Sinnatamby R. Niloshini (Orcid ID: 0000-0003-1423-6631)

Considering multiple anthropogenic threats in the context of natural variability: Ecological processes
in a regulated riverine ecosystem

Running Head: Ecological processes in a regulated riverine ecosystem

R. Niloshini Sinnatamby¹, Bernhard Mayer², Mary K. Kruk², Stewart B. Rood³, Anne Farineau¹, John R.
Post¹

¹Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada, T2N 1N4. Email:
ramila.sinnatamby@ucalgary.ca

²Department of Geoscience, University of Calgary, Calgary, Alberta, Canada, T2N 1N4

³Environmental Science Program, University of Lethbridge, Alberta, Canada, T1K 3M4

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/eco.2217

Abstract

Rivers are among the most altered environments globally but identifying which threats are responsible for observed biotic and abiotic changes is complicated by natural drivers of variation.

The Bow River, Canada provides an ideal model to resolve these influences and explore spatial relationships. It originates from pristine Rocky Mountain headwaters and is subsequently impacted by typical human alterations: damming, municipal channelization and effluent release, and agricultural impacts (nutrient enrichment, water withdrawal for irrigation). By coordinating studies of the Bow River's biota, we demonstrate how threat-driver interactions depend on season and the abiotic factor and biotic community or species of interest. We conclude that impact severity and riverine recovery depend on the threat magnitude, its longitudinal position and proximity to other threats and natural drivers. We found that river regulation, water extraction and bank armouring interact to limit geomorphic processes resulting in depleted riparian woodlands and numbers of fish species, though a large, undammed tributary nearby allows quick recovery downstream. We highlight the implications of the longitudinal position of the threats since cold-water fish species are disproportionately impacted through the area where the human impacts on the Bow River overlap. We illustrate how the interactions between flow, nutrients and temperature lead to macrophyte or algae dominated communities and associated shifts in fish composition and biomass. Finally, we applied our increased understanding of ecological riverine processes to conclude that management techniques such as flushing flows or functional environmental flows are likely to have only minimal or conditional success in the Bow River.

Keywords: multiple threats, aquatic ecosystems, hydrology, riparian, aquatic vegetation, dissolved oxygen, fish, nutrients.

1.0 Introduction

1.1 Value and vulnerability of freshwater ecosystems

Freshwater is vital to sustaining life on the planet, providing essential ecosystem services that support anthropogenic activity (Carpenter, Stanley, & Vander Zanden, 2011; Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Freshwater ecosystems services include water supply for power generation, domestic, industrial, and agricultural use, fish and wild life production, recreation, waste management and water quality control, and transportation (Aylward et al., 2005; Postel & Carpenter, 1997). In addition, freshwater ecosystems play a disproportionately important role in global biodiversity, accounting for approximately ten percent of all known species while comprising less than one percent of the Earth's entire water volume (Carpenter et al., 2011; Strayer & Dudgeon, 2010). Rivers make up an even smaller fraction, estimated at 0.006 % of the Earth's freshwater (Shiklomanov, 1993), but have played a crucial role in human settlement and development, and continue to play a disproportionately large role in human activities (Malmqvist & Rundle, 2002; Postel & Carpenter, 1997). As a result, flowing waters are among the most altered ecosystems in the world, modified by damming, water extraction, channelization, inputs from wastewater treatment facilities and agricultural runoff, and species addition or removal (Malmqvist & Rundle, 2002; Vörösmarty et al., 2010). Such anthropogenic modifications result in abiotic and biotic responses and ultimately threaten fluvial biodiversity, water security and ecosystem services (Harrison et al., 2014; Malmqvist & Rundle, 2002; Vörösmarty et al., 2010).

1.2 Terminology

To avoid confusion from multiple terms emerging in the literature (e.g. Carpenter et al., 2011; Cote, Darling, & Brown, 2016; Craig et al., 2017; Malmqvist & Rundle, 2002; Vörösmarty et al., 2010), we refer to anthropogenic causes of ecosystem change, such as dams, as **threats** following Craig et al. (2017), and **natural drivers** to refer to factors responsible for natural variation like climate variability. Anthropogenic threats and natural drivers are often combined into one common term (e.g. *stressor* used by Cote et al., 2016), however, we keep these terms separate to emphasize their

distinct roles and management potential. We use the term **abiotic variation** to refer to chemical or physical factors (e.g. flow) that vary in response to anthropogenic threats and/or natural drivers. The outcome observed at the biotic level is called a **biotic response** (e.g. variations in macrophyte biomass).

1.3 Complexity of understanding multiple threats in the context of natural drivers

As demands on freshwater ecosystems increase, interest in understanding and managing multiple threats in aquatic environments has also grown (Cote et al., 2016; Craig et al., 2017; Nöges et al., 2016; Vörösmarty et al., 2010). Craig et al. (2017) argue the need to identify the threats responsible for observed abiotic variation in freshwater ecosystems and that multiple interacting threats must be considered coincidentally to effectively manage their abiotic and biotic responses. Multiple threats can interact making outcomes difficult to predict (i.e. synergism, antagonism, additive or reversal; Cote et al., 2016; Jackson, Loewen, Vinebrooke, & Chimimba, 2016). As such, identifying threat-abiotic variation relationships can be complicated depending on the number of threats and the type of interactions (reviewed in Craig et al., 2017). This complexity can result in attributing abiotic variation to the wrong threat or just one threat, causing inaction among scientists and managers, and selecting management tools that are ill suited to the problem (Cote et al., 2016; Craig et al., 2017).

Identifying the threats responsible can be further complicated by natural drivers (Feld et al., 2016; Stendera et al., 2012). For example, natural seasonal and annual fluctuations in flow, including floods and droughts, must be disentangled from flow alterations caused by river regulation and water extraction (Malmqvist & Rundle, 2002). Understanding the natural variability of a system can be challenging in riverine systems with a long history of anthropogenic interference where natural baseline conditions are either unknown or unachievable (Acreman et al., 2014). As a linear feature, riverine ecosystems exhibit unidirectional properties (Fausch, Torgersen, Baxter, & Li, 2002), which underpin variations in morphology and many other physical and chemical properties and may provide insight into the natural abiotic variation expected along the river (Thorp, Thoms, & Delong,

2006; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). The unidirectional property of rivers can also lead to cumulative effects of upstream changes that can complicate interpretation of relationships.

Here, we explore how riverine and riparian ecological processes respond to multiple threats and natural drivers using examples from the Bow River in Alberta, Canada. Originating in the pristine, snowmelt and glacier-fed environment of Banff National Park, the Bow River flows through a range of natural regions (e.g. montane, foothills, prairies) but also the most populous district in Alberta. We combine new assessments with previously published studies from several disciplines using different temporal and spatial scales to elucidate the roles of anthropogenic threats versus natural drivers on abiotic variation and biotic responses; we explore their interactions and evaluate longitudinal variation in their relative importance along the river.

2.0 Natural drivers and anthropogenic threats of the Bow River, Alberta, Canada

2.1 Natural drivers

Originating at Bow Lake (51.651° N, 116.420° W) on the eastern slopes of the Rocky Mountains in the province of Alberta (Canada), the main stem of the Bow River flows predominantly eastward approximately 637 kilometres until converging with the Oldman River to form the South Saskatchewan River (Fig. 1). Consistent with the river continuum concept (RCC) and the fluvial geomorphological theories which underpin it (Vannote et al., 1980 and references therein), much of the Bow River's natural variation is associated with distance from headwaters, and we use this term broadly to describe the natural drivers responsible for variations in channel morphology (Table 1).

Although climate (i.e. air temperature and precipitation), in the case of the Bow River, is also highly associated with distance from headwaters, we discuss climate variation as a separate driver, owing to its important role in many ecological processes. We intentionally distinguish between *climate variability* as a natural driver and *climate change* as an anthropogenic threat. Owing to the timescale of the studies included, our discussion largely pertains to climate variability; with distance from headwaters, average air temperatures increase, and precipitation declines as the climate is

more arid in the downstream portions of the watershed. The potential role of climate change in increasing flood events is also not discussed; rather, floods are considered an abiotic response to climate variation. The hydrology of the Bow River watershed, particularly inputs from unregulated tributaries, plays an important role in driving natural variation on the Bow River. Of the main tributaries, the least alteration presently exists on the Pipestone, Ghost and Highwood rivers (Fig. 1, Table 2). The Bow River valley exhibits geological transitions along the length of the river (Hamilton, Price, & Langenberg, 1999).

2.2 Anthropogenic threats

Key anthropogenic threats on the Bow River include dams, weirs, reservoirs and wastewater treatment plants (WWTP), bank armouring, water extractions, and agricultural practices including livestock grazing (Table 1). The Bow River is heavily regulated by dams on some of its primary tributaries (Spray, Cascade, Kananaskis and Elbow Rivers) and on its main stem (Figs. 1, 2, Table 2). The main stem contains two storage reservoirs (associated with Ghost and Bearspaw dams) and two weirs. The Bow River flows through several municipalities and First Nations reserves, but the City of Calgary accounts for the largest population density with approximately 1.25 million people in 2017. Bank armouring, which is often linked to urbanization, is more prevalent within the City of Calgary, compared to areas immediately upstream and downstream of the city (City of Calgary, 2016; East Slopes Aquatic Consulting Inc., 2017). Water is extracted directly from the Bow River throughout the year for municipal and industrial use (Figs. 1, 2). As well, three of Alberta's irrigation districts are supported through surface water extractions from the Bow River, which occur primarily between April and October. Six municipal WWTPs discharge treated effluent directly into the Bow River (Fig. 1), three of which exist within the City of Calgary limits. Anthropogenic threats related to agriculture include water extraction, nutrient runoff from agricultural practices, and grazing. Most agricultural practices along the river occur downstream of the City of Calgary (Forcorp Solutions Inc, 2012).

