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Effects of Tag Type and Environment on Migratory Success of Sockeye Salmon (Oncorhynchus nerka) Smolts Through a Counting Fence

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Effects of Tag Type and Environment on Migratory Success of Sockeye Salmon
(*Oncorhynchus nerka*) Smolts Through a Counting Fence

By

Tyler Parent

Bachelor of Science, Wildlife and Fisheries Biology

University of Vermont, 2014

Thesis

Submitted to the University of New Hampshire

In Partial Fulfillment of

The Requirements for the Degree of

Master of Science

In

Biological Sciences: Integrative and Organismal Biology

May, 2023

This thesis was examined and approved in partial fulfillment if the requirements for the degree of

Master of Science in Biological Sciences: Integrative and Organismal Biology by:

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On March 20th, 2023

Approval signatures are on file with the University of New Hampshire Graduate School.

Acknowledgements

More than anyone, I need to thank my wife, Val. We have really been grinding to build our lives for the last few years. Your support as I worked towards my graduate degree has been so important to my success and added challenges such as COVID and my surgery have certainly made things even harder. Thank you.

Next, I'd like to thank my family for being the best cheerleaders ever and for never questioning my crazy plan to get my degree while I continue to work full time. I am lucky to have so many role models in my family to inspire me to pursue another degree. You all have helped me to unwind and de-stress whenever we spend time together and that has helped me more than you know.

I also need to say a huge thank you to my advisor, Dr. Nathan Furey. You took a big risk by accepting me as a student knowing that I would take longer to finish my degree than a full-time student and that I would have less time in a week to devote to school. I know it hasn't always been easy, but I so appreciate the opportunity you gave me. I also can't forget the other students from the Furey Lab! There were tons of instances when I needed assistance with challenges in my code, and the lab came to my rescue and taught me so much.

In addition to my advisor, I would like to thank my other Committee members Dr. Adrienne Kovach and Dr. Scott Hinch. Your guidance and patience as I worked through my degree for longer than a typical student is so appreciated.

I was very lucky to have the opportunity to work with high quality existing data that originated from projects at the University of British Columbia. Thank you to everyone who is a part of the Pacific Salmon Ecology and Conservation Laboratory at UBC who helped to collect

the dataset and for allowing me to use it in pursuit of my degree. In addition, I would like to thank the Xeni Gwet'in First Nation for allowing this research to be conducted on your land.

Thanks to all of you for this experience.

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Abstract

Understanding behavior and quantifying survival is vital to the conservation of anadromous fishes. Sockeye Salmon (*Oncorhynchus nerka*) are one of the most economically and culturally important fish in the world, but some populations are declining, particularly in the Fraser River watershed in British Columbia, Canada. Within the Fraser River basin, Chilko Lake is one of the most prolific Sockeye Salmon populations, and Fisheries and Oceans Canada (DFO) has operated a counting fence at the mouth of the river for several decades to enumerate outmigrating smolts. Previous studies identified the clear water landscapes immediately downstream of the fence as high-risk, with high mortality of migrating smolts relative to larger, more turbid systems further downstream. In this thesis, I used passive integrative transponder (PIT, n = 358 age-1 smolts and n = 251 age-2 smolts) and acoustic telemetry (n = 208 age-2 smolts) to assess behavior and estimate survival of Chilko Lake Sockeye Salmon smolts in the 1.3-km upstream of the counting fence. Mark-recapture Cormack-Jolly-Seber models indicate that this 1.3-km stretch of the migration is high-risk (survival ranging from 37.7% - 62.2%). Survival estimates were similar among age classes and tag types, but age-2 fish may experience slightly higher survival than age-1 fish, with age-1 fish representing ~96% of the outmigrating population. Travel duration from release to the counting fence varied widely (1.3 hours – ~18 days days), suggesting complex behavioral patterns in this specific area. After investigating several covariates, fork length, mass, and a condition metric (residuals of a mass-length relationship) appeared correlated with survival, but the directions of relationships were not consistent across age and tag types. Further investigations of fine-scale behavioral patterns revealed that it is common for smolts to make several attempts to pass the fence, potentially causing delay and a depletion of energy stores. Consistent with previous studies, I presented

evidence that increased co-migrant density appears to promote successful escapement at the fence. I identified a new high-mortality landscape and showed that a counting fence used by fisheries managers annually over the past 70 years is likely negatively affecting survival and the timely passage of out-migrating smolts.

CHAPTER 1: Introduction

1.2 Pacific Salmon

Pacific salmon (*Oncorhynchus* spp.) are one of the most valuable natural resources on the planet, both economically (Pacific Salmon Commission 2017) and culturally (Groot and Margolis 1991). The status of global populations varies widely with some regionally at record highs while others are in decline (Ruggerone and Irvine 2018). Even populations that are not in decline are seeing other potentially negative changes such as reductions in average body size (Oke et al. 2020). A variety of stressors are contributing to these observed impacts including competition at sea (Ruggerone and Irvine 2018) and warming waters (Islam et al. 2019). External stressors combined with the complex life histories exhibited by salmon can produce many potential bottlenecks that could impact productivity.

1.3 Salmon Life History

Pacific salmon are semelparous and anadromous, with many populations exhibiting long-distance and high-volume migrations (Groot and Margolis 1991; Quinn 2018). At maturity, adults migrate from the ocean to their natal freshwater system to reproduce (Groot and Margolis 1991; Quinn 2018). After spending one or more years progressing through early developmental stages (egg, alevin, fry), the smoltification process begins, during which individuals are drawn to migrate downstream to the ocean (Groot and Margolis 1991). Once a juvenile salmon (called a smolt at this stage) has begun the journey to the ocean, it confronts an entirely new set of challenges, including exposure to new predators (Tucker et al. 2016; Thomas et al. 2017; Nelson et al. 2019), novel infectious agents (Nendick et al. 2011), and changing water quality conditions

including saltwater (Burgner 1991; Quinn 2018), requiring complex physiological changes. These new challenges can have implications for survival.

1.4 Smolt Survival

Juvenile to adult productivity can correlate more strongly with overall population productivity of salmon than spawner to juvenile productivity (Peterman et al. 2010). Thus, it is imperative to identify and understand drivers of variability in survival of downstream migrating smolts to maximize our predictive power of future adult returns. Mortality of smolts as they migrate downstream and in coastal waters can be high and variable. For example, hatchery Sockeye Salmon (*Oncorhynchus nerka*) smolts migrating from Cultus Lake in British Columbia experienced freshwater survival between 50% and 70% and early marine survival between 10% and 30% (Welch et al. 2009) while wild Steelhead (*Oncorhynchus mykiss*) smolts migrating from the Green River through Puget Sound, Washington had an estimated freshwater survival probability of 79.5% ± 2.1 and early marine survival probability to be 12.1% ± 4.4 (Goetz et al. 2015). With mortality high and variable, even a small increase in smolt survival could result in substantial increases in productivity.

Both physical and environmental factors can influence the migratory success of smolts (Hartman et al. 1967; Reed et al. 2010; Griswold et al. 2011). Predators can be a significant source of mortality during migration (Larsson 1985; Furey et al. 2015, 2016b) and include increasing presence of seals (Thomas et al. 2017; Nelson et al. 2019) and birds (Hostetter et al. 2012; Tucker et al. 2016; Evans et al. 2016, 2019, 2022) as smolts approach marine habitat. Infectious agents, including microparasites and viruses (Miller et al. 2014; Furey et al. 2021a) as well as macroparasites such as sea lice (Nendick et al. 2011) can reduce the fitness of a smolt through reductions in foraging efficiency (Godwin et al. 2015, 2018) and growth (Godwin et al.

2017), and increase the likelihood of mortality. In response to these challenges, smolts can exhibit behavioral adaptations to minimize risks and exposure (Hartman et al. 1967). Examples include predator swamping (Furey et al. 2016a), traveling at night (Hartman et al. 1967; Ibbotson et al. 2011; Goetz et al. 2015; Clark et al. 2016), and taking advantage of higher river flows to both reduce travel time (Smith et al. 2002; Griswold et al. 2011) and gain the cover of turbidity (Hembre et al. 2001).

1.5 Influences of Barriers on Juvenile Salmon

Smolt survival can also be influenced by anthropogenic barriers, both directly and indirectly. A disproportionate amount of research has been conducted to determine impacts to diadromous fish caused by large, permanent barriers such as dams (Silva et al. 2018; Hinch et al. 2022). In the case of large hydroelectric dams, direct mortality is possible via interaction with the power production turbines (Mathur et al. 2011). Even without directly causing mortality, barriers can cause delay (Venditti et al. 2000; Marschall et al. 2011; Nyqvist et al. 2017b) or confusion and energy depletion (Hinch et al. 2022), which can presumably affect success downstream. Comparatively, smaller and sometimes temporary barriers have received little attention. Results from the more limited research focused on smaller, non-hydropower structures show a lack of consensus, with some studies showing limited impacts (Newton et al. 2019) and others suggesting that mortality from smaller structures like a weir can be similar to that through a hydroelectric turbine (Havn et al. 2020). The lack of consensus on this topic suggests that anthropogenic barriers need to be individually assessed before any assumptions regarding behavioral or survival impacts can be made.

1.6 Monitoring Movements with Telemetry

Biotelemetry has become a prominent research tool as miniaturization of technology continues to progress (Wilmers et al. 2015). In particular, acoustic telemetry is often used to track the movements of aquatic organisms (Hussey et al. 2015) and has been used extensively to unveil the migration ecology of salmon smolts (Welch et al. 2009; Melnychuk et al. 2010; Rechisky et al. 2013, 2019; Stich et al. 2014; Brosnan et al. 2014; Goetz et al. 2015; Lothian et al. 2018). Acoustic telemetry has allowed researchers to track smolts over vast distances during their migration through rivers and estuarine environments en route to the open ocean. Additionally, migratory routes can be compartmentalized into distinct segments for individual survival assessment (Clark et al. 2016; Lothian et al. 2018). These data allow researchers to compare behavior and survival outcomes over specific landscapes with a host of other measurable factors (Donaldson et al. 2014). Such studies traditionally used acoustic telemetry receivers at distinct but disparate locations to assess migrations over broad scales. However, a densely deployed array of acoustic telemetry receivers over a small area can be used to triangulate animal positions to reveal fine-scale patterns of movement from tagged individuals (Espinoza et al. 2011), allowing for more complex analyses such as characterization of movement types (Breed et al. 2012; Bacheler et al. 2019), identification of important correlates of space use (Furey and Rooker 2013; Alós et al. 2016), and determination of behavioral states (Whoriskey et al. 2017).

One potential limitation of telemetry, particularly when used with fish as small as salmon smolts, is induced tag burden (Brown et al. 2010). Tag burden is defined as the weight of a tag relative to the weight of the fish receiving the tag, generally calculated as a percentage of the mass of the fish (i.e.., (tag mass/fish mass)*100). Tag burdens can impact studies because excessive burdens may result in tagged fish not being representative of the untagged population,

violating a general assumption of tagging studies (Greenstreet and Morgan 1989; Peake et al. 1997; Adams et al. 1998; Collins et al. 2013). Other telemetry tags, primarily Passive Integrated Transponder (PIT) tags, are much smaller but have a reduced detection radius relative to acoustic tags. The lack of an on-board battery allows PIT tags to remain extremely small and a tag can remain operational for the entire life of a tagged organism (Gibbons and Andrews 2004). Thus, PIT tags are more limited in their use but may impose lower tag burdens, potentially leading to differences in behavior or survival. PIT tags have been successfully used to characterize behavior (Teixeira and Cortes 2007; Chase et al. 2013) and estimate survival (Welch et al. 2008; Murauskas et al. 2021) of salmon smolts.

1.7 Sockeye Salmon and the Chilko Lake Population

One particularly important species of Pacific salmon, Sockeye Salmon (*Oncorhynchus nerka*), have been in decline at the southern edge of their range, including British Columbia, Canada. Warm ocean conditions and abnormally high levels of competition at sea have induced declines in productivity (Connors et al. 2020). The warming trend is also evident in freshwater, and over time, increases in freshwater temperatures in spawning and migratory habitat may constrict the number of days when temperatures are suitable for activities imperative to this individuals completing their life cycle (Islam et al. 2019). As with other pacific salmon, the complexity of the Sockeye Salmon life history, particularly during migration, facilitates many opportunities for bottlenecks that can impact successful recruitment. At maturity, Sockeye Salmon adults migrate from the ocean to their native freshwater systems to reproduce (Burgner 1991; Quinn et al. 2009). After spending 1 to 3 years progressing through developmental stages (egg, alevin, and fry) in freshwater, Sockeye Salmon juveniles "smoltify" and begin their seaward migration (Burgner 1991; Quinn et al. 2009). Of particular concern are the Sockeye

Salmon populations native to the southern portion of their range, including British Columbia, Canada, where population declines have been most severe (Connors et al. 2020).

The Fraser River watershed in British Columbia, Canada hosts dozens of distinct spawning populations of Sockeye Salmon, constituting one of the most productive rivers in the world for the species (Northcote and Larkin 1989). As a result, a large portion of Sockeye Salmon research worldwide has occurred in the Fraser River watershed (Martins et al. 2012). Fraser River Sockeye Salmon smolts exhibit seaward migration almost exclusively as yearlings with only a select few waiting one more year to smoltify (Burgner 1991). In the Fraser River, predicting adult returns has become more difficult over time. In 2009, Sockeye Salmon adult returns were the lowest they have been since 1947, leading to a judicial inquiry from the Canadian Government (Cohen 2012). The very next year, in 2010, adult returns were among the highest of the previous century, proving just how difficult it is to predict returns. Then in 2019, the Big Bar landslide temporarily blocked adult Fraser River salmon from upstream migration. Conservation and management would be aided with increased precision in life-stage-specific survival estimates, and further portioning of survival estimates that represent multiple life stages, such as smolt-to-adult (SAR) survival.

One of the most productive Sockeye Salmon populations in the Fraser River watershed occurs at Chilko Lake, with an average of ~ 20 million Sockeye Salmon smolts leaving the lake each spring (Irvine and Akenhead 2013). In addition to being a large population, Chilko Lake smolts travel downriver through the low turbidity water of the Chilko and Chilcotin Rivers before reaching the relative safety of the more turbid Fraser River (Clark 2016; Rechisky et al. 2019). Chilko smolts are age-1 (spawned ~18 months ago) or age-2 (spawned ~30 months ago) when they begin to emigrate, with only 4-5% of the run being age-2 in any given year (Irvine

and Akenhead 2013). Age-2 outmigrants have average lengths 35-mm longer than age-1 fish, but their survival in freshwater (Stevenson et al. 2019b) and to adulthood appear similar (Irvine and Akenhead 2013). However, other studies suggest a positive correlation between fork length of outmigrant Chilko Lake smolts and smolt to adult survival (Henderson and Cass 1991; Bradford et al. 2000). Previous studies assessed the survival of Chilko Lake smolts either broadly (e.g. SAR; Irvine and Akenhead 2013) or via telemetry through freshwater and estuarine landscapes (Jeffries et al. 2014; Clark 2016; Furey et al. 2016a; Rechisky et al. 2019; Stevenson et al. 2019b, 2020; Bass et al. 2020). These studies have successfully compartmentalized the migratory route of Chilko Lake smolts, characterizing landscape-specific trends in survival and behavior (Clark 2016; Furey et al. 2016a; Stevenson et al. 2019b) and revealing much about the migration ecology of these fish.

