

THE MOVEMENTS AND DISTRIBUTION OF BULL TROUT (*Salvelinus
confluentus*) IN RESPONSE TO SOCKEYE SALMON (*Oncorhynchus nerka*)
MIGRATIONS IN THE CHILKO LAKE SYSTEM, BRITISH COLUMBIA

by

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THE MOVEMENTS AND DISTRIBUTION OF BULL TROUT (*Salvelinus confluentus*) IN RESPONSE TO SOCKEYE SALMON (*Oncorhynchus nerka*) MIGRATIONS IN THE CHILKO LAKE SYSTEM, BRITISH COLUMBIA

submitted by Adam Matthew Kanigan in partial fulfillment of the requirements for

the degree of Master of Science

in Forestry

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Abstract

The migrations of animals between discrete locations frequently generate a range of ecological side effects. While many of the consequences of migrations are well understood, migratory coupling – the movements of predators over large spatial scales in response to migrant prey – has received little attention. I sought to describe a potential occurrence of migratory coupling in the Chilko Lake system, British Columbia, where bull trout (*Salvelinus confluentus*) aggregate near the lake outlet during the annual migration of anadromous sockeye salmon smolts (*Oncorhynchus nerka*), presumably to consume migrant smolts. To characterize the influence of the smolt migration on the spatial distribution of bull trout, I surgically implanted acoustic transmitters into 20 bull trout and tracked their movements throughout the Chilko system for one year. Because bull trout generally become increasingly piscivorous with size and age, I also combined acoustic telemetry with age estimates and length measurements to determine whether bull trout size, age, or growth influences their behavioural response to the smolt migration. Bull trout travelled substantial distances and 47% returned to the lake outlet during the smolt migration in consecutive years, suggesting that a portion of the population may be responding to the migrant smolts. However, bull trout returned to the outlet up to three months prior to the arrival of smolts at the outlet, thus their spatial distribution may also be influenced by other factors such as site fidelity. Furthermore, if bull trout are responding to the smolt migration, it remains unclear whether they are anticipating the arrival of smolts at the lake outlet or are following the diffusion of smolts from the lake. There was no detectable difference in age, size, or growth ratio among bull trout that returned to the outlet in consecutive years and those that did not; however, my inability to detect a difference may be a result of my small sample size and narrow range of ages and sizes. Through collecting these data, I also provided the estimates of size-structure, age-structure, and spatial distribution for Chilko bull trout, which has been identified as critical information for the management of bull trout in BC.

Lay Summary

The annual outmigration of juvenile sockeye salmon (*Oncorhynchus nerka*) from Chilko Lake, British Columbia, represents a substantial feeding opportunity for bull trout (*Salvelinus confluentus*), which regularly aggregate near the lake outlet during the salmon outmigration. However, the influence of the sockeye salmon outmigration on the seasonal movements of bull trout is poorly understood. I captured bull trout in the Chilko River, tagged them with acoustic transmitters, and tracked their movements for one year, and I determined that bull trout are capable of moving over large distances. However, whether their movements to the lake outlet are in response to the sockeye salmon outmigration remain unclear, as bull trout displayed high fidelity to the outlet throughout the year. I also characterized the spatial distribution, age-structure, and size-structure for bull trout in the Chilko system, all of which has been identified as critical information for bull trout management in BC.

Preface

This research was conducted in collaboration with the BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development. I held primary responsibility for the study design, the collection and analysis of the data, and for the preparation of the manuscript for submission. I received supervision and guidance from my supervisor, Dr. Scott Hinch, and from my supervisory committee member, Dr. Nathan Furey. I also received support from Lee Williston, Rob Dolighan, and Greg Andrusak at the BC Ministry of Forests, Lands and Natural Resource Operations, who assisted with the deployment and retrieval of acoustic telemetry receivers in Chilko Lake, and with tagging bull trout in the lake. The analysis of bull trout pelvic fin rays for age estimation was conducted by North/South Consultants Inc. (Winnipeg, Manitoba, Canada). I received logistical support from the Chilko Lake field camp (Fisheries and Oceans Canada), and from the Xeni Gwet'in First Nation and the Tsilhqot'in National Government. A version of this thesis will be submitted for publication in September 2019 as "The movements and distribution of bull trout (*Salvelinus confluentus*) in response to sockeye salmon (*Oncorhynchus nerka*) migrations." (Authors: Adam M. Kanigan, Scott. G. Hinch, Nathan B. Furey, Lee Williston, Rob Dolighan, and Andrew G. Lotto.). This study was conducted and written by AMK with assistance from LW, RD, and AGL, under the supervision and guidance of SGH and NBF who helped with the conceptualization of the study and the preparation of the manuscript. All capture, tagging and handling procedures were approved by the University of British Columbia Animal Ethics Committee (animal care permit: A11-0125) in accordance with the Canadian Council of Animal Care

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Introduction

Animal migration – defined as the predictable, directional and persistent movement of an organism between two (or more) locations (Dingle and Drake 2007) – is a ubiquitous phenomenon that is exhibited by every major taxon over a broad range of spatial and temporal scales (Chapman et al. 2014; Dingle 2014). Migration is an adaptive behavioural response to ecological and biogeographic factors such as spatiotemporal variability of resources, habitats, competitors, and predators (Alerstam et al. 2003), and it evolves mainly as a strategy through which individuals can maximize their survival and reproductive success (Åkeson and Hedensröm 2007). The migrations of large numbers of organisms may also generate a range of ecological consequences that can greatly influence recipient ecosystems (Bowlin et al. 2010; Furey et al. 2018). Upon arrival at destination habitats, migrants may deposit energy and nutrients in the form of waste (e.g., feces), reproductive material (e.g., eggs), carcasses (i.e., of the migrants), or sessile organisms from resident habitats or stopover sites, which can potentially spread throughout entire ecological communities (Bauer and Hoyer 2014). For instance, migratory ungulates such as white-tailed deer (*Odocoileus virginianus* Zimm.) may transport seeds tens of kilometers between resident and destination habitats, potentially contributing to the colonization of unoccupied areas (Vellend et al. 2003). Migrating adult anadromous and semelparous Pacific salmon (*Oncorhynchus* spp.) transport substantial quantities of marine-derived nutrients to the freshwater streams where they spawn and die (Moore and Schindler 2004), and the nutrients derived from their carcasses provide a substantial resource subsidy to various species within coastal

ecosystems (Naiman et al. 2002). Furthermore, the long distances that migrants travel, as well as the diverse habitats and species assemblages they encounter, can have far reaching implications for the spread of pathogens (Altizer et al. 2011). One of the most prominent examples of this phenomenon is the annual congregation of millions of migratory birds such as sanderlings (*Calidris alba*), ruddy turnstones (*Arenaria interpres*), and red knots (*Calidris canutus*) in Delaware Bay, northeast U.S.A., which creates a global hotspot for avian influenza virus (Altizer et al. 2011). Despite the breadth of research that has investigated the ecological consequences of animal migrations on recipient ecosystems, the effects of migrations on the behaviour of species at alternate trophic levels has received little attention.

Migratory coupling

Recently, Furey et al. (2018) introduced the concept of migratory coupling, whereby predators engage in large-scale movements that extend beyond their home ranges in response to feeding opportunities provided by migrant prey. Migratory coupling can occur across taxa and can substantially impact ecological food webs as predators redistribute across space to exploit migrant prey. Furey et al. (2018) hypothesized that migratory coupling may induce seasonal trophic cascades through which predation could influence community structure by mediating the impacts of a local consumer. Other associated consequences may include reduced consumptive pressure on resident prey as predators vacate resident habitats, temporary competitive release for a predator that remains in the resident habitat, or seasonal competition between predators that participate in migratory coupling and those that are resident to the destination habitat (Furey et al.

2018). Conversely, by introducing predators that are capable of exploiting seasonally-abundant prey pulses, migratory coupling may act to stabilize food webs by moderating the effects of abundant prey on recipient communities (McCann et al. 2005; Furey et al. 2018).

The potential impacts of migratory coupling should be of particular interest given that both predators and migrant species have experienced large-scale declines in recent decades (Wilcove and Wikelski 2008; Estes et al. 2011; Ripple et al. 2014). Therefore, researchers and resource managers need to identify potential occurrences of migratory coupling and should investigate its potential impacts at the individual-, population-, and community-levels. In North America, the migrations of Pacific salmon (*Oncorhynchus* spp.) and the movements they elicit by predators provide an excellent opportunity to study interspecific interactions within the migratory coupling framework.

Pacific salmon and migratory coupling

The spawning migrations of Pacific salmon provide substantial, and often critical, feeding opportunities to predators at higher trophic levels (Denton et al. 2009; Armstrong and Bond 2013). Terrestrial, avian, and aquatic predators will often aggregate near salmon migration routes and spawning grounds to consume actively migrating salmon, the carcasses of deceased salmon, and the eggs that are deposited during spawning (Weng et al. 2008; Shardlow and Hyatt 2013; Levi et al. 2015). Consumers (i.e., predators and scavengers) can travel considerable distances to exploit the ephemeral resource pulses provided by salmon (Gende et al. 2002; Schindler et al. 2003; Levi et al. 2015). For example, brown bears (*Ursus arctos*) will travel tens of kilometers to exploit

spawning salmon (Glenn and Miller 1980) while bald eagles (*Haliaeetus leucocephalus*) can travel hundreds of kilometers (Wheat et al. 2017) to reach salmon spawning grounds (Elliot et al. 2011; Levi et al. 2015). The outmigration of juvenile Pacific salmon from freshwater rivers and lakes to the ocean can also provide predators with important feeding opportunities. For example, rhinoceros auklets (*Cerorhinca monocerata*) will often consume substantial numbers of juvenile salmon during the early marine phase of their migration (Tucker et al. 2016), and predation by western gulls (*Larus occidentalis*) on juvenile salmon in California catchments has been estimated to cause population declines of up to 30% (Osterback et al. 2013). Similarly, northern pikeminnow (*Ptychocheilus oregonensis*), walleye (*Stizostedion vitreum*), and smallmouth bass (*Micropterus dolomieu*) frequently congregate near hydroelectric dams in the Columbia and Snake Rivers, northwest U.S.A., to feed on migrating juvenile salmon, and the population-level impacts of this predation can be quite significant (Rieman et al. 1991; Beamesderfer et al. 1996; Shively et al. 1996). More recently, predation on juvenile sockeye salmon (*Oncorhynchus nerka*) has been investigated in the Chilko Lake system, British Columbia, Canada.

Chilko Lake sockeye salmon

The Chilko Lake sockeye salmon population is one of the largest in the Fraser River watershed. Each year during the smolt life stage, 10 - 70 million juvenile sockeye salmon migrate from the lake beginning in mid-April and continue to migrate from the lake for 4 - 6 weeks. As an important indicator stock for the management of sockeye salmon in British Columbia (Cass 1989; Irvine and Akenhead 2013), Chilko Lake

sockeye salmon have been intensively studied (Hinch et al. 2006) with recent research investigating the factors that influence the survival of smolts during their migration. For example, Clark et al. (2016) utilized acoustic telemetry to track the first 1,044 km of the smolt migration from Chilko Lake (2010 - 2013; $n > 1800$) and found that smolts exhibited poor survival (57% - 78%) while migrating through the shallow and clear waters of the Chilko and Chilcotin Rivers (80 km). Stevenson et al. (2019) also used acoustic telemetry to track the migratory fate of sockeye salmon smolts (2016; $n = 300$) from Chilko Lake and found similar results, with estimates of survival ranging from 53% - 76% through the first 14 km of the Chilko River. Clark et al. (2016) hypothesized that predation by piscivorous fishes, birds, and mammals was a likely cause of such high levels of smolt mortality during the early migration, as predators such as bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), mergansers (*Mergus* spp.), gulls (*Larus* and *Chroicocephalus* spp.), and river otters (*Lontra canadensis*) can be seen near the lake outlet and along the Chilko River during the smolt outmigration. In fact, resident bull trout – a large piscivorous salmonid – will often aggregate near the spatially-constricted outlet of Chilko Lake during the sockeye salmon smolt outmigration. This behaviour was confirmed by Furey and Hinch (2017) who used acoustic telemetry to track the seasonal movements of adult bull trout in the Chilko Lake outlet (2014 - 2015) and found that bull trout activity and residency in the outlet was greatest during the smolt outmigration, and that 40% of acoustic-tagged bull trout returned to the outlet during the smolt outmigration in consecutive years. Furthermore, bull trout that were captured at the Chilko Lake outlet during the smolt outmigration in 2013 and 2014 were found to be feeding nearly exclusively on sockeye salmon smolts,

and many bull trout frequently exhibited binge-feeding (i.e., feeding beyond the daily sustainable maximum) (Furey et al. 2015).

Together, Furey et al. (2015) and Furey and Hinch (2017) identified a previously unrecognized relationship between sockeye salmon smolts and resident bull trout, whereby the seasonal movements of bull trout seem to be influenced by the feeding opportunities provided by migrant smolts. However, it is not yet known whether the bull trout that aggregate near the Chilko Lake outlet during the smolt outmigration are moving over large spatial scales to exploit the migrant sockeye salmon. If they are, in fact, traveling over large distances in response to the smolt outmigration, this predator-prey interaction may constitute migratory coupling.

Bull trout ecology and conservation status

The bull trout is a species of char that is endemic to western Canada and the U.S. Pacific Northwest, with the majority of its range located in British Columbia (Haas and McPhail 1991). Bull trout reside in lakes, rivers, and streams, but generally have more specific habitat requirements than other salmonids (Rieman and McIntyre 1993) as they require adequate channel and hydraulic stability, the presence of migration corridors, and clean, well-oxygenated water within a temperature range of 5 °C and 9 °C for spawning and below 15 °C for summer rearing (McPhail and Baxter 1996; Selong et al. 2001). Unfortunately, the collective effects of habitat degradation and fragmentation of migration corridors (Rieman et al. 1997; Ripley et al. 2005), overfishing (Post et al. 2003), the introduction of non-native fishes (Leary et al. 1993), and poor water quality (Kiser et al. 2010) coupled with the species' late reproductive maturity (Dunham et al.

2008) have caused substantial declines in the abundance and distribution of certain bull trout populations. However, while an assessment by the Committee on the Status of Endangered Wildlife in Canada determined that many populations in British Columbia are of “Special Concern”, populations in the Pacific region of the province – which includes bull trout in the Chilko system – were assessed as “Not at Risk” (COSEWIC 2012). Nonetheless, concern for the conservation of bull trout throughout the province led to the development of a British Columbia Provincial Bull Trout Management Plan (Pollard et al. 2015), a BC Provincial Assessment of Bull Trout Populations (Hagen and Decker 2011), and a Bull Trout Management Plan for the Middle and Upper Fraser River watershed (Hagen et al. 2017). Collectively, these reports identified a glaring lack of data for many of the bull trout populations in BC (Pollard et al. 2015). In the Chilcotin region of the province, the majority of bull trout monitoring that has been done has focused on populations from Chilko Lake (R. Dolighan, Ministry of Environment, personal communication); however, despite over a decade of monitoring there is still a paucity of information regarding the spatial distribution, size structure, and age structure for bull trout in the Chilko system. To achieve bull trout management objectives, a thorough understanding of the species’ often complex life history is required (Rieman and McIntyre 1993).

