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Collateral benefits: River flow normalization for endangered fish enabled riparian rejuvenation

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Abstract

Like most rivers worldwide, the transboundary North American Kootenay/i River has experienced multiple impacts including watershed developments, river channelization, and floodplain clearing, draining, and diking. Construction of Libby Dam was authorized by the 1964 Columbia River Treaty (CRT) between the United States and Canada, and in 1975 began regulating downstream flows for flood risk management and hydropower generation. Following cumulative impacts, the endemic Kootenai River White Sturgeon population collapsed and was designated as endangered in 1994 (U.S. Endangered Species Act). Subsequent Biological Opinions from the U.S. Fish and Wildlife Service prescribed Libby Dam operations to provide springtime flow pulses for sturgeon spawning. These provided the unanticipated benefit of substantial seedling recruitment of native and introduced riparian cottonwoods and willows. The regulated flow regime was further adaptively managed to provide a more normative (natural) regime, to balance ecological functions with flood risk management and hydropower generation. The broadened ecological considerations would be consistent with the proposed priorities for the modernization of the international CRT. The observed responses revealed that (1) diverse aquatic and riparian organisms are dependent on common river flow characteristics; (2) a normalized flow regime provided substantial ecological benefits; and (3) due to multiple influences, hybrid ecosystems develop along regulated rivers, with a blending of natural and altered processes and communities. For other regulated rivers, we recommend that (1) high springtime flows be allowed, as feasible; (2) followed by the gradual post-peak recession; and (3) the maintenance of sufficient flows through the warm and dry interval of mid to late summer.

KEYWORDS

Acipenser transmontanus, Columbia River Treaty, environmental flows, functional flows, *Populus*, restoration, *Salix*

† Deceased

1 | FUNCTIONAL ENVIRONMENTAL FLOWS

Numerous river dams were constructed across North America through the twentieth century, primarily to attenuate floods and to store and manage water for hydropower generation, agricultural irrigation, and domestic and industrial human uses (Annear et al., 2002; Nilsson & Berggren, 2000; Petts, 1984). Dams were often constructed with limited consideration of their environmental impacts, which include abrupt and permanent changes associated with reservoir flooding, and downstream impacts that extend as far as the water flow, temperature, sediment, and woody debris regimes are altered (Braatne et al., 2008; Kondolf, 1997; Ligon et al., 1995; Wohl et al., 2015).

The environmental impacts are substantially determined by the regulated regime, and Instream Flow Needs (IFN) characterize the seasonal flow requirements for riverine organisms, often fish (Annear et al., 2002; Hoffman et al., 2002). IFN assessments were broadened across other aquatic and riparian organisms, leading to more comprehensive environmental, or ecological flows (Poff & Zimmerman, 2010; Richter & Thomas, 2007). While the natural flow regime paradigm recognizes that riverine organisms are adapted to the natural flow patterns (Poff et al., 1997), it is generally impractical to fully restore natural flows along regulated rivers. Consequently, the concept of functional flows arose as a feasible alternative (Foster et al., 2018; Yarnell et al., 2015, 2020). This emphasizes the essential components of the seasonal flow regime that sustain geomorphic dynamics and satisfy the life history requirements for riparian plants and aquatic animals (Amlin & Rood, 2002; Annear et al., 2002; Hughes, 1997).

Functional environmental flow regimes have been successfully implemented for some smaller rivers (Foster et al., 2018; Rood et al. 2003, 2005; Shafroth et al., 2010), but rarely for large rivers. This paper describes the successful, multiple-decade development and implementation of an adaptive ecological flow regime for a large transboundary river in western North America. With this synthesis, we coordinate published reports and provide further analyses to track the historical flow regulation and riparian responses over the past half-century (Anders et al., 2002; Benjankar et al., 2012; Burke et al., 2009; Polzin & Rood, 2000). The outcomes provide guidance for environmental flows for other regulated rivers, including those in western North America and the many other temperate ecoregions around the Northern Hemisphere where riparian Salicaceae, poplars, and willows, provide the foundations for the diverse and dynamic floodplain ecosystems (Hughes & Rood, 2003; Karrenberg et al., 2002; Rood, Braatne, & Hughes, 2003; Shafroth et al., 2010).

2 | THE KOOTENAY/I RIVER AND LIBBY DAM

The Kootenay River (Canadian spelling) is a tributary of the Columbia River, the largest Pacific drainage in the Western Hemisphere and one of the most extensively dammed river systems worldwide

(Palmer, 1997). The Kootenay and Columbia rivers commence from adjacent Canadian headwaters and flow west and south into the United States (Figure 1). The 1964 Columbia River Treaty (CRT) between Canada and the United States led to the construction and coordinated management of Mica and Keenleyside dams on the Columbia River, and Duncan Dam on the Duncan River in British Columbia (BC), Canada. The CRT also authorized Libby Dam on the Kootenai River (American spelling) in Montana (Figure 1; Cosens & Williams, 2012).

The Kootenay River is the second largest tributary of the Columbia River, behind the Snake River in the Idaho region of the United States (Palmer, 1997). It commences in the Rocky Mountains of BC, and cascades down to the flatter Rocky Mountain Trench (0.6 m/km), where it flows over lacustrine deposits from glacial Lake Invermere (Sawicki & Smith, 1992). At the south end of the Trench, the 128 m tall concrete Libby Dam created the 145 km long Kootenay Reservoir that straddles the international border (Figure 1). Libby Dam is the first dam along the Kootenay River, but there are smaller, run-of-river dams on tributaries, including the Bull (1922) and Elk Rivers (1924) in BC and Moyie River (1923, 1950) in Idaho (Figure 1). After discharge from Libby Dam, the outflows pass downstream through six more hydropower dams on the lower Kootenay River in BC, and then through 11 hydropower dams on the mainstem Columbia River in the United States.