1.8 Current Knowledge

Acoustic telemetry has identified that for Chilko Lake Sockeye Salmon smolts, the first segment of the migration in the Chilko River is consistently high-risk (i.e., high mortality relative to downstream migratory segments) among years (Clark 2016; Rechisky et al. 2019), resulting in further explorations regarding smolt behavior and potential mechanisms of mortality. Chilko Lake Sockeye Salmon smolts exhibit nocturnal movements while in the low turbidity water of the Chilko River and the Chilcotin River (Clark et al. 2016; Furey et al. 2016a). It also appears that smolts can synchronize their movements to migrate in high densities to numerically overwhelm or swamp predators (Furey et al. 2016a, 2021b). Both swamping and nocturnal migration are thought to be in response to the presence of visual predators such as Bull Trout (*Salvelinus confluentus*), which also travel to the area (Furey and Hinch 2017) to feed extensively on the outmigrant smolts (Furey et al. 2016a, 2016b; Cheng et al. 2022). However,

the benefits of migrating at night could in theory be mediated by moonlight, as the additional illumination could facilitate predator foraging (e.g., from artificial light; Czarnecka et al. 2019). Although the effects of water temperature on smolt behavior and survival have not been investigated for the Chilko Sockeye Salmon population, it is possible that increased temperatures could facilitate feeding by Bull Trout (Mesa et al. 2013), which could in turn affect smolts. Similarly, although flow has been found to increase smolt migration rates elsewhere (Hembre et al. 2001; Michel et al. 2013; Stiff et al. 2017), it is unknown if Chilko sockeye smolts can exploit increased flow rates to either migrate more quickly or to increase their chances of survival. Thus, there remains further opportunities to identify factors influencing smolt survival in this high-risk landscape, particularly at finer spatial scales than previously studied.

Most of the acoustic telemetry studies on Chilko Lake Sockeye Salmon have focused on age-2 smolts because of tag burden concerns (but see Stevenson et al. 2019), resulting in questions regarding the applicability of results to the entire population, given that age-2 smolts contribute only ~4% of the outmigrant fish. Furey et al. (2016a) found that PIT-tagged fish (experiencing lower tag burdens than fish given acoustic tags) exhibited faster migratory movement than similarly sized fish tagged with acoustic telemetry tags. This research indicated a relationship between tag burden and behavior, without investigating survival (Furey et al. 2016a). Mortality of smolts with high tag burdens (mean = 9.6%) experienced a mortality rate 1.51 times higher than those with low tag burdens (2.6%) for an assessment of Chilko Lake smolts from the counting fence through the early stages of marine residency (Bass et al. 2020), confirming that tag burden may also affect survival. By directly comparing survival of similarly sized smolts tagged with acoustic tags with those with smaller PIT tags we can investigate if high

tag burdens alter survival of outmigrating smolts in the unstudied landscape upstream of the fence.

1.9 Government Counting Fence: an Understudied Feature

One of the unique aspects of the Chilko Lake-River system is the counting fence that Fisheries and Oceans Canada (DFO) installs each spring in order to enumerate smolts emigrating from the lake (Irvine and Akenhead 2013). Since the early 1950s the Chilko counting fence, ~1.3-km downstream of Chilko Lake, has provided valuable data on the timing and numbers of smolts outmigrating at high temporal resolution (Furey et al. 2016a). As such, it provides a platform for researchers to capture smolts, but also produces a bottleneck that predators could potentially exploit. In fact, predatory Bull Trout that feed extensively on the smolts during this period (Furey et al. 2015) feed at higher rates at the fence than elsewhere in the lake-river region (Furey et al. 2016b; Cheng et al. 2022). However, it remains unclear if the migratory restriction impacts survival of smolts; survival to and through the fence has not been estimated in any of the prior studies. Furthermore, barriers in rivers have been shown to affect behavior in salmonids (Moore et al. 2013), but smolt behaviors in the vicinity of the counting fence have not been described.

1.10 Goals

In this thesis, I investigated the behavior and survival of Sockeye Salmon smolts as they attempt to pass downstream of a government operated counting fence. My findings will contribute to the current knowledge of how downstream migrating fish are impacted by anthropogenic barriers. Chapter 2 estimates survival of outmigrating Sockeye Salmon smolts via mark-recapture modelling in the previously unstudied landscape immediately upstream of a government operated counting fence. Chapter 3 investigates and characterizes complex

behaviors exhibited by smolts while they are upstream of the counting fence using an acoustic telemetry positioning system to further contextualize the survival rates presented in Chapter 2. Chapter 4 summarizes these findings, suggests potential management solutions, identifies opportunities for further research, and discusses the broader implications that our findings may have regarding impacts from small barriers on migratory fish.

CHAPTER 2: Survival of Chilko Lake Sockeye Salmon Smolts from Release to the Fence 1.3 km Downstream

2.1 Introduction

Anadromous Pacific salmon (*Oncorhynchus* spp.) are economically, culturally, and ecologically important (Gustafson et al. 2007; Criddle and Shimizu 2014; Atlas et al. 2021). Unfortunately, southern latitude populations have experienced significant declines in recent decades (Gustafson et al. 2007; Peterman and Dorner 2012) related to several factors including warming freshwater environments (Hinch et al. 2012) and poorer ocean rearing conditions caused by climate change and increased competition at sea (Ruggerone and Irvine 2018; Connors et al. 2020). Southern latitude Sockeye Salmon (*Oncorhynchus nerka*) have experienced particularly sharp declines since ~1990 (Peterman and Dorner 2012; Irvine and Akenhead 2013; Connors et al. 2020). The Fraser River watershed in British Columbia, Canada is home to dozens of distinct spawning populations of Sockeye Salmon, constituting one of the most productive rivers in the world for the species (Northcote and Larkin 1989). In 2009, Sockeye Salmon adult returns to the Fraser River were the lowest they have been since 1947, leading to a judicial inquiry from the Canadian Government (Cohen 2012). The next year (2010), adult returns were one of the highest of the previous century, demonstrating the complexity and uncertainty associated with factors affecting adult returns.

Outmigrating smolt abundance is thought to be an important factor affecting the abundance of returning adults of Sockeye Salmon (Henderson and Cass 1991) and for returning adults of other migratory salmon (Beamish and Mahnken 2001; Sharma et al. 2013) . Downstream migrating smolts face numerous survival challenges, including increased exposure

to predators (Furey et al. 2015; Tucker et al. 2016; Thomas et al. 2017; Nelson et al. 2019), infectious agents (Nendick et al. 2011; Stevenson et al. 2020), and changing water quality conditions including salinity (Burgner 1991), which requires complex physiological changes. In addition, smolts in some systems must pass through human-made barriers to reach the ocean (Welch et al. 2008; Marschall et al. 2011; Stich et al. 2015).

Barriers to migratory salmon smolts vary in size and flow characteristics, including large hydroelectric facilities, sluice gates, temporary weirs, or anthropogenically constricted channels. Among salmon species (*Oncorhynchus* spp. and *Salmo* spp.), these barriers can affect smolt behavior (Kemp et al. 2005; Havn et al. 2020; Renardy et al. 2021) and survival (Mathur et al. 1996; Marschall et al. 2011; Stich et al. 2015; Nyqvist et al. 2017b). However, these impacts are likely to be system-, barrier-, and species-specific (Haro et al. 1998), as not all barriers appear to impact behavior and survival (Welch et al. 2008; Newton et al. 2019; Harbicht et al. 2021). Thus, system-specific research is often needed to characterize behavior and survival of salmon smolts as they migrate through anthropogenic structures.

One of the most productive Sockeye Salmon populations in the Fraser River watershed is the Chilko Lake stock, with 10 – 70 million smolts leaving the lake each spring for the Pacific Ocean (Irvine and Akenhead 2013). This system is the first one where miniaturized acoustic telemetry and biopsy sampling were combined to examine the large spatial scale migration ecophysiology of outmigrating salmon smolts including studies examining the effects of predators, pathogens, migrant transcriptomics, tag burden, size and age, on smolt behavior and survival (Jeffries et al. 2014; Clark et al. 2016; Furey et al. 2016a; Rechisky et al. 2019; Stevenson et al. 2019b, 2020; Bass et al. 2020). A repeated finding is that survival immediately downstream of the rearing lake, in clear waters of the Chilko River, is low relative to that in

larger and more turbid riverine systems further downstream (Clark et al. 2016; Rechisky et al. 2019; Stevenson et al. 2019b). Due to tag burden limitations, most of the studies (with the exception of Stevenson et al. (2019, 2020)), involved the tracking of larger age-2 smolts; however, age-1 smolts represent 96% of the outmigrating population (Irvine and Akenhead 2013).

In part due to the large size of its population, outmigrating smolts from Chilko Lake have been enumerated by Fisheries and Oceans Canada (DFO) using a seasonal counting fence installed nearly every spring since 1952 (Henderson and Cass 1991; Irvine and Akenhead 2013). The counting fence provides valuable data on the timing and numbers of smolts outmigrating at high temporal resolution (e.g., Furey et al. 2016a). However, the fence also produces a spatial bottleneck that predators could potentially exploit. For example, Bull Trout (*Salvelinus confluentus*) feed extensively on smolts during this period (Furey et al. 2015; Cheng et al. 2022), and those captured at the fence had fuller stomachs than those caught elsewhere in the lake-river region (Furey et al. 2016b). However, none of the extensive research involving the tracking of smolts from this population has examined migratory behavior or survival as they immediately leave the lake and pass through the fence.

Given the global importance of understanding how smolt populations are affected by in-stream anthropogenic barriers (Hinch et al. 2022), this study aimed to examine smolt survival from the Chilko Lake outlet through the DFO counting fence using acoustic and passive integrative transponder (PIT) telemetry. PIT telemetry can be used to estimate the migration survival of salmonids (Tiffan et al. 2019; Murauskas et al. 2021), with tags small enough for age-1 smolts. Both age-1 (PIT) and age-2 (PIT and acoustic) smolts were tagged and tracked,

allowing us to determine if survival in this small landscape is age-dependent or varies with other factors related to fish size, condition, or the environment.
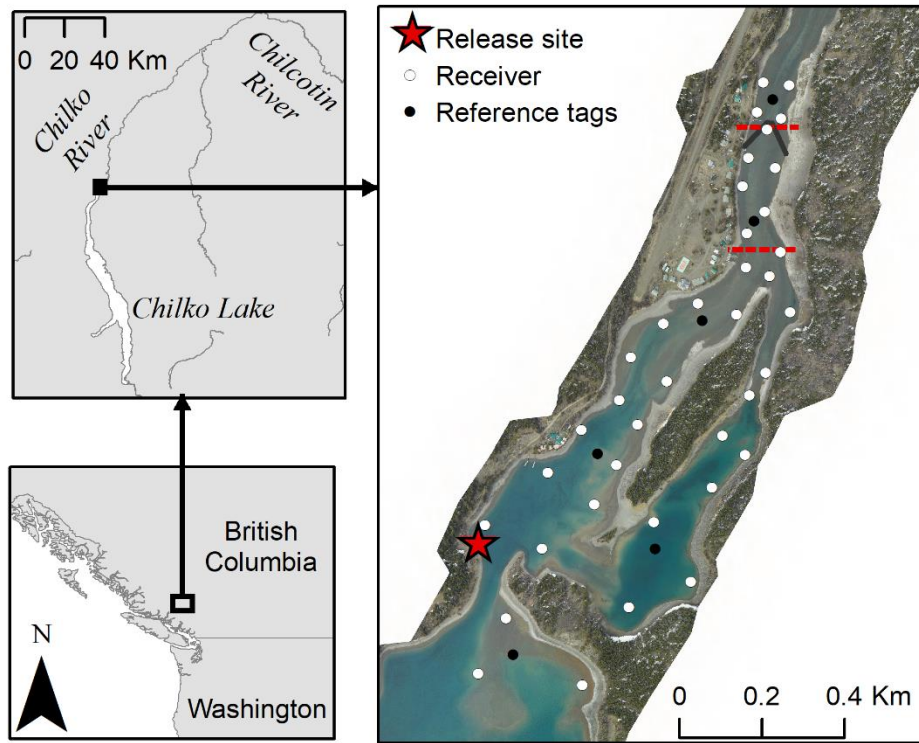
Figure 2.1: Bottom left panel shows the regional location of Chilko Lake relative to the US-Canada Border. Top left panel shows the location of the specific project area relative to broader Chilko Lake. Right panel shows the full study area with the counting fence shown in black (V-shaped line), release site shown with a red star, and the reference tag locations shown with black dots and receiver locations shown with white dots. The southern horizontal red line shows the latitude threshold of the "approach zone" while the red line further north shows the latitude threshold for survival in the acoustic telemetry data.

2.2 Methods

2.2.1 Study Area

Data collection took place in a 1.3-km section of Chilko Lake where it transitions to the Chilko River (Figure 2.1). Chilko Lake has a north-south orientation and flows into the Chilko River at the north end of the waterbody. To commence seaward migration, Sockeye Salmon smolts move northward out of the lake into the Chilko River, first passing through the DFO counting fence installed each spring, generally from mid-April through mid-May (Figure 2.1). In

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this portion of the lake to river transition zone, the more lacustrine environment constricts to an area of increasing flows with an approximate width of 90 m.

2.2.2 Smolt Capture and Tagging

Between April 28, 2014 and May 10, 2014, smolts were captured during the initial segment of their migration within the Chilko River. Smolts were captured from the river immediately upstream of the DFO counting fence with dip nets. Collecting fish in this location ensured that study fish were already attempting migration during that spring rather than waiting another year in the lake.