In general, bull trout exhibit one of three life history forms: stream resident, fluvial (i.e., those that reside in rivers as adults and migrate to tributaries to spawn), and adfluvial (i.e., those that reside in lakes as adults and migrate to tributaries to spawn) (Dunham et al. 2008; Paragamian and Walters 2011); it is possible for multiple forms to coexist within a single population (Nelson et al. 2002; Homel and Budy 2008). Bull trout

are iteroparous (i.e., they are capable of spawning more than once in their lifetime), and the spawning migrations of fluvial and adfluvial bull trout can vary substantially from ly short movements to nearby tributaries (McPhail and Murray 1979) to large-scale movements that can exceed 250 km (McLeod and Clayton 1997; Pillipow and Williamson 2004). Bull trout spawning generally occurs between mid-August and late October (McPhail and Baxter 1996); however, spawning migrations that are particularly long or difficult may be initiated as early as May (Hagen 2003). In addition to spawning opportunities, other factors may provoke bull trout migrations, including better-quality feeding opportunities (e.g., Furey and Hinch 2017).

Bull trout consume a range of prey species depending on their developmental stage and life history form. They have diverse diets, varying from invertebrates to fish (including cannibalism) (Boag 1987; Beauchamp and Van Tassel 2001), and will opportunistically consume the eggs of other fishes (e.g., Lowery and Beauchamp 2015). However, bull trout tend to become increasingly piscivorous as they become larger (and possibly older) (Beauchamp and Van Tassel 2001), which results in an increased rate of somatic growth (Juanes and Conover 1994; Olson 1996) due to the high energy content prey fish provide (Forseth and Jonsson 1994). Thus, an ontogenetic shift to piscivory may lead to behavioural differences among age- and size-classes in response to a feeding opportunity. Still, the majority of current literature on bull trout movements has focused primarily on spawning migrations (e.g., Swanberg 1997; Bahr and Shrimpton 2004; Muhlfeld and Marotz 2005), while the influence of feeding opportunities and age or size on movements across large spatial scales has not received significant attention.

Thesis overview and research objectives

My thesis examines the influence of the migration of Chilko Lake sockeye salmon smolts on the behaviour of bull trout in the context of migratory coupling. My main objective is to use acoustic telemetry to track the movements of bull trout throughout Chilko Lake and the surrounding region (including the Chilko and Chilcotin Rivers) and to determine whether they are moving over broad spatial scales in response to the migration of sockeye salmon smolts from Chilko Lake. I also combine acoustic telemetry data with length measurements for individual bull trout, and with non-lethal pelvic fin biopsies and age estimation techniques to investigate whether bull trout size or age influences their behavioural response to migrant sockeye salmon smolts. I also examine whether fish that are faster-growing relative to the population mean respond differently to the smolt outmigration than fish that are slower-growing. Piscivorous fish typically grow more quickly than those that feed on invertebrates (Forseth and Jonsson 1994), and earlier studies have shown that growth rate may influence piscivory in other species of freshwater fishes (e.g., Jonsson et al. 1999). Specifically, I examine seasonal changes in the spatial distribution, displacement, rates of movement, and direction of movement for individual bull trout and among age- and size-classes, which I compare to the timing of the sockeye salmon smolt migration to answer the following questions:

- 1) Are bull trout moving over large spatial scales in response to the smolt migration?
- 2) If bull trout are responding to the smolt migration, do they anticipate the arrival of smolts at the outlet of Chilko Lake or do they follow the diffusion of smolts out of the lake?

3) Do larger, older, or faster-growing bull trout exhibit a stronger behavioural response to the migrant smolts than smaller, younger, or slower-growing individuals?

I predict that bull trout will display directed movements over large spatial scales in anticipation of the outmigration of sockeye salmon smolts, which I characterize as arrival at the lake outlet prior to the arrival of sockeye salmon smolts, movements that are primarily directed towards the lake outlet, and transit speeds that are greater than what a sockeye salmon smolt could swim. I also predict that the migrant smolts will elicit a stronger behavioural response from larger, older, and faster-growing bull trout than their smaller, younger, and slower-growing conspecifics, such that larger, older, and faster-growing fish will return to the outlet in successive years at higher rates than smaller, younger, and slower-growing fish.

Through investigating these questions, I also characterize patterns of seasonal distribution, size structure, and age structure for bull trout in the Chilko Lake system, none of which has previously been documented. In doing so, I provide critical information for the management and conservation of bull trout in the Chilcotin region of BC.

Methods

Study system

Chilko Lake is a large oligotrophic lake located in the eastern Chilcotin region of British Columbia, Canada (Figure 1). The main body of the lake is 65 km long, averages 3 km in width, and has a maximum depth of 339 m (Desloges and Gilbert 1998). The outlet of the lake is located at its north end (51.61583°N, 124.1517°W) where it drains into the Chilko River (Figure 1). The Chilko River flows northeast from Chilko Lake for 75 km to its confluence with the Chilcotin River, and its main tributary is the Taseko River (Figure 1). From its confluence with the Chilko River, the Chilcotin River flows southeast for approximately 105 km to its confluence with the Fraser River (Figure 1).

Bull trout sampling and acoustic tagging

Between 24 April and 12 May 2017 and between 20 April and 02 August 2018, a total of 200 adult bull trout were captured via angling from Chilko Lake, the Chilko Lake outlet, and the Chilko River (Figure 1). Prior to sampling, individual bull trout were placed in a 50 L cooler that contained aerated river water and an anaesthetic of clove oil emulsified in 95% ethanol (0.5 ml/L; 1-part clove oil to 9-parts ethanol; Gutowsky et al. 2013; Thorley and Andrusak 2017) where they remained for approximately 2 minutes. Following complete anesthetization (characterized as a complete loss of equilibrium and a lack of response to squeezing the caudle peduncle [Gutowsky et al. 2013]) bull trout were weighed to the nearest tenth of a kilogram (kg) and were placed inverted in a V-

shaped sampling trough where they were measured for total length (TL) to the nearest tenth of a centimeter (cm). During sampling, bull trout received a constant supply of recycled aerated river water from a 100 L cooler via a submersible bilge pump (2,271 liters per hour; Shoreline Marine). The water in the 100 L cooler was frequently replaced to ensure that it did not become too warm.

During sampling, non-lethal pelvic fin ray samples were collected for age estimation from a subset of all individuals ($n = 166$), as previous work has identified fin rays as adequate structures for estimating the age of bull trout (Zymonas and McMahon 2009; Erhardt and Scarnecchia 2013). Using steel end-cutting pliers with a 12 mm cutting edge, the leading two rays were excised from one pelvic fin near the base and placed into coin envelopes to dry. Zymonas and McMahon (2006) found that this fin biopsy procedure had negligible effects on the growth and survival of sampled individuals.

Of the bull trout captured in 2017, twenty were surgically implanted with a V-13 acoustic transmitter (36.0 mm length, 13.0 mm diameter, 11.0 g weight in air, randomized nominal delay of between 30 and 60 seconds, and an estimated tag life of 800 days; VEMCO, Amirix Systems, Bedford, NS). Fifteen bull trout were tagged near the outlet of Chilko Lake while five individuals were tagged at various locations throughout the first 13 km of the Chilko River downstream from Chilko Lake (Figure 1). While individuals were inverted in the sampling trough, a small incision (~ 30 mm in length) was made a few centimeters off the midventral line between the pectoral and pelvic fins, through which a coded acoustic transmitter was inserted into the body cavity. Incisions were closed using two interrupted absorbable monofilament sutures (Ethicon size 0 violet monofilament suture with a 26-mm reverse cutting needle). Tag burden (i.e.,

the percent ratio of transmitter weight to body weight) ranged from 0.3% to 0.7% (mean = 0.52% [$\pm 0.11\%$ SD]), which is much lower than the commonly cited rule that cautions against implantation of transmitters that represent burdens greater than 2% (Winter 1996). Prior to release, all bull trout were tagged near the dorsal fin with an external “T-bar” high-reward tag (FD-94 Anchor Tags, Floy Tag and Manufacturing Inc., Seattle, WA). These tags were deployed as part of a concurrent bull trout exploitation study and offered anglers a reward if a tagged bull trout was reported. The reporting of a tagged individual also let me know whether an acoustic-tagged bull trout was harvested. Sampling and surgery instruments were disinfected in 95% ethyl alcohol for 15 minutes between each bull trout. Surgeries and sampling procedures lasted between 2 and 23 minutes per fish (mean = 8.1 minutes [± 3.9 minutes SD]).

Acoustic receiver deployments

In April 2017, twenty-two omnidirectional VR2W acoustic receivers (69 kHz; VEMCO, Amirix Systems, Bedford, NS) were deployed in Chilko Lake, the Chilko River, and the Chilcotin River to track the in-situ movements of bull trout (Figure 1). Thirteen receivers were placed throughout the lake at locations that were believed to be near important bull trout spawning tributaries (R. Dolighan, Ministry of Environment, personal communication) or in areas where the lake narrowed to maximize receiver coverage across the width of the lake. The remaining nine receivers were placed at locations throughout the Chilko and Chilcotin rivers where aggregations of bull trout have previously been observed or near the junction of major tributaries (i.e., the Chilko-

Taseko confluence and the Chilko-Chilcotin confluence) so that individuals entering or leaving the system may be identified.

Preparation of telemetry data

Detection data were downloaded from acoustic VR2W receivers in April and May of 2018 – one year after bull trout were tagged. In preparation for analyses, telemetry data were screened for false detections which can occur due to environmental conditions or collisions between acoustic tag transmissions. Screening for false detections followed the First Scan Acceptance criteria for the False Detection Analysis Tool from VUE software (Amirix Systems, Bedford, NS). Specifically, any detection of an individual transmitter that was not accompanied by a second detection for the same transmitter on the same receiver within 20 minutes (short interval) was flagged as questionable. Additionally, if within a given time frame a greater number of successive detections for the same transmitter on the same receiver were separated by more long intervals (5 hours) than short intervals (20 minutes), those detections were also flagged as questionable and removed from the data. This method of determining the presence of false detections is based on the average programmed delay of the transmitters and is sufficiently strict that no false detections are erroneously accepted. The screening process resulted in three false detections being removed. To account for the stress associated with surgical tagging, which can potentially temporarily affect fish behaviour (Rogers and White 2007), I also removed the first 48 hours of detections for each bull trout following surgical implantation of the acoustic transmitter. Following the detection screening process, 3,190 detections were removed from the data for a total of 527,838 detections.

Further data screening methods specific to each analysis are discussed in the corresponding methods sections.

Spatial distribution and activity space

One disadvantage to using passive acoustic telemetry to track the movements of tagged individuals is that it does not provide position estimates for the individuals being monitored. Instead, detections on an acoustic receiver simply report the presence of an acoustic-tagged animal that has entered the detection range of the receiver, as well as the date and time of the detection (Voegli et al. 2001). One way to overcome this limitation is to estimate short-term centres of activity (COA) for each acoustic-tagged individual following the methods described by Simpfendorfer et al. (2002). Short-term COAs are position estimates that are determined by calculating the weighted arithmetic means of the coordinates for the receiver(s) that detect a signal from an acoustic transmitter during a pre-determined period of time (Δt); it is assumed that the probability that a transmitter signal will be logged by a receiver is proportional to the distance between the receiver and the transmitter (Simpfendorfer et al. 2002). As described by Simpfendorfer et al. (2002), COA estimates for an individual are more accurate when a greater number of telemetry receivers record detections during Δt and when a greater number of transmitter receptions for an individual are recorded during Δt ; however, a Δt interval that is too long will fail to produce a COA estimate that is representative of an individual's actual activity center. To allow for more detailed analysis of the telemetry data, I estimated COAs for each individual at a Δt of 5 days. I chose a Δt interval of 5 days following visual inspection of frequency distributions for the total number of transmitter detections

and the number of unique receivers that logged detections during Δt intervals of 1, 2, 5, 7, and 10 days. COAs were estimated for each bull trout for as long as it continued to be detected.

To characterize the spatial distribution of acoustic-tagged bull trout, I examined the COA estimates for each individual at the seasonal level. The classification of the seasons that I examined included spring (April - June), summer (July - September), fall (October - December), and winter (January - March); these classifications correspond to biologically meaningful periods for bull trout (e.g., the fall is associated with bull trout spawning in lake and river tributaries [Dunham et al. 2008; Nitychoruk et al. 2013]), and are consistent with other studies of bull trout space use (e.g., Gutowsky et al. 2016). Using the COA estimates, I calculated seasonal utilization distributions for each individual. Utilization distributions are probability densities that define an animal's activity space based on relocations (Fieberg and Kochanny 2005). As recommended by Börger et al. (2006), I estimated utilization distributions at the 50% and 90% levels, which represented the seasonal core-use area and home range for each fish, respectively. Estimates of activity space were calculated using the lattice-based approach of Barry and McIntyre (2011), which is based on an approximation to Brownian motion whereby random walks originating from each position estimate (i.e., COA) are restrained to a geographic boundary. Although this method is not as common as others for estimating animal space use (e.g., minimum convex polygons, local convex hulls, or kernel-based methods), it is particularly useful when the movements of tagged animals are restricted by boundaries or when obstructions to movement need to be accounted for. In contrast, more prevalent methods (e.g., kernel utilization distribution; Worton 1989) estimate

utilization distributions in unconstrained space and often fail to account for areas where tagged individuals cannot enter. Consequently, it is common for estimates of animal activity space to extend into areas that should have zero density (e.g., terrestrial areas) when these more traditional methods are applied to telemetry studies of freshwater fish.

The lattice density approach to estimating activity space uses a neighbour relationship whereby a grid of evenly spaced nodes is superimposed over the study area; each node is connected to adjacent nodes in the orthogonal and diagonal directions to create a spatial lattice. Animal density is then estimated using a random walk process where the smoothness of the density estimate is controlled by the length of the random walk, k , and the probability that the random walk remains at a given node, M . Specifically, activity space is estimated as the probability density of the length- k random walk on the lattice, such that when $k = 0$ the probability density is equal to the original animal locations. As the length of k increases, the probability density diffuses to neighboring nodes. I used cross-validation to estimate k , which is analogous to estimating the bandwidth smoothing parameter of kernel-based methods (e.g., Worton 1989). The spacing between nodes in the spatial lattice is user-defined and is a trade-off between computational efficiency and the ability for the lattice to fit complex boundaries (Barry and McIntyre 2011). I chose a node spacing of 200 m for my analyses, which is analogous to estimating bull trout density within 200 m grid cells, as it was sufficient for delineating the complex boundaries of Chilko Lake and the Chilko and Chilcotin Rivers. Finally, I used bull trout COAs to approximate M , the probability that a random walk remains within in the same 200 m grid cell in each time interval. Similar to Citta et al. (2015), I calculated the value of M for each season as the proportion of COA locations

that remained in the same grid cell in sequential 5-day intervals (Δt). I used the *latticeDensity* package (Barry and McIntyre 2011) in R 3.5.2 (R Core Team 2018) to estimate the smoothing parameter, k , via cross-validation and to estimate seasonal activity space for each acoustic-tagged bull trout.

Estimates of activity space were also used to determine the percent overlap between individual core-use areas (50% lattice density) and home ranges (90% lattice density) for each season. Given that activity space was estimated using the same grid of nodes for all individuals, I defined the percent by which each individual's activity space was overlapped by every other bull trout as the proportion of nodes in the activity space of one individual that were also present in the activity space of a different individual.

