

**MIGRATION ECOLOGY OF JUVENILE PACIFIC SALMON SMOLTS: THE ROLE
OF FISH CONDITION AND BEHAVIOUR ACROSS LANDSCAPES**

by

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Abstract

Migrations are utilized across taxa to exploit spatiotemporal variability across landscapes. The benefits of migrations are balanced with costs, and understanding the factors that limit migratory success is needed for proper management and conservation. Sockeye salmon (*Oncorhynchus nerka*) are of economic, cultural, and ecological importance and undergo downstream migrations from natal freshwater systems through rivers to the ocean as juvenile smolts. In this thesis, I describe a series of studies investigating the migration behaviour and survival of sockeye smolts emigrating from Chilko Lake, British Columbia, a large population that experiences poor survival in the Chilko River. First, field sampling and bioenergetics models were used to find that short-term feeding on smolts by bull trout (*Salvelinus confluentus*) in the Chilko River was extreme, not limited by cold temperatures, and resulted in greater exploitation of smolts than expected using traditional bioenergetic assumptions. Examining bull trout stomach contents revealed that consumed smolts had higher rates of infection by hematopoietic necrosis virus and *Flavobacterium psychrophilum* and were smaller than non-predated smolts. Through acoustic telemetry, I found that smolts traversing the upper Chilko River with higher densities of conspecifics experienced improved survival relative to smolts travelling at times when few smolts were migrating. Thus swamping predators can maximize survival. It is more difficult to conduct field studies in the coastal marine environment such as the Strait of Georgia, and even knowledge on migration routes and behaviour is limited. Aggregating telemetry data collected over ~10 years of research on sockeye and steelhead (*Oncorhynchus mykiss*) populations determined that contingents of both species exhibited westward lateral movements within the strait, consistent with predicted currents. Steelhead using the eastern migratory route experienced improved survival through the Strait to a location ~250 km further along the migratory corridor -

a rare example of migration route impacting fitness. Individually, chapters advanced the fields of migration and feeding ecology and tested long-held ecological hypotheses. Important links were identified between smolt migration behaviour and/or survival and components of the movement ecology framework. This thesis has expanded our understanding of the factors influencing the migration of one of the largest sockeye populations in Canada.

Preface

Chapter 2: A version of this chapter is in press at a peer-reviewed journal with the following citation: Furey, N.B., S.G. Hinch, M.G. Mesa, D.A. Beauchamp. Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. *Journal of Animal Ecology*. This study was conducted, analyzed and written by NBF under supervision of SGH, MGH, and DAB. MGM and DAB provided data from former laboratory studies for additional analyses conducted by NBF. All coauthors contributed to editing the manuscript. Ethics Approval: This research was approved by the University of British Columbia Animal Ethics Committee (animal care permit: A11-0125) in accordance with the Canadian Council of Animal Care.

Chapter 3: A version of this chapter is currently in preparation for submission at a peer-reviewed journal with the following citation: Furey, N.B., A.L. Bass, K.M. Miller, and S.G. Hinch. Infection increases predation risk of juvenile salmon smolts during outmigration. This study was conducted, analyzed, and written by NBF under supervision of ALB, KMM, and SGH. ALB and KMM provided laboratory support, and ALB led laboratory work. ALB provided data processing support. ALB and SGH contributed to editing the chapter. Ethics Approval: This research was approved by the University of British Columbia Animal Ethics Committee (animal care permit: A11-0125) in accordance with the Canadian Council of Animal Care.

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List of Symbols

Φ Phi

List of Abbreviations

AIC	Akaike information criterion
AICc	Akaike information criterion corrected for small sample sizes
ANOVA	Analysis of Variance
df	degrees of freedom
DFO	Fisheries and Oceans Canada
FL	fork length
IHNV	infectious haematopoietic necrosis virus
km	kilometer
PIT	passive integrative transponder
SD	standard deviation
SOG	Strait of Georgia
QCS	Queen Charlotte Strait

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Dedication

This thesis is dedicated to my wife Laura, my sisters Allison and Dr. Rachel Furey, and my parents Bruce Furey and Dr. Nancy Redman-Furey.

Chapter 1: Introduction

1.1 Animal migrations

Migrations, or the directed, pre-emptive movements of organisms from one location to another, are displayed across taxa, including insects, birds, mammals, reptiles, and fish. These directed movements are thought to have evolved to allow organisms to take advantage of spatial and temporal variability in habitat quality and/or to reduce or avoid competition (Alerstam et al. 2003). The benefits of exploiting this spatiotemporal variability, however, are balanced with a wide variety of costs that include increased energetic requirements, stressful environmental conditions, and exposure to novel predators (Cresswell et al. 2011). Factors that affect the severity of these costs are varied, specific to both the individual and the landscapes experienced, and can act as strong selection agents for populations that migrate (Alerstam et al. 2003, Dingle and Drake 2007). Furthermore, populations of migratory organisms are in decline across taxa and ecosystems worldwide (Wilcove and Wikelski 2008, Limburg and Waldman 2009, Harris et al. 2009). Thus, understanding the factors that influence migration behaviour and success is imperative for proper management and conservation of migratory species, and the process of migration itself which acts to couple ecological systems worldwide (Bauer and Hoyer 2014).

1.2 A conceptual model for migration experience and survival

Conceptual frameworks are useful for contextualizing complex ecological processes such as migrations into manageable components. The movement ecology paradigm for exploring the causes and patterns of movement (Nathan et al. 2008) can

easily be applied to migrations (Figure 1.1). In short, this framework examines the movement process via three components of an individual migrant: internal state, motion capacity, and navigation capacity, and the external factors the migrant experiences (Nathan et al. 2008).

1.2.1 Internal state

The internal state represents the physiological condition of the migrant and the subsequent motivations for movement (Nathan et al. 2008). Thus the internal state is multidimensional and can encompass the physical health, condition, and physiology. The internal state can also represent whether the organism is alive to continue the migration or has perished, and thus the framework can also examine processes influencing survival during the migration. The process of initiating the migration is often controlled by endocrinology across taxa (Bauer et al. 2011, Chapman et al. 2015) as well as size (Skov et al. 2011). After initiation, the health of the organism can affect further movements or even result in migration failure (Altizer et al. 2011). Individual variability in physiology, including indicators of stress and energy status, has been correlated with migration success in both fish (Cooke et al. 2006, Donaldson et al. 2010) and birds (Angelier et al. 2009, Goymann et al. 2010). These factors can directly influence the other two intrinsic components of the movement ecology framework: motion and navigation capacities.

1.2.2 Motion capacity

Motion capacity refers to an individual's ability to traverse a landscape (Nathan et al. 2008). Such capacity generally refers to the type of movement (flying, swimming, walking, etc.) and the biomechanics that limit such movements. The motion capacity can

be affected by the internal state, as morphology-based (Plaut 2000, Berwaerts et al. 2002, Bowlin and Wikelski 2008), and size-based (Hedenström 2003) effects on movement performance have been observed. Whether due to motion capacity or some other factor, size-selective migration mortality is often observed particularly when migrants are juveniles, including for turtles (Janzen et al. 2000, Myers et al. 2007, Rebelo et al. 2011), coral reef fishes (Brunton and Booth 2003), lampreys (Keefer et al. 2009), and eels (Calles et al. 2010).

1.2.3 Navigation capacity

Navigation capacity defines how an organism orients and navigates the landscape in the context of progressing the migration (i.e., where and when to move; Nathan et al. 2008). The mechanism for navigation capacity over large spatial scales remains largely a mystery across taxa (Alerstam 2006, Holland et al. 2006), but variability in this capacity has been demonstrated (Mueller et al. 2013) and thus could influence migratory success. Magnetic compass sense and the use of the sun and stars, landmarks, odours, and learned migration paths have all been hypothesized to allow for navigation and orientation behaviours (Akesson and Hedenstrom 2007, Bauer et al. 2011). On smaller spatiotemporal scales, navigation capacity can refer to movements in response to diel cycles, predators, conspecifics, and changes in environmental conditions.

1.2.4 The movement path (migration route) and external factors

Ultimately the motion and navigation capacities combine to result in a migrant's movement path or migration route through landscapes (Figure 1.1). Migration routes can vary considerably among individuals (Gschweng et al. 2008, Jonzén et al. 2011, Mueller

et al. 2013), resulting in differing experiences (Felicísimo et al. 2008, Mellone et al. 2011). Thus, migration routes define the external factors to which a migrant is exposed.

External factors within the movement ecology framework include 1) environmental conditions (which can affect the physiology of the migrant, and thus interacting with internal state), 2) the physical structure of the landscape, and 3) biotic components of the landscape including predators, competitors, and conspecific migrants (Nathan et al. 2008). Even when environmental conditions (such as temperature) are sublethal, cumulative or carry-over effects on physiology can impact long-term fitness (Bauer et al. 2008, López-López et al. 2010, Crossin et al. 2010). Landscape structure can either facilitate or impede movement, thus interacting with the motion capacity. Impedances to migration can include wind fields (Felicísimo et al. 2008, Mellone et al. 2011) and oceans (Delmore et al. 2012) for birds, mountain ranges for birds and mammals (Williams et al. 2001, Webster et al. 2002), dams for fish (Dudgeon et al. 2006, Limburg and Waldman 2009, Winemiller et al. 2016), and fences (Harris et al. 2009), roads (Vistnes et al. 2004, Holdo et al. 2011), and railways (Ito et al. 2005) for terrestrial mammals.

Biotic components of landscapes, including predators and conspecifics, are also important external factors that can influence movements and migrations. Predators also vary in distribution and abundance within a landscape (Bouchet et al. 2014), which can impact how migrants move and directly impact survival. Predation risk can influence propensity for emigration in populations exhibiting partial migrations (Skov et al. 2011, 2013), the seasonal timing of migrations (Lank et al. 2003), and the short-term (diel)

timing of movements within the migration (Ibbotson et al. 2011). Thus predator distribution and abundance directly impacts when and where an individual migrates (the navigation capacity; Figure 1.1). The migration experience is also impacted by conspecific migrants; by definition migrations are dependent upon large population contingents moving in a synchronized fashion. Competition for food along the migration can increase with conspecific densities, altering movement behaviours (Hopcraft et al. 2014) and/or energetic status (Moore and Yong 1991). Increased conspecific densities, however, can also result reducing per-capita predation risk, both by swamping predators (Ims 1990), as well increased ability to detect and/or confuse predators (Landeau and Terborgh 1986, Lima 1995). The benefits of increased conspecific densities specifically for migrants, however, have little empirical support. In sum, external factors, including environmental, physical, and biotic, can both directly influence the migratory experience, as well as generate feedback loops to the other intrinsic components of the framework (Figure 1.1).

1.3 Fish migrations and anadromy

Of the 35,000 species of fish, nearly 900 are migratory during at least one stage of their life cycle (Riede 2002, 2004). One form of fish migration is anadromy, where spawning and juvenile stage(s) occur in freshwater after migrating from the ocean as adults. Anadromy is expected to have evolved in response to food resources being greater in marine environments than in freshwater habitats at higher temperate latitudes (Gross et al. 1988). Although anadromous fishes represent a small portion of all fishes, they often support valuable fisheries as their migrations result in predictable spatiotemporal

concentrations of fish that are easily exploited (McDowall 2009). Due to this exploitation, along with loss of habitat and connectivity, anadromous fishes across the North American continent have exhibited dramatic declines (Limburg and Waldman 2009) and thus these species are often a priority for conservation and management.

1.4 Fraser sockeye salmon and juvenile smolt migrations

Among anadromous fishes, Pacific salmon are among the most-studied (Hinch et al. 2006) due to their economic and cultural value. In Canada, sockeye salmon (*Oncorhynchus nerka*) of the Fraser River basin drive commercial, recreational, and First Nations fisheries. Unfortunately, productivity of these populations have declined over the past two decades, resulting in a federal inquiry whose recommendations included several directed towards increasing research efforts on the migration of juvenile smolts (Cohen 2012), the life stage when salmon leave freshwater habitats and migrate to the marine environment. Although less visible than the upstream migration taken by adults, these migrations by smolts are no less impressive as they can involve the synchronous movements of several millions of individuals at a time (Hinch et al. 2006). The migrations of smolts are relatively poorly studied, especially in the marine environment (Drenner et al. 2012). As is common in all anadromous fishes, outmigrating smolts experience multiple landscape types with distinctive characteristics in terms of external factors that could affect experience and migratory success.

The initial outmigration of salmon smolts begins in late spring after natal lakes begin to thaw (Hinch et al. 2006). Both increasing photoperiod and water temperature are both important in initiating migration (Burgner 1991), and photoperiod appears to

directly influence the process of smoltification, the physiological process by which a juvenile salmon prepares for life in the marine environment (Clarke et al. 1981, Hinch et al. 2006). As migrations are generally constrained to occur within specific time periods to be successful (Healey 2000), it is important for initiation timing to be optimal. For hatchery smolts, later releases (forced delayed migration initiation) resulted in lower survival (Welch et al. 2009), and it is expected that variability in timing of wild smolts to also be an important influence on migration success.

Once the migration is initiated and downstream movement has begun, predation is expected to drive survival. As such, much of the research on outmigration has focused on the distribution and abundance of predators. In the Columbia River, for example, the aggregation of piscivorous pikeminnow (Zimmerman 1999, Petersen 2001), and avian predators such as terns, gulls, and cormorants (Schreck et al. 2006, Evans et al. 2012, Osterback et al. 2013), has been shown to influence location-specific mortality of smolts. These studies have largely focused on large rivers with hydropower facilities and/or in estuaries, rather than small, unaltered river systems.

External factors specific to the riverscape may mediate the interactions with predators. River flow is expected to influence the duration of predation risk (Hostetter et al. 2012), as flow has been correlated with downstream migration speeds (Berggren and Filardo 1993, Giorgi et al. 1997). River turbidity can also influence predation risk (Gregory and Levings 1998, Hostetter et al. 2012), but turbidity-risk relationships can vary with predator behaviour (Hostetter et al. 2012). Water temperature, by establishing

the metabolism and energy requirements of predators, can also impact predation risk for smolts in riverine environments (Vigg and Burley 1991, Petersen and Kitchell 2001).

Predation risk is further affected by the smolt's internal state. Smolts in poor condition, either from pathogen presence (Schreck et al. 2006) or injuries from migration (Gadomski and Hallgriswold 1992, Hostetter et al. 2012), can experience increased predation risk and mortality due to assumed reductions in motion and navigation capacities. Similarly, smolt size can influence predation risk (Poe et al. 1991, Hostetter et al. 2012), but size-dependent predation risk is not always observed and can be predator dependent (Sogard 1997). Smolt size can also be correlated with movement behaviour consistent with predator avoidance, such as the propensity for nocturnal movement (Ibbotson et al. 2011).

Much like in the freshwater environment, the mortality experienced by smolts in the coastal marine landscape is generally attributed to predation. Although predation has been difficult to investigate directly in this landscape, lampreys (Beamish and Neville 1995), spiny dogfish (Beamish et al. 1992), and seals (Olesiuk 1993) all feed on smolts. Again due to logistical constraints, it is difficult to directly identify factors influencing risk in this landscape, but fast-growing fish appear to have higher survival to adulthood (Beamish and Mahnken 2001, Beamish et al. 2004), and therefore conditions correlated with smolt growth have been identified as important during this stage of the migration. In particular, regional-scale oceanographic conditions, including temperature and upwelling indices (Ryding and Skalski 1999, Mueter et al. 2002a, 2002b), have been correlated with early marine survival. These correlational studies, however, generally tend to explain

only a small portion of the observed variability in mortality (Mueter et al. 2005), and generally utilize data collected from returned adults (which are thus exposed to potential mortality for an additional 2-3 years beyond the smolt life stage).

Beyond predation, other factors within the coastal marine landscape have been suggested to influence mortality. One of the most immediate changes smolts experience upon entry is an increase in salinity and the subsequent osmoregulatory challenges. Some smolts are not prepared for the increased salinities and perish upon entry into estuarine waters (Hinch et al. 2006). Although the proportion of smolts that are not prepared for increased salinities is unknown, there appears to be a link between stress levels and osmoregulatory preparedness (Franklin et al. 1992, Price and Schreck 2003), and therefore prior migration experience might influence saltwater tolerance. Harmful algal blooms in coastal British Columbia waters during the time of migration have also been linked to high mortality rates (Rensel et al. 2010). Thus spatiotemporal variability in environmental conditions and the distribution and abundance of predators are expected to influence the success of migrant smolts through coastal waters. Although limited, studies on movements in the marine environment suggest that sockeye smolts largely move in a linear fashion through coastal waters, and that migration routes are further influenced by tidal or wind-driven currents (Groot and Cooke 1987, Peterman et al. 1994).

1.5 Recent research: Chilko sockeye smolt migrations revealed through telemetry

Many of our limitations in studying the migration ecology of smolts are tied to the geographical expanse of the landscapes through which a migration occurs, and the inability to track individuals and their fate. The continued advances in biotelemetry, or the use of inserting or attaching an actively-transmitting tags to organisms, however, has provided researchers a means to track in-situ organismal movements throughout multiple environments (Hussey et al. 2015, Kays et al. 2015). Acoustic telemetry has been used on several Pacific salmon smolt species to estimate migration rates and survival through the Strait of Georgia (Melnychuk et al. 2007, Welch et al. 2009, 2011). Because of their relatively smaller size, investigations on sockeye have been limited to hatchery smolts, which tend to be larger and can accommodate the size of commercially available acoustic tags (Welch et al. 2009).

Recently, acoustic telemetry for the first time tracked the migration of wild sockeye smolts ($n > 1600$) from the Chilko Lake population within the Fraser River watershed (2010-2013; Clark et al. 2016). Chilko sockeye provide a good model for investigating smolt migration ecology as they are one of the largest sockeye populations in all of Canada (10 – 40 million smolts emigrate annually), act as an indicator for Fraser River sockeye (arguably Canada's most valuable fish species), and Fisheries and Oceans Canada (DFO) has conducted population assessments for the population for > 60 years. Lastly, two age classes of this wild population migrate, and the older age-two smolts

(which constitute ~5% of the outmigration population; (Irvine and Akenhead 2013)) are large enough to accommodate the size of acoustic tags.

Tagged Chilko sockeye smolts demonstrated landscape-specific trends in both survival and movement behaviour. Smolts exhibited poor survival (57% - 78% over 80 km) early in the migration, while smolts were traversing the small and clear Chilko and Chilcotin Rivers (Clark et al. 2016). In these riverscapes of poor survival, smolts also demonstrated strong nocturnal migrations (Clark et al. 2016). Once in the Fraser River mainstem, however, survival was high (>90%) and migration rates were rapid (i.e. occasionally exceeded 200 km/day), with no evidence of diel influences. In the coastal Strait of Georgia, smolt survival was quite variable, and movements were slower (10 – 20 km/day; Clark et al. 2016). These patterns in survival and migration rates identify small clear tributaries and the marine environment as potentially critical in determining migration survival rates.

1.6 Knowledge gaps

1.6.1 Movement and migration ecology

Significant knowledge gaps exist in both the fields of movement and migration ecology as well as in understanding sockeye smolt migrations. Progression the field of migration ecology beyond the simple characterization of animal movements is considered a “grand challenge” of the field (Bowlin et al. 2010). Although the presented movement ecology framework (Nathan et al. 2008) is useful in conceptualizing the numerous factors influencing movements, many of the suggested relationships have little empirical support, as reviewed by (Holyoak et al. 2008). The vast majority of movement ecology research

has linked motion capacity and subsequent movement paths to external factors, namely environmental conditions (Holyoak et al. 2008). This leaves other components of the framework, including internal state and navigation capacity, as largely unstudied (Holyoak et al. 2008). Integrating across scientific disciplines can help to alleviate these gaps, particularly combining migration ecology with physiology and/or disease ecology (Bowlin et al. 2010, Altizer et al. 2011) to better understand links between the internal state and subsequent movement behaviours and migratory success. Even the role of variability in movements and migration routes in determining fitness or fate is poorly understood (Holyoak et al. 2008). Lastly, there is a distinct lack of research that attempts to test multiple components of the framework within a single study or system (Holyoak et al. 2008), making it difficult to generate a hierarchical understanding of the factors affecting movement and migration success across spatiotemporal scales.

1.6.2 Pacific salmon smolt migrations

To assist with management of Pacific salmon, knowledge is needed to understand 1) where and when mortality occurs, 2) what factor(s) either influence or ultimately causes this mortality, and 3) the variability and strength of these relationships. Recently telemetry has been important in identifying landscapes with poor survival during the smolt outmigration (Clark et al. 2016), but the mechanisms for these landscape-specific relationships are unknown.

Predation can substantially influence smolt survival (Brower and Calvert 1985, Lindström 1989, Rieman et al. 1991, Osterback et al. 2013), and yet little research has focused on specific predator-prey relationships. Predators are easier to identify in

freshwater landscapes, and thus riverine environments provide an opportunity to understand the 1) consumptive capacities of predators feeding on smolts, 2) the characteristics of smolts consumed by predators, and 3) the behavioural mechanisms used by smolts to reduce risk in areas of poor survival. Focusing on relationships between smolts and other taxa can also shed light on the ecosystem-level impacts on smolt migrations, which have largely been ignored relative to those induced by the adult spawning migrations (i.e. (Helfield and Naiman 2001, Naiman et al. 2002)).

In the marine environment particularly little is known about smolt migrations (Drenner et al. 2012). It is assumed that sockeye smolts exhibit linear migrations through the Strait of Georgia, but this paradigm was developed through the use of population-level surveys (purse seines) that inferred movement based on body size (Groot and Cooke 1987, Peterman et al. 1994). Thus, migration routes by sockeye through the Strait of Georgia at the individual level have not been defined. Defining migration routes are imperative for understanding the conditions experienced by migrant smolts in a landscape characterized by variable and poor survival (Clark et al. 2016), particularly when directed studies on predation in coastal waters are difficult. In short, applying the movement ecology framework to smolt migrations should allow for the production of knowledge that has important implications for salmon ecology and management.

1.7 Thesis aims

The broader aim of this thesis is to assess the importance of multiple components of the movement ecology framework for outmigrant smolts in freshwater and marine landscapes across multiple spatial scales. Assessing multiple components of the

framework simultaneously for a given taxa and system is rare (Holyoak et al. 2008) generally due to the logistical constraints. While any single chapter may focus on a single component of the framework, it is possible to build a more comprehensive view of smolt migration ecology through the use of complementary techniques among thesis chapters. Chilko sockeye is used as a model population throughout the thesis to both advance the fields of movement and migration ecology, as well as provide specific context for management purposes. Focus is placed on the early freshwater landscape, where survival is poor (Clark et al. 2016) and the system's manageable size allows for in-depth investigations, but movements in the early marine environment are also examined. While individual chapters focus on a single spatial scale, the thesis is organized to investigate smolt migration ecology at increasing spatial scales, from site-specific (~1 km) to landscape-wide (100s km).

Chapter 2 quantifies the short-term consumption limits of bull trout (*Salvelinus confluentus*) feeding on outmigrant smolts as smolts initiate migration and emigrate from Chilko Lake. This chapter utilizes stomach content collection and bioenergetics to assess how short-term consumption by bull trout varies across temperatures, bull trout mass, and location of feeding. The development of an altered bioenergetics model then determined the potential consequences of binge-feeding by bull trout on total consumption of smolts. Describing the magnitude of consumption by bull trout underscores the potential importance of predation in this riverscape characterized by poor survival (Clark et al. 2016), and sets the stage for later chapters aimed at examining the factors that place smolts at risk for predation.

Chapter 3 progresses to examine how the internal state (infection status and size) of smolts affects risk of predation by these binge-feeding bull trout in the outlet connecting Chilko Lake and Chilko River. The infection status of smolts predated by bull trout was assessed using novel genetic techniques (quantitative reverse-transcriptase real-time polymerase chain reaction; qRT-PCR) and compared to non-predated smolts collected at random from the broader outmigrant population. This chapter focuses on the presence and load of pathogens suspected or known to infect salmon worldwide (Miller et al. 2014). The role of infectious disease has been identified as an important and understudied component of animal migrations (Altizer et al. 2011). Further comparisons were made to determine if smaller smolts tend to be predated at higher rates. In sum, this chapter links smolt internal state to migratory success over a small spatial extent (~1-km reach of river).

Chapter 4 remains in the upper Chilko River to assess the importance of movement behaviours and internal state on smolt migration success over a broader spatial extent (>10 km reach of river). Smolt movements were tracked at a scale of ~1 km with acoustic telemetry and mark-recapture models were used to assess the influence of multiple components of the movement ecology framework on downstream survival. In particular, telemetry data were paired with high-resolution information on smolt outmigrant densities to determine if migration survival was density-dependent. The role of such “predator swamping” was compared to migrating timing at multiple scales and smolt size.

Chapter 5 brings the assessment of the movement ecology framework into the early marine environment: the Strait of Georgia. The use of telemetry data collected over multiple populations of sockeye and steelhead (*Oncorhynchus mykiss*) across ~10 years of research allowed for updating current paradigms on migration routes used by smolts in the Strait of Georgia. Given the broader spatial extent of the migratory corridor examined in the Strait of Georgia (~30-km wide), this environment allows for empirically testing the influence of migration route on survival over broader spatial scales (10s to 100s km), a concept for which few examples exist (Holyoak et al. 2008). Further components of the movement ecology framework were also examined, including migration timing (navigation capacity), and smolt size (internal state and motion capacity).

In sum, this thesis aims to provide a more comprehensive understanding of the factors influencing smolt outmigrations, while also assessing components of the movement ecology framework put forth by Nathan et al. (2008). Collectively, this thesis examines hypotheses regarding the influence of factors within each component (internal state, motion capacity, navigation capacity, and external factors). In addition, a more comprehensive understanding of the factors influencing smolt outmigrations, discussed in the final chapter, provides insight for conservation and management aims.

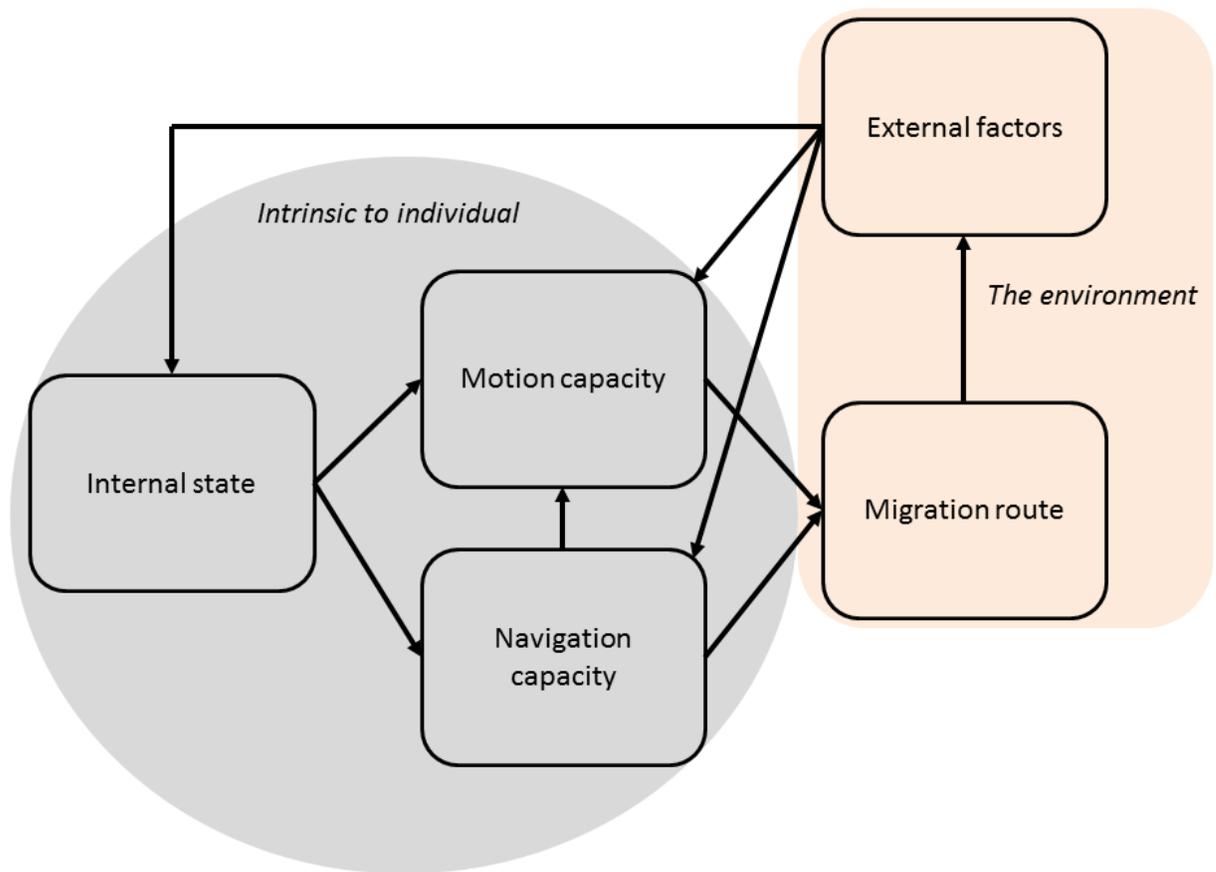


Figure 1.1 The movement ecology framework adapted for examining the causes and consequences of movements during animal migrations. Adapted from Nathan et al. (2008).

Chapter 2: A predator of outmigrant sockeye smolts exhibits binge-feeding

2.1 Introduction

Predation helps to structure ecosystems (Pace et al. 1999, Shurin et al. 2002), but consumption opportunities are patchy in space and time (Fauchald et al. 2000, Ritchie and Johnson 2009) due to the interactions of behaviour, phenology, and landscape conditions (Kauffman et al. 2007, Humphries et al. 2010). In response, predators should have mechanisms to optimize feeding opportunities when they arise. Piscivorous fishes, for example, maintain the digestive capacity to consume and digest two to three times the amount of prey they consume on an average basis (Armstrong and Schindler 2011). Consumption can also exceed this digestive capacity (Green et al. 2011, Armstrong et al. 2013), indicating that satiation may not limit feeding (Essington et al. 2000). Such consumption beyond what can be digested in a day (binge-feeding or hyperphagia), however, is rarely the focus of research (Armstrong et al. 2013). Thus the true short-term consumptive capacity of fish, the factors that limit such binge-feeding, and the potential for binge-feeding to alter predator-prey dynamics are not well-defined.

We expect that hyperphagia is expected to be facilitated by gut volume. The gut not only provides temporary storage of food prior to digestion, but also represents the physical constraint on the volume of food that can be consumed at any one time. This volume, and therefore the amount of food that can be held at any one time, does not change with temperature even though digestion is temperature-dependent (Thornton and

Lessem 1978). At low temperatures, a single meal can take several days to digest (Hop and Tonn 1998, Sweka et al. 2004), while in warm waters the volume of the stomach can be filled, processed, and refilled multiple times within a 24-hr period (Juanes and Conover 1994a). Therefore, stomach volume can provide surplus storage capacity for predators during short periods of high prey availability. Even though the hyperphagia phenomena might be short (duration needed to fill the gut), at low temperatures this increase in consumption could still represent a substantial boost to the predator's energy budget relative to temperature-dependent consumption.

Temperate freshwater systems at higher latitudes or elevations provide a model for investigating hyperphagia, as basin productivity and water temperatures undergo high seasonal variability relative to the tropics (Gross et al. 1988). Furthermore, these systems are often influenced by the life history of anadromous Pacific salmon: the events of spawning and the outmigration of juvenile salmon smolts can provide short but highly predictable and large energy pulses for consumers. Indeed, reports of hyperphagia have coincided with these salmon life history events, with most attention directed towards consumption of eggs deposited by returning adult salmon (Armstrong and Bond 2013, Armstrong et al. 2013, Lowery and Beauchamp 2015). However, massive pulses of outmigrating smolts also provide short-term, intense feeding opportunities (Furey et al. 2015). The outmigration of smolts from lake systems also occurs in late spring shortly after ice break-up when water temperatures are still cold, thus providing a favorable opportunity for testing if hyperphagia is limited by temperature and the potential impacts on predator-prey interactions.

Bull trout (*Salvelinus confluentus*) reside in temperate systems in North America and are considered either threatened or a species of concern across much of its range (Dunham et al. 2008). In addition, bull trout are important predators in many salmon-bearing systems (Lowery & Beauchamp 2015; Furey et al. 2015). To investigate the limits and impacts of hyperphagia, I characterized consumption of bull trout fed *ad libitum* in a controlled laboratory setting and also in the field at a temperate lake-river system where bull trout were reported to binge-feed during a prey pulse of outmigrating juvenile sockeye salmon (*Oncorhynchus nerka*) smolts (Furey et al. 2015). Specific objectives included 1) quantifying the limits of binge-feeding (magnitude and duration) across temperatures and body mass, 2) determining if the limits of binge-feeding are reached in the field, and 3) estimating the potential influence of binge-feeding on bull trout consumption and growth.

2.2 Methods

2.2.1 Laboratory trials

Details of the laboratory trials can be found in Mesa et al. (2013) and are only briefly outlined here. Bull trout (13-592 g) captured from the Metolius River and Lake Billy Chinook in Oregon, U.S.A. were transported to the U. S. Geological Survey's Columbia River Research Laboratory via truck within insulated tanks with aerated water. Bull trout were held in tanks at temperatures of 3, 7, 10, 13, 16, and 20°C (n = 28 at 10°C, n = 16 at 16°C, and n = 6 at each of the other temperatures). Prior to feeding trials, bull trout were fasted for 3 days (or 4 days for fish held at 3°C). During the feeding trials, bull trout were then fed rainbow trout (*Oncorhynchus mykiss*) fry and subyearling Coho

salmon (*Oncorhynchus kisutch*) *ad libitum* (individual prey weighing 0.2-1.4 g) for four consecutive days and total daily consumption was recorded every 24 hours. These data were used to develop functions for mass- and temperature-dependent constraints on maximum daily consumption for sustainable, routine feeding by bull trout when food was not limiting (Mesa et al. 2013). The first day's consumption after fasting was hyperphagic, whereas daily consumption for the subsequent three days was lower and consistent. Because bioenergetics models use the average sustainable maximum consumption rates as the primary variable for fitting consumption to growth and other calculations, the hyperphagic consumption from the first day was omitted from the model development (Mesa et al. 2013). In the current study, I examined the underlying basis for hyperphagia during the first day and implications for the energy budget of the piscivore and predation mortality of its prey.

