabec, A. Buffagni, S. Erba, A. W. Lorenz, T. Ofenböck, P. F. Verdonschot, and D. Hering. 2010. A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. Journal of Applied Ecology 47:671–680.

Jorde, K., M. Burke, N. Scheidt, C. Welcker, S. King, and C. Borden. 2007. 23 Reservoir operations, physical processes, and ecosystem losses. Developments in Earth Surface Processes 11:607–636.

Kail, J., K. Brabec, M. Poppe, and K. Januschke. 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. Ecological Indicators 58:311–321.

Katz, S. L., K. Barnas, R. Hicks, J. Cowen, and R. Jenkinson. 2007. Mass transfer, and perspectives. Limnology and Oceanography: Methods 13:356–374.

Kemp, R. M., and P. M. O’Neil. 2003. A hierarchical framework for assessing environmental impacts of dam operation: Changes in streamflow, bed mobility and recruitment of riparian trees in a western North American river. Journal of Environmental Management 90:S224–S236.

Kemp, R. M., and P. M. O’Neil. 2003. A hierarchical framework for assessing environmental impacts of dam operation: Changes in streamflow, bed mobility and recruitment of riparian trees in a western North American river. Journal of Environmental Management 90:S224–S236.
Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46:303–316.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology 84:701–708.

Killick, R., and I. Eckley. 2014. changepoint: An R package for changepoint analysis. Journal of Statistical Software 58:1–19.

Killick, R., K. Haynes, I. Eckley, P. Fearnhead, and J. Lee. 2016. changepoint: Methods for changepoint detection. R package version 2.2.2. (Available from: https://CRAN.R-project.org/package=changepoint)

Kirkwood, A. E., L. J. Jackson, and E. McCauley. 2009. Are dams hotspots for Didymosphenia geminata blooms? Freshwater Biology 54:1856–1863.

Kootenai Tribe of Idaho. 2016. Kootenai River Habitat Restoration Program: Bonners Ferry Islands and Straight Reach Project update. (Available from: http://www.kootenai.org/documents/KVRJuly2016KRRHPbriefing_001.pdf)

Kuplas, B., D. Hering, A. W. Lorenz, C. Knuth, and B. Gücker. 2017. Hydromorphological restoration stimulates river ecosystem metabolism. Biogeosciences 14:1989–2002.

Levi, P. S., J. L. Tank, J. Rüegg, D. J. Janetski, S. D. Tiegs, D. T. Chaloner, and G. A. Lamberti. 2013. Whole-stream metabolism responds to spawning Pacific salmon in their native and introduced ranges. Ecosystems 16:269–283.

Lord, J. K. 1866. The naturalist in Vancouver Island and British Columbia. Volume 1. Richard Bentley, London, England.

McFann, M., J. Webster, E. Benfield, and M. Neatour. 2003. Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society 22:359–370.

Meyer, J. L., and R. T. Edwards. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology 71:668–677.

Miller, S. W., P. Budy, and J. C. Schmidt. 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: Applications of meta-analysis to river restoration. Restoration Ecology 18:8–19.

Minshall, G. W., B. Shafii, W. J. Price, C. Holderman, P. J. Anders, G. Lester, and P. Barrett. 2014. Effects of nutrient replacement on benthic macroinvertebrates in an ultraoligotrophic reach of the Kootenai River, 2003–2010. Freshwater Science 33:1009–1023.

Morley, S. A., J. J. Duda, H. J. Coe, K. K. Kloehn, and M. L. McHenry. 2008. Benthic invertebrates and periphyton in the Elwha River basin: Current conditions and predicted response to dam removal. Northwest Science 82:179–196.

Munn, M. D., and M. A. Brusven. 2004. The influence of Dworshak Dam on epilithic community metabolism in the Clearwater River, USA. Hydrobiologia 513:121–127.

Naiman, R., H. Décamps, and M. McClain. 2005. Riparia: Ecology, conservation, and management of streamside communities. Elsevier Academic Press, San Diego, California.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98:166–170.

Northcote, T. 1973. Some impacts of man on Kootenay Lake and its salmonoids. Technical Report No. 25. Great Lakes Fishery Commission, Ann Arbor, Michigan. (Available from: http://www.glfic.org/pubs/TechReports/Tr25.pdf)

Ochs, C. A., O. Pongrakham, and P. V. Zimba. 2013. Darkness at the break of noon: Phytoplankton production in the Lower Mississippi River. Limnology and Oceanography 58:555–568.

Olden, J. D., C. P. Konrad, T. S. Melis, M. J. Kennard, M. C. Free- man, M. C. Mims, E. N. Bray, K. B. Gido, N. P. Hemphill, and D. A. Lytle. 2014. Are large-scale flow experiments informing the science and management of freshwater ecosystems? Frontiers in Ecology and the Environment 12:176–185.