Horizontal movement

To assess the scale of horizontal movements by bull trout, I calculated the minimum total displacement, the maximum one-way displacement, the mean distance from the lake outlet by month, the rate of movement between sequential detections, and the direction of movement between sequential detections for each acoustic-tagged individual. Prior to analyzing bull trout movements, acoustic receiver files were filtered to remove any instances where the same individual was detected on multiple receivers within fewer than 30 seconds. This step ensured that any duplicated detections of individuals in areas where receiver detection ranges likely overlapped would not be interpreted as movements between receivers, and a minimum threshold of 30 seconds was chosen as it was the minimum transmission frequency for the V13 transmitters used in this study. For all calculations of distance between relocations, I also subtracted the

detection range for the VR2W acoustic receivers. I assumed that each receiver had a detection radius of 540 m which I calculated using VEMCO's range calculator tool. This detection range was also comparable to the ranges reported for similar acoustic telemetry studies (e.g., Gutowsky et al. 2016).

Total displacement and one-way displacement –To determine whether bull trout moved across large spatial scales, I calculated the cumulative least-cost distance between the release location for each individual and sequential receiver detections, and I also calculated the least-cost distance from the release location of each individual to the furthest receiver on which it was detected (i.e., maximum one-way displacement). Least-cost distance was calculated by first superimposing a transition matrix over the study area. A transition matrix is essentially a grid of nodes that are each assigned a weight based on conductance (i.e., ease of movement), and the least cost path between relocations (i.e., receiver detections) was defined as the shortest node-to-node path, taking into account any obstacles to movement. I assigned any node that was within the boundaries of Chilko Lake or the Chilko and Chilcotin Rivers a conductance weight of 1 and any node that was beyond the boundaries of the lake or rivers received a conductance weight of 0, such that only nodes with a weight of 1 could be included in the calculation of least-cost distance. The spacing between nodes was set at 10 m, which was done to allow for node connections in spatially-constricted areas such as the Chilko Lake outlet, and nodes could be connected to any one of their eight orthogonal and diagonal nearest neighbours during the creation of the least-cost path. Because this method does not account for tortuous movements between relocations, the cumulative least-cost distances between release locations and sequential detections should be considered minimum

estimates of displacement. The least-cost distance between sequential receiver detections was determined using the *gdistance* package (van Etten 2011) in R 3.5.2 (R Core Team 2018).

Mean distance from the lake outlet – One of my approaches for describing the spatial distribution of bull trout in response to the migration of sockeye salmon smolts was to calculate the mean least-cost distance of each individual to the Chilko Lake outlet by month. I chose to calculate mean distance to the lake outlet by month rather than by season because I was also interested in approximating the timing of arrival for any individuals that were detected at the lake outlet in the spring of 2018. Using the same transition matrix as was used to determine the least-cost distances between sequential relocations of individuals, I calculated the least-cost distance between each individual's COAs and a fixed location at the lake outlet (51.61583°N, 124.1517°W) (Figure 1), which I then averaged by month. The least-cost distance between COA locations and the lake outlet was determined using the *gdistance* package (van Etten 2011) in R 3.5.2 (R Core Team 2018).

Rate and direction of movement – One of the primary objectives of my thesis was to determine whether bull trout that aggregate near the outlet of Chilko Lake during the outmigration of sockeye salmon smolts are anticipating the arrival of smolts at the lake outlet (i.e., they are displaying a learned behaviour) or whether they are simply following the diffusion of smolts out of the lake. To achieve this objective, I first determined the direction and rate of movement between sequential detections for each individual that was detected at the lake outlet during the smolt migration in 2018 ($n = 7$). The direction between successive detections was defined as the bearing from one receiver to the next,

and movement rates were calculated as the least-cost distance (converted to mm) between the receivers on which the individual was detected divided by the number of seconds between successive detections. The least-cost distances between receivers were calculated using the same transition matrix that was used to calculate total displacement. Movement rates between detections were grouped by month and compared to a hypothesized average transit speed for Chilko Lake sockeye salmon smolts to determine whether bull trout were moving at rates that were significantly faster than what could be attained by migrant smolts. This was done on the basis that if bull trout are making directed movements towards the lake outlet in anticipation of the smolt migration, they are likely moving at rates that are much faster than what a smolt can swim, and their movements are likely directed towards the north end of the lake. In contrast, if bull trout are following the diffusion of smolts out of the lake it is likely that they are not swimming much faster than what the average smolt can swim. I assumed that the average transit speed for Chilko Lake sockeye salmon smolts was 1.25 body lengths per second, which was estimated using transit speeds for Chilko Lake sockeye salmon smolts that were tracked via acoustic telemetry through the Strait of Georgia (Clark et al. 2016; Stevenson et al. 2019), and is comparable to the range of optimal transit speeds for sockeye salmon smolts (Hinch et al. 2006). I then calculated a mean body length of 84 mm from a random sample of sockeye salmon smolts from the 2018 Chilko Lake outmigration (S. Decker, Fisheries and Oceans Canada, personal communication). Given these estimates, I hypothesized that sockeye salmon smolts migrated through Chilko Lake at a mean transit speed of 105 mm/s ($1.25 \text{ body lengths per second} \times 84 \text{ mm}$). For each month of tracking, I tested whether the mean rate of movement for bull trout was

significantly greater than the hypothesized mean transit speed for sockeye salmon smolts using weighted one-sided one-sample t-tests. I chose to use weighted t-tests to account for any potential bias due to some individuals having more estimates of rate in a given month than other individuals. Therefore, for each month (i.e., for each t-test) I weighted each observation such that the total weight of each individual's rate estimates in the t-test summed to 1. Prior to performing analyses, I filtered the data to remove any sequential detections of the same individual that were separated by an interval of greater than 7 days. This was done to limit the influence of tortuous movements or lengthy intervals between detections, which could decrease the accuracy of movement rate estimates. Given that I was mainly interested in movements in the north and south directions, I also filtered any movements in the east or west directions from the data (i.e., any movement with a bearing between 62.0 ° and 118.0 ° inclusive or between 242.0 ° and 298.0 ° inclusive, respectively). Rate data were \log_{10} transformed so that the assumption of normality would be met, and the hypothesized mean smolt transit speed was also \log_{10} transformed. Statistical analyses were completed with R 3.5.2 (R Core Team 2018), and assumptions (including normality and variances) were visually assessed. Statistical significance was set at $\alpha = 0.05$.

Age and growth

The use of pelvic fin rays for determining the age of bull trout has been identified as a more accurate and precise option than the use of scales and is a suitable non-lethal alternative to using otoliths (Zymonas and McMahon 2009). Pelvic fin rays were used to estimate the ages of individual bull trout ($n = 166$) following the general procedures

outlined by Zymonas and McMahon (2009). Dried samples were first trimmed, dipped in an epoxy resin (Cold Cure, System Three Resins), and allowed to harden for 48 hours. Two cross sections (0.50 - 0.75 mm thickness) were then cut from each fin ray using a low speed sectioning saw (Struers Minitom, Struers Ltd.) and permanently mounted to a glass microscope slide using Cytoseal-60 (Thermo Fisher Scientific). The cross-sectioned fin rays were then viewed under a microscope with transmitted light to determine an estimate of age. Annual growth in fin rays can be identified as an adjacent pair of hyaline (translucent in transmitted light) and opaque bands, which are associated with slow growth during the winter and rapid growth during the summer, respectively (Chilton and Bilton 1986; DeVries and Frie 1996). Each hyaline band present in the cross-section represents one year of growth for the individual from which the sample was taken. Fin ray sample preparation and ageing were conducted by North/South consultants Inc., Winnipeg, Manitoba.

To estimate the ages of the individuals from which a fin ray sample was not taken ($n = 34$) I constructed an age-length key (ALK), which operates on the premise that there is generally a strong relationship between fish length and age (Ogle 2016). Thus, the age structure for a large sample of fish can be reliably estimated by summarizing the relationship between age and length for a subsample of aged fish (n) and then applying this summary to the entire sample of fish that have been measured for length (N). The first step in creating the ALK was to assign each bull trout to a length interval based on its TL measurement. Length intervals began at 40.0 cm, had an interval width of 5.0 cm, and were left-inclusive and right-exclusive, resulting in eight length intervals between 40.0 cm and 80.0 cm to which an individual could be assigned. A multinomial logistic

regression model was then used to model estimated age as a function of length interval for the aged subsample of bull trout using the *nnet* package (Venables and Ripley 2002) in R 3.5.2 (R Core Team 2018). From the fitted model, the probabilities that an individual fish was of a given age were predicted and the ALK was produced (Table A2). I then used a method described by Isermann and Knight (2005) to assign ages to individuals in the unaged subsample; the expected number of unaged individuals in the i^{th} length interval to be assigned the j^{th} age (N_{ij}^*) was computed as:

$$N_{ij}^* = N_i^* P_{j|i}$$

where N_i^* = the number of unaged individuals in each length interval and $P_{j|i}$ = the probability that an unaged individual from the i^{th} length interval is assigned to the j^{th} age class (i.e., the ALK probabilities). Ages were assigned to unaged bull trout according to the Isermann-Knight method using the *FSA* package (Ogle et al. 2018) in R 3.5.2 (R Core Team 2018).

I was also interested in comparing the age structure for my sample of bull trout to other bull trout populations, so I fit a von Bertalanffy growth function (VBGF) (von Bertalanffy 1938) to the age data for the full sample ($n = 200$). The VBGF is a non-linear function that assumes the rate of growth of an organism declines with increasing size, and it uses the known lengths and estimated ages of individuals to produce a model that allows for the prediction of an individual's age based on its known length. The common form of the VBGF is by far the most frequently used growth function in fisheries analyses (Haddon 2011), and it was first described by Beverton and Holt (1957) as:

$$E[L|t] = L_{\infty} (1 - e^{-k(t - t_0)})$$

where $E[L|t]$ = the mean length at age t , L_{∞} = the maximum mean length, K = the instantaneous rate at which the function approaches L_{∞} (note that K is not a growth rate), and t_0 = the x-intercept. The first step in fitting a VBGF to the length and age data was to estimate starting values for the parameters L_{∞} , K , and t_0 , which was done via the *vbStarts* function from the *FSA* package (Ogle et al. 2018) in R 3.5.2 (R Core Team 2018). The starting values for these parameters were used along with the ages for individual bull trout to produce a VBGF. Bull trout TL (cm) was modeled as a function of the VBGF via non-linear regression, and the fitted VBGF was used to predict mean length-at-age for the population, which I compared to other bull trout populations.

One of the primary objectives of my thesis was to determine whether the migration of sockeye salmon smolts from Chilko Lake elicited a stronger behavioural response from older, larger, and faster-growing bull trout than from younger, smaller, and slower-growing individuals. To test this, I compared the ages, total lengths (cm) and growth ratios of bull trout that had a positive response to the smolt migration (i.e., were detected at the lake outlet during the smolt migration in 2018) to those individuals that had a negative response to the smolt migration (i.e., were not detected at the outlet during the smolt migration in 2018). Prior to conducting analyses, I removed any individuals from the data that were harvested during the previous year (i.e., its external tag number was reported) or that were detected for only one day following tagging ($n = 4$). I assumed that any individual that had not been reported as harvested was still in the system, such that even when an individual was not detected on any receivers during the smolt outmigration it was still included in the negative response group. Using the VBGF that I fit to the age-at-length data, I calculated each individual's relative size as the ratio of its

TL (cm) to the predicted mean TL (cm) for the age class to which it belonged (Figure 2). I used the relative size of an individual as a proxy for a growth ratio such that a relative size that was greater than 1.0 suggested fast somatic growth relative to the population mean and a relative size that was less than 1.0 suggested slow somatic growth relative to the population mean. Mean values for age, TL (cm) and growth ratio were compared among the positive and negative response groups using one-way analysis of variance (ANOVA). Statistical analyses were completed with R (R Core Team 2018), and assumptions of ANOVA (including normality and variances) were visually assessed. Statistical significance was set at $\alpha = 0.05$.

Results

Acoustic telemetry detection summary

Between 24 April and 8 May 2017, 20 bull trout were tagged with an acoustic transmitter and released near the outlet of Chilko Lake. In total, 527,838 detections of 19 bull trout were recorded on 18 receivers between May 2017 and May 2018. The number of detections per bull trout ranged from 0 to 134,574 (mean = 27,781 [$\pm 35,424$ SD]; Table 1). The total number of days on which individuals were detected ranged from 0 to 280 (mean = 95.0 days [± 89.3 days SD]; Table 1), and the number of days over which each individual was tracked (i.e., the number of days between the first and last detections for each fish) ranged from 0 to 375 (mean = 192.5 days [± 164.3 days SD]; Table 1). Following the sockeye salmon smolt outmigration in 2017, acoustic telemetry indicated that 14 bull trout (70.0%) moved into Chilko Lake and 6 (30.0%) bull trout remained in the Chilko River; however, those individuals that remained in the river were either harvested within one month of being tagged or were only detected for one day following tagging ($n = 4$). Seven bull trout were detected at the lake outlet during the sockeye salmon smolt migration in 2018 (35.0%), and one individual was never detected following tagging (Table 1).

Activity space size and overlap

Bull trout were estimated to occupy larger activity spaces in the summer than in the spring, fall, and winter at both the 50% and 90% levels (Figure 3). In the summer,

individual 50% core-use areas ranged from 0.32 km² to 16.72 km² (mean = 5.25 km² [± 5.09 km² SD]; Table 2) and 90% home ranges ranged from 1.43 km² to 48.24 km² (mean = 19.00 km² [± 15.26 km² SD]; Table 2). In the spring, fall, and winter, lattice density activity spaces were estimated to cover an area approximately 90% smaller than that of the summer at both the 50% and 90% levels (Table 2; Figure 3). Furthermore, individual activity spaces were distributed throughout Chilko Lake in the summer, while in the spring, fall, and winter, activity spaces were primarily located at the north and south ends of the lake (Figure 4).

Across all four seasons, the amount of overlap between individual bull trout activity spaces ranged from 0% to 100% for both 50% core-use areas and 90% home ranges (Figure 5). Among seasons, the amount of overlap between the activity spaces of individual bull trout was greatest during the winter (90% activity space: mean = 37% overlap [$\pm 35\%$ SD]; 50% activity space: mean = 48% overlap [$\pm 46\%$ SD]), followed by spring 2017 (90% activity space: mean = 29% overlap [$\pm 35\%$ SD]; 50% activity space: mean = 28% overlap [$\pm 35\%$ SD]), spring 2018 (90% activity space: mean = 23% overlap [$\pm 34\%$ SD]; 50% activity space: mean = 26% overlap [$\pm 42\%$ SD]), summer (90% activity space: mean = 19% overlap [$\pm 26\%$ SD]; 50% activity space: mean = 16% overlap [$\pm 30\%$ SD]), and fall (90% activity space: mean = 15% overlap [$\pm 25\%$ SD]; 50% activity space: mean = 16% overlap [$\pm 30\%$ SD]) (Figure 5).

Horizontal movement

The minimum total displacement for acoustic-tagged bull trout ranged from 0 km to 523.2 km (mean = 161.0 km [± 164.9 km SD]; Table 1), while the maximum one-way

displacement ranged from 0 km to 64.9 km (mean = 35.8 km [± 23.4 km SD]; Table 1). Generally, the individuals that travelled the furthest cumulative distances over the duration of tracking were also those that were tracked the longest (i.e., highest number of days tracked; Table 1); however, one individual with one of the longest tracking durations (355 days) had a minimum total displacement of only 61.4 km. Following tagging in April and May 2017, the least-cost distance to the lake outlet increased steadily up until August 2017 at which point the median distance to the outlet was approximately 20 km (Figure 6). Individuals began moving closer to the lake outlet in November 2017, and the median of the individual mean distances to the outlet was approximately 7 km from January to May 2018 (Figure 6). Mean bull trout movement rates were greater than the hypothesized mean smolt transit speed (105 mm/s) in June ($t_{(16)} = 2.34$, $P = 0.002$), September ($t_{(51)} = 2.26$, $P < 0.001$), and October ($t_{(22)} = 2.30$, $P = 0.002$); mean bull trout movement rates for all other months were not significantly greater than the hypothesized mean smolt transit speed (in all cases, $P > 0.05$; Figure 7). Across all months, the proportion of movements directed towards the north end of the lake was greatest in September and October, while movements directed towards the south end of the lake were greatest in July and December (Figure 7).