2.2.2 Field samples

Field research in 2013 and 2014 occurred at the outlet of Chilko Lake into the Chilko River, British Columbia, Canada. Chilko Lake supports one of the largest Fraser River populations of sockeye salmon, with 15-40 million smolts outmigrating each spring between April and May, and thus represent a large pulse of prey that is only available in certain locations over a short period for resident bull trout. To monitor the smolt outmigration, the federal fisheries agency responsible for salmon management (Fisheries and Oceans Canada – DFO) deploys a counting fence across the Chilko River ~1 km downstream of the lake outlet. Bull trout often congregate at and in the general vicinity of the fence to prey on smolts funneled through the spatially-restricted area (Furey,

unpublished data). Water temperatures generally range 2-12 °C during the period of smolt outmigration.

Bull trout (total length [TL] range: 51 – 80 cm; mean TL = 61.9 cm; SD = 6.3 cm; n = 49) were captured via hook-and-line or dipnet at either the counting fence or at the lake outlet. Bull trout mass was measured in 2014 and estimated in 2013 using the following weight-length relationship (Hyatt and Hubert 2000):

$$\log_{10} \text{mass} = -5.327 + 3.115 \times \log_{10} TL$$

This weight-length relationship was used to estimate mass of 2013 fish (rather than from the 2014 fish), as the size range observed in 2013 (51 – 80 cm TL) was greater than in 2014 (51 – 72 cm TL). Exploratory comparisons of weight-length relationships between the two years indicate that the above weight-length relationship was reasonable. Mass of field-caught bull trout ranged between 1.3 and 5.2 kg. Stomach contents were collected from bull trout via gastric lavage, filtered through a 500 um sieve, and weighed to the nearest 0.1 g. Consumption, lengths, and estimated masses of bull trout from 2013 are published in Furey et al. (2015).

2.2.3 Analyses

For each individual, the maximum temperature- and mass-dependent consumption that could be sustained daily (C_{\max}) was calculated using the Wisconsin bioenergetics model (Hanson et al. 1997) specifically parameterized for bull trout (Mesa et al. 2013). Temperatures experienced by lab-held bull trout (3 – 20°C) were continuously maintained. For field-caught bull trout, the temperatures used to calculate C_{\max} were measured daily at the counting fence (2013), or by averaging temperature measurements

of the preceding 24 hours from a datalogger placed in the Chilko River approximately 50 meters downstream from the fence (2014). The degree of binge-feeding exhibited by each bull trout was defined as the ratio between the observed specific consumption (C) and C_{\max} , such that values > 1 indicated binge-feeding or hyperphagia. For lab-held bull trout, C was defined as the 24-hour *ad libitum* consumption during the first 24 h after fasting. For field-caught bull trout C was defined as the observed wet mass of the stomach contents.

I assessed the relationship between the degree of binge-feeding (C / C_{\max}) and temperature. Bull trout mass and the three foraging settings: 1) laboratory, 2) in the field at the government counting fence, and 3) in the field at other locales within Chilko Lake and Chilko River (where prey availability was still high, but less aggregated) were included as further explanatory variables to determine how binge-feeding differed across sizes of bull trout, between the lab and field situations, and among field locales. After exploratory analyses, both degree of binge-feeding and temperature were Ln-transformed. Regression was conducted using a generalised least squares (GLS) approach following the protocols described in Zuur et al. (2009). For information on the modelling approach see Appendix A.1. Briefly, a backwards stepwise selection procedure determined the main effects (temperature, mass, and foraging setting) to be included in the final model via likelihood ratio tests. GLS models were run using the ‘nlme’ package (Pinheiro et al. 2015) in R 3.1.1 (R Core Team 2014).

As our metric for the degree of binge-feeding is a ratio, and thus does not directly reflect meal size, I also assessed how specific consumption ($C /$ bull trout body mass) of

lab-held bull trout related to temperature and bull trout body mass via generalized additive models (GAMs). The significance of explanatory variables (temperature and bull trout body mass) were assessed with F-tests, and variables were removed if insignificant ($P > 0.05$). All GAMs were run with the `mgcv` package (Wood 2006, 2011) in R. For more details, see Appendix A.2. Because I wanted to investigate the limits of binge-feeding, empty stomachs ($n = 2$ for lab-held bull trout; $n = 3$ for field-captured bull trout) were excluded from both degree of binge-feeding and specific consumption models.

2.2.4 Simulations

To estimate the potential consequences of binge-feeding for bull trout consumption and growth, two parallel sets of bioenergetic models were constructed to simulate daily feeding during both the 2013 and 2014 smolt outmigrations from Chilko Lake. The first set of simulations were based on traditional assumptions of bioenergetic models, such that daily consumption is constrained by both temperature- and mass-dependent processes. The second set of simulations used an altered model that allowed for binge-feeding (via storage of food up to the maximum volumetric capacity in the gut on the first day of feeding, followed by model predictions of routine, sustainable daily maximum consumption on subsequent days when prey were available). Bull trout consumption and growth from these two parallel sets of models were then compared to understand the potential consequences of binge-feeding in a realistic ecological setting.

Simulations based on temperature-dependent consumption allowed bull trout to feed on days in which high densities of migrant smolts were available, at the temperature- and mass- dependent C_{\max} as defined in conventional bioenergetics models. In the altered

“binge-feeding” model, bull trout again only fed on days in which high densities of smolts were available, but the total amount consumed was dependent upon stomach volume, estimated as the temperature-independent C_{\max} ($0.1317 \cdot \text{mass}^{-0.1396}$; Mesa et al. 2013). Thus if a bull trout’s stomach was empty and smolts were available, consumption equaled the stomach volume during the first day of this condition. Daily growth and digestion (and therefore emptying of stomach volume), were still limited to the temperature- and mass-dependent C_{\max} , as in the traditional model. On subsequent days, bull trout could only feed to “top off” the remaining stomach volume (i.e., attain sustainable C_{\max} according to the ambient temperature and body mass of the predator). The binge-feeding cycle could be repeated if lapses occurred between pulses of high prey availability.

In both consumption modes (traditional and binge-feeding capable), daily consumption only occurred when a minimum number of smolts (prey) were available. Daily prey availabilities for both years were summarized from high-resolution data on the number of smolts outmigrating from the lake into the river via photography at the counting fence (B. Leaf and K. Benner, DFO, unpublished data). The number of smolts passing through the fence in any given 24-hr period varied between 0 and ~6.1 million during the 2013 smolt outmigration and 0 and ~1.8 million in 2014 (Figure 2.1c-d). As I did not have information on smolt densities needed for bull trout to feed, the minimum smolt abundance needed for feeding to occur in simulations (prey availability threshold) was varied across model runs and ranged between 0 (if any smolts passed in a 24-hour period, feeding was allowed) and ~63,000 (2 smolts per m^2 of the river’s width each

minute at night [8.8 hours each 24-hr period]). A total of 21 equidistant values for the prey availability threshold were used within this range for simulations, with one value used per simulation (more below). Thus within a simulation feeding was allowed for that day if the daily number of smolts passing through the fence equaled or exceeded the prey availability threshold.

All simulations used a daily time step with conditions matching the chronologies of the 2013 and 2014 smolt outmigration in both prey availability and water temperature (Figure 2.1 a-d). Mean temperatures (Figure 2.1a-b) were recorded daily at the counting fence (2013) or calculated using temperature dataloggers (n=34), placed in the river and lake outlet for a separate telemetry study (2014). Each simulation was constructed based on the unique combination of 1) consumption occurring at either traditional rates or allowed for binge-feeding, 2) either the 2013 or 2014 smolt outmigration (smolt densities and water temperatures), 3) prey availability threshold value (one of 21), and 4) bull trout initial mass (1, 2, 3, 4 or 5 kg). In total, 420 simulations were conducted.

For all simulations, bull trout cumulative consumption and cumulative growth were recorded daily over a 35-day (2013) or 33-day (2014) period that encompassed one day prior to smolt outmigration through two days after the last smolts passed the counting fence (when the outmigration can be assumed to have concluded). Further details of the simulations can be found in Appendix A.3. To quantify the potential benefits from binge-feeding, the relative increase in consumption and in relative growth between each set of parallel models (i.e., the only difference between two simulations was the ability to binge-feed) were calculated and summarized for each year.

As I was unsure as to how the benefits of binge-feeding may be affected by consumer size or the prey availability threshold, sensitivity analyses were conducted. The benefit of binge-feeding from each simulation and the model input value for initial bull trout mass and prey availability threshold were analyzed with Pearson correlation coefficients to determine if our responses were dependent upon the value of these two values. All simulations and statistics were constructed and run in R 3.1.1 (R Core Team 2014).

2.3 Results

2.3.1 Degree of binge-feeding

In both the laboratory and the field, bull trout commonly exhibited binge-feeding, with >80% of samples exceeding C_{max} in 1-day feeding trials or gut-fullness observations (even when including empty stomachs). The degree of binge-feeding (C / C_{max}) was negatively related to temperature (both variables ln-transformed; parameter estimate = -1.6; SE = 0.1; t-value = -14.5; $P < 0.001$; Table 2.1). Bull trout held at 3°C consumed 12 to 87-fold more than the sustainable daily consumption rate, but this ratio approached 1 at 20°C (Figure 2.2). There was greatest support (via both AIC and LRT; see Supplemental Material) for equal slopes for the degree of binge-feeding among foraging situations, indicating the overall relationship between temperature and degree of binge-feeding was maintained for field-captured bull trout. Bull trout captured at the fence, where prey were funneled into higher densities, fed at rates quite similar to lab-held bull trout, with some overlap of their 95% confidence intervals (Figure 2.2). However, two of 13 fence-caught bull trout did not exhibit hyperphagia (C / C_{max}) and overall the degree of binge-feeding

was significantly reduced relative to the lab (regression coefficient = -0.8; t-value = -2.3, $p < 0.001$). Bull trout captured elsewhere in the lake or river experienced lower and more variable prey availability and exhibited much lower stomach fullness with 33% (11 of 33) showing C / C_{\max} ratios < 1.0 (regression coefficient = -1.8; t-value = -8.2, $p < 0.001$). Many of these bull trout still experienced hyperphagia, with maximum consumption approaching 20-times C_{\max} . Body mass of the predator was not retained in the model, and thus not suggested to influence the degree of binge-feeding.

2.3.2 Specific consumption

In the laboratory trials, specific daily consumption (consumption/ bull trout body mass) during the first day after fasting was influenced by temperature ($F = 9.9$; $P < 0.001$; $\text{edf} = 1.9$), and demonstrated a parabolic relationship that peaked at $\sim 10^{\circ}\text{C}$ (Figure 2.3) and was lowest at the highest temperatures (Figure 2.3). Overall, however, the specific consumption of similarly-sized bull trout (50-150 g) varied little with temperature, with the mean specific consumption at 3, 7, 10, 13, 16 and 20°C being 0.16 (SD = 0.04), 0.24 (SD = 0.04), 0.22 (SD = 0.06), 0.24 (SD = 0.08), 0.22 (SD = 0.08), and 0.11 (SD = 0.05), respectively. Thus mean specific consumption of bull trout between $7\text{-}16^{\circ}\text{C}$ were generally equivalent. Specific consumption was also inversely related to mass ($F = 12.9$; $P < 0.001$; effective degrees of freedom [edf] = 1.4) with the specific daily consumption of a 750 g bull trout at roughly half that demonstrated by a 50 g bull trout (Figure 2.2). Overall this GAM containing both temperature and mass explained 41.2% of the deviance in specific consumption. Bull trout in the field were larger and thus specific consumption was lower (0-12%) than laboratory-held fish. Although sample sizes were

limited, I also portray specific consumption across temperatures and bull trout mass in the field (Figure 2.3). Due to the high variability in consumption across field-collected samples (as in Figure 2.2), no further analyses were conducted.

2.3.3 Simulations

In total, I ran 420 simulations of bull trout consumption during the 2013 and 2014 Chilko sockeye salmon smolt outmigrations, half using traditional temperature-dependent consumption and half allowing for binge-feeding (Figure 2.1e-h). Simulated cumulative consumption per predator under traditional assumptions for the 35-d 2013 smolt outmigration ranged between 144 g and 744 g. When simulating binge-feeding under the same conditions, cumulative consumption ranged between 187 g and 908 g, representing an increase of 17-32%. Similar results were obtained when simulating 2014 conditions; cumulative consumption under traditional assumptions over the 33-d period was 226 – 1496 g and consumption with binge-feeding was 300-1719 g, representing an increase of 16-34% (Figure 2.1e-f). Across both years of simulations, for any given initial size of bull trout, the mean increase in cumulative consumption over the smolt outmigration period from binge-feeding compared to traditional bioenergetic scenarios ranged between 58 g (for 1-kg predator) to 227 g (5-kg predator).

Simulated bull trout growth under temperature-constrained consumption was 1.1-3.4% of initial body mass over the 35-d smolt outmigration in 2013, and growth with binge-feeding was 2.3-5.3%, representing an increase of 50-110%. In 2014 simulations, traditional-feeding bull trout grew 2.9-10.5% of initial body mass over the 33-d smolt outmigration, while binge-feeding resulted in growth of 4.9-12.5% (an increase of 19-

70%). Across both years of simulations, for any given initial size of bull trout the mean increase in cumulative growth from binge-feeding versus traditional bioenergetic scenarios ranged between 25 g (for a 1-kg bull trout) to 79 g (5-kg bull trout).

Within simulations, the increase (benefit) due to binge-feeding was sensitive to the threshold for prey availability (Figure 2.4); the more smolts needed for binge-feeding to occur was positively correlated with the benefit of binge-feeding in both consumption (Pearson's $p = 0.73$, $P < 0.0001$) and growth (Pearson's $p = 0.57$, $P < 0.0001$). Simulated benefits of binge-feeding were insensitive to bull trout masses 1 – 5 kg, as no correlation was found between mass and increase of either consumption (Pearson's $p = -0.03$, $P = 0.67$) or growth (Pearson's $p = 0.02$, $P = 0.76$).

2.4 Discussion

I demonstrate that binge-feeding by bull trout not only occurs regularly in both the laboratory and in the field but also at high rates. First-day specific consumption was similar across temperatures (< 10% difference between 7 °C and 10-16 °C), and thus stomach volume may limit short-term consumption rather than temperature-induced satiation. Similar meal sizes across temperatures resulted in consumption at low temperatures ($\leq 5^\circ \text{C}$) being 10-87 times the daily sustainable maximum (C_{max}) across foraging situations, and only 1-10 times C_{max} at temperatures $>5^\circ \text{C}$. Short-term feeding was most limited at high temperatures, with specific consumption at 20 °C being 20-40% less than maximum values. This decrease at high temperature may be due to bull trout being a cold-water char (Dunham et al. 2008) and 20°C exceeds the thermal optima for consumption and growth (Mesa et al. 2013). Binge-feeding has been observed in other

field studies (Essington et al. 2000; Green et al. 2011; Armstrong et al. 2013), but to my knowledge this is the first to 1) specifically quantify the limits of binge-feeding, and 2) closely integrate field and lab observations.

In addition, the prevalence and degree of binge-feeding observed in this study generally exceeds others. Essington et al. (2000) observed consumption that exceeded C_{\max} in 13% of temperate largemouth bass (*Micropterus salmoides*) examined, and all consumption rates were within a 10-fold value of C_{\max} . Similarly, Green et al. (2011) found tropical lionfish to consume ~3-times expected consumption as determined by studies on captive lionfish. Only Armstrong et al. (2013) observed hyperphagia at a similar extreme as this study, finding 2-g to 20-g juvenile coho salmon (*Oncorhynchus kisutch*) to consume ~13% of their body mass in 20 minutes while feeding on salmon eggs (a rate that was 200-to-400-fold their digestive rate). These juvenile coho, however, were at minimum 50-times smaller than the adult bull trout observed binge-feeding at Chilko Lake that were binge-feeding at ~3 to 20 times C_{\max} . Binge-feeding is rarely the primary focus of research (Armstrong et al. 2013), however, and I encourage authors to report evidence of binge-feeding whenever observed so that we can begin to understand its prevalence across systems.

For predators, hyperphagia allows for securing energy beyond C_{\max} without sacrificing the ability to further feed when prey are available. The consumption during the first day of feeding exceeded what could be sustainably consumed over the 3-day fasting period, and these bull trout continued to feed, at lower rates, in successive days following the initial day of binge-feeding (Mesa et al. 2013). Furthermore, wild Chilko

bull trout consumed up to 20-times their sustainable maximum and yet separate fish tracked with acoustic telemetry consistently demonstrated foraging behaviours each night near the fence during the smolt outmigration (Furey, unpublished data). Thus, the lab and field results support the conceptual model of binge-feeding: filling the gut beyond C_{\max} when possible and then “topping off” as digestion allows. These results also suggest bull trout can consume greater prey amounts than suggested by using traditional bioenergetics models (i.e., use of C_{\max}) alone.

Simulating consumption using realistic smolt outmigration conditions demonstrate that bull trout benefit by binge-feeding, with cumulative growth increases of 19-110% over the smolt outmigration period compared to the traditional bioenergetics model. At the beginning of a pulse, binge-feeding allows for storage of excess energy that will continue to be digested during lulls in the prey pulse (or once the pulse ends), resulting in increased growth. Similarly, if lulls in prey availability are long enough, binge-feeding will result in additional benefits upon the pulse resuming. In systems characterized by high-magnitude energy pulses, these short-term events have the potential to contribute large portions of the annual energy budget of consumers (Armstrong and Bond 2013), and thus large stomachs and binge-feeding appears to be adaptive mechanisms to exploit such pulses (Armstrong et al. 2013). Thus far, the best examples of binge-feeding occur in temperate salmon-bearing systems, potentially due to the predictable and high-magnitude energy pulse events associated with salmon life history.

Under our assumptions, the benefits of binge-feeding will be dependent upon water temperature, the duration of prey availability during pulses, and the timing (gaps) between peaks of prey availability within pulses. As I hypothesize that binge-feeding occurs due to storage of food within the gut, increases in temperature such that routine sustainable consumption approximates gut volume would result in decreased importance of binge-feeding. Similarly, the relative importance of binge-feeding decreases as the duration of consistently high prey availability increases. Binge-feeding provides benefits when the gut is not full, and thus if prey availability remains high, hyperphagic-based consumption is limited to the pulse's initiation. As the duration of a prey pulse increases, the average consumption and growth of the predator will converge on the conventional bioenergetics-based estimate of C_{max} . Thus it is important to recognize that not only pulse duration but also the timing between peaks and the number of peaks within the pulse will influence consumer ability to binge-feed. The Chilko sockeye smolts studied generally have two or three peaks of outmigrants each spring, resulting in limited opportunities for consumers to experience hyperphagia. Outmigrations or pulses that are further fragmented into multiple distinct peaks could result in increased importance of binge-feeding and increased predation pressure on migrants. Theoretical-based research could quantify the potential impacts of varying pulse compositions on predation risk to better understand the selection pressures on migrants. In our model system, the benefits of binge-feeding already appear large, but could be extended if consumers have mechanisms or adaptations to further facilitate binge-feeding during times of high prey availability.

A variety of spatial, behavioural, and physiological factors could facilitate or mediate binge-feeding to further alter predator-prey relationships. Prominent landscape structures can alter both predator distributions and feeding success (reviewed in Bouchet et al. 2014), and our study demonstrated that the presence of an extreme spatial constriction (an anthropogenic counting fence) allowed bull trout to feed consistently at levels similar to observed in the lab, where fish were fed *ad libitum*. Bull trout caught elsewhere, however, still exhibited binge-feeding regularly, indicating binge-feeding can be common even in unaltered systems. Beyond spatial constrictions, spatial variability in water temperature can be exploited to increase digestion, and subsequently growth, between feeding bouts (Wurtsbaugh and Neverman 1988, Armstrong et al. 2013). For example, movements by juvenile coho to warmer waters (9-11°C) between bouts of feeding on salmon eggs (where water was 6-7°C) resulted in roughly double the assimilation rates of fish that did not exploit the thermal heterogeneity (Armstrong et al. 2013). Physiological adaptations may also further facilitate binge-feeding. For example, Dolly Varden (*Salvelinus malma*) in Alaska undergo seasonal changes in digestive machinery, such that energy needed for digestive physiology is reduced during times of low productivity and fish can gorge during the annual energy pulse provided by sockeye salmon spawning (Armstrong & Bond 2013). In addition, standard metabolic rate (SMR) can increase directly with food availability (Auer et al. 2015), although this has not been demonstrated in tandem with binge-feeding nor in the natural environment. Now that we understand the potential for binge-feeding to affect consumption, the prevalence of environmental and physiological influences on binge-feeding needs to be further

examined to develop a hierarchical understanding of the limits of feeding and consumption's flexibility.

Binge-feeding also has important implications for prey. A predator's ability to binge-feed and continue to feed can result in increased prey mortality, especially during short episodic events. Our simulations revealed that bull trout predation on smolts increased 16-32% via binge-feeding, without any further adaptations to facilitate hyperphagia. Depending on bull trout size, the mean increase in per capita consumption represented 58-227 g, or roughly 12-47 additional smolts during outmigration (average age-one smolt mass = 4.86 g; Irvine & Akenhead 2013). Bull trout in this study contained as many as 100 fish within the gut, with up to 69 prey items identifiable as smolts (Furey et al. 2015). Thus the selection on prey due to predation is expected to be even higher than formerly appreciated, and I expect prey to employ as many risk-reducing mechanisms as possible in systems with binge-feeding predators. In fact, Chilko sockeye smolts exhibit both nocturnal migration and swamping of predators (including bull trout) while traversing the early Chilko River to reduce predation risk (Chapter 4). Predation is already an important component of migration mortality for many fishes, including juvenile anadromous salmonids (i.e. Beamesderfer, Ward & Nigro 1996; Schreck et al. 2006; Evans et al. 2012), and acoustic telemetry studies have found high mortality rates of smolts in freshwater environments (Melnychuk et al. 2014; Clark et al. 2016; Chapter 4). I have quantified how binge-feeding can contribute to this predation mortality.

Attempts to quantify predator impacts on prey are often driven by conservation and/or management goals, but predation rates alone may not be sufficient to prescribe

action. In particular, poor health of migrants can result in reduced behavioural and physiological performance (Miller et al. 2014), which presumably could lead to mortality regardless of the landscape and/or predator encountered (i.e. ‘migratory culling;’ Altizer et al. 2011). Steelhead (*Oncorhynchus mykiss*) smolts with external signs of disease were less likely to survive through the Snake and Columbia Rivers (Hostetter et al. 2011). Furthermore, sockeye smolts positive for infectious haematopoietic necrosis virus within our study system were unlikely to survive their outmigration through the upper Chilko River (Jeffries et al. 2014). Neither of these studies, however, was able to directly link compromised condition to predation by specific consumers, as directly observing predation in the field is difficult (Miller et al. 2014). If migrant fate is indeed condition-dependent, management actions to reduce predation at one locale or by a single predator may not improve survival at broader spatial scales. Research could aim to fully integrate prey health and predator foraging to better understand population-level consequences of predation, particularly in difficult management scenarios such as this where both predator and prey have economic, cultural, and ecological importance (Marshall et al. 2015).

Estimating the degree of binge-feeding and the effects of binge-feeding on consumer growth and consumption relies on both accurate measures of consumption as well as an accurately parameterized bioenergetics model. Field estimates of daily consumption were limited to stomach contents, leaving the possibility that some contents were consumed over multiple days. Consumed sockeye smolts, however, generally demonstrated similar levels of digestion, indicating they had been consumed at similar

times. In fact, some stomachs only contained freshly ingested smolts that showed no evidence of digestion (see Furey et al. 2015). To quantify the benefits of binge-feeding, I altered a bioenergetics model for bull trout (Mesa et al. 2013). The conceptual framework for binge-feeding (filling of the gut regardless of temperature, and subsequent “topping off” as digestion occurs) appears to be supported both by laboratory observations and telemetry data of Chilko bull trout movements, but modelling the benefits of binge-feeding is highly sensitive to parameterizing prey availability. Although visual-based foraging models exist to estimate prey fish capture in pelagic systems (Beauchamp et al. 1999, Hansen et al. 2013a, Hansen and Beauchamp 2014), further research should test the efficacy of such models during times of high prey availability (i.e., prey pulses). Although untested, I also expect the benefits of binge-feeding to be dependent upon gut volume, which were estimated as the temperature-independent C_{\max} (~4-5% of bull trout body mass). This value may be an underestimate, however, as in general stomach contents of Chilko bull trout represented a greater proportion of body mass (median of >6% for fence-caught bull trout, and a maximum of >12%). Therefore I expect the benefits to be greater than estimated here, even without accounting for aforementioned potential mechanisms to facilitate binge-feeding.

Binge-feeding can cause traditional applications of bioenergetics models to underestimate feeding or acute short-term predation impacts, and the magnitude of underestimation will be exacerbated with colder temperatures, shorter-duration feeding events, and potentially by a higher number of discrete peaks in prey availability instead of fewer, more continuous peaks within the pulse. However, as the period of “surplus”

food availability increases, the proportional consumption and growth will converge with the estimates from traditional bioenergetics models. Thus, traditional bioenergetics models (i.e, the Wisconsin model; Hanson et al. 1997) are effective in situations for which they were designed: predicting average, routine, and sustainable consumption over longer time scales (seasons to multi-year). I suggest that researchers exercise caution when modelling short-term, acute predation events that occur over the scale of days or weeks during which binge-feeding is possible as the prevalence of binge-feeding, both within and outside the context of prey pulses, is not known.

To conclude, I provide a conceptual model for how binge-feeding may occur that others can begin to test and utilize for such modelling applications. The extreme binge-feeding observed underscores the importance of prey or energy pulses: highly episodic events that can be exploited and relied on by consumers and often due to migratory life histories. The role of acute predation events at the ecosystem-level for both consumers and prey needs further study, particularly given the underappreciated importance of animal migrations in ecosystem functioning (Bauer & Hoyer 2014).

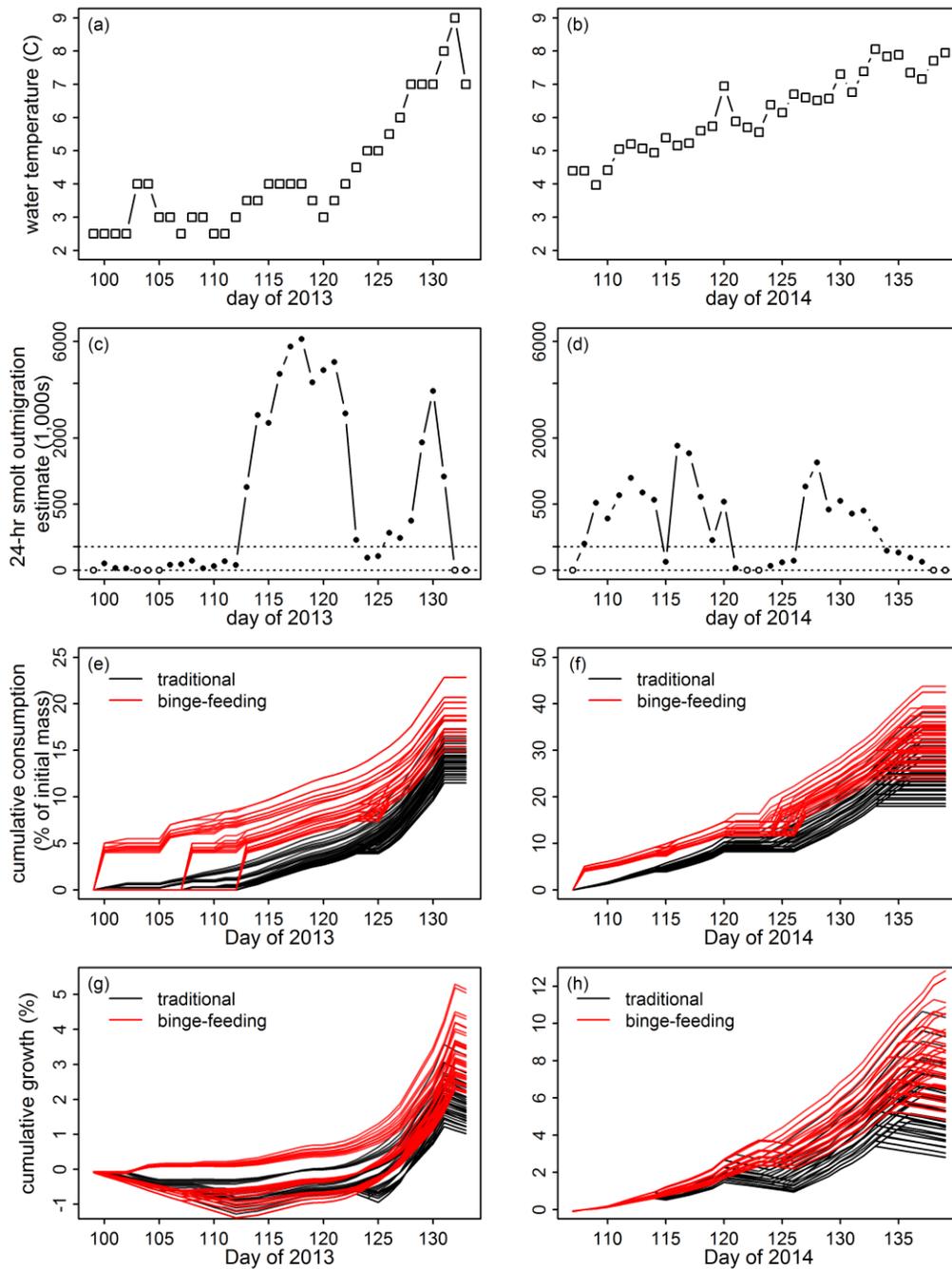


Figure 2.1 Temperatures (a-b), smolt outmigration estimates (c-d), and simulated cumulative consumption (e-f) and cumulative growth (g-h) of bull trout for 2013 (left panels) and 2014 (right panels) smolt outmigration periods. The dashed lines in panels c and d represent the minimum (0) and maximum (63,000) values used as the prey availability threshold parameter in models. In simulations, feeding occurred on any day in

which the smolt outmigration estimate exceeded the prey availability threshold. Note the square-root scaling of unit distance for the y axis for panels c and d. For simulations (e-h) individual lines represent a single simulation scenario, which varied in initial bull trout mass, prey availability threshold, and whether feeding was solely based on temperature-dependent consumption (black) or rather binge-feeding was allowed (red). Note that the y-axis scales differ between panels e and f and g and h.

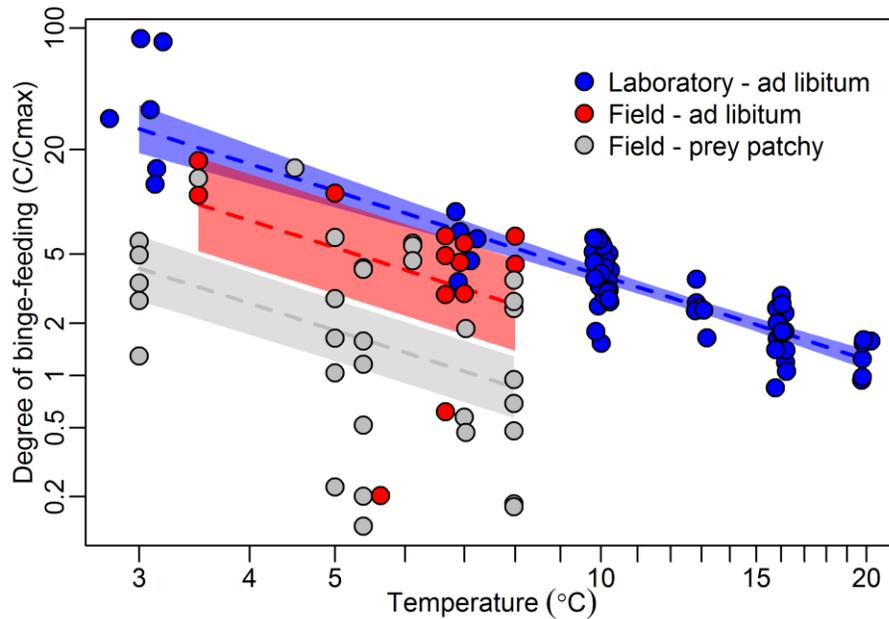


Figure 2.2 Degree of binge-feeding exhibited by bull trout across water temperatures. Dashed lines represent the best fit regression lines from generalised least squares (GLS) regression, and shaded areas indicate 95% confidence intervals of the regression line. Laboratory points (blue) are jittered up to 0.25 units along the horizontal axis to increase visibility. Please note the log-scaling of unit distance for both axes.