Geomorphic transitions downstream of Libby Dam produce four river reaches (Figure 1; Richards, 1997). Below Libby Dam, the river flows through the sediment starved, alluvial Tailwater Reach. The valley subsequently narrows into the confined Canyon Reach, which includes a bedrock segment and Kootenai Falls, one of the last remaining major waterfalls in the western United States. Below the Moyie River, the river slope declines, the valley re-widens, and the channel form transitions into the dynamic, alluvial Braided Reach (Figure 1). After the short straight segment at Bonners Ferry, the gradient further declines, and the river turns north and flows along the Meander Reach through the Purcell Trench northward into Kootenay Lake. Through earlier intervals of the Holocene, Kootenay Lake had extended southward to the present location of Bonners Ferry (Hallett & Hills, 2006), and consequently, the Meander Reach cuts through finer, glaciolacustrine sediments. Prior to levees and regulation, the broad and flat floodplain naturally supported a complex network of braided channels and wetlands, with extensive cottonwood gallery forests (Jamieson & Braatne, 2001; Polzin, 1998; Richards, 1997).

Through more than a century, the Kootenay/i River system was progressively altered, with impacts that are typical along mountain rivers in western North America and worldwide (Hauer et al., 2016; Nilsson & Berggren, 2000; Polzin, 1998; Richards, 1997). Commencing in the 1890s, dikes were built to confine the river flow, the channel was dredged, riparian woodlands were cleared, and canals drained the floodplain wetlands to enable agricultural development. This dramatically simplified the river and floodplain system from Bonners Ferry to Kootenay Lake.

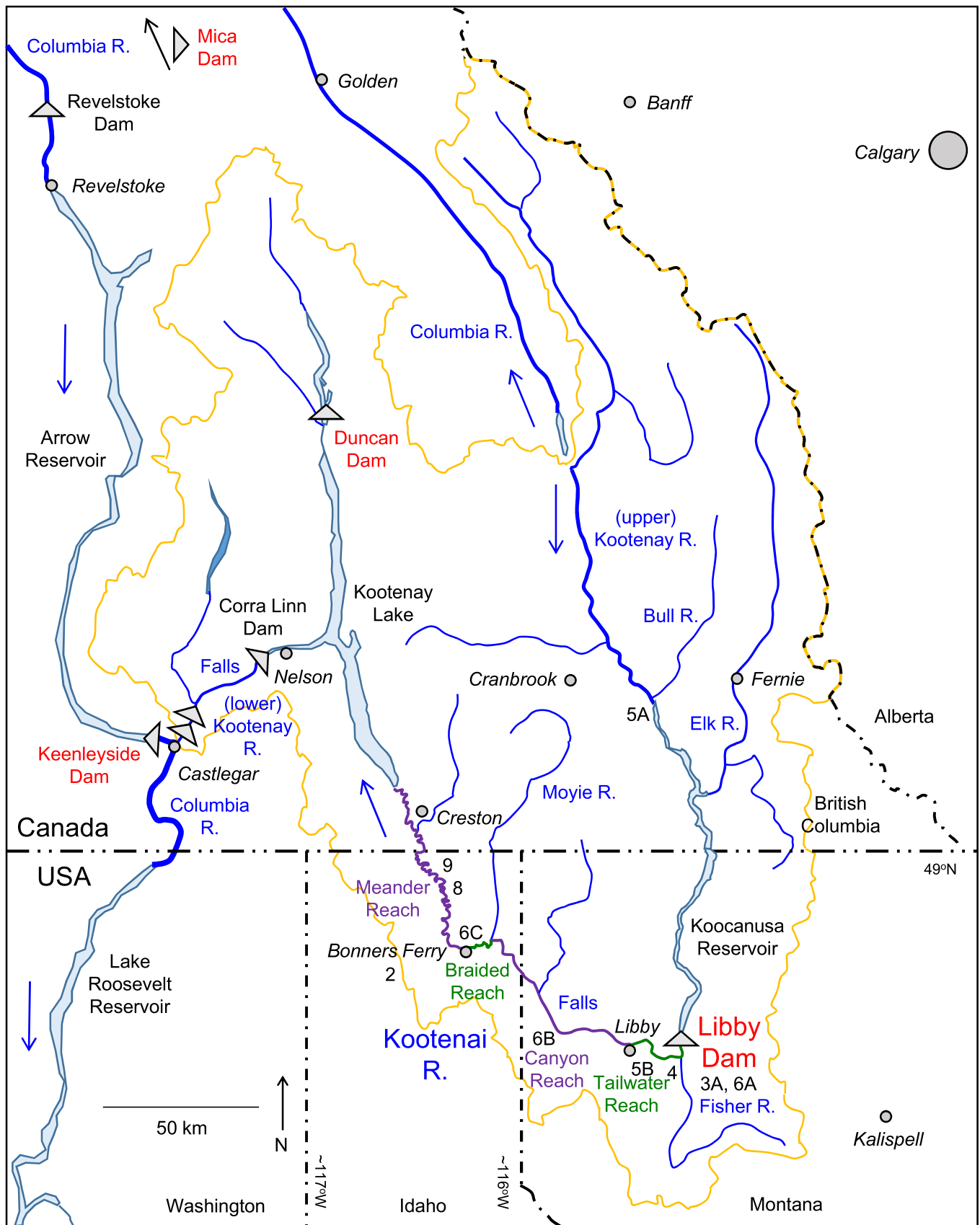


FIGURE 1 Map of the Kootenay River Basin (yellow outline) and upper Columbia River, with dams (Columbia River Treaty dams in red) and referenced tributaries. The four geomorphic reaches of the Kootenai River (American spelling) below Libby Dam are designated and locations of the photographs for subsequent figures indicated (e.g., “5A”). [Color figure can be viewed at wileyonlinelibrary.com]

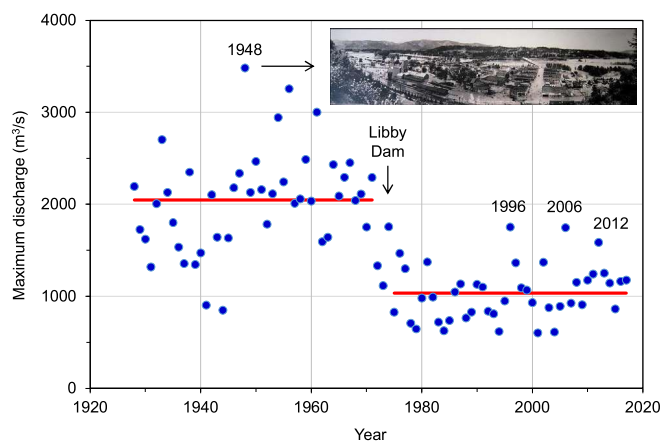


FIGURE 2 Maximum daily discharges (Q_{\max} ; peak streamflow) of the Kootenai River at Leonia (USGS 12305000; 1928). Averages are provided for the pre- and post-dam intervals (1928–1971, 2048 m^3/s ; 1975–2022, 1028 m^3/s ; excluding reservoir filling years). The inset displays Bonners Ferry, flooded in 1948 (City of Bonners Ferry photo). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Corra Linn Dam was completed in 1932 at the outflow of Kootenay Lake (Figure 1) and allows the lake level to be raised up to 2 m. Along with the extensive dike systems from Bonners Ferry to Kootenay Lake, management of the lake elevations through the operation of Corra Linn, Duncan, and Libby Dams can result in Kootenay Lake “backwater” effects through the Meander Reach (Figure 1; USFWS, 1994). This dampens the variation, but river stage patterns through the vegetation growth season are largely determined by flow regulation from Libby Dam (Benjankar et al., 2012, 2014; Burke et al., 2009).

