Migratory diversity of juvenile salmon in a threatened estuary

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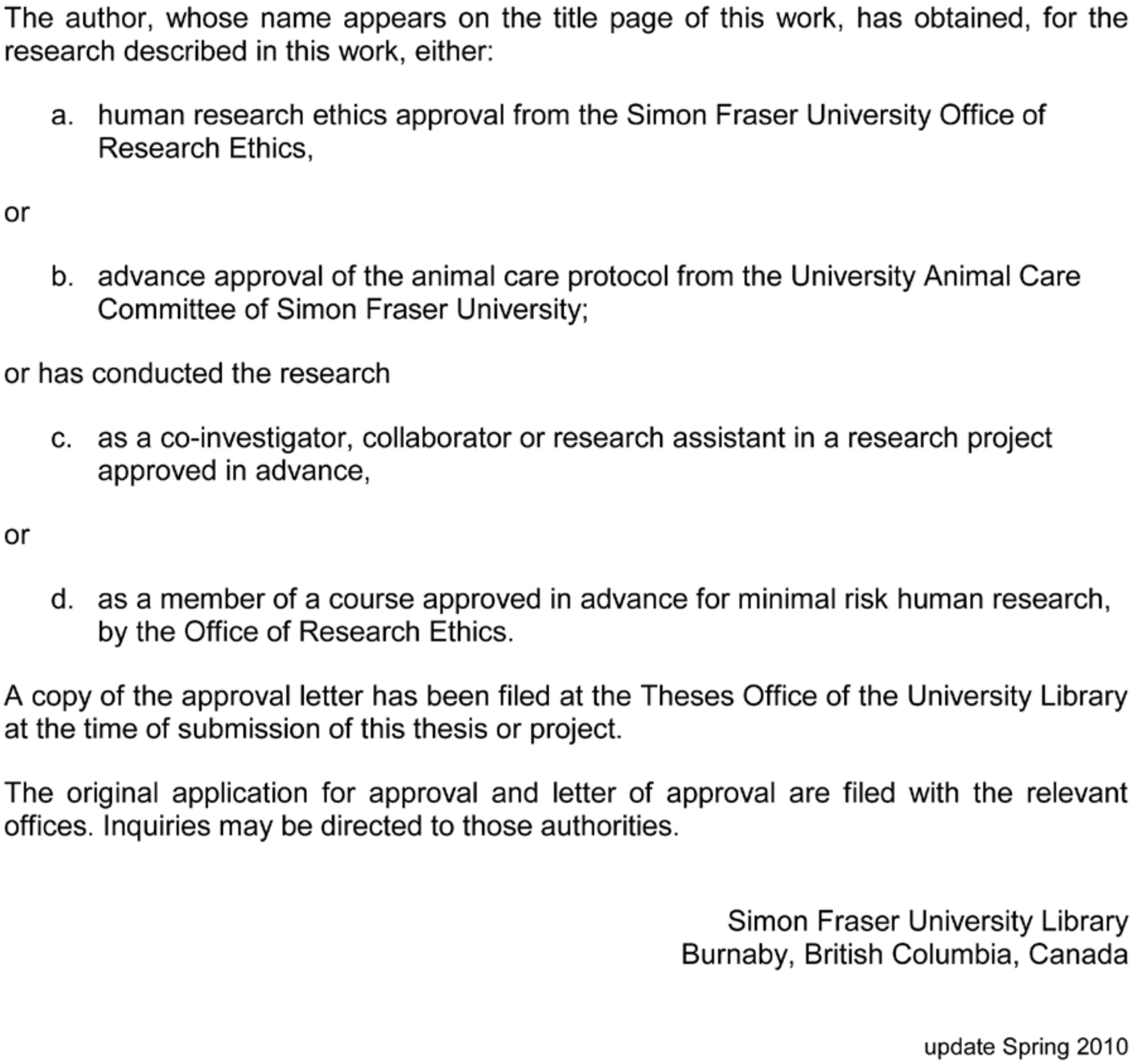

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Abstract

Understanding how migratory species such as juvenile salmon (*Oncorhynchus* spp.) utilize key transition habitats such as estuaries can illuminate their vulnerability to pressures such as habitat alteration or climate change. This thesis examined the diversity of migratory juvenile salmon in the estuary of the vast Skeena River, Canada. First, I compared abundances of different species of juvenile salmon in different regions, and found that sockeye (*O. nerka*) and Chinook (*O. tshawytscha*) salmon were most abundant in areas proposed for development. These estuary salmon were genetically linked to dozens of locally-adapted populations from throughout the Skeena watershed and beyond. I also found that downstream migration timing was population-specific and related to the elevation of the different rearing lakes and distance travelled. Different populations encountered different zooplankton communities in the estuary. These results suggest that the Skeena estuary integrates multiple scales of salmon diversity, which could be compromised by impending habitat degradation.

Keywords: estuary; habitat degradation; migration; phenology; salmon; zooplankton

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Chapter 1. Introduction

Nearshore coastal and estuary habitats are important ecosystems that support rich and diverse aquatic communities and fisheries (Beck *et al.*, 2001). However, in an era of rapid worldwide decreases in biodiversity largely attributable to habitat loss (Pimm & Raven, 2000), anthropogenic activities have reduced the capacity of these habitats to support aquatic resources (Lotze *et al.*, 2006). Coastal and estuary habitats are being developed at rapid rates to support encroaching human settlements, heavy industry, and marine shipping infrastructure. Modifications to wetland, seagrass and fish nursery habitats have resulted in declines in species richness and depletion of marine resources (Lotze *et al.*, 2006). Coastal habitat degradation is one of multiple stressors affecting marine communities, and the cumulative effects of habitat loss, increased fishing pressure, pollution, and climate change to ecosystem structure and function are not well understood (Crain *et al.*, 2008). Diversity protects an ecosystems' capacity to respond to environmental change (Loreau *et al.*, 2001). Decreased species richness may reduce redundancy in ecological interactions (Burkle *et al.*, 2013), while declines in population diversity may contribute to reductions in ecosystem services (Luck *et al.*, 2003). Changes in coastal marine and estuarine communities driven by habitat degradation may therefore reduce their resilience to environmental change, and it is important to consider diversity at multiple scales when assessing the effects of development on these habitats.

Anadromous salmonids are one group of migratory fishes that are thought to rely heavily on estuary habitats (Simenstad *et al.*, 1982). As juvenile salmon transit estuaries, the interface between freshwater and marine habitats, during their seaward migration, they undergo a physiologically challenging transition as they acclimate to new environmental conditions. The downstream migration and early marine life history stages, including the period of estuarine residence, are a critical period of high mortality for some species of juvenile salmon (Parker, 1968; Pearcy, 1992). Previous studies have observed that different species of juvenile salmon appear to utilize different habitats within estuaries at different life history stages (Healey, 1982; Thorpe, 1994; Weitkamp *et al.*, 2014). Some species of juvenile salmon may rely on specific estuary habitat for forage and protection from predators (Simenstad *et al.*, 1982). For example, juvenile Chinook salmon prefer native eelgrass habitats to other benthic habitat types (Semmens, 2008). Furthermore, degradation of estuary habitats has been associated with declines in survival of some species of anadromous salmon, particularly Chinook salmon (Magnussen & Hilborn, 2003; Meador, 2014). However, the estuary component of the juvenile salmon life-cycle is relatively under-studied (Weitkamp *et al.*, 2014). For the estuaries of large rivers in particular, which may support several species and many populations of salmon, understanding how this salmon biodiversity moves through estuaries in time and space is of critical importance for understanding basic salmon biology as well as informing development policy.

This thesis examines the juvenile salmon habitat utilization in the estuary of a large river system, the Skeena River, British Columbia. The 570 km Skeena River and its tributaries support robust returns of hundreds of distinct populations of six species of Pacific salmon, (*Oncorhynchus* spp.) including sockeye (*O. nerka*), pink (*O. gorbuscha*, chum (*O. keta*), coho (*O. kisutch*), Chinook (*O. tsawytcha*), and steelhead salmon (*O. mykiss*), which are targeted by numerous commercial, recreational and First Nations fisheries. There are currently several industrial projects proposed for development in the relatively pristine Skeena River estuary which would alter these habitats through significant dredging and shoreline modifications, construction of jetties, trestles, and increased vessel traffic (Stantec, 2011, 2013; AECOM, 2013). Few studies have considered the direct impact of the proposed developments on these culturally and economically valuable fish populations.

I conducted a two-year juvenile salmon sampling project in the Skeena River estuary using trawl, beach seine, and purse seine sampling. Chapter 1 describes the temporal and spatial distribution of different species of juvenile salmon throughout the estuary. In this first chapter, I sampled juvenile salmon with two different gear types: a beach seine, which sampled nearshore littoral habitats, and a midwater trawl, which sampled deeper waters further offshore. I found that different species of juvenile salmon were more likely to be captured in different habitats at different times during the smolt migration period. For instance, juvenile pink (*O. gorbuscha*) and chum salmon (*O. keta*) were captured exclusively in littoral habitats in April and early May, juvenile coho salmon (*O. kisutch*) were captured in littoral and pelagic habitats in May and June, and juvenile sockeye salmon (*O. nerka*) were only captured in pelagic habitats in late May and early June. Thus, estuary habitat utilization patterns varied by species over time. Next, I examined the horizontal distribution of different species of salmon by comparing trawl capture abundances of different regions throughout the Skeena River estuary in 2013 with data collected in 2007 during a separate juvenile salmon sampling project conducted by Skeena Fisheries Commission. I constructed a series of generalized additive models to assess the relative effects of region on juvenile salmon abundance for the different species after controlling for time. These models revealed that abundances of the different species of juvenile salmon varied by region, and the relative abundances of sockeye and coho salmon were consistent between the different regions across years. The highest abundances of some species, including sockeye and Chinook salmon in both years, and coho salmon in 2013, were captured in the region where industrial development is proposed. Finally, I used microsatellite DNA analysis to determine the populations of origin for the juvenile Chinook and sockeye salmon, the only Skeena salmon species for which baseline genetic data are available, that I captured in the estuary. The genetically identified sockeye and Chinook salmon originated from dozens of spawning habitats in tributary streams and lakes throughout the Skeena watershed and beyond, suggesting that alteration of these habitats has the potential to affect salmon populations far beyond the geographic scope of the projects.