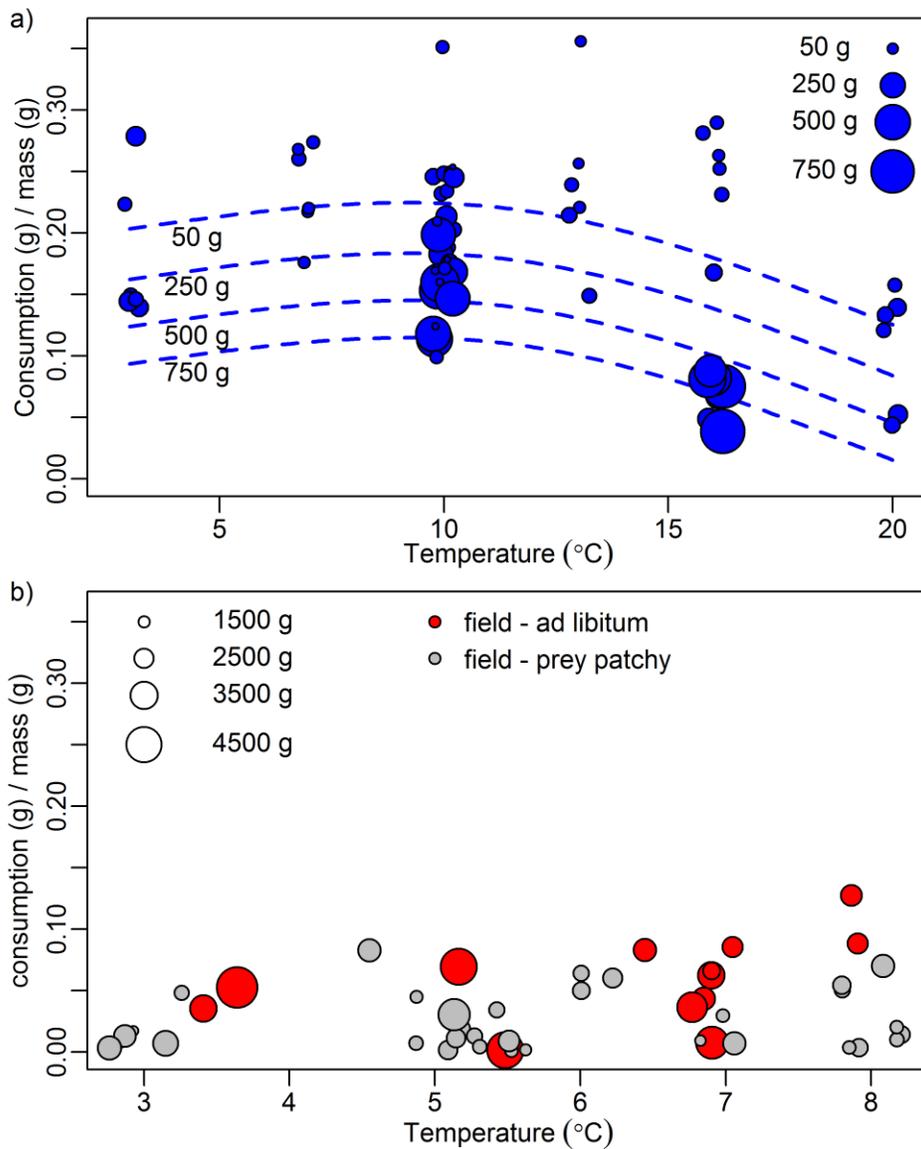


Figure 2.3 a) Specific daily consumption of lab-held bull trout over the first 24 hours of feeding across water temperatures when hyperphagia occurred. Dashed lines represent fitted values from a generalized additive model (GAM) at bull trout body masses of 50g, 250 g, 500 g, and 750 g. b) Specific consumption of field-caught bull trout, either at the fishery counting fence where feeding was considered near ad libitum (red) or elsewhere in the lake or river (grey). Points in both panels are jittered up to 0.25 units along the horizontal axis to increase visibility. In both panels, point size is relative to bull trout mass (see legends). Note that y axis scaling for both panels is the same to demonstrate that specific consumption was lower in the field than in the lab.

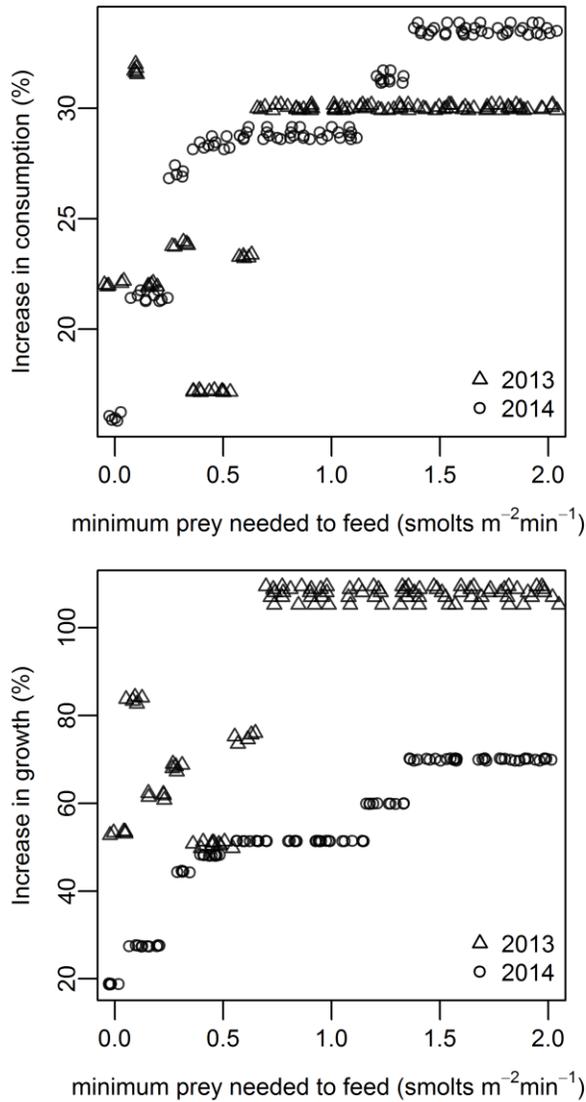


Figure 2.4 The sensitivity of benefits of binge-feeding due to prey availability threshold (minimum prey needed for feeding to occur) on simulated bull trout consumption (top) and growth (bottom). Circles represent a single simulation scenario, which varied in initial bull trout mass and prey availability threshold.

Table 2.1 Parameter coefficients, standard error (SE) and significance values for the generalised least squares (GLS) regression between the degree of binge-feeding ($\ln(C / C_{\max})$) and water temperature across settings. Bull trout mass was not retained in the model.

Parameter	Estimate	SE	t-value	P-value
Intercept (Foraging setting laboratory)	4.3	0.3	17.8	< 0.001
$\ln(\text{temperature})$	-1.6	0.1	-14.5	< 0.001
Foraging setting (fence)	-0.8	0.3	-2.3	0.022
Foraging setting (lake)	-1.8	0.2	-8.2	< 0.001

Chapter 3: Infected and small sockeye salmon smolts experience increased predation risk by piscivorous bull trout

3.1 Introduction

Animal migrations, or the directed movements of large portions of populations, subject migrants to a variety of stressors. These stressors can include increased bioenergetic demands and exposure to both harsh environmental conditions and novel predators. In sum, these stressors can lead to high-risk migrations, with mortality being high relative to non-migratory periods (Sillett and Holmes 2002, Strandberg et al. 2010, Klaassen et al. 2014). The ultimate cause of mortality is difficult to confirm in the field, but predation can contribute substantially (Brower and Calvert 1985, Lindström 1989, Rieman et al. 1991, Osterback et al. 2013).

Numerous factors are expected to influence predation risk of migrants. High migrant densities as a result of migratory synchronization can effectively swamp predators, reducing per-capita risk (Ims 1990, Chapter 4). The timing of migration can reduce predation risk either by reducing exposure to predators (Lank et al. 2003, Ydenberg et al. 2007) or reducing foraging efficiency of predators (i.e. nocturnal migration; (Pechmann and Semlitsch 1986, Ibbotson et al. 2011)). The physical state of migrants can also influence predation risk and migratory success. In particular, predation can be size-specific based on predator behaviour and morphology (Tucker et al. 2016). Physiological or nutritional condition for migration is also often correlated with migratory success (Cooke et al. 2006, Guy Morrison et al. 2007), if not directly to

predation risk. More recently, focus has been placed on migrant health and the role of pathogens in the migratory process (Altizer et al. 2011).

Migrants can be susceptible to infection via exposure to novel pathogens as they traverse landscapes and reduced immune function due to the incurred migration costs (Owen and Moore 2006, Altizer et al. 2011). Pathogens can reduce migratory performance in terms of movement speed and endurance (Barber et al. 2000, Bradley and Altizer 2005) and therefore it is expected that pathogens can alter predation risk. Directly linking migrant health to predation risk is difficult due to the general inability to confirm the fate of infected individuals (Miller et al. 2014), although examples have been provided for both non-migrant *Daphnia* (Johnson et al. 2006) and birds (Hudson et al. 1992). Direct evidence of pathogens influencing predation risk for migrants remains lacking (but see Schreck et al. 2006 and Miller et al. 2014).

Among migratory organisms, Pacific salmon are among the most studied due to their ecological, economic, and cultural value. One of the migrations undertaken during the Pacific salmon life cycle is by juveniles, when smolts leave natal freshwater habitats and migrate downstream to the open ocean. Mortality can be high for smolts from British Columbian watersheds through rivers and the Strait of Georgia to the Pacific Ocean (Welch et al. 2009, Chittenden et al. 2010, Clark et al. 2016). In addition, intense predation on outmigrant smolts has been observed in a number of systems (Beamesderfer et al. 1996, Evans et al. 2012, Osterback et al. 2013). In experimental settings, infection can increase predation risk for juveniles (Mesa et al. 1998), but the ramifications for wild populations are unknown. Recent research has linked smolt migration survival to the

presence and/or prevalence of pathogens (Jeffries et al. 2014), external signs of disease (Hostetter et al. 2011, Evans et al. 2014), and size (Evans et al. 2014, Tucker et al. 2016), suggesting that the physical state of smolts is indeed important to migratory success.

Among British Columbian sockeye salmon (*Oncorhynchus nerka*) populations, the Chilko population is one of the largest; 10-40 million smolts emigrate from Chilko Lake annually. The outmigration of these smolts has been tracked with acoustic telemetry, revealing high mortality (10-37% among years) during the first ~14 km of the migration in the upper Chilko River (Clark et al. 2016, Chapter 4). Furthermore, combining telemetry with non-lethal gill biopsies revealed that Chilko sockeye smolts with infectious haematopoietic necrosis virus (IHNV) were not likely to survive this same initial portion of the migration (Jeffries et al. 2014), but the ultimate cause of mortality for these fish is unknown. No size-based effects on survival have been found through telemetry for this population (Clark et al. 2016, Chapter 4), but only the largest (and oldest) individuals were tagged. A suite of predators has been observed to feed upon outmigrant Chilko sockeye smolts, including bull trout (Furey et al. 2015). Analysis of bull trout stomach contents (Furey et al. 2015) found size-based differences between predated and non-predated smolts to be small, and therefore it is unknown what traits of smolts result in increased predation risk. This study assesses the influence of fish health (prevalence of IHNV and other pathogens) and size on risk of predation by bull trout, by comparing predated and non-predated sockeye smolts.

3.2 Methods

3.2.1 Study area and field sampling

Field sampling occurred at the outlet of Chilko Lake into the Chilko River in British Columbia, Canada, where each spring (April – May) the smolt outmigration occurs. Smolts emigrate as two age classes: those that spend one year in the lake (~18 months age at outmigration) and those that spend two years in the lake (~30 months age at outmigration). Age-two smolts contribute ~4% to the outmigration and in general are 20 – 30 mm longer than age-one smolts (Irvine and Akenhead 2013). To enumerate outmigrant smolts, Fisheries Oceans and Canada (DFO) installs a river-wide counting fence that funnels smolts through one of two counting boxes. To compare fish health between predated and non-predated smolts, individuals were collected from both within stomach contents of bull trout and at random from the outmigrant population. A total of 30 non-predated smolts were collected via dipnet at the counting fence at night during the outmigration (10 smolts were collected on each of April 29, 2014, May 7, 2014, and May 13, 2014). All non-predated smolts were age-one (mean 96.4 mm fork length; standard deviation [SD] = 6.1 mm).

Between April 30, 2014 and May 15, 2014, bull trout were captured via dipnet at the fence or via hook-and-line over a ~1.5 km span between the counting fence and the lake outlet (51 – 69 cm fork length and 1.7 – 4.1 kg). Stomach contents from bull trout were collected via gastric lavage. When possible, smolts were individually wrapped in foil and frozen in liquid nitrogen; when this was not possible, smolts were frozen at -20 C. Smolts were assessed for condition (from 0 to 6) as a proxy for duration in the

stomach (adapted from Berens 2005; Table 3.1). When needed, scores were given in increments of 0.5 if a single category was not appropriate. A total of 50 smolts with a condition score of ≤ 3 (i.e. the least digested) were selected for pathogen screening. These 50 smolts were collected from a total of 12 different bull trout, with the number of smolts used from any given bull trout ranging between 1 and 13 (Table 3.2). Of these 50 smolts, 36 were age-one (mean FL = 92.2 mm; SD = 5.8 mm), and 14 were age-two (mean FL = 129.7 mm; SD = 9.6 mm).

To assess size-based predation risk, fork length (FL) of predated smolts were compared to smolts collected by DFO daily when migration occurred ($n = 7\ 488$). FL was measured from all smolts recovered from bull trout stomachs when possible. When a predated smolt was too degraded to measure FL, either total length (TL) or post-orbital hypural length (POH; distance from the posterior of the eye socket to the poster end of the hypural plate) was measured when possible to estimate FL using regression. Both the regressions between FL and TL or POH had $r^2 > 0.96$. In total, 120 individual predated smolts were either measured for FL or had FL estimated. Any smolt > 116 mm FL was considered age-two (B. Leaf, Fisheries and Oceans Canada, pers. comm.).

3.2.2 Laboratory sampling and analyses

Once in the lab, smolts were dissected to remove gill, brain, kidney, liver, and heart tissues using sterile technique. One set of dissection tools were used to remove a single gill arch and for the initial incisions to access the brain and peritoneal cavity, and a separate set of tools were used for removing internal organs to prevent external surfaces of the body contaminating internal organs. Tissues were put directly into homogenization

boxes placed upon dry ice. Organs were homogenized separately and equal volumes from the aqueous layer of each homogenate were combined for extraction. Extractions were carried out using MagMAX™ -96 for Microarrays Total RNA Isolation Kits with a Biomek FXP automated liquid- handling instrument according to the manufacturer's instructions. Total RNA was used to synthesize cDNA (SuperScript VILO MasterMix) following manufacturer's instructions. qPCR assays were examined using probe-based TaqMan.

Tissue samples were screened for the presence of 44 pathogens (Table 3.3), using quantitative reverse-transcriptase real-time polymerase chain reaction (qRT-PCR). The assessed pathogens are those suspected or known to generate disease in salmon worldwide (Miller et al. 2014); for further details about the selection of pathogens and development of assays, see Miller et al. (2016). Assays were run using the Fluidigm BioMark™ microfluidics platform (Fluidigm Corp. South San Francisco, USA). Total RNA was extracted using methods previously described (Miller et al. 2011, 2014; Jeffries et al. 2012). Briefly, tissues were homogenized in TRI reagent (Ambion Inc., Austin, TX) and 1-bromo-3-chloropropane was added to the homogenate. The assay volume used for qPCR on the BioMark is small (7 µL) and therefore a pre-amplification step is required. Thus, 1.25 µL of cDNA from each sample was pre-amplified with primer pairs corresponding to all assays in a 5- µL reaction volume using TaqMan Preamp Master Mix (Life Technologies) according to the BioMark protocol. Unincorporated primers were removed using ExoSAP-IT High-Throughput PCR Product Clean Up, and samples were diluted 1:5 in DNA Suspension Buffer. The assay mix was prepared containing 10

μL primers and 3 μL probes for the TaqMan assays. All assays were run in duplicate. A serial dilution of artificial positive constructs (APC clones) of all pathogen assays was run as six samples on the dynamic array. This serial dilution allowed for the calculation of assay efficiency. The APC clones contain an additional probe (VIC) that allows for the detection of vector contamination. The qPCR assays were run on the BioMark with dynamic arrays (96 samples x 96 assays). The amplified cDNA was diluted 1:2 with 29 Assay Loading Reagent (Fluidigm). A 5- μL reaction mix was prepared [29 TaqMan Master- mix (Life Technologies), 209 GE Sample Loading Reagent, nuclease-free water and 2.7 μL of amplified cDNA], which was added to each assay inlet of the array following manufacturer's recommendations. After loading the assays and samples into the chip by an IFC controller HX (Fluidigm), PCR was performed with the following conditions: 50°C for 2 min, 95°C for 10 min, followed by 40 cycles of 95°C for 15 s and 60°C for 1 min.

Cycle threshold was manually determined using the Biomark Real-Time PCR analysis software. Reaction curves for each positive sample-assay combination were visually evaluated for abnormal curve shapes, close correspondence between replicates, and presence of APC contamination as indicated by VIC positives. Using R (R Core Team 2015), efficiency was calculated for each assay, results where only one duplicate was positive for a sample-assay combination were removed, limit of detection thresholds (above which, samples were considered negative; Miller et al. 2016) applied, VIC positive samples removed, and duplicates averaged.

3.2.3 Data analyses

As in Jeffries et al. (2014), threshold Ct values were used to determine pathogen presence as defined by Miller et al. (2016). As an example, $Ct < 27.9$ represented pathogen presence for IHNV. To determine if any pathogens were more prevalent in predated smolts than from the general population, a Fisher's exact test was conducted for each pathogen, along with the calculation of the odds ratio for infection in predated vs non-predated samples, and its 95% confidence interval (CI). Ct scores were transformed to represent pathogen load by subtracting Ct from 40 and giving all negative samples a load of zero. In this manner, pathogen loads can be compared across samples, with higher load values indicating potentially higher pathogen productivity.

As little research has attempted to assess pathogens in predated fish (but see Miller et al. 2014), and to my knowledge never in individuals consumed by other fish, further analyses were conducted to identify factors potentially confounding pathogen prevalence in predated smolts. In theory, pathogen transfer could occur within the stomach among predated smolts (resulting in cross-contamination and apparent increased prevalence in predated samples). In response, I assessed if smolt condition score (proxy for time after predation) differed between infected and uninfected smolts with t-tests and estimated effect sizes using Cohen's d (Nakagawa and Cuthill 2007) using the 'effectsize' package (Torchiano 2015) in R (Team 2014). In general, $d < 0.2$ is considered a negligible effect, $d < 0.5$ is small, $d < 0.8$ is medium, and otherwise large (Cohen 1992). If smolts in worse condition (i.e., in the stomach longer) have higher prevalence of a given pathogen, this could indicate that smolts are becoming infected

after being consumed. If pathogens continue to replicate after death, a positive relationship might occur between smolt condition score and pathogen load. In response, I assessed if pathogen load (indicative of pathogen abundance) was dependent upon smolt condition using linear regression. Lastly, as age-two smolts were only in predated samples (14 of 50), I assessed if prevalence of these pathogens differed between the two age classes within predated smolts.

To determine if size (FL) of predated smolts differed from non-predated, Wilcoxon rank sum tests were used and Cohen's *d* estimates of effect sizes calculated. To determine if predation risk was age-specific (rather than size), the proportions of age-two fish within the predated and non-predated samples were compared using a Fisher's exact test and odds ratio calculation. For all tests, $\alpha = 0.05$.

3.3 Results

Among the 44 pathogens screened, nine were found to be in sampled smolts, and six (*Candidatus Branchiomonas cysticola*, *Flavobacterium psychrophilum*, IHNV, *Myxobolus arcticus*, Pacific salmon parvovirus, and *Tetracapsuloides bryosalmonae*) were found to be the most prevalent, and present in at least >30% of samples (Table 3.3). The remaining three pathogens were found in only one or two smolts (*Ichthyophthirius multifiliis*, *Parvicapsula minibicornis*, and *Piscichlamydia salmonis*; Table 3.3). Of the pathogens found in smolts, only IHNV and *Flavobacterium psychrophilum* were significantly more likely to be found in predated smolts than those non-predated (Fisher exact test $P < 0.05$; Table 3.3). The odds of IHNV infection was 34-times greater for predated than non-predated smolts ($P < 0.00001$; Figure 3.1). *Flavobacterium*

psychrophilum was 3-times more prevalent in predated samples than in non-predated, which was marginally significant ($P = 0.03$; Figure 3.2).

Within the predated sample, IHNV-positive smolts were in worse condition (mean condition score = 2.0) than those IHNV-negative (mean condition score = 1.3; t-test, $t = 2.3$, $df = 48$, $P = 0.02$; Figure 3.3), a ‘medium’-sized effect (Cohen’s $d = 0.74$) but the 95% CI was wide and included values implicating effect sizes of ‘negligible’ to ‘large’ (0.07 – 1.40). Salmon parvovirus also had significant differences in condition scores between positive and negative smolts (t-test, $t = -2.2$, $df = 48$, $P = 0.03$), but condition scores were greater for non-positive samples (means of 2.1 and 1.6, respectively). The remaining two most prevalent pathogens with >2 negative samples exhibited no differences in mean condition scores between positive and negative smolts (t-tests, both $P > 0.15$).

For predated, IHNV-positive smolts, IHNV load did not differ among condition scores (regression, $F_{1,34} = 1.0$, $P = 0.32$; Figure 3.4). Condition scores did not differ between smolts found to be positive and negative for *Flavobacterium psychrophilum* (t-test, $t = 0.4$, $df = 48$, $P = 0.69$). Similarly, load of *Flavobacterium psychrophilum* did not differ among condition scores (regression, $F_{1,22} = 0.0$, $P = 0.95$). In fact, of the pathogens with > 2 positives (Table 3.3), only *Myxobolus arcticus* (regression, $F_{1,46} = 3.9$, $P = 0.054$), demonstrated any evidence for loads differing among condition scores. The loads of neither Pacific salmon parvovirus ($F_{1,30} = 0.1$, $P = 0.76$), *Candidatus Branchiomonas cysticola* (ANOVA, $F_{1,47} = 0.2$, $P = 0.67$), nor *Tetracapsuloides bryosalmonae* (regression, $F_{1,20} = 2.3$, $P = 0.15$) differed among condition scores.

IHNV prevalence was the same (71.4%) for both age-one and age-two smolts, and thus our inclusion of age-two smolts in predated samples (14 of 50) should not bias our interpretation of links between infection and predation. Similarly, age was found to have no effect on prevalence of *Flavobacterium psychrophilum* in predated smolts (Fisher's exact test $P = 0.36$), and prevalence was actually greater in age-one smolts (51%) than in age-two (36%). Thus any potential bias would be in reducing the prevalence of *Flavobacterium psychrophilum* in the predated sample.

Comparing mean sizes of predated smolts to those collected at the counting fence revealed that within both age classes of smolts, smaller smolts were predated on more frequently (Figure 3.5). The mean FL of predated and non-predated age-one smolts was 92.5 mm and 98.2 mm, respectively, a significant (Wilcoxon rank sum test; $P < 0.0001$) and "large" size-based effect (Cohen's $d = 0.95$; 95% CI = 0.75 – 1.16). A similar effect was found for age-two smolts (mean predated FL = 134.0 mm; mean non-predated FL = 142.5 mm), resulting in a significant (Wilcoxon rank sum test, $P < 0.0001$) and "medium" size-based effect (Cohen's $d = 0.79$, 95% CI = 0.41 – 1.16). When pooling across both age classes, however, the difference in mean size was negligible (Cohen's $d = 0.03$; 95% CI = -0.21 – 0.15), even though significant (Wilcoxon rank sum test $P < 0.001$). This confounding result appears due to age-two smolts representing a larger proportion within the predated sample (23.3%) than in the non-predated (8.3%; odds ratio = 3.4; 95% CI = 2.1 – 5.2; $P < 0.0001$), increasing the overall mean size observed in predated fish.

As IHNV, *Flavobacterium psychrophilum*, and size were indicative of predation risk, additional analyses examined if infection of either pathogen and size were related.

Comparing mean FL between fish positive and negative for IHNV with t-tests found no significant difference in size, regardless if comparing across all samples ($t = -0.79$; $df=77$; $P = 0.43$), just samples from predated fish ($t = 0.63$; $df = 47$, $P = 0.53$), just age-one fish ($t = 0.63$; $df = 65$; $P = 0.53$), just age-one predated fish ($t = -0.06$; $df = 35$; $P = 0.95$), or just age-two fish (all predated; $t = 1.23$, $df = 10$; $P = 0.25$). Similarly, there was no correlation between IHNV load and FL for IHNV-positive smolts (Pearson correlation = -0.14 ; $t = -0.82$; $df = 35$; $P = 0.42$). For *Flavobacterium psychrophilum*, again, no significant differences in FL were found between positive and negative smolts regardless if comparing across all samples ($t = 0.58$, $df = 77$, $P = 0.57$), predated samples ($t = 1.1$, $df = 47$, $P = 0.28$), age-one smolts ($t = 0.8$, $df = 65$, $P = 0.44$), age-one predated smolts ($t = 0.5$, $df = 35$, $P = 0.60$), or age-two predated smolts ($t = -0.3$, $df = 10$, $P = 0.73$).

3.4 Discussion

This study represents the broadest pathogen screening in wild outmigrant sockeye salmon smolts in freshwater to date, revealing nine pathogens with six of these prevalent in at least one-third of samples. Previous research using a similar technique on the same population of smolts only found three pathogens (Jeffries et al. 2014), however, fewer pathogens were initially assessed (18 vs 44). Jeffries et al (2014) only used gill tissue (some pathogens are found nearly exclusively in other tissues such as *Myxobolus arcticus* [brain] and *Tetracapsuloides bryosalmonae* [kidney]) and used a smaller quantity of RNA. Two of the three pathogens found by Jeffries et al. (2014) in 2012 outmigrant smolts (*Nucleospora salmonis* and Ricksettia-like organism) were of low prevalence and were not found in the 2014 outmigrant smolts. This results in eight pathogens that were

found in 2014 smolts that were either not found during the 2012 outmigration or not assessed by Jeffries et al. (2014), with *Candidatus Branchiomonas cysticola*, *Flavobacterium psychrophilum*, *Myxobolus arcticus*, Pacific salmon parvovirus, and *Tetracapsuloides bryosalmonae* being prevalent. With the exception of *Flavobacterium psychrophilum*, none of these pathogens demonstrated any impact on initial predation risk in freshwater, and thus it is unknown what the potential consequences of these infections might be. Indeed, pathogens and parasites are present in all ecosystems (Hudson et al. 2006), and not all infections result in severe compromises to health. Pathogen influences on hosts can be landscape-specific (Miller et al. 2014) so the potential for effects on smolts further along the migration is possible. These results help to provide important context for the pathogens present in one of the largest wild sockeye salmon populations in Canada.

Fish infection status and physical state significantly influenced predation risk of migrant sockeye salmon smolts because the presence of IHNV and *Flavobacterium psychrophilum*, along with small body size, resulted in increased predation. IHNV-infected smolts were 34-times more likely to be predated than not while *Flavobacterium psychrophilum* infected smolts were 3-times more likely to be found in predated samples. Few studies, across ecosystems and taxa, have been able to make a direct link between the presence of a pathogen and predation risk outside of experimental settings (but see (Hudson et al. 1992, Johnson et al. 2006, Miller et al. 2014). Only Miller *et al.* (2014) has demonstrated pathogen-based predation risk for wild sockeye salmon. Using a similar approach to that of the current study, they found rhinoceros auklets (*Cerorhinca*

monocerata) fed more heavily on marine sockeye salmon smolts that were infected with *Parvicapsula sp.* parasites (Miller et al. 2014). Thus smolt health may influence risk throughout the migratory process.

Our assessment of pathogen influences on predation risk is dependent upon multiple assumptions, including that once ingested, an infected smolt cannot infect others. IHNV-infected smolts, however, were in worse condition (a proxy for longer duration in the gut) than those that were not infected, which may be evidence of transmission post-ingestion. No other pathogen showed evidence of increased digestion time (poor condition) resulting in increased prevalence in predated samples. If cross-contamination of IHNV within the gut does occur, it could be through the gills, which were the only externally-exposed tissue sampled. As IHNV can be present in mucus (LaPatra et al. 1989), it is plausible that cross-contamination could occur (subsequently increasing the prevalence of pathogen-positive fish in the predated sample). Restricting sampling to only internal organs in future studies could minimize this risk. Cross-contamination after ingestion would be more likely if pathogens could persist and proliferate after host death. However, none of the six most prevalent pathogens exhibited loads that varied across smolt condition, implying that pathogen productivity is not increasing after ingestion. Stomach acid is a hostile environment, that is thought to have evolved in vertebrates not only to aid digestion, but to protect against pathogens (Koelz 1992, Tennant et al. 2008), which would help to prevent proliferation after ingestion.

The statistical significance for the difference in condition scores between IHNV-positive and IHNV-negative smolts, however, was marginal and the CI of the effect size

was wide and ranged from “negligible” to “strong.” This relationship was driven by six smolts in the best condition (scores 0 or 0.5), of which only one was IHNV-positive (removing these six samples results in no significant relationship between condition score and being predated). This low prevalence of IHNV in these best-condition samples may be related to where these fish were consumed by bull trout. All six of these smolts were collected from bull trout captured via dipnet at the fence where bull trout feed more closely to *ad libitum* rates than bull trout foraging elsewhere (Chapter 2). Thus selection of smolts by bull trout may be more random at the fence, which could act to decrease IHNV prevalence in these samples. This hypothesis, however, is untested, and the possibility for transmission after ingestion to increase IHNV prevalence in predated samples cannot be discounted. Further research needs to better define such possibilities. Regardless, Jeffries et al. (2014) found most (>80%) IHNV-positive smolts tracked with acoustic telemetry to perish in the first 80 km of migration, suggesting a true ecological relationship between IHNV infection and smolt mortality, and this study provides a plausible link (predation).

Using predated smolts for pathogen screening also assumes that bull trout cannot infect smolts with pathogens upon ingestion. IHNV can infect a variety of North American salmonids (Booy et al. 2005) and *Flavobacterium psychrophilum* is expected to be found in all salmonids (Nematollahi et al. 2003). To my knowledge, IHNV has never been documented in bull trout, albeit implicated in a historical population collapse in Lake Chelan, Washington (Nelson 2012). If bull trout are susceptible to pathogens, it is certainly feasible for these fish to become infected due to repeated exposures via

feeding on smolts during the outmigration. It remains unknown, however, if the ingestion of a smolt would provide an appropriate mechanism for pathogen transfer. Regardless, I present compelling evidence for the influence for fish health to impact predation risk.

IHNV is a single-stranded RNA virus that generates an acute, systemic disease that causes necrosis of hematopoietic tissues of the kidneys and spleen and damage to the pancreas, adrenal cortex, and gastro-intestinal tract (Bootland and Leong 1999). For juvenile sockeye, virulence is particularly high (Miller et al. 2007) and can result in very high mortality (Lapatra 1998). The virus is endemic to western North America and can be found in all continental *Oncorhynchus* species, as well as in farmed Atlantic salmon (*Salmo salar*; (Booy et al. 2005)). IHNV is naturally present within the study system (Chilko Lake, British Columbia) and its presence there has been known for > 40 years (Williams and Amend 1976). Mortality can be rapid and generally occurs 4 – 20 days after exposure (Kim et al. 1999). Prevalence of IHNV in outmigrant Chilko sockeye smolts in 2012 was ~8% (Jeffries et al. 2014), and was ~7% (two of 30) in non-predated samples from 2014. Among acoustic-tagged Chilko sockeye smolts that were IHNV-positive, >80% did not survive the downstream migration through the Chilko and Chilcotin Rivers (Jeffries et al. 2014). In addition, the expression of several genes involved in immune and stress responses and predictive of mortality of these tagged smolts was highly correlated with IHNV presence and load (Jeffries et al. 2014). Jeffries et al. (2014) implicated predation as a source of mortality for IHNV-positive smolts, and I confirm that bull trout are indeed feeding upon smolts that are compromised. Thus IHNV appears to strongly affect a small portion of outmigrant Chilko sockeye smolts.

Flavobacterium psychrophilum affects most salmonid species and select non-salmonids across the globe and results in bacterial cold water disease and rainbow trout fry syndrome (Nematollahi et al. 2003). *Flavobacterium psychrophilum* is particularly virulent for juvenile coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*), but is also found in sockeye and in wild populations even though it is of greatest concern in aquaculture settings (Nematollahi et al. 2003). Mortality rates can vary between 5-90% depending on species, population, and environmental conditions (Barnes and Brown 2011). Mean time from infection to death of juvenile Chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout, and coho salmon is generally < 10 days (Holt et al. 1989). The bacterium can be found in connective tissues in fins, gills, and operculum, as well as in mucus (Madetoja et al. 2002, Nematollahi et al. 2003), and is transferred both vertically and horizontally (Mulcahy and Pascho 1985, Nematollahi et al. 2003). Thus the outmigration (during which smolts synchronize movements into high densities) could provide a pathway for transmission among conspecifics. It is a cold-water pathogen, being most lethal in waters 3 – 18 C (Holt et al. 1989), and therefore its presence in Chilko Lake is unsurprising, as water temperatures during the outmigration is generally 2 – 10 C. To my knowledge this is the first evidence of *Flavobacterium psychrophilum* being associated with predation risk of wild juvenile sockeye.

How infection of either IHNV or *Flavobacterium psychrophilum* results in increased predation risk by bull trout remains unclear. First, it is possible that infection results in smolt death, after which it is eaten by scavenging bull trout. This seems unlikely given the lack of moribund smolts seen in the study system and the active

foraging of bull trout that is observed. If smolts are truly being predated, it is assumed that these pathogens either reduce a smolt's probability of escaping a predation attempt when targeted, or increase the predator's propensity to target the smolt. Either possibility would probably rely on alterations to smolt swimming behaviour and/or performance. Pathogens and parasites can alter swimming performance of fish (reviewed in (Barber et al. 2000)), including stamina, recovery rates, burst swimming speed, and migration orientation (Butler and Millemann 1971, Garnick and Margolis 1990, Moles and Heifetz 1998, Wagner et al. 2003, 2005, Ferguson et al. 2012). Specifically, *Flavobacterium psychrophilum* can induce ataxia (lack of movement control) and/or spiral swimming behaviour in underyearling salmonids (Kent et al. 1989, Nematollahi et al. 2003), but similar work has not been conducted on smolts or sockeye. IHNV can result in lethargy, hyperactivity, and/or erratic swimming (Bootland and Leong 1999). Further work is needed to determine the behavioural consequences of infection on sockeye smolts, and how this might result in increased predation risk by bull trout and other predators.

Predation risk was also size-based; within each age class, predated smolts were on average ~5 – 10 mm shorter than the outmigrant population means. Across systems, the “bigger is better” hypothesis is well supported (Pauly 1980, Sogard 1997), as increased size can both reduce the potential number of gape-limited predators and improve ability to evade predators (Juanes and Conover 1994b, Sogard 1997). Gape is not expected to be limited for bull trout, and thus size-based predation risk may be based on improved swimming abilities of larger smolts that effectively reduce foraging efficiency of the predator. Tucker et al. (2016) found smaller salmon smolts, including sockeye, to be

disproportionately fed upon by rhinoceros auklets in the marine environment. Thus smolt size may continually be selected for throughout the outmigration across landscapes and predators.