Recognizing the ecological losses from the depletion of the biodiverse riparian forest and wetland complexes, initiatives were undertaken to provide habitat for wildlife and especially migratory waterfowl. These included the Kootenai National Wildlife Refuge (1964) and Boundary-Smith Wildlife Management Area (1999) in Idaho, and the Creston Valley Wildlife Management Area in BC (1968).

As intended, flood flows along the lower Kootenai River were substantially reduced due to the operation of Libby Dam and the large storage volume of Kooconusa Reservoir (storage/annual inflow = 0.68; Figure 2). The combination of peak flow attenuation for flood risk management during the spring and summer, and hydropower production during the high-demand winter months, led to flow stabilization and an inversion of the seasonal regime (Figure 3a).

As observed downstream from other dams (Kondolf, 1997; Ligon et al., 1995), Libby Dam also interrupted the flow of suspended sediments, woody debris, fish and other aquatic biota, plant propagules, and nutrients (Figure 4; Fosness & Williams, 2009). Consequently, the downstream channel, bar, and island sands were progressively depleted (Figure 5; Richards, 1997; Polzin & Rood, 2000), altering the aquatic and riparian conditions (Jamieson & Braatne, 2001; Minshall et al., 2014; Polzin, 1998).

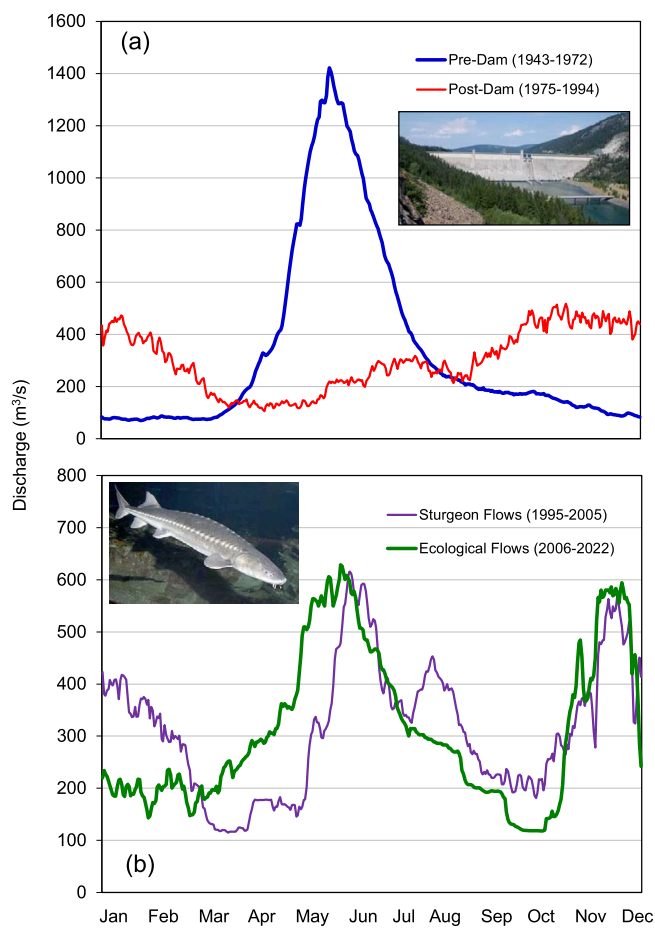


FIGURE 3 Averaged daily hydrographs for the Kootenai River at Libby, MT in four intervals relative to Libby Dam operations. The top pairing (a) provides the pre-dam and initial post-dam flows (discharge, Q). The lower pairing (b) provides the Sturgeon Flows and Ecological Flows (note the expanded y-axis). The transition included a shift from winter (I) to spring (II) release, and progressive summer recession (III). The insets display Libby Dam (upper; photographs by S. Rood, unless indicated), and white sturgeon (lower; creative commons). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

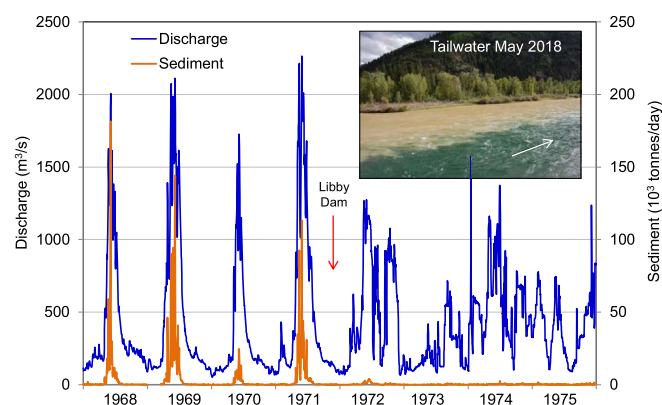


FIGURE 4 Daily discharges (Q) and suspended sediment of the Kootenai River at Leonia within 4 years prior to and after regulation with Libby Dam. The inset photo (B) displays the clear Kootenai River flow (foreground) that contrasts with the turbid Fisher River at the annual peak (opposite, 10 May 2018). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