3.0 Abiotic variation along the Bow River in response to natural drivers and anthropogenic threats

Abiotic variation can look the same regardless of what threat(s) and/or natural driver(s) are generating it. Understanding the underlying cause of variation is essential for determining whether and how to manage the outcome. Here, we discuss variation in six key abiotic factors and the natural drivers and threats that affect them.

3.1 Major natural regions

Alberta uses an ecological land classification system that is based on landscape patterns of vegetation, soil and physiographic features (Natural Regions Committee, 2006). The Bow River flows through three major natural regions: Rocky Mountain (subalpine and montane subregions), Parkland (foothills parkland subregion), and Grassland (foothills fescue, mixed grass, dry mixedgrass subregions, Fig. 2). These regions are influenced largely by natural drivers (i.e. climate, topography, geology; Natural Regions Committee, 2006), but, over a longer timescale, natural climate variations are likely to interact with anthropogenic climate change to shift regions upstream (Schneider, 2013).

3.2 Spatial variation in channel morphology

The Bow River follows a concave longitudinal path with its elevation declining steeply at first from 1983 meters above sea level (MASL), then more gradually to 706 MASL at the confluence with the Oldman River (Figs. 2, 3). Consistent with fluvial geomorphology underpinning the RCC (Vannote et al., 1980), channel width gradually increases with distance from headwaters. Two exceptions to the expected pattern are the area around Canmore where the channel type is frequently braiding and anastomosing, and increased width associated with the reservoirs and other areas immediately preceding dams (excluded from Fig. 2).

From its headwaters to the confluence with the Highwood River, Bow River morphology is fairly straight (sinuosity = 1-1.5) and described largely as a single channel with infrequent braiding. Once a river moves out of the confined valley of its headwaters and is characterized by lower gradient and finer substrate, sinuosity is expected to increase. River damming and consequent flow stabilization are known to reduce erosion, and sediment transport and deposition, and consequently reduce

channel migration and geomorphic processes that occur under natural flow regimes (Williams & Wolman, 1984). Rood et al. (1999) used historical air photos to demonstrate that between the City of Calgary and the Highwood River confluence, the Bow River became less geomorphologically dynamic following the onset of flow regulation. Further, bank armouring, which is also more prevalent in this reach (City of Calgary, 2016; East Slopes Aquatic Consulting Inc., 2017), is known to limit erosion and channel migration (Florsheim, Mount, & Chin, 2008).

From the confluence of the Highwood River to Bassano Dam, sinuosity is notably higher (~ 2) indicating a meandering river (Dey, 2014). This small section of river (~ 154 km) represents a geomorphologically active section with relatively few anthropogenic alterations. Indeed, Rood et al. (1999) noted the role of relatively unregulated flow from the Highwood River in returning geomorphic channel activity to the Bow River main stem. From Bassano Dam to the confluence with the Oldman River, the river is characterized as a single meandering channel (sinuosity > 1.5 ; Dey, 2014).

Throughout its length, Bow River morphology shows varying influence of natural drivers and anthropogenic threats. Natural drivers (i.e. distance from headwater, hydrology, and climate variation) dominate abiotic variation in the headwaters, whereas the effects of anthropogenic threats (i.e. dams, river regulation, bank armouring) are most evident between Kananaskis Dam and the Highwood River.

3.3 Spatial variation in substrate

Substrate is fairly coarse (i.e. gravel, cobble, boulders) throughout the Bow River, though silt deposition over the substrate is prevalent downstream of Carseland weir (Culp, Hamilton, Sosiak, & Davies, 1992; Longmore & Stenton, 1981). The spatial distribution of substrate in the Bow River results from natural drivers (i.e. geology, hydrology, climate variability and resulting geomorphological processes) but anthropogenic threats can alter the expected longitudinal substrate profile. For example, both reservoirs and bank armouring can reduce the amount of sediment being transported downstream (Vörösmarty et al., 2010). Further, the release of sediment-

depleted water from dams can erode fine sediment from the receiving environment, with implications for aquatic biota relying on interstitial spaces of a streambed (Poff et al., 1997). Finally, grazing in riparian areas, which is largely observed downstream of Calgary (Alberta Environment, 2007), is likely to result in more river bank erosion and increased silt in the downstream reaches.

3.4 Spatial and temporal variation in discharge

Flow-ecology relationships have received considerable attention owing to the prevalence of river regulation and its negative impacts on aquatic biota, biodiversity and ecosystem services (Koning, Locke, & Mahoney, 2016; Poff & Zimmerman, 2010). In contrast, unaltered magnitude and timing of discharge helps maintain river geomorphology and the habitats required by aquatic and riparian biota (Bunn & Arthington, 2002). Discharge is expected to increase with distance from headwaters owing to an increase in catchment size, which was indeed demonstrated in the longitudinal discharge profile on the Bow River (Fig. 3A). Discharge during the open water season from the first decade on record (1911-1920) represents natural flows since anthropogenic alterations were minimal. Comparison with a recent decade (2001-2010) highlights the profound impact of anthropogenic threats on river discharge (Fig. 3). The two records diverge substantially following the onset of dams on the river where recent discharge levels are considerably lower (Fig. 3A). A similar comparison of early and recent decades of seasonal hydrographs at Banff (upstream of most flow alterations) and Calgary illustrates how anthropogenic alterations to flow can have different outcomes depending on the season (Fig. 3B). While discharge in Calgary is lower than natural levels during the summer, discharge is higher than natural levels from late fall to early spring.

How natural drivers and anthropogenic threats interact to impact discharge depends on the season because of the strong seasonality of climate variation and anthropogenic water and power demands. In the winter, when natural flows are low and power demands are high, more water is released from reservoirs to generate more electricity, resulting in higher than natural water levels. During late spring and early summer, when peak discharge occurs on the Bow River, natural flow is dampened by water storage in reservoirs, and municipal and agricultural water extractions. Water

levels are of most concern for maintaining ecological function in the late summer when natural declines in flow are exacerbated by water storage in reservoirs and water extraction.

Municipal withdrawals from the Bow River represent a relatively small proportion of the total extracted river water ($\sim 4 \text{ m}^3/\text{s}$ annual average), 90% of which is treated and returned to the river (data provided by Town of Cochrane and City of Calgary). In contrast, water withdrawn for irrigation occurs at a much higher rate ($27 \text{ m}^3/\text{s}$ annual average; data from 2009-2015 obtained from Environment Canada and Climate Change's Historical Hydrometric data website), less than 21 % of which is returned to the river (Alberta Agriculture and Forestry, 2016, 2017). Therefore, municipal extractions do not contribute appreciably to the lower discharge of the Bow River, whereas agricultural withdrawals are a major contributor to the observed pattern (Fig. 3A).

3.5 Spatial variation in water temperature

Environmental temperatures have a pervasive effect on biota and various ecological and biological processes (Caissie, 2006). In addition to natural spatial and temporal variability, water temperatures are also susceptible to anthropogenic threats such as climate change, altered discharge, water releases from reservoirs, and inputs from point sources of thermal effluent (Caissie, 2006). Longitudinal variation of mean July water temperature along the Bow River demonstrated a gradual increase with distance from headwaters – an average of approximately 10°C at Bow Lake to just over 20°C near the confluence with the Oldman River (Fig. 4, Mee et al., 2016). In unaltered rivers that originate at high elevations and are exposed to solar radiation downstream, the longitudinal increase in water temperature occurs at a faster rate closer to the headwaters and the rate of increase declines with distance downstream as the size of the river increases (Fullerton et al., 2015). In the Bow River, however, temperatures increased fastest in the section of river characterized by the highest number of anthropogenic threats (Reach 2, Figs. 1, 4). This deviation from expected may reflect natural drivers particular to the Bow River (e.g. the number of tributaries with high elevation sources in its headwater reach), or anthropogenic threats (e.g. heated effluents from WWTPs, and reduced riparian density; Caissie, 2006; Olden & Naiman, 2010). It should be

noted, however, that thermal deviations related to dam releases typically result in cooler than expected summer water temperatures below dams (Ellis & Jones, 2013).