In Chapter 2, I examined a relatively understudied aspect of phenotypic diversity in a single species, the migration timing of juvenile sockeye salmon. Using genetic data collected in 2013 and 2014, I quantified sockeye salmon smolt migration timing for different Skeena River populations captured in the estuary. I used linear modeling to determine the effects of year and population on the timing of estuarine capture, which I used as a proxy for smolt migration timing. I found that smolt migration timing varied considerably by population, while year had little effect. Next, I used linear mixed effect models to determine the relative effects of geographic factors including migration distance, elevation, latitude, and productivity on smolt migration timing. While I found that smolt migration timing was strongly related to river distance and elevation, population identity explained more of the variability in smolt migration timing than geographic factors. Population-level variation in outmigration timing was greater than predicted based on difference in migration distance and swim speed alone, as indicated by the opportunistic recapture of several tagged fish from a concurrent upstream smolt fence project. The smolt migration timing for different sockeye salmon populations from within the Skeena watershed differed by over six weeks, providing evidence of previously underappreciated phenological diversity.

The diversity in migration timing is important for salmon smolts entering marine waters where successful feeding and growth determine whether they will survive to reproduce (Beamish & Mahnken, 2001; Farley *et al.*, 2007). There is considerable within and across-year variability in the timing and abundance of the zooplankton prey resources on which sockeye salmon post-smolts feed (Mackas *et al.*, 2007; Tanasichuk & Routledge, 2011). While zooplankton phenology has advanced with rising ocean temperatures (Edwards & Richardson, 2004; Hays *et al.*, 2005; Poloczanska *et al.*, 2013), phenologies of secondary and higher consumers are advancing less rapidly than primary producers and primary consumers (Thackeray *et al.*, 2010). Variable rates of temporal advance between different trophic levels could result in phenological mismatch (Cushing, 1990) between juvenile salmon and their zooplankton prey. I conducted a zooplankton sampling program in the Skeena estuary in 2013 and 2014, and found that for both years, the relative abundances of important sockeye salmon food items varied throughout the smolt migration period such that the different populations of salmon, arriving in the estuary at different times, would encounter different prey groups. I then analyzed a long term time series of local temperature data collected within 100 km of our sampling stations and found that mean monthly sea surface temperatures have increased by over 0.7^{o}C over the last 50 years during April and May, the months immediately prior to the timing of ocean entry for sockeye salmon. These results imply that the different populations of juvenile sockeye salmon from the Skeena River, already experiencing different feeding conditions upon arrival in the estuary, may respond differently to shifting ocean temperatures. Conserving the diversity of hereditary traits such as the phenological diversity of smolt migration timing may therefore be important for ensuring that the Skeena sockeye salmon populations maintain the potential to respond to environmental change.

In Chapter 4, I discuss my results in broader context and provide recommendations for future work based on the findings of my thesis research.

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Chapter 2. Juvenile salmon usage of the Skeena River estuary

This paper has been accepted for publication at PloS One, with coauthors Allen Gottesfeld and Jonathan Moore.

2.1. Abstract

Migratory salmon transit estuary habitats on their way out to the ocean but this phase of their life cycle is more poorly understood than other phases. The estuaries of large river systems in particular may support many populations and several species of salmon that originate from throughout the upstream river. The Skeena River of British Columbia, Canada, is a large river system with high salmon population- and species-level diversity. The estuary of the Skeena River is under pressure from industrial development, with two gas liquefaction terminals and a potash loading facility in various stages of environmental review processes, providing motivation for understanding the usage of the estuary by juvenile salmon. We conducted a juvenile salmonid sampling program throughout the Skeena River estuary in 2007 and 2013 to investigate the spatial and temporal distribution of different species and populations of salmon. We captured six species of juvenile anadromous salmonids throughout the estuary in both years, and found that areas proposed for development support some of the highest abundances of some species of salmon. Specifically, the highest abundances of sockeye (both years), Chinook in 2007, and coho salmon in 2013 were captured in areas proposed for development. For example, juvenile sockeye salmon were 2-8 times more

abundant in the proposed development areas. Genetic stock assignment demonstrated that the Chinook salmon and most of the sockeye salmon that were captured originated from throughout the Skeena watershed, while some sockeye salmon came from the Nass, Stikine, Southeast Alaska, and coastal systems on the northern and central coasts of British Columbia. These fish support extensive commercial, recreational, and First Nations fisheries throughout the Skeena River and beyond. Our results demonstrate that estuary habitats integrate species and population diversity of salmon, and that if proposed development negatively affects the salmon populations that use the estuary, then numerous fisheries would also be negatively affected.

2.2. Introduction

Estuaries link freshwater and marine habitats for diadromous species such as Pacific salmon (*Oncorhynchus* spp.). Estuaries are staging areas and transition zones where juvenile anadromous salmon can grow rapidly and physiologically adapt to saltwater environments (Healey, 1980; Levy & Northcote, 1982; Iwata & Komatsu, 1984). The early marine life history stages, including the period of estuarine residence, are among the most critical life history stages for juvenile salmon (Parker, 1968; Healey, 1982; Bax, 1983; Pearcy, 1992; Karieva *et al.*, 2010), and growth attained during this period can determine whether they survive to reproduce (Mortensen *et al.*, 2000; Beamish & Mahnken, 2001). Despite the emerging appreciation of the importance of the estuary phase to the overall dynamics of salmon populations (Karieva *et al.*, 2010), this phase of the salmon life-history is less well-studied than their marine or freshwater phases (Weitkamp *et al.*, 2014).

Estuaries provide juvenile salmon with habitats where feeding and growth opportunities are relatively high (Healey, 1980; Levy & Northcote, 1982) and predation pressure is relatively low. For example, Chinook salmon (*O. tshawytscha*) fry grew over 5% a day in the Nanaimo River, BC (Healey, 1980) and restored Puyallup, WA (Shreffler *et al.*, 1992) estuaries. Estuary-rearing steelhead (*O. mykiss*) grew more rapidly in a seasonally-closed tidal lagoon and exhibited less size-selective mortality than their counterparts that reared in freshwater and went directly to sea (Bond *et al.*, 2008). Active feeding and growth in estuaries has been observed even in salmon populations that migrate rapidly seaward (Weitkamp *et al.*, 2014). Estuaries can provide cover to juvenile salmonids from predators due to higher turbidity (Straty & Jaenicke, 1980), estuarine vegetation, such as seagrass and algae beds (Semmens, 2008), and riparian vegetation (Quiñones & Mulligan, 2005), and rates of predation on juvenile salmon may be lower in estuaries than other habitats. For instance, juvenile Chinook salmon released at estuarine sites were exposed to fewer fish and avian predators than those released to marine sites near Campbell River, BC (Macdonald & Mcallister, 1988). Furthermore, while juvenile salmonids were an important food item for common mergansers (*Mergus merganser*) in freshwater habitats they were rarely consumed by mergansers in estuaries (Wood, 1987). Given the potential importance of estuary food webs and habitats to juvenile salmon, it is perhaps not surprising that juvenile salmon survival rates have been found to be higher in estuaries with less degraded habitat (Magnussen & Hilborn, 2003).

The duration of estuarine residence varies among anadromous salmon species and populations (Thorpe, 1994; Bottom *et al.*, 2005; Weitkamp *et al.*, 2014). Many populations of coho (*O. kisutch*) and sockeye (*O. nerka*) salmon may transit rapidly through estuaries (Thorpe, 1994; Weitkamp *et al.*, 2014), while others such as chum (*O. keta*) and ocean-type Chinook salmon may remain in estuaries for weeks or months (Thorpe, 1994; Weitkamp *et al.*, 2014). Different populations within species also exhibit different timing and patterns of estuarine residence. Juvenile Chinook salmon which enter marine waters in their first year of life may inhabit estuarine habitats for several months (Healey, 1980), while their stream-type counterparts, which rear in freshwater for one year or longer, may occupy estuaries only briefly during their seaward migration (Weitkamp *et al.*, 2014). Ocean-type sockeye fry will rear in estuaries where suitable lake habitat is unavailable, such as in the Situk estuary in Alaska where feeding and growth was observed in age-0 sockeye for 3-4 months (Thorpe, 1994), while age-1 and 2 sockeye salmon swam rapidly through the much larger Bristol Bay estuaries upon ocean entry (Straty & Jaenicke, 1980). Age-0 and age-1 sockeye inhabited brackish waters in the estuary for up to three months in the Chignik, AK system where lake-rearing habitat is available (Simmons *et al.*, 2013). Microchemical analysis combined with daily growth increment counts of otoliths provided evidence of overwintering in estuaries for juvenile coho salmon from two systems in Cook Inlet, AK *(*Hoem Neher *et al.*, 2013). Increased estuarine rearing opportunities following estuary restoration in the Salmon River system in Oregon had increased life-history variability among juvenile Chinook salmon that utilized these habitats (Bottom *et al.*, 2005) which supported five different previously described ecotypes (Reimers, 1973) ranging from immediate ocean entry to prolonged estuary rearing types. There is continued need to understand how estuary habitats support different species and populations of salmon, particularly for the estuaries of large watersheds with high salmon biodiversity (Simenstad & Cordell, 2000).

