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Prepared in cooperation with the University of British Columbia, Biodiversity Research Centre and Beaty Biodiversity Museum and Idaho State University, Department of Biological Sciences, Fish Ecology Laboratory

Evolutionary and Ecological Connectivity in Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and Mountain Whitefish (*Prosopium williamsoni*) in Relation to the Potential Influences of Boundary Dam, Washington, Idaho, and Parts of British Columbia

Open-File Report 2022–1084

U.S. Department of the Interior
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Contents

Figures

Conversion Factors

U.S. customary units to International System of Units

Multiply	By	To obtain
	Length	
foot (ft)	0.3048	meter (m)
mile (mi)	1.609	kilometer (km)
	Flow rate	
cubic foot per second (ft^3/s)	0.02832	cubic meter per second (m^3/s)

International System of Units to U.S. customary units

Multiply	By	To obtain
	Length	
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
	Area	
hectare (ha)	2.471	acre
	Volume	
cubic meter (m^3)	35.31	cubic foot (ft^3)
	Flow rate	
cubic meter per second (m^3/s)	35.31	cubic foot per second (ft^3/s)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

°F = (1.8 × °C) + 32.

Datums

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Abbreviations

WDFW	Washington Department of Fish and Wildlife
SNP	single nucleotide polymorphism
PIT	passive integrated transponder
PoR-C	Pend Oreille and Columbia Rivers

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Abstract

In this report, we consider evolutionary and ecological connectivity for westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and mountain whitefish (*Prosopium williamsoni*) within the Pend Oreille River in northeastern Washington State, northern Idaho, and adjacent portions of southeastern British Columbia, Canada. Specifically, we focused on the rationale for active translocation of individuals of these species upstream from Boundary Dam both in the context of natural patterns of pre-dam evolutionary connectivity as well as preserving contemporary ecological and evolutionary characteristics of local extant populations. Boundary Dam impounds the Pend Oreille River (called the Pend d'Oreille River in Canada) with the resulting reservoir inundating two historical barriers to upstream movement of fish (Metaline Falls and Z Canyon). Historically, it was thought these barriers impeded the upstream movement of westslope cutthroat trout and mountain whitefish, as well as Pacific salmon (*Oncorhynchus* spp.), steelhead trout (*O. mykiss*), and other resident species such as bull trout (*Salvelinus confluentus*). To address connectivity, we consider historical and contemporary processes and features. This review includes an assessment of postglacial processes within the Pend Oreille River and systems upstream that include Priest Lake, Lake Pend Oreille, the Clark Fork River, features of Boundary Reservoir and its tributaries, and areas downstream in the Pend Oreille River such as the Salmo River. Based on this information, we then give a more detailed review of existing genetic and ecological data to summarize what is known about connectivity for westslope cutthroat trout and mountain whitefish. Our assessment of the collective evidence leads us to conclude that moving fish upstream over Boundary Dam is not warranted if the management objective is to maintain natural patterns of evolutionary and ecological connectivity or to conserve unique ecological and evolutionary characteristics of extant local populations of these species in the system. These findings parallel that of a previous analysis of bull trout. Although we were able to arrive at well-supported conclusions in relation to Boundary Dam, we suggest that more work on connectivity further upstream in the Pend Oreille River would help to better understand the role of historical processes and dams further up in the system.

Introduction

Across the United States, there are over 91,000 large dams[1] on rivers (U.S. Army Corps of Engineers, 2018[2]). Assessing their effects on riverine ecosystems is complicated because dams have influences downstream and upstream from their location and create novel reservoir habitats within the waters they hold back (Bellmore and others, 2019). Furthermore, the unique setting of where dams are constructed, how they are operated, their relationships to other barriers, and a host of other potential influences defy simple generalizations. Accordingly, it is important to consider the unique context within which any given dam is located. Although dams influence riverine ecosystems in many ways, one of the most fundamental involves how they influence evolutionary and ecological connectivity of physical and biological systems.

Here, we consider how dams impact connectivity for two species: westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and mountain whitefish (*Prosopium williamsoni*) within the Pend Oreille River in northeastern

[1]The Army Corps of Engineers National Inventory of Dams includes dams that either (1) pose a threat to human life if the dam fails, (2) pose economic loss, environmental damage, disruption of lifeline facilities or other important concerns, (3) equal or exceed 7.6 meters in height or 82,000 square meters of storage, or (4) equal or exceed 1.8 meters in height and exceed 164,000 square meters of storage.

[2]Army Corps of Engineers National Inventory of Dams database can be accessed at https://nid.usace.army.mil/#/

Washington State and adjacent portions of southeastern British Columbia, Canada (where the river is known as the Pend d'Oreille River). The geographic focus of this report is Boundary Dam (fig. 1), which is located on the Pend Oreille River near the U.S. - Canada border, and is one of several dams in this watershed (fig. 2). Like most salmonid fishes, westslope cutthroat trout and mountain whitefish are influenced by and rely on connectivity within river networks or riverscapes (Northcote and Ennis, 1994; Neville and others, 2006a). Our specific objective in this report is to evaluate historical and contemporary evolutionary and ecological connectivity for westslope cutthroat trout and mountain whitefish to address the rationale of potentially providing upstream passage over Boundary Dam for these species. A previous analysis (Dunham and others, 2014) examined similar questions concerning connectivity in bull trout (*Salvelinus confluentus*) in relation to Boundary Dam (app. 1).

To address our objective, Part 1 of this report begins with a review of historical and contemporary processes and features of the riverscape that influence connectivity relative to Boundary Dam within the lower Pend Oreille system. Historically, it was thought that the upstream extent of anadromous Pacific salmon (*Oncorhynchus* spp.) and migratory rainbow trout (*O. mykiss*, commonly referred to as steelhead trout) in the Pend Oreille River was just downstream from Metaline Falls, the current approximate location of Boundary Dam (Scholz and others, 1985). From this foundation, in Part 2, we review existing genetic and ecological information to evaluate what is known about connectivity for westslope cutthroat trout and mountain whitefish within the system. In Part 3, we assess this evidence with respect to the evolutionary or ecological rationale for passing these species upstream over Boundary Dam. Throughout, we identify important uncertainties and information gaps that could be addressed to inform management decisions and actions to benefit westslope cutthroat trout and mountain whitefish within the area.

Figure 1. Boundary Dam (downstream view) photographed after dark, December 8, 1998 (from City of Seattle Archives, Item 126710, Record Series 0207–01).

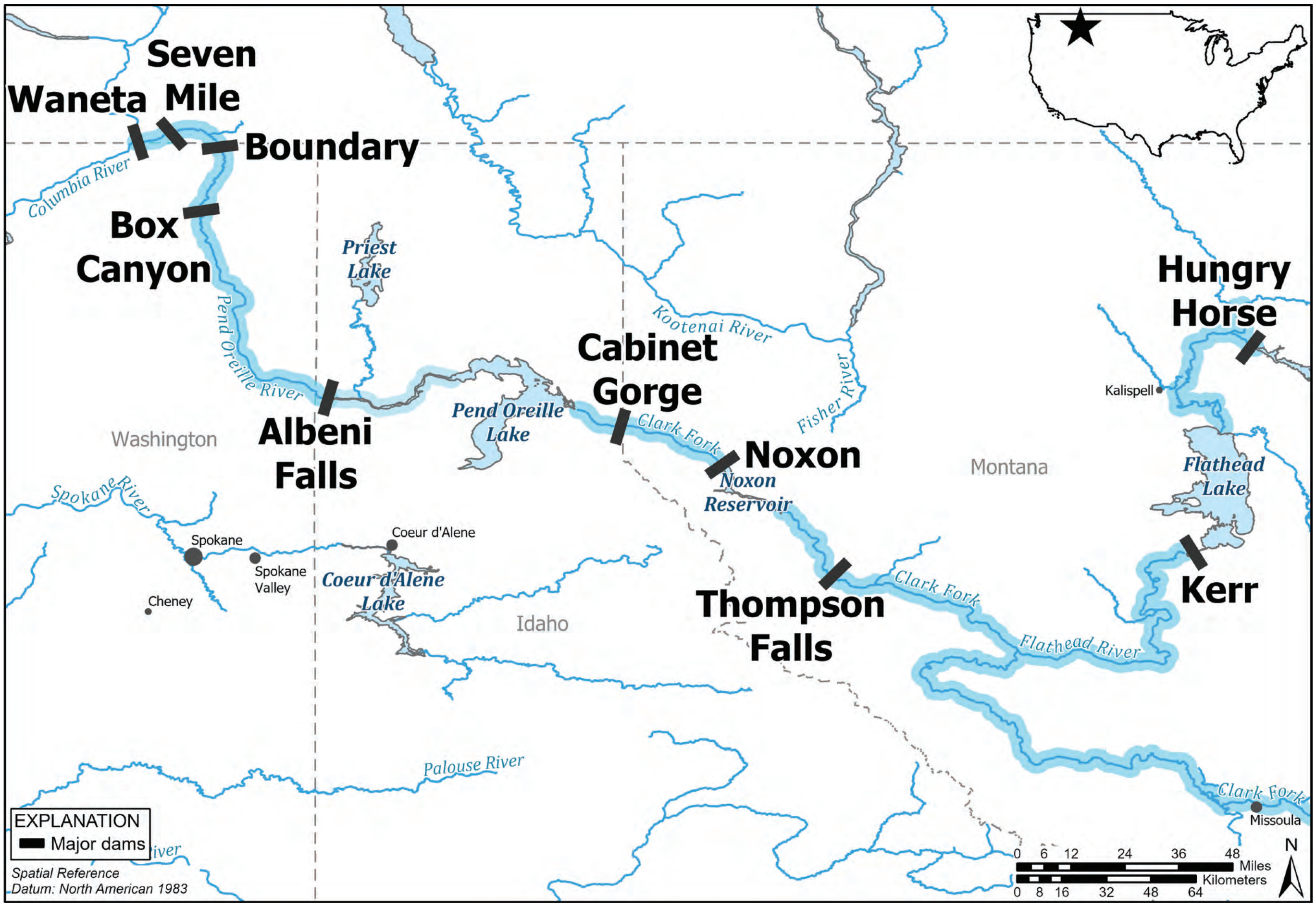

Figure 2. Lower Clark Fork River, Lake Pend Oreille, and Pend Oreille River with major dams indicated.