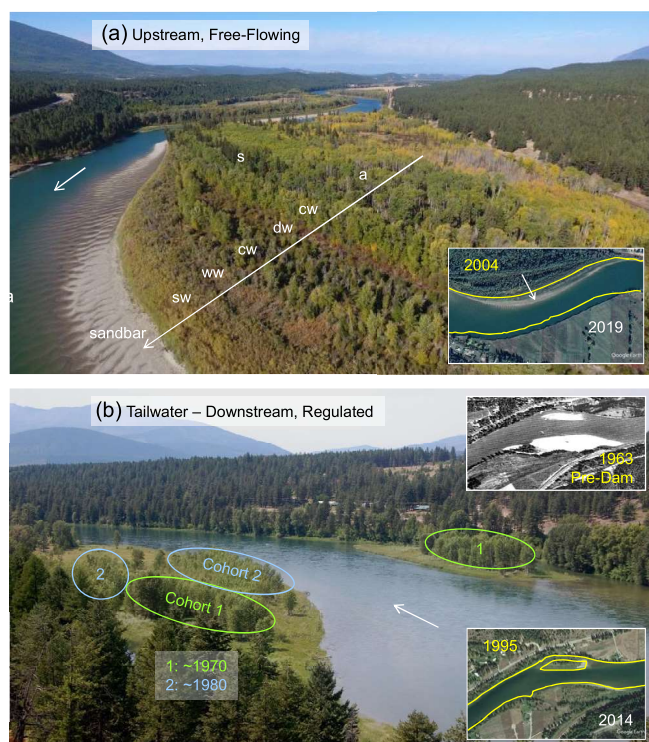


FIGURE 5 (a) An upstream view over a meander lobe of the free-flowing upper Kootenay River upstream of Koocanusa Reservoir (6 October 2017; Upper Kootenay Site 3, Egger et al., 2015; Polzin & Rood, 2000). The arrow indicates the point bar extension, with arcuate bands of riparian vegetation, commencing from the exposed barren sandbar to sandbar willow (sw), wolf willow (ww, *Elaeagnus commutata*), black cottonwood (cw), dogwood (d, *Cornus stolonifera*), aspen (a, *Populus tremuloides*), and spruce (s, *Picea × glauca*) and then a step up to the upland coniferous forest (cf). The inset aerial photograph displays the site in 2019, with the 2004 shorelines traced, revealing the meander extension and opposite concave cut-bank erosion (27 m/15 years). (b) A meander lobe and island along the Kootenai River near Libby, MT (Jul 2007; Lower Kootenai Site 3; Polzin & Rood, 2000). These were colonized by black cottonwoods in two establishment pulses (cohort patches 1 and 2), along with sandbar willows and understory grasses following flood flow attenuation by Libby Dam. The inset aerial photographs display the barren sand bar and island in 1963, before damming (Polzin, 1998), and in 2014, with the 1995 shorelines traced and revealing minimal change after damming. Further analyses of elevations, surface substrates, and vegetation at these and other upstream and downstream sites are contrasted by Polzin and Rood (2000) and Egger et al. (2015). [Color figure can be viewed at wileyonlinelibrary.com]

3 | ECOSYSTEM IMPACTS FROM KOOTENAI RIVER DAMMING

There are two primary comparisons that can be applied to analyze the ecological impacts of river damming: temporal and spatial (Braatne et al., 2008; Ligon et al., 1995). The hydrographs and sediment plots display major physical changes through the temporal comparison of the pre-dam versus post-dam conditions (Figures 2–4; Polzin & Rood, 2000). An instructive spatial comparison is upstream versus

downstream from a dam and reservoir (Braatne et al., 2008; Ligon et al., 1995).

Upstream of Koocanusa Reservoir, the free-flowing Kootenay and Elk River channels were dynamic, with progressive migration and more abrupt movement with flood events (Figure 5a; Polzin & Rood, 2000, 2006; Rood et al., 2015; Pomeroy et al., 2016). This resulted in a sequence of older vegetation bands away from the river, commencing with an initial band of the highly flood-tolerant sandbar willow (*Salix exigua*; Figure 5a; Polzin & Rood, 2000; Rood et al., 2011) and then other riparian shrubs. Progressively older bands of black cottonwood trees (*Populus trichocarpa*) followed, leading to successional woodlands with aspen (*Populus tremuloides*), and conifers (Egger et al., 2015). This stratified banding provides a space-for-time chronology that reveals historical meander migration, plant colonization, alluvial aggradation, and woodland succession, including pulses of geomorphic disturbance and riparian recruitment following flood events (Hughes, 1997; Junk et al., 1989; Philipsen et al., 2021; Polzin & Rood, 2006). These dynamic patterns persisted along the upper Kootenay River (Figure 5a), with similar patterns along nearby free-flowing rivers: the Elk River in BC, Fisher River Montana, and the transboundary North Fork of the Flathead River (Figure 1; Polzin & Rood, 2000, 2006, Kalischuk et al., 2001; Egger et al., 2015).

In contrast, along the Kootenai River downstream of Libby Dam, the floodplain substrates and vegetation dynamics were substantially altered after damming (Figure 5b; Richards, 1997; Jamieson & Braatne, 2001; Polzin & Rood, 2000). Following initial flood flow attenuation, riparian cottonwoods and willows expanded downwards onto the sand and gravel bars and islands that were previously barren due to periodic inundation, and sediment scour and deposition (Figure 5b). Similar downward riparian woodland expansion followed flow stabilization along other regulated, alluvial rivers (Hughes, 1997; Johnson, 1998).

Black cottonwood colonization was abundant, with two pulses of seedling recruitment (Figure 5b; Jamieson & Braatne, 2001; Egger et al., 2015). One cohort represented the survival of seedlings established in the final years before dam closure. These would otherwise have been killed with subsequent high flows of the natural regime (Johnson, 1998; Polzin & Rood, 2006). The second cohort followed a few years after dam closure, around 1980 (Figure 5b). These seedlings colonized the barren surfaces that still retained favorable surface and interstitial sands but were no longer flooded and scoured.

The lower banks and bars were also extensively colonized by sandbar willow (Polzin & Rood, 2000; Rood et al., 2011). This shrub has similar colonization requirements as cottonwoods but favors sandy substrates and has later seed dispersal, which enables colonization at lower positions in the seasonally inundated varial zone (Amlin & Rood, 2002; Karrenberg et al., 2002; Rood, Braatne, & Hughes, 2003). Following seedling establishment, sandbar willow vigorously expanded through clonal suckering. Black cottonwoods are also capable of clonal expansion, which is promoted by favorable water patterns and root scarification through ice or flood scour (Egger et al., 2015; Rood, Gourley, et al., 2003).

