SURVIVAL AND MIGRATION CHARACTERISTICS OF JUVENILE SOCKEYE SALMON (Oncorhynchus nerka) SMOLTS THROUGH COMPLEX NEARSHORE COASTAL

MIGRATION CORRIDORS

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SURVIVAL AND MIGRATION CHARACTERISTICS OF JUVENILE SOCKEYE SALMON (*Oncorhynchus nerka*) SMOLTS THROUGH COMPLEX NEARSHORE COASTAL MIGRATION CORRIDORS

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Abstract

Telemetry tracking of Fraser River Sockeye salmon (Oncorhynchus nerka) smolts from Chilko Lake to the open ocean has revealed relatively high mortality through some coastal areas of British Columbia, and that coastal migratory routes may influence survival. Acoustic arrays were strategically deployed through the Discovery Islands region to track tagged smolts across all possible migratory routes, including three major entrances: Discovery Passage (DP), Sutil Channel (SC), and Desolation Sound (DS). A total of 465 smolts were tagged and released at Chilko Lake in 2017 (n = 315) and in the Northern Strait of Georgia in 2018 (n = 150) using a combination of VEMCO V4, V5 and V7 transmitters. Smolts were observed using all three routes with SC (n = 101), the most central, having the greatest proportion of use, followed by DP (n = 44) and DS (n = 13). Survival of the 2018 smolts was estimated using a Cormack Jolly Seber framework adjusted to account for variable distances of the major migratory routes. Highest survival was in DS (84% /100 km, 95% CI: 46 - 97%), followed by DP (71%, 95% CI: 39 - 90%), and lastly SC (48%, 95% CI: 37 - 60%). Each route presents variable environmental conditions that may influence smolt survival likely through variable exposure to predators. Smolts migrated through DP with mean travel rates of 36 km.d⁻¹ (SE \pm 1.8) which was 1.7 times faster than through SC (mean travel rates of 21.5 km.d⁻¹ (SE \pm 1.8) and 2.4 times faster than through DS (mean travel rates of 15 km.d⁻¹ (SE \pm 2.9). Extreme tidal currents present with DP provide rapid transport of smolts through the route, while other routes provide beneficial currents further along their migration path. Survival and travel rates did not appear to be linked as survival was poorest through SC which had the 'intermediate' travel rate. This study provides the most detailed picture of behaviour and mortality of Pacific salmon smolt migrations in marine coastal areas to date and highlights the potential of spatiotemporal variability of migration to impact survival in early marine migrations of smolts.

Lay Summary

Pacific salmon (*Oncorhynchus spp.*) beginning their seaward migration must leave their freshwater environments and transition into the marine environment. Not all juveniles use the same routes within early marine segments of migration, and these routes may vary in levels of predation, competition and disease transfer, and thus could variably impact survival of those that choose different routes. This study was the first to capture, tag, and track juvenile sockeye salmon (*O. nerka*) exclusively within the marine environment using acoustic telemetry. I was able to identify regions of high relative mortality and observe how different migration routes, body size, and behaviours led to different survivorship among juvenile sockeye. The variation was likely driven by predation and, specifically, the environmental conditions within each route that provide better opportunity for predators. My thesis highlights the large scale impact that a small scale spatial variation can have on population survival.

Preface

This project was completed as part of the collaborative Salish Sea Marine Survival Project that has brought together scientists from across national and disciplinary boundaries. Additionally, Canada's Ocean Tracking Network, the Pacific Salmon Foundation, and Kintama Research Services have provided integral financial, operational and analytical support related to acoustic telemetry infrastructure. Acoustic tags were provided by Fisheries and Oceans Canada (Dr. Jay Parsons), Canada's Ocean Tracking Network, the Pacific Salmon Foundation and the Hakai Institute. This work represents a continuation of nearly a decade of previous studies from many members of the Pacific Salmon Ecology and Conservation Laboratory. I was responsible for research design planning, along with data collection and analysis, in addition to preparation and submission of manuscripts. None of this would be possible without the guidance of my supervisor, Dr. Scott Hinch, who has been an integral part of the foundation of research that developed the research questions associated with my study. Dr. Brian Hunt provided significant support through developing key relationships with industry partners that allowed this research to be carried out in both field and laboratory settings, along with securing funding through the Mitacs Accelerate program. Dr. Eric Peterson and the Hakai Institute's Juvenile Salmon Program provided the operational and technical support necessary to obtain smolts within the marine environment along with accommodation, technician, and vessel support within the study area. I received support from David Welch, Erin Rechisky, Aswea Porter, Nathan Furey, Andrew Lotto and Christine Stevenson in field techniques, data management, analysis and presentation. Daniel Johnston provided a vessel for transportation of smolts among the capture, tagging and release sites. The Campbell family provided access on their property to a site we used for tagging surgeries. Procedures related to the capture, handling, tagging and transport of salmonids were approved by the University of British Columbia Animal Care Committee (AUP #A19-0193).

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Introduction

Migrations are a phenomenon that occur on large spatial and temporal scales across many taxa in distinct regions of the world (Alerstam et al. 2003; Chapman et al. 2014). Migrations are a directed movement across geographic environments that provide individuals a benefit relative to prior environments (Chapman et al. 2014). Such large-scale movements are energetically demanding, but the demographic benefits of accessing resources (Melnychuk et al. 2010; Freshwater et al. 2017), large congregations of mates (Chapman et al. 2012), areas with less predators (Clark and Levy 1988; Manuel and O'Dor 1997), and superior environmental conditions (Hodgson and Quinn 2002), may outweigh the costs of completing these movements (Chapman et al. 2014). Risks incurred during migrations are often experienced within transitory environments where predators may take advantage of increased densities due to natural and anthropogenic bottlenecks (Furey et al. 2015a; Evans et al. 2016), decreased condition caused by lack of feeding (Chapman et al. 2013; McKinnell et al. 2014; Miller et al. 2014; Godwin et al. 2015; James et al. 2020), or exposure to infectious agents (Miller et al. 2014; Godwin et al. 2017). These factors likely drive the impacts on survival that are observed with spatiotemporal variability in migrations of conspecifics (Nathan et al. 2008).

Pacific salmon (*Oncorhynchus spp.*) are semelparous anadromous fishes born in freshwater, rear as juveniles in riverine and lacustrine environments, spend part of their adult life in the ocean, and return to freshwater to spawn, then die (Groot and Margolis 1991). Thus, their life-cycle consists of distinct stages occurring in different aquatic environments. Generally, eggs are deposited in the fall, alevins hatch in the late winter or early spring, fry emerge from the gravel in the spring, and smolts migrate to sea following a few days to years of residence within their freshwater environments. Following one to seven years in which they complete growth and maturation at sea, they return from the saline environment to their natal rivers to spawn (Groot

and Margolis 1991). While such migrations among environments provide many benefits including enhanced growth rates (Quinn 2018), there are large risks associated with moving among environments (Alerstam et al. 2003) including energetically demanding physiological shifts (Hoar 1988), exposure to different suites of predators and pathogens (Miller et al. 2014; Godwin et al. 2015; Tucker et al. 2016), and anthropogenic barriers such as dams (Welch et al. 2008; Marschall et al. 2011).

Pacific salmon have deeply rooted cultural, economic and ecological significance on the north Pacific coasts. The largest salmon-producing river in Canada, the Fraser River, flows into the Salish Sea near Vancouver, British Columbia, and drains a watershed of approximately 220,000 km² (McDaniels et al. 2010; Chandler et al. 2015). Populations of five Pacific salmon species are supported within this watershed and can migrate over 1000 km inland, historically providing a rich supply of nutrients to the land and food for local animals and indigenous peoples (First Nations). Interannual variability of population productivity is a trademark of salmon populations globally, however, stark declines in stock-specific recruitment and abundance of local stocks have been observed since the early 1990s (Irvine and Fukuwaka 2011).

Sockeye salmon (*O. nerka*) are the second most abundant Pacific salmon species in the Fraser River. They are arguably the most important salmon for First Nations food, social and ceremonial fisheries (Jacob et al. 2010), and provide the greatest economic benefit to commercial fisheries (McKinnell et al. 2014). They are unique in their increased reliance on lacustrine environments, relative to other species of Pacific salmon (Groot and Margolis 1991). Upon emerging from gravel beds, fry migrate to their natal lake systems where they may spend one to two years rearing, however, some populations remain as long as three years within the lake (Groot and Margolis 1991). As with all Pacific salmon, the anadromous nature of sockeye salmon means they must make arduous return migrations between inland spawning habitats and offshore pelagic feeding grounds, covering tens of thousands of kilometers in their life (Groot and Margolis, 1991). Adult return migrations of sockeye salmon are well known globally due to the conspicuous nature of these brightly coloured individuals and the important harvest that occurs with their return. However, our understanding of the seaward migration remains limited (Hinch et al. 2006), specifically the early marine segments of migration that occur upon ocean entry. Yet, survival during this life stage has been proposed to have a disproportionate effect on returning population sizes and thus the overall population productivity (Tucker et al. 2018).

Fraser River sockeye salmon are near the southern distribution of the species (Rand et al. 2012), which can exacerbate negative impacts of climate change and highlights the spatial variation of stock-recruitment (Irvine and Fukuwaka 2011; Irvine and Akenhead 2013; Miller et al. 2014). Record low adult sockeye returns to the Fraser River in 2009 and a decade of declining productivity led to a judicial inquiry (Cohen 2012a, 2012b), only to be followed in subsequent years by two of the largest adult returns ever observed (Neville et al. 2016). Highlighting the erratic interannual variability of Fraser River sockeye populations, adult returns in 2019 set a new record low of an estimated 485,700 individuals, or approximately 10% of the pre-season forecasted returns (PSC 2019). Reasons for the highly variable and generally decreasing productivity among sockeye populations are still being debated (McKinnell et al. 2014). Many theories have been developed as to what drives the declines, including increased predators (Berejikian et al. 2016; Nelson et al. 2019), increasing presence of pathogens (Miller et al. 2014; Tucker et al. 2018), and shifting oceanic productivity and associated increased competition (Irvine and Fukuwaka 2011; Beamish et al. 2012; Irvine and Akenhead 2013; Ruggerone et al. 2015). One of the key recommendations emerging from The Cohen Commission was for greater investigation and understanding of the early marine life phase of sockeye salmon (Cohen 2012b). Although survival of Pacific salmon varies among life stages, the brief smolt life stage which involves physiological transformations, and transitions between fresh and salt water, is thought to represent a significant survival bottleneck (Welch et al. 2008; Cohen 2012b; Tucker et al. 2018). Smoltification is a process of physiological and behavioural adaptation that is thought to be triggered by increasing photoperiod, and is mediated by changes in thyroid hormone production (Keefer and Caudill 2014). The physiological changes enable juvenile salmon to better cope with the marine environment, by enhancing ability to osmoregulate in salt water (Keefer and Caudill 2014), and increasing schooling behaviour which is a known anti-predator technique (Furey et al. 2016). However, these changes also increase the total energy demand necessary to sustain growth and active feeding, leaving smolts potentially more vulnerable to predators resulting from the need to increase foraging rates (McCormick and Saunders 1987; Keefer and Caudill 2014).