3.6 Spatial variation in nutrient flux and source

Nutrients play an important role in supporting aquatic productivity, and rivers can act as a vital conduit transferring land derived nutrients to lakes and marine environments (Peterson et al., 2001). Anthropogenic nutrient inputs, on the other hand, are a pervasive issue in aquatic ecosystems and can lead to eutrophication with negative impacts, such as excessive aquatic vegetation and reduced dissolved oxygen, with implications for biota, drinking water quality, and transportation (Sosiak, 2002). Bow River nitrate fluxes (i.e. nitrate concentrations x discharge), are low in the headwaters (<5000 kg/day) and increase substantially (>25000 kg/day) below the Calgary WWTPs, followed by a slight decline downstream of the city (Fig. 5A). The substantial increase has been attributed to nitrate inputs predominantly from WWTPs in Calgary (Chao, 2011). Compared to nitrate, dissolved phosphorus fluxes are much lower in the Bow River and exhibit a small increase below the Calgary WWTPs attributed to WWTP inputs but a more drastic increase further downstream (~525 km from headwaters) potentially caused by agricultural inputs (Fau, 2015). Riverine boron concentrations provide an additional indicator of anthropogenic impacts. Boron fluxes display a more gradual increase with distance from headwater and continues to increase further downstream of Calgary, declining again towards the confluence with the Oldman River (Kruk, Mayer, Nightingale, & Laceby, 2020).

Comparison of $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ nitrate values from Bow River water samples allows estimation of the major nitrate source contributions if the isotopic compositions of those sources are sufficiently different, as is the case for four major nitrate sources: (1) atmospheric nitrate deposition, (2) nitrate-containing synthetic fertilizers, (3) nitrate derived from nitrification e.g. in soils or ammonium or urea-based fertilizers, and (4) nitrate in manure and wastewater effluents (Fig. 5C, see Supplemental Information). The isotopic composition of nitrate in Bow River water samples indicated that atmospheric deposition and synthetic nitrate-containing fertilizer are not significant sources of

riverine nitrate (Fig. 5C). $\delta^{15}\text{N}$ values of nitrate are low ($<+4\text{‰}$) in headwater (Lake Louise, Banff) and upstream (Canmore to upstream of City of Calgary WWTPs) sections of the river, suggesting that nitrate is predominantly derived from nitrification of organic N (e.g. in forest soils). In contrast, midstream and downstream samples have elevated $\delta^{15}\text{N}$ values ($>+8\text{‰}$) of nitrate indicating that effluents from WWTPs and/or manure are the predominant sources of riverine nitrate.

It is typically not possible to distinguish between nitrate from WWTP effluents and manure due to their similar ranges of $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ values (Fig. 5C). To distinguish nitrate from these two sources, boron isotope ratios have proven to be a useful co-tracer (Kruk et al., 2020). Boron isotope ratios in Bow River water revealed that samples from the midstream section are dominated by WWTP-derived nutrients (Fig. 5C). In contrast, samples from the downstream section had elevated $\delta^{11}\text{B}$ values suggesting some manure-derived nutrient inputs via agricultural return-flows.

The approximate contributions from each nitrate source (soil nitrification, WWTP effluent, and manure-derived agricultural nitrate) to samples from each section of the river was estimated based on dual isotope mixing models using $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ values by Chao (2011) and $\delta^{15}\text{N}$ and $\delta^{11}\text{B}$ values by Kruk et al. (2020; Fig. 5B) and revealed that nitrate in headwater samples were predominantly derived from nitrification in soils with some minimal input from WWTPs. Nitrate in the upstream samples revealed approximately equal proportions of soil nitrification and WWTP effluent. Midstream samples revealed riverine nitrate was derived predominantly (~84 to 92%) from municipal WWTP effluents and a small proportion of soil nitrification (~8%), with the remainder (up to 8%) from unknown sources (e.g. synthetic fertilizers, but not atmospheric deposition). In the agricultural downstream section, municipal wastewater-derived nitrate remained the dominant source of riverine nitrate, while manure-derived nitrate from agricultural return flows constituted a secondary source.

4.0 Biotic responses to threats and drivers illustrated by case studies from the Bow River

4.1 *Spatial assessment of the riparian woodland community*

4.1.1 Riparian community composition

We assessed riparian woodland composition and abundance using Google Earth satellite imagery at 2 km intervals along the Bow River, excluding reservoirs because of artificially widened channels (Fig. 6). The longitudinal variation in community structure was largely consistent with expected natural drivers of variation, including climate and elevation. Community composition transitioned from primarily coniferous species in the headwater reach to a mixed community of coniferous and deciduous species between Canmore and Cochrane and finally to a predominantly deciduous community from Cochrane to the confluence with the Oldman River. While our coarse assessment suggests that riparian woodland community composition is regulated mainly by natural drivers (e.g. consistency with major natural regions), a previous, finer scale assessment conducted by Alberta Environment and Parks (AEP; previously Alberta Environment, Alberta Environment and Sustainable Resource Department) found evidence of anthropogenic threats (e.g. disturbance-tolerant and grazing-resistant species, Alberta Environment, 2007).

4.1.2 Riparian abundance

We assigned a score to represent the estimated riparian woodland abundances from negligible (0) to very dense and extensive (5). Longitudinal variation of riparian woodland abundance reflects combined natural and anthropogenic influences and can be interpreted as four main reach segments (Fig. 6), which are consistent with the four reaches depicted in Fig. 1. In Reach 1, where the river is relatively unaltered by anthropogenic activity, riparian woodland abundances are high (~3.8 on average). Reach 2 contains the largest number of anthropogenic threats. Even with reservoirs excluded, the average index value was lower than that of Reach 1 (2.1). The downstream decline in riparian health was previously attributed, at least in part, to dewatering from irrigation water withdrawals and alterations of peak flow volumes and timing (due to upstream reservoir operations; Alberta Environment, 2007; Rood, Taboulchanas, Bradley, & Kalischuk, 1999). From the inflow of the

Highwood River to Bassano Dam (Reach 3), riparian woodland abundance increased to index values (3.7) similar to that of the pristine headwater reach, suggesting a return to improved riparian health.

The improved riparian community in this reach was attributed to the return to a more natural flow regime from the inflow of the Highwood River, which is undammed and relatively unregulated (Alberta Environment, 2007; Rood et al., 1999).

Reach 4 is characterized by the lowest riparian woodland abundances of the entire river (0.4), consistent with the previous report which reported negligible tree communities (<1% cover, Alberta Environment, 2007). Land use in the reach is dominated by grazing, but this was thought to have only slight impact on the riparian community (Alberta Environment, 2007). Flows are the most diminished in this reach relative to natural flows as a result of cumulative impacts from upstream dams and the largest agricultural water withdrawal occurring at Bassano Dam (Fig. 3, >25% withdrawn, Alberta Environment, 2007). While these alterations likely contribute to poor riparian abundance, we conclude that this region was also naturally impoverished, as evidenced by mapping of the riparian woodlands by Dawson and McConnell (1884), prior to any damming or diversion. East of Bassano Dam, the major natural region switches to dry mixedgrass which is the driest subregion in Alberta (Natural Regions Committee, 2006), marking a regional shift in ecoclimatic condition. This coincides with the river shifting southward into a constrained valley, resulting in a static channel and limited floodplain in marked contrast with the dynamic alluvial channel and extensive riparian woodlands upstream.

4.2 Spatial and temporal variation in aquatic vegetation and dissolved oxygen concentrations

Potential eutrophication of the Bow River from WWTP effluents in Calgary has been a concern for decades (Culp et al., 1992; Sosiak, 2002; Taube, He, Ryan, & Valeo, 2016). Macrophyte and epilithic algae biomass assessments have been conducted by AEP in most years since 1981. Spatial assessments have shown an increase in macrophyte and algal production downstream of the WWTP outflows, which were associated with increased productivity resulting from WWTP effluent inputs (Sosiak, 2002; Taube et al., 2016). Temporal assessments have demonstrated declines in macrophyte

and algae production following upgrades to the City of Calgary WWTPs that have resulted in decreased phosphorus loads since 1982, and decreased nitrogen loads since the mid 1990s (Sosiak, 2002; Taube et al., 2016). High discharge has also been shown to limit aquatic vegetation (Chambers, Prepas, Hamilton, & Bothwell, 1991; Sosiak, 2002) with low end of season macrophyte abundances in years when annual maximum flow exceeds 400 m³/s (Taube et al., 2016). Conversely, algae biomass was not influenced by variations in annual maximum flow (Taube et al., 2016), presumably owing to the quicker regeneration of epilithic algae. Rather, Taube et al. (2016) found that algae was scoured when daily discharge exceeded 120 m³/s. Here, we assess the updated provincial data set (macrophyte and algae biomass) combined with discharge data from the hydrometric gauging station in Calgary and continuously recorded dissolved oxygen (DO) data measured by the City of Calgary DO sensor from 2007 to 2016 (Figs. 1, 7, 8).

4.2.1 Annual variation

Macrophytes typically found downstream of the WWTP outflows were absent in the year of an extreme flood event (2013) consistent with findings by Taube et al. (2016). Further, macrophytes were also absent in 2014, suggesting the possibility of a multi-year impact of the 2013 flood.

Increases in aquatic primary productivity are often associated with high photosynthesis during the day and high respiration at night, resulting in larger diel fluctuations of DO (Wassenaar, Venkiteswaran, Schiff, & Koehler, 2010). The magnitude of diel DO fluctuations measured downstream of the City of Calgary varied among years (Fig. 7). Although the magnitude of diel fluctuations varied, mean DO values were similar among years. Diel DO fluctuations were not significantly related to macrophyte biomass (linear regression $p > 0.05$) but were significantly and positively related to algae biomass ($r^2 = 0.57$, $p = 0.01$), suggesting that algal photosynthesis and respiration may be driving more of the observed fluctuations in DO. The lack of a significant relationship between macrophyte biomass and the magnitude of DO fluctuations may reflect the low abundance of macrophytes in the Bow River in recent years because of two flood events (2005, 2013), and the limited number of years for which continuous DO data exist.