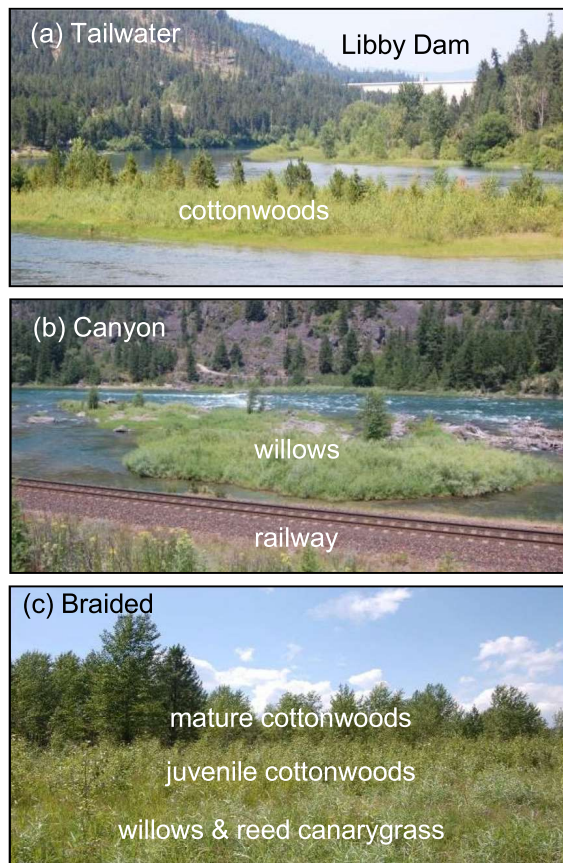


FIGURE 6 Photographs of riparian zones along three geomorphic reaches of the Kootenai River (as in Figure 1) extending downstream from Libby Dam, with vegetation types indicated. (a. Tailwater, June 2016; b. Canyon, July 2007; c. Braided, July 2009). [Color figure can be viewed at wileyonlinelibrary.com]

After the initial riparian woodland expansion, the vegetation on the floodplain zones along the Kootenai River became more static. With exclusion from inundation, upland grasses and other plants expanded down toward the river edge (Polzin & Rood, 2000). While the vegetation was expanding, the bar and island surfaces became coarser as the finer sediments were flushed downstream without replenishment (Figure 4; Polzin & Rood, 2000; Fosness & Williams, 2009). As a further impediment, reed canary grass (*Phalaris arundinacea*) proliferated, with dense mats that impeded colonization by the native willows and cottonwoods (Figure 6c; Jamieson & Braatne, 2001; Benjankar et al., 2012).

There was further channel stabilization by bank armoring to protect the highways and railway that were aligned along the river (Figure 6b). Especially in mountain regions, transportation corridors are commonly positioned along rivers to utilize the gradual valley slopes. Following multiple impacts, cottonwood colonization became sparse, as indicated by the deficiency of younger cottonwoods (Polzin & Rood, 2000; Jamieson & Braatne, 2001). The mature cottonwoods apparently remained healthy, with limited branch or crown die-back (Rood et al., 2003a), but the aging cottonwood population progressively reduced the woodland structure or vertical diversity. This reduced habitat for wildlife, including birds that

provide mobile indicators of riparian woodland health (Merz et al., 2015), iconic carnivores such as grizzly bears and wolves (Hauer et al., 2016), and threatened species such as the Western Yellow-billed Cuckoo (*Coccyzus americanus occidentalis* Wohner et al., 2021).

4 | THE ENDANGERED KOOTENAI RIVER WHITE STURGEON

The white sturgeon, *Acipenser transmontanus*, is the largest and longest-lived freshwater fish in North America, reaching 5 m in length and living up to a century (Fisheries and Oceans Canada, 2014). The ancient fish has declined across North America due to habitat degradation, fishing pressure, and pollution (Anders et al., 2002; Duke et al., 1999; Paragamian et al., 2005). These fish are anadromous or adfluvial, and thus require suitable lentic and lotic environments and connectivity for migration and reproduction (Anders et al., 2014; Duke et al., 1999; Paragamian et al., 2001).

The Kootenai River White Sturgeon occupy Kootenay Lake and the Kootenai River, having been isolated from the Columbia River white sturgeon population by Bonnington Falls at the outflow of Kootenay Lake following glacial retreat (Figure 1; Northcote, 1972; Anders et al., 2002). Along the Kootenai River upstream of Kootenay Lake, Kootenai Falls block upstream passage by this sturgeon, which has subsequently been referred to as “the fish between the falls” (Sibley, 2014). With the limited geographic distribution and reproductive isolation, there was a genetic divergence that produced the distinct, endemic strain or subspecies (Anders et al., 2002; Paragamian et al., 2005; USFWS, 1994).

Habitat critical for sturgeon spawning, recruitment, survival, and growth declined with the extensive diking and drainage along the Meander Reach (Figure 1; Richards, 1997; Anders et al., 2002), and more steeply with the completion of Libby Dam (Duke et al., 1999; Paragamian et al., 2001). Adults were harvested for caviar, and pollution provided a further challenge (Anders et al., 2002). Kokanee salmon (*Oncorhynchus mykiss*) in the Kootenay Lake system provide a primary food source, but that population declined due to multiple impacts, especially following the construction of the two Columbia River Treaty dams, Libby, and Duncan (Anders et al., 2002; Paragamian et al., 2005).

Adapted to the natural flow regime of the Kootenai River, sturgeon spawn during the freshet period from May into June. The artificial, non-normative flow attenuation by Libby Dam reduced the attraction cues and imposed shallower conditions that hindered sturgeon migration to suitable spawning locations (Anders et al., 2002; Paragamian et al., 2001, 2005). The high flows naturally sorted and flushed the riverbed cobbles, and after high flow attenuation following damming, these became embedded with finer sediments, reducing egg survival, cover for larval and juvenile stages, and invertebrate food production (Anders et al., 2002, 2014). Annual recruitment failure in the wild population reflected the spatiotemporal mismatch between spawning and incubation habitat requirements and the availability of suitable sites for eggs and

embryos in the regulated river (Anders et al., 2014; Paragamian et al., 2001).