Even though smaller fish within each age class were more likely to be predated, the larger age-two smolts represented a greater contribution to bull trout consumption (~23%) than expected given their low prevalence in the outmigrant population (~8%). This disproportionate consumption of age-two smolts would suggest bull trout are targeting the largest smolts when possible. The mass of individual age-two smolts is generally 3-times that of age-one animals (Irvine and Akenhead 2013), and therefore consuming these fish would certainly provide greater benefit if capture probabilities are similar. Or, given the small proportion of age-two smolts among migrants, these fish may appear to stand out to predators, thus allowing for the targeting of “odd-sized” individuals within a school (Theodorakis 1989). The fact that within both age-classes smaller fish were at higher risk could indicate that bull trout are more proficient at capturing smaller individuals, regardless of which prey they target.

There was no apparent interaction between smolt size and infection of either IHNV or *Flavobacterium psychrophilum* on predation risk, and thus each factor may affect predation risk independently. The mean size of smolts was similar between infected and uninfected individuals, and neither pathogen load was correlated to smolt size. Both IHNV and *Flavobacterium psychrophilum* affect fish quickly, and thus feeding might not be impacted for a long enough duration to generate size differences among infected and uninfected smolts. Regardless, given the 34-times increase in predation risk

due to IHNV, it appears IHNV may affect predation risk more strongly than fish size in this system, although I am unable to directly compare effect sizes of these two factors, and IHNV prevalence may be confounded by duration spent in the predator's stomach. Likewise, given the marginal statistical significance and small odds ratio of *Flavobacterium psychrophilum*'s impact on predation risk, this pathogen's influence could be tertiary to both IHNV infection and size. The relative importance of size, however, may vary among years, and therefore more research across a longer temporal scale may be needed to properly understand the relative importance of these factors.

Increased predation risk for infected smolts would indicate that infected individuals are effectively removed from the population during the downstream migration. Thus IHNV, and to a lesser extent, *Flavobacterium psychrophilum*, may be subject to 'migratory culling' (Bradley and Altizer 2005, Altizer et al. 2011), where pathogen prevalence in a population reduces via migration. Although unconfirmed, bull trout predation may reduce exposure for healthy fish as they migrate downstream. The use of simulation models that incorporate information on both migrant population density and movements, along with information on pathogen infection processes, could be instrumental in quantifying downstream consequences of predation on pathogen and migration dynamics. The potential for migratory culling has important implications for the management of migratory juvenile salmon as management actions to improve survival via reducing predation may not provide the desired results. If fish are sufficiently compromised upon outmigration, survival may be poor regardless of predator abundance and distribution, or environmental conditions. Avian predators in the marine environment

can also select for compromised migrant smolts (Miller et al. 2014), and thus even reduction of predation in one landscape may not prevent smolts from experiencing infection-based predation further along the migration. Therefore, fisheries management should be focused on the monitoring and evaluation of fish health at the population level, identifying factors that affect pathogen prevalence, and understanding how pathogens interact with other stressors to influence predation and/or mortality risk.

In conclusion, I provide evidence that IHNV and *Flavobacterium psychrophilum* infection, along with small body size, increases predation risk of outmigrant juvenile sockeye salmon smolts by bull trout in the Chilko river. The effects of infection and body size appear to act independently. These results suggest that predation results in a lower probability of IHNV-infected smolts to successfully migrate (Jeffries et al. 2014). Although the mechanism resulting in the consumption of infected fish is unknown, it is hypothesized to be behaviour-based. These results indicate that the physical state of smolts in terms of both health and fish size is important to the migratory process of juvenile salmonids.

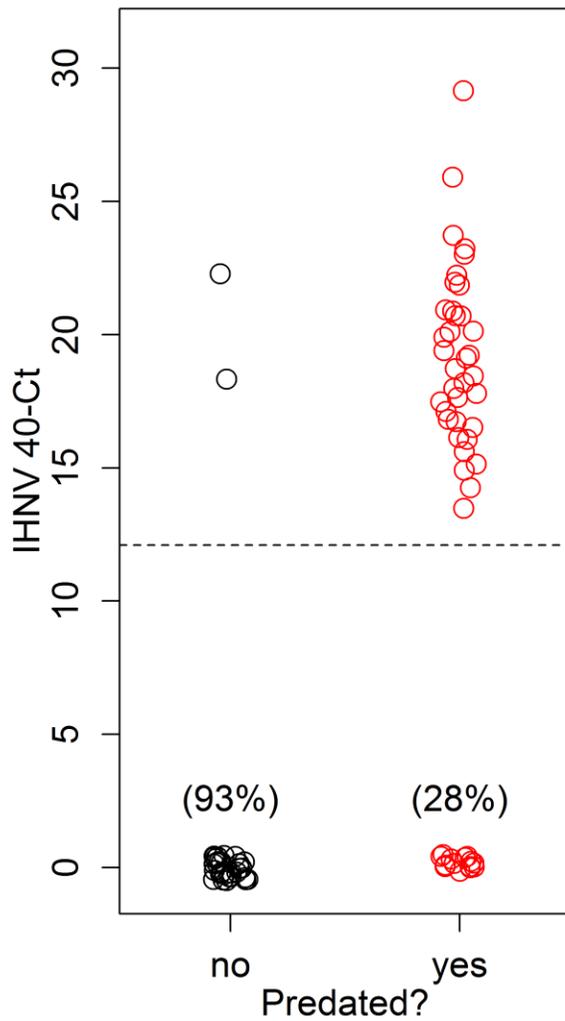


Figure 3.1 Relative loads of IHNV in sockeye salmon smolts predated by bull trout (red) and those collected randomly from the population (black). Numbers in parentheses indicate the percentage of smolts in that category (predated or not) that had a negative result for IHNV. Dashed line represents the minimum load required for a positive detection (see Table 3.3). Points are jittered to aid visibility.

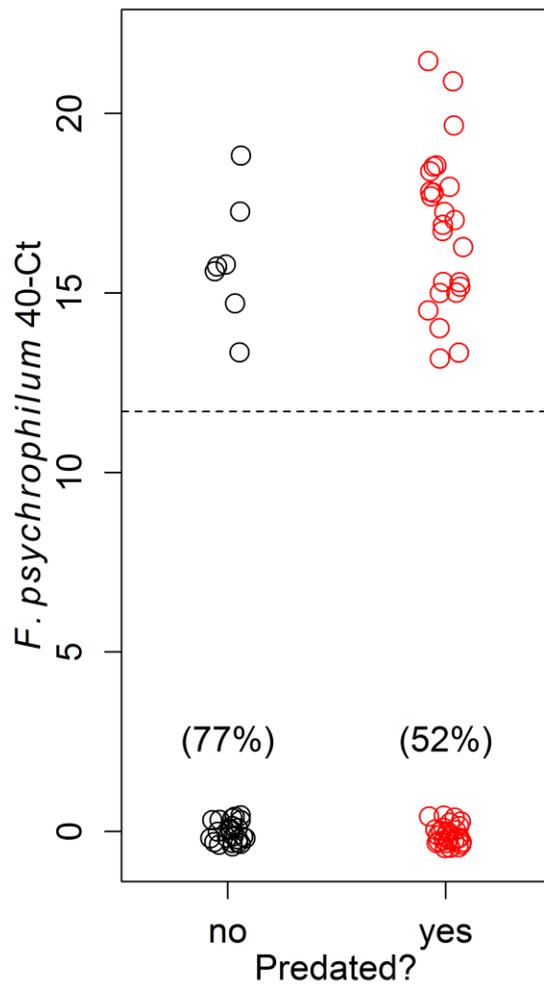


Figure 3.2 Relative loads of *Flavobacterium psychrophilum* in sockeye salmon smolts predated by bull trout (red) and those collected randomly from the population (black). Numbers in parentheses indicate the percentage of smolts in that category (predated or not) that had a negative result for *Flavobacterium psychrophilum*. Dashed line represents the minimum load required for a positive detection (see Table 3.3). Points are jittered to aid visibility.

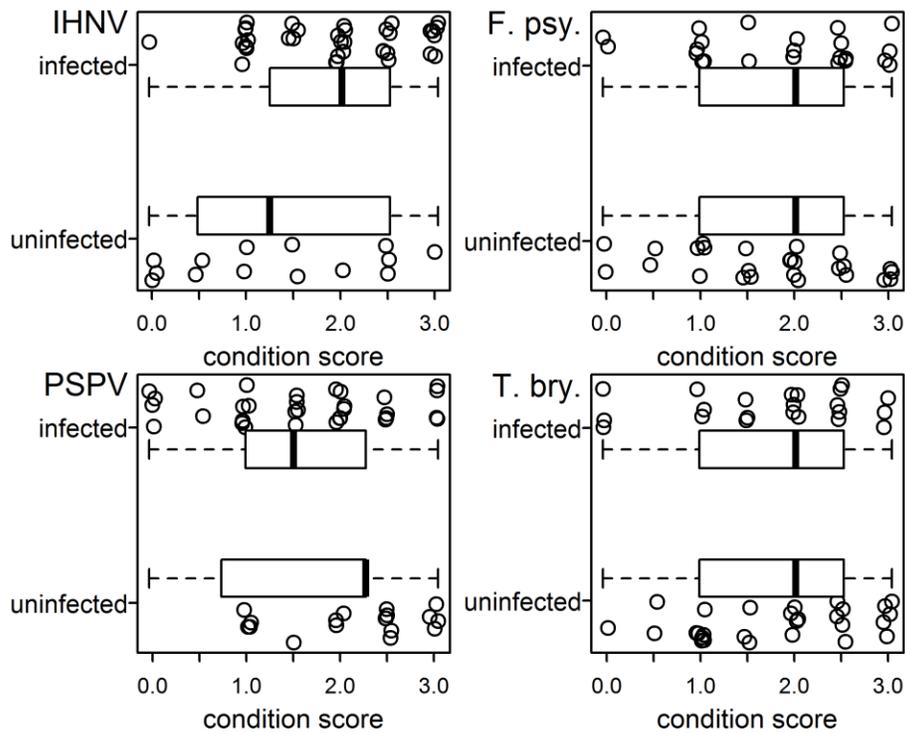


Figure 3.3 Condition scores (proxy for degree of digestion) between smolts testing positive (infected) and negative (uninfected) for the four most prevalent pathogens that had at least 2 samples in each category. Circles represent individual samples (smolts), and are jittered to aid visibility. Boxplot whiskers represent 1.5-times the interquartile range (IQR) and thick lines represent the median value of the sample.

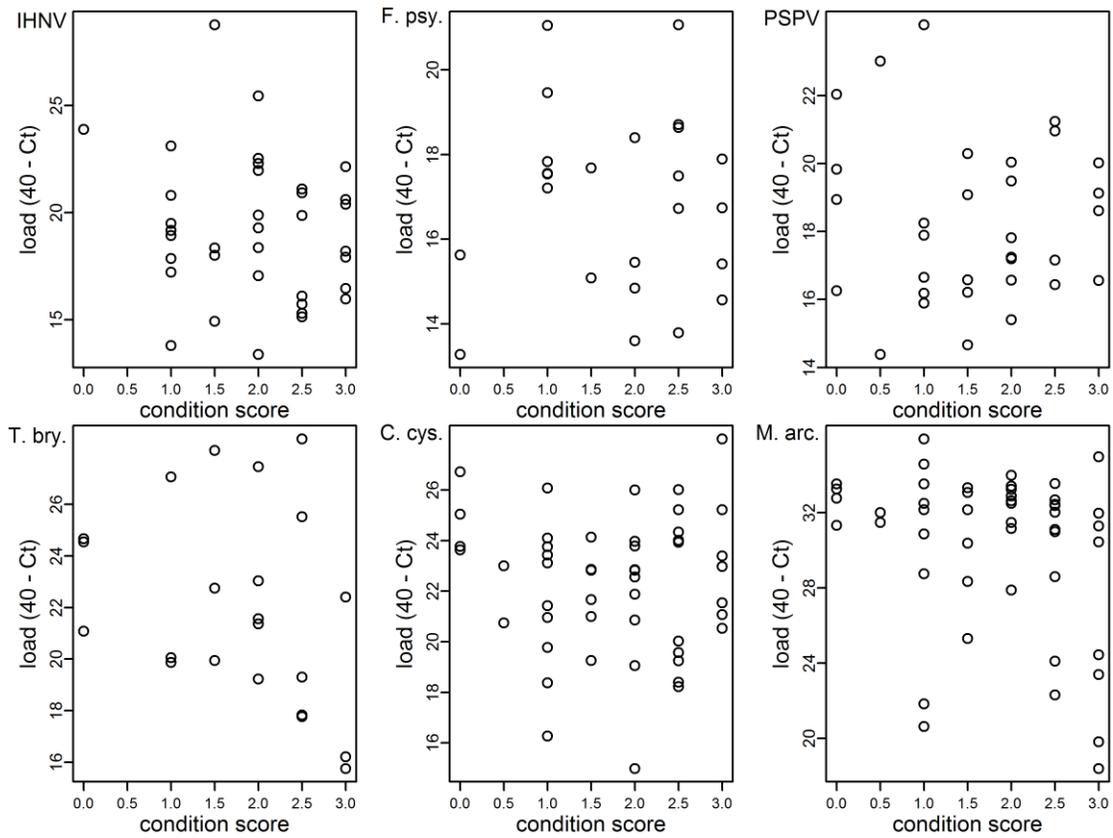


Figure 3.4 Condition scores and loads of the six most prevalent pathogens found in predated sockeye salmon smolts. Circles represent individual smolts. Pathogen abbreviations in the upper right-hand corner of each panel are as follows (starting in top-left and moving clockwise): Infectious hematopoietic necrosis virus (IHNV), *Flavobacterium psychrophilum* (F. psy), Pacific salmon parvovirus (PSPV), *Tetracapsuloides bryosalmonae* (T. bry.), *Candidatus Branchiomonas cysticola* (C. cys.), and *Myxobolus arcticus* (M. arc.).

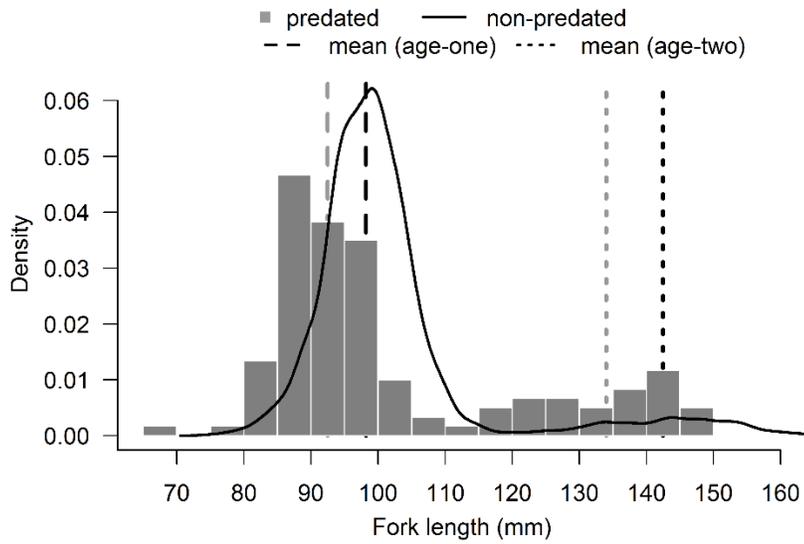


Figure 3.5 Density-based histograms of smolt lengths for predated fish (grey bars) and those from the general population (solid black line). Dashed vertical lines indicate age-specific means for predated and non-predated groups. Any smolt > 116 mm fork length was considered an age-two fish (Brian Leaf, DFO, personal communication).

Table 3.1 Description of digestion codes used on individual prey items found within bull trout stomach contents. Adapted from Berens (2005).

Digestion code	Description
0	Whole fish, most or all skin, head present, all meat, all guts, all bones present, most finrays present, no chyme or digesta
1	Mostly whole fish, most skin present, head present, all or most meat present, all guts and all bones present, some finrays present, no chyme or digesta
2	Recognizable fish, most skin present, most of head present, most meat present, most guts and all bones present, very little chyme or digesta
3	Recognizable fish, some skin present, some or most of head present, some meat present, some guts and all bones present, little chyme or digesta
4	May or may not be a recognizable fish, little skin present, no or partial head, some meat present, some guts and most bones present, some chyme or digesta
5	Not a recognizable fish, bits of or no skin present, no head, little to no meat present, little to no guts and some bones present, chyme or digesta present
6	Not a recognizable fish, no skin, no head, no meat or guts present, some bones present, chyme or digesta present

Table 3.2 Summary of bull trout captured for collection of smolts for pathogen screening. The total number of smolts (and within each age class) used in pathogen screening from each individual bull trout's stomach contents are given.

Bull trout ID	FL (cm)	mass (kg)	# of smolts used in pathogen screening		
			Total	age-one	age-two
BT01	56	2.0	13	12	1
BT02	60	2.5	11	10	1
BT03	57	2.2	8	5	3
BT14	69	4.1	3	3	0
BT15	58.5	2.2	4	3	1
BT16	65	3.8	1	1	0
BT17	51	1.7	1	0	1
BT18	65	2.9	1	0	1
BT20	63	2.9	2	0	2
BT23	55		2	0	2
BT24	59	2.3	2	1	1
BT25	60	2.2	2	1	1
Mean \pm SD	59.9 \pm 5.0	2.6 \pm 0.7	Totals	36	14

Table 3.3 List of pathogens assessed in sockeye salmon smolts using qRT-PCR. The maximum Ct allowed for a positive detection as in Miller et al. (2016), the number and percentage of positives recorded across categories, and the odds-ratio of each pathogen being found in a predated smolt over a non-predated smolt (and the 95% confidence interval [CI]) are given.

Pathogen	Agent	Maximum Ct allowed for positive	# Positives detected (if any)	# positives predated	# positives non-predated	odds-ratio (Predated over non-predated)	95% CI of odds ratio
<i>Aeromonas hydrophila</i>	Bacteria	28.7					
<i>Aeromonas salmonicida</i>	Bacteria	26.5					
Atlantic salmon paramyxovirus	Virus	26.4					
<i>Candidatus Branchiomonas cysticola</i>	Bacteria	26.9	79 (98.8%)	49 (98.0%)	30 (100%)	NA	NA
<i>Ceratomyxa shasta</i>	Myxozoan	28.2					
<i>Dermocystidium salmonis</i>	Fungus/Protozoan	27.5					
<i>Facilispora margolisi</i>	Microsporidium	29.1					
<i>Flavobacterium psychrophilum</i>	Bacteria	28.3	31 (38.8%)	24 (48.0%)	7 (23.3%)	3.0	1.01 - 9.82*
Gill chlamydia (Sch)	Bacteria	27.7					
<i>Gyrodactylus salaris</i>	Ectoparasitic worm	26.3					
<i>Ichthyophonus hoferi</i> (<i>Ichthyophonus Spp</i>)	Protozoan	25.4					
<i>Ichthyophthirius multifiliis</i>	Ciliate	25.2	2 (2.5%)	1 (2.0%)	1 (3.3%)	0.6	0.01 - 48.04
Infectious hematopoietic necrosis virus	Virus	27.9	38 (47.5%)	36 (72.0%)	2 (6.7%)	34.1	7.12 - 332.61*
	Virus	27.7					

Pathogen	Agent	Maximum Ct allowed for positive	# Positives detected (if any)	# positives predated	# positives non-predated	odds-ratio (Predated over non-predated)	95% CI of odds ratio
Infectious pancreatic necrosis virus							
<i>Kudoa thyrsites</i> (<i>Kudoa Spp</i>)	Myxozoan	26.2					
<i>Loma salmonae</i> (<i>Loma Spp</i>)	Microsporidium	26.1					
<i>Myxobolus arcticus</i>	Myxozoan	26.9	78 (97.5%)	48 (96.0%)	30 (100%)	NA	NA
<i>Myxobolus cerebralis</i>	Myxozoan	26.4					
<i>Myxobolus insidiosus</i>	Myxozoan	26.6					
<i>Nanophyetus salmincola</i>	Fluke	25.8					
<i>Neoparamoeba perurans</i>	Amoeba	26.9					
<i>Nucleospora salmonis</i>	Microsporidium	25.3					
Pacific salmon parvovirus	Virus	27	51 (63.8%)	32 (64.0%)	19 (63.3%)	1.0	0.36 - 2.90
<i>Paranucleospora theridion</i>	Microsporidium	28.6					
<i>Parvicapsula kabatai</i>	Myxozoan	27					
<i>Parvicapsula minibicornis</i>	Myxozoan	28.7	1 (1.3%)	0 (0.0%)	1 (3.3%)	NA	NA
<i>Parvicapsula pseudobranchicola</i>	Myxozoan	25.7					
<i>Piscichlamydia salmonis</i>	Bacteria	29.2	2 (2.5%)	2 (4.0%)	0 (0%)	NA	NA
Piscine myocarditis virus	Virus	26.3/25.6*					
Piscine reovirus	Virus	25.4					

Pathogen	Agent	Maximum Ct allowed for positive	# Positives detected (if any)	# positives predated	# positives non-predated	odds-ratio (Predated over non-predated)	95% CI of odds ratio
<i>Piscirickettsia salmonis</i>	Bacteria	25.6					
<i>Renibacterium salmoninarum</i>	Bacteria	26					
Salmon alphavirus 1, 2, and 3	Virus	25.6					
Salmonid herpesvirus	Virus	27.4					
<i>Sphaerothecum destructuens</i>	Fungus	27					
<i>Spironucleus salmonicida</i>	Flagellate	29					
Strawberry disease	Bacteria	26.5					
<i>Tetracapsuloides bryosalmonae</i>	Myxozoan	25.4	34 (42.5%)	22 (44.0%)	12 (40%)	1.2	0.43 - 3.29
<i>Cryptobia salmonistica</i>	Protozoan	27.3					
<i>Vibrio anguillarum</i>	Bacteria	26.5					
<i>Vibrio salmonicida</i>	Bacteria	25.7					
Viral encephalopathy and retinopathy virus	Virus	26.4					
Viral erythrocytic necrosis virus	Virus	25.4					
Viral hemorrhagic septicemia virus	Virus	31.8/25.5*					

Chapter 4: Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape

4.1 Introduction

Migrations, or the directed movements of large portions of animal populations, occur across taxa and evolved as mechanisms to increase fitness via exploitation of spatiotemporal variability in resources or risks (Alerstam et al. 2003; Dingle & Drake 2007; Milner-Gulland et al. 2011). Although the benefits of migration can be numerous, there are inherent costs as well, including metabolic expenses, increased risk of pathogen transmission, and exposure to new abiotic conditions and predators (Alerstam et al. 2003). Due to the myriad costs, migration mortality can be high (Osterback et al. 2013, Lok et al. 2015), even relative to non-migratory periods (Sillett and Holmes 2002, Strandberg et al. 2010, Klaassen et al. 2014). Migrants can be especially vulnerable while traversing high-risk landscapes that allow predators to feed efficiently (Osterback et al. 2013, Bouchet et al. 2014). With sufficient selection pressure due to predation, risk-reduction mechanisms should exist to optimize migration success.

A commonly assumed mechanism available to migrants to reduce risk is to move together in high densities to swamp predators. The theoretical adaptive value of synchronizing life history events is well founded (reviewed in Ims 1990), but empirical demonstrations of this density-dependent benefit are largely limited to insect emergence events (Sweeney and Vannote 1982, Williams et al. 1993) rather than migrations. Using a more experimental approach, Tucker et al. (2008) found that seasonal timing, rather than density, altered individual predation risk of released turtle hatchlings, but the study was limited to few release groups. Outside of emergence

events, penguins from larger colonies experienced lower individual risk of seal predation during regular foraging trips indicative of a swamping effect (Ainley et al. 2005), but the densities of predators across penguin colonies were not known. Thus we still lack strong evidence for the value of density-dependent predator swamping, particularly in the context of animal migration.

Behavioural risk-reduction mechanisms includes the timing of migration; migrants can travel at times that either reduce exposure to or reduce foraging efficiency of predators. These timing effects can occur at multiple temporal scales. Diel cycles, for example, are often exploited by migrants to reduce foraging efficiency of visual-based foragers, even outside the context of diel vertical migrations (Pechmann and Semlitsch 1986, Ibbotson et al. 2006, 2011). At longer, seasonal scales, migrations can reduce overlap with predators (Lank et al. 2003, Ydenberg et al. 2007, Tucker et al. 2008). In sum, synchronizing migrations to both increase density and to decrease foraging opportunities for predators are behavioural or movement-based mechanisms that could impact experience and ultimately survival.

Aside from movement-based mechanisms, the “bigger is better” hypothesis suggests that larger migrants would experience reduced predation risk. Outside of the migratory context, reduced risk for larger individuals has consistent support across ecosystems (Pauly 1980, Sogard 1997, McCoy and Gillooly 2008), as predators are typically larger than their prey (Peters 1986, Brose et al. 2006). This hypothesis, however, is less tested for migrants (but see Tucker et al. 2016 and Chapter 3) outside the context of juvenile ungulates comigrating with adults where juveniles are targeted by predators (Grange et al. 2004, Middleton et al. 2013) or lipid reserves in birds where increased fuel storage can actually reduce predator avoidance capabilities (Lima 1986). Size has been implicated in the propensity for movement by fish in populations with

partial migration, with smaller individuals at higher risk of predation more likely to migrate (Skov et al. 2011). In general it is difficult to assess the strength of any risk-reducing mechanism during migration due to the difficulties in tracking individual experience and success of migrants, but landscapes with high predation should provide opportunities for studying the relative importance of mechanisms for reducing risk.

Of migratory animals, Pacific salmon are among the most oft-studied due to their economic, ecological, and cultural value. Although less visible than the upriver spawning migrations by adults, the downstream migrations undertaken by juvenile smolts through rivers and to the open ocean are no less impressive. The Fraser River watershed in British Columbia is the greatest producer of wild salmon in Canada, but smolt-to-adult survival of sockeye salmon (*Oncorhynchus nerka*) in this system has declined precipitously in recent years (Cohen 2012; Irvine & Akenhead 2013). Mortality of migrant smolts can be substantial due to a suite of piscivorous fishes and avian predators (Beamesderfer et al. 1996; Hostetter et al. 2012; Osterback et al. 2013).

Recently, acoustic telemetry was used to examine the individual migration experience of wild sockeye salmon (*Oncorhynchus nerka*) smolts outmigrating from Chilko Lake within the Fraser watershed (Clark et al. 2016). Chilko Lake is one of the largest sockeye salmon populations in all of Canada, with 10-40 million smolts outmigrating downstream annually, and is used as an indicator of all sockeye populations in the Fraser River. Outmigrant smolts are enumerated at a counting fence by the federal fisheries agency responsible for salmon management (Fisheries and Oceans Canada - DFO), using (in recent years) high temporal resolution photography. Outmigrant survival in the small and clear Chilko River is consistently

poor across years relative to the larger and turbid Fraser River (Clark et al. 2016). Nocturnal-timed migrations by smolts and the presence of a multiple avian predators (mergansers, Bonaparte gulls, loons, etc.) and bull trout (*Salvelinus confluentus*; Clark et al. 2016) suggests that predation is a large factor influencing survival in this landscape. Using sockeye smolts and the Chilko River as a model system, I used acoustic and passive integrative transponder (PIT) telemetry to examine movements and survival at the kilometer-scale during outmigration to understand the relative contributions of swamping, timing, and size to predation risk.

4.2 Methods

4.2.1 Study site and species

Field research was conducted at the outlet of the Chilko Lake into the Chilko River in British Columbia (Figure 4.1). Chilko Lake has a north-south orientation and is 3km wide and 60 km long (Desloges and Gilbert 1998). The northern end of the lake outlets into the Chilko River (Figure 4.1). During the time of field research (April-May), the Chilko River is narrow, slow-moving, and clear. Every spring since the early 1950s for a 5-8 week period, the DFO has operated a counting fence 1.3 km downstream from the lake outlet (Figure 4.1). This fence spans the entire width of the river and is used to concentrate smolts into a small area during their initial migration in order to photographically enumerate and generate density estimates of outmigrant smolts every 5 minutes. Two age classes of smolts emigrate: those that were spawned ~18 months prior (age-one) and those that spent two years in the lake (spawned ~30 months prior to smolt emigration; age-two). Age-two smolts generally constitute ~4-5% of outmigrants, and the smolt-to-adult survival ratios of both age classes are statistically similar (Irvine & Akenhead

2013). In addition, age-two smolts are on average ~35 mm longer than age-one smolts (Irvine & Akenhead 2013).

4.2.2 Telemetry infrastructure

Acoustic telemetry receivers (Vemco VR2W; 69 KHz) were placed at 8 stations across the first 13.5 km of the Chilko River downstream of the counting fence, hereafter referred to as arrays A through H (Figure 4.1). Clark et al. (2016) found smolt survival to range between 63% and 90% for this portion of the Chilko River across years (2010-2013). Additional receivers were placed further downstream and detections from the first of these (80 km downstream of array A) were used to estimate the detection efficiency of array H: the last site used in the current analyses (see ‘Mark-recapture survival models’ below).

In addition to acoustic telemetry, PIT telemetry was used to compare migration rates across smolt sizes and tag types. PIT arrays were constructed in two locations. First, an array was constructed on the back-end of each of the two traps of the counting fence through which virtually all downstream migrating smolts must pass. These traps were ~50-m upstream of the release site for acoustic-tagged fish, and thus in our analyses is considered the same location as array A. The second array was constructed ~11.4 km downstream, and was placed with acoustic receivers at array G. The array consisted of two parallel pass-through antennae that spanned the entire river width (~28 m), separated by a horizontal distance of ~3-5 m. Low detection efficiency and periods of malfunction prevented using detections at this second PIT array for survival analyses (see ‘Mark-recapture survival models’ below), but allowed us to calculate migration rates for detected smolts to compare to acoustic-tagged smolts.

4.2.3 Smolt tagging and release

Smolts were captured at night via dipnet at the counting fence (Figure 4.1). Prior to tagging all smolts were anesthetized using MS-222 (100 mg l⁻¹ buffered with 200 mg NaHCO₃ l⁻¹), and measured for fork length (FL) and mass. Individual smolts receiving acoustic tags were placed in a custom-made V-shape trough with water continuously flowing over the gills (with a maintenance dose of 50 mg l⁻¹ MS-222 buffered with 100 mg NaHCO₃ l⁻¹). Vemco V7 tags (7 mm diameter, 18 mm length, 1.4 g in air, 123 d estimated battery life) were implanted through a ~7 mm incision on the smolt's ventral side. The incision was closed with two interrupted surgeon's knots using monofilament sutures (Ethicon monocril 5-0 monofilament 3/8 circle reverse cutting 13mm [P-3]). Smolts receiving PIT tags were held by hand and a 12mm x 2.12 mm (0.1 g) tag was implanted using a hypodermic syringe along the ventral side proximal to the ventral line. Due to tag burden concerns, only age-two smolts ≥ 120 mm FL were implanted with acoustic tags; PIT tags were implanted into both age-classes. After tagging, all smolts were given ~10 minutes to recover in an aerated cooler of river water prior to being transferred to buckets for later release. Release buckets had mesh sides to allow water flow, and were placed within larger tanks with flow-through ambient river water.

Smolts were released in the river at two locations: just downstream of the counting fence (array A), or ~1.3 km upstream of the fence (Figure 4.1). The upstream release site was used for a separate study examining the fine-scale movements of smolts (Furey, unpublished data), but smolts that reached array A were also included in analyses to increase sample size. Releases occurred the night after capture between 23:00 and 02:00 to match the general pattern of smolt outmigration; thus, the total holding time for all smolts was approximately 20-26 hours. For this

study, only smolts released or detected at array A were used (i.e. smolts that were released upstream were only considered if they were detected at array A or downstream). All releases occurred between 2015 April 29 and 2015 May 9.

In total, 235 acoustic-tagged and 576 PIT-tagged smolts were either released or detected at array A and were included in analyses. Acoustic-tagged smolts ranged in fork length between 121 and 183 mm (mean = 146 mm, SD = 9 mm), while PIT-tagged smolts ranged between 82 mm and 161 mm (mean 123 mm, SD = 22 mm). Of the PIT-tagged smolts used in analyses, 264 were age-one and 312 were age-two smolts.

4.2.4 Holding study

To investigate the short-term impacts of tagging on smolt survival and tag retention, 49 individuals were PIT tagged (both age-one and age-two), and 42 were implanted with dummy acoustic transmitters of the same mass and dimensions as those used. These fish were then located in a 200-L tank held streamside to the Chilko River. Ambient river water was pumped continuously through the tank, and each day the tank was checked for mortalities. Fish were held for 9 days, after which tag retention for all remaining smolts was verified. Over the 9 days, 100% of acoustic-tagged smolts and 96% of PIT-tagged smolts survived. Tag retention was 100% for both tag types.

4.2.5 Mark-recapture survival models

Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965) were used to estimate downstream survival of acoustic-tagged smolts. CJS models use the number of individuals passing an array and the detection efficiency of the array to estimate segment-

specific survival. Individual covariates were included in CJS models to test our hypotheses regarding the importance of predator swamping, timing, and body size on smolt survival. To test the influence of swamping, for each smolt the density of co-migrant conspecifics was estimated using the fine-scale temporal outmigration data collected at the counting fence (B. Leaf and K. Benner, DFO, unpublished data). Co-migrant density equaled the estimated number of smolts passing through the counting fence within 1 hour (between 30 minutes before and 30 minutes after) of either the individual's last detection at array A or the release time at array A, whichever was later. Hourly outmigration densities ranged between 0 and ~600,000 smolts during the 2014 outmigration (Figure 4.2), of which acoustic-tagged individuals experienced between 0 and nearly 420,000 co-migrants as they left array A (mean = 119,000; SD = 111,000; Figure 4.2). Co-migrant density values were square-root transformed to improve normality. Timing variables included the time of last detection at array A (calculated as the number of hours from midnight, with negative values indicating before midnight and positive values indicating a time after midnight), and the release date (as Julian day). For smolts released at array A that were not detected at array A, the release time was used to calculate the number of co-migrants. Size-based covariates included fork length, mass, and Fulton's condition index ($\text{mass}/\text{FL}^3 * 10,000$). Prior to CJS model construction, variables were standardised by subtracting the mean and dividing by two-times the standard deviation (Gelman 2008).

Survival was estimated for each segment between arrays A and H, with arrays B through H being located 2.9, 4.6, 7.9, 9.0, 10.1, 11.4, and 13.5 km downstream of the release site (Figure 4.1). Detections from a site further downstream (80 km from array A) were used to estimate detection probability and survival for the final array used in the current study (array H). Models

allowed detection probability p to vary by array, with the exception of the additional array used downstream of the study area. The detection probability (p) for this further site was fixed at 0.97, which is the mean value determined by similar CJS models constructed for four years of broad-scale telemetry in the system on smolts (Clark et al. 2016).