Part 1. Lake Pend Oreille and Pend Oreille River—Past to 2022

Overview

The system of interest includes Lake Pend Oreille in northern Idaho and its outlet: the Pend Oreille River (fig. 2). Lake Pend Oreille is the terminus of the Clark Fork River, which flows westward and drains much of western Montana, with some drainages extending north of the U.S. - Canada border. The Pend Oreille River produces an annual average discharge of 26,267 cubic feet per second (ft^3/s) according to a U.S. Geological Survey streamgage (USGS streamgage 12396500, 68 water years of record) located near Box Canyon Dam, which is 55.2 kilometers (km) upstream from the confluence of the river with the mainstem of the upper Columbia River in southeastern British Columbia. From Lake Pend Oreille to the Columbia River, the Pend Oreille River flows for 210 km. A major Pend Oreille River tributary near the outlet of Lake Pend Oreille and just upstream from Albeni Falls (fig. 2) is the Priest River, which drains Priest Lake and discharges an annual average of 1,705 ft^3/s (USGS streamgage 12395000, 71 water years of record) into the system.

Basin History: 15,000 Years to 2022

Between approximately 13,000–15,000 years ago, most of the Pend Oreille River was beneath the Purcell Lobe of the Cordilleran Ice Sheet. The Purcell Lobe covered the bottom of present-day Lake Pend Oreille and dammed the Clark Fork River, forming glacial Lake Missoula. This massive water body (over 320 km long and 610 meters [m] deep) was the largest ice-dammed lake known to have existed (O'Connor and others, 2020). The waters behind the ice dam were released with catastrophic flooding downstream extending across eastern Washington and occurring several times as the dam re-formed and failed in relation to fluctuations in the Ice Sheet. Following glacial retreat about 11,000 years ago, Lake Pend Oreille and the Pend Oreille River began to assume their present forms (McPhail and Lindsey, 1986; Pielou, 1991; Link and Keeley, 2018; O'Connor and others, 2020).

With the river and lake system formed, native fishes gained access to the area from glacial refugia located upstream and downstream from the influence of the Cordilleran Ice Sheet (McPhail and Lindsey, 1986). Although native salmonids such as bull trout, mountain whitefish, and westslope cutthroat trout were able to colonize throughout the system, anadromous Pacific salmon and rainbow trout in the Pend Oreille River are thought to have been limited to areas below the hydraulic barriers posed by Z Canyon and Metaline Falls (near the present site of Boundary Dam, see below; Scholz and others, 1985). Historical accounts indicate that anadromous fishes were limited by the falls and cascades in the lower Pend Oreille River. There is some uncertainty, however, if any single waterfall completely blocked the passage of salmon and steelhead trout in all years, at least up to Albeni Falls (Scholz and others, 1985). Within most tributaries to Boundary Reservoir (the impoundment above Boundary Dam), natural waterfalls and steep cascades also likely acted to restrict the movement of native fishes and this continued with the construction of Boundary Dam. Beyond migratory fishes, accounts of resident fish consumption by the Kalispel tribe indicate significant whitefish, char (*Salvelinus*, sp.), trout, and sucker (Catostomidae) populations in the Pend Oreille River (Scholz and others, 1985).

Contemporary Conditions

Today the Pend Oreille River is influenced by a series of large dams, beginning with Cabinet Gorge Dam, which is located just upstream from Lake Pend Oreille on the Clark Fork River and controls flows into the lake (fig. 2). Downstream from Lake Pend Oreille, major dams include the Priest Lake Outlet Dam on the Priest River, and on the Pend Oreille River, three dams in the United States (Albeni Falls, Box Canyon, and Boundary dams) as well as two in British Columbia (Seven Mile and Waneta dams). There are a few dams on key tributaries, including Mill Pond Dam (removed in 2017) and Sullivan Lake Dam in the Sullivan Creek basin. Numerous stream-road crossings (for example, culverts) and other human-built structures are present and sometimes hinder or prevent fish passage. A host of nonnative aquatic animals, ranging from mysid shrimp (*Mysis* spp.) to northern pike (*Esox lucius*) and dozens of other species have become established in the Pend Oreille system from intentional human introductions and subsequent dispersal. Active suppression efforts are occurring to control nonnative lake trout (*S. namaycush*; Hansen and others, 2010), brook trout (*S. fontinalis*; Dunham and others, 2002), and northern pike (Carim and others, 2019) to minimize their influences on native species and ecosystem processes. In short, flow regulation, introductions and invasions of nonnative species, and other changes wrought by humans to Lake Pend Oreille and the Pend Oreille River have fundamentally transformed the ecosystem. Despite such transformations, native species persist throughout much of the system.

Boundary Dam and Reservoir

This report focuses on the specific question of how Boundary Dam influences connectivity for westslope cutthroat trout and mountain whitefish. Accordingly, it is important to describe a few essential details of the dam, the associated reservoir, and tributaries. The salient characteristics of Boundary Dam were summarized from the City of Seattle's description of the project (Frantilla, 2022, https://www.seattle.gov/cityarchives/exhibits-and-education/online-exhibits/boundary-dam). Construction of Boundary Dam was completed in 1967, stands at just over 100 m tall, and can produce 127 million kilowatts of electricity on an annual basis. The impoundment upstream from Boundary Dam, the Boundary Reservoir, has a maximum depth of about 82 m, a maximum surface area of about 726 hectares (ha), and extends for 28 km upstream to the base of Box Canyon Dam. Water flow through the reservoir is relatively fast, with a residence time that ranges between 2 and 4 days (Pickett, 2004). Correspondingly, temperatures are fairly consistent up and downstream, and the reservoir is not thermally stratified at any time of the year (Seattle City Light [SCL], 2006).

Seattle City Light’s (2006) assessment listed 28 tributaries to Boundary Reservoir that offer a total of nearly 25 km of stream distance that is accessible to upstream-migrating salmonids (Washington Department of Fish and Wildlife [WDFW], 2020). For individual tributaries, accessible stream distance ranges from 0 km (barrier falls at the confluence) to potentially 32 km in Sullivan Creek after the 2017 removal of Mill Pond Dam (Federal Energy Regulatory Commission [FERC], 2011). Despite the removal of this dam, however, a seasonal velocity barrier approximately 1 km from the mouth of Sullivan Creek remains (Powers, 2008).

Part 2. Evolutionary and Ecological Connectivity for Westslope Cutthroat Trout and Mountain Whitefish

In this section, we review evidence describing historical and contemporary patterns of connectivity for westslope cutthroat trout and mountain whitefish. Although the focus of our review is on upstream passage over Boundary Dam, we review salient local and regional factors influencing connectivity. In Part 3 below, we rely on the body of evidence reviewed here to draw conclusions regarding the value of providing passage for these species upstream over Boundary Dam. In addition to considering these species, we briefly revisit the case for bull trout (Dunham and others, 2014; app. 1) to provide a more complete and updated review of upstream passage over Boundary Dam.

Westslope Cutthroat Trout

Biogeography

The Pend Oreille River represents a transitional region in the distribution between two native trout species in western North America: rainbow trout and westslope cutthroat trout. The natural biogeographic history of the boundary area is thought to have been strongly influenced by the various Pleistocene glaciations (roughly 2.8 million to 18,000 before present [B.P.]) that covered vast swaths of land and had dramatic influences on streamflow and watershed connectivity over time (McPhail and Lindsey, 1986; Pielou, 1991). Although the exact biogeographic history of the area cannot be fully reconstructed today, recolonization of ice-covered areas by fish species must have occurred following glacial retreat. Areas outside of the extent of glaciation may have also been greatly affected by historical floods, elevated stream flows, and interconnection of watersheds, allowing dispersal of fish species over areas now presently isolated from each other. Based on historical records and observations from the late 1800s, Z Canyon (immediately upstream from the present-day location of Boundary Dam and Metaline Falls on the Pend Oreille River 15 km farther upstream) appears to have limited or at least impaired upstream movement of anadromous fishes, which would likely have included steelhead trout (Scholz and others, 1985; Nellestijn and Ells, 2008).

Contemporary evidence for connectivity of westslope cutthroat trout relative to Boundary Dam is available from genetic and distribution data as well as from studies of fish movements and demographic characteristics of populations within tributary systems. Arguably, the most comprehensive description of trout distribution patterns in North America was written by R.J. Behnke (1992, 2002). He described the native distribution of westslope cutthroat trout to follow the west side of Kootenay Lake in British Columbia and south into Idaho but outside most of the Priest Lake watershed and the downstream sections of the Pend Oreille River (fig. 3). Although McPhail (2007) recorded observations of westslope cutthroat trout in the watersheds noted by Behnke (1992, 2002) around the Kootenay River of southeast British Columbia, McPhail (2007) also reported that westslope cutthroat trout populations occur in the Salmo River downstream from Boundary Dam and in other tributaries of the upper Columbia River outside of the continuous distribution estimated by Behnke (1992, 2002). More recent sampling in the boundary area established that westslope cutthroat trout populations exist in tributaries of the Pend Oreille River and in the Priest Lake watershed (fig. 3; Small and others, 2020).

Genetic Evidence of Connectivity

As with bull trout (Dunham and others, 2014), the relationship of westslope cutthroat trout in the Salmo River to populations upstream from Boundary Dam and historical barriers to upstream passage (in other words, Metaline Falls and Z Canyon) in the Pend Oreille system can provide important clues about historical and contemporary connectivity. Overall, there is little evidence that suggests any appreciable connectivity between native westslope cutthroat trout below Boundary Dam and upstream areas. For instance, genetic analysis of westslope cutthroat trout began with an analysis of 10 microsatellite DNA loci in 2007 by the Washington Department of Fish and Wildlife (Washington Department of Fish and Wildlife [WDFW], 2020; Small and others, 2007). This study included 77 localities within the Pend Oreille and Priest Lake watersheds as well as several groups of hatchery fish used in various stocking programs (westslope cutthroat trout, Yellowstone cutthroat trout, and rainbow trout). The Salmo River collection included samples from near the confluence with the Pend Oreille River (Swift Creek, about 12 km upstream) and a small lake in the headwaters (Waldie Lake). Unfortunately, owing to variable and uncertain scoring of microsatellite loci for the Salmo River samples, little insight was gained on the status of these fish (M. Small, oral comm., May 2020). The few analyses that were completed indicated that the Waldie Lake and Swift Creek samples were quite distinct from one another (both were more similar to samples outside the Salmo River drainage than they were to each other) as well as from other fish from the Pend Oreille study area.