Acoustic telemetry technology has been used for several years to investigate individualbased behaviour, travel rates, and survival of out-migrating Pacific salmon smolts and characterize environmental and regional factors associated with patterns of mortality (Welch et al. 2003). The first study that involved acoustically tracking Fraser sockeye salmon smolts investigated the endangered Cultus Lake population (2004 – 2007; Welch et al. 2009). This population travels only a short distance (~ 100 km) from natal areas to the ocean and the fish that were tagged were all hatchery reared. More recently, acoustic tracking of Chilko Lake sockeye salmon has taken place. This is one of the largest sockeye salmon populations in the Fraser River; it has a long freshwater migration, is not enhanced by hatcheries, and is used as an indicator population by Fisheries and Oceans Canada, the federal agency that manages Pacific salmon. For the past 60 years, a counting fence has been erected at the lake outlet to enumerate the smolt outmigration and provide a means to access smolts for tagging. From 2010 to 2017,

nearly 3000 smolts have been acoustically tagged and tracked from Chilko Lake to where they enter the open ocean, a total distance of > 1000 km (~ 700 km in freshwater and an additional 400 km in the marine environment; Clark et al. 2016; Rechisky et al. 2019; Stevenson et al. 2019). Survival during the freshwater portion of the migration ranged among years from 20% to 70%, with much of the mortality occurring early in the migration near the natal lake and largely attributed to predation (Furey et al. 2015a; Clark et al. 2016). Survival during the shorter coastal marine portion of the migration was relatively poor with only 3% to 20% of the tagged smolts that left the natal lake reaching the open ocean (Clark et al. 2016; Rechisky et al. 2019).

In the middle of this coastal migratory route are the Discovery Islands, a complex archipelago that separates the continental coast from Vancouver Island and represents a significant spatial bottleneck (Figure 1). Smolts migrate from the northern Strait of Georgia into narrow migratory routes of fast currents (Foreman et al. 2012) where they would encounter high densities of co-migrating populations of salmon smolts, and predators. High density of smolts provides an opportunity for predators to utilize these narrow migratory routes to access prey (Zimmerman and Ward 1999; Evans et al. 2016; Furey and Hinch 2017). The oceanographic conditions in this region are believed to create poor feeding opportunities for migrating smolts and it is thought that increased residence here could therefore result in reduced growth and survival (McKinnell et al. 2014, James et al. 2020). The complex nature of the migratory corridors through the Discovery Islands could affect residence time and travel rates for individuals that experience different routes, conferring a competitive advantage to individuals that traverse this region more rapidly.

Indeed, route utilization by smolts in coastal migratory areas is an important determinant of survival. Furey et al. (2015b) examined the migratory routes of > 850 acoustically tagged sockeye salmon and steelhead (*O. mykiss*) smolts which travelled through the Northern Strait of

Georgia and found that both species had better survival to the open ocean if they migrated more along the western side of the Strait than the eastern side. Furey et al. (2015b) were not able to specifically examine migration survival through Discovery Island routes because acoustic receiver arrays were not in place in those locations during their study. However, Healy et al. (2017) were able to examine this for > 240 acoustically tagged steelhead smolts tracked through the Discovery Island region. They found that survival was nearly two times greater for smolts migrating through the western-most route of the several routes that were available. These studies highlight the importance of spatiotemporal variability in smolt migrations within the early coastal marine life-history.

All acoustic telemetry studies discussed above examined relatively large bodied smolts (e.g. hatchery fish, Welch et al. 2009; Healy et al. 2017; age-2 wild fish, Clark et al. 2016; Rechisky et al. 2019). This use of large fish occurred because of limitations due to the size of acoustic tags that were available for those studies. Recent advancements in tag miniaturization have permitted smaller smolts to be tagged and tracked. Stevenson et al. (2019) were the first to utilize miniature acoustic tags to track 200 wild age-1 Chilko Lake sockeye smolts from natal areas into the marine environment. Age-1 sockeye represent ~95% of the out-migrating population (Irvine & Akenhead, 2013). Stevenson et al. (2019) found similar survival patterns in freshwater and marine segments to what the previous Chilko smolt studies found with the larger and older smolts (Rechisky et al. 2019; Clark et al. 2016). Because only ~ 20% of tagged age-1 smolts survived to migrate through the Discovery Islands, Stevenson et al. (2019) were not able to statistically examine route-specific survival, though their limited data suggested the western-most route may support higher survival, as was found with larger steelhead smolts (Healy et al. 2017).

Travel rates are an important factor that can affect smolt survival. In freshwater, travel rates for Chilko smolts were extremely slow (~ 10 km/d) immediately downstream of their natal lake, which was attributed to the fact that they only migrated during night time (Clark et al. 2016) owing to the large predator presence and clear water (Furey and Hinch 2017) and the fact that the river was very shallow and slow. Survival was lowest in these areas out of all freshwater migratory locations (Clark et al. 2016; Stevenson et al. 2019). As smolts traversed further from their natal lake, riverine environments became more turbid and faster flowing, and both travel rates and survival increased significantly. Their 600-km downstream migration in the highly turbid Fraser River mainstem had individuals travelling at 120 to 200 km/d, depending on the year, with nearly 100% survival (Clark et al. 2016; Stevenson et al. 2019). Travel rates slowed substantially when smolts entered the marine environment, with transit through the Strait of Georgia ranging from 10 to 20 km/d depending on the year (Clark et al. 2016), though travel rates nearly doubled during passage through the Discovery Island region (Clark et al. 2016; Stevenson et al. 2019). Stevenson et al. (2019) is the only study to compare survival and travel rates in the same year between age-1 and age-2 smolts. They found no differences in travel rates between age groups in the freshwater migration but had too few age-2 individuals to contrast ages in the marine environment. The relationship between survival rates and travel rates in the marine area needs to be more fully explored to understand the impact of residence within the Discovery Islands.

My thesis will characterize the migration behaviour, travel rates, and survival patterns of age-1 and -2 sockeye salmon smolts as they migrate through the Discovery Island region in coastal British Columbia. This research will be the first to capture, acoustically tag and track sockeye smolts solely in the marine environment, and aims to address the following questions:

- 1) Do smolts disproportionately utilize specific migratory routes?
- 2) Do travel rates and routes affect survival of migrating sockeye smolts?
- 3) Do physical characteristics of smolts affect travel rates and survival?

Given recent results from acoustically tracked steelhead smolts and their route-specific survival patterns (Healy et al. 2017), I predict that sockeye smolts will utilize the western-most route through the Discovery Islands more frequently, and these fish will exhibit the highest survival through the Discovery Islands. Also, because larger smolts can swim faster than smaller smolts, and the study region is known to have high levels of smolt predators, I predict that larger smolts will display the highest survival.

Methods

Study system

The Salish Sea is an inland body of water bounded by Vancouver Island and the Olympic Peninsula to the west and the mainland of British Columbia and Washington State to the east (Figure 1). Sub-basins include Puget Sound, Strait of Georgia (SOG), Juan de Fuca Strait, and the Discovery Islands (DI) (Figure 1). Water is exchanged with the open Pacific Ocean primarily via Juan de Fuca Strait in the south and to a limited extent with Johnstone Strait (JS) in the north (Khangaonkar et al. 2017). The Fraser River is the largest source of both freshwater and Pacific salmon (Oncorhynchus spp.) to the Salish Sea, draining a watershed of nearly 220,000 km² into the SOG (Pawlowicz et al. 2007; Beamish et al. 2012). Sockeye smolts emigrating from the Fraser River almost exclusively migrate north through the SOG, traversing the DI and JS before entering the open Pacific Ocean through Queen Charlotte Strait (QCS) (Clark et al. 2016). The DI represents the northern boundary of the Salish Sea and consists of 12 major islands that develop a complex network of channels and passages used by migrating salmonids. Transition from the northern SOG to the DI occurs via three primary entrances, Discovery Passage (DP), Sutil Channel (SC) and Desolation Sound (DS). The islands of Vancouver, Quadra and Cortes, along with the continental coast, make up the landmasses that delineate these primary routes. Upon entering the primary routes, additional secondary routes are available to migrants (SC = 9, DS = 5, DP = 0; Figure 1; Table 2).

Acoustic receiver arrays

Acoustic telemetry receiver infrastructure was situated within the Fraser River and throughout the SOG, DI, JS and QCS (Figure 1). The receivers and their maintenance were managed by Canada's Ocean Tracking Network (OTN), the Pacific Salmon Foundation (PSF) and Kintama Research Services (KRS). Receiver arrays consist of several anchored buoys that suspend VEMCO VR2W (69 kHz) or VR4 (69/180 kHz) receivers within the water column perpendicular to and crossing the complete channel width, creating a curtain of detection designed to detect all tagged individuals passing the region. Northern SOG (NSOG) and QCS receiver arrays were installed as part of the Pacific Ocean Shelf Tracking project in 2003 and are now managed by OTN (Welch et al. 2008). These receivers consist primarily of VR2W receivers that are only capable of detecting larger 69 kHz tags. Receivers in the eastern component of the NSOG array (Figure 1), were converted to dual-frequency VR4s capable of detecting both 69 kHz and 180 kHz tags. In 2015, arrays consisting of VEMCO VR4 receivers were deployed at the southern boundary of the DI in Discovery Passage (n = 6, $w_{channel}(w_c) = 2.25$ km), Sutil Channel (n = 20, $w_c = 7.05$ km), and Desolation Sound (n = 9, $w_c = 2.40$ km), spanning all potential primary entrance routes to the region (Figure 1). An array was placed in JS (n = 8, $w_c =$ 2.70 km) at a location where these migratory pathways converge. Additional receivers deployed in 2017 captured finer-scale movements within the DI region in Hoskyn Channel (n = 6, w_c = 1.25 km), Hole in the Wall Passage (n = 2, $w_c = 0.34$ km), Okisollo Channel (n = 6, $w_c = 1.05$ km), and within a fish farm tenure at Venture Point within Okisollo Channel (n = 1). Further deployments occurred in 2018 with receivers placed at Cordero Channel (n = 4, $w_c = 0.85$ km), White Rock Passage (n = 1, $w_c = 0.50$ km), and near active Atlantic salmon (*Salmo salar*) open net-pen farm tenures within Okisollo (Brent Island and Okisollo Point) (n = 2) and Nodales Channels (Sonora Point) (n = 1) (Figure 1). This network of sixty-six receivers captured all potential migratory pathways around the ten major southern islands of the archipelago and provided the highest resolution picture of smolt migration to date.