4.2.2 Spatial assessment of seasonal variation

A comparison of seasonal flow, algae abundance and DO profiles reveals a difference between the sites upstream and downstream of Calgary WWTPs (Fig. 8). Notably, the diel DO fluctuations varied little at the upstream sites (<0.5 mg/L on average) compared to the patterns observed downstream (>4 mg/L on average). The large diel DO fluctuations at the downstream site are likely the effect of WWTP effluent-enhanced photosynthesis and respiration activity in the river (Wassenaar et al., 2010). Consistent with this, upstream algae biomass was typically lower than biomass measured at the downstream site. However, low upstream diel DO fluctuations may also result from releases from Bearspaw Dam immediately upstream of the water DO sensor location.

4.3. *Spatial and temporal variations in macroinvertebrate metrics*

Early studies indicated that benthic macroinvertebrate species distribution along the Bow River was largely related to terrestrial vegetation zones (Donald & Mutch, 1980; Reynoldson, 1973). The upper reach of the river contained shredders and grazers, whereas the lower river reaches contained scrapers, filter-feeders and deposit-feeders, a pattern consistent with the RCC and which authors attributed to shifts in hydraulic, geomorphic and climatic conditions (Culp et al., 1992). Reynoldson (1973) did, however, identify a decrease in species richness and biodiversity between Calgary and Carseland, and an increase in density, which he attributed to the WWTP inputs to the river.

Here, we assess spatial and temporal variability of AEP's macroinvertebrate data which has been collected periodically since 1983 (Anderson, 1991; Saffran & Anderson, 2009). Overall macroinvertebrate density varied among years with no directional pattern (mean density of all five sites (number/m²): 1985 – 43000, 1993 – 62540, 2006 – 63450, 2007 – 42860, 2014 – 59630). There were no significant relationships found between macroinvertebrate densities and mean daily discharge or algal biomass (linear regressions, $p>0.05$). When viewed in finer detail both density and proportion of *Ephemeroptera*, *Plecoptera*, and *Trichoptera* (EPT) failed to show clear spatial or temporal patterns (Fig. 9A). Two-way ANOVAs identified significant interactions between year and site (density: $F_{16,100} = 13.435$, $p<0.0001$; EPT proportion: $F_{16,100}=12.821$, $p<0.0001$) so that any

observed spatial patterns were not consistent year over year. The large amount of spatial and temporal variation in both metrics makes it difficult to identify the threats or natural drivers responsible. The lack of a meaningful pattern may be the result of infrequent or insufficient sampling or the ability of macroinvertebrates to migrate vertically into the hyporheic zone in response to changes in flow (Stubbington, 2012). Caution should be taken when interpreting this type of data from limited sampling. A review by Ellis and Jones (2013) of dam impacts on benthic invertebrate communities indicated varying response, noting the challenges of identifying a single abiotic variable responsible for invertebrate community characteristics.

4.4 Spatial variation in fish species distribution and sport fish biomass

The spatial distribution of fish species was assessed along the Bow River (Mee, Robins, & Post, 2018; Robins, 2009). Overall, the number of fish species increased with distance from headwaters, generally in agreement with patterns of species addition often observed in montane lotic environments (Fig. 10; Rahel & Hubert, 1991). Explored at a finer scale, species numbers fluctuated longitudinally, indicating an inconsistent rather than gradual pattern of increase that can be interpreted as four main reach segments, as depicted in Fig. 1. The number of species present was fairly stable in Reach 1, showing only one distinct increase; on average, 10.7 species were observed in this reach, all of which had cold-water preferences (Mee et al., 2018). Contrary to the expected pattern of species addition, Reach 2 was characterized by a large amount of fluctuation and on average had a lower number of fish species than Reach 1 (9.5). Reach 3 displayed a return to the expected gradual increase in fish species indicative of recovery, until a sharp decline immediately before the last dam on the river. Reach 4 shows a general increasing trend with some fluctuation. Overall, the longitudinal patterns in number of fish species on the Bow River correspond with the expected pattern of species addition (Horwitz, 1978; Rahel & Hubert, 1991) with deviations occurring in areas of high anthropogenic disturbance.

An assessment of species distribution in relation to physicochemical variables conducted by Mee et al. (2018) indicated that mean July water temperature was the best predictor of species

distribution along the river (Fig. 10). The authors noted two areas along the Bow River with high community turnover (low Czekanowski coefficient, Fig. 10); these occurred at approximately 260 and 445 km downstream from headwaters, where mean July water temperatures were approximately 15 and 19 °C, respectively. These high turnover zones and the temperatures that characterized them were remarkably consistent across the three largest rivers in the South Saskatchewan River Basin that originate in the Rocky Mountains – the Bow River, the Red Deer River to the north, and the Oldman River to the south (Mee et al., 2018).

The findings by Mee et al. (2018) provide a new perspective with which to consider spatial patterns in sport fish biomass in and downstream of the City of Calgary presented by Askey et al. (2007). Askey et al. (2007) observed a drastic increase in rainbow trout biomass (25x) and a smaller increase in brown trout biomass (5x, Fig. 11) consistent with an expected response to the nutrient input from Calgary's WWTPs (Fig. 5); however, they also observed an unexpected decrease in mountain whitefish biomass (45x). The authors suggested several potential hypotheses for the observed change, which could not be evaluated because of limits to the empirical data (Askey et al., 2007). The first of the two high species turnover zones identified along the Bow River by Mee et al. (2018), occurred within the City of Calgary, immediately upstream of the first Calgary WWTP. As such, the large shift in sport fish biomass identified by Askey et al. (2007), mountain whitefish in particular, may be related to the change in water temperature in addition to the previously identified role of nutrients (Fig. 5A). The location of the first species turnover (at ~15 °C) is likely related to natural climate variation along the river but could be influenced by anthropogenic thermal effluents (i.e. WWTP outflows) and exacerbated by diminished riparian abundances. The second key shift in fish community structure (at ~19 °C) occurs just upstream of the Bassano dam, near other key shifts in the river (i.e. natural region, low riparian abundance, shifts to more silt-covered substrate).

5.0 Elucidating relative roles of anthropogenic threats and natural drivers

5.1 Longitudinal structure of anthropogenic threats and natural drivers on the Bow River

A review of the relative roles of primary natural drivers and anthropogenic threats lends itself to considering the Bow River as four distinct longitudinal reaches (Fig. 1): Reach 1 is mainly influenced by natural drivers; Reach 2 contains the highest number of anthropogenic threats; Reach 3 undergoes recovery; and Reach 4 displays combined and cumulative effects of natural drivers and anthropogenic threats.

Between the headwaters and the first mainstem dam, Reach 1 contains the fewest anthropogenic threats and we can conclude that most of the observed abiotic variation and consequent patterns in biota are primarily caused by natural drivers. This reach was characterized by a mostly unaltered flow regime, low water temperatures and low nutrient fluxes despite containing three small WWTPs. Biota were characterized by the highest riparian abundances, a macroinvertebrate community typical of headwater systems (Culp et al., 1992), and fish community made up of a low number of cold-water species (Mee et al., 2018).

Reach 2 contains the highest number of anthropogenic threats on the Bow River, which include dams, weirs and on-river reservoirs that facilitate channel widening, water storage and river regulation, alter the magnitude and timing of discharge, and impede fish movement. This reach also contains the City of Calgary, the most populous area in Alberta, which is associated with a higher prevalence of bank armoured and contains three wastewater treatment plants that release treated effluent directly into the river. As a result of these threats, this reach is characterized by a higher rate of temperature increase than expected, an altered flow regime, a marked increase in nutrient fluxes, and lower than expected sinuosity. Lower sinuosity likely occurs as a result of channel armoured and regulated flows which both act to limit natural geomorphic processes (Florsheim et al., 2008; Williams & Wolman, 1984). The high number of anthropogenic threats is reflected in lower riparian abundance, increased aquatic vegetation and consequent DO fluctuations, and a shift in fish community structure and biomass including lower numbers of fish species than predicted.

Reach 3 represents an area of recovery following the heavily altered upstream Reach 2. The inflow of the Highwood River, a large, relatively unregulated river, returns some of the natural magnitude and timing of discharge to the Bow River, restoring geomorphic processes to a natural state and promoting riparian communities. In this reach, a shift in macroinvertebrates to scrapers, filter feeders and deposit feeders was observed (Culp et al., 1992), consistent with the RCC (Vannote et al., 1980). The fish community gradually increases in number of species, consistent with predicted patterns in species addition (Horwitz, 1978; Rahel & Hubert, 1991) which may be linked to increased habitat availability resulting from geomorphic processes and large woody debris (Gibeau, Connors, & Palen, 2017; Pusey & Arthington, 2003). Closer to Bassano Dam, the fish community shifts to mainly warmer water species, a change likely related to natural longitudinal shifts in temperature. Despite recovery in many aspects, nutrient fluxes remain high due to relatively high contributions of urban WWTP effluent, but, toward the downstream end of this reach, agricultural return flows constitute a secondary nutrient source.