Furthermore, Small and others (2017) reported the results of analyses of about 1,850 samples, including fish from five sites within the Salmo River watershed, using a panel of 215 single nucleotide polymorphism (SNP) loci. In this analysis, fish were first screened for hybridization with rainbow trout using four loci that were diagnostic for differences between the species. Results indicated that 29 percent of fish sampled from the Salmo River sites (range 3–68 percent) were interspecific hybrids between rainbow trout and cutthroat trout (table 3 in Small and others, 2017). Even the most upstream sample sites (Crutch and Watch Creeks) showed some evidence of introgression with rainbow trout although at much lower levels (3–6 percent) than in downstream reaches of the Salmo River system. Of the remaining Salmo River fish that were deemed to be westslope cutthroat trout from four sites (two were pooled as they were so similar to one another), all showed very high genetic affinity to the King's Lake (Priest Lake drainage origin) hatchery samples of westslope cutthroat trout (fig. 4). These fish showed a similar “hatchery genetic signal” to fish from other localities within the Pend Oreille drainage that have been subject to hatchery supplementation (for example, Sweet, Slate, Lunch, Lost, and Harvey Creeks). The U.S. part of the Salmo River has also received at least some supplementation of westslope cutthroat trout using the King's Lake hatchery source (Small and others, 2017).

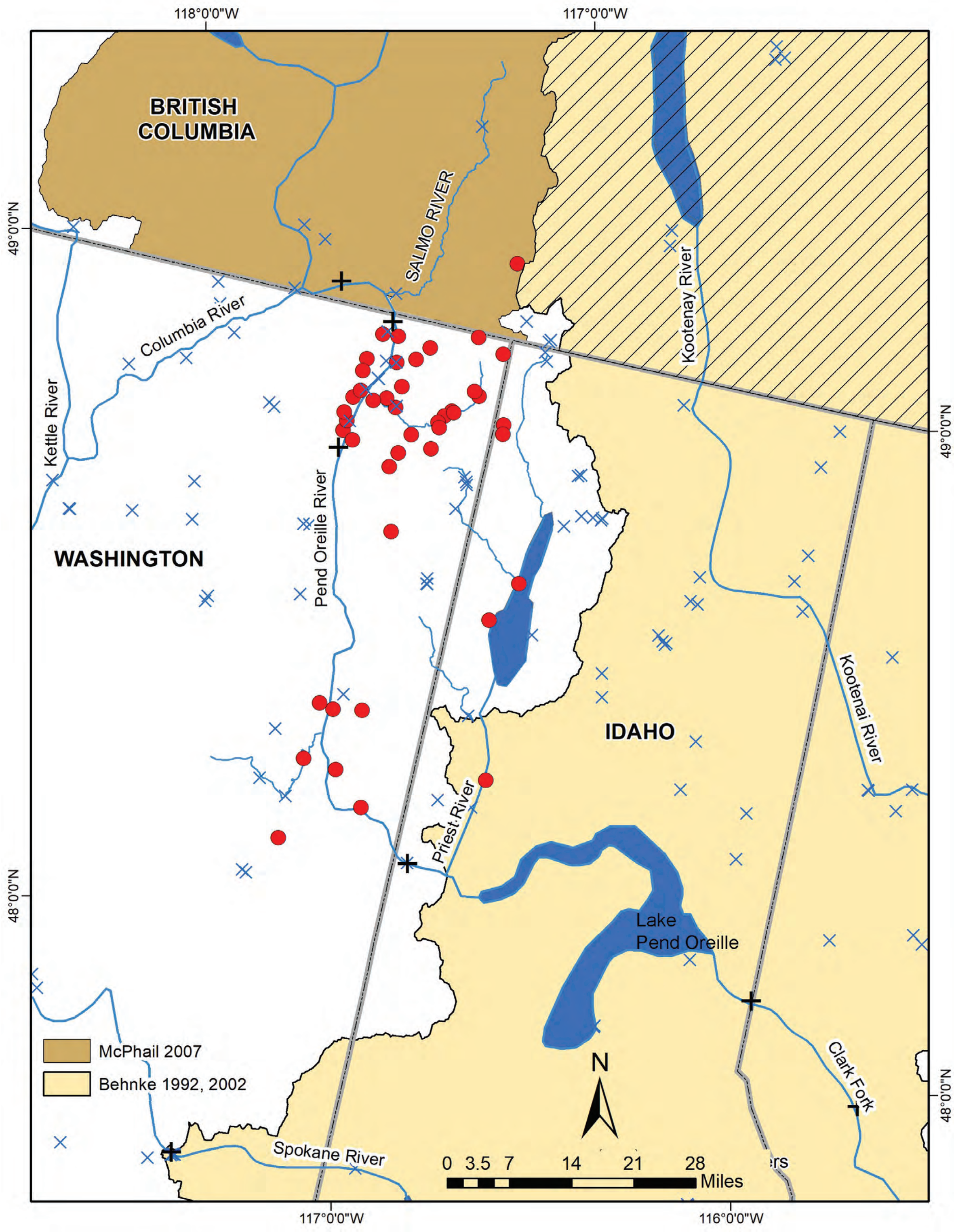

Figure 3. Pend Oreille River and associated major rivers (blue lines) of British Columbia, Washington, Idaho, and Montana. Brown polygon represents the estimated western extent of the native distribution of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) in southeastern British Columbia (McPhail, 2007). The light brown polygon is the estimated extent of westslope cutthroat trout by Behnke (1992, 2002). Hatched area indicates the estimated overlap in range between McPhail (2007) and Behnke (1992, 2002). Red circles represent sampling locations for westslope cutthroat trout populations reported in Small and others (2020). Black crosses indicate the location of major dams in the region. Blue crosses indicate the location of known waterfalls (World Waterfall Database, 2022, https://www.worldwaterfalldatabase.com/).

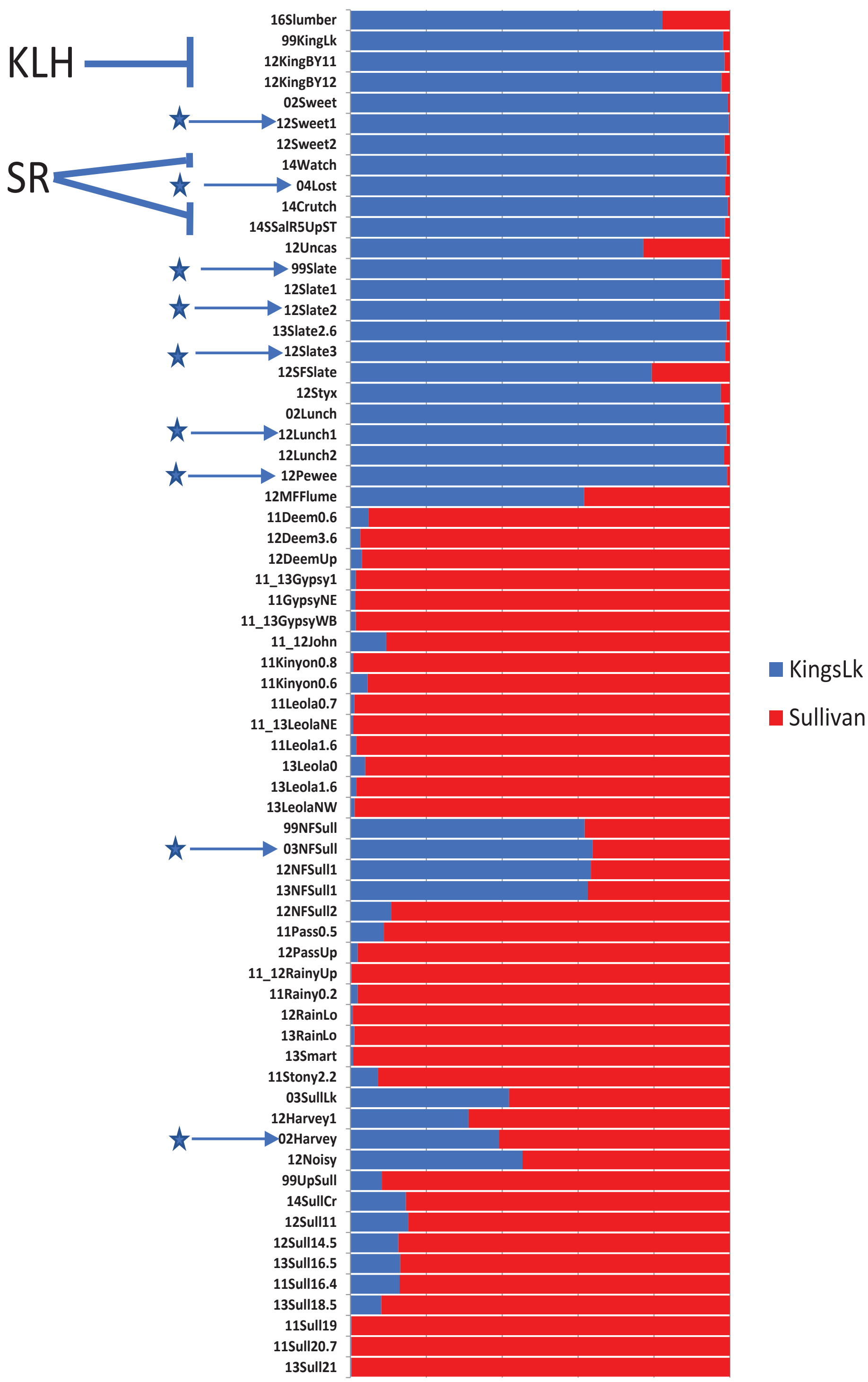

Figure 4. Bar graphs showing proportional composition of samples of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) with respect to two major genetic groups (blue and red shading) based on the single nucleotide polymorphism analysis of Small and others (2017). Each bar represents the mean proportional contribution (0.0 to 1.0) of fish from each locality across multiple admixture analyses. Fish from the King's Lake hatchery (KLH, three samples) are predominantly composed of the blue genetic group. Fish from localities within the Salmo River (SR, three samples) are also predominantly composed of the blue group, as are some tributaries of the Sullivan Creek ("Sull") drainage and the Pend Oreille River upstream from Boundary Dam that have been subject to hatchery supplementation with King's Lake hatchery westslope cutthroat trout (indicated by blue stars; for example, Harvey, Lunch, Lost, Slate, North Fork Sullivan (NFSull) Creeks, see Small and others 2017, table 1 and fig. 2). The red genetic group is thought to be characteristic of native fish from the Sullivan Creek watershed.