Olden, J. D., and R. J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55:86–107.

Oliver, R. L., and C. J. Merrick. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biology 51:1131–1148.

Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? Freshwater Biology 55:205–222.

Paragamian, V. L. 2000. The effects of variable discharges on burbot spawning migrations in the Kootenai River, Idaho, USA, and British Columbia, Canada. Pages 111–123 in V. L. Paragamian and D. W. Willis (editors). Burbot: Biology, ecology, and management. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.

Paragamian, V. L., R. C. Beamesderfer, and S. C. Ireland. 2005. Status, population dynamics, and future prospects of the endangered Kootenai River White sturgeon population with and without hatchery intervention. Transactions of the American Fisheries Society 134:518–532.

Paragamian, V. L., V. Wakkinen, and G. Kruse. 2002. Spawning locations and movement of Kootenai River White sturgeon. Journal of Applied Ichthyology 18:608–616.

Paragamian, V. L., V. Whitman, J. Hammond, and H. Andruskas. 2000. Collapse of burbot fisheries in the Kootenai River, Idaho, USA, and Kootenay Lake, British Columbia, Canada. Pages 155–164 in V. L. Paragamian and D. W. Willis (editors). Burbot: Biology, ecology, and management. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.

Perry, S. A., and J. E. Huston. 1983. Aquatic insect study. Pages 1–70 in Kootenai River investigations final report 1972–1982. Montana Department of Fish, Wildlife and Parks and The US Army Corps of Engineers.

Perry, S. A., and W. B. Perry. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. Hydrobiologia 134:171–182.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Polzin, M. L., and S. B. Rood. 2000. Effects of damming and flow stabilization on riparian processes and black cottonwoods along the Kootenay River. Rivers 7:221–232.

Pringle, C. M. 2000. Managing riverine connectivity in complex landscapes to protect ‘remnant natural areas’. Internationale
Redwing Naturalists. 1996. History of diking on the Kootenay River floodplain in British Columbia. Report of Redwing Naturalists to Habitat Enhancement Branch, Department of Fisheries and Oceans, British Columbia, Canada. (Available from: https://science-catalogue.canada.ca/record=4042772−56)

Revenga, C., J. Brunner, N. Henninger, R. Payne, and K. Kassem. 2000. Pilot analysis of global ecosystems: Freshwater systems. World Resources Institute, Washington DC.

Richards, D. 1997. Kootenai River biological baseline status report: Annual report, 1996. Technical Report BP-40364-1. United States Department of Energy, Bonneville Power Administration, Portland, Oregon.

Rosenberg, D. M., P. McCully, and C. M. Pringle. 2000. Global-scale environmental effects of hydrological alterations: Introduction. BioScience 50:746−751.

Slavik, K., B. Peterson, L. Deegan, W. Bowden, A. E. Hershey, and J. Hobbie. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. Ecology 85:939−954.

Snyder, E. B., and G. W. Minshall. 2005. An energy budget for the Kootenai River, Idaho (USA), with application for management of the Kootenai white sturgeon, Acipenser transmontanus. Aquatic Sciences 67:472−485.

Spaulding, S., and L. Elwell. 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom Didymosphenia geminata: Recommendations for response. White Paper. United States Environmental Protection Agency, Region 8, Denver, Colorado.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrenick, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118−146.

Thorp, J. H., and M. D. Delong. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96:543−550.

Uehlinger, U., B. Kawecka, and C. Robinson. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). Aquatic Sciences 65:199−209.

Van de Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnology and Oceanography: Methods 5:145−155.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130−137.

Vörösmarty, C. J., and D. Sahagian. 2000. Anthropogenic disturbance of the terrestrial water cycle. American Institute of Biological Sciences Bulletin 50:753−765.

Ward, P. R. B., P. J. Anders, G. W. Minshall, C. Holdeman, G. M. Hoyle, and H. Yassien. 2017. Nutrient uptake during low-level fertilization of a large, seventh-order oligotrophic river. Canadian Journal of Fisheries and Aquatic Sciences 75:569−579.

Whitton, B., N. Ellwood, and B. Kawecka. 2009. Biology of the freshwater diatom Didymosphenia: A review. Hydrobiologia 630:1−37.

Williams, G. P., and M. G. Wolman. 1984. Downstream effects of dams on alluvial rivers. Geological Survey Professional Paper 1286. United States Government Printing Office, Washington, DC.

Woods, P. F. 1982. Annual nutrient loadings, primary productivity, and trophic state of Lake Koocanusa, Montana and British Columbia, 1972−80. Geological Survey Professional Paper 1283. United States Government Printing Office, Washington, DC.

Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins Jr, L. E. Stevens, S. Hueffle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. Ecological Modelling 183:157−172.