Candidate CJS models were constructed by allowing segment-specific survival (Φ) to vary among arrays and with a single fish-based covariate. Exploratory analyses found that performance of models were not improved by including interactions between a covariate and site (reported in Appendix B). An array-only model (i.e. Φ and p could vary with each array but were not influenced by other factors) and a null model (i.e., a single Φ and p estimated that was common to all arrays) were also constructed for comparison. A global model was assessed for overdispersion by calculating the overdispersion parameter c . If c was found to be >1 , standard errors (SE) of model results were inflated by the square root of this value. Candidate models were compared and ranked via quasi-Akaike information criterion corrected for small samples sizes (QAICc) and QAICc weights (w_i). Models were constructed using the program MARK (White and Burnham 1999) within the ‘RMark’ package (Laake and Rexstad 2007) in R (R Core Team 2014). CJS models were constructed with the following assumptions: 1) tagged smolts are representative of the population, 2) survival of tagged and untagged smolts is the same, 3) every tagged smolt had equal probabilities of survival and detection after release, 4) no tags are lost, 5) sampling is instantaneous, 6) each smolt’s fate is independent of other smolts, and 7) smolts swim downstream. From the final model, per-km survival was estimated from segment-specific Φ as:

$$k = \Phi^{1/d}$$

where k is distance-based survival rate, Φ equals segment-specific survival, and d equals segment distance (km).

4.2.6 Diel effects on migration

Most smolts pass through the counting fence at night. To determine diel patterns in downstream movements, I categorized the first detection of acoustic-tagged smolts at each array as either occurring during daytime or nighttime hours (sunrise and sunset calculated using coordinates for array D; National Resource Council Canada 2015). For each array, the proportion of smolts arriving at night was compared to the proportion of nighttime hours in a 24-hour diel period using a one-sample proportions test.

4.2.7 Migration rates

Migration rates were calculated based on the length of each river segment's thalweg (the deepest portion of the channel, as estimated using aerial imagery of the study site and ArcMap [ESRI, Redlands CA]), and the duration of time between segments. The duration between segments was defined by the difference in time between the first detection at the segment's first array and the first detection at the next array, with exception of the first segment (between arrays A and B). For this segment, the difference between the last time of detection at array A and the first detection at array B was used. If a smolt was released at array A but had no detections, the release time was used. For PIT-tagged fish, migration rate was only assessed between array A and array G.

To identify factors influencing downstream migration rates, a linear modelling approach was used. To be able to include both acoustic- and PIT-tagged smolts, migration rates between

array A and array G (the only shared locations) were calculated and used as the response variable. Conspecific outmigration density (as described in ‘Mark-recapture survival modelling’ above) was included as an explanatory variable to understand if migration rates were density-dependent. Timing-based explanatory variables included time of night (calculated as hours from midnight as described previously) and date of release/passage at array A (in Julian date). Size and fish-based explanatory variables included fork length (FL), Fulton’s condition index ($[\text{mass}/\text{FL}^3]*100000$), and a single factor combining age and tag type (resulting in three levels: age-one PIT, age-two PIT, and age-two acoustic). Because FL and age were highly correlated (Pearson correlation coefficient = 0.87), the FL was entered as the residuals between a regression of FL and age (as suggested in Graham 2003), and thus represent smolt FL relative to their age class. All continuous variables were standardised by subtracting the mean from each value and dividing by two-times the standard deviation (Gelman 2008). Collinearity was examined using variance inflation factor (VIF) and all VIF scores were less than 3.

I employed all-subsets regression using the MuMIn package (Barton 2015) in R (R Core Team 2014). All models were ranked based on AICc. For each model, the difference in AICc from the top model (ΔAICc), AICc weights (W_i), R^2 , and log-likelihood values were calculated. Model averaging, using the zero-method, was then employed across all models with $\Delta\text{AICc} < 4$ to estimate effect sizes and their variability. For each variable’s effect size, 95% confidence intervals were calculated to assess significance.

Because tag implantation has the potential to impair or alter swimming ability, and these effects can vary depending upon tag type (Cooke et al. 2011b), I directly compared the migration rates between PIT- and acoustic-tagged smolts to array G (shared by both tag types) using a

Mann-Whitney U test. In addition, migration rates were compared by combining tag type and age using a Kruskal-Wallis rank-sum test.

4.3 Results

4.3.1 Survival

Cumulative smolt survival over the first 13.5 km of the Chilko River was 68%. Of the seven river segments, the first two (array A to array B and array B to array C) resulted in the poorest survival (Table 4.1). The top CJS model estimating survival for acoustic-tagged smolts accounted for 100% of the total weight (Table 4.2), and thus was the only model further examined. Survival varied with array and the outmigration density of conspecifics (Table 4.2). Estimated survival probability of smolts co-migrating with ~2,000 conspecifics was ~50% while those travelling with ~350,000 conspecifics was ~95% (Figure 4.3). Detection probability was array-dependent and ranged between 0.80 (array G, which is in a more turbulent and fast-flowing section of river, and thus louder) and 1.00 (arrays E and H; Table 4.1). Using the median \hat{c} test in MARK (White and Burnham 1999) there was evidence of limited overdispersion ($\hat{c} = 1.20$), and all SE values were adjusted by a factor of the square root of \hat{c} . Although both timing variables performed better than null models (Table 4.2), both associated models contained 0% of the total weight and thus had little support.

4.3.2 Movements

Arrival times of smolts to all receivers were predominantly during nighttime hours (proportions tests, all p-values < 0.0001; Figure 4.4). The strongest nocturnal migration occurred at array C, where 96% of first detections occurred at night, while nighttime use was weakest at

array H, where 69% of smolts first arrived at night. Nighttime represented ~37% (8.8 hours) of the 24-hour diel cycle.

Smolts spent between 4.2 and 74.5 hours migrating the ~13.5 km downstream of array A (mean = 16.1 hours), resulting in maximum migration rates exceeding 0.8 m/s (mean = 0.23 m/s, or ~1.75 BL/s). These speeds generally exceeded river flow (0.1 – 0.3 m/s, as estimated at array A). There was a bimodal distribution in travel times, with one group of smolts taking between 4 and 13 hours to traverse the study area, and a second group taking between 16 and 29 hours; there was also a small contingent of fish requiring > 40 hours (Figure 4.5). These trends also persisted for PIT-tagged smolts detected at array G (Figure 4.5). The multimodal distribution for acoustic-tagged smolts was largely a result of migration experience in the segment between arrays B and C. In fact, 47 of the 155 (~30%) acoustic-tagged smolts detected at both of these arrays took at least 12 hours to travel the ~1.7 km to reach array C (i.e. passing the following night), indicating that smolts paused migration until the next sunset. Further analyses demonstrated that this pausing behaviour was linked to timing; smolts that paused between arrays B and C arrived to array B later than those that continued to array C in the same night (Mann-Whitney U test; $W = 258.5$; $p\text{-value} < 0.00001$; Figure 4.6). The proportion of smolts pausing migration between any two other successive arrays was less than 7%.

In models explaining variability in migration rate, time of night and the combined factor of tag type and smolt age were retained in all models with $\Delta\text{AICc} < 4$ (Table 4.3). Of these, only time of night had an effect size for which the 95% confidence intervals excluded zero (Figure 4.6), indicating it to be a strong predictor of migration rate. The effect size was negative, signifying that smolts leaving array A later (into the morning hours) had reduced migration rates.

This effect appeared largely due to the bimodal distribution in travel times and apparent pausing behaviour noted above. Smolts leaving array A at 01:00 or later exhibited migration rates (< 0.2 m/s) that were half or one-third of the rates exhibited by smolts moving downstream earlier ($\sim 0.4 - 0.8$ m/s). Aside from time of night, the effect size for age-2 PIT-tagged smolts was the largest, but its confidence intervals narrowly included zero (Figure 4.7). Models with $\Delta AICc < 4$ explained 41-44% of the variability in migration rates. Other variables were not retained consistently across models, including date of migration initiation, outmigration density, condition, and FL.

Even though there was no difference in migration rates between PIT- and acoustic-tagged smolts (Mann-Whitney U test; $W = 4168$; $P = 0.13$), differences were found when accounting for age in addition to tag type. Age-2 PIT-tagged smolts migrated at consistently faster rates than age-1 PIT-tagged smolts (Kruskal-Wallis rank sum test; chi-square = 5.36; $df=1$, $P = 0.021$ Figure 4.8). Acoustic-tagged smolts (all age-2) were not different in migration rate compared to age-1 PIT tagged fish (Kruskal-Wallis rank sum test; chi-square = 0.05; $df=1$, $P = 0.817$), though they were slower in general than age-2 PIT-tagged smolts (Kruskal-Wallis rank sum test; chi-square = 5.97; $df=1$, $P = 0.008$).

4.4 Discussion

Survival of smolts was poor (68%) in the first 13.5 km of the Chilko River even though migration rates were rapid and smolt duration in the system was generally less than 48 hours. These results are consistent with previous telemetry research in the system and confirm this landscape to be high-risk for migrant sockeye salmon smolts, as survival is nearly 100% once smolts reach the large, fast-flowing, and turbid Fraser River (Clark et al. 2016). I am confident

that poor survival is not a result of holding and/or tagging effects. Survival of dummy-tagged smolts was 100% survival, similar to the 96-100% survival of held dummy-tagged smolts 2010-2012 (Clark et al. 2016). In addition, Clark et al. (2016) found no effect of tagging on either Chilko sockeye smolt burst swimming speeds or time to fatigue, indicating there should be little effect of tagging on behaviour, although I cannot discount the possibilities for interactions between tagging and other stressors of migration. Furthermore, I believe the disappearance of tagged smolts in the system to be a strong proxy for predation-based mortality, even though fate of tagged individuals cannot be confirmed. A suite of predators exist in the upper Chilko River (Clark et al. 2016) and bull trout have been confirmed to congregate in large aggregations and binge-feed on smolts during the smolt outmigration (Furey et al. 2015; Furey unpublished data). Furthermore, transportation of smolts beyond the upper Chilko River in prior years improved survival of smolts (Clark et al. 2016), indicating that this landscape is high-risk. The apparent primary mechanism for reducing predation risk was travelling in high densities to swamp predators during the strongly nocturnal migration. Smolt size and inter-seasonal timing did not appear to modify predation risk. The relative importance of mechanisms in reducing predation risk is probably due to specific features of this system and landscape.

Increased densities of co-migrants improved survival of individual smolts, providing rare empirical example of swamping effectively reducing predation risk across individuals during a migration. Pairing pseudo-experimental releases of telemetry-tracked individuals with high-resolution data on population-level movements and densities allows us to extend evidence of swamping beyond classic examples associated with the emergence of insects such as mayflies (Sweeney and Vannote 1982) and cicadas (Williams et al. 1993) to migrants moving across a

landscape. I suggest researchers focus on systems for which predation rates could be high for migrants, such as post-emergence movements of sea turtle hatchlings or river crossings by wildebeests, to begin to understand conditions under which swamping is effective.

The large population size of Chilko smolts could facilitate swamping efficacy in our study system; an average of ~20 million emigrate from the lake each year (Irvine & Akenhead 2013) over a period of 3-5 weeks. Although swamping may be non-beneficial if migration synchronization results in predator aggregations, I surmise that the smolt population is large enough that predators would respond to outmigrations regardless of smolt timing. Thus, there appears to be strong selective pressure to synchronize outmigration to overwhelm predators. The timing of smoltification (the changes in physiology and morphology required to prepare for living in the marine environment) appears linked to daily photoperiod, and subsequent migration of smolts may be cued by the warming of lake water post ice break-up (Burgner 1991). Environmental cues for initiating migration should aid synchronization of movements across the population. The Chilko smolt outmigration is generally characterized by two or three large peaks of outmigrants, as was evident in our study year (2014), but variability on shorter time-scales (hourly to daily) is quite high. Future research should further investigate the variability in outmigration densities to better quantify the effects of density-dependent predation risk at the population level, and to identify factors (behavioural, environmental, or otherwise) resulting in variability in migration densities.

In addition to swamping predators by synchronizing migration, smolts outmigrate from the lake primarily at night, and continue this nocturnal migration through the upper Chilko River. To ensure nocturnal migration, many smolts paused migration, particularly within the first two

river segments where survival was poorest. Pausing resulted in travel durations 2-5 times longer than smolts completing the migration in a single night, hinting at strong selection against moving during the day. These observations are consistent with nocturnal migration being important in reducing predation risk, although I was unable to make a direct link between timing and survival. The predators feeding on smolts (birds and bull trout; Clark et al. 2016; Furey et al. 2015) are visual-based foragers, and thus nocturnal migration should reduce foraging efficiency. In addition, the upper Chilko River is clear during smolt outmigration; therefore individuals receive little protection from turbidity (Gregory and Levings 1998, De Robertis et al. 2003, Hansen et al. 2013b). Once downstream of the Chilko River, however, migrations become less nocturnal and smolts travel day and night in the turbid waters of the large Fraser River and in the estuarine Strait of Georgia (Clark et al. 2016). Atlantic salmon (*Salmo salar*) smolts migrate nocturnally as well, but such behaviour is only prominent for small individuals and with reducing prevalence throughout the season (Ibbotson et al. 2006; Ibbotson et al. 2011). Thus the predation risk of smolts in the current study might be more extreme and/or consistent to result in adaptive behavioural mechanisms across smolt sizes and seasonal timing.

Outside of salmonids and diel vertical migrations, nocturnal migrations as a mechanism to reduce predation appears rare. Sea turtle hatchlings might be the best comparison, as emergence often occurs at night, both to reduce predation and to avoid intense heat (Mrosovsky 1968). Birds also often migrate at night, and could potentially reduce predation rates, but the largest benefit is potentially optimizing foraging efficiency at stopover sites during the day (Alerstam 2009). Migrations are metabolically costly; energy expenditure is high due to directed and often constant movements and feeding is often completely repressed or reduced while

migrating (Dingle and Drake 2007, Sapir et al. 2011). Thus the decision to migrate nocturnally is not made solely on the risk of predation, but rather is a balance among the varying associated costs. Further theoretical investigations could provide insight into the conditions necessary for nocturnal movement of migrants as an adaptive predation-reducing mechanism.

At broader time-scales, I found no evidence of intra-seasonal timing influencing behaviour or survival, which is counter to the findings of (Scheuerell et al. 2009). Hypotheses regarding the importance of smolt timing, however, revolve around variable marine conditions experienced after exiting freshwater (McCormick et al. 1998, Scheuerell et al. 2009), and thus the impacts of timing might be landscape-specific. Our results may also be limited as tagging began ~10 days after outmigration began. Timing can also be of greater importance in systems with generalist predators that employ prey-switching such as those that consume turtle hatchlings (Tucker et al. 2008), or when predators themselves undergo seasonal migrations that can be avoided, as demonstrated in migrant birds (Lank et al. 2003; Ydenberg et al. 2007).

Although swamping and nocturnal migrations are both likely to influence predation risk of smolts, our results did not support the “bigger is better” hypothesis. Our lack of support for this hypothesis appears due to only acoustic-tagging age-two smolts, as large size-based effects were found, with smaller fish within both age classes experiencing higher risk, by examining predation risk via bull trout stomach contents on this same year class (Chapter 3). The impacts of size may vary year-to-year, as only slight (but significant) size-based selection by bull trout was found in the 2013 outmigration by examining stomach contents (Furey et al. 2015). Avian predators also feed on smolts, and often select for intermediate or even large smolts (Hostetter et al. 2012; Osterback et al. 2014). Tucker et al. (2016) found larger smolts of multiple Pacific

salmon species, including sockeye, to have reduced predation risk in the early marine environment, and other research has placed importance of size on smolts once in the marine environment (Holtby et al. 1990).

Survival was poorest in the first two river segments, indicating variable predation risk across the landscape. Landscape structure can influence predator aggregations via modifying energetic costs and foraging efficiency (Bouchet et al. 2014), and the riverscape structure of the first two segments studied might allow high foraging efficiency of predators. The first segment (arrays A to B) occurs immediately downstream of the counting fence, an extreme bottleneck for smolts that aggregates bull trout. The subsequent segment (arrays B to C) also resulted in poor survival, and contains the largest natural spatial bottleneck, where the river quickly narrows after ~1-km of deep (>10-m), lake-like conditions (Figure 4.1). Bull trout also aggregate at this bottleneck (Furey unpublished data). It is interesting that nocturnal migration by smolts was strongest in these earlier segments with spatial bottlenecks and high mortality. Comparative studies across river systems would help to determine the universality of use of spatial bottlenecks by predators exploiting downstream smolt migrations, subsequent spatial variability in risk due to bottlenecks, and behavioural reactions of migrants to perceived risk.

Poor survival occurred even though migration was rapid. Migration rates of smolts were as fast as ~0.8 m/s (~6 body lengths/s) for individuals completing the migration within one night (mean of ~0.2 m/s across all fish or ~1.33 body lengths/s), providing evidence for directed migration. These migration rates are comparable to other downstream smolt migrants (Johnson et al. 2010, Michel et al. 2013) and to previous years of this population (Clark et al. 2016), although variability probably due to river size occurs across species and populations (Melnichuk et al.

2010). The greatest predictor of migration rate in our study was time of day, such that smolts migrating downstream earlier in the night could complete the studied section in a single night without pausing, while later-timed migrants required at least one additional nighttime period. Migration rates were also reduced for age-one PIT-tagged fish relative to age-two PIT-tagged fish, and could be indicative of size-based differences in swimming speed or behaviour.

Our ability to effectively characterize the migration experience of smolts is limited by how tagged fish behave relative to non-tagged fish. Although I have no evidence that tagging influenced survival (informed by our and previous tag-holding studies; Clark et al. 2016), I did find age-2 smolts with acoustic tags migrated at rates more comparable to PIT-tagged age-one smolts than PIT-tagged smolts of the same age. This result was surprising given Clark et al. (2016) found no difference in burst swim endurance or speed between acoustic-tagged and untagged Chilko sockeye smolts. I also note that this effect on migration rate was weak in relation to other factors, and was not found to be significant, via the model-averaging approach (Figure 4.7). Regardless of the strength or mechanism, however, our results indicate that our use of acoustic telemetry may reduce migration rates of smolts. Such reduction in speed could result in a greater proportion of tagged smolts pausing migration relative to untagged age-two smolts. Although I cannot estimate the potential effects of PIT-tagging on migration rates for either age class relative to non-tagged smolts, (Newby et al. 2007) did not find an influence of PIT tagging on swim performance of juvenile rainbow trout (*Oncorhynchus nerka*). If PIT-tagging effects are negligible, it is possible that acoustic-tagged age-2 fish swim at similar rates relative to untagged age-one smolts, which make up the vast majority (~95%) of the outmigrant population.

In conclusion, I provide evidence that swamping behaviour is an important mechanism for increasing outmigrant juvenile sockeye salmon smolts survival during nocturnal migration through an area of high risk. These movement-based mechanisms were more important than individual size, and underscore the importance of quantifying and investigating movements in attempting to understand the migratory process (Nathan et al. 2008). I provide a rare example of density-dependent swamping effectively reducing predation risk of individual migrants. Additional empirical examples are needed to understand the generality of risk-reducing mechanisms such as swamping across taxa and landscapes. I hypothesize that density-dependent predator swamping is a common and effective behavioural mechanism for migrants across systems and taxa, but remains difficult to directly measure in the field. However, this research demonstrates the power in combining individual-based telemetry with population-level assessments in successfully demonstrating swamping efficacy.

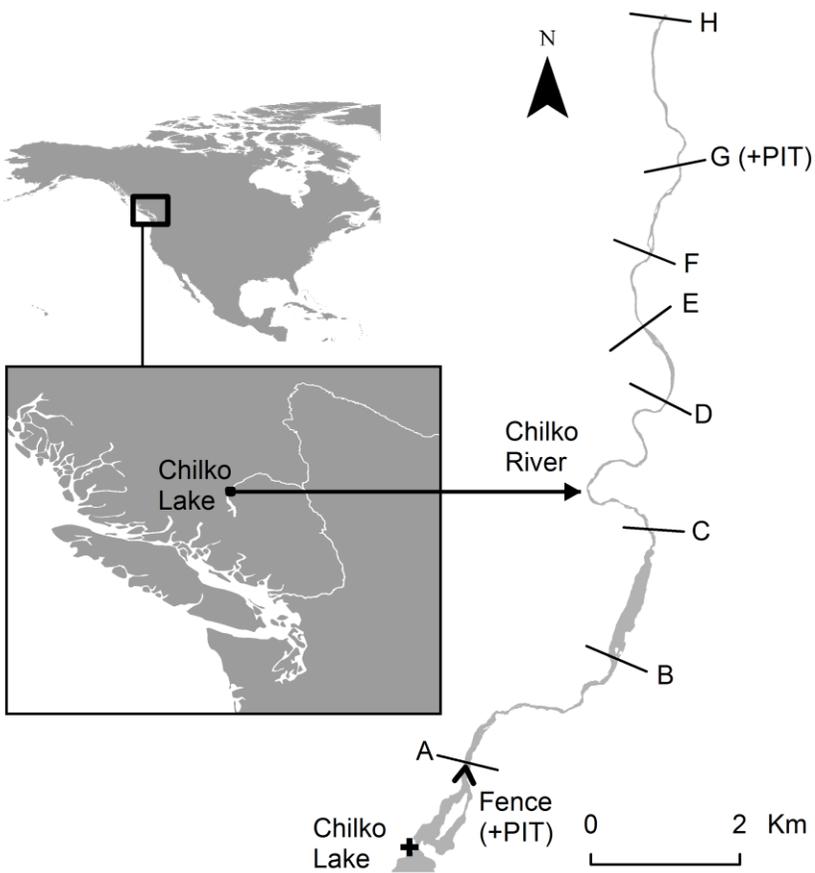


Figure 4.1 The upper Chilko River, British Columbia, Canada. The study occurred in the first 13.5 km of the Chilko River immediately downstream of the counting fence. Locations of acoustic telemetry receivers and PIT arrays are given. Smolts were released at array A and at the cross symbol.

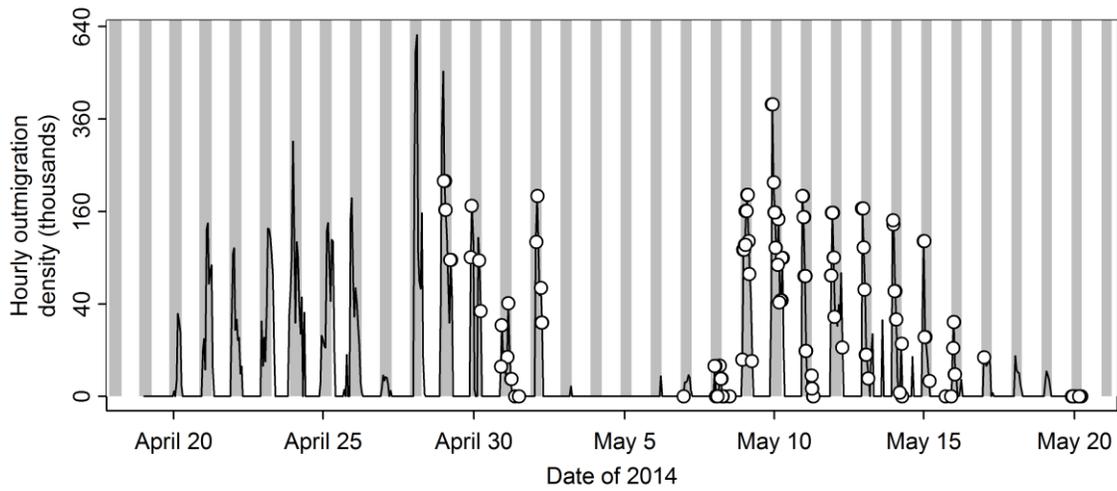


Figure 4.2 Hourly outmigration densities of Chilko sockeye salmon smolts passing through the counting fence. Lines indicate the hourly outmigration counts through the study period in 2014. Grey bars indicate nighttime hours. Circles represent the time of last detection or release (whichever was later) of individual acoustic-tagged smolts.

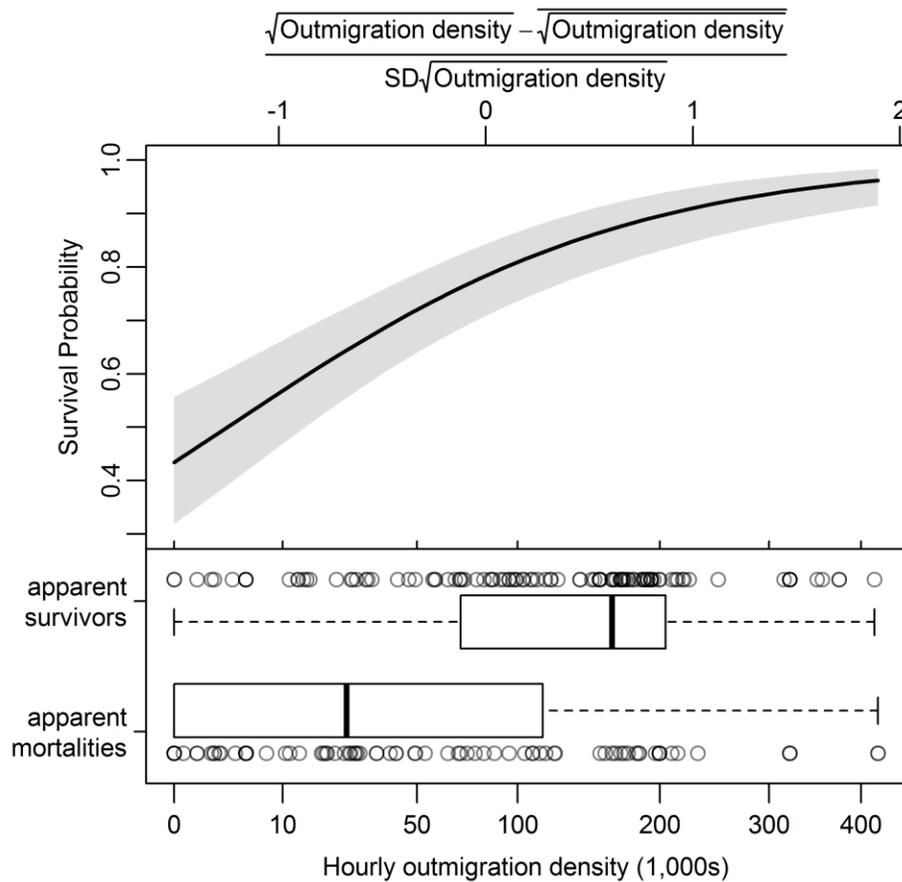


Figure 4.3 Density-dependent effects on survival of downstream-migrating juvenile sockeye salmon smolts. Top panel depicts survival probability across experienced outmigration densities as predicted by the top CJS model. Bottom panel displays the outmigration density values for individual smolts (circles) that were detected at array H (apparent survivors) and those not detected at array H (apparent mortalities), as well as boxplots depicting their distributions. Left-hand and right-hand edges of boxes are the 25th and 75th percentile of experienced outmigration densities, and boxplot whiskers extend to the range of all values observed. The upper x-axis depicts outmigration densities in terms of the number of standard deviations (SD) from the mean square-root transformed value.

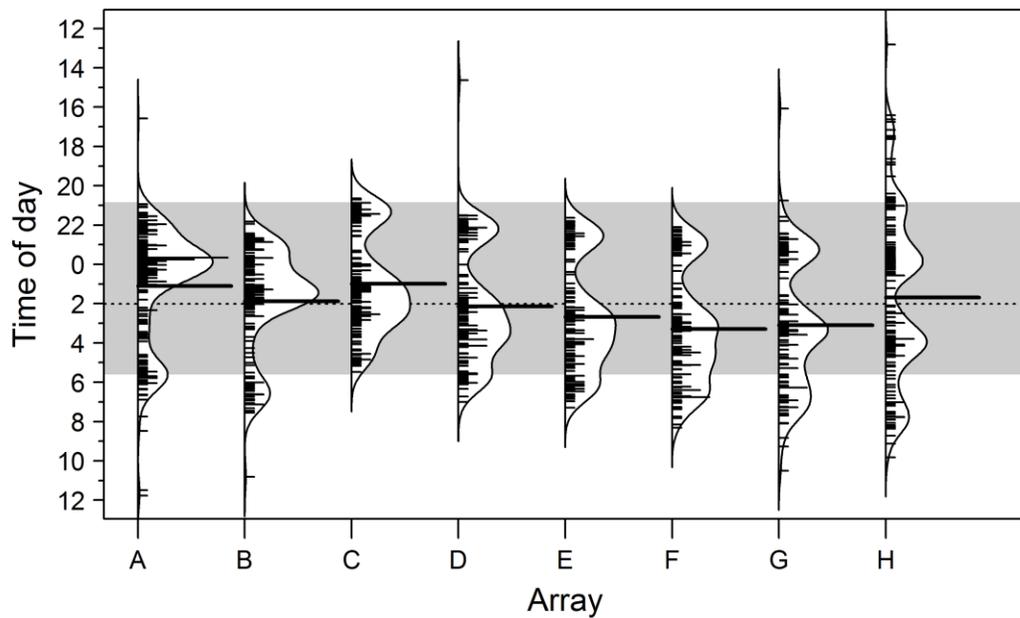


Figure 4.4 Beanplots of arrival times (except array A, which are times of last detections) of sockeye salmon smolts migrating downstream at each array. Grey shading indicates nighttime hours. Dashed line indicates the mean arrival time across all smolts and arrays. Thick lines indicate the mean arrival time for each array. Thin lines represent arrival times of individual fish for an array.

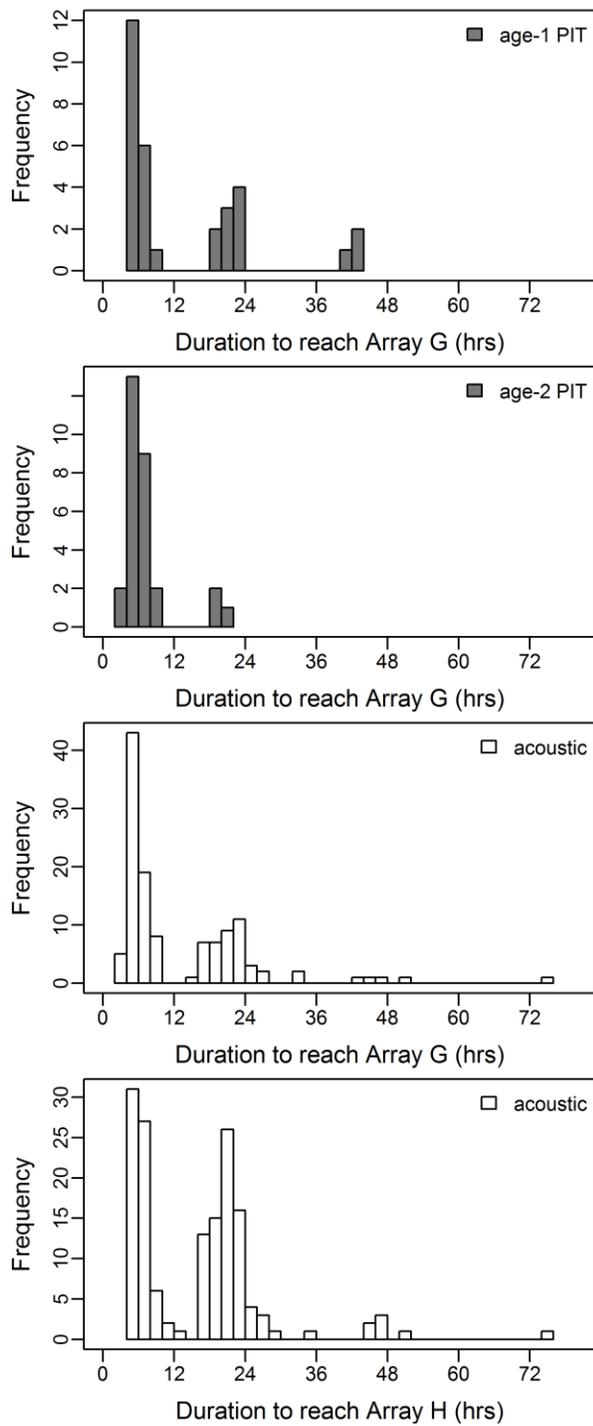


Figure 4.5 Histograms of the duration of time to reach either array G (shared array for PIT-tagged and acoustic-tagged sockeye smolts) or array H (the final array for acoustic-tagged smolts). Note values along the y-axes differs among histograms.

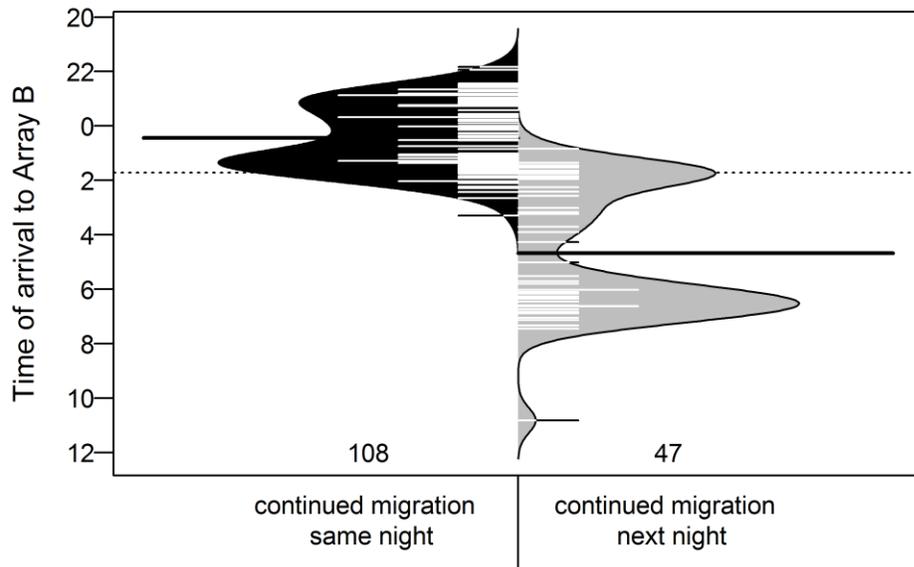


Figure 4.6 Beanplot characterizing the distributions of smolt arrival times to array B between smolts that continued to array C the same night (black) or smolts that paused migration and continued to array C the next night (grey). White horizontal lines represent individual smolts, and the solid black line represents each group's mean. The dashed horizontal line represents the mean value across all smolts. Numbers denote sample sizes for each behaviour. During the study mean sunrise was 05:37 and mean sunset was 20:50.