Age and growth

Based on pelvic fin ray ageing techniques, bull trout in the Chilko Lake system appeared to be relatively long-lived; the subsample of bull trout from which pelvic fin rays were collected ranged in age from 3 to 9 years ($n = 166$; Appendix, Table A1) while the subsample of individuals that were not sampled for fin rays ranged in estimated age

from 3 to 8 years ($n = 34$; Appendix, Table A1), as was determined by the ALK (Appendix, Table A2). The mean age for the total sample was 5.5 years (± 1.3 years SD) and the mean age for individuals that were tagged with an acoustic transmitter was also 5.5 years (± 1.1 years SD). The TL of all individuals ranged from 41.0 cm to 79.5 cm (mean = 58.0 cm [± 6.8 cm SD]; Appendix, Table A1) while the TL of acoustic-tagged bull trout ranged from 54.0 cm to 65.6 cm (mean = 59.6 cm [± 3.2 cm]; Table 1). There was substantial variability in length at age for fish in the age-4 to age-8 range (Figure 2), with the highest variability occurring in age-4 fish (41.0 to 73.0 cm). The lowest variability in length at age occurred in age-9 fish (61.0 to 61.5 cm) followed by age-3 fish (45.1 to 54.5 cm).

The VBGF-predicted estimate for the mean asymptotic TL for the population (L_{∞}) was 69.11 cm (Table 3; Figure 2), and the VBGF-predicted mean TL for each age class was within 7% of the observed mean TL for the corresponding age class (Table 4). ANOVAs failed to detect any differences in age ($F_{1, 13} = 0.50$, $P = 0.49$), TL ($F_{1, 13} = 0.35$, $P = 0.56$), or growth ratio ($F_{1, 13} = 0.03$, $P = 0.87$) among fish that returned to the outlet and those that did not (Figure 8). Growth ratio ranged from 0.93 to 1.11 (mean = 0.97 [± 0.1 SD]) for individuals that were included in the outlet return analysis.

Discussion

This thesis characterized the movements and spatial distribution of bull trout (*Salvelinus confluentus*) in response to the annual migration of sockeye salmon (*Oncorhynchus nerka*) smolts from Chilko Lake, British Columbia, and attempted to identify potential migratory coupling of bull trout and sockeye salmon. Using acoustic telemetry, I found that Chilko bull trout engage in large-scale movements; however, whether these movements are related to migratory coupling with migrant sockeye salmon smolts remains unclear. By combining acoustic telemetry with size-at-age data, I also found that bull trout age, TL, and growth ratio did not appear to influence their behavioural response to the smolt migration.

Of the bull trout that were acoustic-tagged at the Chilko Lake outlet ($n = 15$), seven (47%) returned to the outlet in the spring of 2018, presumably to exploit the resource pulse provided by migrant smolts. These individuals also traveled some of the furthest distances of the fish that were tagged with acoustic transmitters; bull trout that returned to the outlet had a greater average total displacement (310.7 km) than those individuals that did not return to the outlet (100.9 km). However, my results are likely biased by tracking duration, as the bull trout that returned to the outlet were tracked for an average of 362 days while those that did not return to the outlet were tracked for an average of 130 days. The scale of movements observed in this study are generally similar to others (e.g., Swanberg 1997; Starcevich et al. 2012), and these observations suggest that at least some bull trout will travel across large distances and return to the outlet in consecutive years. In fact, three individuals that returned to the outlet had a maximum

one-way displacement greater than 64.0 km, indicating that these fish traveled from their release locations in the outlet to the southern-most end of the lake and back.

The outlet return rate for bull trout in this study (47%) is similar to the 40% return rate reported by Furey and Hinch (2017), who used acoustic telemetry to characterize the seasonal use of the Chilko Lake outlet by bull trout and found that the daily probability of bull trout residency in the outlet was strongly linked to the timing of the sockeye salmon smolt migration. However, Furey and Hinch (2017) also noted that because they restricted sampling to the lake outlet, their sample may have been biased towards individuals that show site fidelity to the outlet. Previous telemetry studies have also demonstrated that bull trout can exhibit some degree of site fidelity. Swanberg (1997) reported that 86% of radio-tagged bull trout in the Blackfoot River in Montana, U.S.A., returned to pre-spawning locations following spawning, suggesting high fidelity to their home range. Similar behaviour was reported by Carson (2001), who found that 50% of radio-tagged bull trout in the McLeod system in Alberta, Canada, occupied a small home range to which they exhibited post-spawning homing behaviour. Although I did not directly investigate spawning and homing behaviour, there is some evidence to suggest the long-distances traveled by bull trout were in response to the interactive effects of spawning opportunities and site fidelity. For example, during the spring, fall, and winter seasons, bull trout home ranges were relatively small and the median distance of individuals to the lake outlet was 10 km, suggesting some degree of site fidelity. Furthermore, bull trout that returned to the outlet were aged between 5 and 7 years, and thus were likely reproductively mature during the previous spawning season (Dunham et al. 2008). Three of these individuals also displayed behaviour consistent with spawning,

which I identified as sequential detections on the same receiver, but that were separated by a hiatus in all detections for at least four weeks during August and September (Thorley and Andrusak 2017). Since many of the receivers in Chilko Lake were placed near assumed bull trout spawning tributaries, it is likely that the gaps in detections for these three individuals were a result of spawning activity. Therefore, it is possible that movements to the lake outlet by at least a portion of bull trout in this study are a result of site-fidelity to their home range following a spawning migration, and, like Furey and Hinch (2017), I must consider the potential influence of tagging-location bias on my results.

Predators that travel over large distances to intercept migratory Pacific salmon generally anticipate the arrival of salmon at a particular location (e.g., Hulbert et al. 2005; Elliot et al. 2011; Schindler et al. 2013; Deacy et al. 2016); however, it remains unclear in the present study whether bull trout that returned to the outlet anticipated the arrival of sockeye salmon smolts. Bull trout arrived at the lake outlet as early as January – approximately three months earlier than sockeye salmon smolts began migrating through the outlet on April 13th (S. Decker, Fisheries and Oceans Canada, personal communication) – suggesting that bull trout may have anticipated the smolt migration. Although bull trout movements were not disproportionately directed towards the north end of the lake in the months leading up to their arrival at the outlet, the average transit speed for bull trout during those months was significantly greater than the hypothesized transit speed for smolts. This supports the idea that bull trout engage in directed movements towards the outlet prior to the smolt migration; however, because bull trout movements towards the outlet seemed to begin in the fall, it does not appear that bull

trout aggregate near the outlet in anticipation of the smolt migration. A possible explanation is that bull trout movements and fidelity to the lake outlet are influenced by alternate feeding opportunities. Bull trout will frequently consume the eggs of other fishes (Lowery and Beauchamp 2015), including Pacific salmon, and previous research has found that bull trout residency in the Chilko River increased during adult sockeye salmon spawning (Furey and Hinch 2017). Furthermore, in addition to sockeye salmon, the Chilko River also supports populations of Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) which spawn in the river each year between August and October and between November and December, respectively. Thus, it is possible that bull trout are making directed movements from Chilko Lake towards the lake outlet in the fall to feed on the eggs of spawning Pacific salmon, and are remaining near the outlet through the winter in anticipation of the sockeye salmon smolt migration.

Although bull trout generally exhibit opportunistic foraging behaviour (Dunham et al. 2008), there is some evidence to suggest that they become progressively more piscivorous as they become larger (Beauchamp and Van Tassell 2001). However, my assessment of the differences in fish size (TL) among bull trout that returned to the outlet (presumably to consume migrant smolts) and those that did not failed to detect any differences among the groups. A possible explanation is that bull trout switch from generalist foraging to primarily piscivorous behaviour at a smaller size than was represented in my sample. In the present study, acoustic-tagged fish ranged in TL from 54.0 to 65.5 cm. Earlier studies of the relationship between body length and foraging behaviour by bull trout identified a switch to piscivory at a range of lengths all smaller

than the fish I acoustic-tagged. For example, Beauchamp and Van Tassell (2001) found that bull trout greater than 45.0 cm fork length primarily consumed other fishes such as kokanee salmon (*Oncorhynchus nerka*), rainbow trout (*Oncorhynchus mykiss*), and mountain whitefish (*Prosopium williamsoni*), while bull trout that were smaller than 45.0 cm fork length mainly consumed invertebrates. Similar feeding behaviour was also reported by Lowery and Beauchamp (2015), who found that bull trout of lengths greater than 30.0 cm were more likely to consume other fishes across all seasons than bull trout of lengths smaller than 30.0 cm. Therefore, my inability to detect a difference in bull trout TL among fish that returned to the outlet and those that did not may be due to the lack of smaller fish in my sample.

In addition to size, age has also been shown to influence the ontogenetic shift of fishes from generalist consumers to piscivores. Often, fish will become piscivorous as they age as a way to maintain energetic efficiency as they grow (Keast 1985), and a shift to piscivory by a predator results in an increased rate of growth (Juanes and Conover 1994; Olson 1996) due to the high energy content prey fish provide (Forseth and Jonsson 1994). My assessment of the differences in age and growth ratio among bull trout that returned to the outlet (presumably to consume migrant smolts) and those that did not failed to detect any differences among the groups. As with body length, a possible explanation is that bull trout switch to piscivory at a younger age than was represented in my sample of acoustic-tagged fish, which would also explain the lack of difference in growth ratio among the groups. The correlation between age and a shift to piscivorous behaviour has not been examined for bull trout; however, it has been documented that other char species such as lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus*

fontinalis) exhibit piscivorous behaviour beginning at age-2 (Mittelbach and Persson 1998). Ages of acoustic-tagged fish in the present study ranged from age-3 to age-8. Thus, if shifts to piscivory occur at earlier ages and growth rates are influenced by this shift, it should come as no surprise that I was unable to detect a difference. Further research with a broader range of bull trout size- and age-classes may be required to better understand whether a behavioural response to migrant smolts is influenced by body size or age.

Potential implications of migratory coupling

Ecological interactions and their associated consequences may be facilitated by the movements of predators in response to migrant prey through two pathways: (1) the increasing density of predators as they move from one area to another; and (2) the decreasing density of predators in areas from which they move (Furey et al. 2018). Although it is unclear in the present study whether the migration of sockeye salmon smolts from Chilko Lake influences large-scale movements by bull trout from nearby systems, the distances moved by bull trout in this study suggest that it is plausible. For example, a portion of bull trout in the present study ($n = 5$) had a maximum one-way displacement greater than 64 km, which is approximately the distance between the outlet of Chilko Lake and the confluence of the Chilko and Taseko Rivers. If migratory coupling is occurring between bull trout and sockeye salmon smolts in the Chilko system, the movement of bull trout to the lake outlet from alternate areas could directly and indirectly affect food web and community structure through interactions with other resident species.

In addition to bull trout, Chilko Lake and the Chilko River support populations of resident rainbow trout (*Oncorhynchus mykiss*) and mountain whitefish (*Prosopium williamsoni*). Like bull trout, rainbow trout are generalist consumers (McPhail and McPhail 2007); however, they may also opportunistically consume other fishes and have been observed at the Chilko Lake outlet during the sockeye salmon smolt migration (Clark et al. 2016), presumably to prey migrant smolts. With migratory coupling causing greater predator densities at the lake outlet, resident fishes such as rainbow trout would likely face increased competition or could be displaced entirely if bull trout from nearby systems are participating in migratory coupling. Furthermore, in years with few migrant sockeye salmon smolts, bull trout can shift to consuming other prey such as mountain whitefish (A. M. Kanigan, unpublished data), which could induce a seasonal trophic cascade. If bull trout predation substantially decreases the density of mountain whitefish in the Chilko system, the density of aquatic invertebrates that mountain whitefish normally consume (McPhail and McPhail 2007) could potentially increase. These interactions represent only a few of the possible ecological consequences of migratory coupling between bull trout and sockeye salmon smolts in the Chilko system, as there are other piscivores in the system such as mergansers (*Mergus* spp.), gulls (*Larus* and *Chroicocephalus* spp.), and river otters (*Lontra canadensis*; Clark et al. 2016) that may be affected. Furthermore, if bull trout are moving from other areas to the Chilko system, it is likely that the areas they temporarily vacate are also affected at some level. However, more research is required to determine the prevalence of migratory coupling in the Chilko and surrounding systems, as well as how it affects predators, prey, and the structure of communities.

Bull trout management objectives

The migration of sockeye salmon smolts from Chilko Lake can often exceed 200,000 individuals per hour (Furey et al. 2016a) and thus represents a large energy source for predators in the system. Bull trout will often feed on migrant smolts at high rates (Furey et al. 2016b) and use of the lake outlet by bull trout has been linked to the timing of the smolt migration (Furey and Hinch 2017). Thus, the concentration of small home ranges (90% activity space) and a high proportion of home range overlap near the lake outlet in consecutive spring seasons can likely be attributed to feeding opportunities for resident bull trout. Aggregations of predator fishes in response to smolt migrations have been observed in other freshwater systems (e.g., Rieman et al. 1991; Petersen 2001); however, these predator aggregations are usually associated with an anthropogenic alteration to the system (e.g., a hydroelectric dam) that acts to funnel downstream-migrating smolts to the waiting predators. In contrast, the characteristics of the Chilko Lake outlet (a spatial constriction with low water volume) act to funnel smolts into high densities. It is likely that Pacific salmon smolts are exploited by bull trout in other systems with similar characteristics; however, this is the first system in which it has been identified.

In the summer, the large home ranges are most easily explained as horizontal movements associated with the reproductive migratory behaviour of bull trout. Most bull trout spawn between mid-August and late October (McPhail and Murray 1979; Rieman and McIntyre 1996); however, bull trout in northern temperate systems may spawn earlier (Pollard and Down 2001). Indeed, home range sizes were greatest during the summer, presumably because at least a proportion of acoustic-tagged individuals

migrated from the lake outlet towards lake tributaries to reach spawning grounds. While little is known about bull trout in the Chilko system, spawning has been documented in one tributary (~ 40 km south of the outlet), and there are several other tributaries that have been identified as potential bull trout spawning streams. Furthermore, the small proportion of overlap between summer home ranges suggests that, if the summer distribution of bull trout is a result of spawning migrations, they are likely utilizing various tributaries throughout the lake. Although bull trout are iteroparous, the frequency of bull trout spawning can be quite variable. Some bull trout will spawn each year, while other individuals spawn in alternating years (DeHann and Bernall 2013). Thus, the expansive summer home ranges may also be associated with summer foraging throughout the lake rather than spawning migrations.