Next, Small and others (2019a) reported the results of genetic tests that used a baseline of SNP information on potential source populations to genetically assign fish (N = 16) sampled from various non-tributary localities to these potential source populations. One fish was sampled from the Boundary Dam tailrace, and it was estimated to have originated from either Watch Creek (a tributary of the uppermost reaches of the Salmo River in Washington) or Slate Creek, a tributary of the Pend Oreille about 10 km upstream from the Boundary Dam. Consequently, identification of this tailrace westslope cutthoat trout was ambiguous relative to whether it may have originated from upstream or downstream from the dam site. The remaining 15 fish were all sampled from areas upstream from the dam and were identified as either rainbow trout (N = 1), westslope cutthroat trout x rainbow trout hybrids (N = 3 fish of varying levels of admixture between the two species), King's Lake hatchery westslope cutthroat trout (N = 1), either native or hatchery fish (N = 2), or native fish from localities upstream from the dam, including the Sullivan Creek drainage (N = 8).

Finally, A similar analysis was conducted by Small and others (2020) for a sample of 47 fish, all but seven of which were sampled in river sections between Boundary and Box Canyon dams. The largest percentage of fish were either introgressed (up to 75 percent introgression) with rainbow trout (19 of 47 fish, 40.4 percent), or were assigned to the King's Lake westslope cutthroat trout hatchery stock (13 of 47 fish, 27.7 percent). Two more fish were identified as rainbow trout. Of the remaining 13 fish, a single individual was considered to have originated from the Salmo River or King's Lake hatchery, and another was assigned to the Salmo River or Granite Creek (one of the original brood sources for the King's Lake hatchery strain; Small and others, 2007, 2020), three fish were assigned as Salmo River watershed westslope cutthroat trout, and eight fish were assigned to various localities between Boundary and Box Canyon dams. In summary, of 40 fish sampled above the Boundary Dam, only one was unequivocally assigned to the Salmo River drainage (and thus suggests some historical connectivity between the Salmo River and the Pend Oreille River upstream of Metaline Falls). Additionally, of the seven fish sampled below Boundary Dam, only one could be unequivocally assigned to a site upstream from the dam (to Lunch Creek), suggesting either entrainment through the dam or some historical connectivity through Metaline Falls.

In sum, the extensive genetic sampling and analysis by WDFW strongly suggest that westslope cutthroat trout sampled from the Salmo River (and the few fish sampled in the tailrace sections and genetically assigned to the Salmo River baseline) are either: (1) hybrids between rainbow trout and westslope cutthroat trout or, (2) are genetically indistinguishable from the King's Lake hatchery strain. Small and others (2017) concluded that Salmo River westslope cutthroat trout included in their study were either a population founded from hatchery plantings or a native population that has been substantially influenced by introgression with hatchery fish. The likelihood of a hatchery origin of westslope cutthroat trout in at least the mainstem reaches of lower Salmo River is considered to be high by fisheries workers in the Nelson, BC, area (J. Baxter, FortisBC, written commun. with Eric Taylor, May 2020). Furthermore, consultation with local authorities could not confirm any native populations of westslope cutthroat trout between the confluence of the Salmo and Pend Oreille Rivers and the confluence of the latter with the Columbia River (C. Lee, WDFW, Spokane, and T. Anderson, Kalispel Tribe Fish and Wildlife Dept., written commun. with Eric Taylor, May 2020).

The lack of significant historical connectivity between populations of westslope cutthroat trout downstream and upstream from Boundary Dam is consistent with conclusions for bull trout (Dunham and others, 2014). Finally, Chinook salmon (*O. tshawytscha*) and steelhead trout have migrated to the confluence of the Salmo River (formerly referred to as the "Salmon" River) and the Pend Oreille River as well as upstream in the Salmo River, but Metaline Falls and Z Canyon probably represented barriers to further upstream migration for anadromous fish in the Pend Oreille River, and thus almost surely served as barrier to upstream migration for westslope cutthroat trout and mountain whitefish (Nellestijn and Ells, 2008).

Ecological Evidence of Connectivity

Inferences from molecular markers can provide important insights into potential patterns of historical and contemporary connectivity (Neville and others, 2006a, b). Many forms of connectivity cannot be easily evaluated using molecular markers alone, however. Complex patterns of fish movement and consequences for growth, survival, and reproduction require tracking of tagged fish or indirect methods (for example, observational or modeling studies) to evaluate the importance of connectivity in riverscapes (Young, 1996; Falke and Fausch, 2010).

Direct evidence of movement of westslope cutthroat trout in Boundary Reservoir and its tributaries comes from tagging and tracking studies. In the reservoir and tailrace, 56 westslope cutthroat trout were tagged and tracked using acoustic telemetry between 2016 and 2019 (Hydroacoustics Technology, Inc., 2018, 2020). Tagged fish were tracked between the tailrace of Boundary Dam and downstream areas, as well as in Boundary Reservoir up to the base of Box Canyon Dam. Available reports mention that the length and mass of tagged individuals were recorded, but were not reported, so effects of size on movement cannot be evaluated (for example Monnot and others, 2008). These fish were captured over the course of 24 electrofishing events, each of which involved at least 1 day of effort and yielded a catch rate of less than two fish per event. Interestingly, over the course of the 3-year study and sampling efforts,10 of the 56 (18 percent) tagged fish were recaptured. Of all fish tagged and tracked over 3 years, eight individuals (14 percent) were entrained downstream through Boundary Dam. The average size of westslope cutthroat trout entrained ($\bar{x}$ = 286 millimeter fork length; standard deviation [SD]= 61) were statistically indistinguishable to those that were not entrained ($\bar{x}$ = 310 mm fork length; SD = 66; Hydroacoustics Technology Incorporated, 2018, 2020, 2021).

Overall, studies of westslope cutthroat trout indicate that very few individuals currently occupy Boundary Reservoir, though precise density estimates are not available. Furthermore, only a few of these individuals were entrained downstream through Boundary Dam (14 percent). Low numbers of tagged and tracked individuals, uncertainties about size-related movement patterns, and lack of tracking of individuals from the reservoir into tributaries limit what can be concluded from this work in terms of patterns of connectivity beyond the simple question of entrainment.

Tagging of westslope cutthroat trout in tributaries to Boundary Reservoir has involved considerably more locations and individuals relative to work in the main-stem river (West Fork Environmental, 2020). Tributary studies have used Passive Integrated Transponders (PIT tags), and results from work conducted from 2012 to 2019 were available for this report. Of the 28 tributaries identified by Seattle City Light (2006), tagging of individual westslope cutthroat trout has been conducted in Peewee, Slate, Sullivan, Flume, Pocahontas, and Sweet-Lunch Creeks. It is important to note these tributaries have complete or partial natural barriers to upstream movement of fish that occur near their confluences with Boundary Reservoir, and that PIT tagging has occurred upstream from these barriers. Over 8 years (2012–19), a total of 13,975 westslope cutthroat trout were PIT-tagged. Individuals were recaptured by electrofishing at locations distributed across tributaries. Between 2014 and 2019, numerous 200 m locations have been annually sampled 1–6 times by single-pass electrofishing. The total number of sites sampled across all years was not reported, but in 2018, for example, efforts included 46 sites sampled in previous years and 32 new sites located next to previously sampled sites.

Based on existing tagging and electrofishing efforts and the distribution of sites sampled in space and time, few westslope cutthroat trout were recaptured within or beyond the site of initial capture. Recaptured individuals in 2019 represented fish that were tagged in previous years, including 71, 19, 6, 3, and 1 percent for fish initially PIT-tagged in 2018, 2017, 2016, 2015, and 2014, respectively. A total of six PIT-tag arrays are being used for the detection of tagged individuals as they swim past the antennas, including five in Sullivan Creek and one in Slate Creek. All but one of the PIT array locations include three channel-spanning arrays to ascertain the directional movement of detected individuals. Since the antennas were installed in 2014 and 2015, the PIT tag arrays have recorded a total of 516,602 detections from 486 unique fish. This low number of unique fish suggests that movement across PIT arrays is generally infrequent and that tagged fish reside primarily within tributaries (Lukacs and Landguth, 2020). While data from the PIT arrays suggests very few individuals leave Sullivan Creek for Boundary Reservoir, there have been considerable challenges with maintaining the most downstream antenna near the outlet of Sullivan Creek, adding an unknown degree of uncertainty to these findings (Lukacs and Landguth, 2020). Overall, captured fish (tagged and untagged) were relatively small (43–228 mm, fork length) but is consistent with sizes that may be expected for small streams. Growth rates based on recaptured fish did not exhibit any obvious outlying values or bi-modality as may be expected of a population composed of a mixture of resident and migratory individuals (Kendall and others, 2015).

Environmental Conditions

Current conditions within Boundary Reservoir are marginal for supporting westslope cutthroat trout due in part to warm seasonal water temperatures. Consistently colder water temperatures are available in tributary systems feeding Boundary Reservoir and at tributary mouths. A recent report (Environmental Science Associates [ESA], 2019) documenting seasonal temperatures within Boundary Reservoir indicated extended seasonal (July–Sept) occurrences of temperatures above 20 °Celsius (C) at all locations sampled. Temperatures in the Boundary Reservoir forebay recorded at 10 m depth exceeded 20 ° C from July 10th through September 14th, 2019, with a maximum of 23 °C. Temperatures recorded at 60 m were similar, reflecting isothermal conditions that should be expected in a system with water discharge that has a short residence time. Small, coldwater refuges at Boundary tributary mouths (H. Rich and R. Simmons, Seattle City Light, oral communication, April 2021) are not apparent in that dataset. Similarly, some locations of the Pend Oreille River upstream from Box Canyon Dam, have colder patches or thermal refuges near tributary confluences. It is not clear, however, if the use of these cold refuges can be expected to improve conditions for coldwater fish (for example, mountain whitefish, westslope cutthroat trout, bull trout) as the benefits of thermal refuge use depend on many contingencies such as other measures of habitat quality, including vulnerability to predators, lack of feeding opportunities (Snyder and others, 2020), poor water quality (for example, low dissolved oxygen), or possibly the presence of other nonnative species, such as brook trout.