Hundreds of millions of salmon smolts from a variety of populations and species funnel through the estuaries of large watersheds (Weitkamp *et al.*, 2014) such as the estuary of the Skeena River, British Columbia, Canada. All species of semelparous eastern Pacific salmon and steelhead spawn throughout this 55,000 km^2 watershed, representing hundreds of distinct populations including up to 70 sockeye, 55 Chinook, 133 coho, 75 even-year pink (*O. gorbuscha*), 81 odd-year pink, and 34 chum salmon populations associated with specific spawning areas (Morrell, 2000). There is considerable genetic, phenotypic and life-history diversity among the different populations of each species, encompassing variation in run timing, age structure, and preferred spawning habitats (Gottesfeld & Rabnett, 2008). Salmon escapements to the Skeena River included approximately 668,000 sockeye, 2.5 million pink, 88,000 coho, and 36,000 Chinook salmon in 2009 (Pacific Salmon Commission, 2014). The total returns are higher when the various fisheries are taken into account--the Northern Boundary Technical Committee of the Pacific Salmon Commission estimate an average run size of nearly 3,000,000 sockeye salmon (1985-2012) with an average exploitation rate of 41% (Pacific Salmon Commission, 2014), and an average exploitation rate for Chinook salmon of about 50% (Pacific Salmon Commission, 2014). Chum salmon are the least numerous of the commercially-exploited anadromous species, with estimated escapements of several thousand in recent years (English, 2012), considerably less than historical abundances (Price *et al.*, 2013). Steelhead returns to the Skeena River during the past decade have been between 20,000 and 50,000 (Hooton, 2011). These different salmon species support Canadian and USA commercial fisheries, both tidal and freshwater recreational fisheries, and numerous First Nations food, social and ceremonial (FSC) fisheries that occur throughout the watershed. During the peak of the commercial fishing industry in the early 1900s, millions of salmon were captured annually by seine and gillnet fleets that supported dozens of fish canneries in the Skeena estuary (Blyth, 1991; Argue & Shepard, 2005). Variability of these salmon populations and unpredictable returns now threatens fisheries; for instance low sockeye salmon returns in 2013 led to the unprecedented closure of Skeena commercial, recreational, and First Nations fisheries due to conservation concerns (Pacific Salmon Commission, 2014).

The high salmon biodiversity of the Skeena River system necessarily passes through the downstream estuary during their seaward migration, but it is thought that the duration of estuary residence and resource utilization varies among the different species and populations of salmon (Thorpe, 1994; Weitkamp *et al.*, 2014). For example, pink and chum salmon enter marine waters immediately after emergence at 30-40 mm in length (Healey, 1982) and feed on small zooplankton such as calanoid copepods in nearshore littoral habitats (Manzer, 1969). Coho salmon, which spend one or two years in freshwater prior to their downstream migration, are partially piscivorous when they arrive at sea, sometimes preying on juvenile pink and chum salmon in addition to larval smelt and sand lance in the estuary (Parker, 1971). In addition to the Skeena River, salmon from other watersheds such as the Nass River and several smaller coastal systems in the region may also utilize the Skeena River estuary. While the freshwater life-history stages of many populations of Skeena River salmon have been extensively studied (Macdonald *et al.*, 1987; Rutherford *et al.*, 1995; Gottesfeld & Rabnett, 2008; Cox-Rogers & Spilsted, 2012), there have been comparatively few studies of juvenile salmonids in the Skeena River estuary. The federal Department of Fisheries conducted a survey of juvenile salmon in the Skeena River estuary in 1955 (Manzer, 1956), and the British Columbia Ministry of Environment conducted a biological assessment of aquatic resources in the Skeena River estuary in 1972 (Higgins & Shouwenberg, 1973). During both of these surveys, thousands of juvenile salmon were captured by beach and purse seine and trawl sampling and juvenile salmon were observed in all parts of the estuary that were sampled. More recently, the Skeena Fisheries Commission conducted a large-scale juvenile salmon sampling project throughout the Skeena River estuary as part of a baseline sea lice research project from 2004-2007 (Krkosek *et al.*, 2007; Gottesfeld *et al.*, 2009; Price *et al.*, 2011), and also observed juvenile salmon in all parts of the estuary that were surveyed. Thus, while there has been some historic research on juvenile salmon in the Skeena River estuary, it is relatively understudied compared to other large salmon-bearing rivers.

There are currently several large-scale industrial development projects pending in the Skeena River estuary, including a bulk potash loading facility and two liquefied natural gas (LNG) terminals (Stantec, 2011, 2013; AECOM, 2013;Figs. 2.1, 2.2). The causeway and berth for one of the proposed LNG terminals is situated between Lelu and Kitson Islands on Flora Bank, which represents 50-60% of tidal and subtidal eelgrass habitat in the Skeena estuary. As part of the application process for industrial development, project proponents are required to submit environmental assessments of ecosystem components that could be adversely impacted by the proposed development. Environmental assessment studies conducted by project proponents provide an opportunity to collect information on important ecosystem components such as juvenile salmon and their habitats. However, the scope and time frames of environmental reviews, as well as the number of projects that must complete a federal environmental assessment, have been recently reduced (Gibson, 2012). Previous understanding of estuaries in general (Simenstad & Cordell, 2000) and the Skeena River estuary in particular (Manzer, 1956; Higgins & Shouwenberg, 1973) suggest that these habitats support juvenile salmon. For example, Flora Banks was previously found to be among the most important early marine habitats for pink salmon from the Skeena watershed, and past proposals for industrial development in the vicinity of Flora Banks were rejected because of concerns about the potential environmental risks to salmon productivity (Hoos, 1975). However, consulting agencies on behalf of the project proponents have submitted environmental assessment applications to the Canadian Environmental Assessment (CEA) Agency for approval of these projects (AECOM, 2013; Stantec, 2013) without conducting field studies of juvenile salmon. Despite the lack of data from field studies of juvenile salmon, environmental assessment applications have consistently come to the conclusion that proposed projects will have no significant residual negative impacts on salmon populations (Stantec, 2014). At the time of writing, the proposed potash terminal had completed the CEA Agency's review process under an older version of Canadians Environmental Assessment Act which has since been replaced by new legislation, and was approved to proceed to the permitting stages. The two LNG terminals entered the environmental assessment process under the new regulations. There is thus a pressing need for scientific data on the usage of the Skeena River estuary by juvenile salmon.

Here we examined the usage of the Skeena River estuary by juvenile salmon. In particular, we examined the geographic and temporal habitat utilization of juvenile anadromous salmon in the greater Skeena River estuary in relation to the footprints of the proposed industrial development projects. Furthermore, we used genetic identification to illuminate connections between the estuary habitat and the specific population of origin. These data can help illuminate the current status of salmon biodiversity in the Skeena River estuary, and guide decisions regarding its future.

2.3. Methods

2.3.1. Study area

The main stem of the Skeena River is approximately 570 km long with a mean discharge of about 1,750 m^3/s. The Skeena River enters the ocean near the village of Port Edward on the north-west coast of British Columbia, where it divides into three channels at a group of islands near the mouth of the river. All of the proposed developments fall within the jurisdiction of the Prince Rupert Port Authority and are located near the exit of the northernmost and central channels, both of which flow northward. At peak discharge, the zone of freshwater influence extends well past this area, approximately 50 km southwest through Ogden Channel, and over 85 km northwest through Chatham Sound and out Dixon Entrance (Figs. 2.1 and 2.2).

2.3.2. Fish sampling

We collected juvenile salmonids by trawl between May 26 and July 5, 2007, and from May 5 to July 1, 2013. Trawl sampling was conducted using a modified trawl which was fished from an 11 m ex-gillnet vessel, HMV Pacific Coast. The trawl net was 18 m long with an opening 5 m wide and 4.6 m deep, with a rigid, baffled holding box designed for live capture (Gottesfeld *et al.*, 2009), and sufficient flotation to maintain a position at top of the water column while fishing. Therefore, only the surface layer of the water column was sampled for all trawls, where juvenile salmon are known to feed during the daylight hours when we sampled (Barraclough & Phillips, 1978; Straty & Jaenicke, 1980). The trawl net was deployed for a targeted duration of at least 15 min and up to 20 min for an approximate tow length of 1 km depending on the velocity of prevailing currents. All trawls were conducted within 1 km from shore over water depths ranging from approximately 5 m to over 800 m. Trawl sites were aggregated into generalized regions according to their relative proximity to the northern or southern exit of the Skeena River (Fig. 2.1). The 2007 trawl sampling program was more extensive than in 2013, and encompassed five regions (Inside North (IN), Outside North (ON), Middle (MID), Inside South (IS), and Outside South (OS)), while the 2013 program encompassed only three regions (IN, IS, and OS) (Fig. 2.1). Hereafter we refer to these as “regions”. The IN region contains the proposed industrial development footprints.

Beach seine sampling was carried out from April 29 to June 13, 2013 to sample the nearshore fish community. Beach seining occurred weekly at shoreline sites close to proposed industrial activities near the northern entrance to the Skeena River (Fig. 2.2). The beach seine net was 35 m long and 3 m deep, with 13 mm mesh at the tow ends and 6 mm mesh at the bunt. Each beach seine sampling event consisted of a single set, during which the seine net was deployed down-current from an anchor point on the beach using a 3 m vessel. The beach seine sites were all located within the IN region and were grouped according to the island or inlet where each site was located (Fig. 2.2). Hereafter we refer to these as “sub-regions”. The Ridley Island and Lelu Island sub-regions are within proposed industrial development footprints.