The size and distribution of home ranges in the fall were similar to the spring, with relatively small home ranges concentrated near the outlet of the lake and in the first few kilometers of the Chilko River. Although bull trout can spawn during the fall (i.e., until late October) and fluvial populations of bull trout spawn in the tributaries of river systems, Chilko bull trout are not expected to spawn in tributaries of the Chilko River. Thus, it is unlikely that this distribution is associated with spawning. Another possible explanation is that bull trout are returning to the outlet in response to the spawning migration of adult sockeye salmon, presumably to exploit feeding opportunities. Although it has not been observed in the Chilko system, bull trout will frequently consume the eggs of other fishes (Lowery and Beauchamp 2015), including Pacific salmon. Furthermore, Furey and Hinch (2017) found that bull trout residency in the Chilko River increased during adult sockeye salmon spawning. Such behaviour has also

been documented for other species of char. Denton et al. (2009) found that Dolly Varden (*Salvelinus malma*) in southwestern Alaska moved into areas of sockeye salmon spawning synchronously with the arrival of the salmon and fed almost exclusively on salmon eggs once spawning began. Similarly, Dennert et al. (2016) found that sockeye salmon eggs dominated the diets of both Dolly Varden and Arctic char (*Salvelinus alpinus*) during sockeye salmon spawning in tributaries to Lake Aleknagik, Alaska. Thus, it is possible that the concentration of bull trout near the outlet of the lake in the fall is associated with opportunities to feed on sockeye salmon eggs.

Consistent with Furey and Hinch (2017) bull trout showed strong site fidelity to the outlet during the winter. Home range sizes were smaller during the winter than in any other season and the degree of overlap between home ranges was greatest during the winter. Indeed, fidelity to overwintering locations and relatively constricted winter ranges have been documented for other populations of bull trout (Starcevich et al. 2012). For example, 74% of radio-tagged bull trout in the Morice River basin returned to within 1 km of overwintering locations in consecutive years (Bahr and Shrimpton 2004) and, in the Blackfoot River, Montana, 86% of radio-tagged bull trout returned to within 20 m of the same overwintering location from the year prior (Swanberg 1997). The reasons for this distribution remain unclear; however, given that bull trout will opportunistically consume the eggs of Pacific salmon (Lowery and Beauchamp 2015), it is possible that bull trout arrive at the lake outlet in the fall during the spawning of adult sockeye salmon and remain near the outlet until the migration of sockeye salmon smolts from the lake in the spring.

Across all four seasons, home ranges reported in this study were generally smaller than those reported for previous studies of bull trout in lacustrine environments. For example, Gutowsky et al. (2016) estimated that bull trout in the Kinbasket Reservoir, British Columbia, occupied 90% home ranges of approximately 50 km² in the spring and fall and 35 km² in the summer and winter, which are 2 - 45 times larger than what I estimated for Chilko bull trout. The relatively small home ranges that I report can likely be attributed to the feeding opportunities provided by migrant sockeye salmon smolts and spawning adults, as it is possible that the high abundance of resources in the spring and fall may not necessitate larger home ranges during these seasons (i.e., optimal foraging theory; Pyke 1984). Home range sizes may have also been influenced by variability in the density and detection efficiency of the acoustic receivers. Since the receivers that were set out in the main body of the lake were all near shore it is possible that some individuals were able to move throughout the lake undetected. Detection efficiency can be affected by receiver placement, ambient noise, environmental conditions, and tagging procedures (Clements et al. 2005; Gjelland and Hedger 2013; Dance et al. 2016). Because sentinel tags were not available for this study (Kessel et al. 2014) I was not able to determine seasonal variability in the detection efficiency of individual receivers. Inadequate detection efficiency may explain why fish that entered the Chilko River following the smolt migration in spring 2017 failed to be detected by downstream receivers, as the noise of the river may have interfered with transmissions from acoustic tags. Regardless, the movements of bull trout in the Chilko River and downstream systems should be investigated further to determine whether individuals are moving from other systems to exploit the downstream migration of sockeye salmon smolts.

Bull trout life history strategy largely influences diet, which in turn influences growth. Generally, adfluvial bull trout experience greater growth than fluvial individuals (Ratcliff et al. 1996) as adfluvial fish are predominantly piscivorous, which plays a large role in their more rapid growth (Mushens and Post 2000). Although I did not characterize Chilko bull trout as either fluvial or adfluvial, I assume that the majority were adfluvial given the proportion of acoustic-tagged fish that entered Chilko Lake and continued to be detected in the lake during tracking. Using fin ray age estimation, I found that bull trout in the Chilko system can be relatively long-lived. Bull trout ages ranged from age-3 to age-9, and TL measurements ranged from 41.0 cm to 79.5 cm. This age structure is similar to that of other populations of bull trout (e.g., Mogen and Kaeding 2005; Al-Chokhachy and Budy 2008); however, length-at-age data indicated that Chilko bull trout are generally larger than fluvial bull trout in other systems, especially at younger ages. For example, age-3 bull trout in the present study had an average TL of 49.5 cm. In comparison, the average TL for age-3 bull trout from the St. Mary River drainage, Montana and the South Fork Walla Walla River in northeastern Oregon was approximately 19.0 cm (Mogen and Kaeding 2005; Al-Chokhachy and Budy 2008). Relatively few studies have characterized the age- and size-structure of bull trout, and those that do often neglect to fit a growth function to the size-at-age data. In once exception, McCubbins et al. (2016) characterized the size- and age-structure for adfluvial bull trout in Lake Pend Oreille, Idaho, and found that mean length-at-age ranged from 12.0 cm for age-1 fish to 80.0 cm for age-15 fish. A comparison of von Bertalanffy growth parameters from this study and those reported by McCubbins et al. (2016) suggests that on average, Chilko bull trout grew from a younger age at length zero (t_0) at

a slower instantaneous rate (K : 0.27) to a shorter asymptotic length (L_{∞} : 69.1 cm) than male (K : 0.91; L_{∞} : 105.5 cm) and female (K : 1.04; L_{∞} : 101.6 cm) bull trout in Lake Pend Oreille. The difference in growth between the two populations is likely due to differences in the consistency of feeding opportunities, as Lake Pend Oreille supports a vast assemblage of potential prey species including westslope cutthroat trout (*Oncorhynchus clarkii lewisi*), mountain whitefish (*Prosopium williamsoni*), pygmy whitefish (*Prosopium coulterii*), slimy sculpin (*Cottus cognates*), peamouth (*Mylocheilus caurinus*), northern pikeminnow (*Ptychocheilus oregonensis*), longnose dace (*Rhinichthys cataractae*), redbside shiner (*Richardsonius balteatus*), longnose sucker (*Catostomus catostomus*), and largescale sucker (*Catostomus macrocheilus*), as well as a number of non-native species. However, in a comparison of mean length-at-age, the two populations are relatively similar. For example, at age-8, Chilko bull trout have a mean length-at-age of 61.5 cm, while bull trout from Lake Pend Oreille have a mean length-at-age of 59.0 cm (female) and 57.0 cm (male). Therefore, differences in growth parameters among the populations may be a result of my inability to age younger and older bull trout. Nonetheless, future studies of age and growth should fit growth functions to their data and report growth parameters to allow for comparison among populations.

Conclusion

My thesis provides the first estimates of broad-scale movements by bull trout in the Chilko Lake system, as well as the first estimates of age- and size-structure for Chilko bull trout. I confirmed that bull trout will return to the Chilko Lake outlet during the sockeye salmon smolt migration in consecutive years, as previously identified by Furey and Hinch (2017), and that the movements by bull trout between the lake and the outlet can be substantial. However, it remains unclear whether the movements of bull trout to the lake outlet constitute migratory coupling with migrant sockeye salmon smolts. In the present study, a portion of bull trout returned to the lake outlet up to three months earlier than the start of the sockeye salmon smolt migration, and it seems that these movements are related to site fidelity. However, even if bull trout exhibit fidelity to the lake outlet it is still possible that they are participating in migratory coupling with sockeye salmon smolts. A possible explanation for this spatial distribution is that bull trout are moving towards the lake outlet in the late fall to feed on the eggs of spawning Pacific salmon, and that they remain near the outlet through the winter in anticipation of the smolt migration. Finally, although bull trout tend to become increasingly piscivorous as they become larger and older, which contributes to faster somatic growth, I did not detect any differences in the sizes, ages, or growth ratios of bull trout that returned to the lake outlet during the smolt migration and those that did not. Because the bull trout that I tagged seem to display fidelity to the outlet, future work should distribute tags evenly throughout Chilko Lake and the downstream river systems.

Data collected in the Chilko lake system also provided critical information for conservation of bull trout. Seasonal home ranges were relatively small in the spring, fall, and winter, and were largely concentrated near the Chilko Lake outlet, suggesting site fidelity. In contrast, summer home ranges were expansive, and their distribution suggested that bull trout spawn in tributaries throughout the lake. Such work is important, as characterizing the spatial distribution of bull trout can help to identify patterns of space use which can inform management decisions regarding the protection of critical bull trout habitat.

Tables

Table 1. Detection summary for bull trout (*Salvelinus confluentus*) that were tagged with an acoustic transmitter following capture in the Chilko River, British Columbia, between 24 April and 8 May 2017. Days tracked = the difference between the first and last days on which an individual was detected on an acoustic telemetry receiver. Days detected = the number of unique days on which an individual was detected on an acoustic telemetry receiver. Total displacement (km) = the minimum total displacement for the duration of tracking. One-way displacement (km) = the maximum distance an individual was detected from the release site. COAs = the number of 5-day centers of activity that were estimated from acoustic receiver detections for each individual. TL = total length. Outlet return = an indication of whether an individual was (1) or was not (0) detected at the lake outlet during the 2018 sockeye salmon smolt migration.

ID	Date tagged	Total detections	Days tracked	Days detected	Total disp. (km)	One-way disp. (km)	COAs	TL (cm)	Mass (kg)	Age (years)	Outlet return
1	2017-04-24	93858	373	237	495.9	35.0	60	62.0	2.40	6	1
2	2017-04-24	27572	361	155	337.5	64.3	54	62.5	2.15	6	1
3	2017-04-25	13591	28	28	33.4	14.0	6	60.5	2.25	6	NA
4	2017-04-25	33519	361	169	213.2	47.7	51	57.0	1.80	8	1
5	2017-04-25	8549	88	66	88.5	64.3	15	63.0	2.10	6	0
6	2017-04-25	54299	375	171	162.6	64.3	40	63.0	2.65	6	0
7	2017-04-25	34116	356	184	523.2	47.7	61	58.0	2.10	5	1
8	2017-04-25	6950	25	22	27.3	14.0	6	59.0	2.40	5	NA

ID	Date tagged	Total detections	Days tracked	Days detected	Total disp. (km)	One-way disp. (km)	COAs	TL (cm)	Mass (kg)	Age (years)	Outlet return
9	2017-04-26	35603	374	124	254.7	22.0	42	65.5	2.85	6	1
10	2017-04-26	800	28	19	15.2	13.4	5	58.5	2.10	5	NA
11	2017-04-26	716	14	11	21.4	34.5	3	58.0	2.00	5	0
12	2017-04-26	28237	152	88	262.2	48.3	23	58.0	1.50	5	0
13	2017-04-26	11969	355	64	61.4	13.4	22	60.5	2.40	5	1
14	2017-04-26	42655	295	177	205.5	64.9	51	54.0	1.60	4	0
15	2017-04-26	134574	356	280	288.7	64.9	67	59.0	2.10	4	1
16	2017-04-29	792	15	4	6.4	6.4	3	63.0	3.30	6	0
17	2017-05-06	NA	NA	NA	NA	NA	NA	55.5	1.80	5	NA
18	2017-05-06	3	1	1	0	0	1	56.5	1.75	6	NA
19	2017-05-08	5	1	1	9.0	9.0	1	54.5	1.70	3	0
20	2017-05-08	30	99	4	51.9	51.9	3	63.0	3.10	7	0
mean	-	27780	192.5	95.0	161.0	35.8	27	59.6	2.20	5.5	-
SD	-	35423	164.4	89.3	164.9	24.4	24	3.2	0.49	1.1	-

Table 2. Estimates of 50% and 90% activity space (km²) by season for bull trout (*Salvelinus confluentus*) that were captured in the Chilko River, British Columbia, between 24 April and 8 May 2017, and tracked via acoustic telemetry. NA = an individual for which an activity space could not be estimated. Estimates of activity space were determined using the lattice density approach of Barry and McIntyre (2011).

Fish ID	Activity space (km ²)									
	spring 2017		summer 2017		fall 2017		winter 2018		spring 2018	
	90%	50%	90%	50%	90%	50%	90%	50%	90%	50%
1	0.80	0.32	48.24	16.72	3.34	0.48	1.27	0.32	0.64	0.32
2	0.64	0.32	16.87	4.14	1.27	0.32	0.48	0.16	3.34	0.80
3	9.87	2.07	NA	NA	NA	NA	NA	NA	NA	NA
4	1.11	0.32	32.00	9.71	0.80	0.32	0.32	0.16	0.48	0.16
5	6.85	0.64	9.55	3.50	NA	NA	NA	NA	NA	NA
6	0.32	0.16	NA	NA	0.96	0.48	1.27	0.32	1.91	0.64
7	1.75	0.48	13.69	3.98	2.87	0.80	0.48	0.16	0.64	0.16
8	9.87	2.07	NA	NA	NA	NA	NA	NA	NA	NA
9	2.71	0.96	1.43	0.32	1.11	0.32	0.80	0.16	0.64	0.16
10	0.80	0.32	NA	NA	NA	NA	NA	NA	NA	NA
11	4.62	1.59	NA	NA	NA	NA	NA	NA	NA	NA
12	1.11	0.32	18.31	4.78	NA	NA	NA	NA	NA	NA
13	0.32	0.32	NA	NA	NA	NA	1.11	0.32	NA	NA
14	1.43	0.32	1.59	0.48	1.75	0.48	0.80	0.32	NA	NA
15	0.16	0.16	29.29	3.66	0.16	0.16	0.80	0.16	0.16	0.16
16	0.16	0.16	NA	NA	NA	NA	NA	NA	NA	NA
17	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
18	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
20	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
mean	2.66	0.66	19.00	5.25	1.53	0.42	0.81	0.23	1.11	0.34
SD	3.34	0.66	15.26	5.09	1.08	0.19	0.35	0.08	1.13	0.27

Table 3. Estimates (LL = lower 95% confidence limit; UL = upper 95% confidence limit) of asymptotic total length (L_{∞} = cm), instantaneous rate at which length approaches L_{∞} ($K = 1/\text{age}$), and age at length = 0 (t_0 = age) for a von Bertalanffy growth function fitted to individual length at age for $n = 200$ bull trout (*Salvelinus confluentus*) captured via angling in Chilko Lake and the Chilko River, British Columbia, between 24 April and 12 May 2017 and between 20 April and 2 August 2018.

Parameter	Estimate	LL	UL
L_{∞}	69.11	63.43	102.26
K	0.27	0.07	0.52
t_0	-1.52	-7.06	0.51

Table 4. Observed mean total length (TL) for each age class of bull trout (*Salvelinus confluentus*) captured in Chilko Lake and the Chilko River between 24 April and 12 May 2017 and between 20 April and 2 August 2018. n = sample size. SD = standard deviation of the observed mean. VBGF mean TL = the mean total length-at-age for the population as predicted by a von Bertalanffy growth function.