The last reach on the Bow River, between Bassano Dam and the confluence with the Oldman River, represents a combination of anthropogenic threats within the reach, cumulative effects of upstream threats and natural drivers. Although discharge along the river is the most altered in this reach, evidence of similar conditions pre-dating most anthropogenic alterations (Dawson & McConnell, 1884) suggests that low riparian abundances here cannot be attributed solely to anthropogenic activity. The fish community is not similarly impoverished; rather, it is characterized by increased numbers of species, consistent with expected patterns of species addition (Horwitz, 1978; Mee et al., 2018; Rahel & Hubert, 1991). The fish community inhabiting this reach is likely unimpeded by low riparian abundances since it comprises relatively warm water species (Mee et al., 2018).

5.2 Serial discontinuity vs. river continuum concepts

We use the RCC and its underlying fluvial geomorphological theory to present an expected gradient of abiotic variation and biotic responses along an unaltered river (Vannote et al., 1980).

However, both abiotic and biotic parameters on the Bow River illustrate deviations from the expected continuum. This is unsurprising given the prevalence of anthropogenic discontinuities and in fact, the serial discontinuity concept (SDC) was proposed to address deviations from the RCC caused by on-river dams (Ward & Stanford, 1983). But deviations from the expected continuum can also be caused by other types of anthropogenic threats such as WWTP outflows, water extractions and bank armouring.

Further complicating our ability to decipher natural from altered abiotic variation and biotic responses is that natural drivers can also cause abrupt changes to response variables, and conversely, anthropogenic threats can occur in a diffuse manner. Tributaries provide water and sediment that can create a discontinuity in the main stem (Rice, Greenwood, & Joyce, 2001), the impact and magnitude of which depend on the size of the tributary (Sabo, Bestgen, Graf, Sinha, & Wohl, 2012). This is evident on the Bow River following the input of the Highwood River where much recovery is observed. A primary example of a diffuse anthropogenic threat on the Bow River is nutrient input from agricultural sources. Whether natural drivers and anthropogenic threats are discrete or diffuse has implications for how easily their impacts can be identified, quantified, and in the case of threats, mitigated.

5.3 Complexity of threat-driver interactions

Understanding the relationship between anthropogenic threats and natural drivers is necessary to inform decisions on if and how threat management should occur. Since our assessment of the Bow River combines data from vastly different disciplines at different temporal and spatial scales, we did not quantify the relative roles of threats and drivers on abiotic variation and biotic responses. A more quantitative assessment is needed to determine what types of threat/driver interactions are at work (i.e. additive, synergistic, antagonistic, reversal, Jackson et al., 2016). Instead, we discuss interactions here as either cooperative or conflicting. A cooperative interaction is when the effect of each threat or driver results in the same direction of change in the abiotic variable or biotic response, whereas a conflicting interaction results in opposing responses.

Bank armouring, water extraction and river regulation can act cooperatively to diminish riparian abundances, whereas hydrology (i.e. tributary inputs) can suppress impacts of river regulation and water extraction and promote recovery in riparian communities. A return to natural geomorphic processes (e.g. creation of gravel bars, side channels, pools) and increased availability of large woody debris provided by the healthier riparian community likely contributes to the apparent recovery of the fish community (Gibeau et al., 2017; Pusey & Arthington, 2003). Further, cooperative interactions between natural climate variability, geology, river regulation and water extraction result in the riparian conditions observed in reach 4 with all drivers and threats contributing to the impoverished riparian conditions.

During the summer, river regulation and water extraction interact cooperatively where both threats reduce flow. When combined with anthropogenic nutrient inputs, reduced flow can have ecological impacts such as increased aquatic vegetation biomass (macrophyte and/or algae), increased fluctuations in dissolved oxygen concentrations and potential negative impacts on fish. Whether aquatic vegetation community composition predominantly comprises macrophytes or algae depends on a conflicting interaction between natural climate variation (i.e. annual freshet magnitude), river regulation (i.e. lowered daily summer flows) and anthropogenic nutrient inputs. That is, in years when the annual freshet is large, high flows counteract the impact of nutrients by scouring vegetation beds, with a longer lasting effect on macrophytes. Conversely, when the annual freshet is small, reduced flows from river regulation and anthropogenic nutrient inputs interact cooperatively to facilitate increased aquatic vegetation biomass, the composition of which will depend on competition between algae and macrophytes (Hilton, O'Hare, Bowes, & Jones, 2006; O'Hare et al., 2018).

Nutrient concentrations and temperature can interact cooperatively or in conflict to impact fish, depending on species. Natural climate variability (i.e. temperature) along the river and anthropogenic nutrient inputs work together to increase biomass of rainbow trout and brown trout.

However, for mountain whitefish, which have lower thermal tolerances, the interaction between temperature and nutrients is conflicting; nutrients lead to increased biomass, but temperature leads to decreased biomass.

Not all ecological processes and outcomes are equally understood, resulting in gaps in our ability to characterize interactions and their impacts. For example, river regulation conflicts with natural climate variations when winter flows are higher than the natural hydrograph would predict owing to increased winter power demands. However, the potential impact of high winter flow on fish is not clear. A review by Heggens et al. (2018) suggests that high winter flows may increase available habitat and result in higher salmonids productivity. But the authors also note that higher winter flows can lead to loss of spawning redds or increased egg mortality if the substratum is disturbed. The authors conclude that the specific effects of high winter flows will depend on species and life stage, as well as habitat and flow characteristics. The interaction between threats and drivers can get complicated quickly as more factors are included and variables of seasonality, species and life stage are considered.

5.4 Implications for management

Our exploration of threat-driver interactions has improved our understanding of ecological processes in the Bow River. That knowledge can help evaluate whether management techniques used in other systems are likely to succeed on the Bow River. The known impact of river regulation on the natural hydrograph, and its impact on riparian abundances has prompted the alteration of dam operations to mimic natural flow in order to promote cottonwood seedling colonization and woodland development (called functional flows, Mahoney & Rood, 1998). This method has had success for some regional rivers (Foster, Mahoney, & Rood, 2018; Rood et al., 2016, 2005) but has not been conducted on the Bow River. Our analysis identified Reaches 2 and 4 with lower than expected riparian abundances as candidates for management intervention. The continued presence of other anthropogenic threats, specifically bank armouring, and dampened geomorphic processes

in Reach 2 suggests that functional flows may have limited effectiveness here. In Reach 4, historical low riparian abundances suggests that management intervention is unnecessary.

High macrophyte growth is controlled in some rivers using flushing flows or mechanical removal (Hussner et al., 2017; Ochs, Rivaes, Ferreira, & Egger, 2018). If DO fluctuation management is desired, low frequency flushing flows or relying on large annual freshets would not be an adequate course of action for the Bow River since these do not have long term effects on algae and DO is mainly linked to algae photosynthesis and respiration. Therefore, managing nutrient inputs, maintaining higher daily flow or using periodic flushing flows (e.g. Fovet et al., 2012) would be needed.

5.5 Relative impacts of threats and implications for recovery

The size of each threat has implications for its impact and recovery of the riverine ecosystem downstream. For example, even though WWTPs are responsible for approximately 50% of the nutrients in the upstream reach, the low nutrient fluxes coupled with low water temperatures suggests a meaningful biotic response is unlikely. On the other hand, the large WWTP nutrient contribution from the City of Calgary has resulted in macrophyte patches and has a long downstream footprint. However, a threat's impact and river's recovery are also influenced by interactions with other threats and natural drivers, as discussed in Section 5.3. Although Reach 2 contains a high concentration of threats with considerable ecological impacts, downstream recovery is remarkably quick (e.g. geomorphic processes, riparian community and fish community recovery observed in Reach 3) owing mainly to the proximity of a large relatively unregulated tributary (Highwood River). The longitudinal position of a threat also influences the severity of its impact. Although recovery of many variables is observed in Reach 3, the longitudinal position of anthropogenic threats in Reach 2 has disproportionate impacts on cold-water fish species since they are thermally excluded from the region of recovery in Reach 3. Indeed, anthropogenic development

likely contributed to declines and extirpation of cold-water native salmonids in the foothills of the Bow River basin (Sinnatamby, Cantin, & Post, 2019).