Average beach seine catches for each species were calculated for each sub-region and sampling week. Trawl catches were normalized based on trawl duration by multiplying the catch by typical duration (20 min) and dividing by the observed duration to obtain a catch per unit effort (CPUE). Average normalized trawl catches were calculated for each species and trawl region.

2.3.3. Statistical analysis

We analyzed trawl CPUE for sockeye, coho and Chinook salmon with generalized additive models (Wood, 2006). Specifically, generalized additive models were constructed to estimate the overall mean CPUE for each species in each region in each year by applying a non-parametric smooth function to day-of-year and treating the different regions as parametric factors. The resulting model is of the form

$$\log Y = f(d) + \beta(x)$$

where Y is the CPUE (mean normalized catch per 20 min set) for a given species, f is a thin-plate regression spline smoother (Wood, 2003) for day of year d, and the β coefficient is the mean abundance for each region x. In essence, these models examine the relative effect of each region on catch rate, after controlling for time. We used a negative binomial distribution which accounted for the large number of empty sets, or zeroes in the trawl abundance data, andran a separate model for each species and each year using a log link. β is thus an estimate of the relative CPUE of each region on day 0, and is on a log-scale. We used the fitted models to predict the relative abundances of each species at regular intervals in each region during the sampling period, which were back transformed to produce estimates of the CPUE at each region for each prediction interval. To determine the relative support for including region in the model, we used Akaike's Information Criterion (AIC) to compare the model for each species-year combination with an analogous model that excluded region. Generalized additive models were constructed using the mgcv package (Wood, 2006) in the R programming environment (R Core Team, 2013).

2.3.4. Genetic analysis

We used genetic stock identification to determine the spawning location of origin of estuary-caught juvenile salmon. Specific populations of salmon can be separated by their degree of genetic differentiation, which varies according to gene flow; i.e. the rate of migration between populations (Waples, 1998). Thus the genetic structures of the different pink, chum and coho salmon populations, which have higher straying rates, are less well defined than for Chinook and sockeye salmon populations (Quinn, 2005). At present, there are 29 Chinook and 29 sockeye salmon populations from the Skeena River for which baseline genetic data are available that can be reliably separated using microsatellite variation (Beacham *et al.*, 2005, 2006). These populations represent geographically and genetically distinct spawning stocks throughout the Skeena watershed, and the baselines are continually modified as new populations are added (Beacham *et al.*, 2014). The 29 Skeena sockeye salmon populations of the genetic baseline includes populations from 15 different lakes and four river-type populations. Some lakes contain more than one population. For example, Babine Lake, the largest sockeye salmon rearing lake in British Columbia, accounts for up to 90 percent of Skeena River sockeye salmon production and contains at least ten known populations. Populations are spatially related, such that multiple populations from a single lake are more closely related than populations from different lakes. Thus the overall population structure groups the different populations into reporting units that roughly cluster the populations within the different rearing lakes (Beacham *et al.*, 2014).

Tissue samples were collected for DNA analysis from a subsample of Chinook and sockeye salmon specimens. Small pieces of the upper caudal fins were preserved by desiccation on filter paper. DNA was extracted and amplified by polymerase chain reaction (Withler *et al.*, 2000) at 13 microsatellite loci for Chinook salmon (*Ots2, Ots9, Ots100, Ots101, Ots102, Ots104, Ots107, Ssa197, Ogo2, Ogo4, Oke4, Oki100, Omy325*) (Beacham *et al.*, 2006) and 14 microsatellite loci for sockeye salmon (*Ots2, Ots3, Ots100, Ots103, Ots107, Ots108, Ok1a, Oki1b, Oki6, Oki10, Oki16, Oki29, One8, Omy77*) (Beacham *et al.*, 2005). The polymerase chain reaction products were size-fractionated on denaturing polyacrylamide gels, and allele sizes were determined with an ABI 3730 capillary DNA sequencer. Genotypes were scored with GeneMapper software v3.0 (Applied Biosystems) using an internal lane sizing standard (Beacham *et al.*, 2005). Allele frequencies were compared with coast wide baselines of 243 sockeye salmon populations from 20 regions, and 207 Chinook salmon populations from 39 regions using a Bayesian procedure (Pella & Masuda, 2001), in which individual probabilities and stock proportions were assigned using a modified, C-based version of the program BAYES (Neaves *et al.*, 2005). Genetic analyses were performed at Molecular Genetics Laboratory of Fisheries and Oceans Canada at the Pacific Biological Station.

The population of origin for each specimen was determined based on the geographic distribution of the most likely genetic assignments. We accepted individual assignments above a probability threshold of 90%. Where the probability of assignment to a specific population was less than 90%, we assigned populations to coarser resolution groups of lake, sub-basin, basin, or larger areas depending on the geographic distribution of the five most likely population assignments. Genetic resolution is expected to improve as the baseline is expanded (Beacham *et al.*, 2014).

All fish sampling activities were conducted under a license to fish for scientific, experimental or education purposes issued by Fisheries and Oceans Canada. Fish sampling activities were approved by Simon Fraser University’s Animal Care Committee.

2.4. Results

2.4.1. Spatial and temporal distribution of juvenile salmonids

We captured juvenile salmonids at all trawl and beach seine sites that were surveyed. Numerous non-target species were also caught, of which Pacific herring (*Clupea pallasii*) and surf smelt (*Hypomesus pretiosus*) were the most numerous. The total catches by surface trawl were 733 juvenile sockeye salmon, 180 coho salmon, 149 Chinook salmon, 186 pink salmon, 8 chum salmon and 4 steelhead in 2007, and 567 juvenile sockeye salmon, 96 coho salmon, 23 Chinook salmon, 50 pink salmon, and 3 steelhead in 2013. The 2013 total beach seine catch was 132 coho salmon, 11 Chinook salmon, over 250 chum salmon, and thousands of juvenile pink salmon.

Temporal patterns of abundance varied among the different species of salmon captured in the Skeena River estuary. High abundances of juvenile pink salmon were observed during early-season beach seine sets, and were captured in diminishing abundance from the first day of sampling until the second week of May 2013. The highest abundances of juvenile chum salmon were captured by beach seine between the second and fourth weeks of May. Smaller numbers of pink and chum salmon were captured by trawl in 2007, and pink but not chum salmon in 2013. Juvenile coho salmon were observed in trawls from the middle of May onward in both years, and in high abundances in beach seine sets in the third and fourth weeks of May 2013. Juvenile Chinook salmon were captured throughout the sampling period in both years and by both gear types in 2013, and with higher abundances in 2007 than in 2013. Juvenile sockeye salmon, which were only captured by trawl, were the most abundant species captured by trawl in both 2007 and 2013. Sockeye salmon were continually present in the study area from May 26 (the first day of sampling) to July 5 in 2007, and from May

13 until July 1 (the last day of sampling) in 2013, with peak abundances observed between the last week of May and the first week of June in both years (Fig. 2.3).

The prevalence of each species of juvenile salmon varied by gear type, sub-region, and region (Figs. 2.4, 2.5). Sockeye salmon were not caught in beach seine sets but were abundant in nearshore trawls, in some cases within 20 m of shore. Pink salmon were most abundant in beach seine sets, especially at Kinahan Islands and at Ridley Island close to the proposed industrial developments (Fig. 2.4a). Most chum salmon were captured in the Tsum Tsadai Inlet area, outside of the proposed development footprints (Fig. 2.4b). The highest beach seine catches for coho and Chinook salmon were near proposed developments at Lelu and Ridley Islands (Fig. 2.4c and d). The highest abundances of juvenile sockeye salmon in trawl sets were captured in the IN region in both years (Fig. 2.5), the region containing proposed industrial developments. For regions that were sampled in both years, the abundances of juvenile sockeye and coho salmon captured by trawl were similar within regions across years (Fig. 2.5). The highest abundances of juvenile Chinook salmon were captured by trawl in the IN region in 2007, and evenly distributed between the IN and IS regions in 2013 (Fig. 2.5). In 2007, the highest abundances (mean normalized trawl catches for all weeks) of both pink and chum salmon were captured in the ON region (not sampled in 2013) at two of the northernmost sites close to Portland Inlet, which drains the Nass River and empties into Chatham Sound (Fig. 2.5c and e). In 2013, the highest abundances of pink salmon captured by trawl were found in the OS region (Fig. 2.5c).

Our observations of the relative abundances of the different salmon species among the different regions were supported by general additive modeling which accounted for seasonal variation. Specifically, the GAMs statistically indicated that juvenile sockeye salmon were most abundant in the IN region in both years, and juvenile coho salmon were most abundant in the IN region in 2013 (Figure 2.6). The *β* coefficient for sockeye salmon in the IN region was 1.74 ± 0.36 ($p < 0.0001$, this and the following represent the best estimate of the coefficient ± 1 SE and P-value of the coefficient) in 2007 and 1.56 ± 0.34 ($p < 0.0001$) in 2013 (Fig. 2.6). The predicted abundances for sockeye salmon in the IN region were 2-8 x higher than in the other regions in both years. For example, the back transformed predicted abundances of sockeye salmon for May 28 were 24 sockeye salmon (per 20 minute set) in the IN, 11 in the IS, and 7 in the OS region in 2013, and 27 in the IN, 13 in the IS, 9 in the OS, 3 in the MID and 4 in the ON in 2007. The β coefficients for coho salmon in the IN region were 0.63 ± 0.28 ($p = 0.0262$) in 2007 and 0.45 ± 0.19 ($p = 0.022$) in 2013 (Fig. 2.6). The predicted abundances of coho salmon were 2-7 x higher in the IN than in other regions in 2013, and 2-7 x higher in the IN and MID regions than in other regions in 2007. Chinook salmon appeared to be most abundant in the IN region in 2007 and in the IS region in 2013, however neither of these values were significant ($p > 0.05$). The delta-AIC score comparing each species-year model to an analogous version that excluded region was greater than 2, thus demonstrating support for including region for all year-species combinations except Chinook salmon in 2013. Because we sampled the top 4.5 meters of the water column over sites of varying depth, the juvenile salmon abundances are representative only of the surface layer of each region--this surface layer is where juvenile salmon are known to feed during the daylight hours in which we sampled (Barraclough & Phillips, 1978; Straty & Jaenicke, 1980).