Although temperatures within the Boundary Reservoir exceed levels considered suitable for coldwater taxa such as salmonids (Richter and Kolmes, 2005), tributaries within the system are a potential source of cold-water habitat. Modeled presence of cold-water species such as westslope cutthroat trout is predicted to be high in many locations, particularly within Sullivan Creek (Isaak and others, 2016; fig. 5).

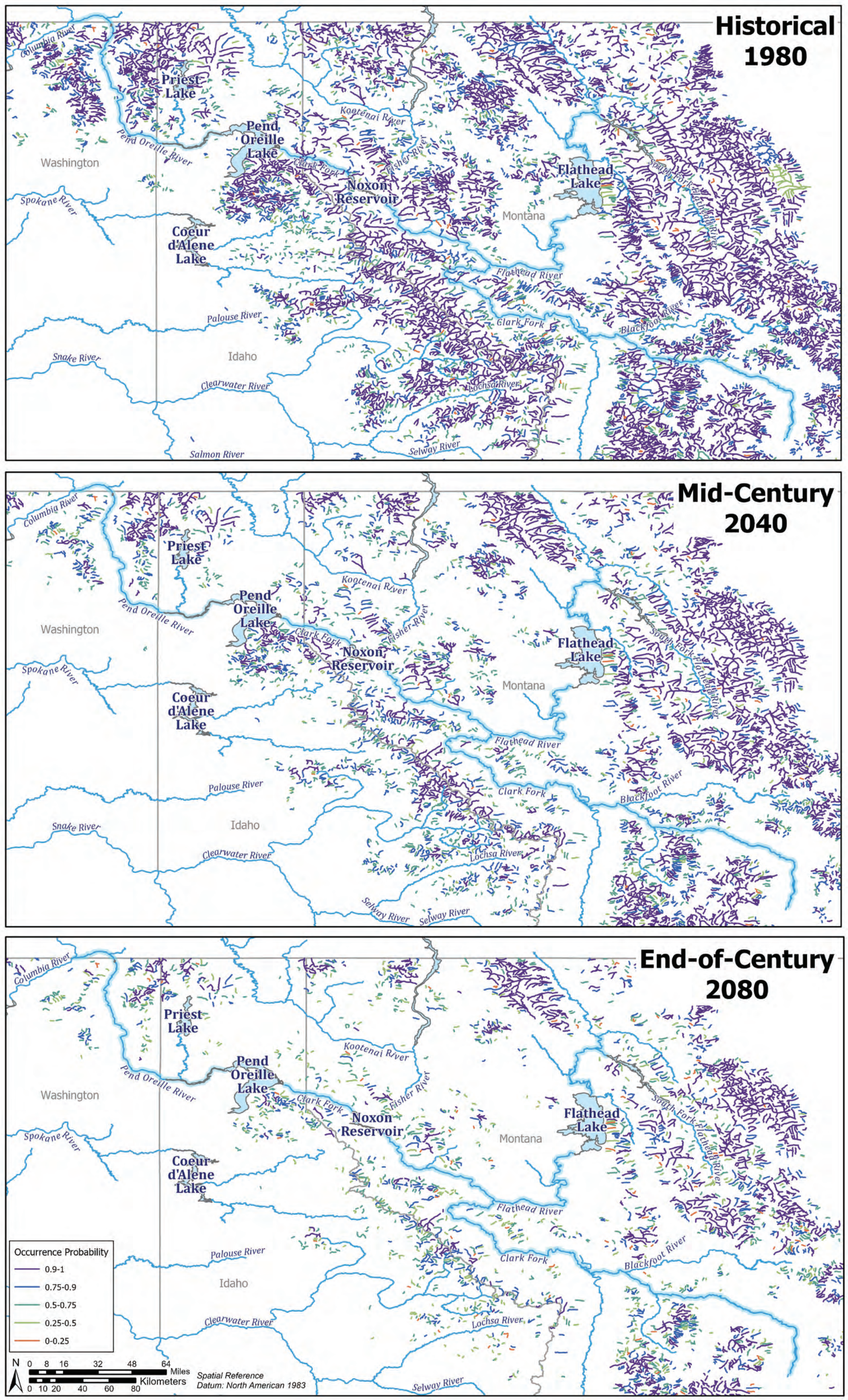

Figure 5. Historical, mid-century, and end-of-century (based on climate change scenarios in 1980, 2040, and 2080) predicted presence of native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), assuming the absence of nonnative brook trout (*S. fontinalis*) within the Lake Pend Oreille–Pend Oreille River system (fig. 2) in the United States (from Isaak and others, 2016).

Colder tributaries to Boundary Reservoir could act as thermal refuges if they are accessible. In the largest system, Sullivan Creek, a series of chutes and cascades begin about 1 km upstream from the confluence with Boundary Reservoir. Such conditions are considered to pose a barrier to upstream passage of bull trout less than 457 mm when flows exceed about 3 m^3/s Existing stream discharge records (USGS gage 12398000) indicate that flows often exceed those levels during much of the year, but larger fish may be able to move upstream into Sullivan Creek as flows decline in late summer through fall. It is worth noting that none of the 16,980 westslope cutthroat trout captured in tributary surveys from 2012 to 2018 were larger than 350 mm (West Fork Environmental, 2020). Sizes of individuals tracked using acoustic telemetry in Boundary Reservoir averaged 276 mm (SD 47.3) with a maximum length of 395 mm. Access to other tributaries of Boundary Reservoir with available cold water is not possible due to the presence of natural barriers near the confluences of Peewee, Slate, Sweet, Flume, and Sand Creeks.

Before large dams were constructed in the Pend Oreille system, it is possible that westslope cutthroat trout exhibited migratory patterns that were similar to those exhibited by bull trout in the system (DuPont and others, 2007, Dunham and others, 2014). Historical patterns of movement by bull trout included a strong influence of seasonal emigration of individuals from systems upstream from the Pend Oreille River, with some of these individuals passing downstream over the barriers of Z Canyon and Metaline Falls. There is little doubt that the numbers of westslope cutthroat trout from the Priest Lake, Lake Pend Oreille, and Clark Fork River systems could also have produced individuals that migrated downstream seasonally into the Pend Oreille River. Such individuals would, however, have been unable to historically access downstream tributaries between present-day Boundary and Box Canyon dams due to natural barriers near their confluences with the Pend Oreille River. Furthermore, the presence of such migratory individuals would be limited to the section of the river (which is now part of Boundary Reservoir) that is located upstream from Metaline Falls (just downstream from the confluence of Sullivan Creek). Individuals moving downstream from Metaline Falls would not have been able to return upstream.

Today, westslope cutthroat trout in Boundary Reservoir represent a mixture of origins, including individuals from populations upstream from Box Canyon Dam (see “Genetic Evidence of Connectivity” above, and fig. 6). Of 40 westslope cutthroat trout sampled for fin tissues in Boundary Reservoir during 2018–19, the proportion of individuals genetically assigned to populations upstream in Box Canyon Reservoir or Priest River tributaries (35 percent; n = 14) was double that assigned to Boundary Reservoir tributaries (15 percent, n = 6; fig. 6; Small and others, 2020). The proportion of individuals assigned to the King's Lake Hatchery was even higher (40 percent; n = 16) in Boundary Reservoir. A similar genetic analysis of westslope cutthroat trout in Box Canyon Reservoir (n = 202) showed only 2 percent (n = 3) assigning to King's Lake Hatchery (fig. 6; Small and others, 2020).

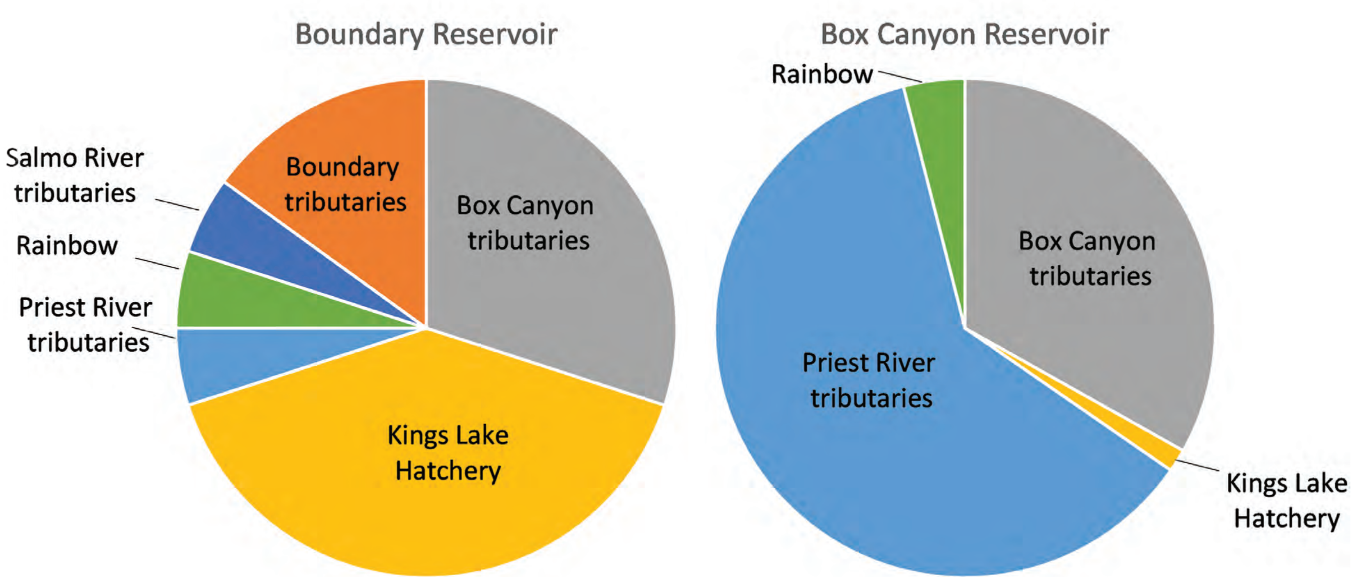

Figure 6. Genetic assignment of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) sampled from Boundary Reservoir (n = 40; left panel) and Box Canyon Reservoir (n = 202; right panel) into major spatial groupings (Boundary Reservoir tributaries, Box Canyon Reservoir tributaries, Priest River tributaries, King's Lake Hatchery, and phenotypic westslope cutthroat trout that were assigned as rainbow trout (*Oncorhynchus mykiss*); Small and others 2020).