Smolt collection and release

Between 24 April and 3 May 2017, smolts (n = 307) were captured at the outlet of Chilko Lake, at the Fisheries and Oceans Canada counting. Smolts were sampled directly from the river as they passed the counting fence and were completed using a dip-net during nighttime hours (22:00-02:30) as smolts migrate at night during this stage of migration (Stevenson 2018). Surgeries commenced the following day and smolts were held for ~10 hours post-surgery in a flow-through, covered tank and released at night (23:30 - 01:30; Stevenson 2018). These smolts comprised both age-1 (n = 160) and age-2 smolts (n = 79) tagged with VEMCO-V4-180 kHz (V4) transmitters, along with an additional group of age-2 smolts (n = 75) tagged with VEMCO-V7-69 kHz (V7) tags (Table 1). Between 25 May and 22 June 2018, sockeye smolts were captured and tagged with VEMCO-V5-180 kHz (V5; n = 100) and V7 tags (n = 50) exclusively in the marine environment. These smolts were selected for a specific size, with required minimum masses of 10g and 20g for V5 and V7 tags, respectively. This ensured tag burdens remained below 8%, a threshold that if exceeded is known to impact survival and swimming performance (Collins et al. 2013). These variable tagging locations, years, and tag types provide the related 'tagging groups' of smolts that are grouped together for analyses when appropriate.

All marine collections used a small-scale modified purse seine with net construction and capture methods similar to those described in Godwin et al. (2015). Collections occurred in proximity to Venture Point (Zone 10 U 333382 m E 5574064 m N) within Okisollo Channel, separating Sonora and Quadra Islands (Figure 1), from 06:56 to 14:15 each day, and were limited to a maximum of three seine sets to ensure time within the transportation and holding tanks was minimized. Surface activity of smolts indicated expected direction of movement; capture vessels were then positioned in the expected path, and the seine net was set out in a crescent shape ahead of the target school. Recovery of the bunt (portion of net with collection mesh; ¹/₄" mesh) end

enclosed smolts within the net and retrieval of the purse line ensured no escape occurred via descent. The resulting net 'basket' provided ample space for smolts to freely swim without interaction with the net, while this also provided the necessary density of fish for species identification and collection to occur.

Smolts were collected using modified 1-gallon containers to ensure they remained submerged throughout the collection procedures and were never air-exposed. Sockeye smolts were identified and selected for size, then transferred from seine net to a transport tank which contained approximately 300L of recirculated seawater. An additional group of conspecific smolts were collected to provide a school of comigrants that were released along with tagged individuals. After completion of surgical procedures, smolts were placed in an aerated recovery tank and allowed to regain natural swimming behaviour prior to reintroduction to the transportation tank. Smolts were then transported 46 km south to the north-central SOG (Zone 10 U 356169 m E 5532152 m N) for release (Figure 1). Upon arrival, smolts were collected into a smaller, vessel side container that allowed warmer sea surface water (14-17°C) to mix with the water collected from sampling and surgical sites (10-11°C) and provided opportunity for the entire school to be released in a single event.

Tag implantation

In 2017 smolts were surgically implanted with tags in the freshwater environment at the outlet of Chilko Lake as part of another study (Stevenson 2018). In 2018, additional smolts were surgically implanted with tags in the marine environment - 100 with V5 tags (12.7 mm L x 4.3 mm H x 5.6 W mm; mass = 0.65 g in air) and 50 with V7 tags (20 mm L x 7mm W; 1.6 g in air). Surgical procedures followed those described in Collins et al. (2013). Smolts collected at Chilko Lake outlet were dipped netted from the river and placed in holding tanks prior to surgeries

occurring hours later. Comparatively, marine captured smolts were collected without net interaction and without a long duration of holding, only residing in the transport tank for approximately one to two hours prior to surgery. Smolts were removed from transport tanks and placed in aerated five-gallon buckets with five to six conspecifics prior to surgery. Individuals were selected from pre-surgery holding and placed into an anaesthetic solution of MS-222 (tricaine methanesulfonate, 100 mg/L) buffered by sodium bicarbonate (NaHCO₃, 200 mg/L) for one to two minutes, or until reaction to a physical stimulus (i.e. caudal pinch) had ceased. Smolts were then placed in a V-shaped trough with their ventral surface exposed. A narrow tube placed within the buccal cavity provided a continuous flow of aerated maintenance anaesthetic solution (MS-222, 50 mg/L; NaHCO₃, 100 mg/L), ensuring ample oxygen and anaesthetic exposure was sustained. An incision (5 - 6 mm, V4 and V5 tag; 7 - 8 mm, V7 tag) along the ventral surface beginning midway and progressing posteriorly, allowed tag insertion with a pair of curved forceps. Initial tag insertion occurs vertically with force to provide entry in the coelomic cavity, whereupon the tag is rotated to the longitudinal plane of the smolt, allowing the tag to shift forward into the larger portion of the cavity. Either one (V4 and V5 tags) or two (V7 tags) single-interrupted sutures closed the incision using an Ethicon MONOCRYL 5-0 monofilament 3/8 circle reverse cutting 13 mm packaged suture. Procedures times (mean = 4:23 [range = 03:00-07:00]) were recorded from the point of entry into the anaesthetic solution until the smolt was released into the aerated recovery bucket.

Tag programming

Tag programs were designed to maximize detection efficiency while within the DI receiver arrays and to account for the slower migration rates expected for age-1 Chilko smolts, knowing that body length will influence smolt travel rates (Stevenson et al. 2019). Each tag has a

unique identification code that allows for individual identification upon recorded detections. Three tag-types were used in this study: V7, V5 and V4 VEMCO acoustic transmitting tags (Table 1). V7 tags released in Chilko age-2 smolts in 2017 had an estimated battery life of 79 days, with a transmission rate of one ping every 20-40 seconds from time of activation until time of battery life failure. V7 tags release in marine captured smolts in 2018 had a faster ping rate, with transmissions occurring every 18-24 seconds, and an estimated battery life of 60 days. V5 tags released in the marine environment in 2018 were programmed with an estimated battery life of 41 days and a transmission rate of 10-14 seconds after activation. Due to the far greater migration distances and times from Chilko Lake, smolts tagged with V4 tags at the counting fence had tags programmed to help ensure battery life was sufficient for detection at terminal receivers within JS. Tags were implanted in groups of age-2 and age-1 smolts that were expected to migrate at different rates due to variable body sizes among these groups (Ware, 1979). V4 tags designed for age-2 smolts had a programmed expected battery life of 43 days, with an initial transmission period of 6 days at a rate of 45-105 second intervals, followed by a nontransmission period of 6 days, after which a transmission rate of 15-35 seconds until battery failure. V4 tags designed for age-1 smolts were expected to last 46 days, accounting for the slower migration speeds, with an initial ping rate of 45-105 seconds, followed by a 13 day period of non-transmission, and finally by a 15-35 second transmission period until battery failure.

Smolt route use and distribution

Smolts were assigned to a primary migratory route using the last detection among the three entrance subsubarrays located within Discovery Passage, Sutil Channel and Desolation Sound (Figure 1; Table 2). The proportion of individuals using each route was calculated among four groups of smolts released over two years (2017 and 2018), consisting of marine V5 and V7

tagged smolts and Chilko age-2 V7 and V4 tagged smolts. V4 tags deployed in age-1 smolts released at Chilko Lake (n = 160) were within the manufacturer's calculated period of expected tag failure when reaching the DI, therefore, they were removed from route distribution analyses as these effects were unequally distributed across the routes. Secondary routes were classified as those where detections on DI subsubarrays occurred upon departure from the primary DI subarrays en route to JS subarrays (Figure 1; Table 2). Secondary routes were observed within Sutil Channel and Desolation Sound, where a total of fourteen potential observable routes existed between them. Detection frequencies were summarized with histograms of the primary entrance arrays to determine overall proportion of use by each tagging group and for the sample as a whole (Figure 2). Distribution of smolts was compared among primary routes through a Chi-squared test of deviance that compared the total number of individual within each route to the total number of receivers (a proxy for channel width) within each route (Furey et al. 2015b).

Travel rates and travel time

All tagged, released and detected smolts were used in travel time and rate calculations as variation in tag-life does not confound travel estimates. Travel time (d) was calculated from time of release or last detection on an array, until time of first detection on a subsequent receiver subarray (Healy et al. 2017). Segment travel times were calculated only for smolts migrating within the marine environment, including the following segments: Northern Strait of Georgia (NSOG arrays or release to DI arrays), Discovery Islands (DI to JS arrays), Queen Charlotte Strait (JS to QCS subarrays), and northeast Vancouver Island (NEVI; NSOG to QCS arrays; Figure 1). When referencing Discovery Islands subarrays, only the most southern, or entrance arrays (Discovery Passage, Sutil Channel, Desolation Sound) were used for travel time calculations. Travel rates (km d⁻¹) were calculated using the distance travelled between segments,

or along routes, divided by the number of days to traverse that segment. Distances were calculated as the shortest point between the central portion of the departure subarray and that of the subsequent subarray (Healy et al. 2017). Travel rates were also converted to body lengths per second (BL s⁻¹) to standardize travel rates among smolts of different body sizes. Linear models were created to compare travel times (d) and rates (km d⁻¹ or BL s⁻¹) among routes and tagging groups, which were then compared using both the 'anova' function (R Core Team, 2019) that compares model fit among those tested and the 'Ismeans' (Lenth, 2016) package that performs a paired t-test of each pair of possible model parameters to indicate where significant variation exists. Tagging groups were grouped by age in some analyses (all marine releases were grouped as 'unknown') as there was no significant variation among the like-age classed individuals for the associated travel characteristics, based on a least-squares mean comparison with Bonferroni corrected P-values.

Segment and route-specific survival rates

I excluded the Chilko Lake V4 tagged fish from survival analyses because subsequent battery-life assessments indicated that the tag programming may have resulted in some fish arriving at DI and JS subarrays at times when batteries may have been dead. Survival analyses only include age-2 V7 tagged smolts captured and released at the Chilko Lake outlet in 2017, and marine-released smolts tagged with V5 and V7 tags in 2018.

Estimates of survival (ϕ) and detection probability (ρ) were calculated using a variate of the Cormack-Jolly-Seber (CJS) mark-recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965). This was completed using the 'RMark' (Laake 2013) package within the R-Studio platform (R Core Team, 2019), utilizing the program 'MARK' (White & Burnham 1999) to complete model construction and testing (Clark et al., 2016). CJS models assume instantaneous

sampling, equal survival probability and equal probability of detections among all individuals (Healy et al. 2017). Parameter (ϕ and ρ) estimates are based on a maximum log-likelihood function, developed from each individual capture history. A capture history describes the detection profile of a single individual as they migrate along their path, where initial release and subsequent detections on a receiver array are each considered a capture event (1), creating a series of 1s and 0s used by the 'MARK' platform to determine both survival and detection probability estimates. In some cases 0s do not represent a mortality event, rather that the individual was missed by the receiver array and subsequent detections occur. This provides the 'MARK' platform the necessary data to create detection probabilities, that will inherently increase estimates of survival compared to observed survival (redetection on JS).

CJS model comparisons were completed with a corrected Akaike's Information Criterion (AIC) for low sample sizes and overdispersion called the Quasi-AIC (QAIC) (Healy et al. 2017). Segment survival, or the probability an individual smolt surviving from one array to the next, was estimated among all marine subarrays and route-specific survival was estimated from DI to JS subarrays, along each specific primary route (Discovery Passage, Sutil Channel, Desolation Sound). To account for the variable distances and travel times required to traverse each route, we converted the model estimates of survival to survival rates. This occurred for variable time as survival rate per day ($S^{1/t}$), where *S* is the modelled survival estimate and *t* is the mean travel time for that segment or route (Healy et al. 2017). Also, accounting for variable distances travelled among routes, a survival rate per 100km ($S^{100/d}$) was created, where *d* is the distance travelled among receivers (Healy et al. 2017).