6.0 Conclusions

Understanding the ecological processes underpinning observed biotic responses is key to elucidating the relative roles of multiple anthropogenic threats and natural drivers and determining best tools and priorities for management. Determining the relative roles of drivers and threats and how they interact is a challenging task, made more complex with increasing numbers of factors. In the Bow River, we have made advances using new analytical methods, applying new findings to old theories, extending long-term datasets and merging different types of data. By combining new and existing assessments from several disciplines we identified primary threats and drivers, described their roles, and characterized how they interact to generate the observed variation in abiotic factors and biotic responses. Our analysis illustrates how even a well-studied and simple system can be further understood by combining information from different fields, advancing analytical methods, and growing datasets, providing a stronger foundation on which to evaluate potential management actions. However, this work is not exhaustive and there remain many physical, chemical, and biological connections to consider. For example, we have not considered threats that act directly on biota (fishing, Cahill et al., 2018; forestry, Forcorp Solutions Inc, 2012; or whirling disease). As well, we did not consider the role of feedback loops or biotic interactions (e.g. algal shading of macrophyte, competition among fish species, etc.). To further develop management tools to address anthropogenic impacts, we must consider natural variability and threats as they modify ecosystem structure and function across the spatial and temporal scales of regulated riverine ecosystems. The inability to unravel complex driver-threat relationships may result in attributing abiotic variation and biotic responses to the wrong threat, or just one threat when several are involved, leading to selecting management tools that are ill suited to the problem, or even causing paralysis among scientists and managers. As threat and driver interactions become numerous and more complex, a mechanistic model may be necessary to identify and quantify those interactions and their outcomes.

Acknowledgements

The authors thank Wendell Koning and two anonymous reviewers for providing helpful comments to earlier versions of this manuscript. The authors thank the City of Calgary and the Province of Alberta for access to data - restrictions apply to the availability of these data, which were used under license for this study. Bow River discharge data were extracted from Environment and Climate Change Canada Historical Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html) on March 7, 2018. Financial support from Alberta Innovates and the Discovery Grant program of the Natural Sciences and Engineering Research Council of Canada (NSERC) is also gratefully acknowledged.

References

- Acreman, M., Arthington, A. H., Colloff, M. J., Couch, C., Crossman, N. D., Dyer, F., ... Young, W. (2014). Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing world. *Frontiers in Ecology and the Environment*, 12(8), 466–473. <https://doi.org/10.1890/130134>
- Alberta Agriculture and Forestry. (2016). *Alberta Irrigation Information* (Vol. <http://www>). Accessed online January 2018.
- Alberta Agriculture and Forestry. (2017). *Alberta Irrigation Information* (Vol. <http://www>). Accessed online August 2018.
- Alberta Environment. (2007). *Aquatic and Riparian Condition Assessment of the South Saskatchewan River Basin*. Edmonton, Alberta: Alberta Environment.
- Anderson, A. M. (1991). *An overview of long-term zoobenthic monitoring in Alberta Rivers (1983-1987)*. Edmonton, Alberta: Alberta Environment.
- Askey, P. J., Hogberg, L. K., Post, J. R., Jackson, L. J., Rhodes, T., & Thompson, M. S. (2007). Spatial patterns in fish biomass and relative trophic level abundance in a wastewater enriched river. *Ecology of Freshwater Fish*, 16(3), 343–353. <https://doi.org/10.1111/j.1600-0633.2007.00221.x>
- Aylward, B., Bandyopadhyay, J., Belausteguigotia, J.-C., Börkey, P., Cassar, A., Meadors, L., ... Voutchkov, N. (2005). Freshwater Ecosystem Services. In R. Constanza, P. Jacobi, & F. Rijsberman (Eds.), *Ecosystems and Human Well-being: Policy Responses* (pp. 213–255). Washington, D.C: Island Press.
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30(4), 492–507. <https://doi.org/10.1007/s00267-002-2737-0>
- Cahill, C. L., Mogensen, S., Wilson, K. L., Cantin, A., Sinnatamby, R. N., Paul, A. J., ... Post, J. R. (2018). Multiple challenges confront a high-effort inland recreational fishery in decline. *Canadian Journal of Fisheries and Aquatic Sciences*, 1–44. <https://doi.org/10.1139/cjfas-2018-0086>
- Caissie, D. (2006). The thermal regime of rivers: a review. *Freshwater Biology*, 51(8), 1389–1406. <https://doi.org/10.1111/j.1365-2427.2006.01597.x> ER
- Carpenter, S. R., Stanley, E. H., & Vander Zanden, M. J. (2011). State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources*, 36, 75–99. <https://doi.org/10.1146/annurev-environ-021810-094524>
- Chambers, P. A., Prepas, E. E., Hamilton, H. R., & Bothwell, M. L. (1991). Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecological Applications*, 1(3), 249–257. <https://doi.org/10.2307/1941754>
- Chao, Y. J. (2011). *Major ion and stable isotope geochemistry of the Bow River, Alberta, Canada*. University of Calgary, Calgary, Alberta.
- City of Calgary. (2016). *Calgary Rivers Morphology and Fish Habitat Study*. Calgary, Alberta: City of Calgary.
- Cote, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B-Biological Sciences*, 283(1824), 20152592. <https://doi.org/10.1098/rspb.2015.2592>

- Craig, L. S., Olden, J. D., Arthington, A. H., Entekin, S., Hawkins, C. P., Kelly, J. J., ... Wooten, M. S. (2017). Meeting the challenge of interacting threats in freshwater ecosystems: A call to scientists and managers. *Elementa Science of the Anthropocene*, 5, 72. <https://doi.org/10.1525/elementa.256>
- Culp, J. M., Hamilton, H. R., Sosiak, A. J., & Davies, R. W. (1992). Longitudinal zonation of the biota and water quality of the Bow River system in Alberta, Canada. In C. D. Becker & D. A. Neitzel (Eds.), *Water quality in North America river systems*. Columbus, Ohio: Battelle Press.
- Dawson, G. M., & McConnell, R. G. (1884). Map showing wooded and prairie tracts & c. in the vicinity of the Bow and Belly Rivers. Ottawa, Canada: Geological and Natural Survey of Canada.
- Dey, S. (2014). *Fluvial hydrodynamics: Hydrodynamic and Sediment Transport Phenomena*. New York: Springer.
- Donald, D. B., & Mutch, R. A. (1980). The effects of hydroelectric dams and sewage on the distribution of stoneflies (*Plecoptera*) along the Bow River. In *Quaestiones entomologicae*. (Vol. 16, pp. 657–670). Dept. of Entomology, University of Alberta. Retrieved from <https://www.biodiversitylibrary.org/part/204332>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., ... Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, 81(2), 163–182. <https://doi.org/10.1017/S1464793105006950>
- East Slopes Aquatic Consulting Inc. (2017). *Bank Armouring and Riparian Disturbance Inventory, 2016 : Bow, Elbow, Highwood, and Sheep Rivers*. Calgary, Alberta: Trout Unlimited Canada.
- Ellis, L. E., & Jones, N. E. (2013). Longitudinal trends in regulated rivers: A review and synthesis within the context of the serial discontinuity concept. *Environmental Reviews*, 21(3), 136–148. <https://doi.org/10.1139/er-2012-0064>
- Fau, V. (2015). *Identifying the sources and tracing the fate of phosphate in the Bow River basin, Alberta, Canada, using oxygen isotope analyses*. University of Calgary.
- Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience*, 52(6), 483–498. [https://doi.org/10.1641/0006-3568\(2002\)052\[0483:LTRBTG\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2)
- Feld, C. K., Birk, S., Eme, D., Gerisch, M., Hering, D., Kernan, M., ... Malard, F. (2016). Disentangling the effects of land use and geo-climatic factors on diversity in European freshwater ecosystems. *Ecological Indicators*, 60, 71–83. <https://doi.org/10.1016/j.ecolind.2015.06.024>
- Florsheim, J. L., Mount, J. F., & Chin, A. (2008). Bank erosion as a desirable attribute of rivers. *BioScience*, 58(6), 519–529. <https://doi.org/10.1641/b580608>
- Forcorp Solutions Inc. (2012). *Regional Forest Landscape Assessment: South Saskatchewan Region*. Edmonton, Alberta: Alberta Environment and Sustainable Resource Development.
- Foster, S. G., Mahoney, J. M., & Rood, S. B. (2018). Functional flows: an environmental flow regime benefits riparian cottonwoods along the Waterton River, Alberta. *Restoration Ecology*, 26(5), 921–932. <https://doi.org/10.1111/rec.12654>
- Fovet, O., Belaud, G., Litrico, X., Charpentier, S., Bertrand, C., Dollet, P., & Hugodot, C. (2012). A model for fixed algae management in open channels using flushing flows. *River Research and Applications*, 28, 960–972. <https://doi.org/10.1002/rra>
- Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Faux, R. N., Steel, E. A., Beechie, T. J., ... Leibowitz, S. G.