Age class (years)	n	Observed mean TL (cm)	SD	VBGF mean TL (cm)
3	8	49.45	3.69	49.19
4	35	53.02	6.11	54.69
5	68	56.94	5.15	57.89
6	43	60.98	6.39	59.75
7	34	60.91	6.27	60.84
8	10	65.85	5.49	61.48
9	2	61.25	0.35	61.84

Figures

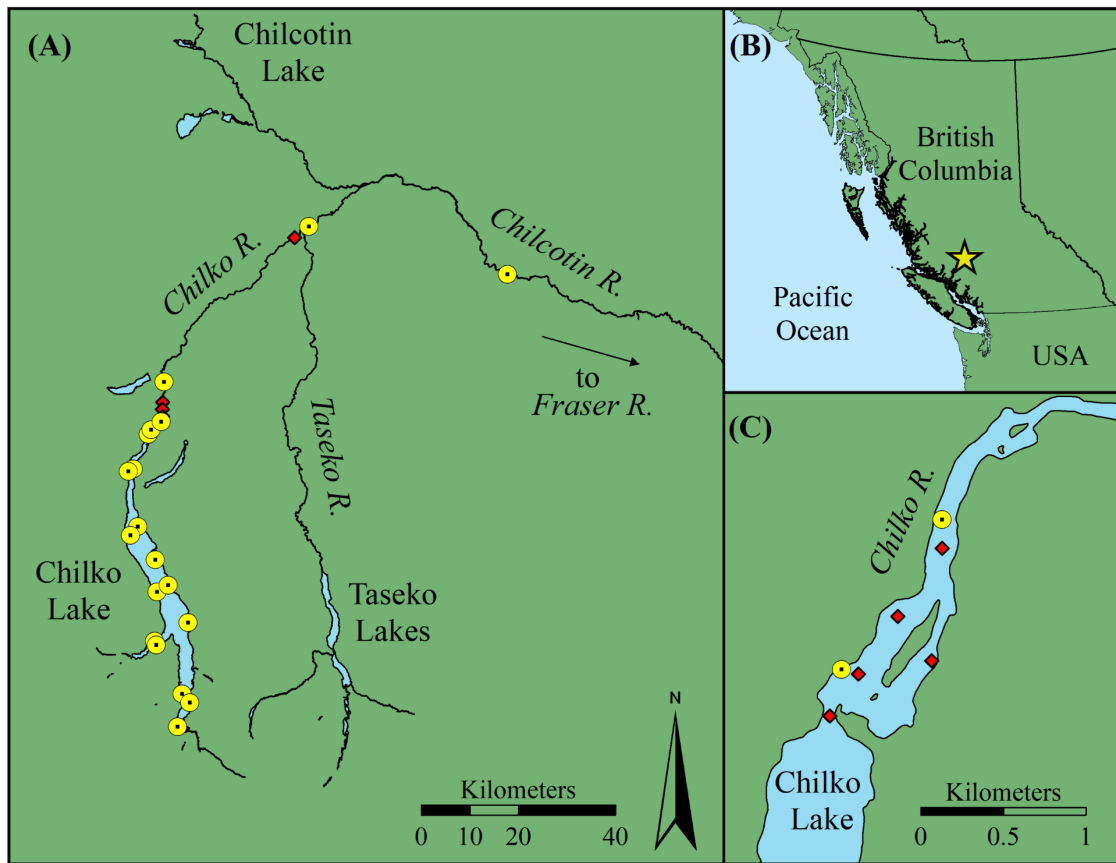


Figure 1. **A)** A map of the study area, including Chilko Lake and the Chilko and Chilcotin Rivers. Yellow and black circles represent the locations of acoustic receivers. Red diamonds represent the capture locations for bull trout (*Salvelinus confluentus*) that were tagged with an acoustic transmitter between 24 April and 8 May 2017. **B)** A map showing the location of the study area in British Columbia, Canada. **C)** The outlet of Chilko Lake and the Chilko River. Yellow and black circles represent the locations of acoustic receivers. Red diamonds represent the capture locations for bull trout (*Salvelinus confluentus*) that were tagged with an acoustic transmitter between 24 April and 8 May 2017.

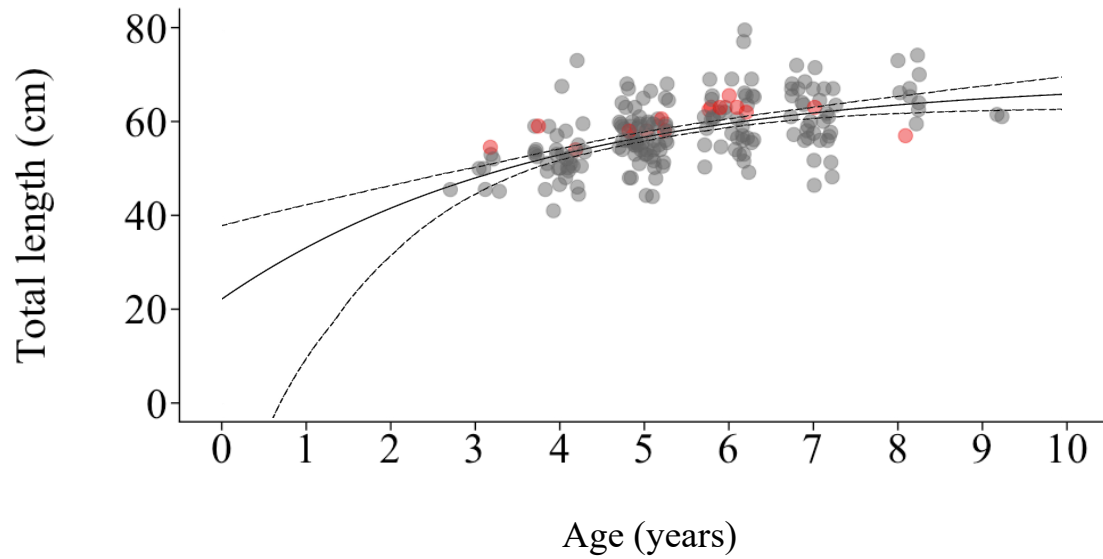


Figure 2. von Bertalanffy growth curve fitted to age-at-length data for bull trout (*Salvelinus confluentus*) that were caught in Chilko Lake and the Chilko River between 24 April and 12 May 2017 and between 20 April and 2 August 2018. Each data point represents an individual bull trout. The solid line represents the predicted mean length-at-age for the population; dashed lines represent the $\pm 95\%$ confidence intervals. Red data points indicate individuals that were included in an analysis of the differences in age, total length (cm), and growth ratio between bull trout that were detected at the lake outlet in the spring of 2018 and those that were not (see Figure 8).

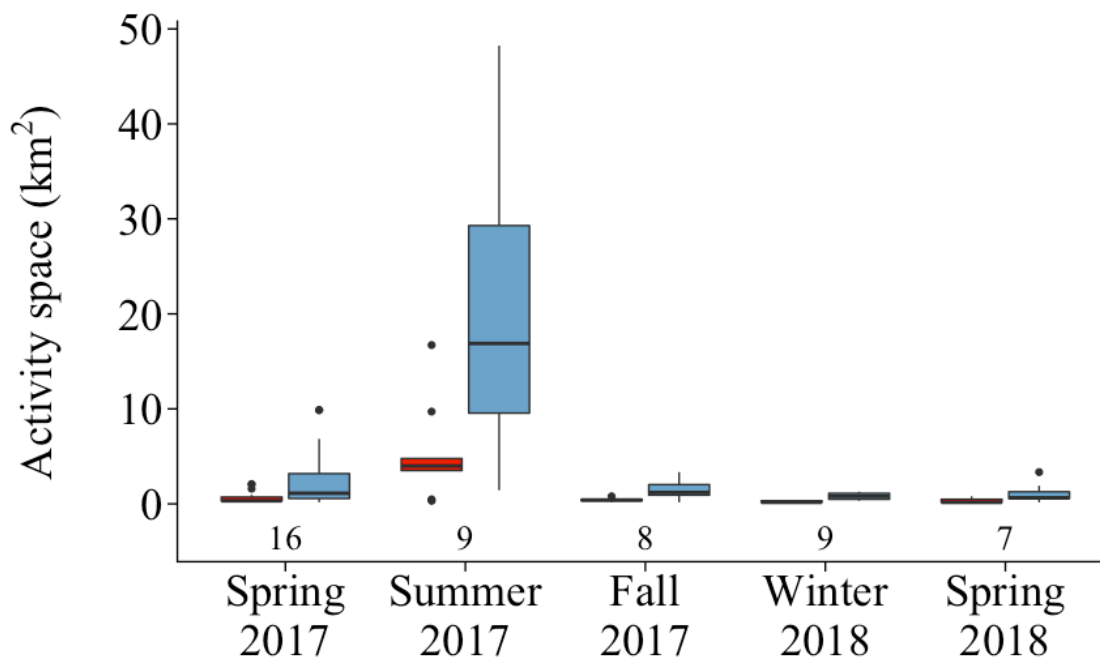


Figure 3. Distribution of estimates of 90% (blue) and 50% (red) seasonal activity space (km^2) for individual bull trout (*Salvelinus confluentus*) that were tagged with acoustic transmitters between 24 April and 8 May 2017 near the Chilko Lake outlet. Boxes represent the first (bottom) and third (top) quartiles, horizontal lines indicate the median, and vertical whiskers depict the maximum and minimum values. Outliers are shown as black dots and sample sizes are shown underneath each paired set of boxes.

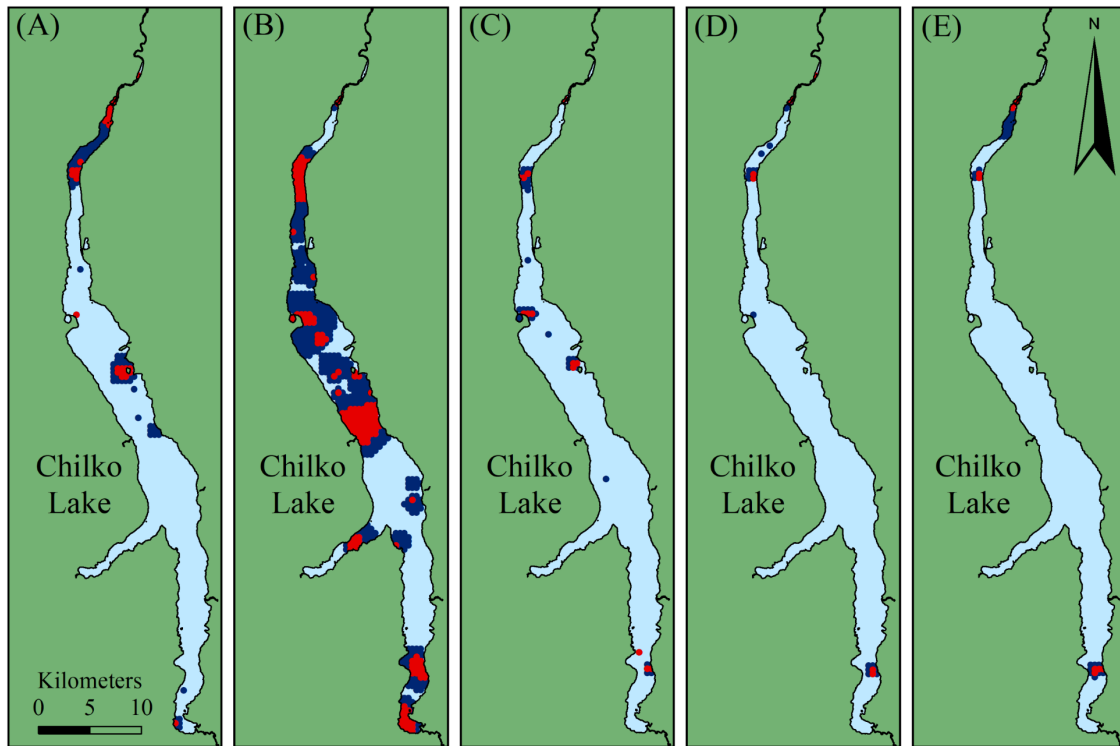


Figure 4. Seasonal home range maps (A: spring 2017; B: summer 2017; C: fall 2017; D: winter 2018; E: spring 2018) for all bull trout (*Salvelinus confluentus*) that were tagged with an acoustic transmitter between 24 April and 8 May 2017 near the Chilko Lake outlet. Dark blue areas represent the total 90% seasonal activity space and red areas represent the total 50% seasonal activity space.

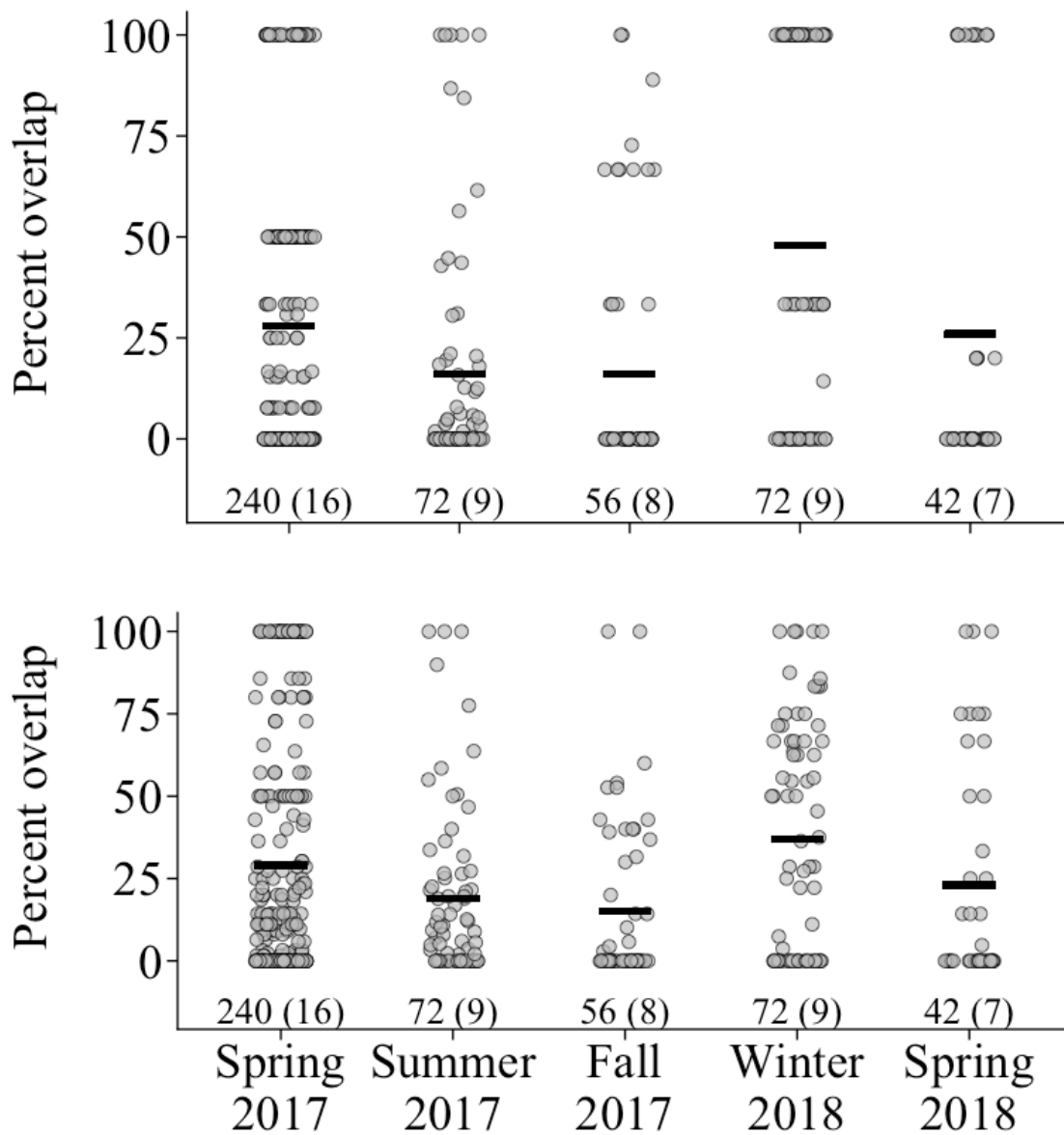


Figure 5. Percent overlap between 50% (top panel) and 90% (bottom panel) seasonal activity space (km^2) for individual bull trout (*Salvelinus confluentus*) in the Chilko Lake system between May 2017 and May 2018, inclusive. Data points represent the percent overlap between the seasonal activity space (km^2) for two individual bull trout, and solid lines represent the mean percent overlap among all individuals. Non-bracketed numbers indicate the number of activity space comparisons, while bracketed numbers indicate the number of bull trout in the sample.