All fish to be tagged were first anesthetized (100 mg/L Tricaine Methanesulfonate [MS222] buffered with 200 mg/L NaHCO$_3$). Once anesthetized, fish were measured for fork length (FL; mm) and mass (g), then placed on a custom V-shape tagging trough ventral side up with a small hose feeding water with a maintenance dose of anesthetic (50 mg/L MS222, 100 mg/L NaHCO$_3$) over the gills to ensure that the fish remained under anesthesia during the tagging procedure. Next, a small incision (6-8 mm) was made in the ventral surface of the smolt, through which the Innovasea V7 tag was inserted (similar to Furey et al. (2016a); Stevenson et al. (2019, 2020)). Incisions were closed using two interrupted sutures using monofilament (Ethicon monocryl 5-0 monofilament 3/8 circle reverse cutting 13 mm [P-3]). After surgery, fish were transported in tanks with circulating water to the release site 1.3-km upstream of the DFO counting fence (Figure 2.1). A total of 208 fish were tagged with acoustic tags. In 2014, Chilko Sockeye Salmon smolts ≤ 116 mm FL were considered age-1, while those larger were considered age-2 via scale analyses (Brian Leaf, DFO, personal communication). All fish that received acoustic telemetry tags were age 2, exceeding 116 mm in FL. Mean FL of smolts with acoustic tags was 143.5 mm (Standard Error [SE] = 0.6 mm) and mean mass was 23.97 g (SE =

0.32 g). For smolts with acoustic telemetry tags, the mean tag burden (tag mass divided by fish mass) was 6.93% (SE = 0.09%; Figure 2.2). V7 tags (69 kHz) were 7-mm diameter, 18-mm length, 1.4 g mass in air, and were programmed to transmit every 20-40 seconds, with 123 days estimated battery life.
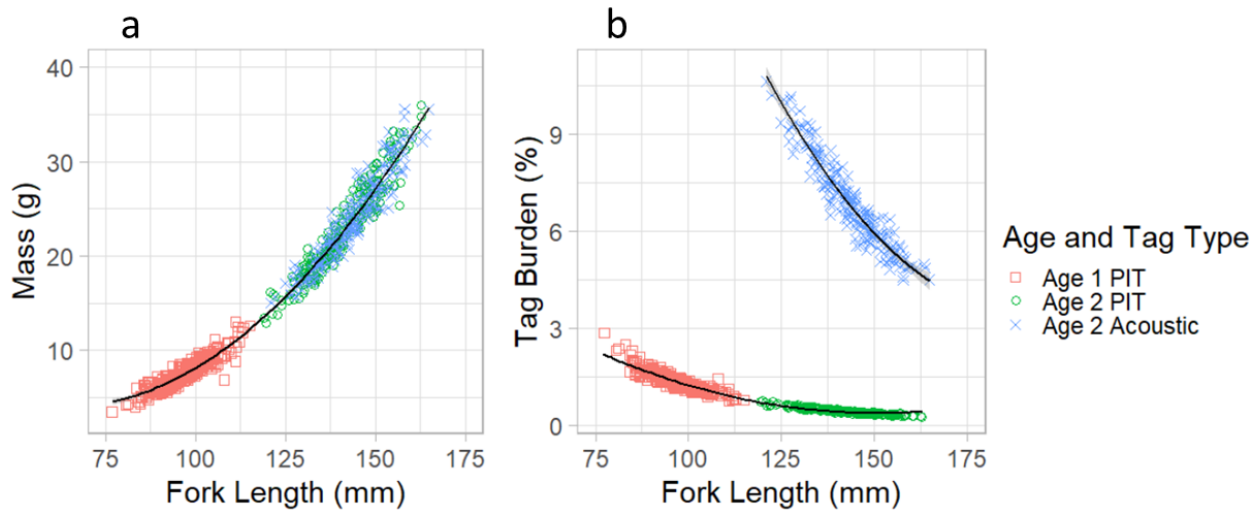
Figure 2.2: (a) Mass and fork length for all tagged fish, separated by age and tag type. Trendline in the left panel shows second order polynomial regression for all fish. (b) Tag burden for all tagged fish, separated by age and tag type. Trendline in the right panel shows second order polynomial regression of burdens for each tag type separately.

Smolts implanted with PIT tags (Oregon RFID tag: 12.0 mm x 2.12 mm, mass: 0.1 g), were held in hand after anesthesia and measurements and then tagged near the ventral line using a syringe. PIT-tagged fish consisted of a mix of age-1 (n = 358) and age-2 (n = 251) smolts (total n = 609 fish). Mean FL of all PIT-tagged fish was 115.3 mm (SE = 0.9 mm) while mean mass was 13.92 g (SE = 0.33 g). For age-1 PIT-tagged fish, mean FL was 97.3 mm (SE = 0.3 mm) and mean mass was 7.70 g (SE = 0.08 g). For age-2 PIT-tagged fish mean FL was 141.0 mm (SE = 0.6 mm) and mean mass was 22.79 g (SE = 0.29 g). Mean tag burdens for PIT-tagged fish were 0.98% (SE = 0.02%) across all fish, 1.35% (SE = 0.01%) for age-1 fish, and 0.46% (SE = 0.01%) for age-2 fish (Figure 2.2). All collection and tagging procedures followed animal use protocols approved by the University of British Columbia, Animal Care Committee.

Regardless of tag type, after ~ 10 minutes of recovery in an aerated cooler, all fish were transferred to release buckets with mesh sides placed in a 1000-L tank with ambient river water pumped through the tank constantly. That night, fish were transported in the same tank with aerators to the release site 1.3-km upstream of the DFO counting fence (Figure 2.1) for release. Releases occurred during nighttime hours (23:00-02:00) to mimic the natural migratory patterns of the fish (Clark et al. 2016; Furey et al. 2016a).

2.2.3 Telemetry Receiver Infrastructure

We used acoustic telemetry and PIT telemetry to assess smolt survival from the release point within Chilko Lake to the counting fence. To track movements of smolts implanted with acoustic telemetry transmitters, we used a Vemco Positioning System (VPS; Innovasea; Halifax, Nova Scotia) which consists of an array of closely spaced telemetry receivers to triangulate positions of tags using a time-distance-of arrival algorithm (Espinoza et al. 2011). A total of 38 acoustic telemetry receivers (Innovasea VR2W-69 kHz) were placed ~100 meters apart to create our VPS for tracking the fine-scale movements of acoustic tagged smolts (Figure 2.1); each of these receivers also had a co-located Innovasea V13 acoustic telemetry transmitter (13-mm diameter, 30.5-mm length, 9.2 g in air, programmed to transmit every 500-700 seconds, 69 kHz) to synchronize internal clocks among receivers. In addition, we placed six stationary tags (reference stations) throughout the array. Reference stations are used to collect positions for known locations during data collection to aid in the calculation of positions for tagged fish. Receivers and reference stations were placed throughout the downstream portion of Chilko Lake, with four receivers and one reference station just downstream of the counting fence (Figure 2.1). In shallow locations, receivers and references tags were attached directly to sandbags via

industrial cable ties; in deeper waters, receivers were attached to line running from the sandbag to a small surface float. Detections from receivers were downloaded after the migration and sent to Innovasea for processing. From these data, we received positions and timestamps for individual tagged smolts, as well as an estimate of positional precision (horizontal position error [HPE] described further below). In this study, we used estimated positions from the VPS to determine whether a smolt passed specific locations for survival modelling.

Each estimated position is accompanied by a HPE value. HPE is a unitless measure of error that is only comparable within a given study. In addition to positions estimated for fish tags, a VPS dataset includes estimated positions for both reference tags and sync tags. Reference tags are stationary transmitters installed within a VPS, and sync tags are a part of an acoustic receiver that acts as an on-board reference tag. Both components are deployed in a known location using as accurate a GPS as possible. Having these stationary transmitters allows a VPS dataset to include estimated positions for reference tags and sync tags that include both a measure of HPE (unitless) as well as HPEm. HPEm represents the distance (in meters) between the known location of a stationary transmitter and the estimated location, thereby providing us with a measure of accuracy within a VPS. Using the methods described in Meckley et al. (2014) we described the relationship between HPE and HPEm for our reference and sync tag locations. We grouped our calculated reference positions into bins that were 1-HPE wide and calculated a 2DRMS (twice the distance root mean square) of HPEm (m) for each bin to better understand how actual error varied with increases in HPE. We chose to only include positions with HPE $\leq$ 23 in our analyses; these values maintained a 2DRMS < 10 m across remaining HPE values which we identified as an acceptable level of accuracy. Our initial dataset contained 58,955

estimated smolt positions, with 56,151 positions 95.2% remaining after removing values with

HPE > 23.

In addition to the acoustic telemetry receivers, PIT arrays were constructed at each of the

two exits of the DFO counting fence. Arrays and tags (Oregon RFID) were both half-duplex. The

arrays were constructed at the downstream end of each trap box where smolts pass over the

counting board. Each of these antennas consisted of 12-gauge wire attached to a ~1 m x ~2.5 m

wood frame affixed to the downstream openings in the counting fence. Additionally, plastic

mesh was used to connect the antenna frames to the counting fence itself to ensure that all smolts

would be forced to pass through an antenna. We conducted a detection efficiency test to

determine the probability of tagged smolts being detected as they passed. On May 11, 2014, 48

PIT-tagged fish were released just upstream of the counting fence (age-one and age-two fish

portions approximately equal) at ~30-second intervals to minimize tag collision. Of the 48 fish

released, 45 fish (93.75%) were successfully detected at the counting fence PIT array with no

difference observed between fish age classes.

2.2.4 Tag Holding Study

To determine the potential short-term impact of tagging on smolts, additional fish were

tagged with dummy acoustic telemetry transmitters or PIT tags and held in a tank for

observation. On May 3, 2014, 42 smolts had dummy tags with the same dimensions and mass of

the Innovasea V7 acoustic tags surgically implanted using the same tagging procedures as the

released fish. Mean FL of all acoustic-tagged holding study fish was 147.5 mm (SE = 1.2 mm)

and mean mass was 25.83 g (SE = 0.65 g), 2.8% and 7.8% larger, respectively than smolts

released with acoustic telemetry tags. In addition, 49 additional smolts received identical PIT

tags as those released. Mean FL of all PIT-tagged holding study fish was 121.0 mm (SE = 3.7

mm) and mean mass was 15.96 g (SE = 1.32 g), 4.9% and 14.7% larger, respectively than smolts released with PIT tags. Smolts of both tag types were held in a 200-L tank on the bank of the Chilko River for nine days. For the duration of the study, ambient river water was pumped through the tank, and each day the tank was checked for any mortalities. After the nine days, all fish were checked for tag retention and wounds. Zero fish with acoustic tags experienced mortality or tag loss. Two PIT-tagged fish died (4.1%), but no tag loss was observed.

2.2.5 Survival Analysis

To estimate survival of tagged smolts through the counting fence, we used a mark-recapture approach in which detections within specific areas (determined from acoustic telemetry positional data) or at the PIT arrays at the fence constituted a "recapture" event. Specifically, we used a Cormack-Jolly-Seber model (CJS; Cormack 1964; Jolly 1965; Seber 1965) to estimate survival of outmigrating smolts (e.g. Hammill et al. 2012; Conner et al. 2015; Raabe et al. 2019) from release through the fence. CJS models use a combination of both the number of individuals successfully detected at and the detection efficiency of an array to estimate segment-specific survival along the migratory route. Assumptions of the CJS models are 1) tagged individuals are representative of the population; 2) survival of an individual does not change by being tagged; 3) after release, all tagged individuals have equal likelihood of detection and survival; 4) tags remain attached and functional; 5) sampling is instantaneous; 6) the outcome of one tagged individual is independent of the other individuals; and 7) individuals can move downstream through the array. Analyses were performed separately for the acoustic telemetry data and the PIT telemetry data. Splitting the analysis was necessary because the two tag types represent different technologies and tags were detected by distinct arrays; thus, detection efficiency was expected to vary independently between tag types. Additionally, the positional data from

acoustic telemetry data allowed for developing more distinct "zones" within the landscape

between the release site and counting fence and therefore capture history lengths differed

between the tag types. CJS models were constructed using Program MARK (White and Burnham

1999), through the 'RMark' package (Laake 2013) in R 4.1.0 (R Core Team 2020).

To prepare data for CJS models, any smolt that did not have complete values for

covariates (FL or mass) or had obviously erroneous values due to transcription errors were

removed (three fish, or 0.4%). Next, covariates were assigned to each smolt. Co-variates

included FL, mass, release date, tag burden, mass-FL residuals (defined as residuals from a

second-order polynomial between mass and FL, representing smolt mass relative to FL), Fulton's

condition index (calculated as (mass/FL^3)*100000)), percent of time the counting fence was

open the night of that smolt's release (from 00:00 through 08:00 the night of release), and

density of co-migrants (i.e., how many fish passed the counting fence from 00:00 to 08:00 on the

night of release as estimated from passage data collected at the counting fence; Figure 2.3; B.

Leaf, DFO, Pers. Comm.).
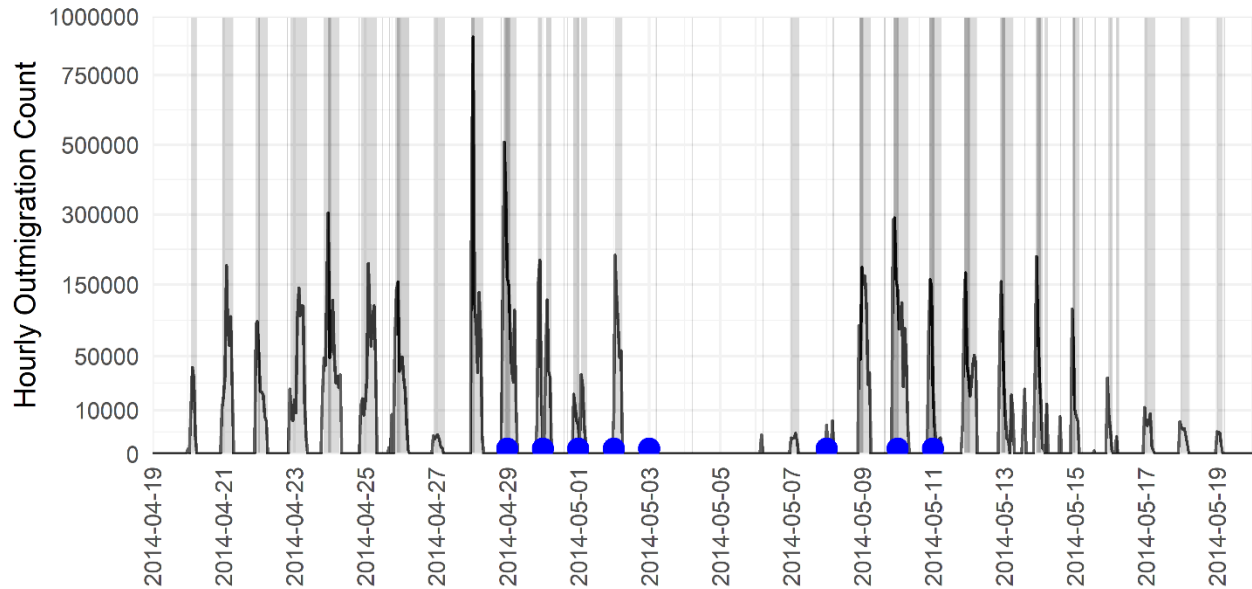
Figure 2.3: Outmigration structure at the Chilko Lake counting fence in 2014. Black line shows hourly outmigration counts determined at the DFO counting fence. Blue dots show dates on which tagged fish were released. Gray bars show time periods during which the counting fence was reported to be open by DFO. Note the unequal scaling of values on the y axis.

Each smolt was then assigned a capture history: a series of zeroes and ones indicating whether the fish was "recaptured" (i.e., detected) at set locations from release through the counting fence. For PIT-tagged fish, the capture history was only two events long. The first "event" was the release (all fish receive a 1 for this event) and the second was the PIT array at the fence; If a fish was detected at the PIT array at the fence, it was given a 1, otherwise a 0. To provide a finer examination of migration through this corridor, we developed longer capture histories for acoustic-tagged fish (four events), using the VPS positions of smolts to assign additional zones between the release and the fence. As with PIT-tagged smolts, release corresponded to the first event in the capture history (all fish receiving a 1). The second event described if a smolt was ever positioned between latitudes 51.625465°N and 51.622800°N, the area where Chilko Lake transitions into a more river-like environment of the Chilko River (narrow and shallow; 1 km from release; Figure 2.1). The third event described if a smolt

successfully passed through the fence, with a position lying in a region starting 10 meters

upstream of the fence (to conservatively account for potential error in position estimates) through

~115-m downstream of the VPS (0.3 km from second event area; Figure 2.1). The fourth and

final capture event represented a detection on any receiver placed downstream of the VPS along

the migratory corridor to the Pacific Ocean (e.g., Clark et al. 2016). This fourth event was

included solely to determine the detection efficiency of the fence-passage region of the VPS; we

only present survival through the fence (third event) as survival and detection efficiency are

confounded at the final event for any CJS mode. Survival downstream of the fence has been

quantified and explored extensively (e.g. Clark et al. 2016; Rechisky et al. 2019; Stevenson et al.

2019, 2020).