- (2015). Rethinking the longitudinal stream temperature paradigm: Region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. *Hydrological Processes*, 29(22), 4719–4737. <https://doi.org/10.1002/hyp.10506>
- Gibeau, P., Connors, B. M., & Palen, W. J. (2017). Run-of-River hydropower and salmonids: potential effects and perspective on future research. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(7), 1135–1149. <https://doi.org/10.1139/cjfas-2016-0253>
- Hamilton, W. N., Price, M. C., & Langenberg, C. W. (1999). Geological Map of Alberta. Alberta Energy and Utilities Board, Alberta Geological Survey, Map 236.
- Harrison, P. A., Berry, P. M., Simpson, G., Haslett, J. R., Blicharska, M., Bucur, M., ... Turkelboom, F. (2014). Linkages between biodiversity attributes and ecosystem services: A systematic review. *Ecosystem Services*, 9, 191–203. <https://doi.org/10.1016/j.ecoser.2014.05.006>
- Heggenes, J., Alfredsen, K., Bustos, A. A., Huusko, A., & Stickler, M. (2018). Be cool: A review of hydro-physical changes and fish responses in winter in hydropower-regulated northern streams. *Environmental Biology of Fishes*, 101(1), 1–21. <https://doi.org/10.1007/s10641-017-0677-z>
- Hilton, J., O'Hare, M., Bowes, M. J., & Jones, J. I. (2006). How green is my river? A new paradigm of eutrophication in rivers. *Science of the Total Environment*, 365(1–3), 66–83. <https://doi.org/10.1016/j.scitotenv.2006.02.055>
- Horwitz, R. J. (1978). Temporal variability patterns and the distribution patterns of stream fishes. *Ecological Monographs*, 48, 307–321. <https://doi.org/10.2307/2937233>
- Hussner, A., Stiers, I., Verhofstad, M. J. J. M., Bakker, E. S., Grutters, B. M. C., Haury, J., ... Hofstra, D. (2017). Management and control methods of invasive alien freshwater aquatic plants: A review. *Aquatic Botany*, 136, 112–137. <https://doi.org/10.1016/j.aquabot.2016.08.002>
- Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., & Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology*, 22(1), 180–189. <https://doi.org/10.1111/gcb.13028>
- Koning, C. W., Locke, A. G. H., & Mahoney, J. M. (2016). Determining environmental flows for the South Saskatchewan River Basin, Alberta, Canada. In B. Németh (Ed.), *Engineering and Industry* (Vol. Watershed, pp. 86–93). Trivent Publishing. <https://doi.org/10.22618/tp.ei.20162.120011>
- Kruk, M. K., Mayer, B., Nightingale, M., & Laceby, J. P. (2020). Tracing nitrate sources with a combined isotope approach ($\delta^{15}\text{N}_{\text{NO}_3}$, $\delta^{18}\text{O}_{\text{NO}_3}$ and $\delta^{11}\text{B}$) in a large mixed-use watershed in southern Alberta, Canada. *Science of the Total Environment*, 703, 135043. <https://doi.org/10.1016/j.scitotenv.2019.135043>
- Longmore, L. A., & Stenton, C. E. (1981). *The fish and fisheries of the South Saskatchewan River basin*. Edmonton, Alberta: Alberta. Dept. of Energy and Natural Resources.
- Mahoney, J. M., & Rood, S. B. (1998). Streamflow requirements from cottonwood seedling recruitment — an integrative model. *Wetlands*, 18(4), 634–645. <https://doi.org/10.1007/BF03161678>
- Malmqvist, B., & Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, 29(2), 134–153. <https://doi.org/10.1017/S0376892902000097>
- Mee, J. A., Robins, G. L., & Post, J. R. (2018). Patterns of fish species distributions replicated across three parallel rivers suggest biotic zonation in response to a longitudinal temperature gradient. *Ecology of Freshwater Fish*, 27(1), 44–61. <https://doi.org/10.1111/eff.12322>

- Natural Regions Committee. (2006). *Natural Regions Committee 2006*. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852.
- Nöges, P., Argillier, C., Borja, Á., Garmendia, J. M., Hanganu, J., Kodeš, V., ... Birk, S. (2016). Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. *Science of the Total Environment*, 540, 43–52. <https://doi.org/10.1016/j.scitotenv.2015.06.045>
- O'Hare, M. T., Baattrup-Pedersen, A., Baumgarte, I., Freeman, A., Gunn, I. D. M., Lázár, A. N., ... Bowes, M. J. (2018). Responses of aquatic plants to eutrophication in rivers: A revised conceptual model. *Frontiers in Plant Science*, 9, 1–13. <https://doi.org/10.3389/fpls.2018.00451>
- Ochs, K., Rivaes, R. P., Ferreira, T., & Egger, G. (2018). Flow management to control excessive growth of macrophytes – an assessment based on habitat suitability modeling. *Frontiers in Plant Science*, 9, 1–11. <https://doi.org/10.3389/fpls.2018.00356>
- Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 55(1), 86–107. <https://doi.org/10.1111/j.1365-2427.2009.02179.x>
- Peterson, B. J., Wollheim, W. M., Mulholland, P. J., Webster, J. R., Meyer, J. L., Tank, J. L., ... Morrall, D. D. (2001). Control of nitrogen export from watersheds by headwater streams. *Science*, 292, 86–90. <https://doi.org/10.1126/science.1056874>
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., ... Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, 47(11), 769–784. <https://doi.org/10.2307/1313099>
- Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55(1), 194–205. <https://doi.org/10.1111/j.1365-2427.2009.02272.x>
- Postel, S., & Carpenter, S. R. (1997). Freshwater ecosystem services. In G. C. Daily (Ed.), *Natures services: Societal dependence on natural ecosystems* (pp. 195–214). Washington DC: Island Press.
- Pusey, B. J., & Arthington, A. H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: A review. *Marine and Freshwater Research*, 54(1), 1–16. <https://doi.org/10.1071/MF02041>
- Rahel, F. J., & Hubert, W. A. (1991). Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: Biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society*, 120(3), 319–332. [https://doi.org/10.1577/1548-8659\(1991\)120<0319:FAAHGI>2.3.CO;2](https://doi.org/10.1577/1548-8659(1991)120<0319:FAAHGI>2.3.CO;2)
- Reynoldson, T. B. (1973). *Macrobenthic fauna surveys of the Oldman, Bow, Red Deer and North Saskatchewan rivers*. Edmonton, Alberta: Alberta Environment.
- Rice, S. P., Greenwood, M. T., & Joyce, C. B. (2001). Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 824–840. <https://doi.org/10.1139/f01-022>
- Robins, G. L. (2009). *Spatial distribution of 33 fish species in the mainstem rivers of the South Saskatchewan River Basin under changing thermal regimes*. University of Calgary, Calgary.
- Rood, S. B., Kaluthota, S., Gill, K. M., Hillman, E. J., Woodman, S. G., Pearce, D. W., & Mahoney, J. M. (2016). A twofold strategy for riparian restoration: combining a functional flow regime and direct seeding to re-establish cottonwoods. *River Research and Applications*, 32, 836–844.

<https://doi.org/10.1002/rra.2919>

- Rood, S. B., Samuelson, G. M., Braatne, J. H., Gourley, C. R., Hughes, F. M. R., & Mahoney, J. M. (2005). Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, 3(4), 193–201. [https://doi.org/10.1890/1540-9295\(2005\)003\[0193:MRFTRF\]2.0.CO](https://doi.org/10.1890/1540-9295(2005)003[0193:MRFTRF]2.0.CO)
- Rood, S. B., Taboulchanas, K., Bradley, C. E., & Kalischuk, A. R. (1999). Influence of flow regulation on channel dynamics and riparian cottonwoods along the Bow River, Alberta. *Rivers*, 7(1), 33–48.
- Sabo, J. L., Bestgen, K., Graf, W., Sinha, T., & Wohl, E. E. (2012). Dams in the Cadillac Desert: Downstream effects in a geomorphic context. *Annals of the New York Academy of Sciences*, 1249(1), 227–246. <https://doi.org/10.1111/j.1749-6632.2011.06411.x>
- Saffran, K. A., & Anderson, A.-M. (2009). *Review of benthic invertebrates and epilithic algae at long-term monitoring sites in the Bow River*. Edmonton, Alberta: Alberta Environment.
- Schneider, R. R. (2013). *Alberta's natural subregions under a changing climate: past, present and future*. Edmonton, Alberta: Alberta Biodiversity Monitoring Institute.
- Shiklomanov, I. (1993). World fresh water resources. In P. H. Gleick (Ed.), *Water in crisis: a guide to the world's fresh water resources* (pp. 13–24). New York: Oxford University Press. <https://doi.org/0-19-507627.3>
- Sinnatamby, R. N., Cantin, A., & Post, J. R. (2019). Threats to at-risk salmonids of the Canadian Rocky Mountain region. *Ecology of Freshwater Fish*. <https://doi.org/10.1111/eff.12531>
- Sosiak, A. (2002). Long-term response of periphyton and macrophytes to reduced municipal nutrient loading to the Bow River (Alberta, Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, 59(6), 987–1001. <https://doi.org/10.1139/f02-071>
- Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., ... Hering, D. (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: A review. *Hydrobiologia*, 696(1), 1–28. <https://doi.org/10.1007/s10750-012-1183-0>
- Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), 344–358. <https://doi.org/10.1899/08-171.1>
- Stubbington, R. (2012). The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research*, 63(4), 293–311. <https://doi.org/10.1071/MF11196>
- Taube, N., He, J., Ryan, M. C., & Valeo, C. (2016). Relative importance of P and N in macrophyte and epilithic algae biomass in a wastewater-impacted oligotrophic river. *Environmental Monitoring and Assessment*, 188(8), 494. <https://doi.org/10.1007/s10661-016-5493-y>
- Thorp, J. H., Thoms, M. C., & DeLong, M. D. (2006). The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. *River Research and Applications*, 22(2), 123–147. <https://doi.org/10.1002/rra.901>
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130–137. <https://doi.org/10.1139/f80-017>
- Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., ... Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467(7315), 555–561. <https://doi.org/10.1038/nature09440>

Ward, J. V. & Stanford, J. A. (1983). The serial discontinuity concept of lotic ecosystems. In T. D. Fontaine & S. M. Bartell (Eds.), *Dynamics of Lotic Ecosystems* (pp. 29–42). Ann Arbor: Ann Arbor Science.