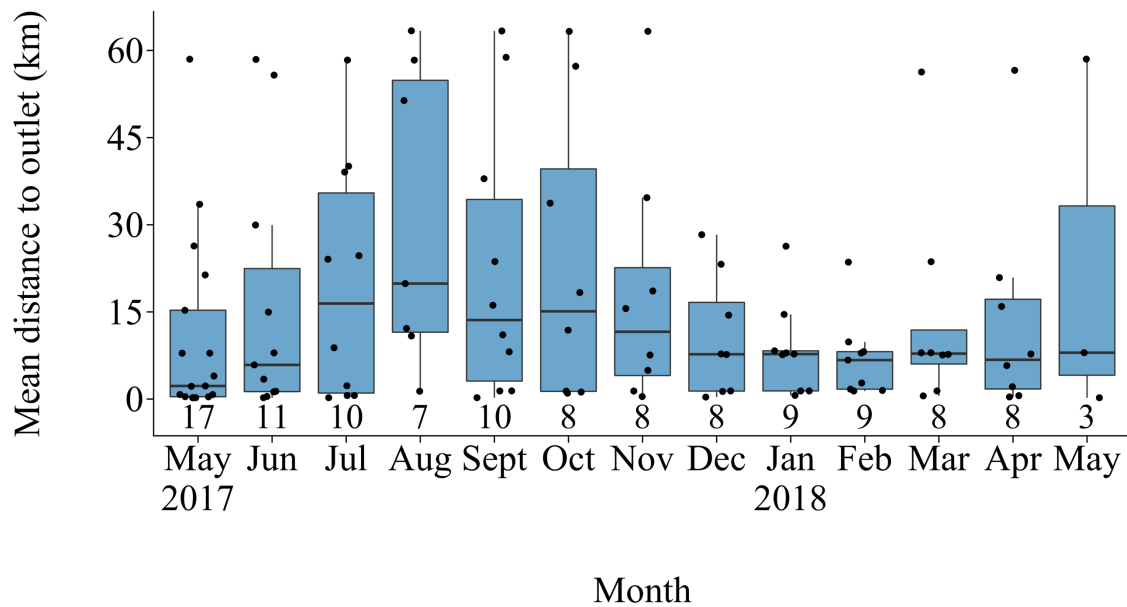


Figure 6. Distributions of mean least-cost distances (km) to the Chilko Lake outlet for bull trout (*Salvelinus confluentus*) for each month from May 2017 to May 2018, inclusive. Boxes represent the first (bottom) and third (top) quartiles, horizontal lines indicate the median, and vertical whiskers depict the maximum and minimum values. Black dots represent individual bull trout, and sample sizes are shown underneath each box.

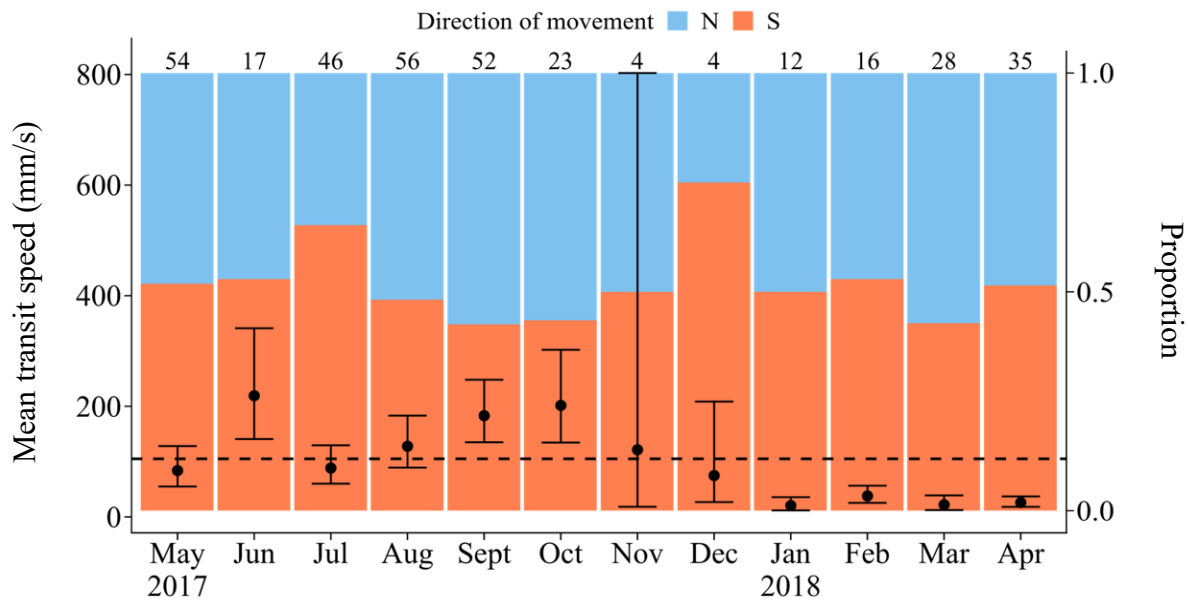


Figure 7. Back-transformed transit speeds (mm/second; mean \pm 95% CI; weighted one-sample t-test) for bull trout (*Salvelinus confluentus*) that were tagged with an acoustic transmitter near the outlet of Chilko Lake, British Columbia, between 24 April and 8 May 2017 and returned to the lake outlet in April 2018. The horizontal dashed line represents the hypothesized mean transit speed for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Stacked bars represent the proportion of bull trout movements in either the north (blue) or south (orange) direction for each month. Numbers at the top of each bar indicate the sample size of individual movements for each month.

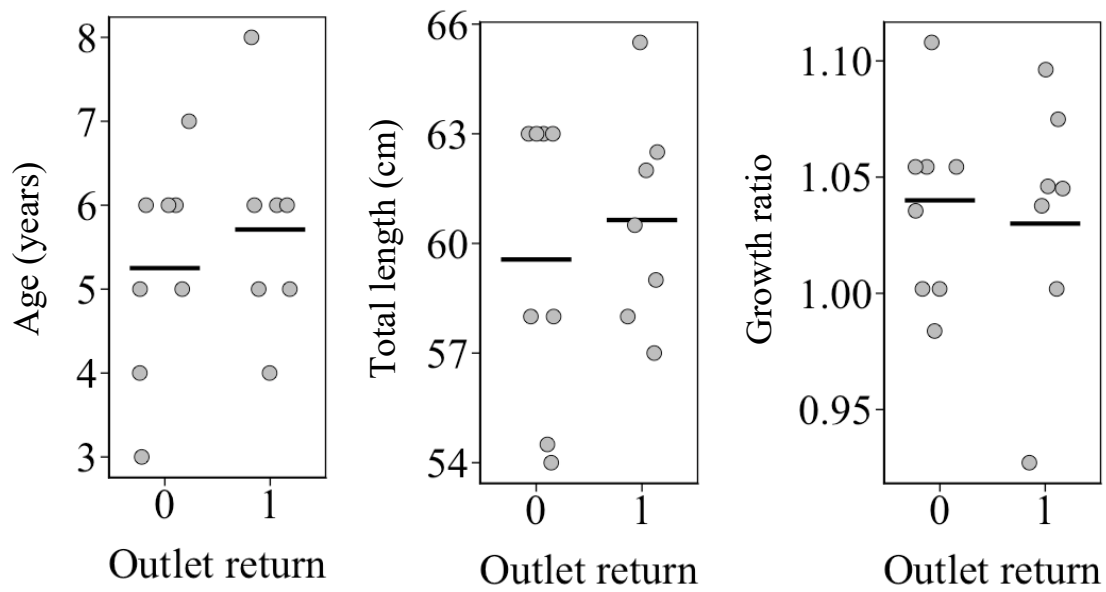


Figure 8. Ages (left plot), total lengths (center plot), and growth ratio (right plot) for bull trout (*Salvelinus confluentus*) that were not detected (0) or that were detected (1) at the outlet of Chilko Lake during the outmigration of sockeye salmon (*Oncorhynchus nerka*) smolts between April and May of 2018. Each data point represents one bull trout. Solid lines represent mean values.

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Appendix Tables

Table A1. Summary of bull trout (*Salvelinus confluentus*) that were captured in Chilko Lake and in the Chilko River between April and May 2017 (n = 68) and between April and August 2018 (n = 132). Transmitter ID is the unique identification number associated with the acoustic transmitter that was surgically implanted in the bull trout. FL = observed fork length. TL = observed total length. Age = the age of the fish in years as estimated from the analysis of pelvic fin rays. ALK age = the age of the fish in years as estimated from an age-at-length key that was created using estimates of fish age obtained from analysis of pelvic fin rays and observed TL measurements (see Table A2). Growth ratio = a measure of growth of individual bull trout relative to the average TL of individuals in the associated age class as predicted with a von Bertalanffy growth function (see Figure 2). Latitude and Longitude = the coordinates for the release location. Date = the date of capture and release.

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
1	64955	2.40	60.0	62.0	-	6	1.04	51.62146	-124.14574	2017-04-24
2	64954	2.15	59.5	62.5	6	-	1.05	51.62146	-124.14574	2017-04-24
3	64961	2.25	57.5	60.5	-	6	1.01	51.62146	-124.14574	2017-04-25
4	64960	1.80	55.0	57.0	8	-	0.93	51.62146	-124.14574	2017-04-25
5	64957	2.10	60.5	63.0	-	6	1.05	51.62146	-124.14574	2017-04-25
6	64956	2.65	60.5	63.0	6	-	1.05	51.61979	-124.14290	2017-04-25
7	64958	2.10	56.5	58.0	-	5	1.00	51.61979	-124.14290	2017-04-25
8	64959	2.40	57.5	59.0	5	-	1.02	51.61979	-124.14290	2017-04-25
9	64946	2.85	64.0	65.5	-	6	1.10	51.61815	-124.15046	2017-04-26
10	64962	2.10	57.0	58.5	5	-	1.01	51.61815	-124.15046	2017-04-26
11	64963	2.00	57.0	58.0	-	5	1.00	51.61578	-124.15213	2017-04-26
12	64952	1.50	55.5	58.0	5	-	1.00	51.62575	-124.14285	2017-04-26
13	64953	2.40	58.5	60.5	-	5	1.05	51.62575	-124.14285	2017-04-26

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
14	64949	1.60	52.0	54.0	4	-	0.99	51.62575	-124.14285	2017-04-26
15	64945	2.10	57.0	59.0	-	4	1.08	51.62575	-124.14285	2017-04-26
16	64939	3.30	61.0	63.0	-	6	1.05	51.66484	-124.10907	2017-04-29
17	64948	1.80	54.0	55.5	5	-	0.96	52.00763	-123.67853	2017-05-06
18	64940	1.75	55.5	56.5	-	6	0.95	52.00763	-123.67853	2017-05-06
19	64944	1.70	53.0	54.5	3	-	1.11	51.65155	-124.10688	2017-05-08
20	64947	3.10	61.5	63.0	-	7	1.04	51.67837	-124.10900	2017-05-08
21	-	3.25	66.5	68.0	7	-	1.12	51.61815	-124.15046	2017-04-27
22	-	2.50	58.5	60.5	-	6	1.01	51.61815	-124.15046	2017-04-27
23	-	1.90	54.0	56.0	7	-	0.92	51.61979	-124.14290	2017-04-28
24	-	3.20	65.0	67.0	7	-	1.10	51.61815	-124.15046	2017-04-30
25	-	4.00	65.5	67.0	-	7	1.10	51.61815	-124.15046	2017-04-30
26	-	1.20	50.5	52.0	4	-	0.95	51.61815	-124.15046	2017-04-30
27	-	5.70	74.5	77.0	-	6	1.29	51.62146	-124.14574	2017-05-01
28	-	4.80	77.0	79.5	6	-	1.33	51.62146	-124.14574	2017-05-01
29	-	1.80	57.0	59.5	-	5	1.03	51.62146	-124.14574	2017-05-03
30	-	1.50	49.5	51.5	-	6	0.86	51.62146	-124.14574	2017-05-03
31	-	2.25	62.5	65.5	7	-	1.08	51.62146	-124.14574	2017-05-03
32	-	1.50	51.5	54.0	5	-	0.93	51.62146	-124.14574	2017-05-03
33	-	2.00	59.5	61.0	-	7	1.00	51.62146	-124.14574	2017-05-03
34	-	2.60	62.0	63.5	6	-	1.06	51.62146	-124.14574	2017-05-03
35	-	1.60	56.5	59.0	-	5	1.02	51.62146	-124.14574	2017-05-03
36	-	2.00	52.5	54.0	4	-	0.99	51.61815	-124.15046	2017-05-07
37	-	2.10	56.0	57.0	-	6	0.95	51.61815	-124.15046	2017-05-07

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
38	-	1.80	54.0	56.0	5	-	0.97	51.61815	-124.15046	2017-05-07
39	-	1.80	57.5	59.0	-	5	1.02	51.27391	-124.02377	2017-05-07
40	-	1.80	51.0	53.0	3	-	1.08	51.61815	-124.15046	2017-05-07
41	-	2.10	57.0	58.0	-	5	1.00	51.61815	-124.15046	2017-05-07
42	-	3.10	66.0	67.5	4	-	1.23	51.61815	-124.15046	2017-05-07
43	-	1.70	53.0	54.0	-	4	0.99	51.61815	-124.15046	2017-05-07
44	-	2.20	58.0	59.5	5	-	1.03	51.61815	-124.15046	2017-05-07
45	-	2.30	58.5	59.5	-	4	1.09	51.61815	-124.15046	2017-05-07
46	-	1.60	51.0	53.0	5	-	0.92	51.61815	-124.15046	2017-05-07
47	-	1.40	51.0	53.0	-	5	0.92	51.61815	-124.15046	2017-05-07
48	-	1.90	56.0	59.0	4	-	1.08	51.61815	-124.15046	2017-05-07
49	-	2.20	57.0	59.5	-	5	1.03	51.61815	-124.15046	2017-05-07
50	-	1.70	53.5	55.5	6	-	0.93	51.62575	-124.14285	2017-05-07
51	-	3.40	66.0	68.0	-	5	1.17	51.62575	-124.14285	2017-05-07
52	-	2.30	59.0	61.0	5	-	1.05	51.61815	-124.15046	2017-05-09
53	-	1.80	55.0	56.0	-	5	0.97	51.61815	-124.15046	2017-05-09
54	-	1.90	55.0	56.0	5	-	0.97	51.61815	-124.15046	2017-05-09
55	-	1.70	58.5	59.0	-	5	1.02	51.61815	-124.15046	2017-05-09
56	-	1.80	55.5	57.0	4	-	1.04	51.61815	-124.15046	2017-05-09
57	-	1.20	49.5	51.0	-	4	0.93	51.62146	-124.14574	2017-05-09
58	-	1.30	50.5	52.5	5	-	0.91	51.61815	-124.15046	2017-05-10
59	-	1.80	55.0	56.0	-	7	0.92	51.61815	-124.15046	2017-05-10
60	-	1.20	46.5	48.0	5	-	0.83	51.61815	-124.15046	2017-05-10
61	-	1.70	54.5	56.0	-	5	0.97	51.61815	-124.15046	2017-05-10