    We built separate CJS models from acoustic telemetry and PIT telemetry data to estimate

segment-specific survival (Φ) and detection efficiency (p). Candidate CJS models for acoustic

telemetry data were built by allowing Φ to vary both with each segment of the study area as well

as one additional covariate per candidate model (mass, FL, mass-FL residual, Fulton's condition

index, percent of time the counting fence was open, or density of co-migrants). We also allowed

detection efficiency to vary with each segment. CJS models of PIT data only had a single

survival segment, and thus Φ only varied with a single covariate per model. Detection efficiency

(p) for the PIT array was fixed at 93.75% via the field test. Models were subsequently ranked

using Akaike's Information Criterion corrected for small samples sizes (AICc) and AICc weight

(w_i), which represents the probability that an individual model is the most parsimonious among

candidate models (Burnham and Anderson 2002). For any model with an AICc score lower than

a null model (where Φ only varied with segment or did not vary at all; i.e., intercept-only

models), we predicted relationships between survival and the retained covariate to visualize each covariate's potential influence on smolt survival.

For models estimating survival from acoustic telemetry data, cumulative survival from release through the fence was obtained by multiplying the two segment-specific survival estimates together. To provide further context for our estimates of survival, cumulative survival estimates were concerted to survival per kilometer and survival per day using the equation

$$S^{1/d}$$

where S = cumulative survival from release through the fence and d = median transit time in hours or the distance from release to the fence (1.3 km). Transit time from release to the fence was calculated for each surviving fish to create a median transit time in hours for each of the three age and tag type combinations in the study.

To account for potential overdispersion in the acoustic telemetry data, we assessed the goodness of fit (GOF) of the data using the GOF Test Two and Test Three available through Program MARK (White and Burnham 1999). The sum of chi-square values of tests two and three are summed and divided by the degrees of freedom to provide an estimate of ĉ (Cooch and White 2002). After the bootstrapping tests were performed, we estimated the overdispersion parameter ĉ by determining the deviance. The value of ĉ (2.4) was used in acoustic telemetry CJS models to adjust AIC values and to inflate the standard errors of calculated survival estimates to account for overdispersion in the dataset.

2.3 Results

2.3.1 Survival Estimates

Survival from the release site through the counting fence was calculated in two segments for the acoustic telemetry fish and a single segment for the PIT-tagged fish. Estimated

cumulative survival through the fence was 62.2% (SE = 6.1%; Figure 2.4) for acoustic telemetry fish (age-2) and 45.2% (SE = 4.8%) for PIT-tagged fish (combined age-1 and age-2). Estimated survival through the fence for PIT-tagged age-1 fish was 37.7% (SE = 2.7%) and for age-2 fish was 46.1% (SE = 3.4%; Figure 2.5). For fish with acoustic tags, estimated survival over the first 1.0 km to the lake-river transition was 65.8% (SE = 5.2%). Of those fish that survived the first kilometer, 93.3% (SE = 6.0%) survived to pass through the counting fence. Detection efficiencies (p) for each migratory step within the acoustic telemetry models were variable between the two segments estimated. At the approach zone (between latitudes 51.625465°N and 51.622800°N), p was 91.5% (SE = 4.0%). In the zone immediately downstream of the fence (North of latitude = 51.622800°N), detection efficiency was lower at 79.3% (SE = 6.91%).

Estimated survival rates per kilometer was 69.7% for age-2 acoustic telemetry fish, 47.2% for age-1 PIT fish, and 55.1% for age-2 PIT fish. Estimated survival rates per day were based on calculated travel times for each age class and tag type combinations (Figure 2.5) 88.6% for age-2 acoustic telemetry fish, 73.9% for age-1 PIT fish, and 82.3% for age-2 PIT fish.
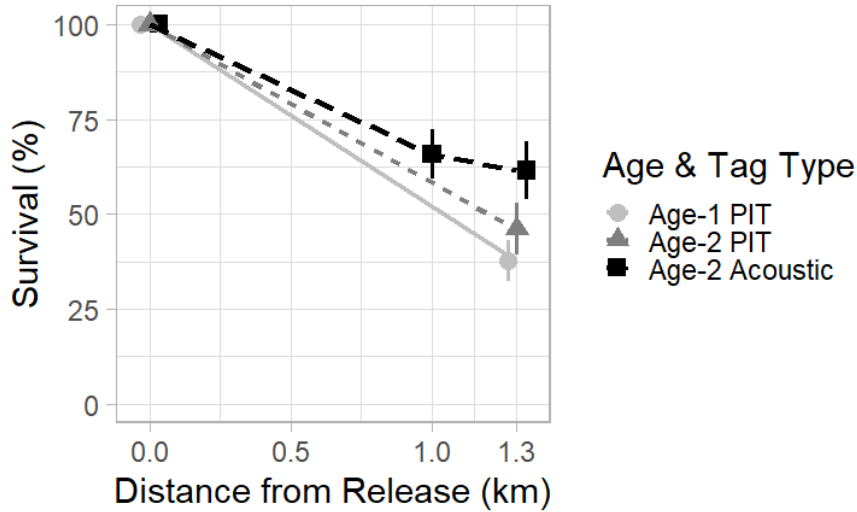
Figure 2.4: Estimated survival over distance traveled from the release site. Color and line type represent age-tag combinations. Error bars show 95% confidence interval. Note that standard error, and therefore the 95% confidence interval, was inflated for the age-2 acoustic telemetry results based on the $\hat{c}$ value determined in the goodness of fit testing. Values are jittered slightly in the horizontal direction to improve visibility among age-tag combinations.
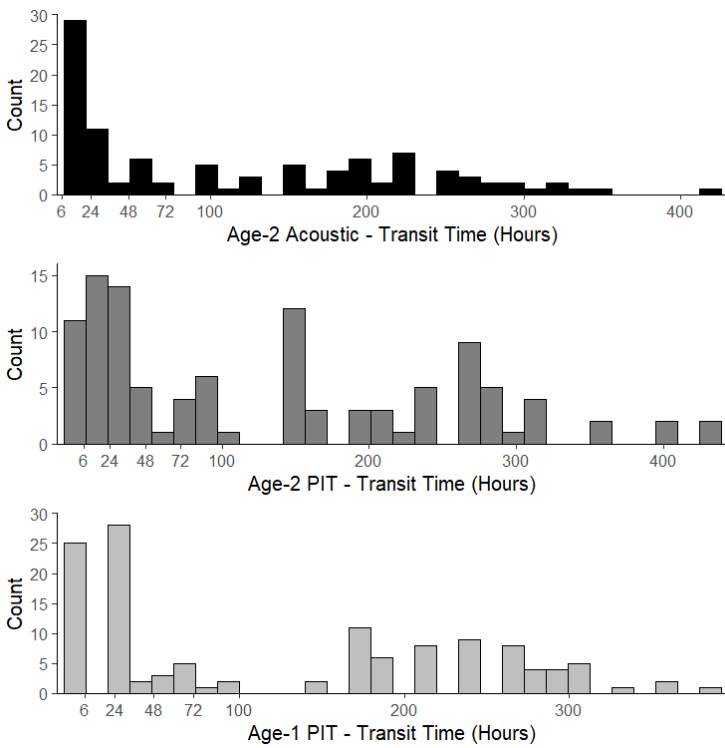
Figure 2.5: Distribution of transit times for all surviving fish from the release location to the fence (1.3 km) separated by age and tag type.

2.3.2 Covariates of survival

Across age-tag combinations, highly ranked models tended to include covariates of FL, tag burden, mass, mass-length residuals, or Fulton's condition index (Table 2.1; Full details on estimated coefficients from top-ranked models in Appendix 2). However, none of these covariates appeared consistently among the highly ranked models across age class and tag type. The top-ranked model for Age-2 acoustic tagged fish included Fulton's condition index (Table 2.1; AICc of 678.25 and model weight of 0.19). The second- and third-ranked models had similar weights (0.18 and 0.14) and contained the covariates of mass-FL residuals and FL, respectively (Table 2.1). Among these models, survival exhibited a slight positive relationship with Fulton's condition index and mass-FL residuals, and a slightly negative relationship with FL (Figure 2.6). Models containing other covariates had higher AICc values than a "null" model (where survival only varied by segment, with no influence of further covariates). All top-ranked models using acoustic telemetry data had detection efficiency (p) vary with migratory segment (Table 2.1), indicating p indeed varied among regions of the VPS.

For age-2 PIT tagged fish, the top-ranked model contained FL and contained a majority of the model weight (0.53; AICc of 335.22; Table 2.1). The second-ranked model for age-2 PIT-tagged fish contained mass (model weight = 0.27) and the third-best model contained tag burden (model weight = 0.19). Collectively, these top three models contained ~99% of the model weight (Table 2.1). Among these variables, FL appeared to have a negative effect on survival for Age-2 PIT tagged fish, while burden had a positive relationship with survival and mass maintained a negative relationship with survival (Figure 2.6). For age-1 PIT-tagged fish, the top-ranked model contained tag burden (Table 2.1; AICc of 465.89 and model weight of 0.30). Tag burden appeared to have a slightly negative effect on survival for age-1 PIT tagged fish (Figure 2.6). The

second-ranked model for age-1 PIT-tagged fish contained mass, with mass having a slightly

positive relationship with survival, but this model had the same weight (0.12) as the null model

(no covariate influencing survival; Table 2.1).

Table 2.1: Ranked CJS model outputs, including models that contributed to the cumulative top 95% of model weights for a given tag type and age combination. Models are ranked by AICc. For each model, the number of covariates (npar), the difference in AICc from the top-ranked model (ΔAICc), model weight (weight), and cumulative weight (Cum. Weight). Parameters after "Phi" are those that were assessed for correlation with survival for a particular model while parameters after "p" are those assessed for correlation with detection efficiency. Parameters include Fulton's Condition Index (Fulton), smolt mass relative to fork length (Residuals), fork length (FL), tag burden (Burden), time the tagging fence is open after release (Open), smolt mass (mass), number of smolts crossing the counting fence after release (co-migrant), and release group (Release). Numbers preceding parameters show estimated coefficients from CJS models (See Appendix 2 for full details on top-ranked models).

Model Rank	Model	npar	AICc	ΔAICc	Weight	Cum. Weight
	Acoustic Age-2					
1	Phi(~segment + 3.94*Fulton) p(~segment)	6	678.2519	0	0.19	0.19
2	Phi(~segment + 0.13*Residuals) p(~segment)	6	678.3420	0.09013	0.18	0.36
3	Phi(~segment + -0.02*FL) p(~segment)	6	678.8428	0.59092	0.14	0.50
4	Phi(~segment) p(~segment)	5	679.2963	1.044376	0.11	0.61
5	Phi(~segment + 0.09*burden) p(~segment)	6	680.2552	2.0033	0.07	0.68
6	Phi(~segment + 1.49*open) p(~segment)	6	680.3822	2.1303	0.06	0.75
7	Phi(~segment + -0.02*mass) p(~segment)	6	680.5307	2.27878	0.06	0.81
8	Phi(~segment + -0.01*Release) p(~segment)	6	681.0013	2.749440	0.05	0.86
9	Phi(~segment + 0.0*co-migrant) p(~segment)	6	681.3203	3.068380	0.04	0.90
10	Phi(~segment + 0.13*Residuals) p(~1)	5	682.7111	4.459176	0.02	0.92
11	Phi(~segment + 3.94*Fulton) p(~1)	5	682.7231	4.471256	0.02	0.94
12	Phi(~segment) p(~1)	4	683.3703	5.118409	0.01	0.95
	PIT Age-2					
1	Phi(~-0.05*FL) p(~1)	2	335.2238	0	0.53	0.53

Model Rank	Model	npar	AICc	ΔAICc	Weight	Cum. Weight
2	Phi(~-0.10*mass) p(~1)	2	336.553	1.32926	0.27	0.80
3	Phi(~4.81*burden) p(~1)	2	337.2606	2.03688	0.19	0.99
	PIT Age-1					
1	Phi(~-0.85*burden) p(~1)	2	465.8882	0	0.30	0.30
2	Phi(~0.11*mass) p(~1)	2	467.6424	1.75419	0.12	0.42
3	Phi(~1) p(~1)	1	467.6524	1.764143	0.12	0.55
4	Phi(~0.28*Residuals) p(~1)	2	467.8912	2.00301	0.11	0.66
5	Phi(~2.26*Fulton) p(~1)	2	468.2576	2.36937	0.09	0.75
6	Phi(~0.02*FL) p(~1)	2	468.2595	2.37127	0.09	0.84
7	Phi(~0.87*open) p(~1)	2	469.2171	3.32892	0.06	0.90
8	Phi(~0.01*release) p(~1)	2	469.4893	3.601040	0.05	0.95
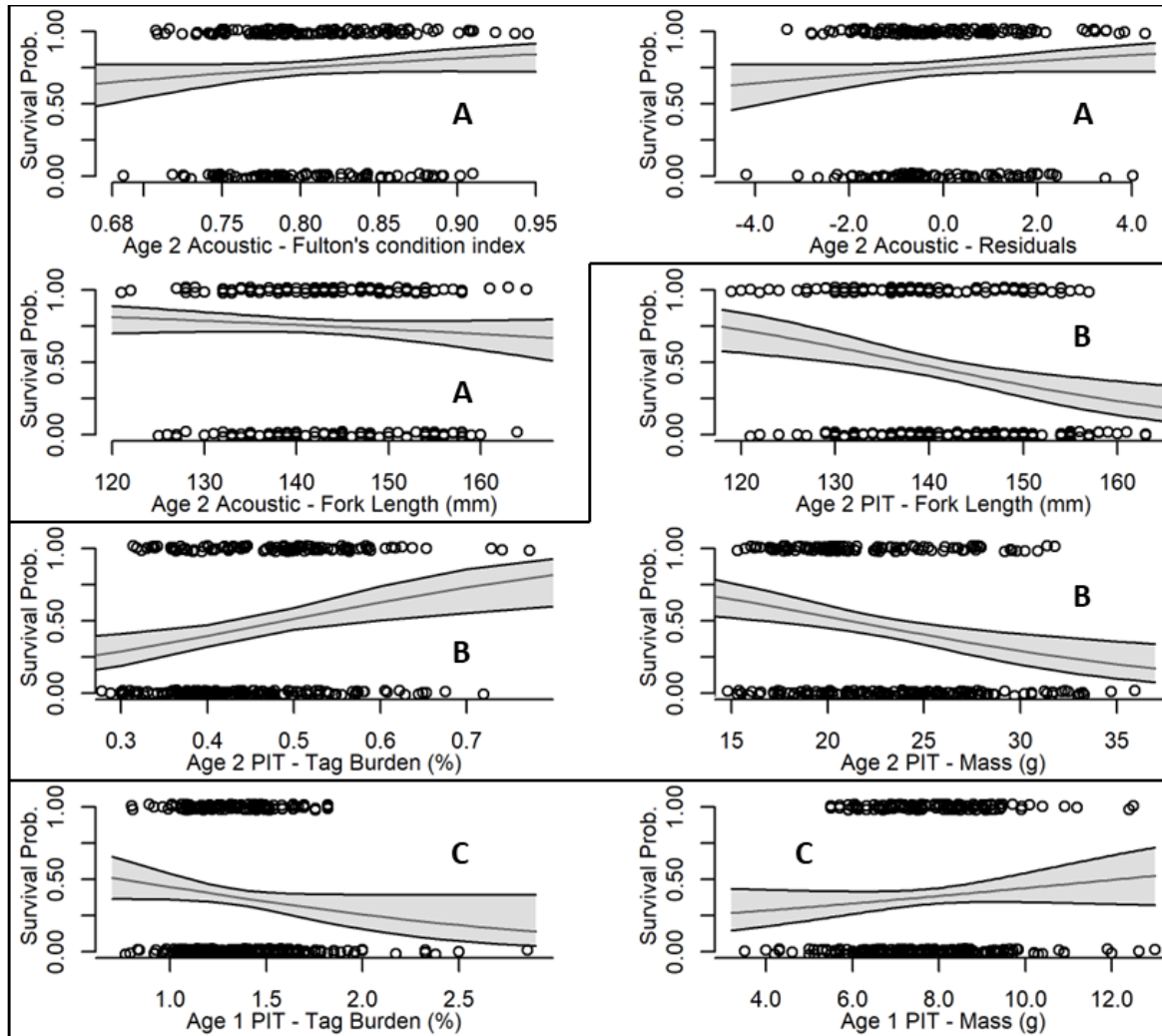
Figure 2.6: Predicted relationships between modeled covariates and survival through the counting fence. Panels labeled "A" include data from age-2 acoustic telemetry fish. Panels labeled with "B" include covariates for age-2 PIT telemetry data. Panels labeled "C" include covariates for age-1 PIT telemetry data. Individual open circles represent fish from the respective dataset which we presumed survived to the fence (1) or did not (0; was not detected at or downstream of the fence). Values are jittered slightly in the vertical direction to improve visibility.