Mountain Whitefish

Biogeography

Mountain whitefish is one of the most widely distributed yet least studied inland salmonid fishes in western North America. The species occurs south from the Lahontan and Bonneville basins within the hydrographic Great Basin desert into the Columbia River basin, upper Missouri River and in other inland and coastal tributary streams north to the Mackenzie River in the Northwest Territories, Canada (Warren and Burr, 2014). Its widespread distribution suggests a complex historical biogeography, but this has not been well studied (Miller, 2006). Unlike westslope cutthroat trout and other salmonids, mountain whitefish have not been widely introduced by humans. Thus, indirect inferences from molecular markers are not as subject to biases from this potential influence.

Genetic Evidence of Connectivity

Limited work has been conducted on mountain whitefish in the Pend Oreille River. The most salient data are those of Small and others (2019b), who examined variation at 15 microsatellite DNA loci in 163 individuals. The samples ranged from one fish collected in the Boundary Dam tailrace to fish from the former Mill Pond Dam area of the Sullivan Creek watershed, fish from Sullivan Creek itself, and fish from a range of localities between Boundary Dam forebay and Albeni Falls.

This analysis showed a major difference between samples in the Mill Pond/Sullivan Creek area and those collected between Boundary Dam and Albeni Falls (fig. 7). The one sample collected in the Boundary Dam tailrace was very similar to the fish collected from the Boundary Reservoir to Albeni Falls area, suggesting that it originated in this area and was entrained downstream through the dam. Furthermore, one fish collected in the Pend Oreille River upstream from Boundary Dam appeared to originate above the former site of Mill Pond Dam (fig. 7, grey symbol indicted by grey arrow). By contrast, there were no differences found among samples collected between Boundary Dam to Albeni Falls, nor between fish from the Mill Pond area and upper Sullivan Creek (although sample sizes were very small in the latter group).

This analysis was augmented by further work on 41 Mountain whitefish collected from Sullivan Lake and five fish collected from the Pend Oreille River between Boundary Dam and Box Canyon Dam (Small and others, 2020). The Sullivan Lake fish were strikingly distinct from those

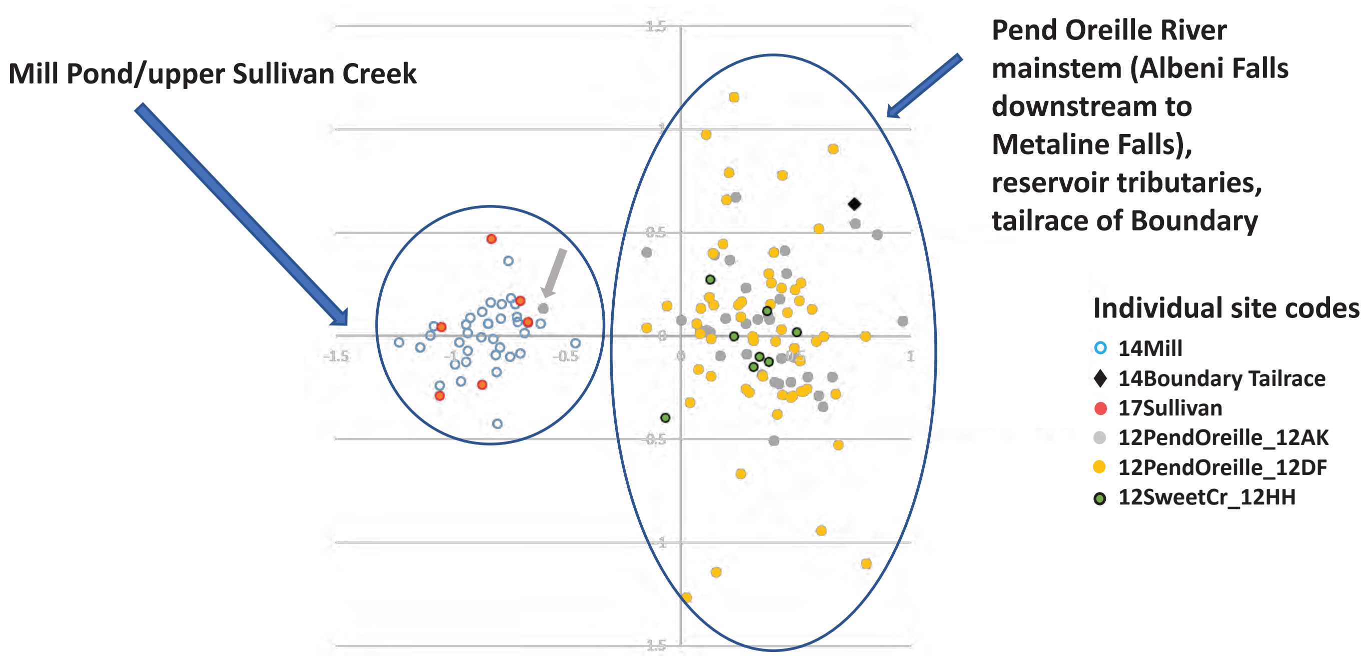

Figure 7. Major genetic groups of mountain whitefish (*Prosopium williamsoni*) in the Boundary Area resolved using microsatellite DNA analysis. Samples are projected in factorial correspondence analysis space and the ellipses denote two genetic groups of mountain whitefish: Mill Pond/upper Sullivan Creek and Pend Oreille main stem and tributaries, and membership of individual fish within those two groups. Modified from Small and others (2019b). The grey closed symbol within the left-most ellipse represents a fish sampled from the Boundary Reservoir and the black solid diamond within the right-most ellipse represents a fish sampled from the Boundary Dam tailrace.

collected from the Pend Oreille River (F_{ST} ranged from 0.10 to 0.11) but were only modestly (but significantly) distinct from Mill Pond Mountain whitefish (F_{ST} = 0.025, fig. 8). Despite these average differences among the different groups of mountain whitefish, three fish collected in the mainstem Pend Oreille River (between upstream from Boundary Dam and downstream from Box Canyon Dam) were genetically similar to fish from the Sullivan Lake/Mill Pond group and remarkably similar to the Mill Pond fish (fig. 8). These data suggest the occasional downstream movement of Sullivan Lake/Mill Pond fish into the area between Boundary Dam and Box Canyon Dam. Notwithstanding occasional downstream movements, the difference between the Mill Pond/Sullivan Creek/Sullivan Lake samples and the Boundary Dam/Albeni Falls samples suggests that there has been restricted movement of fish between these areas, even though the Sullivan Creek watershed enters the Pend Oreille River above Metaline Falls. Alternatively, it is possible that the distinction between areas could be an artifact of the isolation created by the Mill Pond Dam that was removed in 2017. This, however, seems unlikely given that there was a natural water velocity barrier in Sullivan Creek where the Mill Pond Dam was located and another at the outlet of Sullivan Lake (Small and others, 2020). Furthermore, despite smaller sample sizes, the Mill Pond/Sullivan Creek/Sullivan Lake samples contained ten alleles (at low to moderate frequencies of 1–12 percent) not observed in the Boundary Dam/Albeni Falls samples. This observation suggests the Mill Pond/Sullivan Creek/Sullivan Lake fish have been isolated long enough from the Pend Oreille fish for these novel mutations to accumulate. Furthermore, strong genetic drift induced by isolation from Mill Pond Dam construction would be expected to eliminate rare, unique

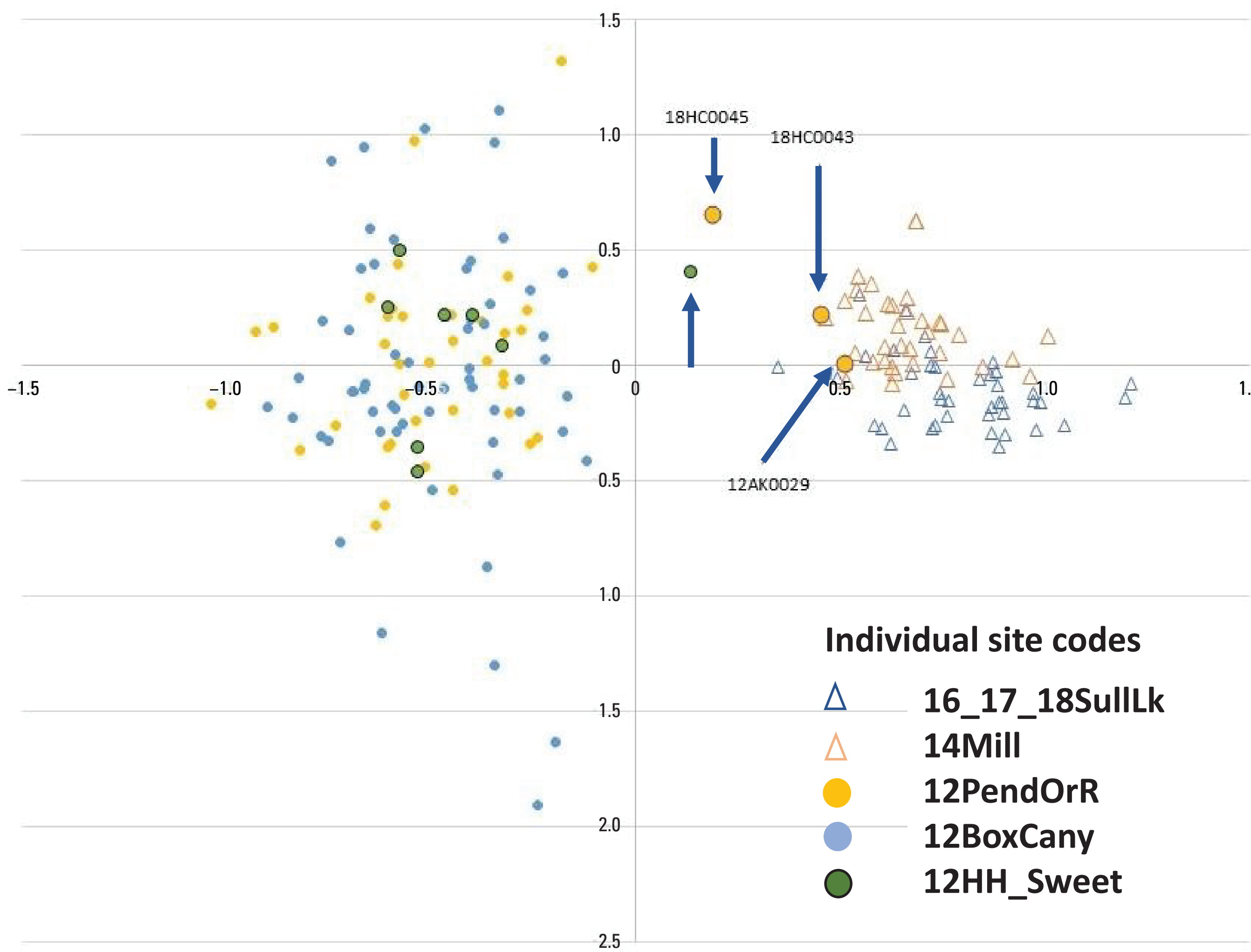

Figure 8. Major genetic groups of mountain whitefish (*Prosopium williamsoni*) in the Boundary Area resolved using allelic variation at microsatellite DNA loci projected using factorial correspondence analysis. The genetic group to the right of the thin vertical grey line consists of mountain whitefish from Mill Pond and Sullivan Lake as well as three fish sampled from the Pend Oreille River (large orange symbols with arrows) and one fish sampled from a tributary above Metaline Falls (Sweet Creek, green symbol with arrow right of grey vertical line). From Small and others (2020) and also includes fish assayed in Small and others (2019a, b).

alleles. Consequently, the substantial divergence between the Mill Pond/Sullivan Creek/Sullivan Lake and Boundary Dam/ Albeni Falls mountain whitefish is probably not an artifact of Mill Pond Dam or Sullivan Lake Dam construction.