As the sturgeon population collapsed, the sport fishery was closed in 1983, and the Kootenai Tribe of Idaho commenced a conservation aquaculture program in 1988 (Anders et al., 2002; Duke et al., 1999; Paragamian et al., 2005). The Kootenai River White Sturgeon was listed as endangered under the U.S. Endangered Species Act in 1994 and under the Canadian Species at Risk Act in 2006 (COSEWIC, 2012; USFWS, 1994). The population had been in decline since the 1950s and there has been minimal recruitment of young sturgeon since the early 1970s when Libby Dam was constructed (Anders et al., 2002; Paragamian et al., 2005).

Among the multiple factors that influenced the species decline, there was agreement that the peak-flow attenuation contributed to the lack of spawning success (USFWS, 1999, 2006). Consequently, commencing in 1992, “Sturgeon Flow” pulses were released from Libby Dam in late spring (Figure 3b). The volumes were released in a tiered fashion based on water supply forecasting for Kootenai Reservoir, and provided outflows intended for sturgeon conservation while maintaining the dam's authorized purposes of flood risk management and hydropower production. The opportunity to shape and time the tiered outflows was increased under the 2006 U.S. Fish and Wildlife Service Biological Opinion (“USFW BiOp”; USFW, 2006), and the subsequent “Ecological Flows” included a more normative pre- and post-peak flow regime (Figure 3b). Variations in water supply enabled larger pulses in 1996, 2006, and 2012, although these remained well below the pre-dam peak flows (Figure 2).

The 2006 USFWS BiOp created the Flow Plan Implementation Protocol (FPIP) Team to experimentally shape the sturgeon tiers and adapt annual sturgeon operations. These sought to attain ecological conditions in the river conducive to sturgeon migration upstream into appropriate spawning habitats, as well as conditions downstream to enable off-channel habitat connectivity for larval development and survival. The former objective is frequently met under most water supply conditions, but the efficacy of the latter objective is dependent on the springtime elevation of Kootenai Lake and the associated backwatering up the Kootenai River that raises the river stage. Management of Kootenai Lake elevations is governed by the 1938 International Joint Commission Rule Curve and currently limits the seasonal aquatic ecological function of the lower river corridor, including adequate habitat and temperature conditions for larval sturgeon.

5 | COLLATERAL BENEFITS—RIPARIAN REJUVENATION

The partial recovery of a more natural seasonal flow regime provided rapid benefits for riparian vegetation. Along the Tailwater Reach, the spring pulses promoted clonal suckering of black cottonwoods (Figure 6a), and through the constrained Canyon Reach, sandbar willow was similarly promoted through clonal expansion

(Figure 6b). The alluvial Braided Reach is the most dynamic river segment and the Sturgeon Flow and then Ecological Flow operations promoted extensive clonal suckering of the black cottonwoods and willows (Figure 6c). Additionally, with growth promotion from the spring flow pulses, the cottonwoods and willows overtopped the reed canarygrass, providing a competitive advantage over that invasive plant (Figure 6c).

Studies followed the major flood of 1995 to assess cottonwood seedling recruitment along regional rivers (Kalischuk et al., 2001; Polzin & Rood, 2000, 2006). That flood resulted in prolific colonization along the Elk and Kootenay Rivers upstream of Kootenai Reservoir, and along the Fisher River, near Libby Dam (Figure 1). In contrast, there was limited cottonwood colonization along the Tailwater or Canyon Reaches of the Kootenai River (Polzin, 1998; Polzin & Rood, 2000). Conversely, along the Meander Reach, abundant cottonwood seedlings were observed on some meander lobes without cattle grazing (Burke et al., 2009; Jamieson & Braatne, 2001). With aging based on ring counts and growth scars, the cottonwood seedling recruitment occurred in 1996 and 1997, when the river stage pattern was favorable for cottonwood seedling establishment (Figure 7; Benjankar et al., 2014; Burke et al., 2009). Unexpectedly, most of these new recruits were an introduced popular species, plains cottonwood (*Populus deltoides*), rather than the native black cottonwood (Burke et al., 2009; Jamieson & Braatne, 2001).

In years with favorable river stage patterns consistent with the Recruitment Box model (Figure 7; Mahoney & Rood, 1998; Amlin & Rood, 2002), new seedlings survived and grew to provide substantial arcuate bands of juvenile trees at common elevations above the river (Burke et al., 2009; Benjankar et al., 2014). A primary study site was near The Nature Conservancy's Ball Creek Ranch, where a typical band of mature cottonwoods occurred along the river-side base of the dike (Figure 8a), (a). There was a subsequent gap (b) to the juvenile cottonwood band (c), revealing the deficiency of cottonwood colonization over an extended interval, probably due to a combination of an inadequate flow regime and cattle use.

The woodland along the dike is about 135 m from the river shoreline (Figure 8b) and the pre-dam meander extension rate of ~2 m/year would be typical for regional rivers (Nanson & Hickin, 1986). With flood flow attenuation after Libby Dam, the meander lobe extended by only 14 m from 1992 to 2004, providing a reduced migration rate of 0.63 m/year (Figure 8b). While this is much less dynamic than in the pre-dam interval, this location was more dynamic than some other meanders since the woodlands had been cleared above the cut bank across the river, removing that stabilizing influence (Figure 8; Rood et al., 2015). The riverside band included cottonwoods from 1996 and 1997 and younger cottonwoods and had apparently been browsed by deer (*Odocoileus hemionus*), somewhat resembling a pruned hedge (Figure 8a, c). Subsequent beaver (*Castor canadensis*) activity has also reduced stem densities in the cottonwood bands.