2.4 Discussion

We identified notably low survival (37.7% - 62.2%) across age classes and tag types for Sockeye Salmon smolts migrating downstream in a ~1.3-km reach between their natal lake and the outlet river, which included passage through a counting fence. Survival of smolts immediately downstream of natal waters has frequently been found to be low—this fact is not unique to Chilko Lake Sockeye Salmon smolts. Elsewhere in British Columbia, similar patterns

have been documented for Steelhead (*Oncorhynchus mykiss*) smolts (Healy et al. 2017), Coho Salmon (*Oncorhynchus kisutch*) smolts (Chittenden et al. 2010), and for a hatchery population of Sockeye Salmon from the Fraser River watershed (e.g. Cultus Lake; Welch et al. 2009). Low survival of salmonid smolts during freshwater migration has been observed in rivers around the world, including Atlantic Salmon in Scotland (Lothian et al. 2018) and both Atlantic Salmon (Serrano et al. 2009) and Brown Trout (*Salmo Trutta*) in Sweden (Aldvén et al. 2015). With juvenile to adult recruitment being a strong driver of overall population productivity of salmon (Peterman et al. 2010), it is thus imperative that we understand factors that affect freshwater smolt survival.

For the Chilko Lake population, outmigration smolt survival is lower in the clear waters of the upper Chilko River, immediately downstream of the counting fence, than in the turbid Fraser River further along the migration (Jeffries et al. 2014; Clark et al. 2016; Rechisky et al. 2019; Stevenson et al. 2019). Prior work found that survival over the first 14 km downstream of the fence ranged from 68% (Furey et al. 2016a) to greater than 90% (Bass et al. 2020). But our study is the first to estimate smolt survival in this short transitional landscape between lake and river habitat immediately upstream and through the counting fence. Our results suggest that this area immediately upstream of the fence is the highest risk landscape assessed to date of the smolt out-migration from Chilko Lake.

Contextualizing our survival estimates to be respective of time or distance allows us to further confirm this area between the lake and counting fence as 'high-risk'. Stevenson et al. (2019) estimated per-km survival in early freshwater for age-1 smolts at 97.9% and for age-2 smolts at 95.2%. Stevenson et al. (2019) calculated survival in early freshwater to be approximately 80% per day for age-1 and 60% per day for age-2 smolts. Across five years,

Rechisky et al. (2019) estimated per-kilometer survival within the clear waters of the Chilko River from a low of 99.3% per km in 2010 to a high of 99.7% per km in 2013. Rechisky et al. (2019) also estimated survival per day during freshwater migration (Chilko counting fence to the Fraser River mouth) with values ranging from 82.0% per day in 2012 to 89.5% per day in 2013. Our per-km survival estimates are lower than previous studies; our highest estimate remaining below 70% per km (age-2 acoustic telemetry fish), and lowest below 50% per km (age-1 PIT-tagged fish). However, our per day estimates (ranging from 73.9% to 88.6%) are more similar to previous estimates for the landscape downstream of the fence. This discrepancy between per-distance and per-time survival rates may be explained by the extremely variable transit times experienced by tagged smolts. Transit times to the counting fence across age groups and tag types ranged from 1.3 hours to greater than 18 days (Figure 2.5). This extreme variability may suggest that smolts exhibit complex behaviors in the area immediately upstream of the fence that could be subjecting them to delays that may lead to reduced survival (Nyqvist et al. 2017b).

Complex behaviors and long transit times in this landscape are potentially a consequence of the counting fence. The outlet of Chilko Lake is a naturally constricted landscape, but passage is then further artificially narrowed each spring by the fence to enumerate outmigrant smolts. Habitat constrictions such as this can have impacts on the success and survival of smolts by altering behavior of both migrating fish (Moore et al. 2013) and predators (Yurk and Trites 2000). For example, a floating structure (the Hood Canal Bridge) that artificially constricts a migratory corridor used by Steelhead smolts caused measurable migration interference and concentrated smolts in a way that may increase mortality risk via predation (Moore et al. 2013). In addition, harbor seals (*Phoca vitulina*) use the shadows and artificial lights below two bridges on the Puntledge River in Courtenay, British Columbia, Canada feed on smolts at an abnormally

high rate (Yurk and Trites 2000). Although we simplified our acoustic telemetry positioning data to estimate survival through specific regions to and through the counting fence, these high-resolution data can provide important and novel insights into animal behavior and movement ecology (Nathan et al. 2022). Preliminary qualitative investigations of the fine-scale VPS positioning data suggests that many smolts make repeated trips back and forth between the lake outlet and the fence before finally crossing downstream or perishing (Furey unpublished data). Thus, future research using these data could define the specific behaviors and routes taken by smolts in this high-risk landscape and determine if biological or environmental factors correlate with such complex behaviors. Further, approaches such as time-to-event analyses (Castro-Santos and Perry 2012) could allow for understanding linkages between behavior and survival.

Complex behaviors and low relative survival in this region are likely due to interacting effects between the counting fence and local piscivorous predators. In the outlet of Chilko Lake, Bull Trout prey heavily on outmigrating Sockeye Salmon smolts in the vicinity of the counting fence (Furey et al. 2015, 2016b; Cheng et al. 2022), with consumption rates higher for Bull Trout caught at the counting fence compared to elsewhere in the lake-river system (Furey et al. 2016b). It is possible that both the presence of Bull Trout upstream of the fence, where we observe them aggregating at high densities, as well as the fence itself affects the behavior of smolts, resulting in slow migratory rates here relative to landscapes downstream of the fence. Predation on smolts is regularly observed among diadromous salmon-bearing rivers (e.g., Blackwell and Juanes 1998; Kekäläinen et al. 2007; Berejikian et al. 2016; Evans et al. 2019, 2022; Hanssen et al. 2022), given these migrations represent large pulses of energy in constrained riverine landscapes for predators to exploit. However, human alterations to the migratory pathway could further mediate predator-prey relationships by aggregating predators or consumption, reducing smolt

migration speeds, or increasing foraging efficiency of predators (Collis et al. 1995; Sabal et al. 2016; Evans et al. 2016; Huusko et al. 2018; Nelson et al. 2021; Moore and Berejikian 2022). Thus, we presume that any linkages between smolt survival and biological and environmental factors are a consequence of their impacts on predation, the ultimate cause of mortality, although it should be noted that proximal causes can be hard to identify (Miller et al. 2014).

Our survival estimates among age classes and tag types were similar through the fence, with overlapping 95% confidence intervals (Figure 2.4). The apparent similarity in survival for this portion of the migration is consistent with the overall returns (smolt-to-adult survival; SAR) of age-1 and age-2 smolts emigrating from this system (Irvine and Akenhead 2013). Similarity in survival rates between age-1 and age-2 smolts improves the ability to use prior telemetry studies that focused on age-2 fish, even with age-1 smolts making up ~96% of the outmigration on average (Irvine and Akenhead 2013). However, we do acknowledge that the survival estimates were slightly higher for age-2 smolts (46.1%-62.2%) than age-1 smolts (37.7%). This trend of age-1 smolts exhibiting poorer survival contrasts with the findings of Stevenson et al. (2019), who identified much higher (double) survival of age-1 smolts relative to age-2 smolts, using acoustic telemetry, in this system in 2016. However, that study acknowledged that these age-specific differences were confounded with tag burden, as age-1 smolts, with smaller tags, experienced lower tag burdens (mean = 7.3%) than age-2 smolts with larger tags (mean of 10.3%; Stevenson et al. 2019). Further work experimentally manipulated tag burden for age-2 smolts and demonstrated high tag burdens indeed could decrease survival (Bass et al. 2020).

The effects of tag burdens are important to consider in any telemetry study (Brownscombe et al. 2019), and our use of PIT and acoustic telemetry allowed us to not only tag both age classes of smolts but also assess survival across a wide range of tag burdens (minimum

0.28% in an age-2 PIT-tagged fish to a maximum of 10.63% in an acoustic-tagged fish). The

lowest tag burden previously assessed during a survival study of Chilko Lake Sockeye smolts is

2.2% (Bass et al. 2020); thus with PIT telemetry we were able to assess survival with much

lower tag burdens. Even with relatively low tag burdens of age-1 PIT-tagged smolts (mean

0.46%), tag burden was still weakly but negatively correlated with survival, with no age-1 smolt

experiencing a tag burden > ~2% surviving (Figure 2.6). In addition, survival of acoustic-tagged

age-2-smolts was lower with increasing tag burdens, further suggesting tag burden affects

survival (Bass et al. 2020), at least initially shortly after release. Although our PIT tag results

suggest support for the debated 2% rule (Winter 1983; Brown et al. 1999; Jepsen et al. 2005), it

should be noted that PIT tags are implanted via syringe vs surgically implanted acoustic

telemetry tags, and that appropriate tag burdens likely remain system- and method-specific. For

example, Bass et al. (2020) found tag burden to impact survival, but only in the first portion of

the migratory corridor (the upper Chilko River). For age-2 PIT tagged fish in our study, tag

burden was weakly positively correlated with survival. Although unintuitive, this relationship is

likely driven by larger age-2 smolts experiencing poor survival; body mass and FL were

negatively correlated with survival, with similar model performance (via AICc and weights) to

the tag burden model. Thus, body size, independent of tag burden, may exhibit age-specific

influences with survival.

Within ages, we identified relationships between smolt survival and both body condition

(mass relative to length) and overall body size. Two metrics of condition (mass-length residuals

and Fulton's condition index) were positively associated with survival, consistent with higher

condition being indicative of broader health (Wilson et al. 2021). For age-1 smolts, increased

mass correlated with increased survival, consistent with both the tag burden effect but also the

hypothesis that larger fish experience increased survival via lower predation rates (Tucker et al. 2016). Across age-2 smolts, both PIT-tagged and those with acoustic telemetry tags, FL was negatively associated with survival, contrary to previous studies in this system that largely observed little to no relationship between fish size and survival (Furey et al. 2016a; Rechisky et al. 2019) and the idea that larger fish should experience higher survival, particularly with abundant predators. However, given that these older smolts constitute < 5% of the outmigrant population, it is possible that age-2 fish, and particularly very large individuals, are conspicuous and more readily targeted by bull trout and other predators smolts relative to the rest of the school (Theodorakis 1989). In fact, age-2 smolts were found to occur at higher-than-available rates within bull trout stomachs, potentially suggesting bull trout target age-2 fish (Furey 2016). Larger smolts can also be targeted by other predators, including birds (Hostetter et al. 2012; Osterback et al. 2014).

In response to intense predation pressures, it appears Chilko Sockeye Salmon smolts synchronize their migrations to both pass through the fence at night, but also in high densities to effectively swamp predators downstream of the fence (Furey et al. 2016a, 2021a). However, in this study we found no evidence that predator swamping improved smolt survival upstream of the fence, unlike the consistent effect observed among years in the 14 km reach downstream of the fence (Furey et al. 2016a, 2021a). However, our ability to assess the influence of predator swamping in the present study may be limited by the method we used to determine density of co-migrants. Furey et al. (2016a, 2021) were able to link co-migrant density in the same hour that each smolt was last detected initiating migration downstream of the fence, where fish were released. However, given we released fish well above the fence, we were limited to characterizing the total density of smolts initiating migration downstream of the fence on the

same night as tagged smolts were released upstream of the fence. Thus, we were less able to directly link the actual densities of co-migrant conspecifics to our tagged smolts, particularly because of the great variability in transit times to the fence experienced among smolts (Figure 2.4). Along with increases in transit times to the fence come increased opportunities for interactions with predators.

Survival or susceptibility to predation by Bull Trout or other predators can be influenced by numerous other biological and environmental factors that we did not assess or did not find to correlate with success in this short landscape. Beyond smolt size or body condition, the presence of pathogens or infectious agents has correlated with survival or predation risk of salmonid smolts (Jeffries et al. 2014; Healy et al. 2018; Furey et al. 2021a). Environmental factors such as turbidity (Gregory and Levings 1998; Clark et al. 2016), diel period (Clark et al. 2016; Flávio et al. 2020), and flow (Hembre et al. 2001) have also correlated with survival by impacting susceptibility to predation. In our study, we assessed the effect of lunar illumination on smolt survival, but this co-variate did not appear in highly ranked models (Table 2.1). We hypothesized that decreased light (i.e., lower lunar illumination) would result in increased cover and reduced predation risk. However, our ability to assess the impact of lunar illumination on smolt survival was likely limited by potential variability in cloud cover. In addition, the counting fence is lit at night for the safety of technicians, potentially providing artificial light in a consistent manner for predators.

Diadromous salmonids such as Sockeye Salmon face substantial challenges throughout their life cycle, with survival and productivity becoming increasingly difficult to predict. Proper management requires long-term monitoring to identify shifts in productivity, including the use of structures such as the counting fence to enumerate the annual smolt outmigration from Chilko

Lake. However, our results suggest that this specific tool has the potential to alter behavior and negatively affect survival of the smolts. Thus, there is a conflict between providing robust data necessary for management and minimally affecting populations of conservation concern. We have presented evidence to suggest that even a small, temporary, and water-porous barrier may influence the downstream survival of salmonid smolts. Thus, although large, permanent barriers have received increased research and efforts to mitigate impacts on fish passage (Silva et al. 2018; Hinch et al. 2022), more attention is likely needed on smaller barriers for which mitigation may be more feasible or less expensive. Potential solutions could include widening the counting boxes in the fence and allowing volitional passage at all hours, or abandoning the fence altogether in favor of other methods such as acoustic imaging (e.g., Dual-frequency Identification Sonar [DIDSON]) to assess behavior, enumerate fish, or assess passage (Maxwell and Gove 2007; Doehring et al. 2011; Magowan et al. 2012). Identifying feasible opportunities to facilitate fish passage is important when other complex and integrating stressors exist for which solutions are likely more challenging. In the Fraser River basin, both broad-scale impacts of climate change as well as acute events (e.g., the Big Bar Landslide that has affected upstream passage of adult Chilko salmon) require adaptive approaches and novel solutions. Just as research needs to quantify and mitigate *in situ* impacts (i.e., tag burden or handling effects as we observed), monitoring programs will need to adapt to meet the conservation and management needs in the Anthropocene.