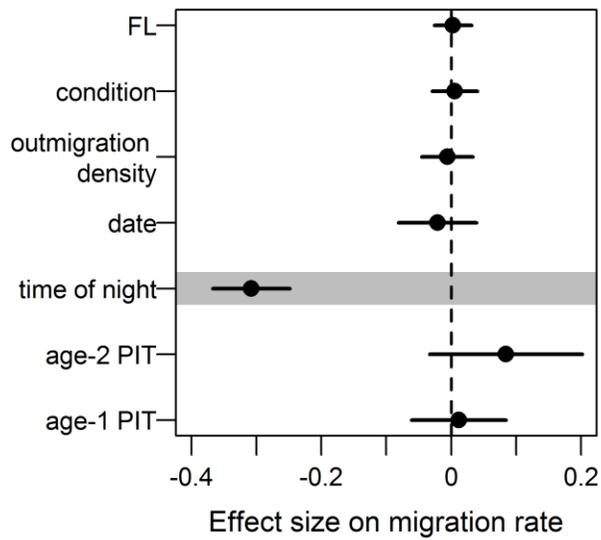


Figure 4.7 Relative effect sizes of variables on downstream migration rates of sockeye smolts, as determined by model averaging of all-subsets regression. Time of night, the only variable for which the 95% confidence intervals exclude zero, is high-lighted in grey.

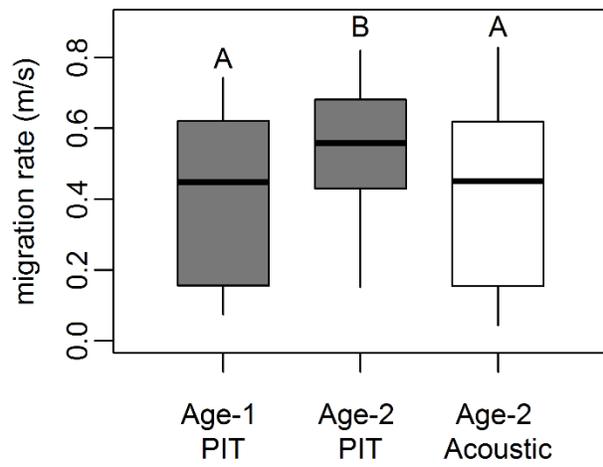


Figure 4.8 Boxplots of migration rates of smolts by age and tag type combination. PIT-tagged fish are in grey, and acoustic-tagged fish in white. Different letters indicate significant differences in migration rates (Kruskal-Wallis rank-sum test; $\alpha = 0.05$).

Table 4.1 Summary of segment-specific survival and detection probability, per-km segment-specific survival, and cumulative survival of downstream migrant smolts from the top CJS model. Segment length (km) and cumulative length (km) are also given. Standard error (SE) values were adjusted by $\hat{c} = 1.20$.

Segment	Survival Φ		Segment length	Per-	Cumulative	
	(SE)	p (SE)	(km)	km	Φ (SE)	Cumulative
				Φ		length (km)
A to B	0.78 (0.03)	0.99 (0.01)	2.877	0.92	0.78 (0.03)	2.877
B to C	0.94 (0.02)	0.98 (0.01)	1.725	0.96	0.73 (0.04)	4.602
C to D	0.96 (0.02)	0.90 (0.03)	3.293	0.99	0.70 (0.04)	7.895
D to E	0.98 (0.01)	1.00 (0.00)	1.075	0.98	0.69 (0.04)	8.970
E to F	0.99 (0.01)	0.94 (0.02)	1.178	0.99	0.68 (0.04)	10.148
F to G	0.99 (0.01)	0.80 (0.04)	1.300	0.99	0.68 (0.04)	11.448
G to H	1.00 (0.00)	1.00 (0.00)	2.055	1.00	0.68 (0.04)	13.503

Table 4.2 Ranking of CJS models based on QAICc. Terms in parentheses indicate factors across which survival (Φ) or detection probability (p) varies. The array-only and null models are presented for reference.

Model	npar	QAICc	Delta QAICc	weight
Φ (~array + conspecific density) p (~array)	16	758.9	0.0	1.00
Φ (~array + time of night) p (~array)	16	794.6	35.7	0.00
Φ (~array + date) p (~array)	16	802.1	43.2	0.00
Φ (~array) p (~array)	15	803.8	44.9	0.00
Φ (~array + mass) p (~array)	16	805.5	46.6	0.00
Φ (~array + FL) p (~array)	16	805.7	46.8	0.00
Φ (~array + condition) p (~array)	16	805.7	46.8	0.00
Φ (~1) p (~1)	2	910.5	151.6	0.00

Table 4.3 Descriptions and summary statistics for all models with $\Delta\text{AICc} < 4$ for models explaining variability in migration rates (as well as the null model). ‘logLik’ is the log-likelihood, and W_i is the AICc weight of the model. The combination of smolt age and tag type was used as a single factor variable, and thus depicted in parentheses.

Model	R ²	logLik	AICc	ΔAICc	W_i
(Tag+Age)+Time of Night+Date	0.44	49.09	-85.67	0.00	0.13
(Tag+Age)+Time of Night	0.43	47.94	-85.51	0.16	0.12
(Tag+Age)+Time of Night+Date+Density	0.44	49.44	-84.18	1.49	0.06
(Tag+Age)+Time of Night+Date+Density	0.44	48.32	-84.12	1.55	0.06
Time of Night	0.41	45.11	-84.08	1.59	0.06
(Tag+Age)+Time of Night+Date+Condition	0.44	49.24	-83.79	1.87	0.05
(Tag+Age)+Time of Night+Date+FL	0.44	49.19	-83.69	1.98	0.05
(Tag+Age)+Time of Night+FL	0.43	48.05	-83.59	2.08	0.05
(Tag+Age)+Time of Night+Density	0.43	47.97	-83.42	2.25	0.04
Time of Night+Date	0.42	45.61	-82.98	2.68	0.03
Time of Night+Density	0.42	45.42	-82.59	3.08	0.03
Time of Night+Condition	0.42	45.39	-82.53	3.14	0.03
Time of Night+Date+Density	0.42	46.38	-82.39	3.28	0.03
(Tag+Age)+Time of Night+Date+Density+FL	0.44	49.60	-82.30	3.37	0.02
(Tag+Age)+Time of Night+Condition+FL	0.44	48.48	-82.27	3.40	0.02
(Tag+Age)+Time of Night+Date+Density+Condition	0.44	49.57	-82.23	3.44	0.02
(Tag+Age)+Time of Night+Date+Density+Condition+FL	0.44	48.36	-82.02	3.65	0.02
Time of Night+FL	0.41	45.11	-81.98	3.69	0.02
(Tag+Age)+Time of Night+Date+Condition+FL	0.44	49.37	-81.85	3.82	0.02
Null	0.00	0.03	4.01	89.68	0.00

Chapter 5: Variability in migration routes influences early marine survival of juvenile salmon smolts

5.1 Introduction

An organism's movements directly impacts its ecology, as changes in spatial locations over time influence interactions among conspecifics, competitors, predators, and/or resources (Nathan et al. 2008). Migrations are a unique subset of directed movements that are observed across taxa including mammals, birds, reptiles, invertebrates, and fish (Wilcove and Wikelski 2008, Milner-Gulland et al. 2011). The movement trajectory or route defines the landscapes traversed and consequently the conditions experienced (Nathan et al. 2008). In theory, migration routes should be optimized to improve probability of survival, but routes can still vary considerably among individuals (Gschweng et al. 2008, Jonzén et al. 2011, Mueller et al. 2013), resulting in differing energetic costs and conditions being experienced (Felicísimo et al. 2008, Mellone et al. 2011), presumably due to either suboptimal behaviour or individual-specific optima (Bauer et al. 2009). At present, few empirical examples relate variability in movements to future fitness or survival to confirm the importance of movements to an organism's ecology (Holyoak et al. 2008, Nathan et al. 2008). Characterizing the variability in the specific routes utilized and relating this individual variability to survival is needed to better understand the migratory process.

Among migratory fish, anadromous salmon are among the most studied due to their economic, cultural, and ecological value (Hinch et al. 2006). Juvenile salmon smolts enter marine waters after rearing in freshwater, and survival during the early coastal migration has

been suggested to be size or growth dependent (Beamish and Mahnken 2001, Beamish et al. 2004) and influence overall population productivity (Beamish and Mahnken 2001, Beamish et al. 2004, Chaput et al. 2005, Mckinnell et al. 2014). Migratory behaviour in the early marine environment, however, remains understudied (Hinch et al. 2006, Drenner et al. 2012), and there has been a call to assess the impacts of migration patterns on smolt survival (Melnychuk et al. 2010). The current paradigm for Pacific smolt movements in estuarine and coastal waters describes linear migratory paths (Groot and Cooke 1987, Peterman et al. 1994), whereby smolts move northward upon entry into the Strait with few lateral movements, but this paradigm has largely been constructed on population-level sampling using purse seine of unmarked individuals during the migratory period and inferring the migration biology from the size and relative abundance of individuals in the catches. The proposed movement patterns have not been verified directly. Therefore, there is a need to characterize migration routes of individuals and to identify factors that result in variability in migratory experience.

For many Pacific salmonids, including those of the productive Fraser basin, the Strait of Georgia, a narrow semi-enclosed marine sea, represents an important component of the migratory corridor. Of these species, smolts across populations of both sockeye salmon (*Oncorhynchus nerka*) and steelhead trout (*Oncorhynchus mykiss*) are thought to move quickly through the Strait of Georgia and then along the continental shelf before eventually reaching offshore feeding grounds, unlike other species that can remain in the Strait of Georgia for extended periods (Quinn 2005, Tucker et al. 2009, Melnychuk et al. 2010, Welch et al. 2011, Preikshot et al. 2012, Beacham et al. 2014). Coastal migrations are assumed to be a result of using local cues to assist in migratory navigation (reviewed in (Byron and Burke 2014)). Large-

scale acoustic networks have been used to describe migration rates and survival in coastal waters for outmigrant juvenile salmon (Melnichuk et al. 2007, 2010, 2013, Welch et al. 2009, 2011, Rechisky et al. 2014), but the fine-scale migration routes used in marine waters have largely remained undescribed nor has their relationship with survival been assessed.

The characterization of movement has become increasingly possible with the advent and continued development of biotelemetry (Cooke et al. 2004b). For small-bodied fishes such as smolts, acoustic telemetry in particular provides a balance between tag size and detection efficiency. Fine-scale arrays have been used to track movements of individual fishes using triangulation methods (Klimley et al. 1998, Espinoza et al. 2011, Furey et al. 2013), but generating these arrays at spatial scales large enough to determine marine migration routes of smolts would be cost-prohibitive. Conversely, large-scale telemetry networks, such as the Pacific Ocean Shelf Tracking (POST; (Welch et al. 2002)) system and the Ocean Tracking Network (Cooke et al. 2011a, Hussey et al. 2015), utilize multiple arrays spaced at greater distances, but are generally used for broad-scale estimates of migration rates and survival rather than characterizing specific migration routes (i.e., (Welch et al. 2009, 2011)). These networks, however, are often made up of “curtains” or arrays of many individual receivers to help ensure detection at specific checkpoints along movement corridors (Heupel et al. 2006), and therefore it is possible that more detailed information on behaviour could be obtained by examining data within a single array rather than simply among arrays.

The current study aims to determine the migratory routes used by juvenile sockeye and steelhead smolts in the Strait of Georgia, and to determine the influence of individual variability in movements on survival. Using acoustic telemetry data collected across populations from

2004-2013 (Melnychuk et al. 2007, 2010, 2013, Welch et al. 2009, 2011, Rechisky et al. 2014) (Table 5.1), I examined detections at a single large-scale array: the northern Strait of Georgia (NSOG; Figure 5.1). I assessed initial east-to-west distributions of >850 smolts arriving at this array, the direction and magnitude of subsequent movements, and survival to the next array at Queen Charlotte Strait (QCS), located ~250 km farther along the migration path (Figure 5.1).

5.2 Methods

5.2.1 Acoustic telemetry studies

I examined marine movement patterns from acoustic telemetry data for three sockeye populations (Cultus Lake [2004-2007], Sakinaw Lake [2004-2007], and Chilko Lake [2010-2013]), and three steelhead populations (Englishman [2004-2006], Seymour [2006-2008], and Cheakamus [2004-2005 and 2007-2008]) whose natal streams (or hatcheries) lie in watersheds of the lower Strait of Georgia (Figure 5.1 and Table 5.1). These populations share a similar early marine migration during the late spring and/or early summer (release dates of tagged smolts occur mid-April to early-June), in which smolts migrate to the north through the Salish Sea region (Figure 5.1) to the open Pacific (Welch et al. 2011). For sockeye, body size and rearing origin differ between Chilko and Cultus sockeye. Chilko sockeye smolts are from a wild and large population (up to 40 million smolts outmigrate each year) for which tagged fish are generally 120-130 mm FL. In comparison, Cultus sockeye is an endangered population and the smolts tagged were reared under hatchery conditions as part of a conservation program to rebuild this population, and all tagged individuals were larger in comparison (generally 175-190 mm FL). In addition, Englishman steelhead are the only population in the current study that originates on Vancouver Island rather than the British Columbia mainland.

For all studies, smolts were captured in natal freshwater systems or collected from a hatchery, and then implanted with either VEMCO (Halifax, NS) 69 kHz V7 (Chilko sockeye) or V9 (all other populations for both species) acoustic tags through a small abdominal incision along the ventral side of the body. Further details regarding surgeries can be found within references cited in Table 5.1.

5.2.2 Acoustic receiver arrays

This study focuses on the detections of tagged smolts at the northern Strait of Georgia (NSOG) array (Figure 5.1), which was installed by the Pacific Ocean Shelf Tracking project (Welch et al. 2002) and subsequently maintained by the Ocean Tracking Network (Cooke et al. 2011a). The NSOG array spans the Strait of Georgia and Malaspina Strait, and contains 26 separate acoustic telemetry receivers which are spaced at approximately 800 m intervals (Figure 5.1), with the 7th and 8th receivers separated by ~8km on either side of Texada Island (Figure 5.1). A 27th receiver was also part of the array for some of the studies, but only a total of 4 smolts were ever detected on this receiver. Due to the geometry of this array, it is possible to characterize the east-to-west distribution in detections of smolts as they approach from the south, and then examine their subsequent behaviours. Smolts could then be subsequently detected at the Queen Charlotte Strait (QCS) array approximately 250 km to the northwest as they exit the Strait of Georgia (Figure 5.1). Detections at the QCS array can be utilized to determine subsequent survival of smolts initially detected at the NSOG array. Depending on the year, arrays were made up of VEMCO 69 Khz VR2, VR3, or VR4 receivers. Smolts could also be detected on the western Juan de Fuca Strait array (JDF; Figure 5.1), but < 2% of smolts were detected here, and thus detections on this array were not analyzed.

5.2.3 Detection data

Large-scale acoustic monitoring systems such as the NSOG array generate large quantities of detection data, much of which is redundant (in the sense that multiple detections of the same animal at closely spaced time intervals does not constitute new information but merely verification of occurrence at a particular time). Analyses were based on ‘detection sequences’ rather than just ‘detections’, allowing detections be grouped in order to represent distinct occurrences at the array. I define a detection sequence as one or more detections of a unique tag (i.e., individual smolt) on a receiver array such that 1) consecutive detections are less than one hour apart, and 2) consecutive detections occur within two receivers’ distance of the previous detection (≤ 1.6 km). Individual detection sequences can be summarized by the following characteristics: 1) the date, time, and receiver position number (or distance in km) of the first detection, and 2) the date, time, and receiver position of the last detection.

5.2.4 Data analysis

The initial distribution of smolts from each species was examined by determining the number of smolts whose first detection sequence was initiated at each of the 27 receivers in the NSOG array. To test for disproportional use of Malaspina Strait (receivers 1-7, spanning the coastal ocean between the British Columbia mainland and Texada Island) versus the Strait of Georgia (receivers 8-27, spanning the coastal ocean between Texada Island and Vancouver Island; Figure 5.1), a proportional test was conducted for each species, weighted on the relative width (number of receivers in the array) of each strait. To examine how distribution might be influenced by release point (natal location), the same analysis was conducted using only Englishman River steelhead (the only population to originate on Vancouver Island).

The difference in receiver position between the first and last detection within the initial detection sequence at NSOG gives insight as to whether the smolt was moving directly through (i.e., perpendicular to) the array, or moving at an angle towards the east or west. The difference in receiver position between the last and first detections within the initial detection sequence was calculated for each smolt, such that movements to the west resulted in a negative value, and movements to the east resulted in a positive value. For each species, a Mann-Whitney U test determined if the difference in receiver position significantly differed from zero.

By comparing the locations of the first detection sequence and second detection sequence, a smolt's migratory experience or "migratory route" was defined. A "counterclockwise" migration route occurred if the second detection sequence occurred to the west of where the first ended, and a "clockwise" migration route occurred if the second detection sequence occurred to the east of where the first ended. If the second detection sequence occurs not on the NSOG array but at the QCS array, I define the smolt as not undergoing detectable east-west movements in the immediate area of the NSOG array. Although a smolt's movements elsewhere between the NSOG and QCS arrays are unknown, for the purpose of characterizing the variability in movements observed, I define this detection history as a "linear" migration route. Linear routes also included instances when the second detection sequence began at the same receiver as the last detection of the first sequence. The proportion of each migratory route (linear, counterclockwise, and clockwise) was calculated for each release group (year and population combination) for each species, as it was expected that the routes experienced within a release could be correlated. Analysis of variance (ANOVA) was used for each species to compare proportions among migratory routes. In addition, ANOVAs were weighted by the

number of individuals within each release group that exhibited one of the three routes (i.e., as release groups varied greatly in sample size (Table 5.1). When the ANOVA was significant, pair-wise comparisons among all migration routes were made with Tukey's honestly significant differences (HSD).

Once migratory routes were defined, the scale of movements along the NSOG array were calculated. East-to-west differences (Δx) between the end of the first and the beginning of the second detection sequences (Δx_{12}) and similarly between the second and third (Δx_{23}) were calculated as the difference in the number of receivers between these sequences (two adjacent receivers represents a Δx of 0.8 km; if the subsequent detection is to the east of the original $\Delta x = 0.8$ and if the subsequent detection is to the west of the original $\Delta x = -0.8$ km). If the second detection sequence began at the location of the first, a Δx of zero was assigned. In addition, for movements spanning Texada Island along the NSOG array (Figure 5.1), Δx was adjusted by 8.0 km (positive for eastward directions, negative for westward directions) as the mean distance between each receiver in the array (804 m) is approximately one-tenth that of the receivers on either side of the island (7.9 km). One-sample Wilcoxon signed-rank tests were used to determine if the mean Δx_{12} or Δx_{23} for each species differed significantly from zero to determine if an overall bias in directional movement was present. Mann-Whitney U tests examined if Δx_{12} or Δx_{23} was significantly different between the two species, or if Δx_{12} differed among sockeye populations. Kendall's τ correlations were assessed between Δx_{12} and the duration of time between the first and second detection sequences. Assumptions of parametric

tests were assessed visually, and if assumptions were not met non-parametric equivalents were used. For all hypothesis-based testing, I specified $\alpha = 0.05$ to determine significance.

For each smolt that was detected at the NSOG array, its subsequent apparent survival (hereafter referred to as ‘survival’) was assessed using detections at the Queen Charlotte Strait (QCS; Figure 5.1) array lying ~250 km to the northwest of the NSOG array and well beyond the exit from the Strait of Georgia. Thus smolts that had any detections at the QCS array were considered survivors, and all others are assumed mortalities. Estimates of detection efficiency for the marine arrays for the tag types used (V7 and V9) range from 60-90%, respectively (Welch et al. 2009). For each species, two sets of binomial general linear models (GLM) were constructed to relate movement and migration experience to subsequent survival to QCS (S_{QCS}), with the first focusing on metrics pertaining to the entry of smolts to the NSOG array using all smolts that were detected at the array, and the second focusing on lateral east-west movements after initial NSOG detection using all smolts with at least two NSOG detection sequences. Constructing two sets of GLMs allowed for maximizing sample size, as the number of smolts with two or more distinct detection sequences (and therefore able to examine east-west movements for) is substantially smaller than the total number of smolts detected at the NSOG array (Table 5.1). In the first set of GLMs, explanatory variables included the receiver position of the initial NSOG detection ($P_{Initial}$), the date of the initial NSOG detection, FL, natal population, and year of release. The interactions between natal populations and both Julian date and initial receiver position were also included. For the second set of GLMs, explanatory variables included the difference in receiver position between the first two NSOG detections (Δx_{12}), the time between the first two NSOG detections (“duration”), FL, natal population, and year of release. The

interactions between natal populations and both the difference in receiver position and the duration between detection sequences were also included. Year of release and FL were not included as variables for both sets of sockeye models as these variables were highly correlated with natal population. For the second set of steelhead models, only 6 Seymour smolts had at least two detection sequences at the NSOG array, and were removed from analyses.

All continuous variables in both sets of GLMs were centered by subtracting the mean from each value and dividing by two-times the standard deviation (Gelman 2008). For each set of models, an all-subsets regression was conducted using the ‘MuMIn’ package (Barton 2014) in R (Team 2014), and all models were ranked based on the corrected Akaike Information Criterion (AICc). For each model, the change in AICc from the top-ranked model (Δ AICc) was also calculated. Model coefficients, and 95% confidence intervals of these coefficients, were calculated using a model averaging approach across all models for which Δ AICc \leq 2 (Burnham and Anderson 2002). Model fit was further assessed using AICc weight (W_i), R^2 , adjusted R^2 , and log-likelihood. For variables whose 95% confidence intervals of the model-averaged coefficient did not contain zero, prediction plots were generated to visualize the modeled effect of the variable(s) on S_{QCS} . Because relating migration metrics to survival can be confounded by migration rate (i.e., smolts with the same daily survival rate will exhibit different net survival to QCS if they take different amounts of time to reach QCS), I assessed the correlation (Pearson correlation coefficient) between these variables and the time taken to reach the NSOG from the previous array (entrance to the SOG). In addition, I assessed the correlation between each of these variables and the time taken to reach QCS among survivors.

5.3 Results

Across the releases used in this study, 3017 sockeye and 728 steelhead smolts were tagged and released (Table 5.1). Of these releases, 582 sockeye and 219 steelhead smolts were detected at least once on the NSOG array, and 146 sockeye and 68 steelhead had multiple detection sequences at NSOG. In addition, 78 sockeye and 49 steelhead had three or more detection sequences at NSOG (Table 5.1). The mean date of arrival at the NSOG array across all releases was May 27 for both sockeye (SD = 16 days) and steelhead (SD = 11 days). Only 28 sockeye (0.9%) and 14 steelhead (1.9%) were detected using the westward route through the Strait of Juan de Fuca rather than northward through the Strait of Georgia (i.e., through the NSOG array; Figure 5.1).

5.3.1 Initial arrival

The majority of sockeye (~66%) arrived to the NSOG array via Malaspina Strait between Vancouver Island and the British Columbia mainland (Figure 5.2). Significantly more sockeye arrived via Malaspina Strait than the Strait of Georgia when accounting for each strait's width ($p < 0.0001$). The median initial position at the array for steelhead was in the Strait of Georgia (Figure 5.3), and although only 38% of steelhead arrived via Malaspina Strait, this use was disproportionately higher than expected given the strait's width ($p < 0.001$). The proportion of Englishman steelhead, the only population between the two species found on Vancouver Island (Figure 5.1), arriving via Malaspina Strait was only 30%, which was not more than the use of the Strait of Georgia ($p = 0.34$).

The difference in receiver position between the first and last detections within the initial detection sequence was significantly different from zero for both sockeye ($p < 0.001$) and

steelhead ($p < 0.001$). This difference in receiver position within the first detection sequence was not significantly different between sockeye (0.3 km to the west ± 0.3 km [mean \pm SD]) and steelhead (0.4 km to the west ± 0.2 km) smolts ($p = 0.55$).

5.3.2 Lateral movements

The proportional use of migratory routes (“clockwise,” “counterclockwise,” and “linear”) among release groups of sockeye smolts differed significantly ($p < 0.0001$; Figure 5.4). Pairwise comparisons determined that the proportion of sockeye smolts taking linear routes (as measured by the NSOG array) was greater than the proportion of smolts moving both counterclockwise ($p < 0.0001$) and clockwise ($p < 0.0001$). There was no significant difference, however, between the proportion of sockeye smolts taking counterclockwise and clockwise routes ($p = 0.14$).

For steelhead, there were also significant differences among migration routes experienced ($p < 0.0001$; Figure 5.4), with smolts taking counterclockwise and linear routes more often than clockwise ($p < 0.0001$ and $p < 0.0001$, respectively). There was no difference between the proportions of counterclockwise and linear smolts ($p = 0.66$).

A significantly smaller mean proportion of sockeye smolts (0.25 ± 0.14 [mean \pm SD]) exhibited a counterclockwise migration route than steelhead (0.41 ± 0.10 [mean \pm SD]) smolts ($p = 0.02$; Figure 5.4). No differences were found between sockeye and steelhead in the mean proportion of linear ($p = 0.12$) and clockwise ($p = 0.60$) migrants.

Overall, the displacement in receiver position between the first and second detection sequences (Δx_{12}) of sockeye smolts along the NSOG array was westward (4.8 km to the west ± 8.8 km [mean \pm SD]) and significantly different from zero ($p < 0.0001$), with the median receiver position of the second detection sequence located in the Strait of Georgia (Figure 5.2) and the

distribution of smolts between the two straits non-uniform ($p = 0.04$). No significant differences in the westward displacement of sockeye smolts were found among populations ($p > 0.05$). Of the 146 sockeye smolts having multiple detection sequences at NSOG, 37 (25%) either spanned Texada Island or had a displacement of at least 8 km (10 receivers) between their first and second detection sequences. The mean duration between first and second detection sequences of sockeye was 69 hours (SD = 98 hours). A significant positive relationship was found between the duration between first and second detection sequences and the change in receiver position ($p < 0.0001$; Appendix C).

Similarly, Δx_{12} of steelhead smolts along the NSOG array also indicated a westward displacement (9.6 km to the west \pm 9.6 km [mean \pm SD]) that significantly differed from zero ($p < 0.0001$), and the mean duration between first and second detection sequences was 72 hours (SD = 71 hours). The overall magnitude of movements of steelhead was greater than those of sockeye ($p < 0.001$), and the second detection sequence for the majority of steelhead occurred in the Strait of Georgia (Figure 5.3). Of the 68 steelhead to have multiple detection sequences at NSOG, 36 (53%) had westward displacements that either spanned Texada Island or at least 8 km distance. A significant positive relationship was found between the duration between the first two detection sequences and the absolute difference in receiver positions ($p < 0.0001$; Appendix C).

The difference in receiver position between the second and third detection sequences (Δx_{23}) for sockeye (0.6 km to the west \pm 6.8 km [mean \pm SD]) was not significantly different from zero (Wilcoxon signed-rank test; $V = 976$, $P = 0.83$). For steelhead, this difference from zero was significant (1.5 km to the east \pm 4.4 km [mean \pm SD]; $p = 0.02$; Figure 5.5), but was not

significantly different compared to sockeye ($p = 0.07$). By the third detection sequence, the majority of smolts for both species (72% for sockeye and 98% for steelhead) were found in the Strait of Georgia rather than Malaspina Strait (Figure 5.2, Figure 5.3), with distribution of sockeye not different from uniform across the array ($p = 0.65$), while steelhead were found almost exclusively in the Georgia Strait, and significantly so ($p < 0.0001$). The lateral movements of individual smolts (i.e., initial positions and Δx_{12} and Δx_{23}) of both species are visualized in Figure 5.6.

The duration between first detection at NSOG array and first detection at QCS array was similar for both sockeye (12.5 ± 5.2 days [mean \pm SD]) and steelhead smolts (12.4 ± 4.1 days [mean \pm SD]). This duration for sockeye was not influenced by migration route ($p = 0.10$). Steelhead smolt residence was significantly influenced by migration route ($p < 0.001$), as duration was 4.3 days shorter for linear migrants (11.2 ± 3.4 [mean \pm SD]) than counterclockwise (15.5 ± 4.1 days [mean \pm SD]) migrants ($p < 0.001$).

5.3.3 Survival

Model averaging of GLMs identified movement metrics that influenced probability of survival to the QCS array (Table 5.2, Figure 5.7). For initial arrival of sockeye to the NSOG array, the top-ranked model included all variables (initial position on the array, Julian date, natal population, and a population's interactions with the preceding two variables), and was the only model for which $\Delta \text{AICc} \leq 2$ (Table 5.2). Chilko and Sakinaw sockeye smolts (Figure 5.1, Table 5.1) arriving via eastern NSOG receivers experienced poorer survival to QCS (Figure 5.8), with sockeye detected migrating west of Texada Island via the Strait of Georgia 1.4-times more likely to be detected at Queen Charlotte Strait than those detected migrating via Malaspina Strait,

although these odds were not significantly different from one (Fisher's exact test, $P = 0.09$). Sockeye smolts arriving via Malaspina Strait took less time to arrive to the NSOG array ($p < 0.001$), but these same smolts took longer to reach the QCS array among survivors ($p = 0.02$).

Chilko sockeye smolt survival also increased with Julian date of initial detection at NSOG, while both Sakinaw and Cultus populations demonstrated a negative relationship with Julian date of arrival (Figure 5.8). Although later Chilko smolts took longer to arrive to the NSOG array ($p < 0.0001$), among Chilko fish to survive to QCS, later migrants took less time to reach QCS ($p = 0.05$). For sockeye smolts with at least 2 detection sequences, the duration between NSOG detection sequences was retained in all models with $\Delta AICc \leq 2$, with longer durations decreasing survival probability (Figure 5.8).

For steelhead, both initial position along the NSOG array and Julian date of arrival were retained within all but one of the NSOG entry models (Table 5.2), but only for initial position did the 95% confidence interval of the model-averaged coefficients not contain zero (Figure 5.7). Unlike sockeye, no effects of natal population on survival were observed, despite Englishman River steelhead entering the Strait of Georgia from the western side (Vancouver Island) rather than from the eastern side (British Columbia mainland). Collectively, steelhead that migrated via Malaspina Strait were twice as likely to be detected at QCS than those that did not (Fisher's exact test, $P = 0.02$). Steelhead arrival position was not correlated with migration speed either to the NSOG array ($p = 0.97$) nor the QCS array among survivors ($p = 0.20$). All of the variables within lateral movements models had 95% confidence intervals of model-averaged effects that contained zero, indicating overall weak relationships with subsequent QCS survival. However,

the two variables “Duration between NSOG detections” and “FL” were included in multiple models with $\Delta AICc \leq 2$ (Table 5.2).

5.4 Discussion

5.4.1 Migration routes

Although detections of smolts occurred across the entire NSOG array, both species preferentially migrated via Malaspina Strait, and extremely few (<2%) used the “westward” migration route through Juan de Fuca Strait, providing further support that upon exit from freshwater, most smolts move northward within the Strait (Groot and Cooke 1987, Burgner 1991, Melnychuk et al. 2010) near the eastern coastline (Groot and Cooke 1987, Peterman et al. 1994, Welch et al. 2009). Juvenile salmon are thought to orient towards marine feeding grounds using a “magnetic map sense” (Putman et al. 2014a, 2014b) that would allow smolts entering the Strait of Georgia to orient to the northwest (i.e., through the Strait of Georgia rather than Juan de Fuca Strait). In addition, tendencies to migrate near shore have been observed in smolts across systems (Hartt and Dell 1986, Groot and Cooke 1987, Lacroix et al. 2004, Burke et al. 2014), a behaviour that possibly facilitates fine-scale orientation and navigation (Byron and Burke 2014) that would result in increased use of Malaspina Strait relative to the main body of water forming the Strait of Georgia. Quickly turning northward may also help to explain why the Englishman River steelhead stock did not display a disproportional use of Malaspina Strait, as their ocean migration initiated along the shore of Vancouver Island rather than the British Columbia mainland.

Approximately 40-60% of smolts of both species did not experience multiple bouts of geographically separate detections on the NSOG sub-array, and therefore may be

moving in a relatively linear fashion northward through the Strait of Georgia. Linear movements are consistent with the current paradigm for smolt outmigrations presented by Groot and Cooke (Groot and Cooke 1987) that sockeye and steelhead exhibit relatively rapid coastal migrations (Burgner 1991, Quinn 2005, Tucker et al. 2009). The combination of a consistent migration heading (or “compass bearing”) and active swimming would help to facilitate such linear migration paths. Although these presumed-linear migrants were among the largest contingents for both species, it was surprising that more smolts were not classified as linear migrants given the mean speed at which migration occurs (~1 BL/s achieved speed over ground, or 13-17 km/day; (Melnichuk et al. 2010, Welch et al. 2011)).

I present evidence that substantial contingents of both species (20-40% of sockeye and 30-50% of steelhead) experience westward or even fully counterclockwise movements while in the Strait of Georgia, particularly for steelhead. First, within initial detection sequences both species exhibit slight westward movements that indicate an angular trajectory across the array, although it should be noted that the array itself is slightly angled from the southwest to the northeast (Figure 5.1 inset). Second, a westward displacement was primarily observed between first and second detection sequences for both species, equating to westward movements of ~5km for sockeye and ~9.5 km for steelhead, with 25% of sockeye and >50% of steelhead experiencing lateral movements exceeding 8 km. As a result, the distributions of the subsequent detection sequences were more frequently recorded in the western Strait of Georgia, particularly for steelhead who rarely had subsequent detections in Malaspina Strait. It should be noted that steelhead had both greater prevalence and magnitude of westward movements even though steelhead used more western routes than sockeye initially, indicating that westward movements

were not simply random. Third, westward displacements of steelhead were followed by a mean eastward displacement of ~1.5 km between the second and third detection sequences, indicating the potential presence of “loop-like” trajectories. Collectively, these observations indicate counterclockwise motions within the Strait of Georgia, with steelhead experiencing more pronounced counterclockwise movements than sockeye that appear to persist through three detection sequences that result in a net-transport of smolts from Malaspina Strait to the Strait of Georgia. This differs from previous research that suggested initial migrants use Malaspina Strait followed by use of the Strait of Georgia by later migrants that was based on purse seine surveys (Groot and Cooke 1987). The westward transport described provides another potential mechanism for the observations by Groote and Cooke (Groot and Cooke 1987).