The distinction between Mill Pond/Sullivan Creek/ Sullivan Lake mountain whitefish and those from below the Mill Pond site is also consistent with similar differences found in westslope cutthroat trout (for example, Small and others 2017, 2020).

Five fish that were collected below falls, as well as current or former dam sites were more similar to fish above these sites suggesting that mountain whitefish can survive entrainment through natural geographic barriers and dams. In the case of the single fish inferred to be of upper Sullivan Creek origin that was collected in the Boundary Dam to Box Canyon Dam area, the "baseline" sample of fish from the Sullivan Creek area was likely sufficient to support the inference of downstream movement from Sullivan Creek. By contrast, the single fish collected in the Boundary Dam tailrace that was inferred to have originated above the dam (Small and others, 2019a, b) could not be compared to mountain whitefish from the mainstem Pend Oreille River downstream from Boundary Dam or the Salmo River because there were no baseline samples available for these areas. Given the limitations of these small sample sizes and their spatial distributions, a different result could arise once baseline samples from below Boundary Dam are analyzed.

Whiteley and others (2006) used six microsatellite DNA loci to assay variation among samples of mountain whitefish, including those collected at the confluence of the Pend Oreille and Columbia Rivers (PoR-C) and upstream from this area in the Clark Fork River. The PoR-C sample was more similar to samples upstream in Canadian portions of the Columbia River (Beaver Creek, BC, and Kootenay Lake each about 100–110 km upstream from PoR-C) and localities from the upper (Eagle River, BC) and lower Fraser River (Chilliwack River, BC, both several hundreds of km away and in a distinct drainage from PoR-C) than it was to samples from the Clark Fork drainage (at least 170 km upstream from Boundary Dam, Z Canyon, and Metaline Falls; Whiteley and others, 2006). High similarity of lower Pend Oreille River mountain whitefish to fish from the Fraser River compared to fish from the Clark Fork is inconsistent with high levels of historical gene flow between the lower Pend Oreille River and areas upstream.

Ecological Evidence of Connectivity

As for westslope cutthroat trout, water temperature is a major control on the distribution of mountain whitefish in stream networks (Isaak and others, 2017a). In a comprehensive analysis of thermal requirements of 73 fish species in Wyoming, Mandeville and others (2019) classified species into five thermal guilds: cold, cool-cold, cool, cool-warm, and warm. Cutthroat trout (*O. clarkii*) was identified as one of two species (including nonnative brook trout, *S. fontinalis*) belonging to the cold-water species guild. Mountain whitefish was classified as a member of the cool water guild of fishes. Isaak and others (2017a) modeled the presence of mountain whitefish based on estimated August mean temperatures (Isaak and others 2017b) in streams located in the upper Columbia River (including the Pend Oreille River), Snake River, and Missouri River headwaters. August mean temperatures associated with estimated probabilities of occurrence of 0.5 for mountain whitefish were 15.3 °C and 9.7 °C for univariate and multivariate models. It is worth noting that confidence bounds associated with these estimates were relatively wide, which should be expected with field-based studies of thermal associations, as numerous factors interact with temperature to determine species presence (Mandeville and others, 2019). Furthermore, associations can vary, depending on descriptors used to associate fish with thermal regimes (for example, magnitude, timing, duration, frequency of thermal exposures; Benjamin and others, 2016). While many uncertainties remain, available evidence suggests that mountain whitefish are more likely to be observed using water that is a few degrees warmer than what can be generally expected of cutthroat trout (Isaak and others, 2017b). As discussed for westslope cutthroat trout, summer maximum temperatures within Boundary Reservoir approach and potentially exceed levels that could lead to physiological stress in mountain whitefish (Quinn and others, 2010).

While limited data are available, inferences from molecular markers (preceding section) indicate little gene flow and connectivity in the Pend Oreille River downstream from Boundary Dam for mountain whitefish. Similarly, within Boundary Reservoir, only six mountain whitefish have been tagged and tracked, but no individuals were detected being entrained through Boundary Dam (Hydroacoustics Technology Incorporated, 2018, 2020, 2021). More individuals would need to be tracked to draw more definitive conclusions. Movement studies of mountain whitefish in other systems, along with knowledge of constraints on connectivity in the Boundary Reservoir system and Pend Oreille River, can be applied to draw a few qualified inferences. Direct tracking of individual movements as well as inferences from otolith microchemistry of mountain whitefish in other systems indicate seasonal movements are extensive (for example, up to and potentially extending over 100 km), complex, and generally limited to larger streams within riverscapes (for example, Davies and Thompson, 1976; Northcote and Ennis, 1994; Baxter, 2002; Benjamin and others, 2014; Boyer and others, 2017). An improved understanding of spatial and temporally dynamic habitat features that mountain whitefish may depend on within Boundary Reservoir could provide useful insights for maintaining or improving connectivity within the system. For instance, Davies and Thompson (1976) proposed a host of proximate (for example, environmental conditions) and ultimate (for example, growth, survival, reproduction) drivers of diverse seasonal movements they observed for mountain whitefish throughout the life cycle.

Aside from the isolated distribution of mountain whitefish in the Sullivan Lake/Creek watershed and the lowest reach of Sweet Creek, tributary connectivity within Boundary Reservoir may have little ecological significance. Given the lack of access (upstream movement barriers) and limited suitability (that is, small size) of many tributaries to Boundary Reservoir, opportunities for mountain whitefish to exploit seasonally variable conditions within the system are limited. Evidence from molecular genetic markers indicating lack of genetic drift in isolated populations of mountain whitefish in the Sullivan Creek watershed indicates that current and recent historical population sizes are large enough to overcome the effects of genetic drift, in spite of their isolation or lack of connectivity to the Pend Oreille River. Such patterns have been observed for other salmonid fishes upstream from human-constructed barriers (culverts), where only the smallest systems show evidence of loss of genetic diversity (Neville and others 2009). Although some studies have identified loss of genetic diversity in some instances upstream from human-constructed and natural passage barriers (for example, Wofford and others, 2005; Neville and others, 2006a, b; Carim and others, 2016), populations of westslope cutthroat trout often persist upstream from barriers (Loxterman and others, 2014; Peterson and others, 2014), and at least in the case of culverts, population persistence times may exceed the lifespan of culverts (Reagan, 2015). Other structures (for example, concrete and metal erosion control dams; Morita and others, 2009) may last longer and pose threats to the long-term persistence of isolated populations.

The importance of upstream connectivity to the Pend Oreille River above Box Canyon Dam is less clear for mountain whitefish. As with westslope cutthroat trout, the ecological importance of connectivity of mountain whitefish to the Pend Oreille River and associated lakes upstream from Albeni Falls Dam is unknown. Movements of mountain whitefish observed in other systems have been extensive however (for example, Davies and Thompson, 1976; Northcote and Ennis, 1994; Baxter, 2002; Benjamin and others, 2014; Boyer and others, 2017), so this is a potential consideration. As with westslope cutthroat trout and bull trout (Dunham and others, 2014), there is little possibility, however, that mountain whitefish were able to move upstream over Z Canyon and Metaline Falls.

Part 3. Conclusions and Recommendations for Upstream Passage over Boundary Dam

Westslope Cutthroat Trout

The historical biogeography of the Pend Oreille River system, molecular genetic analyses, and contemporary ecological observations were assembled to draw conclusions regarding westslope cutthroat trout and the role that Boundary Dam plays in affecting connectivity for this species. Notably, the available molecular genetic evidence suggests westslope cutthroat trout in the Salmo River may: (1) be introgressed with rainbow trout, and (2) derived from a source outside of the Salmo basin (King's Lake hatchery strain). We discuss each of these in turn below.

Introgression between cutthroat trout and rainbow trout can lead to reduced fitness (Strait and others, 2021) and thus pose a threat to westslope cutthroat trout if one or both species are introduced outside their natural ranges. There are likely remnants of native and nonnative rainbow trout in the Salmo River, owing to historical stocking of rainbow trout and isolation by downstream dams that have prevented anadromous (steelhead trout) life history expression (Hagen and Baxter, 2004). Consequently, westslope cutthroat trout likely coexist with a mix of native and introduced rainbow trout in the Salmo River. The potential spread of hybridization between westslope cutthroat trout and rainbow trout throughout connected river networks has been documented in tributaries upstream from the Pend Oreille River (Muhlfeld and others, 2014), which may be exacerbated by rapid climate warming observed across the western United States (Isaak and others, 2016). Similar outcomes are possible if Salmo River westslope cutthroat trout are connected to native westslope cutthroat trout in the Pend Oreille River. Given the evidence from upstream systems, threats posed from hybridization with nonnative rainbow trout or backcrossing with hybrids merit serious consideration when evaluating the potential risks and benefits of connecting to isolated native populations of westslope cutthroat trout in the Pend Oreille River. One option to facilitate fish passage but protect upstream populations from introgression would be to remove hybrid individuals passing over fish passage structures during spawning migrations between mainstem habitats and tributaries, but this can be a costly endeavor.