CHAPTER 3: Fine-Scale Behaviors of Sockeye Salmon Smolts Above a Counting Fence

3.1 Introduction

Smolts migrate to the ocean to mature and grow before returning to their natal waters to complete their life cycle through spawning (Groot and Margolis 1991). The trip to the ocean can range widely in both distance and survivability. Sockeye Salmon are a particularly important species that exhibit large-scale migrations that can exceed 1000 kilometers and tens of millions of smolts. (Burgner 1991; Quinn 2018). Among the many rivers with extant spawning migrations of Sockeye Salmon, the Fraser River in British Columbia hosts dozens of tributary lakes that are home to some of the most prolific spawning populations for the species (Northcote and Larkin 1989). One lake in particular, Chilko Lake, has been the setting for extensive research on the survival of downstream migrating Sockeye Salmon smolts (Irvine and Akenhead 2013; Clark et al. 2016; Furey et al. 2016a; Bass et al. 2019; Rechisky et al. 2019; Stevenson et al. 2019b). Chilko lake has been intensively studied in part due to the Canadian government's annual installation of a counting fence used to enumerate outmigrating smolts. This added infrastructure along with the sheer volume of smolts emigrating from the lake each year results in Chilko Lake being an indicator population for all Sockeye Salmon in the entire Fraser River system.

A seaward migrating Sockeye Salmon smolt born in Chilko Lake must migrate through several landscapes associated with poor survival (Clark et al. 2016; Stevenson et al. 2019a; Rechisky et al. 2019). It appears the highest-risk landscape is the short (1.3-km) region immediately upstream of the counting fence; a lake-to-river transition area where Chilko Lake begins to narrow (Chapter 2). Anthropogenic structures that constrict already narrow migratory corridors can result in behavioral shifts in outmigrating smolts (Moore et al. 2013), as well as

their predators (Yurk and Trites 2000). Through migratory delay, structures such as the Chilko Lake counting fence could be increasing the time smolts spend exposed to heightened predation risk, potentially resulting in reduced survival (Huusko et al. 2018). Results from survival modeling in the 1.3-km stretch upstream of the fence (Chapter 2) bring up new questions regarding what smolts might be experiencing that would create such limited survival in such a small landscape.

In addition to poor survival, variable transit times of smolts from release to the counting fence suggest that behavior may be quite complex in the lake-to-river transition area. Transit times of smolts that were deemed survivors in Chapter 2 ranged from 1.3 hours to greater than 18 days. It is common for migratory fish to be delayed during encounters with barriers such as dams (Nyqvist et al. 2017b; Hinch et al. 2022), while they exhibit complex behavior associated with finding a passage route (Scruton et al. 2007), or waiting for the right conditions for passage (Steel et al. 2013). Variations in behavior within a single population such as individual boldness can also impact survival in fishes (Mittelbach et al. 2014). Although the Chilko Lake counting fence is quite different than a dam because the fence is water-permeable, its constrictions have the potential to induce delays and complex behavior.

An unexpected finding from the survival modeling in Chapter 2 was that estimated survival for age-2 acoustic tagged smolts was lower than for age-2 PIT tagged smolts. Acoustic tags are larger than PIT tags, resulting in mean tag burdens ~15-times higher for acoustic-tagged smolts than those of smolts receiving PIT tags (Chapter 2). Increased tag burdens are presumed to reduce performance or directly lower survival (Brown et al. 2010; Collins et al. 2013). Thus, further investigating smolt behavior, as well as the impacts of analytical methods on estimating

survival from positional data, could reveal if the trends observed (Chapter 2) are biologically relevant or methodological artefacts.

The primary objective of Chapter 3 is to investigate the potentially complex behaviors exhibited by Chilko Lake Sockeye Salmon smolts upstream of the counting fence that result in variable durations of exposure to Bull Trout in the area (Chapter 2). By visualizing smolt movement patterns via the acoustic telemetry positioning system, we quantified behaviors in the approach to and in the vicinity of the fence. We also investigated how the densities of co-migrating smolts and fence operations (e.g., whether either or both fence openings were open or closed) impacted the number and success of fence passage attempts made by each fish. Lastly, by more closely examining the specific paths taken by smolts through the counting fence, we refined definitions for smolt passage.

3.2 Methods

In this analysis we focused on the lake-to-river transition habitat at the downstream end of Chilko Lake in British Columbia, Canada. Specifically, we were interested in the survival and behavior of migrating Sockeye Salmon smolts as they interact with the Chilko Lake counting fence which the Canadian government installs each spring to enumerate outmigrants (Henderson and Cass 1991; Irvine and Akenhead 2013). Between April 28, 2014, and May 10, 2014, 208 smolts were captured at the counting fence and surgically implanted with Innovasea V7 acoustic telemetry tags. All smolts implanted with acoustic tags in this study exceeded the age-2 length threshold of 116 mm in FL determined for the 2014 smolt population (Brian Leaf, DFO, personal communication). Smolts were then released 1.3-km upstream of the counting fence during nighttime hours to mimic the natural migratory patterns of the fish (Clark 2016; Furey et al.

2016a). Additional information on fish capture, size range, tagging, and release is provided in Chapter 2.

To track tagged smolts we used a Vemco Positioning System (VPS; Innovasea; Halifax, Nova Scotia) which consists of an array of closely spaced telemetry receivers to triangulate positions of tags using a time-distance-of arrival algorithm (Espinoza et al. 2011). A dense array of 38 acoustic telemetry receivers along with six stationary transmitters were deployed to create our VPS for tracking the fine-scale movements of acoustic tagged smolts (Figure 3.1). Chapter 2 contains additional specific information regarding the receiver infrastructure used to track acoustic telemetry tagged smolts. In this chapter, we took the additional step of visualizing positional data for each smolt to quantify behaviors on the approach and assess more directly passage success for each fish.
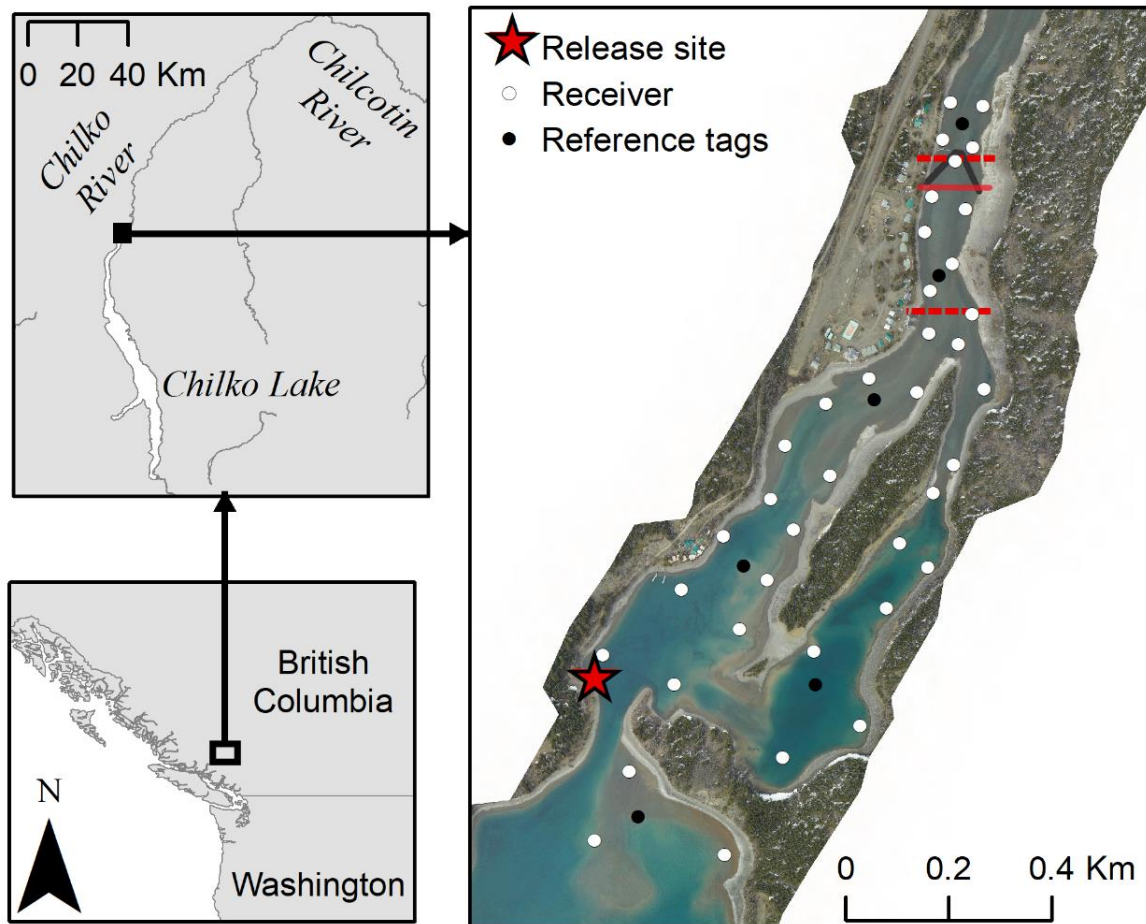
Figure 3.1: Bottom left panel shows the regional location of Chilko Lake relative to the US-Canada Border. Top left panel shows the location of the specific project area relative to broader Chilko Lake. Right panel shows the full study area with the counting fence shown in black (V-shaped line), release site shown with a red star, and the reference tag locations shown with black dots and receiver locations shown with white dots. The southern horizontal red line shows the latitude threshold of the "approach zone", middle red line shows the immediate fence area threshold, and the red line furthest north shows the latitude threshold for survival in the acoustic telemetry data.

For each smolt deemed a survivor in Chapter 2 and that was detected in our VPS in proximity to the fence (i.e., north of the approach zone cutoff; 51.6228; Figure 3.1), we visualized positional data to determine the maximum downstream extent traveled. Determining the extent of downstream travel in Chilko Lake was simplified by the north-south orientation of the waterbody; the farther north a fish swam, the more progress it made along its migration. To examine the acoustic telemetry positioning data visually, a plot was made for each acoustic telemetry tagged smolt that was detected in proximity to the fence (n = 101; examples in Figure

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3.1; all plots in Appendix 3). From these figures, we quantified smolt passage through important regions along the short migratory corridor, including the southern end of the "approach zone" used in the CJS models (Chapter 2, 51.622800°N), the immediate fence area threshold (i.e., the latitude at which the migratory corridor begins to be constricted by the fence; 51.62506°N), and the latitude used to define survival in Chapter 2 in CJS models (i.e., 10 m upstream of fence gates; 51.625465°N). To explore repeated fence approaches using the latitude figures, the number of passage attempts was recorded. A passage attempt was defined as any instance of a fish crossing the immediate fence area threshold (dotted line; 51.62506°N; Figure 3.2) from south to north. In addition, we assessed if a fish truly passed the fence by examining the final known position of each fish; if the final position was north of the survival cutoff from the CJS models (51.625465°N), the fish was deemed a survivor, otherwise the fish was assumed to have died while still upstream of the fence. It is important to note that in Chapter 2, 17 fish were deemed survivors when they were detected downstream of our VPS, but never had a calculated position downstream of the fence while in the VPS. These 17 smolts were omitted from the present Chapter 3 analysis because we do not know when they passed the counting fence. In total, 101 latitude plots were used to assess behavioral interactions with the fence.
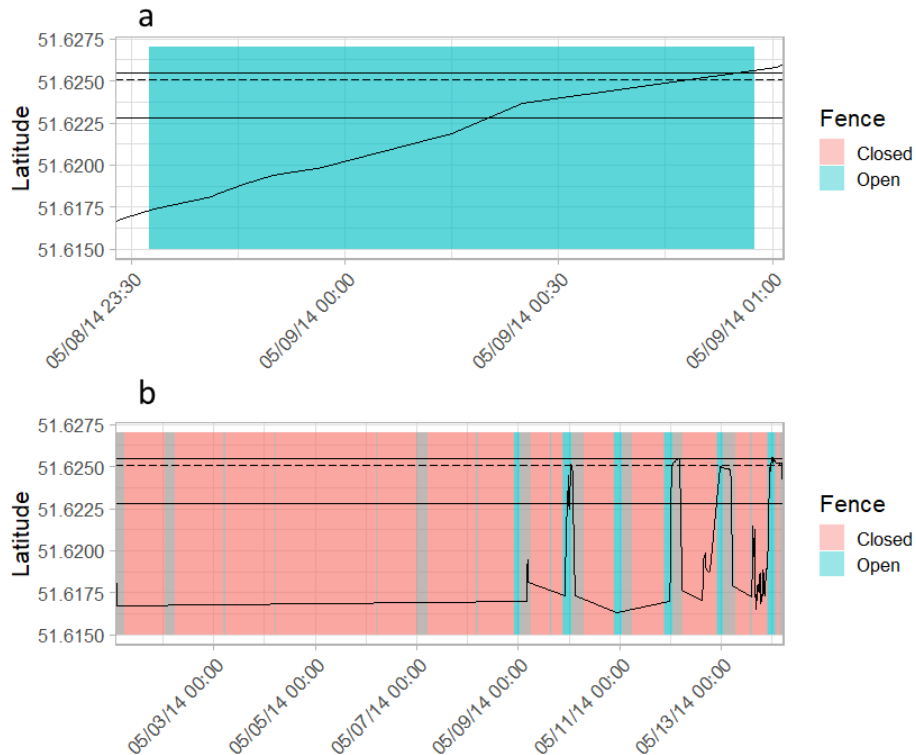
Figure 3.2: Example figures used to visualize tagged smolt behavior upstream of the fence. Panel "a" shows an example of a smolt that approached and passed the fence quickly in a single attempt. Panel "b" shows an example of a smolt that approached the fence several times without successful passage. Bottom solid line represents the cutoff used for "approach zone" in the CJS analysis from Chapter 2. Dotted line represents the immediate fence area. Top solid line represents the cutoff for survival in the CJS analysis in Chapter 2. Shading indicates whether fence was open or closed with green = both gates open, red = both gates closed, and intermediate color = one gate open.

After defining the behaviors and survival metrics for each individual smolt tracked in the VPS, we summarized data by each date and diel period (daytime and nighttime hours) for further analysis. We defined daytime periods as 06:00 until 20:00 and nighttime periods as 20:00 until 06:00 the following morning. The study period began 20:00 on April 28, 2014 and ended 06:00 on May 21, 2014. Within each diel period for each date of migration, several metrics of smolt activity were created from positional data among smolts (Table 3.1). Metrics included: 1) the number of individual smolts detected within the VPS during the diel period, 2) the number of times any smolt crossed into the immediate vicinity of the fence (Figure 3.1), 3) how many unique smolts were detected in the immediate vicinity of the fence, 4) how many fish were

determined to have survived by the CJS model (Chapter 2), 5) how many fish were determined

to have survived based on the latitude plots of the positional data, and 6) mean hourly smolt

density determined by the DFO fence data (details on how this density is calculated in Chapter

2). From these metrics, we explored the relationship between smolt behavior upstream of the

fence and survival. Scatter plots along with linear (for continuous response variables) or logistic

regressions (for binary response variables) were assessed using R 4.1.0 (R Core Team 2020) to

visually show how survival (both from CJS analyses and from the Chapter 3 dataset) varied with

each variable and whether the relationship was statistically significant ($p < 0.05$).