Impact of physical and behavioural traits on apparent survival

Individual physical and behavioural characteristics of smolt migrants were compared among three routes using a one-way ANOVA with the 'aov' function in the 'stats' package (R Core Team, 2019). Milling, a behavioural characteristic, was defined as the amount of time that an individual resided within the detection radius of a single DI subsubarray, calculated as the time difference from the first to last detection (i.e. Sutil Channel, non-inclusive of other Discovery Islands subsubarrays). This varies from previous definitions that included lateral movement among migration routes and the reversed movements along expected migration paths (Healy et al. 2017). Milling was calculated as the difference in time (hours) from first to terminal detection on a single subsubarray. The effects of physical and behavioural traits on apparent survival, or redetection on JS subarrays, were compared among primary routes by creating generalized linear models constructed with the 'stats' package (R Core Team, 2019) in RStudio (RStudio Team, 2015). These regressed the binomial distribution of detection (1) or nondetection (0) against physical and behavioural traits hypothesized to influence survival. Both single- and two-factor ANOVAs were used to determine the significant variation those smolts detected on JS subarrays and those that were not.

Results

Migration behaviour

A total of 465 smolts were tagged and released from the Chilko Lake outlet counting fence in 2017 (n = 315) and the marine environment in 2018 (n = 150; Table 1). Proportions listed below represent the proportion of the total number of tags released (p_T) or the total number of released individuals within their respective tagging groups (p_C) (Table 1). Marine movements were described for all smolts detected in the marine environment (n = 209, $p_T = 0.45$), including detections on the NSOG subarray (n = 33, p_T = 0.07), DI subarray (n = 218, p_T = 0.47), JS subarray (n = 109, $p_T = 0.23$), and the terminal QCS subarray (n = 31, $p_{T-V7} = 0.25$) (Figure 3). Marine-released individuals were detected making a reverse migration from point of release to the NSOG array (~25km) a total of 6 times in 2018, including four ($p_c = 0.04$) V5 tagged individuals, which were only detectable on the array within Malaspina Channel and two ($p_c =$ 0.04) V7 tagged individuals that were detectable across the entire subarray (Figure 3). Of these six individuals, three were later detected returning to their expected direction of migration through the DI with subsequent detections on JS subarrays, including two V5 and one V7 tagged individuals, with that V7 fish being detected on the terminal subarray at QCS. Generally, smolts followed directed migration paths from the NSOG through the DI routes to JS, following roughly a northwest-southeast tangent. Additionally, east-west movements were observed within White Rock Pass and Hole in the Wall (Figure 1) with smolts moving between Calm Channel and either Hoskyn or Okisollo Channels (Table 2).

Route distribution

Smolts released from the Chilko Lake counting fence in 2017 (n = 315) and the marine environment in 2018 (n = 150) were observed within all three primary migration routes

throughout the Discovery Islands (Figure 2; Table 3). The greatest proportion of all smolts detected on Discovery Islands subarrays (n = 167) were within the Sutil Channel route (p = 0.61, n = 101), followed by Discovery Passage (p = 0.26, n = 44) and Desolation Sound (p = 0.08, n = 101) 13). Chi-square tests comparing channel width, or the number of receivers, to the number of smolts detected within each route were completed for both Chilko (χ^2 (2) = 3.9, P = 0.15) and Marine (χ^2 (2) = 4.6, P = 0.10) release groups and indicated no disproportionate distribution of smolts across routes and is the same result when tagging groups are combined (χ^2 (2) = 4.5, P = 0.10; Figure 2; Table 3). This result indicates that route distribution was not statistically skewed, however, there does appear to be some variation in size or age of individuals and the routes they are more likely to utilize (Figure 2). Discovery Passage is unique among the primary routes in having only a single pathway of observed use by smolts after their departure from the entrance array directly to JS. Both Sutil Channel and Desolation Sound contained secondary routes of migrations due to the complexity of the subsequent paths following entry to the DI (Figure 1). Within Sutil Channel, a greater proportion of smolts utilized the Sutil Channel-Cordero Channel (SC-CRD) secondary route (n = 59, p = 0.58), followed by Sutil Channel-Hoskyn Channel-Okisollo Channel secondary route (n = 31, p = 0.31), and lastly a group observed utilizing Sutil Channel-Hoskyn Channel-Cordero Channel secondary route, traversing either White Rock Pass or Hole in the Wall (n = 11, p = 0.11; Figure 1; Table 3). Of the 59 smolts identified within the SC-CRD secondary route, 45 (p = 0.76) were not detected after their entrance, and were thus assumed to have used the SC-CRD secondary route as this was the route with least telemetry infrastructure. Smolts that utilized Desolation Sound were more likely to do so through Cordero Channel (n = 10, p = 0.77) rather than Okisollo Channel (n = 3, p = 0.23), which required traversing Hole in the Wall, White Rock Pass, or Hoskyn Channel.

Travel rates and times

Sockeye smolts captured and released in the marine environment travelled from point of release (10 U 356169 m E 5532152 m N) an approximate distance of 18.1 km to Sutil Channel subarray, 20.0 km to Desolation Sound subarray and 46.1 km to Discovery Passage subarray (Figure 1). I found no differences among tagging groups in travel times from release to DI (ANOVA, $F_{1, 114} = 0.3$, P = 0.6), therefore they were grouped for subsequent analyses, whereas travel times differed among routes (ANOVA, $F_{3, 114} = 3.6$, P = 0.02) as expected, due to differing distances to respective receivers. Mean travel time (days; d) to the DI subarrays were fewest for Desolation Sound (2.39 ± 0.37 d SE) and most for Discovery Passage (4.98 ± 0.85 d SE), however, travel rates (km·d⁻¹) accounted for the variable distances traversed and showed no differences among groups that experienced each route (ANOVA, $F_{2, 111} = 2.3$, P = 0.08) (Figure 4; Table 4). Smolts from Chilko Lake outlet (n = 28) and the marine environment (n = 5) were detected on the NSOG array and these groups did not differ in mean travel times (4.14 ± 0.73 d SE; $t_{2.6} = -0.3$, P = 0.8) or rates (22.2 ± 2.6 km d⁻¹ SE; $t_{3.2} = 0.9$, P = 0.5) to the DI subarrays (Figure 4).

Travel times through the Discovery Islands (DI to JS subarrays) did not differ among tagging groups (ANOVA, $F_{4, 90} = 1.2$, P = 0.3), but travel rates differed among routes within DI (ANOVA, $F_{9, 92} = 32$, P < 0.001). Smolt tagging groups did not differ in travel rates through Desolation Sound (ANOVA, $F_{4, 10} = 1.1$, P = 0.4) or Sutil Channel (ANOVA, $F_{4, 42} = 1.5$, P =0.2) but did differ through Discovery Passage (ANOVA, $F_{4, 28} = 4.0$, P = 0.01). Specifically, age-2 V7 tagged Chilko smolts (mean = 48.0 ± 4.3 km d⁻¹ SE) were significantly faster than marine V5 tagged smolts (mean = 31.1 ± 3.24 km d⁻¹ SE; least-squared means t-test with Bonferroni adjustment; $t_{28} = 3.2$, P = 0.04). Travel times differed among routes (ANOVA, $F_{2, 74}$ = 28, P < 0.001) and among tagging groups (when routes were pooled; ANOVA, $F_{4, 72} = 3.1$, P =
0.02). Mean travel times through the Discovery Islands were greatest for passage through Desolation Sound (11.2 \pm 1.72 d SE) and shortest through Discovery Passage (2.18 \pm 0.15 d SE; Figure 5). Travel times differed among routes and years with the exception of passage through Sutil Channel in 2017 (5.1 \pm 0.5 d SE) and through Discovery Passage in 2018 (2.4 \pm 0.2 d SE) (least-squared means t-test with Bonferroni adjustment; t₉₇ = 2.7, P = 0.21). The fastest mean travel rates were observed in Discovery Passage (37.2 \pm 1.8 km d⁻¹ SE;) and specifically for the Chilko age-2 group (48.0 \pm 4.3 km d⁻¹ SE), whereas the slowest rates were observed in Desolation Sound (14.6 \pm 2.9 km d⁻¹ SE) and again in the Chilko age-2 V7 tagging group (8.6 \pm 5.3 km d⁻¹ SE; Figure 5).

Comparison of the Northeast Vancouver Island (NEVI) segment, only possible for V7 tagged individuals, found that mean travel time (ANOVA, $F_{2, 26} = 24$, P < 0.001) and rate (ANOVA, $F_{2, 26} = 5.8$, P = 0.008) differed among primary routes. A least-squares means comparison with Bonferroni correction showed that migration times in Sutil Channel (11.9 d ± 0.8 d SE) and Desolation Sound (22.0 ± 1.5 d SE) differed significantly ($t_{26} = 6.0$, P < 0.0001), along with Discovery Passage (10.5 ± 0.8 d SE) and Desolation Sound ($t_{26} = 6.8$, P < 0.0001), however, Sutil Channel and Discovery Passage did not differ ($t_{26} = 1.2$, P = 0.8). Travel rates through Sutil Channel (19.2 ± 1.8 km d⁻¹ SE; 1.5 ± 0.2 BL s⁻¹ SE) did not differ from Desolation Sound (10.4 ± 3.3 km d⁻¹ SE; 0.9 ± 0.3 BL s⁻¹ SE) or Discovery Passage (23.3 ± 1.9 km d⁻¹ SE; 2.1 ± 0.2 BL s⁻¹ SE), whereas the latter two differed from each another ($t_{26} = 3.4$, P = 0.007; $t_{26} = 3.2$, P = 0.01).

Segment survival and route-specific survival estimates

Apparent survival (S^A) was calculated for each segment and primary route within the Discovery Islands for all tagging groups, as the proportion of individuals that were detected

within that route, with later detections on JS subarrays (Table 5). Primary route apparent survival was greatest for those migrating through Desolation Sound in 2018 ($S^A = 78\%$), followed closely by Discovery Passage in 2018 ($S^A = 70\%$), with passage through Sutil Channel in 2018 having the lowest apparent survival ($S^A = 40\%$) among any route or year. Survival was more similar among routes in 2017, with apparent survival ranging from 40 % (Sutil Channel) to 50% (Desolation Sound).

Modeled estimates of survival (ϕ) and detection probability (ρ) were assessed for Chilko Lake released smolts tagged with V7 tags and all marine released smolts in 2018. Segment specific estimated survival from NSOG to DI arrays for Chilko released age-2 V7 tagged individuals was 88% (95% CI: 64 – 98%) and 100% (95% CI: 100-100%) from DI to JS (Figure 6; Table 7). Estimated segment survival for marine V5 smolts from release to subsequent DI subarrays was 80% (95% CI: 71 – 87%) followed by 48% (95% CI: 36 – 60%) through the Discovery Islands to Johnstone Strait. Survival of the marine V7 tagging group from release to DI was 86% (95% CI: 73 – 93%), but lower (73%) for survival through the Discovery Islands (95% CI: 56 – 85%) (Figure 6).