2.4.2. Genetic analysis

Genetic determinations were obtained from 476 sockeye salmon captured in 2007, 361 sockeye salmon in 2013, and 19 Chinook salmon in 2013. Of these, 92% of the sockeye salmon captured in 2007, 96% sockeye salmon captured in 2013, and all of the Chinook salmon originated in the Skeena watershed. If we consider only the highest precision genetic determinations, those for which probability of assignment exceeded 90%, five Chinook salmon populations were represented in ten individual fish, and at least seven of the remaining nine came from the more broadly defined Skeena watershed. Four of the five Chinook populations that exceeded the 90% probability threshold were captured in the IN region, including Chinook salmon from Nangeese River in the Kispiox sub-basin, Morice River, and Kitsumkalum River. A total of 220 individual sockeye salmon determinations from both years exceeded 90% probability, representing 25 individual populations including 15 from the Skeena, two from the Nass, and several from smaller coastal watersheds of the north and central coasts of British Columbia.

The highest genetic diversities for sockeye salmon were observed in the IN and OS regions. Twelve of the 13 different sockeye salmon populations that were captured in the IN region originated in the Skeena watershed, including populations from Alastair, Kitsumkalum, and Lakelse lakes in the lower Skeena, Morice Lake in the Bulkley system, Sustut Lake in the high interior, and several different populations of Babine Lake sockeye. Sockeye salmon from 14 different populations were captured in the OS region, of which eight were from the Skeena, and one was from the Kwinageese River in the Nass watershed. Several juvenile sockeye salmon that were captured in the OS region originated from nearby coastal lakes including Lowe Lake in Grenville Channel and

Freda and Kooryet Lakes on Banks Island. At least one sockeye salmon came from Namu Lake on BC's central coast. Most of the specimens whose first probability of assignment did not exceed the 90% threshold were from the Babine drainage within the Skeena watershed (n=548 of 616). The others, which were grouped by lake, sub-basin, watershed or statistical area came from the other Skeena sockeye salmon lakes, coastal systems, and the Stikine drainage.

2.5. Discussion

Our results indicate that the Skeena River estuary, especially the areas containing the proposed development footprints, supports diverse and abundant populations of juvenile salmon. During our two years of sampling, we found that the different species of juvenile salmon occupied the estuary from the middle of May until at least the beginning of July. Some of the highest abundances of some species were observed in areas proposed for development. Specifically, sockeye salmon were 2-8 times more abundant in the IN region compared with other regions in both years of sampling, coho salmon were 2-7 times more abundant in the IN and MID regions, and Chinook salmon were 2-6 times more abundant in the IN region in 2007. Juvenile Chinook and sockeye salmon were genetically identified as originating from populations throughout the Skeena watershed and beyond. These data provide evidence that the Skeena River estuary in general contains high abundances and population diversity of juvenile salmon. Within the greater Skeena River estuary, the highest densities and highest population diversity of the most ecologically and economically important species of Skeena River salmon were found in the inside north region where development is proposed.

We captured thousands of juvenile pink salmon by beach seine within the proposed development footprints in the IN region. Pink salmon, which enter marine waters soon after emergence and return to spawn after a single year at sea, occupy estuarine habitats for several weeks as they gradually move further offshore (Manzer, 1956). For pink salmon, the earliest marine life-history stage is a critical period of high mortality (Parker, 1968), and the abundance of pink salmon smolts captured up to two months after emergence is used as an indicator to predict adult returns in the following year in Southeast Alaska (Orsi *et al.*, 2012). Thus, adult salmon recruitment, and therefore the productivity of fisheries, may be determined by survival of juveniles during the early marine life-history stages such as those that we observed in our beach seine samples in the Skeena River estuary. Juvenile chum salmon were also captured in high numbers in beach seine sets early in the sampling season. Several dozen larger juvenile chum salmon were captured in an experimental purse seine set in a nearby area in early August (Carr-Harris, unpublished), supporting the possibility that some populations may utilize these habitats for months (Manzer, 1956; Weitkamp *et al.*, 2014), however further studies are required in order to determine the duration of estuarine residence and importance of these habitats for the species and populations of salmon that were captured in 2007 and 2013.

The region with proposed development contained the highest densities of juvenile sockeye and coho salmon in both years, and juvenile Chinook salmon in 2007. Abundances of sockeye and coho salmon were consistently higher in this region compared with other regions in the two years sampled, suggesting that the IN region contains consistently important rearing areas for out-migrating salmon smolts. These results are supported by historical studies of juvenile salmonids in the estuary of the

Skeena River (Manzer, 1956; Higgins & Shouwenberg, 1973) that concluded that the areas currently proposed for development including the waters around Flora Bank and southeast Ridley Island are critical habitat for juvenile salmonids (Hoos, 1975). While these results are perhaps not surprising because it is well known that estuaries are important habitat for juvenile salmon (Heard, 1991; Simenstad & Cordell, 2000; Beck *et al.*, 2001), they differ from the recent reports by proponents' consulting groups that have not reported significant numbers of juvenile salmon in this area (Stantec, 2011, 2013; AECOM, 2013). The highest abundances of most species of juvenile salmon were observed within 10 km of the northern entrance of the Skeena River, either within the development footprints, or in habitats that juvenile salmon would have to transit through the proposed developments to access.

Our data indicate that the estuary of the Skeena River in general, and the area proposed for developments in particular, is an ecologically significant habitat that integrates diversity of all species of anadromous salmonids from the Skeena River and surrounding areas. We captured Chinook salmon from at least five different populations and sockeye salmon from 25 different populations from throughout the Skeena drainage and beyond, and sockeye salmon from most of the Skeena River populations currently represented in the DNA baseline. Specifically, 23 of the 29 sockeye salmon populations in the genetic baseline were represented in the probability distributions for genetic assignment for the combined 2007 and 2013 trawl samples, with over 90% probability of genetic assignment for 15 different Skeena sockeye salmon populations (Fig. 2.7). On a finer scale, the proposed development region contained particularly high salmon population diversity, with individual fish assigned to 13 sockeye salmon and 4 Chinook salmon populations. Some of the fish that we captured in this proposed development region are of conservation concern, such as sockeye salmon from Morice and Lakelse lakes and chum salmon from throughout the Skeena watershed, for which low escapements in recent years compared with historical abundances have prompted calls for recovery planning (Price *et al.*, 2013). Our data indicate that the Skeena River estuary, especially the areas where development projects are proposed, represents important habitat for multiple salmon species and populations.

The salmon populations that we sampled near the proposed developments support important commercial, recreational, and First Nations fisheries. For example, we captured Chinook salmon from Morice River, which are targeted by the Wet'suwe'ten First Nation in Moricetown, approximately 450 km upriver from our capture sites, and from the Kitsumkalum River, approximately 120 km upriver, which are targeted by recreational fisheries in the Lower Skeena river and in coastal waters (Gottesfeld & Rabnett, 2008). The majority of the sockeye salmon smolts from the proposed development zone were genetically identified as being from Babine Lake. Babine Lake sockeye salmon are targeted by the Area 4 commercial gillnet fishery in Chatham Sound and the mouth of the Skeena River, a commercial terminal fishery in Babine Lake, and as well as First Nations food, social and ceremonial (FSC) fisheries that support thousands of individuals in 20 communities on the coast and along the Skeena River (Gottesfeld & Rabnett, 2008). Fish that support fisheries are protected by the Fisheries Act, and First Nations fisheries are protected by the Canadian constitution (Government of Canada, 1982). Our data indicates that the estuary habitat is linked to fish that sustain a diversity of fisheries, warranting apparent protection under the terms of the revised Fisheries Act of 2013 (Government of Canada, 2012) and the constitution (Government of Canada, 1982).

Our research supports past findings that the Skeena river estuary is utilized extensively by six species of diadromous Pacific salmon during the critical marine entry stages, and may constitute a bottleneck. The term bottleneck has several meanings. First, migratory bottlenecks refer to areas along migratory routes where migration is constrained, leading to high abundances and diversity during migration (Berger *et al.*, 2008). For example, the oasis at Eilat (Elat), Israel is an important resting stop used by many species of Old World bird species during flights between Europe and sub-Saharan Africa (Safriel, 1968). Alternatively, a bottleneck is used to describe a specific phase of a life-cycle that limits overall productivity of population (e.g., (Mobrand *et al.*, 1997; Buehler & Piersma, 2008)). Estuaries may act as both migratory bottlenecks as well as life-cycle bottlenecks for anadromous salmon. First, given the dendritic structure of river networks, the abundance and diversity of juvenile salmon from throughout river networks will necessarily be funneled through the base of the network. The Skeena River estuary, which represents a small portion of the area of the vast Skeena watershed, funnels hundreds of millions of juvenile salmon through the transition from freshwater to marine habitats each year. Our study found that the estuary was utilized by salmon populations from throughout the Skeena River estuary and beyond, together representing spawning areas ranging from local coastal streams to Sustut Lake in the high interior which is over 575 km inland from our sampling area. Second, the estuary and early marine period may also act as a life-history bottleneck. While mortality occurs throughout the life-cycle of anadromous salmon, past research indicates that the period upon marine entry is particularly important (e.g.. Parker, 1968; Healey, 1982; Pearcy, 1992). Thus, this area may represent a bottleneck that may control salmon productivity by geographical and biological means. The identification of either type of bottleneck can facilitate management or conservation activities.