An organism’s migration route or trajectory can be influenced by the medium through which it is traversing (Nathan et al. 2008), which is especially true for small-bodied organisms, such as salmon smolts, in marine environments (Paris et al. 2007, Burke et al. 2014). The region is characterized by strong tidally-influenced currents in the northern passage (Discovery Passage/Johnstone Strait) as well as weaker currents in the central Strait of Georgia driven largely by tide and freshwater discharge, including the region of the NSOG array (Thomson 1981, 2014, Foreman et al. 2012). Estuarine flow results in a net northward flow in the surface layer over the tidal cycle in the central-to-northern Strait (Thomson 1981, 2014), and these tidal currents are thought to influence outmigration routes of smolts (Groot and Cooke 1987, Peterman et al. 1994). Due to the shape and structure of the central Strait of Georgia, the current direction at any given location turns counterclockwise throughout the tidal period, such that rotary tidal currents develop (Thomson 1981). Furthermore, fine-scale ocean simulation models

predict areas of overall counterclockwise circulation in the region extending from the NSOG array northward (Foreman et al. 2012). In particular, the region of the NSOG array exhibits mean surface currents flowing northward through Malaspina Strait and much of the Strait of Georgia west of Texada Island, and then strong mean currents flowing southward along the most western 3-5km of the Strait (Foreman et al. 2012). I propose that these currents contribute to the counterclockwise movements observed in both sockeye and steelhead. Although I did not find the same evidence for such movements at the QCS array (not shown), sample sizes at this site were limited due to smolt losses from mortality. However, it certainly seems possible that similar circular smolt movements will occur elsewhere where tidally-rectified eddies develop.

Juvenile smolts are larger and stronger swimmers than the larval fish which are often the focus of marine connectivity studies (i.e., (Cowen et al. 2006, Paris et al. 2007)). In fact, simulation studies have suggested that smolts in nearshore environments cannot act as passive particles to complete known migrations (Peterman et al. 1994, Burke et al. 2014). Therefore the movement behaviours of smolts should play a large role in defining overall migratory trajectories or routes (Burke et al. 2014), although the balance between oceanography and self-directed movements is largely unknown (Quinn 2005). Movement behaviours encompass swim speed, swim depth, the use of navigation and/or orientation capabilities, and fine-scale responses to variability in resources, gradients in water quality, and/or predators (many of these factors reviewed in (Byron and Burke 2014)). It is possible that the use of navigation and/or orientation capabilities in the Strait of Georgia allows smolts to orient towards the northwest (thus exiting the Strait of Georgia and facilitating movement towards presumed marine winter feeding areas in

the offshore North Pacific (Putman et al. 2014b)), but that the ability to maintain linear routes is limited by oceanographic currents and/or swimming capabilities.

In particular, swimming depth has the potential to influence the trajectory of migrating salmon smolts (Burke et al. 2014, Byron and Burke 2014). Smolts are believed to swim in shallow near-surface waters (Beamish et al. 2007, Gerbrandt 2013). Although currents in the region are dominated by tidal flow (Thomson 1981, Foreman et al. 2012), northwesterly winds are present during the spring and summer migrations of smolts that can modify currents at the surface (Thomson 1981, 2014). These winds generally act to decrease the mean northward flow of surface waters in the central-to-northern Strait, but this influence decays with depth via the processes creating Ekman spirals (Sverdrup and Armbrust 2009), which have been observed in the Strait of Georgia (Stacey et al. 1986). Thus, variability in swim depth among individuals and between populations and species would alter the exposure and relative impact of wind-altered surface currents on migratory trajectories. In freshwater, juvenile steelhead have been found to swim at shallower depths (<3 m) than other salmonids (Beeman and Maule 2006), and in the pelagic offshore environment of the open ocean immature steelhead swim much closer to the surface than the other species of Pacific salmon, based on the relative vertical distribution of species-specific catches in gill nets (DWW, unpublished observations). Steelhead swimming at shallower depths than sockeye provides a potential mechanism for the observed increase in westward transport of steelhead within the Strait of Georgia and the increase in the measured magnitude of counterclockwise movements relative to sockeye (Figs. 5 and 6). Unfortunately, depth-sensing acoustic tags still remain too large to implant into smolts, and therefore it is unknown what patterns may exist in swim depth across individuals and species.

In addition to swim depth, the relative impact of currents on the migration trajectory is dependent upon individual swim speed of smolts. In general, migration rates (speed over ground) of smolts approach 1 BL/s across species ((Melnychuk et al. 2010, Welch et al. 2011)). If size-dependent swim speeds are consistent, larger fish would be expected to have increased overall swim speeds and therefore be proportionately less influenced by surface currents. I did not observe any differences, however, in the overall magnitude of western movements across populations of sockeye smolts, even though Cultus sockeye smolts were generally 40% longer (~50 mm) than Chilko smolts. In addition, steelhead experienced larger westward movements than sockeye even though they were generally of the same size (or larger). Thus size differences of this order might not be of measurable influence on migration behaviour and/or routes. In fact, more robust migration speed analyses on a similar dataset found that body size did not have a large impact on straight-line migration rates (Melnychuk et al. 2010).

Caution is needed, however, when interpreting straight-line estimates of migration rates, as they do not account for complex movement behaviours such as those observed in this study. In fact, due to the prevalence and magnitude of lateral movements observed in both species, I suggest that straight-line estimates of migration speed (speed over ground) may substantially underestimate true swimming speeds. I cannot provide further information regarding actual swim speeds, however, as I am unable to determine the relative influence of swim speed and current speed on overall migration rate given the current resolution of marine telemetry arrays. The development of high-resolution individual-based models (IBMs) to simulate movements within a realistic oceanographic environment can be used to test hypotheses regarding the balance between swim speeds, movement behaviours, and ocean currents (i.e., (Burke et al. 2014, Byron

and Burke 2014)), while the use of fine-scale 3D tracking arrays could provide direct measurements of the degree of tortuosity in at least some environments (e.g., (Andrews et al. 2011, Espinoza et al. 2011)).

The ability to determine migratory behaviours or routes in the current study is dependent upon the NSOG array's ability to detect smolts as they migrate through. V9 tags have an estimated 90% detection efficiency at the NSOG array, while smaller V7 tags have an estimated 60-75% efficiency (Welch et al. 2009). Imperfect detection efficiency will result in underestimating the extent and nature of rotary movements, as 1/3rd of the first detections of individual V7 tags likely actually represents the second visit to the array. Thus a significant fraction of the apparently clockwise movements recorded (first detection to the west of the second set of detections) may actually come about because the initial point of contact of V7 tagged smolts with the NSOG array went undetected (a similar argument applies to the 2nd and 3rd bouts of detection on the array). These differences in detection efficiency among tag types complicate our comparisons among sockeye populations and between the two species, as all steelhead and Sakinaw and Cultus sockeye were implanted with V9 tags where this "aliasing" effect will be substantially less, while Chilko sockeye were implanted with smaller V7 tags. Although these differences exist, and individual variability in migratory experience was observed, it is evident in the current study that the behaviours described occur across populations and in both species, and thus appear to be common among smolts rather than anomalous observations.

5.4.2 Survival

Smolt survival in the Strait of Georgia to QCS varied among initial NSOG entry positions for both species, suggesting that conditions important to the migratory process are spatially variable in the Strait of Georgia. Post-release survival was highest for steelhead arriving along western receivers, even though steelhead disproportionately arrived via Malaspina Strait to the east. Steelhead arrival position was not correlated with migration speed either to the NSOG array nor the QCS array among survivors and thus I don't expect this result to be confounded by differences in migration rates among routes taken. Therefore the specific migration route taken by steelhead through the Strait of Georgia appears an important part of the migration process.

For sockeye, although the 95% interval of the effect size narrowly included zero, Chilko sockeye also experienced poorer survival to QCS when arriving via Malaspina Strait. Among sockeye populations, only for Sakinaw smolts did the 95% interval of the effect size exclude zero. Of the three sockeye populations investigated, Sakinaw had the lowest sample size, and the release point for Sakinaw sockeye lies within Malaspina Strait, quite close to the eastern receivers (Figure 5.1), and therefore I limit our interpretations of this finding. Future studies should focus on identifying the factors that influence smolt survival on finer spatial and temporal scales to better understand why migration routes affect smolts, and why the observed relationships between migration routes and survival may differ between species.

Texada Island (separating receivers 7 and 8; Figure 5.1 inset) is a natural barrier that could contribute to variable conditions experienced by smolts. The factors that could vary spatially in the Strait and influence smolts are numerous. Variability in currents and zooplankton could influence both swimming and feeding efficiency. Zooplankton communities have been

assessed on longer (decadal) time scales (Li et al. 2013, Mackas et al. 2013) but spatiotemporal variability within the spring and summer in the Strait of Georgia is very difficult to assess at present (but see (Price et al. 2013)). Feeding and energy use affects smolt growth, which has been suggested to influence coastal survival by altering predation risk along the migration (Beamish and Mahnken 2001, Beamish et al. 2004). Although research has identified individual taxa that predate on smolts (e.g., seals (Olesiuk 1993), dogfish (Beamish et al. 1992), lamprey (Beamish and Neville 1995)), the spatial and temporal distribution of these predators, and which predators have the biggest impacts on specific species of smolts, are largely unknown. Further studies should aim to better understand the movement, distribution, and behaviour of smolt predators, as well as utilize technologies capable of examining predator-prey interactions directly (i.e., (Lidgard et al. 2014)).

In addition to the initial migration route used, the timing of arrival at the NSOG array was identified as an important variable in predicting subsequent sockeye survival. Arrival date was also retained in nearly all of the top models for steelhead, but the effect was weaker and the 95% confidence intervals of its effect size contained zero. Later migrants for Cultus and Sakinaw sockeye experienced poorer survival but examining the prediction plots reveals that these effects were quite weak. Later arriving wild Chilko migrants, however, experienced improved survival. Salmonid migrations are generally thought to occur within specific time periods as a result of evolutionary selection (Healey 2000, Quinn et al. 2000, Crozier et al. 2008). Timing has repeatedly been found to influence migratory success of adult salmon during spawning migrations (e.g., (Cooke et al. 2004a, Crossin et al. 2009, Mathes et al. 2010)), but examples for juvenile smolts are less common (but see (Scheuerell et al. 2009, Satterthwaite et al. 2014)).

Satterthwaite et al., (Satterthwaite et al. 2014) demonstrated improved survival of juvenile hatchery Chinook released 70 to 115 d after the spring transition, indicating potentially important bottom-up influences. Scheuerell et al., (Scheuerell et al. 2009) found increased survival for earlier migrants of juvenile Chinook and steelhead outmigrating from the Columbia River system, which they attributed to temporally variable nearshore environmental conditions and predator distributions. In particular, regional-scale oceanographic conditions, including temperature and upwelling indices (Ryding and Skalski 1999, Mueter et al. 2002b), have been correlated with early marine survival of smolts. These studies, however, focus on interannual variability rather than changes in intra-seasonal conditions that our results suggest might be important. Future work should attempt to characterize the differences in migration experience among outmigration dates of smolts. Regardless, the importance of timing suggests that factors influencing survival not only vary spatially but also temporally within the Strait of Georgia.

Sockeye smolts with longer durations between the first two detections sequences experienced poorer survival to QCS, while this effect was found to be weaker for steelhead, such that the 95% confidence interval of the effect size contained zero. Furthermore, for sockeye both initial position and migration timing were correlated with migration rate for those surviving to QCS, such that migration rate may explain the identification of these variables as important. Combined, our results suggest that smolts milling near the array for extended periods of time can experience poorer survival and that sockeye survival in the Strait of Georgia is proportional to time at some level. Even though sockeye survival appears time-dependent, it should not be ignored that migration timing and route resulted in varying durations to reach QCS, and thus variability in route still has an influence on smolt experience within the SOG. Given that

duration between detections sequences at NSOG was correlated with the size of the lateral movements, it is still difficult to assess how strongly survival is linked to time rather than distance travelled. Regardless, excessive milling of smolts presumably decreases survival at least in proportion to the longer time spent within the region monitored by the array.

Growth and/or size of migrant smolts has been implicated as an important process in determining survival during the marine migration (Beamish and Mahnken 2001, Beamish et al. 2004, Osterback et al. 2014), as larger smolts should have increased swim speeds to better evade predators and have fewer gape-limited predators. Although FL was not included in sockeye models (due to collinearity with population), I was still surprised that FL had little support across steelhead models, and confidence intervals of the estimated effect of FL always included zero. This apparent lack of importance of smolt size could be a result of the narrow size ranges of tagged fish, as well as the largest fish in populations being selected for acoustic tagging for both species (the standard deviation of FL within steelhead release groups was ≤ 17 mm, and ≤ 15 mm for sockeye). In addition, Cultus hatchery sockeye were ~ 100 mm larger than their wild conspecifics (Welch et al. 2009) and of Chilko fish, only the larger age-2 smolts could be tagged, which in general make up $< 10\%$ of the outmigrant population (Irvine and Akenhead 2013) and are ~ 50 mm larger than age-1 smolts. Therefore it is possible that our narrow range of sizes tagged, relative to the broader population, prevented our ability to detect size-specific differences. Irvine and Akenhead (Irvine and Akenhead 2013), however, found no difference in average smolt-to-adult survival rate for age-1 and age-2 wild Chilko sockeye smolts over a ~ 50 year time series. Nevertheless, it is interesting that migration route-related factors were found to be more tightly linked to survival than body size.

In summary, our ability to link migration metrics to subsequent survival at a location ~250 km away is promising evidence of the power of sophisticated marine telemetry arrays to make important (and previously impossible) measurements of the importance of migration routes and movement behaviours on the migratory process. Using individual-based telemetry, I have characterized smolt movements in the marine environment at previously undescribed spatial scales and temporal resolutions. Our results confirm that smolts use Malaspina Strait disproportionately, but although most smolts move linearly through the NSOG array, both species demonstrate substantial contingents of individuals (~25-50%) that move in westward or counterclockwise pattern that result in a net transport of smolts from Malaspina Strait to the Strait of Georgia, especially steelhead. Counterclockwise movements may be due to the predominate currents in this area during the time of outmigration, as well as biological differences in swimming behaviour. Beyond identifying the main migration routes and characterizing variability in these routes among smolts, links were established between survival and characteristics of the migration, including initial migration route and timing, and the duration of time spent in the Strait of Georgia, suggesting that the factors important to migratory success are both spatially and temporally variable within the Strait of Georgia. In particular, steelhead appear affected by migration route regardless of migration rate. Our results provide a rare empirical example for how movements can affect survival within the field of movement ecology (Holyoak et al. 2008, Nathan et al. 2008), and confirm that variability in movements are an important part of the migratory process.

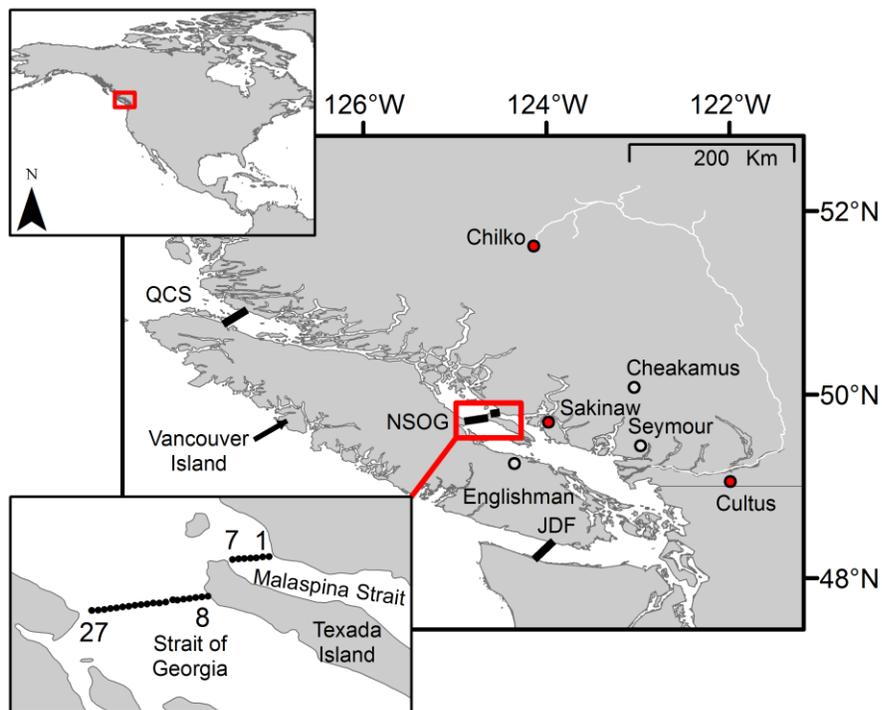


Figure 5.1 The location of acoustic telemetry receiver arrays (black lines) and natal freshwater rearing areas for sockeye salmon (red dots) and steelhead (grey dots). The bottom-left inset depicts the arrangement of acoustic telemetry receivers within the northern Strait of Georgia (NSOG) array. First (1) and last (27) receivers are labeled to reference the numbering scheme used in analyses.

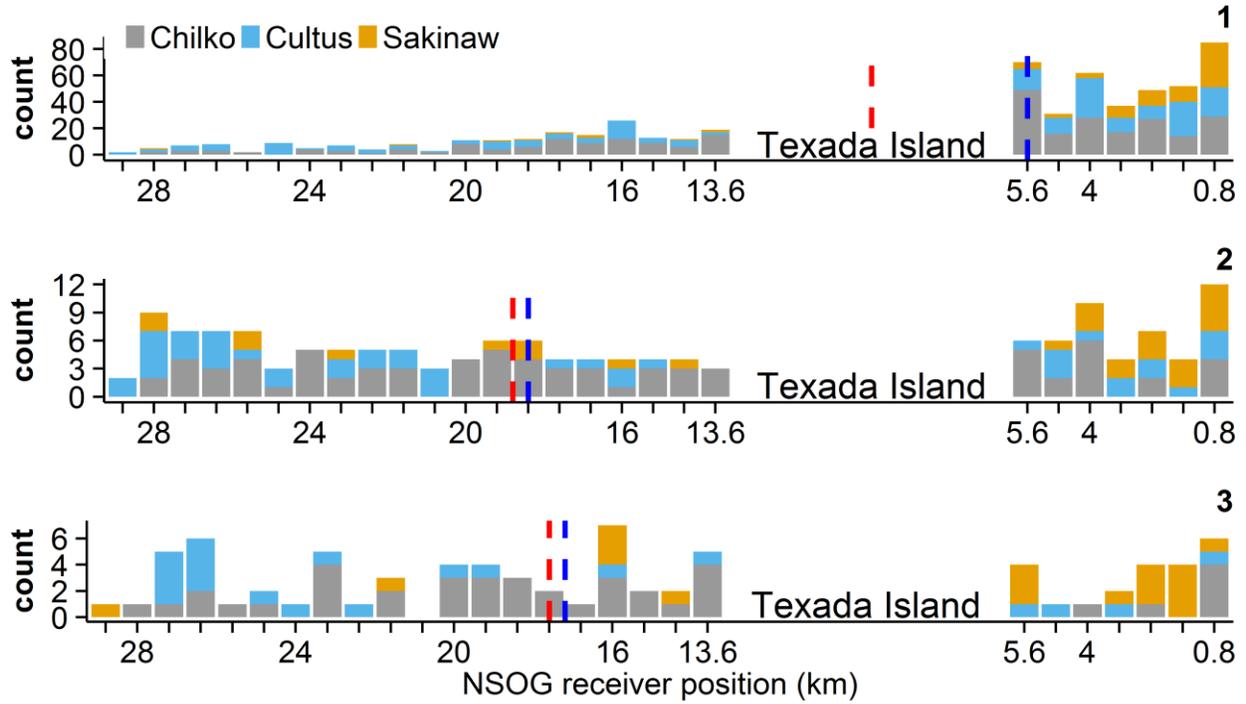


Figure 5.2 The distribution of sockeye salmon smolts on the northern Strait of Georgia (NSOG) array for the first (1), second (2) and third (3) detection sequences. Stacked colors indicate populations. Receiver positions represent those shown in the inset of Figure 5.1, and the gap between receivers 7 (5.6 km) and 8 (13.6 km) indicate the position and relative width of Texada Island. Dashed vertical lines indicate the mean (red) and median (blue) positions of sockeye smolts for each detection sequence. Note that the mean position of the first detection sequence was directly between Malaspina Strait (receiver positions 1-7) and Strait of Georgia (receiver positions 8-27).

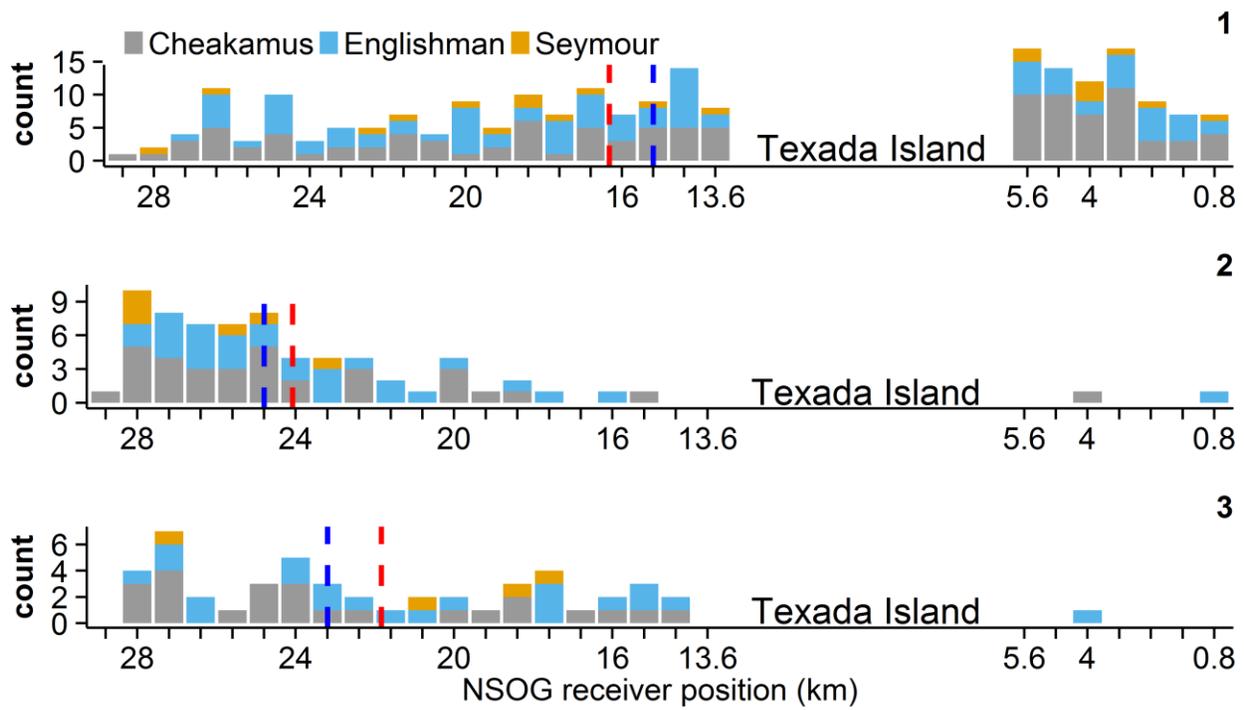


Figure 5.3 The distribution of steelhead smolts on the northern Strait of Georgia (NSOG) array for the first (1), second (2) and third (3) detection sequences. Details as in Figure 5.2.

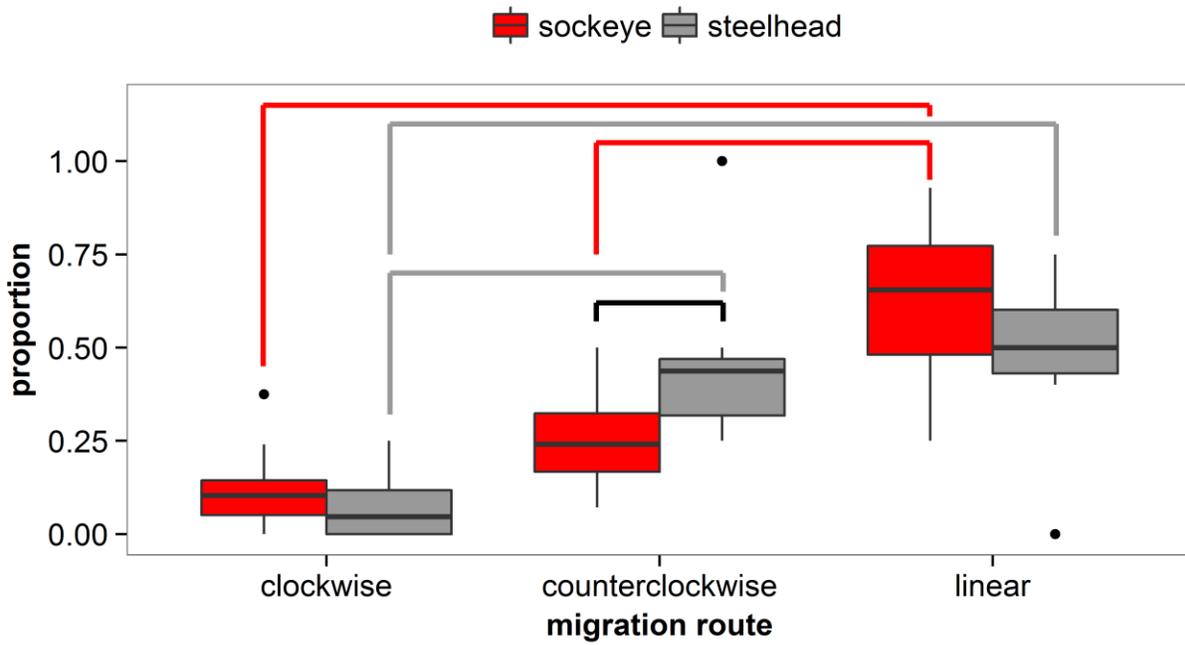


Figure 5.4 Boxplots of the proportion of sockeye salmon and steelhead smolts exhibiting linear, counterclockwise, and clockwise migration behaviours. Box limits represent the 25th and 75th percentile values. Lines indicate significant differences in proportions between migration routes for sockeye (red; Tukey HSD), and steelhead (grey; Tukey HSD), or between species within a migration route (black; t-test).

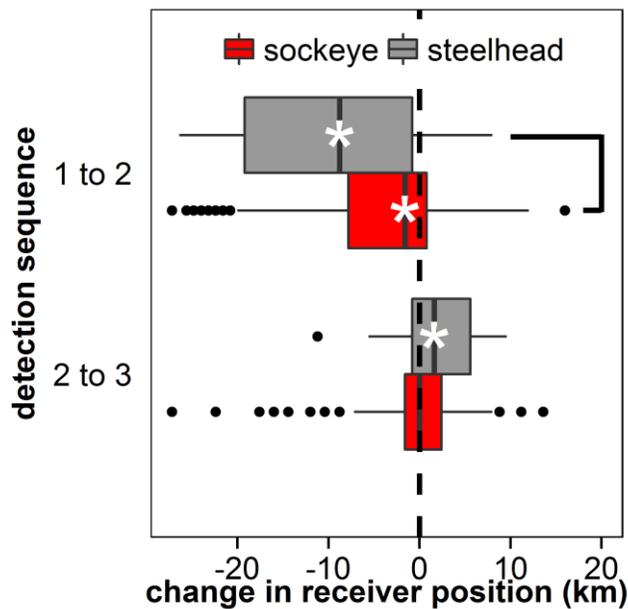


Figure 5.5 Differences in position (km) of sockeye (red) and steelhead (grey) smolts at the northern Strait of Georgia (NSOG) array between detection sequences. (1) Between first and second detection sequences, and (2) between second and third detection sequences. Negative values indicate westward movements, and positive values indicate eastward movements. Asterisks indicate significant differences from zero (Wilcox-signed rank test). Lines indicate significant differences in change in position between species (black; Wilcox signed-rank test). As described in the Materials and Methods, the change in receiver position for any movements that spanned Texada Island were adjusted by 8 km.

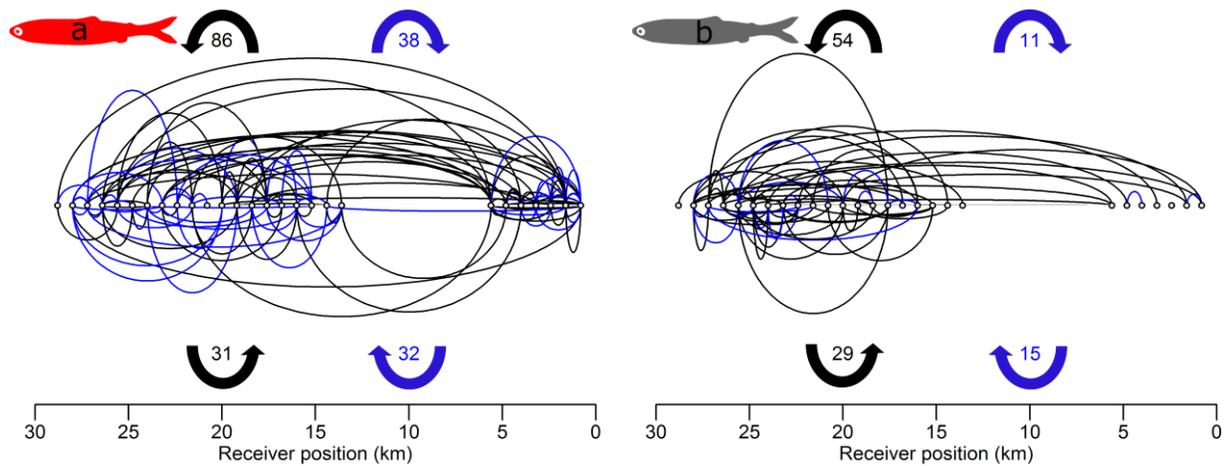


Figure 5.6 Visual representation of lateral movements taken by sockeye (a) and steelhead (b) smolts. Open circles represent the 27 receivers at the northern Strait of Georgia (NSOG) array. Lines indicate counterclockwise (black) or clockwise (blue) movements by individual smolts between either the first and second detection sequence (above receivers) or between the second and third sequence (below receivers). Line length is set equal to a distance travelled assuming each smolt swims continuously at 1 BL/s for the entire time duration between detection sequences. This distance (half of an ellipse’s perimeter) was used to estimate the vertically-oriented radius of the ellipse for plotting purposes using Ramanujan’s first approximation (Ramanujan 1914). Vertical scale (not shown) is equal to horizontal scale. Ellipses were drawn using the plotrix package (Lemon 2006) in R (Team 2014). Smolts exhibiting linear migration routes (see 5.2 Methods) are not shown.

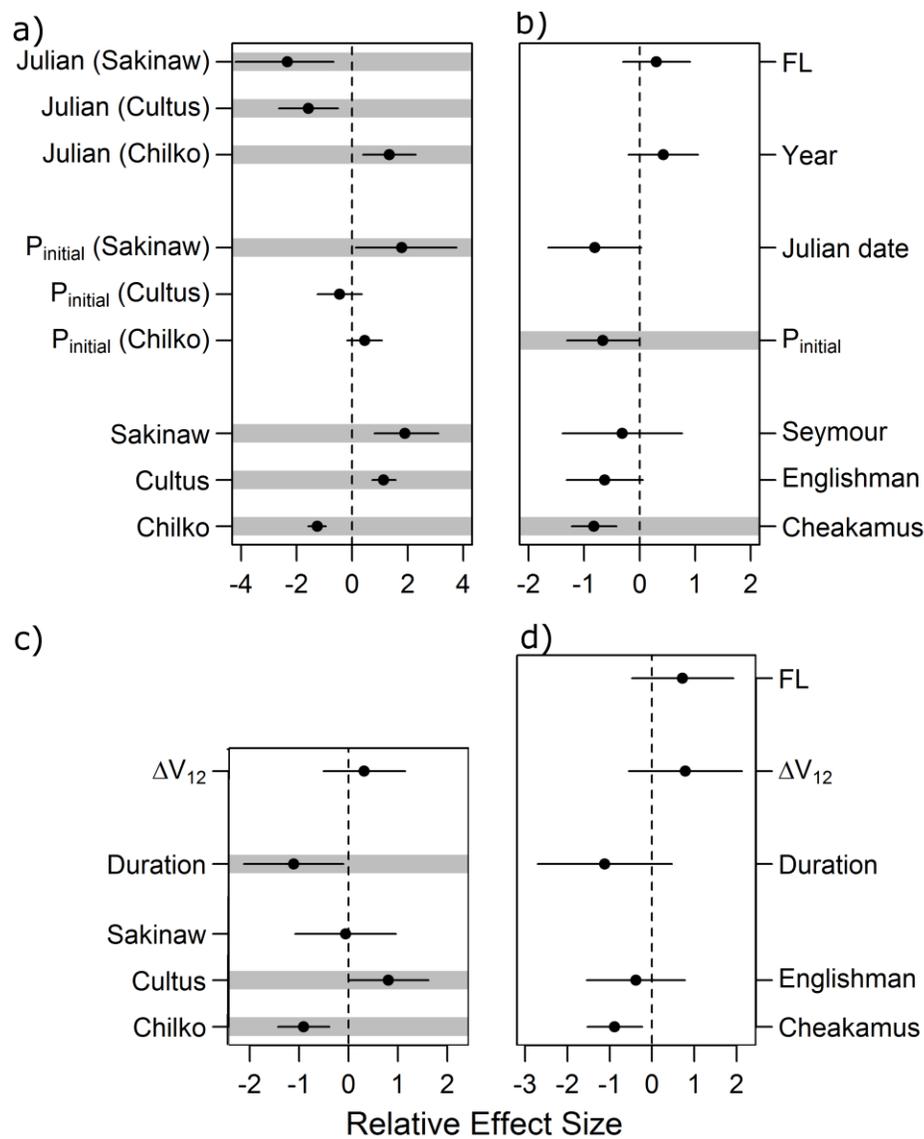


Figure 5.7 Relative effect sizes of model-averaged coefficients from general linear models (GLMs). Grey bars indicate variables for which the 95% confidence interval of the effect size does not include zero. As described in the Materials and Methods, separate models for each species were created using all smolts detected at the NSOG array (sockeye “a”, steelhead “b”), and for smolts detected for multiple periods at the NSOG array (sockeye “c”, steelhead “d”).