Modeled estimates of survival for each primary route followed the same trend as apparent survival, with passage through Desolation Sound ($\phi = 0.81 \pm 0.73$ SE) and Discovery Passage ($\phi = 0.79 \pm 0.65$ SE) having similar, and relatively higher survival compared to Sutil Channel ($\phi = 0.42 \pm 0.56$ SE) (Figure 7). After accounting for differences in distance travelled within each segment and route by creating a rate of survival per 100 km, the trends remain the same with Desolation Sound (S¹⁰⁰ = 84% [46 – 97%]) having the highest rate of survival, followed by Discovery Passage (S¹⁰⁰ = 71% [39 – 90%]) and Sutil Channel (S¹⁰⁰ = 48% [37 – 60%]) (Figure 7). However, when accounting for travel time among the various routes, or survival rates per day, survival through Desolation Sound (S^d = 98% [92 – 100 %]) was the highest (with

overlapping 95% CIs) among all routes, whereas passage through Discovery Passage ($S^d = 91\%$ [76 – 97%]) and Sutil Channel ($S^d = 89\%$ [85 – 92%]) was lowest but relatively similar (Figure 6).

Survival from JS to QCS was only observable for V7 tagged smolts and ranged from 73 to 100% among years, whereas survival rates ranged from 73 to 100% per 100 km and from 94 to 100% per day (Figure 6; Table 7). Survival estimates were consistently higher among V7 tagged smolts and across the entire NEVI segment, from NSOG to QCS, the survival estimate ranged from 46 to 76% (Table 7). Cumulative survival varied through the DI among marine V5 and V7 tagged individuals where estimates to JS were 36% and 73%, respectively (Figure 8). Chilko age-2 V7 smolts demonstrated near perfect survival through the NEVI region, with only minor decreases in survivorship through the NSOG and QCS segment and present perfect survival within the Discovery Islands segment (Figure 8).

Effect of behavioural traits on apparent survival

Milling was observed on all DI entrance subarrays and ranged from 0 to 418 hours (median = 1.9 ± 4.3 SE) for smolts tracked in both 2017 and 2018 (Figure 9). There were no differences in milling time among observed routes (ANOVA, F_{2, 206} = 0.6, P = 0.5). The longest median milling times were in Discovery Passage (2.47 [0 - 282] hours), followed by Desolation Sound (2.33 [0.05 – 170] hours) and Sutil Channel (1.65 [0 – 417] hours). However, mean milling times were greatest in Sutil Channel (38 ± 5.8 SE hours; LR $\chi^2(1) = 5.2$, P = 0.02) followed by Discovery Passage (32 ± 7.7 SE hours; LR $\chi^2(1) = 1.2$, P = 0.3) and Desolation Sound (23.3 ± 9.6 SE hours; LR $\chi^2(1) = 1.6$, P = 0.2), highlighting the greater variability in travel rates observed in Sutil Channel. Smolt survival decreased with milling time from Sutil Channel to JS (-0.20 ± 0.08 SE; Likelihood Ratio Test (LRT) $\chi^2 = 7.4$, P = 0.006) but there was not a significant relationship between survival and milling time in Discovery Passage and Desolation Sound (0.14 \pm 0.1 SE; LRT $\chi 2 = 2.03$, p = 0.15; Figure 9).

Discussion

Acoustically tagged sockeye smolts were tracked during a portion of their migration in coastal British Columbia in order to examine their behaviour and survival. This is the first study to acoustically tag and track wild salmonid smolts in the marine environment. My thesis aimed to answer several questions regarding migration of juvenile sockeye smolts through the Discovery Islands. First, what migratory routes do smolts utilize, and is there a skewed distribution and if so, why? Second, does migratory route and travel characteristics (rates and times) have an effect on survival? And lastly, does smolt size affect their migratory patterns and survival?

Migration Routes and Travel Rates

Salmonid smolts of all species that migrate from the northern Salish Sea to the open Pacific Ocean need to traverse the Discovery Islands, and they do so through one of three passage routes (Melnychuk et al. 2010; Beacham et al. 2014). I found that routes were not all used to the same degree and a pattern emerged suggesting a general western and central skew particularly for the larger tagged fish in my study. Use of these routes have been characterized by Healy et al. (2017) for a population of tagged hatchery steelhead smolts, two-thirds of which utilized Discovery Passage, the western most route. Tagged age-1 smolts released from Chilko Lake in 2016 showed similar route usage to the steelhead smolts with a large component (50%) using Discovery Passage and 45% using Sutil Channel (Stevenson et al. 2019), however, their sample sizes were small (total n = 20). In my study, age-1 smolts released in 2017 from Chilko Lake, which are smaller fish than the other groups in the study, displayed a more even spatial spread among routes with a slight eastern skew (Discovery Passage 16%, Sutil Channel 50%, Desolation Sound 26%) however, 2017 age-2 smolts exhibited a stronger western skew (Discovery Passage 39%, Sutil Channel 43%, Desolation Sound 9%). In 2018, sockeye smolts that were released 25-km south of the Discovery Islands utilized all migratory routes, and the central route was most used (22% Discovery Passage, 66% Sutil Channel, 7% Desolation Sound) which may be attributed to the release location being geographically closest to the entrance of this route. Nonetheless, these results indicate that on the whole, the central route (Sutil Channel) is an important migratory smolt corridor whereas the most eastern route (Desolation Sound) is not.

Each route presents unique oceanographic conditions (Foreman et al. 2012; McKinnell et al. 2014) that would generate different experiences for migrants and which may confer various benefits or costs (Furey et al. 2015b; Healy et al. 2017). Discovery Passage provides the shortest (69 km) and most direct route of transit from the northern Strait of Georgia to JS where smolts encounter significant tidal currents up to 4.0 m s⁻¹ (or \sim 30 BL s⁻¹) in certain areas (Foreman et al. 2012). These currents could provide assistance to smolt marine migration, much like their downstream freshwater migration, however, these currents switch during tidal cycles and would flow in the direction opposing their directed migration path. Yet, smolt migrations persist at remarkable speeds up 68 km d⁻¹, or 6.5 BL s⁻¹ suggesting that smolts may not only use oceanographic currents to aid in their migration (Putman et al. 2014; Burke et al. 2016), but are also taking an active swimming role.

The longest route to JS (122 km) is Desolation Sound which provides narrow channels with modest currents that follow in the directed paths of migration northwest to Cordero Channel, where currents then increase and appear to aid in continued migrations to JS. Sutil Channel is the most complex route with two broad sub-routes leading through Cordero or Okisollo Channels. Access to both routes require directed movement to the east, a behaviour known to be less common for two year old sockeye on the NSOG subarray (Furey et al. 2015b), and those in SC must transit a region of a large scale cyclical current (Foreman et al. 2012) that may inhibit further progress. However, smolts that proceed north from Sutil Channel are exposed to greater directed currents upon reaching Hoskyn and Cordero Channels. Discovery Passage provides quick access to cool water and highly directed, though often reversing, tidal currents, whereas, the entrance of the central and eastern routes contain warmer water with less substantial and directed currents (Foreman et al., 2012).

The oceanographic conditions at the entrances to the main routes may contribute to the type of smolt that utilize them. For instance, smolts that migrated volitionally through the Salish Sea to the Discovery Islands (e.g. released at Chilko Lake in this study, or from the Seymour Hatchery, Healy et al. 2017) revealed that fish size influenced route selection with larger bodied fish (e.g. hatchery steelhead and age-2 sockeye smolts) more likely to enter and utilize the western and central routes. Smaller age-1 sockeye smolts released from Chilko Lake did not show this pattern and few took the western route. Larger, stronger swimming smolts are probably more able to take advantage of, and cope with, the fast tidal currents in Discovery Passage. I estimate that the marine tagged sockeye smolts would have been larger but probably more similar in size to the Chilko-released age-1 fish, than Chilko-released age-2 fish, at the time these freshwater tagged smolts migrated through the Discovery Islands, which may help explain why the marine tagged smolts utilized all the routes though the majority used the western and central ones. Another factor that could lead to larger smolts using the most western and central routes could relate to their behaviour upon leaving the Fraser River. Larger sockeye smolts can be more variable in their swim behaviour and often migrate further offshore (Kemp et al. 2005; Beacham et al. 2014), which, upon emigrating from the Fraser River, potentially means a greater chance of migrating on the western side of the SOG which would propel them more directly through western routes in the Discovery Islands region.

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Smolts traversed the Discovery Islands region on average in just under six days which is a remarkably fast travel rate at approximately 2.5 BL s⁻¹. A meta-analysis of studies examining migration rates in marine salmonids found that most species travel at about 1 BL s⁻¹ which is believed to approximate metabolic optimal swimming speeds (Drenner et al. 2012). The fact that some smolts were travelling well above optimal speeds suggests that they are receiving assistance from tidal or other oceanographic features. This is supported when we consider the significant currents present within Discovery Passage, where travel rates averaged 3.5 BL s⁻¹. In contrast, Desolation Sound where currents are much slower had travel rates which were much closer to metabolic optimal (average 1.5 BL s⁻¹). Clark et al. (2016) studied the travel rates of acoustically tagged Chilko Lake age-2 sockeye smolts, over several years, as they migrated through freshwater and coastal marine areas. Though they could not examine detailed movements in the Discovery Island region but were able to estimate that age-2 smolts moved through the broad Northeast Vancouver Island (NEVI) region at ~30 km d⁻¹. This rate was similar to the rate I measured for age-2 Chilko smolts (average 26.0 km d⁻¹) within the northern Strait of Georgia, though much faster than the smaller bodied age-1 smolts travel rates (average 18.3 km d⁻¹). In contrast, smolts that I captured, tagged and released in the marine environment, approximately 25-km north of the NSOG subarray, travelled initially much slower, possibly because of a 'tagging release recovery effect' that seemed to increase residence time in the northern Strait of Georgia near the release area. The marine released smolts migrated through the northern Strait of Georgia to the closest Discovery Island subarrays at an average rate of 10.2 km d⁻¹ or only 0.9 BL s⁻¹. Conversely, marine released smolts that initially migrated south, to the NSOG subarray (n = 5) and completed a return migration to the Discovery Island subarrays (n = 5)3), did so at a mean rate of 17.5 km d⁻¹. Comparatively, age-1 Chilko smolts completed this same segment travelling 18.3 km d⁻¹ and age-2 smolts doing so at 26 km d⁻¹. Any tagging and transport effect on travel rates of marine released smolts seemed to disappear once smolts were within the Discovery Islands, as travel rates, corrected for body size, were similar among tagging groups for a given route.