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
62	-	2.60	63.0	64.0	7	-	1.05	51.61815	-124.15046	2017-05-10
63	-	1.90	55.0	56.5	-	7	0.93	51.61815	-124.15046	2017-05-10
64	-	3.30	64.0	65.5	6	-	1.10	51.62575	-124.14285	2017-05-10
65	-	1.90	54.0	56.0	-	6	0.94	51.62575	-124.14285	2017-05-10
66	-	2.70	64.0	65.5	6	-	1.10	51.62575	-124.14285	2017-05-12
67	-	1.30	52.5	54.0	-	5	0.93	51.62575	-124.14285	2017-05-12
68	-	5.50	72.5	73.0	4	-	1.33	51.62575	-124.14285	2017-05-12
69	-	1.30	53.0	55.0	4	-	1.01	51.61950	-124.14540	2018-04-20
70	-	2.90	67.0	68.5	7	-	1.13	51.61950	-124.14540	2018-04-20
71	-	3.20	66.0	67.0	7	-	1.10	51.61950	-124.14540	2018-04-20
72	-	2.10	62.5	64.0	8	-	1.04	51.61950	-124.14540	2018-04-20
73	-	2.25	61.0	63.0	6	-	1.05	51.61950	-124.14540	2018-04-20
74	-	2.60	62.0	64.0	5	-	1.11	51.61950	-124.14540	2018-04-20
75	-	2.75	59.5	62.0	6	-	1.04	51.61950	-124.14540	2018-04-20
76	-	3.70	70.5	72.0	7	-	1.18	51.65155	-124.10688	2018-04-21
77	-	2.20	58.5	60.5	6	-	1.01	51.65155	-124.10688	2018-04-21
78	-	2.70	62.0	63.5	7	-	1.04	51.65155	-124.10688	2018-04-21
79	-	1.40	58.5	61.0	6	-	1.02	51.61815	-124.15046	2018-04-22
80	-	1.90	57.5	60.0	7	-	0.99	51.61815	-124.15046	2018-04-22
81	-	1.70	58.0	60.5	5	-	1.05	51.61815	-124.15046	2018-04-22
82	-	2.55	59.5	60.0	5	-	1.04	51.61815	-124.15046	2018-04-22
83	-	1.40	52.0	54.0	5	-	0.93	51.61815	-124.15046	2018-04-22
84	-	3.15	69.0	69.0	6	-	1.15	51.65155	-124.10688	2018-04-23
85	-	3.20	66.0	66.5	5	-	1.15	51.65155	-124.10688	2018-04-23

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
86	-	2.25	62.0	63.0	5	-	1.09	51.65155	-124.10688	2018-04-23
87	-	1.85	57.5	59.0	5	-	1.02	51.65155	-124.10688	2018-04-23
88	-	1.80	54.0	56.0	5	-	0.97	51.65155	-124.10688	2018-04-23
89	-	2.00	56.5	58.5	5	-	1.01	51.65155	-124.10688	2018-04-23
90	-	3.50	66.0	67.0	7	-	1.10	51.65155	-124.10688	2018-04-23
91	-	2.60	63.5	65.5	6	-	1.10	51.65155	-124.10688	2018-04-23
92	-	0.90	45.0	45.5	3	-	0.92	51.65155	-124.10688	2018-04-23
93	-	3.15	66.0	69.0	6	-	1.15	51.65155	-124.10688	2018-04-23
94	-	1.80	55.5	57.5	6	-	0.96	51.61578	-124.15213	2018-04-24
95	-	2.00	56.5	59.0	4	-	1.08	51.61578	-124.15213	2018-04-24
96	-	1.45	52.0	54.0	5	-	0.93	51.61578	-124.15213	2018-04-24
97	-	3.70	72.0	73.0	8	-	1.19	51.65155	-124.10688	2018-04-25
98	-	2.60	66.5	67.0	8	-	1.09	51.65155	-124.10688	2018-04-25
99	-	2.50	63.0	65.0	5	-	1.12	51.65155	-124.10688	2018-04-25
100	-	3.00	66.0	67.0	7	-	1.10	51.65155	-124.10688	2018-04-25
101	-	2.05	59.0	61.0	7	-	1.00	51.65155	-124.10688	2018-04-25
102	-	1.65	53.0	54.0	6	-	0.90	51.65155	-124.10688	2018-04-25
103	-	2.80	69.0	70.0	8	-	1.14	51.65155	-124.10688	2018-04-25
104	-	2.90	64.0	64.5	7	-	1.06	51.65545	-124.10840	2018-04-25
105	-	2.10	57.0	58.5	6	-	0.98	51.65545	-124.10840	2018-04-25
106	-	1.75	56.0	56.5	6	-	0.95	51.65545	-124.10840	2018-04-25
107	-	1.60	49.5	50.0	3	-	1.02	51.65545	-124.10840	2018-04-25
108	-	1.50	51.5	52.5	4	-	0.96	51.65545	-124.10840	2018-04-25
109	-	2.45	60.0	61.0	9	-	0.99	51.65545	-124.10840	2018-04-25

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
110	-	1.10	49.0	50.0	3	-	1.02	51.65545	-124.10840	2018-04-25
111	-	1.70	56.5	57.0	5	-	0.98	51.65545	-124.10840	2018-04-25
112	-	0.90	45.0	45.5	3	-	0.92	51.65545	-124.10840	2018-04-25
113	-	1.60	52.5	53.0	4	-	0.97	51.65545	-124.10840	2018-04-25
114	-	0.95	44.0	44.5	4	-	0.81	51.65545	-124.10840	2018-04-25
115	-	1.65	52.0	53.0	4	-	0.97	51.65545	-124.10840	2018-04-25
116	-	2.30	63.0	65.0	5	-	1.12	51.65545	-124.10840	2018-04-25
117	-	2.30	57.0	58.0	4	-	1.06	51.65545	-124.10840	2018-04-25
118	-	2.70	67.5	68.0	5	-	1.17	51.65155	-124.10688	2018-04-26
119	-	2.60	63.0	64.5	5	-	1.11	51.65155	-124.10688	2018-04-26
120	-	1.20	51.5	52.0	3	-	1.06	51.65545	-124.10840	2018-04-26
121	-	1.70	53.0	53.5	4	-	0.98	51.65545	-124.10840	2018-04-26
122	-	2.90	62.0	63.0	5	-	1.09	51.65545	-124.10840	2018-04-26
123	-	1.45	52.0	52.5	4	-	0.96	51.65545	-124.10840	2018-04-26
124	-	1.50	52.0	53.0	5	-	0.92	51.65545	-124.10840	2018-04-26
125	-	1.35	49.0	50.0	4	-	0.91	51.65545	-124.10840	2018-04-26
126	-	2.55	61.5	62.0	6	-	1.04	51.65545	-124.10840	2018-04-26
127	-	1.45	50.5	51.0	5	-	0.88	51.65545	-124.10840	2018-04-26
128	-	1.50	50.0	51.0	4	-	0.93	51.65545	-124.10840	2018-04-26
129	-	1.70	53.0	53.5	4	-	0.98	51.65545	-124.10840	2018-04-26
130	-	2.25	59.5	59.5	5	-	1.03	51.65545	-124.10840	2018-04-26
131	-	2.55	59.0	60.0	7	-	0.99	51.65155	-124.10688	2018-04-29
132	-	3.10	66.0	67.0	5	-	1.16	51.65545	-124.10840	2018-04-29
133	-	1.50	52.5	53.0	6	-	0.89	51.65545	-124.10840	2018-04-29

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
134	-	1.90	55.5	56.0	5	-	0.97	51.65545	-124.10840	2018-04-29
135	-	3.30	69.0	69.0	6	-	1.15	51.65545	-124.10840	2018-04-29
136	-	1.50	53.5	54.0	5	-	0.93	51.65545	-124.10840	2018-04-29
137	-	1.85	55.0	55.5	5	-	0.96	51.61815	-124.15046	2018-05-02
138	-	4.30	71.0	71.5	7	-	1.18	51.61815	-124.15046	2018-05-03
139	-	2.00	57.8	65.2	6	-	1.09	51.53635	-124.19250	2018-05-09
140	-	3.10	73.0	74.1	8	-	1.21	51.52830	-124.18984	2018-05-09
141	-	1.60	55.2	56.0	7	-	0.92	51.54198	-124.19302	2018-05-09
142	-	1.80	58.1	59.5	5	-	1.03	51.52696	-124.18950	2018-05-09
143	-	2.20	63.0	66.1	6	-	1.11	51.53647	-124.19167	2018-05-09
144	-	1.85	59.4	61.7	7	-	1.01	51.56403	-124.18879	2018-05-09
145	-	1.15	55.3	56.1	6	-	0.94	51.55841	-124.19299	2018-05-09
146	-	1.80	61.3	63.6	7	-	1.05	51.56007	-124.19204	2018-05-09
147	-	1.05	49.6	51.7	7	-	0.85	51.56575	-124.18588	2018-05-09
148	-	1.10	47.3	49.4	4	-	0.90	51.56842	-124.18311	2018-05-10
149	-	1.90	57.1	59.9	5	-	1.03	51.56488	-124.18636	2018-05-10
150	-	2.60	63.5	64.7	6	-	1.08	51.56601	-124.18550	2018-05-10
151	-	1.10	49.0	51.3	5	-	0.89	51.56601	-124.18550	2018-05-10
152	-	1.60	56.5	57.7	7	-	0.95	51.56028	-124.19141	2018-05-10
153	-	2.15	60.5	61.5	9	-	0.99	51.54368	-124.19370	2018-05-10
154	-	1.55	54.7	55.5	5	-	0.96	51.54180	-124.19392	2018-05-10
155	-	0.90	44.5	46.4	7	-	0.76	51.22866	-124.11480	2018-07-30
156	-	1.00	48.0	50.5	4	-	0.92	51.27688	-124.09013	2018-07-30
157	-	1.60	51.3	54.6	6	-	0.91	51.27688	-124.09013	2018-07-30

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
158	-	0.75	49.0	50.5	4	-	0.92	51.27688	-124.09013	2018-07-30
159	-	1.05	45.5	46.6	4	-	0.85	51.27688	-124.09013	2018-07-30
160	-	1.40	53.0	55.0	5	-	0.95	51.36420	-124.15461	2018-07-31
161	-	0.90	49.7	51.6	5	-	0.89	51.36420	-124.15461	2018-07-31
162	-	1.40	54.5	55.0	5	-	0.95	51.27688	-124.09013	2018-07-31
163	-	1.30	53.6	55.4	5	-	0.96	51.27688	-124.09013	2018-07-31
164	-	1.30	49.3	50.0	4	-	0.91	51.32597	-124.11556	2018-07-31
165	-	1.45	53.0	55.1	5	-	0.95	51.32597	-124.11556	2018-07-31
166	-	1.00	47.4	48.0	5	-	0.83	51.32597	-124.11556	2018-07-31
167	-	2.20	64.8	66.1	8	-	1.08	51.32597	-124.11556	2018-07-31
168	-	1.70	57.3	59.0	7	-	0.97	51.32597	-124.11556	2018-07-31
169	-	0.90	45.3	47.9	5	-	0.83	51.32597	-124.11556	2018-07-31
170	-	1.80	64.2	65.3	8	-	1.06	51.28011	-124.02318	2018-07-31
171	-	0.85	47.3	48.2	7	-	0.79	51.32283	-124.06110	2018-07-31
172	-	1.00	49.4	50.3	6	-	0.84	51.32283	-124.06110	2018-07-31
173	-	0.80	49.4	51.3	7	-	0.84	51.32283	-124.06110	2018-07-31
174	-	0.80	47.9	49.2	6	-	0.82	51.32283	-124.06110	2018-07-31
175	-	1.70	55.7	57.5	7	-	0.95	51.32283	-124.06110	2018-07-31
176	-	2.00	59.6	62.5	8	-	1.02	51.32283	-124.06110	2018-07-31
177	-	1.00	46.5	48.0	4	-	0.88	51.20784	-124.00998	2018-08-01
178	-	1.00	51.7	53.0	4	-	0.97	51.20784	-124.00998	2018-08-01
179	-	1.40	53.9	55.0	6	-	0.92	51.20784	-124.00998	2018-08-01
180	-	0.70	44.9	45.5	4	-	0.83	51.20784	-124.00998	2018-08-01
181	-	0.70	42.7	44.0	5	-	0.76	51.25200	-124.02332	2018-08-01

ID	Transmitter ID	Mass (kg)	FL (cm)	TL (cm)	Age	ALK age	Growth ratio	Latitude	Longitude	Date
182	-	1.25	52.2	54.9	5	-	0.95	51.25200	-124.02332	2018-08-01
183	-	1.65	58.2	59.5	8	-	0.97	51.27391	-124.02377	2018-08-01
184	-	0.90	48.3	50.2	5	-	0.87	51.27391	-124.02377	2018-08-01
185	-	1.80	57.5	59.0	6	-	0.99	51.61815	-124.15046	2018-08-01
186	-	1.70	58.3	61.0	6	-	1.02	51.27391	-124.02377	2018-08-01
187	-	1.50	54.9	57.2	7	-	0.94	51.27391	-124.02377	2018-08-01
188	-	1.70	57.8	59.9	5	-	1.03	51.34030	-124.13506	2018-08-01
189	-	0.70	39.8	41.0	4	-	0.75	51.34030	-124.13506	2018-08-01
190	-	0.80	43.0	45.1	3	-	0.92	51.34030	-124.13506	2018-08-01
191	-	1.30	54.7	57.0	5	-	0.98	51.34030	-124.13506	2018-08-01
192	-	1.40	50.8	53.0	6	-	0.89	51.48878	-124.19064	2018-08-02
193	-	0.80	43.0	44.2	5	-	0.76	51.48878	-124.19064	2018-08-02
194	-	1.10	48.0	50.1	4	-	0.92	51.48878	-124.19064	2018-08-02
195	-	1.40	52.0	54.5	5	-	0.94	51.47012	-124.17652	2018-08-02
196	-	1.10	48.0	49.5	4	-	0.91	51.47012	-124.17652	2018-08-02
197	-	1.60	56.0	58.0	7	-	0.95	51.47012	-124.17652	2018-08-02
198	-	0.90	44.0	46.0	4	-	0.84	51.47012	-124.17652	2018-08-02
199	-	1.50	54.0	56.8	7	-	0.93	51.47012	-124.17652	2018-08-02
200	-	1.20	49.0	50.5	5	-	0.87	51.47012	-124.17652	2018-08-02

Table A2. An age-length key (ALK) for bull trout (*Salvelinus confluentus*) captured in Chilko Lake and in the Chilko River, British Columbia, between April and May 2017 and between April and August 2018. The ALK was constructed using estimates of fish age obtained from analysis of pelvic fin rays and observed total length measurements. It was used to assign ages to unaged bull trout based on the length interval to which the individual belonged.

Length interval (cm)	Estimated age (years)						
	3	4	5	6	7	8	9
40.0 - 44.9	0.32	0.45	0.21	0.02	0.01	0.00	0.00
45.0 - 49.9	0.18	0.41	0.33	0.05	0.03	0.00	0.00
50.0 - 54.9	0.08	0.30	0.41	0.12	0.08	0.01	0.01
55.0 - 59.9	0.03	0.16	0.39	0.21	0.16	0.03	0.01
60.0 - 64.9	0.01	0.07	0.29	0.29	0.24	0.08	0.02
65.0 - 69.9	0.00	0.02	0.17	0.32	0.29	0.17	0.02
70.0 - 74.9	0.00	0.01	0.08	0.29	0.30	0.30	0.03
75.0 - 79.9	0.00	0.00	0.03	0.22	0.26	0.46	0.02