Previous studies have found that anthropogenic alteration of estuary habitats can negatively impact juvenile salmon. Overwater structures such as piers or bridges impair juvenile salmon habitat usage and decrease their movement underneath these structures (Toft *et al.*, 2007; Munsch *et al.*, 2014). Such structures may also facilitate predation of juvenile salmonids. For instance, predation activity by cormorants and Caspian terns on juvenile Chinook in the Columbia River estuary was higher in areas near pile dykes, and the size of the bird colonies themselves increased following the formation of the artificially created Rice Island from disposed dredge material (Lyons *et al.*, 2007). Juvenile salmon also have been found to exhibit preference for unaltered estuary habitat; for example, tagged juvenile Chinook salmon had a strong preference for and better survival in native eelgrass habitat compared to human-altered habitats (e.g., oyster aquaculture; Semmens, 2008). Degradation of estuary habitat has also been found to be associated with population-level declines of salmon. A study of tagged juvenile Chinook and coho salmon over 37 years from 14 estuaries in the Puget Sound (Washington, USA) area found that Chinook salmon survival was 45% lower in estuaries contaminated by industrial pollutants (Meador, 2014). A similar study found that survival of tagged Chinook salmon released in estuaries in the western states was significantly lower in more human-altered estuaries compared with pristine systems (Magnussen & Hilborn, 2003). Other studies have found that juvenile salmonid rearing activities increased following the restoration of previously degraded estuaries (Shreffler *et al.*, 1992; Roegner *et al.*, 2010). For example, estuarine rearing opportunities for juvenile Chinook salmon increased along with variation in life history strategies among subpopulations following removal of dikes in the Salmon River estuary (Bottom *et al.*, 2005). There is evidence that estuary habitat degradation can negatively impact salmon populations.

Our study highlights the challenges of relying on proponent-funded research to assess potential environmental impacts of proposed developments. The environmental assessment studies conducted by project proponents provide an opportunity to collect information and identify important juvenile salmonid nursery habitats within the Skeena River estuary; but the data collected on behalf of private industries are generally proprietary and inaccessible to independent review. For example, in 2010, a consulting organization on behalf of the proposed Canpotex potash terminal conducted fish sampling with similar gear, timing, and site selection as the current study. While the project's eventual approval was based on an environmental impact statement that concluded that the juvenile salmon that had been observed at those sampling stations were not likely part of a major migration (Stantec, 2011), these data were not disclosed to the public. In addition, recent changes to Canada's environmental legislation may facilitate industrial development (Hutchings & Post, 2013). Economic co-dependency between industry and their private scientists will exert great pressure on the openness and integrity of environmental science (Moore & Moore, 2013)

The Skeena River watershed is a region where annual salmon migrations sustain the ecosystem, culture, and economies of First Nations, commercial, and recreational fishing sectors (Gottesfeld & Rabnett, 2008). Our data indicates that all surveyed parts of the estuary support salmon, especially the regions that are slated for development (Fig. 2.8). Proposed industrial projects would remove foreshore habitat, dredge benthic habitat, install causeways and berths, potentially mobilize contaminants in sediments, as well as increase tanker traffic. If industry projects are approved and proceed, and if these potential alterations to estuary habitats follow previously documented associations between estuary alteration and salmon declines (e.g., Magnussen & Hilborn, 2003;

Meador, 2014), these alterations of this habitat could degrade nearby and distant fish populations and their fisheries.

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2.7. Figures

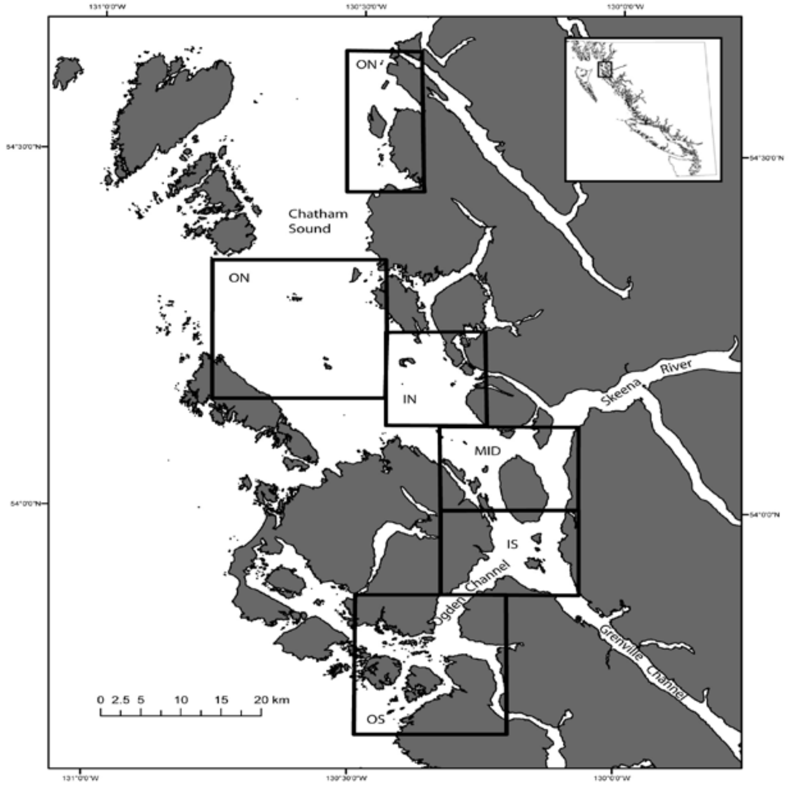

Figure 2.1. The Skeena River estuary, proposed development, and distribution of juvenile salmon sampling.

Note. During the period of highest flow, the zone of freshwater influence extends from the mouth of the Skeena south to Ogden and Grenville Channels, and northwest through Chatham Sound, which also receives freshwater from the Nass River. The study area is shown divided into our analysis regions indicated by the letters IN for inside North, ON for outside north, MID for middle, IS for inside south, and OS for outside south. The IN region contains the focal industrial developments. Note that the ON region includes two polygons.

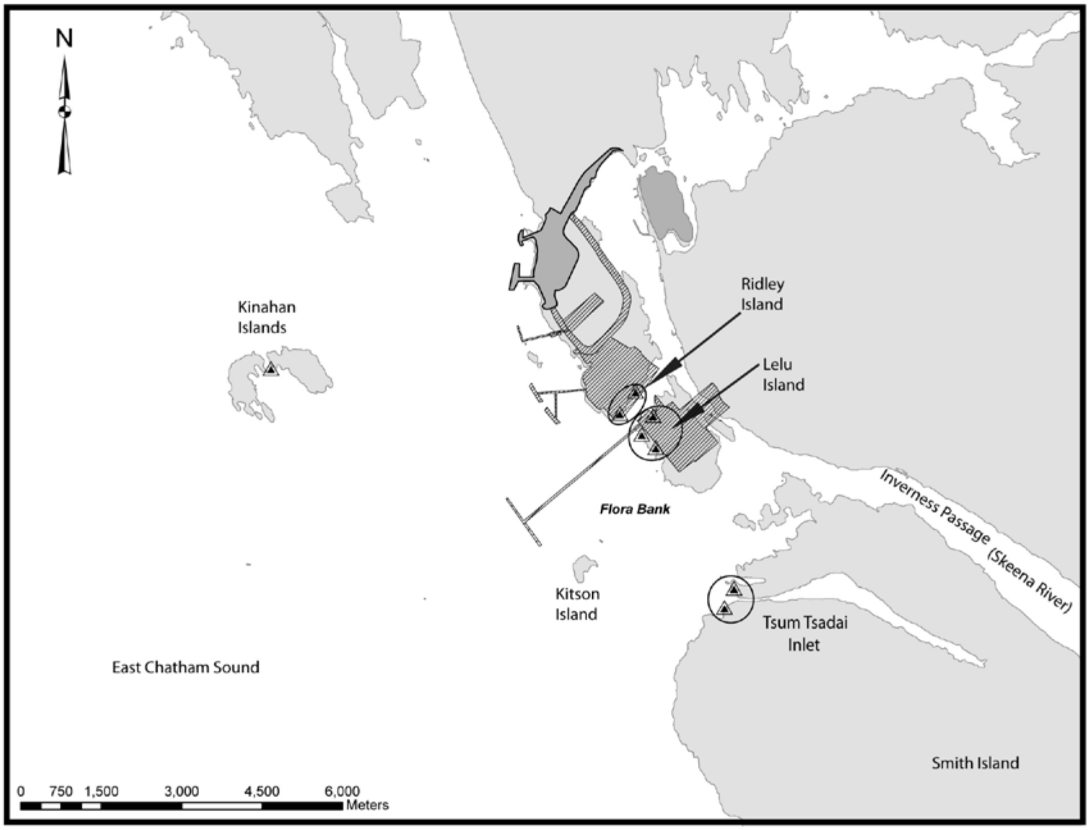

Figure 2.2. Beach seine sampling stations within the IN region indicated in Figure 2.1.