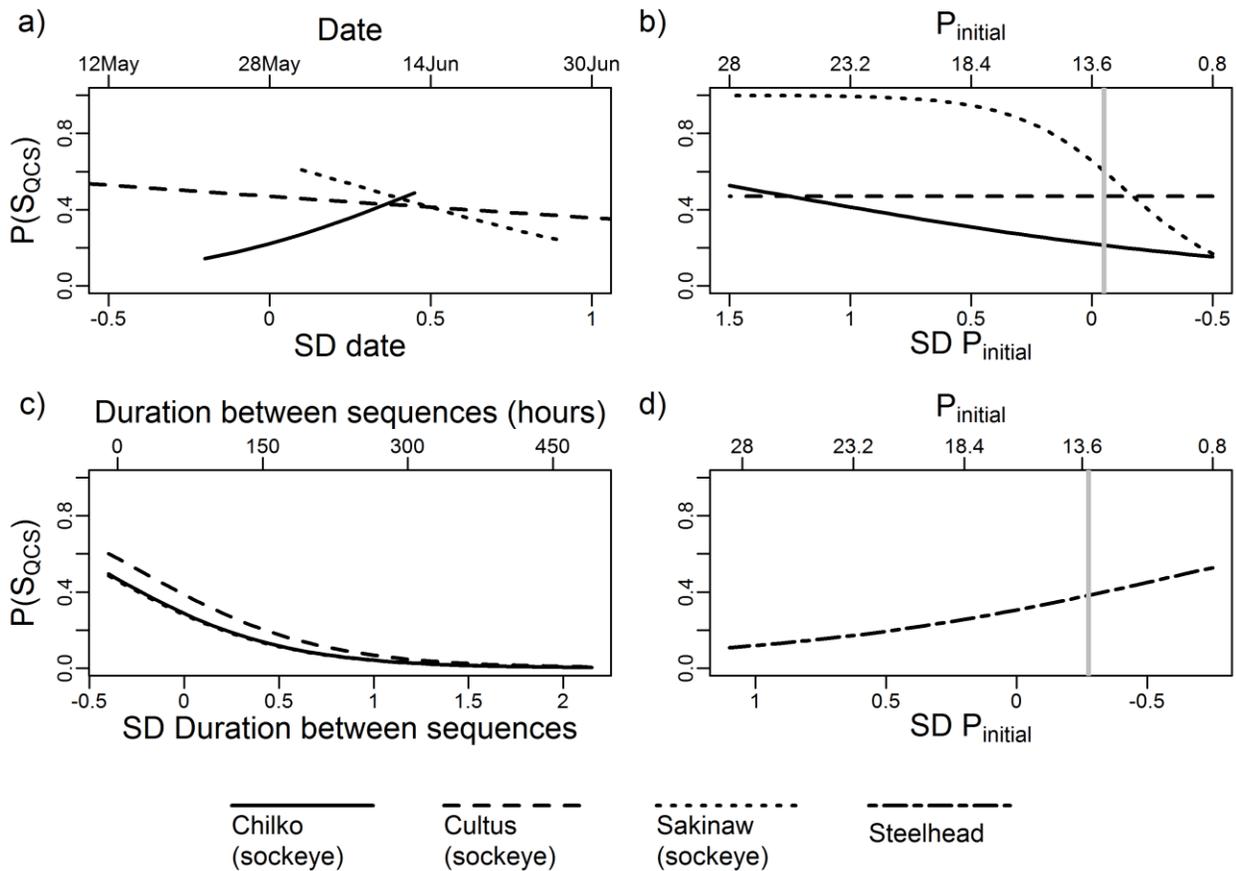


Figure 5.8 Prediction plots for the probability of survival to the Queen Charlotte Strait acoustic telemetry array [$P(S_{QCS})$]. Effects of (a) date of arrival at NSOG for sockeye, (b) receiver position of the initial detection sequence on NSOG ($P_{initial}$) for sockeye, (c) duration between the first and second NSOG detections for sockeye, and (d) $P_{initial}$ for steelhead. For all effects shown the 95% confidence interval of the model-averaged effect size did not contain zero (Figure 5.7). The upper x axis depicts the actual values of the variable, and the lower x axis are these values as standard deviations (SD) from the mean. For sockeye date of arrival (a), only the range of dates observed are predicted for each population. Vertical gray bars (panels b and d), indicate the separation of Malaspina Strait (receivers 1-7) from the Strait of Georgia (receivers 8-27). The predictions for survival of Chilko and Sakinaw sockeye across duration values (panel c) are very similar and therefore little separation of the prediction lines occur.

Table 5.1 Summary of sockeye salmon and steelhead smolts tagged with acoustic telemetry transmitters and tracked in the Strait of Georgia. The number of smolts detected at the Northern Strait of Georgia (NSOG) array and subsequently at the Queen Charlotte Strait (QCS) array are given, as well as the number of each migratory route (linear, counter, and clockwise) as defined in the Materials and Methods. Populations are labeled as hatchery origin (H), wild (W), or a mix of both (H/W).

Year	Species	Population	Mean FL ± SD (mm)	Number released	Number detected at NSOG	Number detected at QCS	Number linear	Number counter	Number clockwise	Data sources
2004	sockeye	Cultus (H)	178 ± 13	100	34	13	13	1	0	(Welch et al. 2009, 2011, Melnychuk et al. 2010)
2004	sockeye	Sakinaw (H)	193 ± 15	97	38	16	16	4	1	(Melnychuk et al. 2010, Welch et al. 2011)
2005	sockeye	Cultus (H)	177 ± 14	378	44	22	17	8	4	(Welch et al. 2009, 2011, Melnychuk et al. 2010)
2005	sockeye	Sakinaw (W)	191 ± 12	47	13	3	2	3	3	(Melnychuk et al. 2010, Welch et al. 2011)
2006	sockeye	Cultus (H)	178 ± 9	200	54	30	26	6	3	(Welch et al. 2009, 2011, Melnychuk et al. 2010)

Year	Species	Population	Mean FL ± SD (mm)	Number released	Number detected at NSOG	Number detected at QCS	Number linear	Number counter	Number clockwise	Data sources
2006	sockeye	Sakinaw (H/W)	206 ± 14	136	40	15	12	7	6	(Melnychuk et al. 2010, Welch et al. 2011)
2007	sockeye	Cultus (H)	182 ± 11	319	107	64	58	12	4	(Welch et al. 2009, 2011, Melnychuk et al. 2010)
2010	sockeye	Chilko (W)	130 ± 4	199	25	4	3	4	1	(Rechisky et al. 2014)
2011	sockeye	Chilko (W)	133 ± 7	443	54	24	23	2	0	(Rechisky et al. 2014)
2012	sockeye	Chilko (W)	123 ± 4	386	60	18	19	7	3	(Rechisky et al. 2014)
2013	sockeye	Chilko (W)	123 ± 2	432	184	48	42	32	13	(Rechisky et al. 2014)
Totals sockeye				2737	653	257	231	86	38	
2004	steelhead	Cheakamus (W)	184 ± 17	51	26	10	7	7	2	(Melnychuk et al. 2007, 2010, 2013, 2014, Welch et al. 2011)

Year	Species	Population	Mean FL ± SD (mm)	Number released	Number detected at NSOG	Number detected at QCS	Number linear	Number counter	Number clockwise	Data sources
2004	steelhead	Englishman (W)	174 ± 17	67	41	10	8	9	3	(Melnychuk et al. 2010, Welch et al. 2011)
2005	steelhead	Cheakamus (W)	178 ± 14	49	26	13	10	5	1	(Melnychuk et al. 2007, 2010, 2013, 2014, Welch et al. 2011)
2005	steelhead	Englishman (W)	159 ± 15	43	20	5	4	2	2	(Melnychuk et al. 2010, Welch et al. 2011)
2006	steelhead	Englishman (W)	169 ± 12	50	34	12	9	10	2	(Melnychuk et al. 2010, Welch et al. 2011)
2006	steelhead	Seymour (H)	207 ± 16	50	5	1	0	3	0	(Balfry et al. 2011)
2007	steelhead	Cheakamus (H)	183 ± 11	100	12	3	3	1	0	(Melnychuk et al. 2010, 2013, 2014, Welch et al. 2011)
2007	steelhead	Seymour (H)	186 ± 13	60	6	1	1	1	0	(Melnychuk et al. 2010, Balfry et al. 2011)
2008	steelhead	Cheakamus (H/W)	180 ± 12	198	55	20	17	14	1	(Melnychuk et al. 2014)

Year	Species	Population	Mean FL ± SD (mm)	Number released	Number detected at NSOG	Number detected at QCS	Number linear	Number counter	Number clockwise	Data sources
2008	steelhead	Seymour (H)	184 ± 14	60	9	4	4	2	0	(Balfry et al. 2011)
Totals steelhead				728	234	79	63	54	11	

Table 5.2 Descriptions and summary statistics of all models with $\Delta \text{AICc} < 2$ for all smolts detected at the NSOG array (A) and for all smolts with ≥ 2 detection sequences at the NSOG array (B) for both sockeye and steelhead smolts. ‘logLik’ is the log-likelihood, and W_i is the AICc weight of the model.

Species	Model	R ²		logLik	AICc	ΔAICc	W_i	
		R ²	Adj R ²					
(A) sockeye	$P_{\text{Initial}} + \text{Julian} + \text{Population}$ + $P_{\text{Initial}}:\text{Population} +$ $\text{Julian}:\text{Population}$	0.11	0.15	-331.61	681.54	0.00	0.71	
	steelhead	$P_{\text{Initial}} + \text{Julian} + \text{Year}$	0.05	0.07	-126.41	261.00	0.00	0.10
		$P_{\text{Initial}} + \text{Julian}$	0.04	0.06	-127.48	261.07	0.06	0.10
		$P_{\text{Initial}} + \text{Julian} + \text{Population}$	0.06	0.08	-125.49	261.26	0.25	0.09
		$P_{\text{Initial}} + \text{Julian} + \text{FL}$	0.04	0.06	-126.95	262.09	1.09	0.06
		$P_{\text{Initial}} + \text{Julian} + \text{Year} + \text{FL}$	0.05	0.08	-125.96	262.21	1.21	0.06
		P_{Initial}	0.03	0.04	-129.13	262.31	1.30	0.05
		$P_{\text{Initial}} + \text{Julian} + \text{Year} +$ Population	0.06	0.09	-125.09	262.58	1.57	0.05
$\text{Julian} + \text{Year}$	0.03	0.05	-128.43	262.98	1.98	0.04		
(B) sockeye	$\text{Duration} + \text{Population}$	0.08	0.11	-86.66	181.60	0.00	0.30	
	Duration	0.05	0.06	-88.97	182.03	0.43	0.24	
	$\text{Duration} + \text{Population} +$ Δx_{12}	0.08	0.11	-86.40	183.24	1.64	0.13	
	$\text{Duration} + \Delta x_{12}$	0.05	0.07	-88.65	183.46	1.87	0.12	
	steelhead	Duration	0.04	0.05	-36.18	76.57	0.00	0.12
		$\text{Duration} + \text{FL}$	0.06	0.09	-35.40	77.22	0.65	0.08
		$\text{Duration} + \text{FL} + \Delta x_{12}$	0.06	0.08	-35.48	77.37	0.80	0.08
		FL	0.02	0.03	-36.64	77.49	0.92	0.07
		Stock	0.01	0.01	-37.03	78.27	1.70	0.05
		$\text{Duration} + \text{Stock}$	0.04	0.06	-36.05	78.51	1.94	0.04

Chapter 6: Conclusions

This thesis describes the migratory behaviour of juvenile sockeye salmon smolts and advanced several important concepts in feeding and migration ecology. Chapter 2 defined the limits of short-term consumption of a predator exploiting the smolt outmigration, provided a simple conceptual model for binge-feeding, and explored the potential impacts of acute predation events on migrants. Chapter 3 provides intriguing evidence of infection status increasing predation risk. Chapter 4 provides arguably the strongest evidence to date for the ability of migrants to swamp predators in order to reduce risk. Chapter 5 provides a rare example of variability in migration routes influencing migration survival. Thus each individual chapter represents important contributions to basic ecology. In addition, these findings can be placed within the movement ecology framework (Nathan et al. 2008) to assess the relative importance of each component for smolt outmigrations. It was expected that each component (internal state, motion capacity, navigation capacity, and external factors) had the ability to influence smolt behaviour and/or survival during the outmigration process.

6.1 Advances in the movement ecology framework

6.1.1 Internal state

Within the movement ecology framework, the internal state encompasses the physiology of an organism (Nathan et al. 2008). In Chapter 3, I found smolts with specific infections were at higher risk for predation during the initial outmigration, and therefore less likely to be successful in migration. This research confirms the ability for infection to impact smolt outmigration success (Jeffries et al. 2014), and demonstrates the potential for internal state to dramatically affect the migration.

6.1.2 Motion capacity

An organism's motion capacity describes its physical capability to move (Nathan et al. 2008) and is manifested in movement rates. Throughout thesis chapters, the influence of smolt size on movements and survival were investigated, as a proxy for swimming capability. Chapter 3 demonstrated that smaller smolts were at greater risk of predation. Although the mechanism by which smaller fish are predated more frequently is unknown, it is assumed increased risk is due to reduced predator avoidance capabilities (i.e. a reduced motion capacity). Chapter 4 did not find size-based effects on smolt survival or movements over ~14 km of the migration in the Chilko River, but a small difference in migration rates was observed between the two age classes of smolts tagged with PIT tags. Thus large differences in size may affect downstream migration rates. Chapter 5, which focused on the early marine environment, did not find evidence of size-based effects on smolt migration rates, size of lateral movements within the Strait of Georgia, or survival to the open ocean. This lack of size-based effects on smolt migrations in the Strait of Georgia are corroborated by other telemetry studies (Melnychuk et al. 2010), but telemetry work, including the studies within Chapter 5, is generally constrained by tagging a narrow size range of the population that can handle the burden of surgical implantation of a tag. Research has consistently linked early marine growth to subsequent survival to adulthood (Beamish and Mahnken 2001, Beamish et al. 2004), and thus its presumed fish size may be of importance in the marine environment, but the mechanisms or conditions under which such a relationship with migratory behaviour or success are unclear. The continued miniaturization of electronic transmitter tags (non-RFID) may soon allow for smolts of all sizes and age classes to be tracked.

6.1.3 Navigation capacity

Navigation capacity within the movement ecology framework refers to when and to where an organism moves (Nathan et al. 2008). In this thesis, the timing of migration was investigated as a component of navigation capacity, including 1) the timing of the migration initiation (inter-seasonal effect), 2) timing of the migration relative to other conspecifics (synchronization) and the timing of movements over the diel cycle. Chapter 4 demonstrated that strong synchronization is important to the migratory process; smolt survival was highly density-dependent. In this same chapter, strong nocturnal migration was observed in this small riverscape. Although no links between diel timing and survival were found, it is still assumed nocturnal migration is a strongly-selected process to minimize risk of predation from visual-based predators. Neither Chapter 4 nor Chapter 5 found evidence of inter-seasonal effects (i.e. when a smolt initiated migration) on movements or survival. Both the synchronization and diel effects, however, underscore the importance of synchronization in migrations as adaptive traits.

6.1.4 External factors

The movements of organisms through time define the experienced movement path or migration route. These migration routes characterize the external factors experienced by migrants, including environmental conditions and the presence of predators. Former work on Chilko sockeye demonstrated landscape-specific trends in movement rates and diel behaviour (Clark et al. 2016), potentially due to differences in water clarity and flow, as well as the distribution and suite of predators. Although examining environmental conditions on smolt movements and survival was not a specific focus of this thesis, there was evidence that experience was landscape-specific at finer scales than those studied by (Clark et al. 2016). First,

the strength of nocturnal migration by smolts in the upper Chilko River (described in Chapter 4) appeared to vary at the km-scale. Nocturnal migration was strongest in a segment of river characterized by an extreme spatial constriction where bull trout have been observed to congregate; beyond this segment, the propensity for nocturnal migration decreased. Within the marine environment, Chapter 5 determined that survival of outmigrant steelhead was route-specific, indicating that spatiotemporal variability in conditions within the Strait of Georgia can contribute to smolt migration success. The impacts of environmental conditions on smolt migration remains understudied, particularly in the marine environment.

External factors also encompass the biotic components of landscapes, including predators and conspecifics. Chapter 2 demonstrated that the acute impacts of predation on migrants are greater than previously considered, although the population-level impacts could not be directly estimated. More detailed research is needed on predator behaviour to fully quantify the impacts of acute predation events. Regardless, any increases in consumptive capacity of predators would result in increased selection on migrants. Researchers should take care to remember that predators may be adapted for exploiting migrations, just as migrants can demonstrate adaptations to reduce predation. Increased conspecific densities as a result of migratory synchronization increased smolt survival through this high-risk landscape in which bull trout reside (Chapter 4). Conspecific densities of migrants reflect both the navigation capacity (a migrant's decision to travel with others) and external factors (the collective decisions of other conspecifics independent of the focal individual). Thus biotic components of landscapes can contribute substantially to the migratory process.

6.2 Implications for conservation and management

Fraser sockeye salmon are economically important, support First Nations subsistence fisheries, and play important ecological roles in freshwater, marine, and even terrestrial ecosystems. Unfortunately, Fraser sockeye have exhibited precipitous declines, including a record low return of adults in 2009 that sparked the Cohen Commission (Cohen 2012). In particular, smolt-to-adult survival ratios have declined over the past couple of decades (Irvine and Akenhead 2013), resulting in increased attention to a better understanding of the smolt life stage. In addition to providing contributions to basic science, observations from this thesis can also help to inform conservation and management of smolt migrations.

6.2.1 Use of telemetry data to estimate smolt survival

Fishery managers use life-stage-specific survival estimates within population models to predict adult returns and set preseason harvest rates. For salmon smolts, survival has been historically difficult to estimate, and thus estimates are limited to smolt-to-adult survival (SAR) that encompasses multiple years and stages of the life cycle (smolt migration through freshwater and coastal marine waters, growing periods in the open ocean, and adult homing migration). Telemetry has been successful in further partitioning survival by focusing on the brief period of smolt outmigration (Welch et al. 2009, 2011, Clark et al. 2016). These estimates have generally not been incorporated into management models, partly due to concern that tagged smolts do not represent the broader population. This skepticism is generally due to low survival estimates that would indicate little to no mortality could occur beyond the last array (i.e. one to three years in the open ocean) which is unrealistic. The impacts of tagging on survival are generally of greatest

concern, even though repeated research has found little effect of tagging on behaviour and/or survival (Brown et al. 2006, Collins et al. 2013, Clark et al. 2016).

Chapter 4, however, provides another mechanism beyond tagging effects by which research action may affect survival; smolts released at times when migratory activity is low experience dramatically reduced survival. This finding underscores the need for researchers to consider not only the effects of the tagging procedure itself, but also how and when fish are released relative to the broader population of interest. Although this indicates that there are more factors affecting survival estimates than previously considered, it also demonstrates the powerful potential to refine estimates of survival from telemetry data in systems where population-level characteristics are being tracked (such as Chilko sockeye). By releasing tagged smolts over a variety of densities, density-dependent predictions of survival can be generated (Figure 4.3). This density-dependent relationship can be applied to hourly outmigration densities measured at the DFO counting fence data to provide a population-level survival estimate that would account for 1) the low probability of survival at low outmigrant densities, and 2) the small proportion of the population that migrate at low outmigrant densities. Such estimates could be valuable to management in partitioning survival of tagged smolts from the time spent in the open ocean in a more realistic manner.

6.2.2 Assessing and managing predator-smolt relationships during migration

Understanding the impacts of predators on species of conservation and/or commercial interest is often a priority for managers in order to understand patterns in distribution and survival. Studies of diet and predator distribution and abundance are generally “scaled-up” to estimate population-level influences on prey through the use of numerical techniques, including

bioenergetics models. In the particular case of acute predation phenomenon (such as salmon smolt migrations), however, care needs to be taken to properly quantify predator-prey relationships.

Migrations by nature are dynamic; migrants are continually moving towards a destination, and therefore interactions with a given suite of predators are expected to be short, resulting in acute impacts of predation that are imposed over a period of days to weeks instead of over a season or throughout the year. This type of relationship has several implications for studying predation impacts on migrants. First, the spatial distribution and behaviour of predators need to be carefully defined. Predator phenology may be adapted to both concentrate predator densities within the migratory corridor (Bouchet et al. 2014) as well allow for predators to follow migrants downstream to increase the duration of consumption. In fact, the concept of consumers following “resource waves” across landscapes to exploit consumption opportunities has recently been brought to light (Armstrong et al. 2016). Second, predators may be particularly adapted to exploit prey during short encounters. Chapter 2 reviews some of these potential adaptations, as well as demonstrated how the simple concept of filling the gut can substantially increase predation on prey over short time scales. Thus it is becoming quickly apparent that predator-prey dynamics during short events such as smolt outmigration differ from those that occur in a more “typical” setting.

In addition to assessment of predation impacts, more active management in the form of predator control or removal is often considered and sometimes used in fisheries (Beamesderfer et al. 1996, Beamesderfer 2000). The logic behind such practices is simple; reducing predator abundance will reduce predation-based mortality and thus increase survival, which in theory

should persist throughout the life cycle. This approach is only effective, however, if fish are being selected by predators either 1) at random, or 2) for characteristics that will not be selected for by other predators or factors further along the migration. Given that the factors resulting in increased predation by bull trout for smolts (infection status and size) are assumed to be related to predator avoidance behaviours, it seems unlikely that predators encountered further along the migratory corridor would not select for similar attributes. In fact, both small size and infection (albeit from different pathogens than found in Chapter 3) have been found to influence avian predation risk on smolts in the Strait of Georgia (Miller et al. 2014). Thus, even if bull trout predation was reduced, unless the health or size of smolts improved quickly during the migration (seemingly unlikely given the rapid nature of freshwater migration; Clark et al. 2016), chances are that these smolts would still experience higher rates of mortality, just in a subsequent landscape. Indeed, the results from predator control programs are mixed at best and often do not result in benefit (Mueller 2005). Further complications occur when predators are native and of conservation concern (Marshall et al. 2015). Therefore comprehensive understanding of the migratory phenomenon is required before predator control is considered.

6.3 Future directions

As in all research, the results from this thesis has spurred the development of several new lines of questioning regarding smolt migrations. In this section, I outline selected areas of research that I especially believe would be beneficial. Where applicable, I describe potential methodologies and sampling designs to be utilized in such endeavors.

6.3.1 Pathogen transmission dynamics relative to the migration process

Chapter 3 identified the potential for infection to alter predation risk and therefore migratory success of wild sockeye salmon smolts. Interest in the role of pathogens in ecology has recently increased both broadly (Hudson et al. 2006, Altizer et al. 2011) and directly for salmon (Miller et al. 2014). A distinct lack of understanding remains, however, in terms of pathogen transmission and subsequent prevalence rates throughout the migratory process (Altizer et al. 2011). Chapter 3 hypothesizes that ‘migratory culling’ is possible, which would act to reduce pathogen prevalence throughout the migration. However, smolt migrations are highly synchronous (Chapter 4), and thus smolts are in high density and it assumed transmission rates can be high. Thus it appears the potential for migratory culling (vs pathogen prevalence being relatively constant or even increasing over the migration) is dependent upon the balance between the severity of the pathogen’s effects on behaviour and survival, the density of conspecifics migrating, and the speed at which migration occurs. To attempt to tease these factors apart for a given pathogen, research could combine focused challenge experiments (to understand transmission dynamics) with simulation models (informed by these challenge experiments along with outmigration data) to understand under which scenarios migratory culling is likely. Results of such simulations could be further tested empirically with field sampling along the migratory corridor to assess spatial variability of pathogen prevalence within a population such as Chilko. These comparisons will be further complicated by the mixing of smolts among populations downstream, but could provide at least the theoretical basis for when migratory culling might occur.

Aside from transmission dynamics during the migration, it is evident that simply more knowledge on the presence and prevalence of pathogens across salmon populations and years is needed. Only through broad and consistent monitoring of fish health will potential impacts of pathogens on population productivity and changes through time and/or changes in environmental conditions be understood. Care is currently taken to quantify the number of smolts outmigrating each year and their size and condition; I suggest we also monitor fish health as well.

6.3.2 Synchronization of migrations: mechanisms and manifestations across scales

Part of the human fascination with animal migrations is generated by the sheer volume of individuals moving simultaneously, resulting in incredible visual spectacles. By definition, migrations are the result of synchronizations of movements at the population level. Such synchrony appears to have strong value in reducing predation risk (Chapter 4), and this value has theoretical support (Ims 1990). Indeed, the Chilko smolt outmigration is quite synchronous, with 10 – 40 million smolts outmigrating annually over a ~4-week period each year. However, there is considerable day-to-day variability in outmigrant densities (Chapter 4) as well as interannual variability (Chapter 2). Simulations of bull trout feeding presented in Chapter 2 showed the potential for variability in the magnitude, timing, and spacing of peaks outmigrant smolts to influence bull trout consumption, and therefore smolt mortality. Thus the dynamics of such synchronization can have important population-level impacts.

The causes of variability in synchronized densities are unknown, but could include timing in smoltification (i.e. physiological), or the spatial variation in smolt locations when smoltification occurs. Chilko Lake is ~70 km long, and the distribution of smolts prior to the spring outmigration is largely unknown. Synchronization occurs at multiple scales. Chilko

sockeye certainly swamp predators in the upper Chilko River, but do these benefits of population-level synchronization persist downstream? And does inter-population (and even potentially inter-species) timing of outmigration result in swamping of predators further along the migratory corridor (i.e. in the estuary or coastal waters)? Again, theoretical investigations could provide important first steps in estimating potential consequences. Identifying factors that both result in synchrony within and among populations, as well as the landscapes at which swamping is effective, could contribute to understand the potential effects of both population fragmentation and climate change, if environmental factors appear to affect timing.

6.3.3 Understanding potential interactions among factors in smolt migrations: the use of simulation models

This thesis successfully identified factors influencing smolt migrations within the context of the movement ecology framework (Section 6.1), but the remaining challenge is to properly synthesize across these findings (and the broader knowledge on smolt ecology) to develop a hierarchical understanding of the factors influencing smolt migration survival. It is important to understand where and when each factor is of most importance and the relative balance among these factors in determining migratory success. This thesis demonstrates the capability of using complementary techniques (telemetry, predator diet analysis, bioenergetics, and genetics) simultaneously to provide a more comprehensive understanding of the migration process within a given landscape, and further field studies could attempt to extend these techniques to investigate more factors simultaneously. A field study that 1) combines the use of gill biopsies with telemetry (as in Jeffries et al. 2014), 2) tags both age-one and age-two fish (either with new acoustic tags or PIT tags), and 3) combines telemetry results with population density information

(as in Chapter 4), could directly assess the impacts of fish health, size, and conspecific densities within a single framework, but would require substantial sample sizes.

An alternative approach to at least generate hypotheses of such hierarchies is through the use of simulation modelling and specifically individual-based models (IBM). IBMs are valuable in assessing complex systems that allow population-level predictions to manifest or emerge from interactions among individuals and the external environment (Grimm et al. 2005). Through the development of sub-models to represent important components of the migration (internal state, movement behaviours, and external factors), knowledge from across studies, including this thesis, can be incorporated to build a virtual laboratory within which the effects of each component can be tested under a variety of conditions. Sensitivity analyses can help to identify factors that dramatically influence migratory behaviour and/or success. IBMs are also useful in exploring scenarios that cannot be found in the field, such as changes in climate or species phenology (Stillman et al. 2015).

6.3.4 The role of salmon smolt migrations in ecosystems: importance to consumers across landscapes

Beyond further understanding the factors that affect smolt migrations, there are opportunities to describe and quantify the impacts of the smolt migrations on the landscapes and ecosystems smolts traverse. The ecosystem-level impacts of spawning migrations of adult salmon are heavily researched and well-publicized (Gende et al. 2002, Childress et al. 2014), but smolt migrations still represent the transportation of a large biomass for consumers to exploit.

Chapter 2 demonstrated that resident bull trout, a species that is of conservation concern across most of its range (Dunham et al. 2008), exploited the migration to binge-feed on

outmigrant smolts, but the ecological consequences for bull trout are unknown. Does feeding on outmigrant smolts contribute significantly to annual energy budget of bull trout? Dolly Varden have been found to largely depend on sockeye salmon spawning to fulfill their annual energy requirements (Armstrong and Bond 2013). How far (from within the lake, downstream, or even in neighboring systems) do bull trout move in order to be in optimal position to exploit the migration, and what are the consequences of such behaviour? Other taxa feed on Chilko sockeye smolts, including a number of avian predators (Clark et al. 2016), but it is unknown if the behaviour of these predators is altered by the smolt outmigration and if there are any consequences on fitness. Focused research on the predator consumption, growth, and behaviour could help elucidate the impacts of smolt migrations on higher trophic levels.

Similarly, little is known regarding predator distribution, abundance, and behaviour in the coastal environment relative to smolt outmigrations. The Strait of Georgia is characterized by a number of potential migratory routes and narrow corridors, providing the type of spatial constrictions that could ease exploitation of migrants (Chapter 2; (Bouchet et al. 2014)). Research dedicated to feeding ecology of upper trophic levels in the Strait of Georgia could have the two-fold benefit of not only identifying consumers exploiting smolt migrations (and help to identify the ultimate cause of mortality), but also to again understand the impacts of smolt migrations on the broader marine ecosystem.

6.4 Summary

In sum, this thesis identified important links between the physical state of smolts, smolt size, migration synchronization, and migration route on behaviour and survival. Individually, chapters advanced the fields of migration and feeding ecology by testing long-held hypotheses including that migrants can swamp predators to reduce individual risk, and infected fish are more susceptible to predation. Collectively, the thesis demonstrates the value in pairing biotelemetry with complementary techniques to provide a more comprehensive perspective of the migration process. The movement ecology framework by Nathan et al. (2008) continues to be useful in conceptualizing animal movements and migrations. Using this framework, this thesis has expanded our understanding of the factors influencing the migration of one of the largest sockeye populations in Canada.

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Appendices

Appendix A Detailed methods for analyses of binge-feeding

A.1 Analysis of degree of binge-feeding

To determine how the degree of binge-feeding scaled with temperature and differed among settings, a generalised least squares (GLS) approach was followed as in the protocols by (Zuur et al. 2009). GLS used in exploratory analyses using linear regression resulted in heterogeneity in residuals. A combined variance structure was employed that allowed for unidirectional spread in residuals across temperatures (fixed variance) and for residual spread to vary across the three foraging settings (variance covariate). This model structure performed better (via AIC and likelihood ratio tests [LRT]) than simple linear regression and GLS with simpler variance structures (i.e., fixed variance and locale-only structures). Once the variance structure was selected, a backwards stepwise-selection procedure determined the main effects (temperature, mass, and setting) to be included in the final model. Likelihood ratio tests were used to compare model fits (log likelihood) of nested models (via maximum likelihood; ML), and the more parsimonious model (i.e., with a dropped variable) was selected when an increase in the log-likelihood ratio statistic was significant ($P < 0.05$). The final model was then refitted with restricted maximum likelihood (REML).

A.2 Analysis of specific consumption

For investigating specific consumption of bull trout, exploratory analyses determined that parametric (i.e., linear and GLS models with a variety of transformations and/or correlation structures) models resulted in poor model fit (by visually assessing residuals), and thus generalized additive models (GAM) were used. GAMs are a nonparametric extension of general

linear regression that allow for complex and nonlinear relationships. GAMs were constructed using the *mgcv* package (Wood 2006, 2011) in R (R Core Team 2014). The degree of smoothing was automatically chosen via minimization of the cross validation score. To prevent unrealistic or uninterpretable response curves, the effective degrees of freedom (edf) for each curve was limited to 3 (Sundblad et al. 2009, Furey and Rooker 2013).

A.3 Simulations of bull trout consumption

Parameters for simulation models are described in (Mesa et al. 2013). Briefly, the model by (Mesa et al. 2013) is a Wisconsin bioenergetics model (Hanson et al. 1997) parameterized for bull trout. The model is an energy-balance equation such that growth is balanced between the rate of food consumption and the rates of respiration, egestion, and excretion. Consumption in the model is limited by C_{\max} and the (Thornton and Lessem 1978) water temperature dependence function for coldwater species (consumption equation 3 in (Hanson et al. 1997)). As in (Mesa et al. 2013), specific dynamic action was set at 0.172 and rates of egestion and excretion were based on lake trout values (Hanson et al. 1997, Mesa et al. 2013). For simplicity, smolts were assumed to represent 100% of the diet throughout simulations (Furey et al. 2015), with an energy density of 4172 J/g (Parrish et al. 2006). Smolt indigestibility was set as 0.03 (Beauchamp et al. 2007). No activity multiplier was added into simulations.

Appendix B Summary of CJS models with interactions

Summary of CJS models that included interactions between array location and individual covariates. Models are ranked based on QAICc, and the Delta QAICc refers to the top model from Table 5.2. Terms in parentheses indicate factors across which survival (Φ) or detection probability (p) varies.

Model	npar	QAICc	Delta QAICc
Φ (~array * conspecific density) p (~array)	23	765.7	6.8
Φ (~array * time of night) p (~array)	23	800.4	41.6
Φ (~array * FL) p (~array)	23	812.0	53.1
Φ (~array * date) p (~array)	23	813.2	54.3
Φ (~array * mass) p (~array)	23	814.1	55.2
Φ (~array * condition) p (~array)	23	818.0	59.1

Appendix C Relationship between duration between detection sequences and difference in receiver position

Scatterplot of the relationship between the duration (in hours) between the first and second detection sequences and the difference in receiver position (km) for sockeye and steelhead smolts at the northern Strait of Georgia (NSOG) array. Best-fit regression lines for each species are added for visualization. Points are jittered by up to 0.5 units horizontally to aid visibility. Correlations were significant for both sockeye (Kendall's $\tau = 0.49$; $P < 0.0001$) and steelhead (Kendall's $\tau = 0.38$; $P < 0.0001$) smolts.