Survival

Most Fraser River sockeye smolts migrate northward through the Salish Sea en route to the open ocean. Recent acoustic tagging studies revealed that $\sim 18 - 31\%$ of marine migrating age-2 Chilko smolts survive this ~ 400 km coastal journey (Clark et al. 2016; Rechisky et al. 2019). The locations of the acoustic array network used by those studies provided insight that survivorship was relatively high through the early marine segment (e.g. the first ~ 150 km) of this migration and that much of the decline in survivorship occurred later in the coastal migration. A similar result was also found using the same telemetry infrastructure for acoustically tagged Cultus Lake hatchery sockeye smolts (Welch et al. 2009). Additional telemetry array infrastructure utilized by my study enabled a more detailed spatial examination of smolt survivorship half-way through their coastal migration. Survival was exceptionally high through the northern Strait of Georgia region, ranging among years and release tagging groups from 80 to 87.5%, levels nearly identical to that observed for acoustically tagged hatchery steelhead smolts migrating through the same region (Healy et al. 2017). Also consistent with Healy et al. (2017), I found survival declined as smolts traversed the Discovery Islands region. This was particularly evident for the smaller smolts that were tagged with V5 transmitters (FL = 123 ± 0.9 mm SE) which exhibited 48% survival whereas larger smolts tagged with V7 transmitters (FL = 147 ± 2.0 mm SE) exhibited 73% survival. Interestingly, age-2 Chilko Lake released smolts had 100% survival through this region in 2017, which may be attributed to their putative much larger size than the marine tagged fish. Survivorship through the final migration

segment from the Discovery Islands to Queen Charlotte Strait (the final acoustic array) was relatively high and similar in magnitude to passage through the Discovery Island region (78% marine tagged smolts, 86% age-2 Chilko tagged smolts). Only V7 tagged fish could be detected at the final acoustic array so I have no survival estimates for relatively smaller bodied smolts at the end of their coastal migration. In sum, the Discovery Island region as a whole generated relatively good survival for larger bodied migrating sockeye smolts and passage success was comparatively similar to that observed in the subsequent and final migration segment.

Body size affects smolt swimming speeds (Ware 1979) thus larger and faster swimming smolts are generally believed to be at lower risk of predation (Furey et al. 2015a; Tucker et al. 2016). Recent acoustic tracking studies provide little evidence that size influences survival (Clark et al. 2016; Rechisky et al. 2019), however, these studies only tracked relatively larger age-2 smolts. The present study found that with a larger range of ages and sizes, larger/older smolts were associated with higher survival in the marine environment, and specifically within the Discovery Islands. Recent sockeye smolt tracking studies have found relatively high mortality through clear, shallow, slow moving freshwater regions (Clark et al. 2016; Rechisky et al. 2019) which has largely been attributed to high levels of predation by piscivorous fish (Furey et al. 2016a). It is possible that avian predators may have a more dominant role in marine mortality (Tucker et al. 2016) relative to submarine predators like pinnipeds (Nelson et al. 2019) or fishes (Beamish and Neville 1995; Emmett and Krutzikowsky 2008). Marine smolts generally migrate within the top one-to-three meters of the water column during daylight hours (Davidsen et al. 2008) and body size affects their relative position within a school, with larger bodied individuals near the deeper anterior portions, leaving smaller individuals near the shallow posterior portion (Hemelrijk and Kunz 2005; Folkedal et al. 2012). This confers a greater chance of exposure of smaller smolts to avian predators. However, the nearly identical proportion of

age-1 and age-2 smolts that emigrate and return as adults (Irvine and Akenhead 2013) does not suggest that this size-related survival advantage continues throughout the entire marine life. Additionally, the advantage conferred by larger size at marine entry for age-2 smolts (Freshwater et al. 2016a), and the relative decrease in mortality in respect to smaller age-1 smolts, suggest that larger bodied smolt mortality must increase at a later stage of migration to account for the variability in adult returns. This may be due to salmon migration progressing further offshore and into reduced avian predator densities in the open ocean (Titmus and Hyrenbach, 2011), size limitations of predation on maturing salmon (Huss et al. 2008), or behavioural adaptation related to maturation and related increased swimming depths (Ogura and Ishida 1995; Davidsen et al. 2008). Shifting patterns of mortality may provide evidence of what dominant predator communities exist spatially along large scale migrations as we observe the relative mortality rates shifts among age-1 and age-2 smolts (Irvine and Akenhead 2013; Freshwater et al. 2016a).

Survivorship through the Discovery Island region not only varied with fish size but varied considerably with migration route. There is clear evidence that marine routes and their associated environmental conditions affects smolt migration survival (Furey et al. 2015b; Healy et al. 2017). In this study, route-specific survival appears to be a product of complex interactions of travel and residency time, and local environmental conditions. Survival was greatest for passage through the eastern route, Desolation Sound (82%), and lowest for passage through the central route, Sutil Channel (44%). Migration through these two routes involved very different travel times, with smolts traversing Desolation Sound on average for 11.2 days (\pm 1.0 SE) which was significantly longer than traversing Sutil Channel (average 6.4 days \pm 2.0 SE). Survival through the third and most western route, Discovery Passage (79%), was intermediate relative to the other routes but travel times here were the shortest and least variable among routes (average 2.2 days \pm 0.7 SE). These three routes provide very different environments to migrating smolts.

The environmental conditions within Sutil Channel may generate a relative 'depression' in sea surface elevation (Foreman et al. 2012) and when paired with relatively weak (NW-SE directed) currents may be an effective 'trap' used by predators as smolts may find themselves caught within a tidal vortex circling the depression. Discovery Passage may also exhibit a similar sea surface depression near Seymour Narrows, however, when paired with the much faster tidal currents that routinely occur (30 BL s⁻¹), smolts may be more readily able to traverse this region with the assisted current boost (Foreman et al., 2012; Burke et al., 2016), and thus avoid large levels of predation. Further evidence for this Sutil Channel 'trap' is provided by the Desolation Sound migrants, as their migration paths merge with Sutil Channel migrants that escape this 'trap' entering either Hoskyn Channel, White Rock Pass, Hole in the Wall, or Calm Channel. Desolation Sound migrants express higher levels of apparent survival when transiting through to Cordero Channel ($S_A = 85$ %) and perfect survival if they transition from Calm Channel to Okisollo Channel. This suggests that the mortality observed within Sutil Channel occurs south of their converged migration paths, specifically in Calm Channel. For smolts in Sutil Channel, entering routes to the north, with stronger and more directional currents, appears to improve survival. A transition into Hoskyn Channel, leads to apparent survival of 72% (n = 21/29) when using Okisollo Channel and 82% (n = 9/11) when using Cordero Channel. The remaining fiftynine smolts that enter Sutil Channel are assigned to the Sutil Channel - Cordero Channel route, of which, only 25% (n = 15/59) survived to JS. Forty-five of the smolts classified within this expected path of migration were only detected on Sutil Channel receivers and of sixteen smolts that were detected on Cordero Channel receivers, fifteen ($S_A = 94\%$) were subsequently detected on the JS array. This suggests the majority of mortality within this broadly distributed route occurred near the entrance, and potentially within the sea surface depression (Foreman et al. 2012), which I am referring to as the 'trap'.

Further evidence of the 'smolt trap' is provided by logistic regression models that predict the probability of redetection based on their levels of milling observed among the primary routes. Milling is defined as the time that an individual remains near an entrance array and is calculated as the difference in time from the first detection to the last detection on that array. This behaviour, which is likely environmentally mediated, was observed within all routes and with relatively equal variation among them. However, within both Discovery Passage and Desolation Sound, increased milling time observed for an individual provided no significant impact on redetection, or survival, at JS. However, within Sutil Channel, there was a significant influence on survival observed, such that individuals that resided near the Sutil Channel subarray for a greater amount of time, decreased their chance of survival.

The impact of tag burden on survival (Appendix) was likely minimal in all tagging groups while migrating within the marine environment. Mean tag burdens were greatest in age-1 Chilko V7 tagged smolts (9.6 \pm 0.1 % SE) and lowest in age-2 Chilko V4 tagged smolts (2.6 \pm 0.02 % SE), whereas the marine V5 and V7 release groups were 3.9 % (\pm 0.1 % SE) and 5.5 % (\pm 0.2 % SE), respectively. My results indicate a relationship among decreased size and decreased survival, however, I believe this effect is not driven by tag burdens, due to how low they are relative to a critical level of 6 to 7 %, which is shown to effect swimming performance (Collins et al. 2013) and potentially influence predation. Highlighting the minimal impacts of tag burden in the marine environment are the Chilko age-2 V7 tagged individuals that had perfect survival through the Discovery Islands and the highest observed tag burdens. Additionally, marine V7 tag burdens are less than half the thresholds observed to influence mortality of Chilko Lake smolts, where a mean of 11.6% increased the chance of mortality in only one of five years of observation (Rechisky et al. 2019). These higher tag burdens only seemed to have an effect on survival early freshwater segments of migration (Rechisky et al. 2019) and thus would likely

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have less effect to smolts upon reaching the Discovery Islands after weeks of additional growth. Also, comparison of sample means comparing those that were successful in migration to JS (5.1 $\% \pm 2.4$ SE) and those that were not (4.1 $\% \pm 1.5$ SE) showed the opposite trend that would be expected had tag burden been an important effect on survival.

Conclusion

My thesis highlights the spatiotemporal variation in survival (Perry et al. 2013; Furey et al. 2015b; Healy et al. 2017) within the Discovery Islands and the effects of physical (Beamish and Mahnken 2001) and behavioural (Thorstad et al. 2012; Karppinen et al. 2014) variation on survivorship and migration characteristics of sockeye salmon smolts during early marine migrations. It also provides the most detailed acoustic tracking assessment of any Pacific salmon species within the marine environment during the smolt life-stage. With specific focus given to the Discovery Islands region, it provides the first direct comparison of migration characteristics of age-1 and age-2 sockeye smolts within the marine environment and develops the first estimates of survival among the major routes within this archipelago for wild migrating sockeye smolts. This region is of keen interest due in part to the significant level of open-net pen salmon aquaculture that is present within the waters that represent the migratory route for nearly all southern British Columbian sockeye populations (Melnychuk et al. 2010; Beacham et al. 2014). This study develops an understanding of how smolts distribute and reside within a region of expected increased relative mortality (Rechisky et al., 2019) during a period hypothesized to have the greatest impact of stock population productivity (Peterman et al. 2012; Freshwater et al. 2016b). It also provides a foundation of movement data that may be compared among modelled migration patterns to investigate the environmental variables that influence migration paths, similar to those developed for viral dispersion (Foreman et al. 2015). Comparison of movement and environmental data may provide clues of how climate change may impact the migratory behaviour through this spatially complex region and the related effect on stock recruitment moving forward.

Tables

Table 1. Summary of smolts and associated physical characteristics from all years of study including 2017 and 2018, groups collected in both freshwater (Chilko Lake) and marine environments, total released (n), including known ages (U = unknown; marine capture), tag type, fork length, mass and the relative tag burden.