With respect to the hatchery origin (King's Lake hatchery stock) of westlope cutthroat trout in the Salmo River,the absence of readily detectable and genetically unique westslope cutthroat trout in the Salmo River contrasts strongly with Sullivan Creek immediately upstream, where westslope cutthroat trout likely represent a native population. The King's Lake hatchery stock is derived from tributaries in the Priest Lake watershed (Small and others, 2007) and can be considered native to the Pend Oreille/Priest Lake watershed. Consequently, the Salmo River fish could be a native population and their current similarity to the King's Lake hatchery strain could be a function of the historical connectivity between these areas as part of the Pend Oreille River drainage. Given, however, that the Salmo River watershed is at the lower end of the Pend Oreille drainage, it seems unlikely that the genetic similarity between Salmo River and King's Lake results from historical connectivity when many other systems closer to the King's Lake hatchery source populations in the Priest Lake drainage show no such affinity (Small and others, 2007, 2017). Introgression following known plantings of King's Lake hatchery fish in and around the Salmo River seems a more plausible scenario for the observed genetic structure of Salmo River fish.

Acoustic telemetry in Boundary Reservoir indicates some tagged westslope cutthroat trout were entrained through the dam and moved downstream. It is not difficult to imagine this being the case prior to construction of Boundary Dam when fish could easily pass downstream over Metaline Falls and down through Z Canyon to access the Salmo River or other downstream destinations. Given historical records indicating that anadromous fishes were limited by the falls, any resident fish moving downstream would likely have been unable to return upstream and would have been forced to complete their life cycle downstream. Previous work on bull trout identified a genetic signal of such interactions, indicating that bull trout from upstream in the Pend Oreille River or Lake Pend Oreille may have contributed to populations in the Salmo River but not vice versa, at least historically (Dunham and others, 2014). Additionally, our analyses suggest that if fish were passed upstream from Boundary Dam it is clear that environmental conditions within Boundary Reservoir are not well-suited to support westslope cutthroat trout in the warmer months and it does not appear that fish in the reservoir have easy access to abundant colder thermal refugia within the system, based on the presence of natural movement barriers near the mouths of larger tributaries. In conclusion, the available evidence points to no strong evolutionary or ecological rationale for passing westslope cutthroat trout upstream from Boundary Dam.

Mountain Whitefish

Although less is known about mountain whitefish, relative to westslope cutthroat trout, existing evidence available within Boundary Reservoir and its tributaries, as well as information from within and outside of the Pend Oreille River indicate little support for passing fish upstream over Boundary Dam. In contrast to westslope cutthroat trout and bull trout (Dunham and others, 2014), mountain whitefish within the Pend Oreille River exhibit little population structure, indicating widespread historical gene flow across the upper Columbia River downstream from Lake Pend Oreille, although populations do show structuring at a broader regional extent (Whiteley and others, 2006). A notable exception is the uniqueness of mountain whitefish in Sullivan Lake, which is consistent with the potential existence of a barrier to upstream movement in the lower reaches of this system (fig. 6). Additional spatial sampling and consideration of a larger diversity of molecular markers could potentially resolve additional genetic relationships for mountain whitefish within the Pend Oreille River and upper Columbia River basin and potentially shed more light on the importance of upstream connectivity to the Pend Oreille River and associated lakes (for example, Dupont and others, 2007). An ecological study of mountain whitefish within the Pend Oreille River and Sullivan Creek may reveal important spatial ecological processes that influence populations (possibly implied by patterns of genetic structure, fig. 8) within each of those systems and opportunities for restoration.

Overall Conclusions

Our review of the available evidence for westslope cutthroat trout and mountain whitefish aligns with the case for bull trout (Dunham and others, 2014, app. 1), with respect to the question of whether or not to provide passage of fish upstream over Boundary Dam. Although each species exhibits unique characteristics, current evidence indicates that moving fish upstream over Boundary Dam is not warranted if the management objective is to maintain natural patterns of evolutionary and ecological connectivity or to conserve unique ecological and evolutionary characteristics of extant local populations of these species in the system. There is little evidence of natural upstream connectivity due to the natural, pre-dam influences of barriers posed by Z Canyon and Metaline Falls. In the case of bull trout, moving fish upstream could have adverse consequences for population numbers in the Salmo River and gene flow between populations upstream and downstream from Metaline Falls. Such does not seem to be the case for westslope cutthroat trout, as there is no definitive evidence of native populations in the Salmo River. Additional work could, however, be done to verify that native populations are not present in headwater tributaries of the Salmo River. Even if such populations were discovered, it is not clear they were likely connected to populations upstream from Boundary Dam, as populations of bull trout have been historically.

Mountain whitefish exhibit much less spatial variability with respect to their distribution, which is confined to higher order (larger) streams, and local populations that are weakly differentiated relative to westslope cutthroat trout and bull trout (Whiteley and others 2004; Taylor and others, 2014). An exception is the presence of unique populations of westslope cutthroat trout and mountain whitefish in Sullivan Lake–the largest tributary to Boundary Reservoir. Again, however, the evidence for Sullivan Creek suggests these populations have not been influenced by connectivity with downstream populations.

Our focus in this report was on the role of Boundary Dam and the historical connectivity of the two species considering the upstream migration barriers of Z Canyon and Metaline Falls in the Pend Oreille River. It is important to recognize, however, that we did not consider connectivity farther upstream in the Pend Oreille River such as Box Canyon Reservoir reaches and the associated systems of Priest Lake and Lake Pend Oreille. This could be an important consideration, as the case for bull trout appears to indicate (app. 1). If connectivity for native fishes such as westslope cutthroat trout, mountain whitefish, and bull trout is a major objective within the Pend Oreille River, more work directed at better understanding connectivity in upstream reaches of the Pend Oreille River may be warranted.

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Appendix 1. Summary and Update on Connectivity for Bull Trout (*Salvelinus confluentus*) in the Pend Oreille River since Dunham and Others (2014)

The dynamic historical and contemporary processes and features within Lake Pend Oreille and the Pend Oreille River have likely influenced evolutionary and ecological connectivity for native coldwater fishes in the system. Of the native fishes present within Lake Pend Oreille and the Pend Oreille River, bull trout (*Salvelinus confluentus*) is likely the most sensitive to changes wrought by humans on the system, including potential hydrologic changes associated with a warming climate (Wenger and others, 2011; Isaak and others, 2015). Prior to contemporary human influences on the system, bull trout likely moved widely throughout the Clark Fork River, Lake Pend Oreille, and the Pend Oreille River. Although upstream passage was almost certainly blocked at Z Canyon and Metaline Falls on the lower Pend Oreille River, downstream movement of bull trout likely contributed to populations below these barriers (DuPont and others, 2007; Dunham and others, 2014).

Genetic evidence indicates this is particularly important for downstream populations of bull trout in the Salmo River (Dunham and others, 2014). In fact, human-assisted movement upstream of these barriers could pose threats to downstream populations of bull trout, and would not be consistent with the natural, historical pattern of movement and gene flow in the system. Although no tributaries to the Pend Oreille River from the Priest River downstream to the Salmo River are known to support self-reproducing populations of bull trout, recent modeling of a potential reintroduction suggest that certain tributaries (for example Sullivan Creek and Sullivan Lake) could potentially support local populations if a reintroduction was implemented (Benjamin and others, 2019; Mims and others, 2019). Both of these studies pointed to the importance of maintaining downstream passage into the Pend Oreille River, as well as maintaining connectivity within tributaries where spawning and early rearing of bull trout can be supported.

The case of the Pend Oreille River contrasts with the major inflow to Lake Pend Oreille, the Clark Fork River. In the Clark Fork River, upstream connectivity has been a management priority. In that system, bull trout arriving at the base of Cabinet Gorge Dam upstream of Lake Pend Oreille are transported to upstream populations if they are genetically identified as originating from upstream (Neraas and Spruell, 2001; Epifanio and others, 2003; DeHaan and others, 2011). This program has been effective in connecting individuals to their natal streams in the absence of their ability to naturally migrate upstream (DeHaan and Bernall, 2013). Similar success has been reported for other migratory salmonids (for example, Lusardi and Moyle, 2017).

Existing evidence for the Clark Fork and Pend Oreille Rivers, as well as smaller tributaries (Spruell and others, 1999) to Lake Pend Oreille, suggests that Lake Pend Oreille acts as a major source of bull trout moving in and out of these systems. Evidence also supports a similar dynamic for Priest Lake and Priest River, the largest tributary to the Pend Oreille River upstream of the historical upstream passage barriers of Z Canyon and Metaline Falls. Notably, the movement of bull trout throughout the system influences patterns of genetic connectivity and potentially allows migratory bull trout to exploit spatial and seasonal variability in prey availability and availability of refuge from environmental extremes. It is noteworthy that the current angling record (19 kilograms [kg]) for bull trout was taken from Lake Pend Oreille in 1949. This record was established as the system was beginning to experience significant changes from introductions of a range of species intended to support sport fisheries, including kokanee (*O. nerka*), rainbow trout (*O. mykiss*), lake trout (*S. namaycush*), and Mysid shrimp (*Mysis* spp.) as forage (Vidergar, 2000). These species introductions have dramatically altered food webs within Lake Pend Oreille, and lake trout also prey on bull trout (Corsi and others, 2019; Dux and others, 2019). Despite these challenges to bull trout, Lake Pend Oreille still supports some of the most robust populations of the species within the Columbia Headwaters Recovery Unit recognized by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 2015).

In summary, it appears that Lake Pend Oreille, and to a lesser extent Priest Lake, serve as core habitat for adfluivial bull trout that move in and out of these lakes to areas upstream in the Clark Fork River and smaller tributaries, or downstream through the outlet of the Pend Oreille River, extending to the Salmo River, and possibly farther during historical times (Dunham and others, 2014). Connectivity for bull trout related to these systems, as well as patterns of connectivity within them, have shaped patterns of genetic variability with likely consequences for migratory bull trout to express diverse behaviors and exploit the wide range of conditions available in the system (for example, Benjamin and others, 2020).

For information about the research in this report, contact
Director, Forest and Rangeland Ecosystem Science Center
777 NW 9th Street, Suite 400
Corvallis, OR 97330
https://www.usgs.gov/centers/forest-and-rangeland-ecosystem-science-center

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