FIGURE 7 Daily hydrographs for 1997 for the Kootenai River at Bonners Ferry, ID, upstream of the meander reach. The green Recruitment Box characterizes favorable conditions for cottonwood colonization and the favorable recession limit is provided by the dashed line (~ 3 cm/day or 1 m/month). Typical intervals of seed dispersal for cottonwoods and reed canarygrass (rcg) are displayed—cottonwood seeds have short viability while rcg seeds remain viable for one or more years. [Color figure can be viewed at wileyonlinelibrary.com]

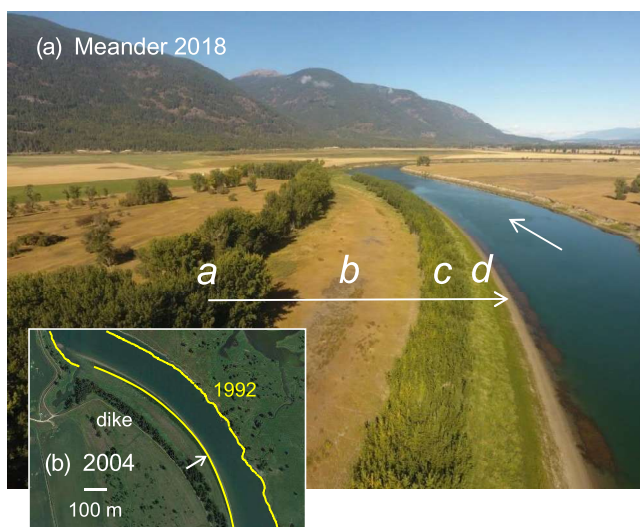


FIGURE 8 (a) A downstream view over the Kootenai River and meander lobe at Ball Creek with the band of mature plains and black cottonwoods along the toe of the dike (a), an extensive band with grasses (b) and then the 24 m band of cottonwoods that were established in 1996 and 1997 (c), and younger seedlings (d) (September 2018). Along the arrow, the distance from the mature cottonwoods to the shoreline was 136 m. The lower, inset aerial photograph (8b; Google Earth) displays the site in 2004, with the 1992 shoreline traced (~ 14 m movement/22 years), and arrows coordinate the positions. [Color figure can be viewed at wileyonlinelibrary.com]

6 | ECOLOGICAL FLOWS AND RIPARIAN RECRUITMENT

The cottonwood recruitment in 1996 and 1997 provided promise for the recovery of seedling reproduction of cottonwoods and willows. As indicated, operational modifications under the 2006 Biological

Opinion (USFWS, 2006) allowed for the development of Ecological Flows, which included a more normatively shaped hydrograph, particularly for the post-peak recession (Figure 3b). The peak was still attenuated relative to the natural regime, but this was followed by a favorable and relatively natural post-peak recession (Mahoney & Rood, 1998; Shafroth et al., 2010).

Subsequently, especially along the Braided and Meander Reaches where suitable nursery sites were available, there was prolific cottonwood seedling establishment in high flow years, including 2006, 2010, and 2012 (Figure 9). To assess the interannual favorability for colonization, we applied an approach similar to Braatne et al. (2007), Foster et al. (2018), and Benjankar et al. (2020), to consider the required flow components, including the peak (1) magnitude, (2) timing, (3) subsequent gradual stage recession, and (4) seedling removal through scour. These requirements were generally satisfied in 1980/1981, 1996/7, 2006, 2010, and 2012, consistent with the field observations (Figure 9; Jamieson & Braatne, 2001; Burke et al., 2009; Benjankar et al., 2014).

Along smaller regulated rivers in western North America, cottonwood seedling colonization has been similarly enhanced with flow normalization and peak shaping to include ramping, gradual post-peak recession (Foster et al., 2018; Kalischuk et al., 2001; Rood, Braatne, & Hughes, 2003; Shafroth et al., 2010). For large or small rivers, deliberate dam operation could influence peak timing, post-peak recession, and subsequent scour, but the peak magnitude is unpredictable. High-flow events are weather-dependent, following combined contributions from winter snow melt and spring rains, including rain-on-snow events (Pomeroy et al., 2016). Sturgeon spawning and cottonwood reproduction are both naturally episodic, probably displaying coincidental population surges in the resulting high-flow years (Paragamian et al., 2005; Philippsen et al., 2021).

There are additional factors that influence river stage patterns and cottonwood reproduction, growth, and development along the

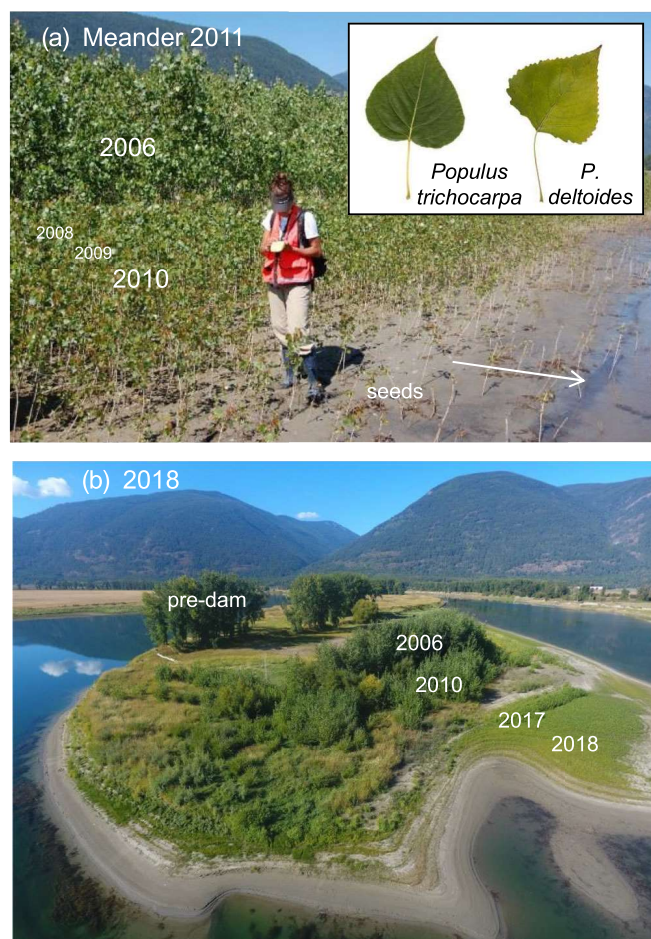


FIGURE 9 (a) A view of prolific cottonwood colonization on a gradual, sandy slope along the Meander Reach (the peninsula near Trout Creek, August 2011). This displays the dense band of juvenile trees from 2006, and overlapping saplings established in 2008, 2009, and especially 2010. These are primarily the introduced plains cottonwood, *P. deltoides*, with some native black cottonwood, *P. trichocarpa*. (b) The tip of a meander peninsula in the Kootenai River near Trout Creek (September 2018). This displays the successful recruitment of plains cottonwoods with the Ecological Flow regime from Libby Dam. The 2006 and 2010 patches are likely to mature but the lower 2017 and 2018 seedlings will probably succumb to inundation and scour. [Color figure can be viewed at wileyonlinelibrary.com]

Meander Reach (Benjankar et al., 2020; Jamieson & Braatne, 2001). As indicated, the operations of Corra Linn and Duncan Dam also influence Kootenay Lake levels and associated backwater effects that can extend upstream along the Kootenai River as far as Bonners Ferry (Duke et al., 1999; Richards, 1997). There are also site-specific effects, primarily from cattle use and reed canarygrass abundance (Braatne et al., 2007; Jamieson & Braatne, 2001; Kalischuk et al., 2001). These compounding impacts from river regulation, livestock grazing, and invasive plants are typical for riparian vegetation along regulated rivers across western North America and worldwide (Naiman et al., 2010; Nilsson & Berggren, 2000).