					Fork L (mi	ength Mas n)		s (g) Tag Bu (%		urden
Collection Location	Year	n	Age	<i>Tag Type</i> ; Frequency	Mean	(± SD)	Mean	(± SD)	Mean	(± SD)
Chilko Lake	2017	76	2	<i>V7-2L</i> ; 69 kHz	129	(3.7)	16.7	(1.5)	9.63	(0.8)
		79	2	<i>V4-1L; 180</i> kHZ	128	(3.4)	16.3	(1.0)	2.59	(0.2)
		160	1	<i>V4-1L; 180</i> kHZ	86	(3.3)	5.0	(0.5)	8.49	(0.9)
Marine	2018	50	U	<i>V7-2L</i> ; 69 kHz	146	(2.4)	31.6	(11.3)	5.5	(0.3)
		100	U	<i>V5-1L; 180</i> kHZ	123	(8.3)	17.6	(3.6)	3.9	(0.9)

Table 2. Summary of migrations routes utilized through the Discovery Islands, distance and number of sockeye smolts (n) observed along each, DP = Discovery Passage, SC = Sutil Channel, DS = Desolation Sound, HSK = Hoskyn Channel, OK = Okisollo Channel, CRD = Cordero Channel, WR = White Rock Passage, HW = Hole in the Wall Passage (Figure 1), and UK = unknown route.

Primary Route	n	Secondary Route	n	Subsubarray Detection Sequence	n	Distance (km)	Width (km)
DP	44	DP	44	DP	44	69	2.3
SC	101	SC-HOK	31	SC - HSK - OK	29	105	7.1
				SC - HW - OK	2	115	
		SC-CRD	59	SC - CRD	14	118	
				SC	45		
		SC-HCRD	11	SC-HSK-CRD	2	120	
				SC - WR - CRD	2		
				SC - HW - CRD	2		
				SC - HSK - WR - CRD	1	122	
				SC - HSK - HW - CRD	4		
DS	13	DS-CRD	10	DS	0	122.5	2.4
				DS - CRD	10		
		DS-OK	3	DS - WR - OK	2	122	
				DS - HW - OK	1	120	
				DS - HSK - OK	0	140	
UK	9						

Table 3. Comparison among release groups (Chilko age1-V4, age2-V4, age2-V7, Marine ageU-V5, ageU-V7) for total number of detections (n) at each marine subarray including Northern Strait of Georgia (NSOG), Johnstone Strait (JS), Queen Charlotte Strait (QCS) and across the primary entrance route subarrays, Desolation Sound (DS), Sutil Channel (SC), Discovery Passage (DP) and Undetected (JS-Unknown) on Discovery Islands (DI), AgeU = unknown age – marine capture, total released (n – total), total detected on marine subarrays (n – marine detections),* indicate counts that occurred when all receivers on subarray are not capable of detecting tag type, ** indicate counts that may be biased low due to battery failure – not included in ALL counts, bolded text highlights values used in Chi-squared comparison tests.

	Chi	lko Lake Ou	tlet	Northern Geor	Strait of •gia	
		2017		201	8	
	Age1-V4	Age2-V4	Age2-V7	AgeU-V5	AgeU-V7	ALL
n – total	160	79	76	100	50	465
n – marine	38	28	18	81	44	209
detections (p)	(0.24)	(0.35)	(0.24)	(0.81)	(0.88)	(0.45)
Subarray – n (p of total ma	rine detectio	ons within tag	ging group)		
NSOG	11* (0.29)	2* (0.07)	15	4*	2	34
11000	11 (0.2 <i>)</i>)	2 (0.07)	(0.83)	(0.05)	(0.05)	(0.16)
DI	38**	27	17	80	43	205
	(1.0)	(0.98)	(0.22)	(0.99)	(0.98)	(0.98)
JS	14**	16**	15	36	28	109
	(0.37)	(0.59)	(0.88)	(0.45)	(0.65)	(0.52)
QCS	-	-	12	-	19	$\frac{31}{(0.15)}$
DI primary rou	ite _ n (<i>n</i> of t	agging grau	n detected on	DI subarrays)	(0.00)	(0.15)
			p detected on	DI subarrays)		
DS	10**	1	3	6	3	13
25	(0.26)	(0.04)	(0.18)	(0.08)	(0.07)	(0.08)
SC	19**	14	5	52	30	101
be	(0.5)	(0.52)	(0.30)	(0.65)	(0.70)	(0.61)
DP	6**	8	9	19	8	44
DI	(0.16)	(0.30)	(0.53)	(0.24)	(0.19)	(0.26)
JS - Unknown	3**	4**	-	3	2	5
te enknown	(0.08)	(0.14)		(0.04)	(0.05)	(0.03)

Table 4. Mean (SE) segment-specific travel time (days) and travel rates (km d⁻¹; BL s⁻¹) for age-1 and age-2 (both V4 and V7) Chilko Lake and marine captured (ageU) sockeye smolts through early marine portions of migration. NSOG = Northern Strait of Georgia, DI = Discovery Islands, Rel = marine release, JS = Johnstone Strait, QCS = Queen Charlotte Strait, na = not applicable due to lacking detections or too few detections to determine times and rates, * indicates an average distance among three entrance arrays and routes.

Marine	Tra	vel Time	e (d)	Trave	el Rate (k	xm d ⁻¹)	Trave	el Rate (l	BL s ⁻¹)
Segment (km)	Age1	Age2	AgeU	Age1	Age2	AgeU	Age1	Age2	AgeU
NSOG to DI (55)	5.8 (1.7)	2.8 (0.4)	4.7 (2.1)	18.3 (4.0)	26.0 (3.9)	17.5 (5.4)	2.5 (0.5)	2.3 (0.4)	1.5 (0.4)
Rel to DI (30)	-	-	3.9 (0.3)	-	-	10.2 (0.7)	-	-	0.9 (0.06)
JS to QCS (102)	-	3.1 (0.2)	3.6 (0.3)	-	34.5 (2.3)	30.6 (2.0)	-	3.1 (0.2)	2.4 (0.1)
Variation by	Route –	DI – JS ((99km)						
Discovery Passage (69)	2.7 (0.2)	1.5 (0.1)	2.5 (0.2)	25.9 (2.0)	47.6 (2.9)	32.1 (2.6)	3.5 (0.4)	4.3 (0.3)	2.9 (0.2)
Sutil Channel (115)	6.0 (1.1)	4.5 (0.6)	7.0 (0.7)	19.0 (2.7)	27.6 (2.6)	18.7 (1.4)	2.5 (0.4)	2.5 (0.2)	1.7 (0.1)
Desolation Sound (120)	9.8 (2.5)	13.5 (3.9)	10.8 (2.8)	13.6 (2.5)	12.4 (4.2)	17.2 (3.1)	1.8 (0.3)	1.1 (0.4)	1.5 (0.3)
NEVI (NSOC	G – QCS)	– Chilk	o V7 Tag	s Only					
Discovery Passage (249*)	-	8.43 (0.5)	-	-	30.1 (1.6)	-	-	2.8 (0.2)	-
Sutil Channel (249*)	-	9.73 (0.6)	-	-	25.9 (2.0)	-	-	2.2 (0.2)	-
Desolation Sound (249*)	-	24.2 (0.9)	-	-	10.3 (2.8)	-	-	0.9 (0.3)	-

Table 5. Summary of apparent (S_A) and Cormack-Jolly-Seber model estimated survival (ϕ) and survival rates per 100 kilometers and per day, for all observed primary routes, counts (n) of individuals from both Chilko Lake (age-2-V4 and V7; 2017) and Marine release (V5 and V7; 2018) tagging groups within each route at Discovery Island (DI) and Johnstone Strait (JS) subarrays, SE = standard error, 95% Confidence Intervals (CI), DP = Discovery Passage, SC = Sutil Channel, DS = Desolation Sound, ALL = all routes or Discovery Islands segment specific, - = not applicable.

Route	Year	n DI det.	n JS det.	S _A (%)	Det. Eff. (ρ) (95% CI)	Survival Estimate (ф) (%) (95% CI)	Survival Rate S 100km ⁻¹ (%) (95% CI)	Survival Rate S d ⁻¹ (%) (95% CI)
DP	2017	17	11	65	-	-	-	-
	2018	27	19	70	-	79.0 (52–93)	71 (39 – 90)	91 (76 – 97)
SC	2017	19	12	63	-	-	-	-
	2018	82	33	40	-	43.5 (32 – 55)	48 (37 – 60)	89 (85 – 92)
DS	2017	4	4	100	-	-	-	-
	2018	9	7	78	-	81.7 (39 – 97)	84 (46 – 97)	98 (92 – 100)
ALL	2017	40	27	68	-	-	-	-
	2018	123	65	53	74.5 (60 - 85)	56.8 (46 – 66)	57 (47 – 67)	90 (87-93)

Parameter	Tagging Group	Segment	Distance (km)	Estimate (%)	Lower 95% CI	Upper 95% Cl
Survival (\$)	Age2-V7	NS to DI	55	87.5	63.7	98.2
		DI to JS	99	100.0	100.0	100.0
		JS to QCS	102	85.7	0.0	100.0
		NEVI	240	76.0	0.0	0.0
	Marine-V5	NS to DI	30	80.0	71.0	86.7
		DI to JS	99	48.0	36.4	59.8
	Marine-V7	NS to DI	30	86.0	73.4	93.2
		DI to JS	99	72.8	55.6	85.1
		JS to QCS	102	77.9	0.0	100.0
		NEVI	240	46.0	0.0	0.0
Survival /100km	Age2-V7	NS to DI	55	78.4	44.0	96.8
		DI to JS	99	100.0	100.0	100.0
		JS to QCS	102	85.9	55.0	100.0
	Marine-V5	NS to DI	30	41.0	25.4	56.5
		DI to JS	99	47.6	36.0	59.5
	Marine-V7	NS to DI	30	54.7	29.0	75.5
		DI to JS	99	72.6	55.3	85.0
		JS to QCS	102	78.3	0.0	100.0
Survival /day	Age2-V7	NS to DI	55	95.3	85.1	99.4
		DI to JS	99	100.0	100.0	100.0
		JS to QCS	102	95.1	82.1	100.0
	Marine-V5	NS to DI	30	94.3	91.4	96.3
		DI to JS	99	89.6	86.0	92.6
	Marine-V7	NS to DI	30	96.4	92.7	98.3
		DI to JS	99	94.1	89.3	96.9
		JS to QCS	102	93.3	0.0	100.0
Detection	Age2-V7	DI	-	100.0	100.0	100.0
Efficiency		JS	-	94.1	74.3	99.8
	Marine V5	DI	-	74.5	60.2	84.9
	& V /	JS	-	89.5	66.3	97.4

Table 6. Cormack-Jolly-Seber model estimates of survival (ϕ), survival rate per 100 km (S¹⁰⁰), survival rate per day (S^d) and detection efficiency (ρ) for Chilko age2-V7 tagged smolts and Marine V5 and V7 tagged smolts, NS* = Northern Strait of Georgia array detection (age2-V7) or release (Marine-V5, V7), DI = Discovery Islands, JS = Johnstone Strait, QCS = Queen Charlotte Strait, NEVI = Northeast Vancouver Island. - = not applicable.

Figures



Figure 1. A) A broad map of study area showing release point of Chilko smolts, Queen Charlotte Strait (QCS) subarray and Northern Strait of Georgia (NSOG) subarray that consists of both single and dual frequency receivers. Pink bars represent acoustic receiver arrays only capable of detecting V7 (69 kHz) tags and those depicted as yellow bars or circles are capable of detecting all tags released, including V5 (180 kHz) and V4 (180 kHz) tags. **B)** Finer scale map of Discovery Islands subarrays, including the primary or entrance arrays of Desolation Sound, Sutil Channel and Discovery Passage, Johnstone Strait, and the marine release point. **C)** More detailed map perspective of the secondary Discovery Islands subarrays including a) Cordero Channel, b) Okisollo Channel, c) Hole in the Wall, d) White Rock Pass, e) Hoskyn Channel and f) Calm Channel, along with capture site represented by the black box, and both marine surgery sites represented by the size of the red circle.