Table 3.1: Full dataset created using the latitude plots for each fish detected in the vicinity of the fence over the course of the study period. Metrics include 1) the number of individual smolts detected within the VPS during the diel period (Fish in VPS), 2) the number of times any smolt crossed into the immediate vicinity of the fence (Crosses into fence area), 3) how many unique smolts were detected in the immediate vicinity of the fence (Fish in Fence Area, 4) how many fish were determined to have survived by the CJS model (CJS Survivals), 5) how many fish were determined to have survived based on the latitude plots of the positional data (Actual Survivals), and 6) mean hourly smolt density

Date	Diel Period	Fish in VPS	Crosses Into Fence Area	Fish in Fence Area	CJS Survivals	Actual Survivals	Hourly Smolt Density
4/28/2014	night	21	5	4	3	1	156154
4/29/2014	day	5	3	4	2	0	354
4/29/2014	night	23	9	9	5	2	61334
4/30/2014	day	7	6	4	0	0	0
4/30/2014	night	27	15	17	10	8	10195
5/1/2014	day	4	1	2	0	0	0
5/1/2014	night	18	14	8	7	6	53756
5/2/2014	day	3	0	0	0	0	0
5/2/2014	night	19	1	1	1	0	49
5/3/2014	day	9	1	1	0	0	0
5/3/2014	night	7	4	3	1	0	0
5/4/2014	day	3	9	2	0	0	0
5/4/2014	night	5	11	3	1	0	0
5/5/2014	day	2	0	1	0	0	0
5/5/2014	night	6	5	2	0	0	193
5/6/2014	day	4	0	0	0	0	0
5/6/2014	night	6	2	2	0	0	705
5/7/2014	day	3	0	0	0	0	0
5/7/2014	night	21	6	7	1	1	1025
5/8/2014	day	9	0	1	0	0	0

Date	Diel Period	Fish in VPS	Crosses Into Fence Area	Fish in Fence Area	CJS Survivals	Actual Survivals	Hourly Smolt Density
5/8/2014	night	46	40	32	18	13	80016
5/9/2014	day	22	7	2	1	0	0
5/9/2014	night	50	27	29	7	2	128790
5/10/2014	day	17	4	4	0	1	3093
5/10/2014	night	37	17	15	6	4	42002
5/11/2014	day	23	22	6	5	0	0
5/11/2014	night	43	49	30	11	8	54862
5/12/2014	day	23	12	3	1	0	0
5/12/2014	night	44	17	23	3	2	35526
5/13/2014	day	30	42	4	3	0	2577
5/13/2014	night	41	31	20	5	3	37838
5/14/2014	day	30	35	13	3	1	527
5/14/2014	night	31	31	17	2	4	18513
5/15/2014	day	22	4	7	0	0	4
5/15/2014	night	28	23	16	2	5	4258
5/16/2014	day	13	0	2	0	0	0
5/16/2014	night	24	11	10	2	0	3505
5/17/2014	day	15	0	2	0	0	0
5/17/2014	night	18	3	7	1	1	1765
5/18/2014	day	13	0	3	0	0	0
5/18/2014	night	19	4	8	0	0	791
5/19/2014	day	12	3	3	0	0	0
5/19/2014	night	17	8	9	0	0	0
5/20/2014	day	10	0	1	0	0	0
5/20/2014	night	0	0	0	0	0	0

3.3 Results

Visual assessments of smolt position (latitude) while in the fence area of the VPS showed that fish exhibited a wide range of behavior while upstream of the fence (Appendix 3). 28 fish (27.7% of the 101 assessed) appeared to experience minimal delay and moved through the fence area and downstream in an hour or less. 45 fish (44.6%) experienced delays greater than 24 hours after initially approaching the fence, with some fish making repeated attempts to pass for greater than a week. Using these visualizations, we gave each of the 101 fish assessed a new fence passage (survival) determination depending on whether their final triangulated positions

remained downstream of the fence or if they retreated back upstream. All 28 smolts that spent an hour or less at the fence after initial approach survived and passed downstream, while only 38% of fish delayed for at least 24 hours survived. Passage attempts tended to occur during times when one or both fence gates were open, while some attempts were made during times when both gates remained closed. Regardless, many fish clearly approached the latitude of the fence gates and were unable to pass, followed by retreats to lower latitudes (i.e., back towards the lake). Within the Chapter 3 dataset, the average number of passage attempts for an individual fish was 3.77 (SE = 0.35). For surviving fish, the average number of attempts was 2.68 (SE = 0.35), significantly less than fish deemed not to have survived averaged 5.62 attempts (average of 5.62 attempts; SE = 0.62; Wilcoxon rank-sum test; p < 0.0001).

These analyses revealed that some smolts were incorrectly deemed survivors in the CJS analysis; these fish had calculated positions north of the required cutoff used in Chapter 2 (which was selected to be conservative in defining passage relative to the potential error in estimated smolt positions), but then retreated back to have their final known positions south of the fence. Using the visualizations (Appendix 3), we determined that of the 118 fish that were deemed survivors by the CJS analysis in Chapter 2, only 80 of them (63 with VPS positions and 17 detected further downstream by other receiver arrays) appear to have truly crossed the fence successfully.

In general, increased hourly smolt density correlated with increased likelihood of survival (Figure 3.3). Linear regressions with survival metrics as the response variable (survival determined by CJS model or by latitude figures) and co-migrant density as the explanatory variable yielded statistically significant positive relationships for survival determined via CJS models from Chapter 2 (p = 0.0081) and via our new assessments (p = 0.0033), however R^2

values were fairly low at 0.17 and 0.21, respectively (Figure 3.3). Logistic regressions with hourly smolt density as the explanatory variable and a binary response variable representing whether zero or at least one smolt survived during a given time period, yielded positive but inconsistent correlation between smolt density and survival. The logistic regression predicting survival to the latitude used in CJS analyses was nearly significant (p = 0.0627). For the logistic regression predicting survival based on the final position yielded from the VPS, a strongly positive and statistically significant relationship between survival and co-migrant density was found (panel b in Figure 3.2; p = 0.0096).

In addition to investigating the impact of co-migrant density on survival, we also produced linear regressions to understand impact on smolt behavior upstream of the fence (Panels e and f in Figure 3.2). Hourly smolt density does not appear to be correlated with the number of times smolts cross into the immediate fence area with a very weak negative effect found (panel e; R^2 = 0.01, p = 0.5081). However, we found a moderately strong positive relationship between co-migrant density and the number of individual smolts spending time in the fence area at some point during a given time period (panel f; R^2 = 0.30, p = 0.0001).
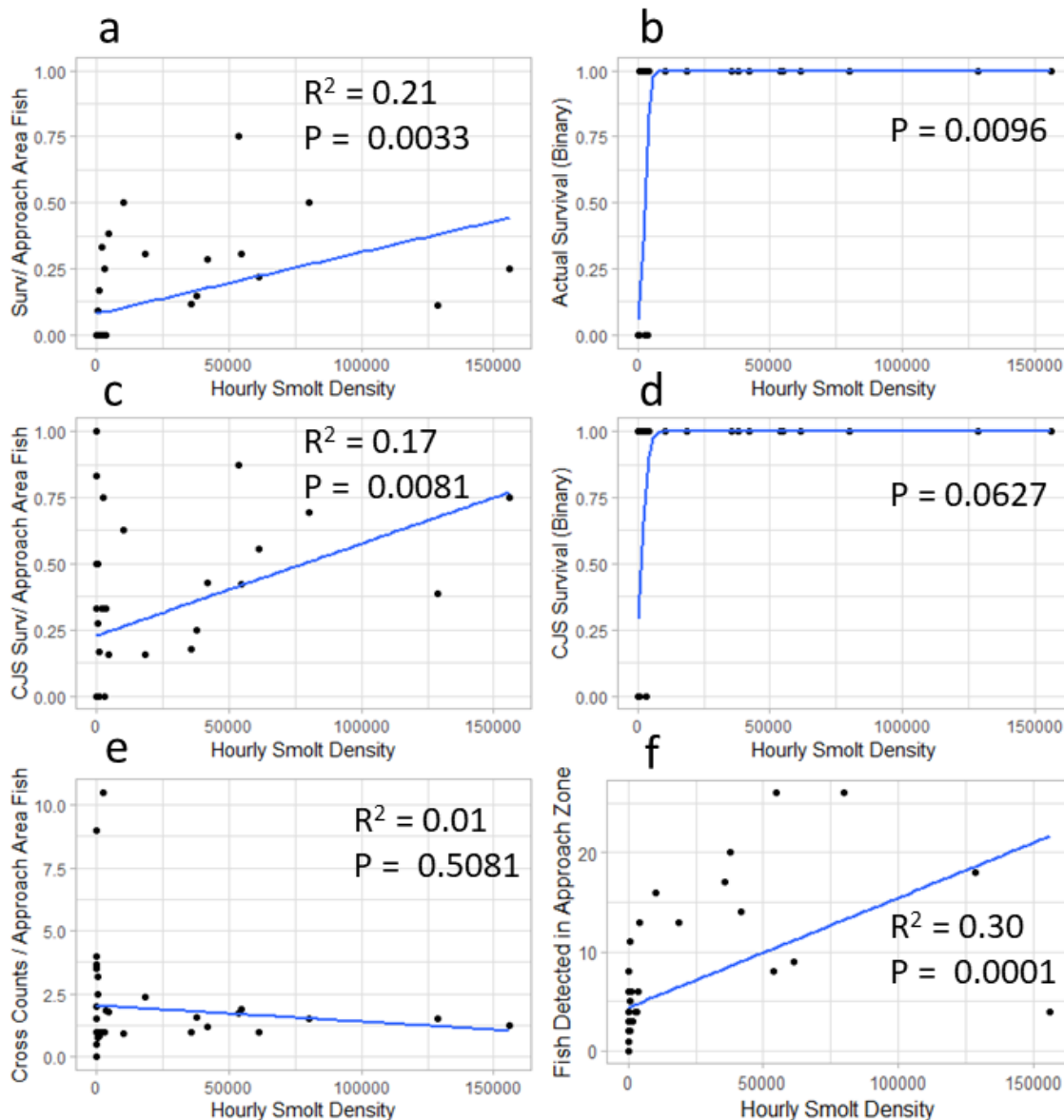
Figure 3.3: Scatter plots showing how hourly smolt density correlated with various metrics of survival or fish behavior in the general fence area. Blue lines show linear regressions for panels a, c, e, and f. Blue lines show logistic regression for panels b and d. All linear regressions include associated R2 and P values while logistic regressions include only P values to determine significance ($P < 0.05$).

3.4 Discussion

These analyses suggest Chilko Sockeye Salmon smolts are exhibiting complex behaviors upstream of the fence and that the fence is potentially causing delay that could affect survival. We visually demonstrated that some smolts approach the fence several times, and sometimes fail to truly pass, even after being within 10 meters of the opening. These fish could be having difficulty finding the openings in the fence meant for passage (Peter et al. 2022) or they may be

waiting for a critical mass of co-migrants to also approach the fence in order to numerically overwhelm (Furey et al. 2016a) the predatory Bull Trout that are likely staged at the fence (Furey et al. 2016b; Cheng et al. 2022). Regardless, these fish appear to be encountering the fence and altering their behavior while they assess how and when to pass (Appendix 3). In addition to our results suggesting that the fence may be causing smolts to pause on their migration, we found Chilko smolts are documented to attempt passage during periods of high co-migrant density, consistent with findings of Furey et al. (2016a).

Co-migrant density appears to be positively correlated with both passage success and the number of fish in the fence area (Figure 3.3). Any amount of active smolt migration (i.e., non-zero level of co-migrant density) appears to promote passage success—this result was consistent for both CJS estimated survival from Chapter 2 and actual survival determined by our latitude plots (Panels b and d in Figure 3.3). One limitation of the Chapter 2 methodology was that a fish could have had one or more calculated positions north of the survival cutoff without successfully passing through the fence. This led us to investigate whether any fish were incorrectly deemed survivors in the Chapter 2 methodology.

Based on the new dataset in this chapter created using the latitude figures in Appendix 3, we determined that 38 fish were potentially categorized incorrectly as survivors using the methods in Chapter 2. Using the methodology in Chapter 2, 56.7% (118 out of 208) of age-2 acoustic telemetry tagged smolts were deemed survivors. When we account for the 38 fish potentially incorrectly categorized as survivors, the survival rate of tagged fish declines to 38.5% (80 out of 208)—a 32.1% reduction. If the CJS model estimated survival for age-2 acoustic telemetry tagged fish in Chapter 2 (62.2% (SE = 6.1%) were adjusted by the same reduction factor, we would estimate survival of 42.2%. This reduced estimate would bring the results closer to the PIT-tagged age-2 survival estimate from Chapter 2 (46.1%; SE = 3.4%). This reduction in survival of acoustic tagged fish is more consistent with the expected effect of increased tag burden; higher tag burdens should be associated with lower likelihood of survival (Bass et al. 2020). Tag burden may impact the survival of smolts through reduced swimming capability (Collins et al. 2013) that could be further exacerbated by multiple fence approaches and increased energy expenditure or disorientation during migratory delay (Hinch et al. 2022).

Our positional data, if further investigated, still hold great potential to further reveal fine-scale movement patterns as Chilko Lake smolts move through our array and encounter the

counting fence. Subsequent analysis should consider using more advanced analyses of the positional data such as the determination of behavioral states of individual fish over time via Hidden-Markov Models (Whoriskey et al. 2017; Bacheler et al. 2019) or state space models (Jonsen et al. 2023). Determination of behavioral states for Chilko Lake smolts could help managers understand the level of energy expenditure smolts are enduring while they are delayed upstream of the fence. These additional analyses could further reveal the true impact of smaller barriers such as counting fences.

Counting fences have been in use for both upstream and downstream migrating salmonids since at least the first half of the 20th century (Blair 1957). These structures have proven to be a valuable tool for research and management by providing researchers with a convenient way to capture study fish (Peake et al. 1997; Whalen et al. 1999; Clark et al. 2016; Furey et al. 2016a; Stevenson et al. 2019b, 2020; Lennox et al. 2019; Bass et al. 2020) and to monitor population trends (Irvine and Akenhead 2013; Cote et al. 2021) to make better informed management decisions. However, it is possible that the very structures that are meant to help a species are actually causing delay that could impact survival. The potential for these structures to cause delay has been suggested before (Cote et al. 2021), but impacts from non-dam structures have been the subject of comparatively minimal research relative to larger barriers. Our results showing the potential for detrimental effects of a counting fence are broadly applicable to downstream barriers that may appear benign, or to any fish passage infrastructure specifically meant so enumerate fish. We believe that any barrier, regardless of the potential benefits (i.e., counting to monitor population trends) needs to be assessed for potential detrimental effects such as migratory delay before assuming that the population of interest is not being negatively impacted by the use of the structure.

CHAPTER 4: Conclusion

Sockeye Salmon must migrate immense distances to and from marine habitat in order complete their life histories (Burgner 1991; Quinn 2018). These migrations create several opportunities for bottlenecks in survival as individuals move through varied landscapes, especially during the smolt lifestage. My thesis used smolt movement data from both PIT and acoustic telemetry to assess smolt survival and behavior during interactions with a small-scale, temporary government operated counting fence. This work provides new context for the potential impacts of such a barrier in a system otherwise rich in understanding of smolt migration ecology (Clark et al. 2016; Furey et al. 2016a; Rechisky et al. 2019; Stevenson et al. 2019b).