7 | A HYBRID RIPARIAN ECOSYSTEM

The riparian woodland community along the Kootenai River has been substantially enriched with the Ecological Flow regime (Figure 6). Through the Braided and Meander Reaches and at some upstream locations the outcome has been a mosaic of shrub and tree patches with different ages, sizes, and composition (Figure 9; Polzin & Rood, 2006; Egger et al., 2015). While this has increased the riparian woodland biodiversity, the spatial extent won't return to the pre-development condition of the nineteenth century. Following channelization and diking, and with the attenuated flow regime, the channel is less dynamic, and the colonization bands and patches are narrower, resulting in a down-scaled floodplain forest.

The vegetation community has also changed. Well prior to Libby Dam, a transition was underway in the woodland composition. There was a change from the native black cottonwood (*P. trichocarpa*) to plains cottonwood (*P. deltoides*; Figure 9), which was extensively planted with the westward European settlement of North America (Braatne et al., 2006). Black cottonwood was reported in the regional cadastral surveys in the late 1800s (Braatne et al., 2006), and photographs around Bonners Ferry revealed some mature plains cottonwood trees by the early 1900s (Polzin, 1998). Black cottonwoods remain as the predominant species along the Tailwater Reach and are also common along the Braided Reach, along with some plains cottonwoods and naturally occurring intersectional hybrids of the two species, *P. × generosa* (*P. trichocarpa* × *P. deltoides*). The proportion of plains cottonwoods increased downstream along the longitudinal river corridor and provided about three-quarters of the mature trees in the Meander Reach around 1995 (Jamieson & Braatne, 2001). Extending the species transition, plains cottonwoods were the predominant seedlings observed along the Meander Reach after 2000 (Figure 9; Burke et al., 2009; Benjankar et al., 2014).

The plains cottonwoods probably favor finer substrate and display greater reliance on seedling recruitment than the black cottonwoods (Braatne et al., 2006; Rood, Gourley, et al., 2003). Conversely, black cottonwoods occur on coarser substrates and display greater clonal expansion through root suckering (Braatne et al., 2007; Polzin & Rood, 2006). The conditions along the Meander Reach apparently favor the plains cottonwood, with the gradual river slope and slow velocities, finer substrate sediments, and a warmer climate (Jamieson & Braatne, 2001; Rood, Braatne, & Hughes, 2003).

While there is commonly a preference for native rather than introduced plant species with ecosystem restoration, in this case, the two cottonwood species are generally similar in size, structural form, and ecophysiology (Rood, Gourley, et al., 2003). There is no practical way to remove the plains cottonwoods, and this might be disfavored in any event, since the altered hydrogeomorphic conditions may favor this species. The Kootenai River valley is only ~250 km west of the native extent of plains cottonwood, likely within the dispersal range of the tiny, wind-blown seeds. With warming weather and changing river flow seasonality accompanying climate change and flow regulation (Schindler & Donahue, 2006), the plains cottonwood might even be better adapted than the native black cottonwood for future

conditions along the Meander Reach of the Kootenai River and along some other regulated river reaches through western North America (Braatne et al., 2006).

With the transition in the foundational tree from the black to the plains cottonwood, the floodplain woodlands along the Kootenai River represent hybrid ecosystems (Hobbs et al., 2014), with this phrase recognizing the altered physical processes, and changes in vegetation community composition and structure. The transition in cottonwood species, sediment depletion, proliferation of reed canarygrass, and occurrences of other non-native plants would alter ecosystem characteristics including the invertebrate communities, and the terrestrial and arboreal wildlife habitats (Naiman et al., 2010). These have been investigated along the Kootenai River (Merz et al., 2015) but coincidental with the changes in river regulation with the Sturgeon Flows and then the Ecological Flows, there were also other deliberate changes, including channel excavations, vegetation plantings, and nutrient additions to promote the aquatic ecosystem productivity (Chowanski et al., 2020; Minshall et al., 2014).

8 | GUIDANCE FOR OTHER REGULATED RIVERS

The Ecological Flow regime along the Kootenai River provided a more normalized pattern, including the partial recovery of the spring peak and subsequently gradual post-peak stage recession (Figure 3b). Different flow patterns across years reflected the varying runoff projections and substantial flow pulses that should particularly benefit sturgeon spawning and cottonwood recruitment were provided following wetter winters. With this adaptive management strategy, it is anticipated that ecological enhancement in wet intervals could increase ecosystem resilience for the inevitable dry periods.

This provides a promising case study with applicability to other dammed rivers in western North America. It also applies to other global, temperate ecoregions where riparian Salicaceae, poplars, and willows, provide the foundation for the biodiverse riparian woodlands (Hauer et al., 2016; Hughes & Rood, 2003; Karrenberg et al., 2002; Naiman et al., 2010). The regulated regime from Libby Dam provides a successful application of the functional flow concept (Foster et al., 2018; Shafroth et al., 2010; Yarnell et al., 2015, 2020) and is relevant to the three other Columbia River Treaty dams. For these, improved ecological function is proposed as a third priority, along with flood risk management and hydropower generation (Baltutis et al., 2018; Cosens & Williams, 2012). Similar balancing of dam operations for socioeconomic and ecological outcomes should be broadly applicable and functional environmental flows are recommended as a widespread strategy for the conservation and restoration of riparian woodlands. These provide rich wildlife habitats, resist bank erosion, and intercept and assimilate surface and groundwater contaminants. The trees and shrubs also contribute leaf and branch litter that benefits the aquatic food web, and there are other valued ecological services, that justify the environmental flow regimes (Naiman et al., 2010; Poff & Zimmerman, 2010; Richter & Thomas, 2007; Rood et al., 2005).

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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

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