Figure 2. Histogram depicting the proportion of smolts within each tagging group distributed across primary routes (DP = Discovery Passage, SC = Sutil Channel, DS = Desolation Sound) through the Discovery Islands subarray with channel widths (km) provided for each route.



Figure 3. Number of detections at each marine subarray, Northern Strait of Georgia (NSOG), Discovery Islands (DI), Johnstone Strait (JS), Queen Charlotte Strait (QCS), for each Chilko Lake (age2-V4, V7) and marine (Marine-V5, V7) tagging groups.



Figure 4. Travel time (days) and rates of kilometers per day (km/d) and body length per second (BL/s) compared among all segments of observed migration within Northeast Vancouver Island (NEVI) for all Chilko Lake (age1-V4, age2-V4, age2-V7) and marine release (Marine-V5, -V7) tagging groups, where NEVI represents the combination of three previous segments. NS = Northern Strait of Georgia and includes both detection on the NSOG receiver subarray and release within the NSOG, DI = Discovery Islands subarray, JS = Johnstone Strait subarray, QCS = Queen Charlotte Strait subarray, the terminal array, only capable of detecting V7-69 kHz tags.



Figure 5. Travel time (days) and travel rates of kilometers per day (km / d) and body lengths per second (BL / s) observed for all smolts migrating through the Discovery Islands, along primary routes Discovery Passage, Sutil Channel and Desolation Sound, comparing Chilko Lake (age1-V4, age2-V4 and age2-V7) and marine release (Marine-V5, Marine-V7) tagging groups, demonstrating an increasing trend of travel time in migration routes moving from west to east along the entrance arrays, and the inverse trend in travel rates, decreasing from west to east, along with variation present among tagging groups.



Figure 6. Cormack-Jolly-Seber model estimated segment specific survival, survival rate per 100 km and survival rate per day (\pm 95% CI) among all modeled tagging groups including Chilko age2 V7-tagged smolts (age2-V7) and marine V5 and V7 tagged smolts captured in 2018 (Marine-V5, Marine-V7), NS = Northern Strait of Georgia, DI = Discovery Islands, JS = Johnstone Strait, QCS = Queen Charlotte Strait.



Discovery Islands Primary Routes

Figure 7. Cormack-Jolly-Seber model estimated primary Discovery Islands route specific survival (S Estimate), survival per 100km (S /100km) and survival per day (S /day) among all primary routes, DP = Discovery Passage, SC = Sutil Channel, DS = Desolation Sound, ALL = all route combined for complete Discovery Islands (DI-JS) segment survival rate, with 95% CI error bars.



Figure 8. Cumulative survival curve depicting the Cormack-Jolly-Seber model survival estimates from point of release to subsequent marine subarrays, for Chilko release tagging group Northern Strait of Georgia (NSOG), and for Marine Release (Rel. - 30km) tagging group, the Discovery Islands (DI - 55km) subarrays were respective subsequent receivers. Johnstone Strait (JS - 154km) subarray that is the terminal array for Marine-V5 tagging group, and Queen Charlotte Strait (QCS - 249km) subarray that is terminal array for Chilko Lake age2-V7 and Marine-V7.



Figure 9. Generalized linear models predicting the redetection of smolts on Johnstone Strait subarrays among three primary routes, Discovery Passage (DP), Sutil Channel (SC), Desolation Sound (DS), Johnstone Strait (JS) with behavioural (Milling Time[hrs]) characteristic compared among routes, for all Chilko age2-V7, Marine V5 and Marine V7 tagged smolts within the Discovery Islands.

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Appendix

Tagging Effects Laboratory Holding Experiment

Holding study design

Previous studies have shown surgical procedures were effective in maintaining a nonsignificant effect on mortality and morbidity in freshwater environments when tag burdens remained under a level of 8% (Collins et al., 2013). However, this study was the first to tag individuals in the marine environment and warranted another test of procedures within this new environment. Construction of necessary infrastructure delayed holding study operations until 24 June 2018, which coincided with the terminal period of sockeye outmigration timing and associated low abundance (Johnson, Gan, Janusson & Hunt, 2018). This necessitated the use of another species, Chum salmon (O. keta), in holding experiments as they were highly abundant at that time, have similar migratory behaviour as the Sockeye migrating through the DI, and are genetically closely related compared among other species of Pacific salmon (Utter, Allendorf and Hodgins, 1973). Two groups of smolts were captured on consecutive days, 26 and 27 June, and placed into two separate flow-through holding tanks (~3000 L) flushed with UV and sand filtered seawater. 'Tank 1' and 'tank 2' were located within an enclosed laboratory setting where water flow (0.83 - 1.08 L min⁻¹), temperature (9.3 – 11.4 °C) and dissolved oxygen (7.46 – 8.79) mg L¹) were monitored twice per day. Each tank consisted of 44 smolts, where 22 were dummy tagged, or treated, and held along with 22 controls. To simulate surgical procedures, pre-surgery and surgical procedures follow those outlined above (Tag Implantation Surgery). Controls were exposed to all surgical procedures and remained on the surgical v-shaped trough for a duration (1-2 minutes) that simulated surgical implantation, incisions and tag implantation were withheld. Total holding time varied among the two tanks, with smolts in 'tank 1' held for a total of 7d 20:36 minutes and those in 'tank 2' for 6 d 19:59 minutes. A log-rank test was used to compare

survival between treatment groups based on the associated Kaplan-Meier Survival Curve (Figure A1). A likelihood-ratio test was completed based on a Cox-proportion Hazard regression model constructed to test for variation between these treatment groups. Resampling of all smolts for fork length and weight were recorded to compare the control and treatment groups to assess the effect of tagging on growth. Feeding was withheld, as previous studies have observed little to no feeding from wild migrating sockeye smolts on the commercially available fish feed products (A. G. Lotto pers. obs.).

Results and Discussion

Tanks 1 (n = 44) and 2 (n = 44) held smolts for a period of 7 d 20:36 minutes and 6 d 19:59 minutes, respectively. Smolts were in either a control group or a treatment group and were evenly distributed among the two tanks. Each tank had a single mortality event, both occurring with a dummy tagged, or treatment, individual at 4d 3:56 minutes and 4d 2:19 minutes in tanks 1 and 2, respectively. A Kaplan-Meier survival curve (Figure ##) comparing the two treatment groups and associated log-rank test indicated no significant variation between the two curves (χ^2 1 = 2, p = 0.155). A Cox-proportion Hazard regression model was also constructed to test for variation between the treatment groups (LR 1 = 2.8, df = 1, p = 0.09) and showed non-significant results.

Previous studies have shown surgical procedures (Collins et al. 2013; Jeffries et al. 2014; Clark et al. 2016; Healy et al. 2017; Stevenson et al. 2019) were effective in maintaining a nonsignificant effect on mortality and morbidity in freshwater environments, specifically, when tag burdens remained under a level of 8% (Collins et al., 2013). Investigations comparing the impact of seawater to fresh water have suggested there is not variation among them (Clark et al., 2016), however, this study was the first to capture and tag sockeye salmon smolts exclusively in the marine environment and warranted another test of procedures carried out entirely within this saline environment.

Construction of necessary infrastructure delayed holding study operations until 24 June 2018, which coincided with the terminal period of sockeye outmigration timing and associated low abundance (Johnson, Gan, Janusson & Hunt, 2018). This necessitated the use of another species, Chum salmon (*O. keta*), in holding experiments as they were highly abundant at that time, have similar migratory behaviour as the Sockeye migrating through the DI, and are genetically closely related compared among other species of Pacific salmon (Utter et al. 1973).

Both tanks held a total forty-four smolts, an equal number of control and surgically treated individuals were distributed among each tank. The specific number of fish were chosen to provide a realistic time frame for operations to occur in manner than best mimicked those tagged and released fish in the tracking component of the study. Total holding periods, 7 d 20.6 h and 6 d 20.0 h, were shorter than most previous studies (Jeffries et al. 2014; Clark et al. 2016; Furey et al. 2016), however the intended outcomes were to observed effects of surgical procedures. Impacts of tagging appeared to fully manifest by ~4.1 days, where both mortality events occurred, one in each tank. This would likely be realized far soon within a natural environment as these individuals would be consumed by a predator in their depleted physical state (Miller et al., 2014). Knowing the procedures did not have a significant impact on survival we can express confidence in the survival estimates produced in this marine investigation.

Additionally, smolts were observed attacking or 'nipping' individuals that were later found dead or were removed and sacrificed due to lethargy (i.e. no reaction to physical stimuli). There were no observed attacks on tagged individuals that survived for the duration of the experimental period and were expressing physically fit behaviour and appearance. This suggests that controls do not observe the treated individuals as sick or a potential threat for disease

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transfer. Three-spined stickleback (*Gasterosteus acule*atus) and killifish (*Fundulus diaphanous*) are known to actively avoid schooling with sick or parasite infected conspecifics (Wisenden et al. 2009). The observed attacking behaviour may represent an attempt to remove these sick individuals from their respective school. This may provide a behavioural indication from conspecifics that tagging has non physically apparent negative impact on smolts and further bolsters the effectiveness of these procedures.

Appendix Tables

Table A1. Measured body characteristics of chum salmon (*O. keta*) smolts collected for holding studies completed to observe the impact of tagging procedures on smolts in the marine environment, at both commencement and termination of holding periods, including calculated changes in sample means for observed characteristics. Where condition factor represents the Fulton's condition factor (K = M (kg) / FL (m) ^3), - = not applicable.

Treatment	n	Fork Length (mm)	Total Mass (g)	Tag Burden (%)	Condition Factor
		Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD
Pre-Holding Period – Commencement of Study					
Control	44	120.1 ± 7.6	15.8 ± 3.0	-	0.90 ± 0.07
Treatment	44	123.6 ± 9.1	17.5 ± 4.5	3.91 ± 0.9	0.91 ± 0.05
Post-Holding Period – Termination of Study					
Control	44	121.8 ± 7.1	15.2 ± 2.9	-	0.83 ± 0.04
Treatment	44	124.6 ± 9.3	17.3 ± 4.2	3.94 ± 0.84	0.88 ± 0.04
Change in Body Characteristics		∆ Mean Fork Length (mm)	∆ Mean Mass (g)	∆ Mean Tag Burden (%)	Δ Mean Condition Factor
Control	44	+1.7	-0.6	-	-0.07
Treatment	44	+1.0	-0.2	+0.03	-0.03

Appendix Figures



Figure A1. Kaplan-Meier survival curve depicting the variation of survival among treatment (n = 44) and control (n = 44) groups of Chum salmon (*O. keta*) used in holding experiments to observe the effect of surgical procedures on smolts within a marine environment, p = p-value of a Chi-square test comparing survival curves.