My work identified a "high-risk" landscape upstream of the Chilko Lake counting fence (Chapter 2). This is not the first research to show that early smolt migration in clear freshwaters of the Chilko River leads to low survival (Clark et al. 2016; Furey et al. 2016a; Rechisky et al. 2019; Stevenson et al. 2019b), but it is the first time that the area upstream of the fence has been assessed—previous studies have only examined survival downstream. During their time upstream of the fence, smolts appear to be exhibiting complex behaviors (Chapter 3) that include repeated passage attempts and days to weeks of time delayed before passage. By causing these behaviors, the Chilko Lake counting fence appears to have a negative impact on smolt survival. These findings add to our understanding of the migratory ecology of salmon smolts and may have broad implications on how managers should view the potential impacts of small, temporary barriers.

4.1 Smolt Survival and Avoiding Predation

In the landscape immediately downstream of the counting fence, specifically the first 14 km, smolts experience low survival ranging from 68% (Furey 2016) to above 90% (Bass et al. 2020) among years. The landscape immediately upstream of the fence has never been previously assessed, but the research in this thesis suggests that the 1.3-km upstream of the fence may be the highest mortality landscape assessed to date. Estimates ranged from 62.2% (SE = 6.1%) for age-2 acoustic tagged fish to 37.7% (SE = 2.7%) for age-1 PIT tagged fish (Chapter 2). The study landscape represents a transition zone between lake and river where flows begin to increase and the corridor narrows, potentially causing the smolts to experience more concentrated exposure to predators.

We observed that smolts tended to avoid staying in the immediate fence area for long periods of time. If a tagged smolt approached the fence and was unable to pass during a particular attempt, it almost always retreated back upstream away from the fence, sometimes traveling upstream greater than 300 m—a seemingly inefficient practice. Swimming against river flow in order to control migration rate or seek shelter has been documented for salmon smolts (Holleman et al. 2022), however, larger forays back upstream appear less common. Although previous studies of the Chilko Lake population did not have the spatial resolution that we did with the VPS, the previous research did not document upstream travel once a smolt had initiated migration. Rather, smolts tended to pause migration and wait for the cover of darkness to move (Clark et al. 2016; Furey et al. 2016a), s consistent with research showing that visual predators have lower feeding efficiency when vision is hindered. The fact that smolts tend to use valuable energy to vacate the fence area after failed passage attempts by swimming upstream presents a potentially novel example of extreme predator avoidance behavior that could deplete precious energy stores that they will need for their migration to the

4.2 Complex Behavior in Response to Barriers

Considerable research has occurred to characterize behavioral and survival impacts of anthropogenic barriers such as dams on migratory fish (Venditti et al. 2000; Marschall et al. 2011; Nyqvist et al. 2017a; Renardy et al. 2021). Much less research has occurred to understand the seemingly more benign impacts of smaller and sometimes temporary barriers (but see Gauld et al. 2013; Newton et al. 2019; Havn et al. 2020). The cumulative impact of delay caused by interaction with barriers can reduce the survival of a downstream migrating smolt (Nyqvist et al. 2017a), and factors such as presence of infections agents can impact survival of smolts via reductions in fitness (Bass et al. 2019; Furey et al. 2021a). Theoretically, anything that reduces the movement ability of a smolt could have a negative influence on survival.

The smolt lifestage has been described as "energy deficient" (Stefansson et al. 2003). This is in part caused by the physiological changes the smolts go through to prepare for the marine environment (Burgner 1991), but it highlights the fact that during the smolt lifestage, energy reserves are naturally low to start and they may be more prone to depletion (Virtanen and Forsman 1987). For Chilko Lake smolts, the energy expenditure involved with repeated fence approaches sometimes coupled with large forays (>300 m) back upstream holds the potential to deplete already reduced energy resources, which could reduce a smolt's ability to avoid predators

during their journey to the ocean. In addition to depleted energy reserves, swimming performance is also thought to be reduced during the smolt lifestage (Smith 1982; Virtanen and Forsman 1987). Smolts that are naturally "energy deficient" and poorer swimmers than during other lifestages need to maintain as much of their energy stores as possible to ensure that they can successfully complete their trip to the ocean. We have presented evidence of complex, potentially energy wasting behavior upstream of a small, temporary, and water porous barrier.

4.3 Delay Impacts Migration Timing

Environmental conditions along freshwater migratory routes (Sykes et al. 2009; Russell et al. 2012; Michel et al. 2013) and in the marine environment (Hvidsten et al. 1998) can change rapidly during the spring migratory season, so the timing of migration can impact conditions experienced by migratory smolts. Climate change is complicating successful recruitment through both a warming marine environment (Cline et al. 2019; Connors et al. 2020) and warming waters along freshwater migratory routes (Hinch et al. 2012). Using the same logic as the "Match-Mismatch Hypothesis" (Cushing 1990) which describes the importance of the timing of juvenile development with food availability, success of migrating smolts requires migrants to match the timing of favorable conditions (Satterthwaite et al. 2014).

Migratory fish react to environmental cues to dictate when it is time for them to move, so it is important both for the cues to remain consistent over time, and fish need to physically be able to move when conditions are right. In order to maximize the likelihood of both immediate and long-term survival, smolts need to match their ocean entry timing as closely as possible with favorable marine conditions (Rechisky et al. 2012). As the timing of marine entry has been shown to correlate with long term survival,(Scheuerell et al. 2009; Satterthwaite et al. 2014) even a few days of delay could cause smolts to miss the ideal window for ocean entry, thereby impacting survival through mechanisms such as water temperature or food availability (Hvidsten et al. 1998, 2009). During the spring downstream migratory season, there are a limited number of days during which smolts have ideal ocean conditions to maximize their survival during ocean entry. A barrier such as the Chilko Lake counting fence could prevent smolts from moving volitionally if the gates are not open, or if smolts have difficulty crossing when they approach to pass, even if the gates are open. Results from Chapter 3 of my thesis showed a correlation between delay and survival outcome, with a negative relationship between number of passage attempts and survival. Even if a smolt is able to make it through the fence, the time that they

spent delayed and potentially depleting their energy stores could impact their likelihood of survival further downstream and into the marine environment (Scheuerell et al. 2009; Satterthwaite et al. 2014) by potentially limiting forage availability (Hvidsten et al. 1998, 2009).

4.4 Potential Solutions for the Counting Fence

Thus far we have only presented problems associated with the Chilko Lake counting fence, but it is important to remember what a valuable tool the structure is. Its intended purpose is to help manage Sockeye Salmon through enumeration of outmigrating smolts (Henderson and Cass 1991; Irvine and Akenhead 2013), providing important indicators of population productivity used in management models. As a result, we need to consider ways to mitigate the potential effects of the fence on smolt behavior, interactions with predators, and survival while still providing robust estimates of the numbers of smolts leaving the lake. At present, the counting fence is only opened when employees can visibly observe a significant number of smolts upstream of the fence. This may result in some smolts being unable to pass when they would otherwise naturally do so. Additionally, the two openings in the fence intended for smolt passage are each only 2.5-m wide, a significant reduction from the width of the Chilko River in this location which is approximately 100 m during the spring migratory season. One suggestion for potentially increasing the passage effectiveness of the counting fence would be to widen the fence openings and keep it perpetually open to allow volitional passage of smolts at any time. Although modifying the fence itself and the way it is operated would likely complicate the currently functioning operation of the fence, perhaps a wider area for the smolts to pass would promote better escapement.

In addition to constricting the migratory corridor and potentially allowing for abnormal prey concentrations for Bull Trout, the fence is artificially lit at night. Having the fence equipped with lights facilitates the photography that occurs at the fence, but it may also be creating artificial daylight conditions which the smolts are known to avoid during migration (Clark et al. 2016; Furey et al. 2016a) and which the Bull Trout could use to forage more efficiently (Nelson et al. 2021). One potential solution used by biologists to avoid the behavioral modifications caused by observation methods requiring light is the use of infrared light (Chidami et al. 2007). By replacing the lights and cameras at a counting fence with infrared capable equipment, it is possible that light-induced behavioral modification could be avoided, resulting in more natural foraging efficiency for the predators and higher survival for the smolts.

Other enumeration methods, albeit potentially more complicated, exist that could allow for monitoring of smolts without constricting their movement at all. One potential method of enumeration without the use of a fence would be through the use of Dual-frequency Identification Sonar (DIDSON) acoustic imaging which has already been used at Chilko Lake to observe smolt interactions with Bull Trout (Cheng et al. 2022). DIDSON has been previously proven as an effective method of enumeration of adult salmon (Holmes et al. 2006), and can be used to enumerate much smaller fish (Maxwell and Gove 2007), although at much shorter distances (i.e., a small proportion of the width of the Chilko River). This solution would likely require some side-by-side comparisons while the fence is still in use to calibrate and determine variability in estimates relative to the robustness of the fence-based counts. By installing and tuning an acoustic imaging system and using it in tandem with the fence to count fish, managers could identify methodologies that would allow for the acoustic imagery counts to eventually replace the fence.

4.5 Summary

This thesis explores survival and behavior of Sockeye Salmon smolts in a previously unstudied landscape for one of the most important populations in the Fraser River basin of British Columbia. We demonstrate that the 1.3-km landscape upstream of the counting fence is high-risk (Chapter 2), similar to the other landscapes previously assessed downstream of the fence (Clark et al. 2016; Furey et al. 2016a; Rechisky et al. 2019; Stevenson et al. 2019b). While upstream, smolts can exhibit complex behavior while attempting to pass through the counting fence, sometimes making several unsuccessful fence approaches before passing or succumbing to predation (Chapter 3), resulting in delays of up to 18 days. The acoustic telemetry data produced by our fine-scale positioning system still hold further potential for understanding smolt experiences in the lake-to-river transition zone, and continued research should focus on fine-scale movements of tagged smolts to attempt to further understand factors driving smolt survival in this initial migratory step. We have demonstrated that smolt behavior and potentially survival is being impacted by the presence of the fence, so managers should consider modifying the way that outmigrating smolts are enumerated. The results in my thesis may even suggest that there are more fish attempting to leave Chilko Lake than we currently think. If the fence is truly preventing a portion of fish from successfully leaving the lake, the current method of enumeration may affect smolt production estimates. My results can also be applied in other

systems where smaller and sometimes temporary barriers are in place—each individual barrier needs to be assessed before impact assumptions can be made.

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Appendices

Appendix 1: Supplemental HPE Figure
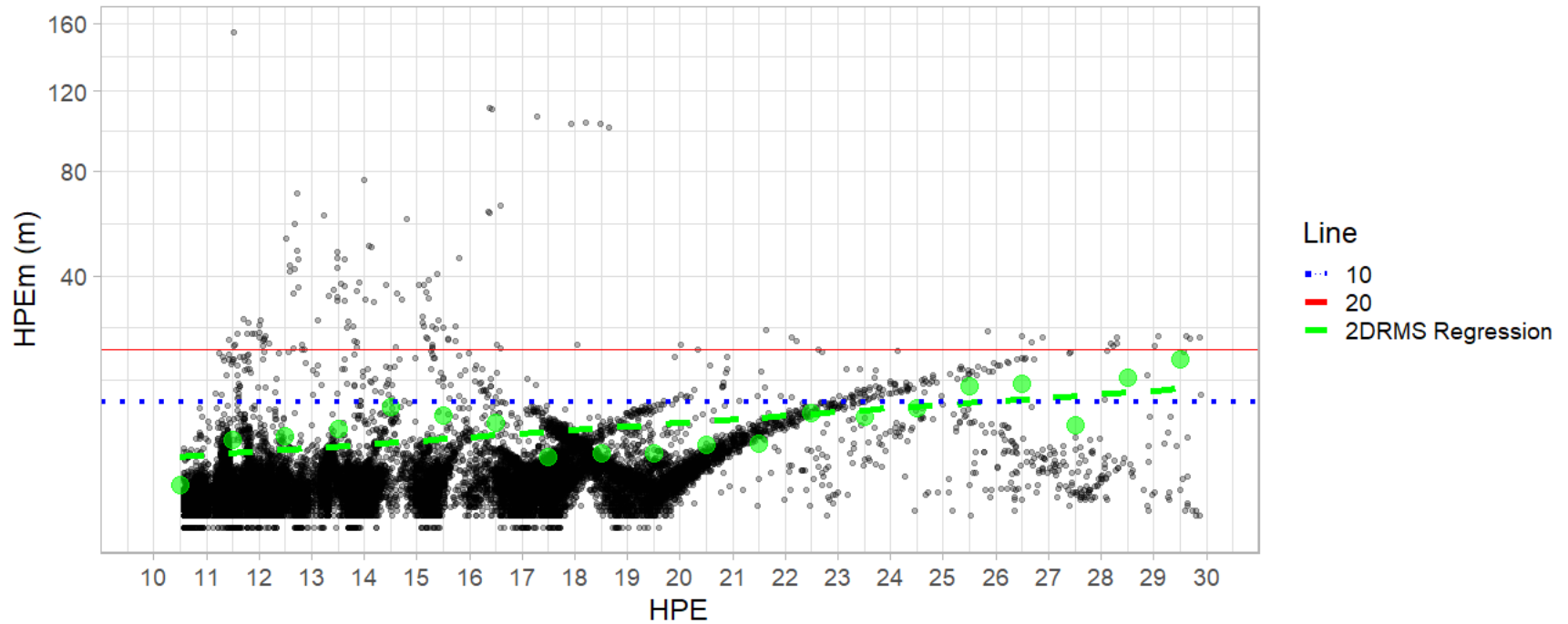
Supplemental Figure 1: Scatter plots of HPEm (m) by HPE for calculated reference positions. Dashed diagonal line represents 2DRMS regression. Larger circles show 2DRMS of HPEm for each HPE bin. Horizontal dotted line is placed at HPEm = 10 m. Solid horizontal shows where HPEm = 20 m.

Appendix 2: Supplemental CJS Parameter Coefficient Table

The following table presents parameter coefficients for top-ranked models separated by age class and tag type. Limits of the 95% confidence interval are for the parameter estimate ("Estimate" column).

Parameter	Intercept	Estimate	Standard Error	Lower Confidence Limit (95%)	Upper Confidence Limit (95%)
Acoustic Age 2					
Fulton	-2.51	3.94	2.26	-0.49	8.38
Residuals	0.66	0.13	0.07	-0.02	0.27
Fork Length	3.48	-0.02	0.01	-0.04	0.00
PIT Age 2					
Fork Length	7.49	-0.05	0.02	-0.09	-0.02
Mass	2.13	-0.10	0.03	-0.16	-0.04
Burden	-2.35	4.81	1.56	1.75	7.86
PIT Age 1					
Burden	0.64	-0.85	0.45	-1.73	0.03
Mass	-1.37	0.11	0.08	-0.04	0.27

Appendix 3: Individual Latitude Plots

The following figures show latitude over time for each fish assessed in Chapter 3. The X axis shows time passing from left to right, and the Y axis represents latitude. The bottom horizontal solid line represents the cutoff used for "approach zone" in the CJS analysis from Chapter 2. The dotted line represents the immediate fence area. The top solid line represents the cutoff for survival in the CJS analysis in Chapter 2. Shading indicates whether fence was open or closed with green = both gates open, red = both gates closed, and intermediate color = one gate open. Slight differences in colors between plots are present when the color shading is more dense due to more time on the x axis being represented on the same size plot. The number in the top left of each panel is the tag ID for the individual sockeye salmon smolt.

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