Note. Existing developments are shown in dark grey, while proposed development areas are diagonally shaded. Beach seine sampling stations are indicated by triangles. Beach seine sub-regions are indicated with open circles, except at Kinahan Islands where there was only one site.

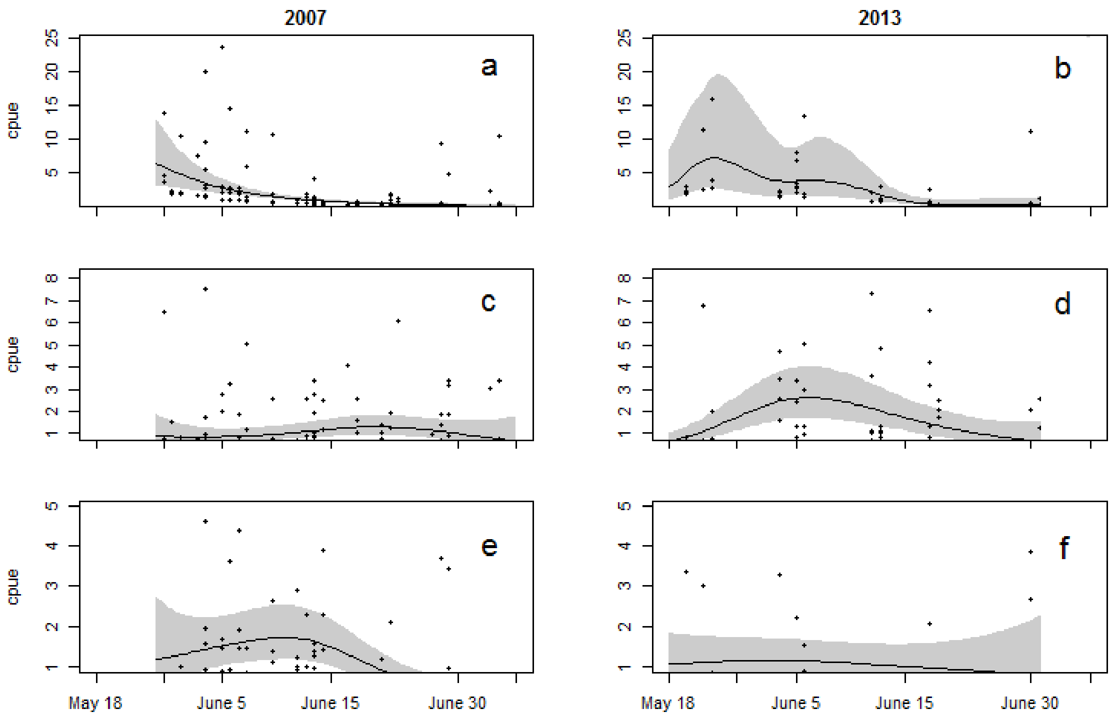

Figure 2.3. **GAM estimates of abundance showing temporal trend for sockeye (a, b), coho (c, d) and Chinook (e, f) salmon abundance during juvenile outmigration season in 2007 and 2013.**

Note. Points indicate normalized trawl catch per 20 min set, note different scales for each species. The smoothed line and shaded region indicate the temporal trend and confidence region for the GAM models.

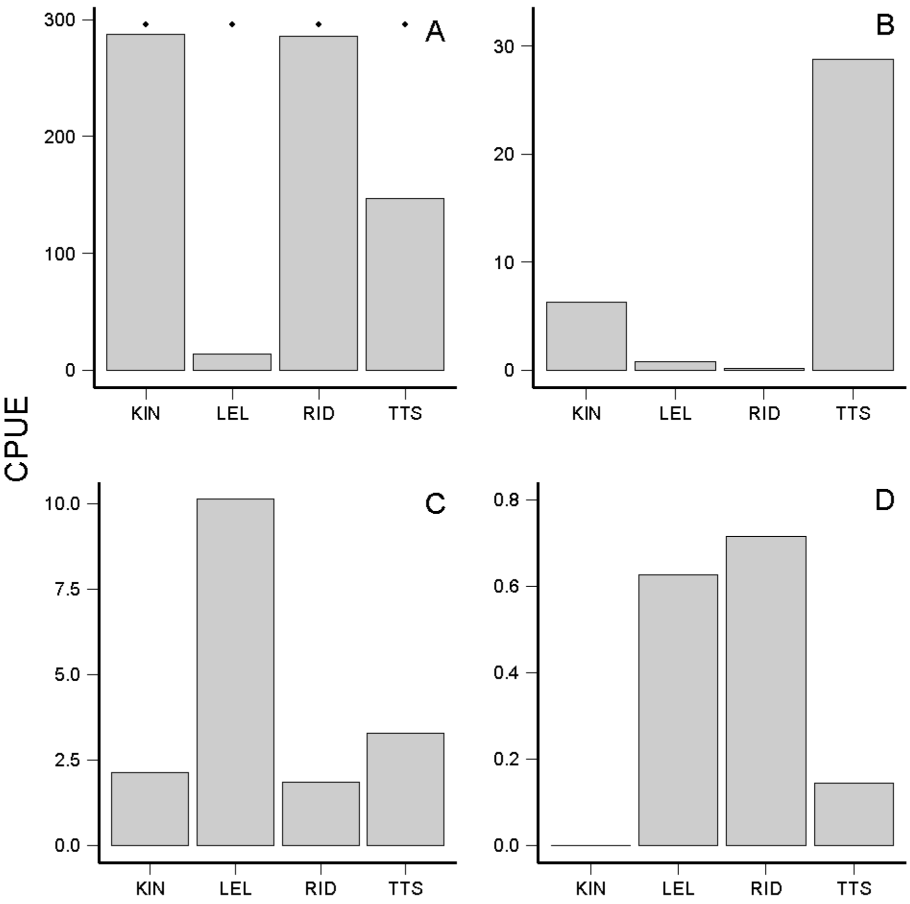

Figure 2.4. **Average beach seine catches of juvenile pink (a), chum (b), coho (c), and Chinook (d) salmon by sub-region, pooled across all sampling dates.**

Note. No sockeye salmon were captured by beach seine. *Pink salmon catches greater than 100 per location are indicated by black dots above bars. Catches greater than 100 or 1000 individuals were calculated as 100 or 1000. Note different scales of y-axes. Locations are as follows: KIN=Kinahan Islands, LEL=Lelu Island, RID=Ridley Island, TTS=Tsum Tsadai Inlet. LEL and RID sites are within footprints of proposed development.*

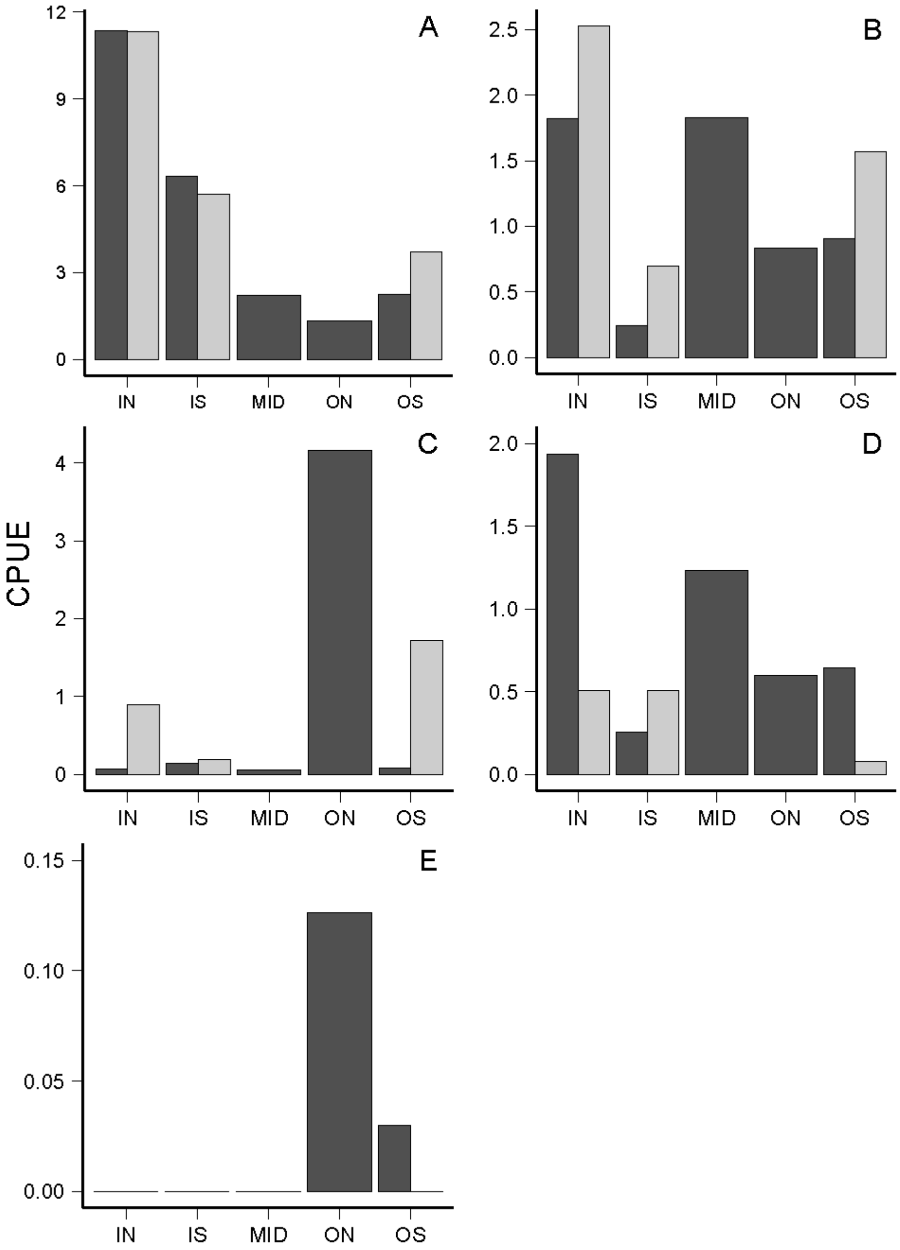

Figure 2.5. **Average normalized trawl catch of all species of juvenile sockeye (a), coho (b), pink (c), Chinook (d) and chum (e) salmon, pooled across all locations and sampling dates and normalized for 20 min sets.**

Note. Dark grey bars indicate 2007 and light grey bars indicate 2013. Note different scales for y-axes for different species. Region boundaries and abbreviations are same as for Fig.2.1.