Wassenaar, L. I., Venkiteswaran, J. J., Schiff, S. L., & Koehler, G. (2010). Aquatic community metabolism response to municipal effluent inputs in rivers quantified using diel $\delta^{18}\text{O}$ values of dissolved oxygen. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(8), 1232–1246. <https://doi.org/10.1139/F10-057>

Williams, G. P., & Wolman, M. G. (1984). *Downstream effects of dams on alluvial rivers* (Vol. Geological). Washington, D.C: United States Government Printing Office.

Table 1. Natural drivers and anthropogenic threats known to act on abiotic variables in the Bow River, and examples of biotic responses discussed in this paper.

Natural Driver/Threat	Abiotic Variation	Biotic Response
<ul style="list-style-type: none"> Distance from headwater Climate variability Geology Hydrology (tributary inputs) Dams, weirs, reservoirs Water extractions Bank armouring Wastewater treatment plants Agriculture Climate Change 	<ul style="list-style-type: none"> Major natural regions Channel morphology Substrate Discharge Water temperature Nutrients 	<ul style="list-style-type: none"> Riparian community and abundance (spatial) Aquatic vegetation abundance (macrophyte, epilithic algae; temporal) Aquatic invertebrate abundance and composition (spatial and temporal) Fish community, species distribution, biomass (spatial)

Table 2. Names of key locations illustrated on the main stem of the Bow River. Number on map corresponds with the numbers displayed on Figure 1.

Number on map	Name
1	Lake Louise
2	Town of Banff
3	Town of Canmore
4	Kananaskis Dam (left), Horseshoe Dam (right)
5	Ghost Dam ^a
6	Town of Cochrane
7	Bearspaw Dam ^a
8	Calgary Weir
9	Stier's Ranch
10	Carseland Weir
11	Bassano Dam

^aDams associated with on-river reservoirs

Figure 1. Map of the Bow River watershed indicating main tributaries. Other key features are shown in the legend and defined in Table 2. Vertical dashed lines indicate delineations between reaches defined and discussed in this paper.

Figure 2. Longitudinal profile of physical properties of the Bow River, including major tributaries, water extractions, population centres, barriers, major natural region, channel type, elevation (grey line graph), channel width (dark grey bar chart), and sinuosity (horizontal black lines). The reaches depicted in Fig. 1 are illustrated at the top. Blue arrows indicate main tributaries, and green arrows indicate water withdrawals by the City of Calgary and the irrigation districts (WID, BRID, EID); the thickness of the arrows indicates relative magnitude within each category (i.e. tributary, water extraction). The orange dots indicate municipalities and reserves except for the City of Calgary which is represented by a grey rectangle. Vertical bars indicate dams (black) or weirs (grey) on the main stem.

Figure 3. Spatial and temporal variability of Bow River hydrology. (A) Mean May to October discharge along the Bow River averaged from early years (1911-1920; dashed line) and recent years (2001-2010, solid line). Key features of the Bow River and river reaches depicted in Fig. 1 are illustrated: municipalities/reserves – orange dots, City of Calgary – grey rectangle, dams – vertical black bars, weirs – vertical grey bars, main tributaries – blue arrows, water withdrawals – green arrows. (B) Mean monthly discharge for Banff and Calgary from early years (1911-1920; dashed line) and recent years (2001-2010; solid line). Discharge data was obtained from Environment and Climate Change Canada's Historical Hydrometric Data web site (https://wateroffice.ec.gc.ca/mainmenu/historical_data_index_e.html) on April 27, 2018.

Figure 4. July water temperatures (grey dots) from water monitoring stations operated by provincial, federal and civic agencies along the mainstem of the Bow River from 1962 to 2001, and water temperature (black line) modelled as a function of distance from headwaters (Robins, 2009). These data were compiled by University of Calgary researchers for the Canadian Water Network into the NCE water quality database. Key features of the Bow River and river reaches depicted in Fig. 1 are illustrated above: municipalities/reserves – orange dots, City of Calgary – grey rectangle, dams – vertical black bars, weirs – vertical grey bars, WWTPs – red diamonds.

Figure 5. (A) Spatial variability of nitrate, phosphorus and boron daily fluxes (concentration x discharge) along the Bow River. Data were compiled from various months (March – November) from different years (2007, 2008, 2012, 2014-16) and vary by element (see Supplemental Information). Wastewater treatment plants (WWTPs; red diamonds) and the City of Calgary (grey rectangle) are illustrated on the line above. The dashed vertical lines divide the river into sections used to discuss nutrient characteristics of the river; these differ slightly from the numbered river reaches depicted in Fig. 1 which are also presented at the top of this figure. (B) Pie charts illustrating the approximated sources of nitrate in the Bow River in the headwater, upstream, midstream and downstream sections. (C) Bi-plots depicting stable isotope space of $\delta^{18}\text{O}$ vs $\delta^{15}\text{N}$ (left) and $\delta^{11}\text{B}$ vs $\delta^{15}\text{N}$ (right). Points indicate water samples and boxes indicate stable isotope values of nutrient sources in the Bow River (atmospheric deposition, fertilizer, manure, WWTP, and soil nitrification).

Figure 6. Estimated riparian abundance index along the Bow River depicting a visual estimate of density and extent of the riparian forest as observed on Google Earth (0=negligible, 1=very sparse, 2=thin, 3=moderate, 4=dense, 5=very dense and extensive). Dark grey represents a coniferous forest, mid-grey indicates a mixed forest, and light grey indicates a deciduous forest. Key features are illustrated above: municipalities/reserves – orange dots, City of Calgary – grey rectangle, dams – vertical black bars, weirs – vertical grey bars, tributaries – blue arrows, water withdrawals – green arrows. Major natural regions, channel type and river reach are also shown.

Figure 7. Annual maximum daily mean discharge of the Bow River at Calgary gauging station (05BH004; grey bars), mean annual epilithic algae biomass (black points), and mean September macrophyte biomass (green points) in all available years between 1980 and 2016. Dashed and solid lines connect consecutive years of data for algae and macrophyte biomass, respectively. Both algae and macrophyte biomasses were measured at sites in the downstream end of Calgary (Stier's Ranch and M8, respectively). Since algae sampling at Stier's Ranch stopped after 2010, data from samples measured at a site near Carseland weir are also shown (grey dots). The horizontal dotted grey line indicates the 400 m³/s discharge level which was suggested by Taube et al. (2016) as the threshold above which scouring flows for macrophytes occur. Vertical blue lines indicate mean diel fluctuation observed in September DO measured continuously at sites downstream of the City of Calgary.

Figure 8. Seasonal DO (blue line) measured continuously at DO sensor sites located upstream (near Bearspaw Dam) and downstream (Stier's Ranch) of the three WWTP outflows in the City of Calgary. Seasonal discharge (grey line) measured at Bearspaw (upstream: 05BH008) and Calgary (downstream: 05BH004) gauging stations. Black points indicate monthly epilithic algae biomass measured at M8 (downstream). The upstream algae biomass data was taken from a site at Cochrane because it was the closest available upstream data.

Figure 9. (A) Macroinvertebrate density (number/m²) (A) and (B) EPT proportion estimated at 5 sites along the Bow River from 5 years between 1985 and 2014. Key features are illustrated: municipalities/reserves – orange dots, City of Calgary – grey rectangle, dams – vertical black bars, weirs – vertical grey bars, main tributaries – blue arrows, water withdrawals – green arrows. River reaches depicted in Fig. 1 are illustrated above.

Figure 10. Total number of fish species present (Robins, 2009) and mean Czekanowski coefficient, indicating areas of high species turnover (low values; Mee et al., 2018). The mean Czekanowski coefficient was calculated in a 50-km sliding window estimated every 5 km along the Bow River. The vertical dashed lines mark the two points along the Bow River where the highest species turnover occurs – at 15.1°C and 18.9°C. Key features are illustrated: municipalities/reserves – orange dots, City of Calgary – grey rectangle, dams – vertical black bars, weirs – vertical grey bars, WWTPs – red diamonds. Mean July water temperature (1961-2001) increases along the Bow River from ~10°C at the headwaters at Bow Lake, to ~20°C at the confluence with Oldman River. The nitrate-nitrite bar indicates variation along the Bow River from 0.03 in grey to 0.8 mg/L in red. River reaches depicted in Fig. 1 are illustrated above.

Figure 11. Loess tricube weight functions of biomass (kg/km) of mountain whitefish (grey), rainbow trout (blue) and brown trout (orange) caught in 2001 in the Bow River over a 177 km section (Askey et al. 2007). The vertical dashed line indicates the location of high species turnover estimated by the mean Czekanowski coefficient at 15.1 °C (Fig. 10; Mee et al., 2018). River reaches depicted in Fig. 1, mean July water temperatures (1961-2001), and dissolved nitrate-nitrite data (1962-2001; Mee et al., 2018), and key features (City of Calgary – grey shading, dams – black vertical bars, weirs – black vertical bars, WWTPs - red diamonds (only two WWTPs existed in Calgary at the time of the study)) are illustrated above.