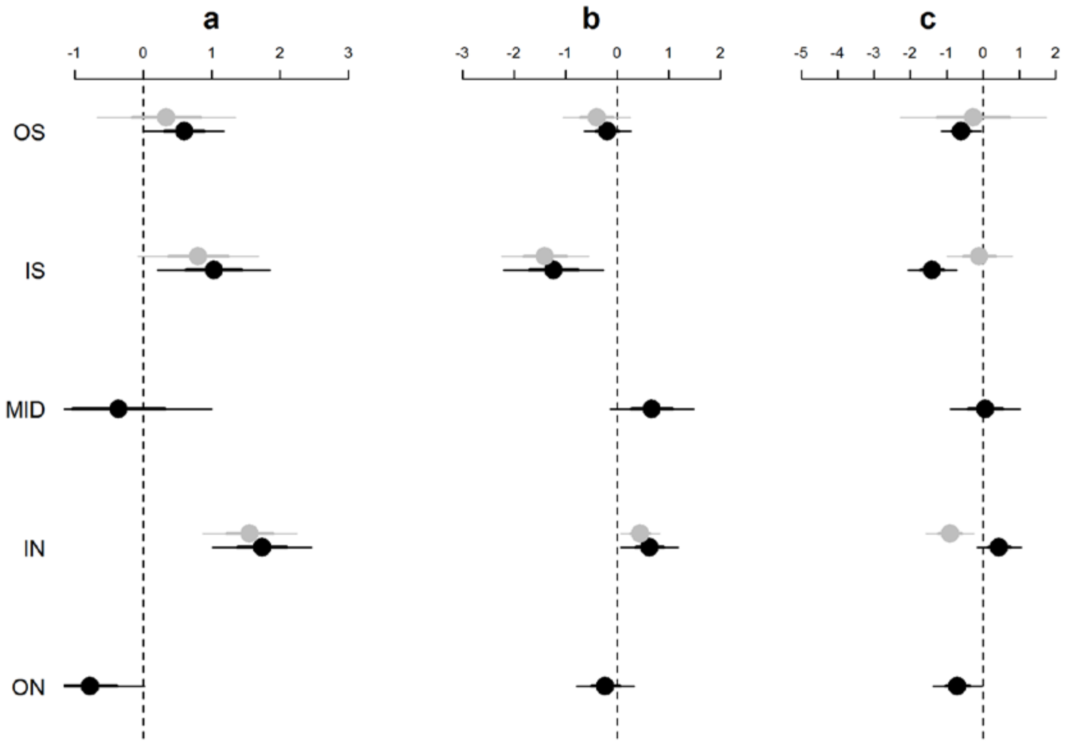

Figure 2.6. GAM coefficients for parametric region covariates for sockeye (a), coho (b) and Chinook (c) salmon.

Note. Coefficients are related to the (log) mean normalized catch per trawl set for each region in 2007 (black) and 2013 (grey). Thus, a value of 0 indicates a mean normalized trawl catch of 1. Error bars indicate + 2 standard errors.

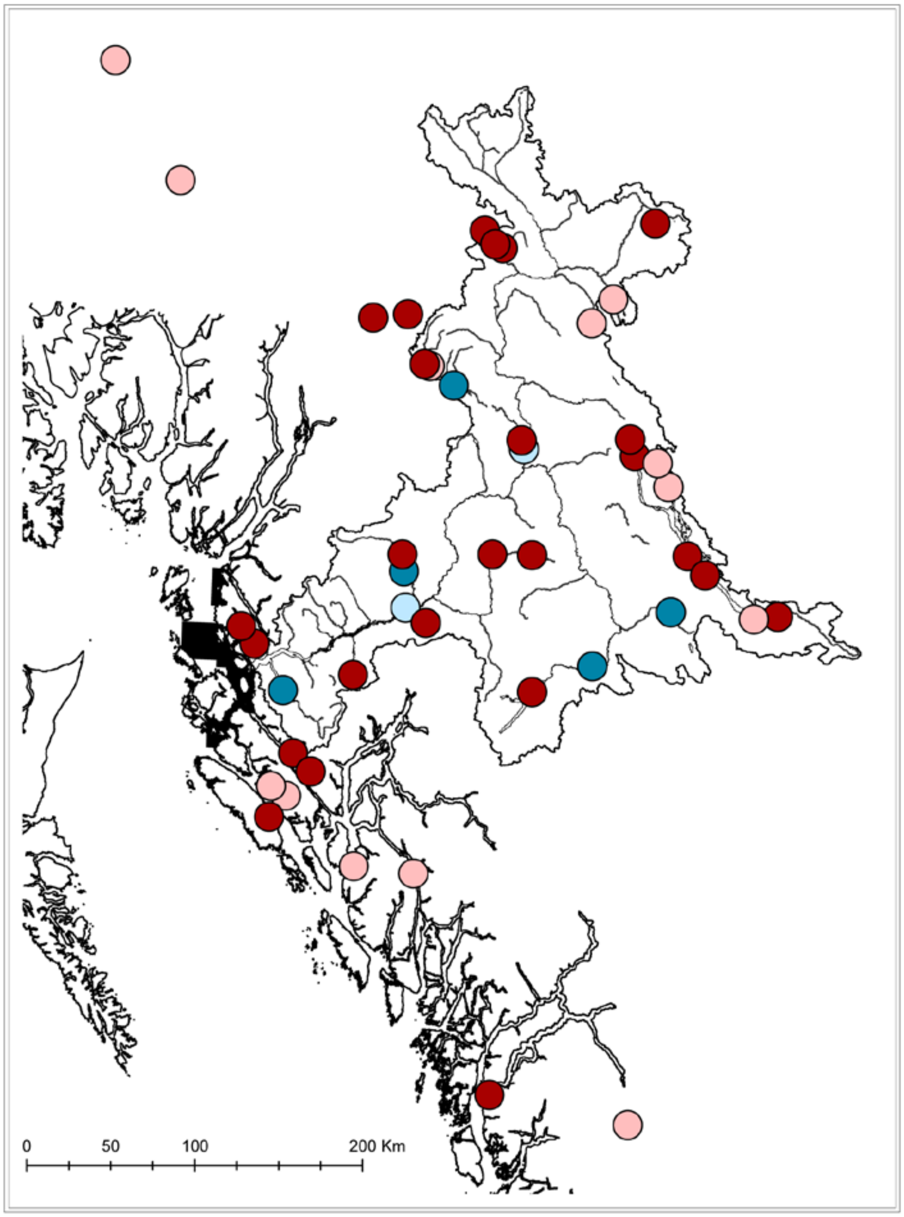

Figure 2.7. Map of the north coast of British Columbia and the Skeena watershed showing locations of origin for genetically identified sockeye and Chinook salmon smolts captured in the Skeena estuary in 2007 and 2013.

Note: Red and pink dots indicate the most likely location of origin for sockeye salmon, with locations that scored above (red) and below (pink) a 90% probability threshold for at least one specimen. Blue dots indicate the highest probability location of origin above (dark blue) and below (light blue) the 90% probability threshold for Chinook salmon. The sampling areas in the estuary of the Skeena River, where all fish were captured, are shown in black.

Figure 2.8. Picture of a pink salmon and a coho salmon smolt caught in the Skeena River estuary, in the area that is proposed to be dredged to accommodate tankers at a proposed terminal for natural gas. A drilling rig is in the background. Photo by J.W. Moore.

Chapter 3. Phenological diversity of salmon smolt migration timing withing a large watershed: implications for match-mismatch dynamics

This paper will be submitted with coauthors Jonathan W. Moore, Allen S. Gottesfeld, Jennifer Gordon, Bill Shepert, James Henry, James Russell, Wade Helin, Dave Doolan, Terry D. Beacham, and Andres Araujo.

3.1. Abstract

While there is growing concern that climate change might drive phenological mismatches between predators and prey, it is possible that within- and among-species phenological variation may provide resilience against such mismatch. One key life-history event that may be vulnerable to climate-induced mismatch is the seaward migration of juvenile salmon, an economically and culturally important group of species, coincident with seasonal abundances of zooplankton. Here we quantified phenological diversity of outmigration timing among salmon subpopulations within a large watershed and its implications for climate mismatches with their marine zooplankton prey. Specifically, we sampled juvenile sockeye salmon throughout the spring and early summer in the estuary of the Skeena River, British Columbia, Canada, a vast watershed with numerous locally adapted salmon populations that supports commercial, recreational, and First Nations fisheries, and used genetic stock identification to link the fish to their population of origin. We found that sockeye salmon were migrating through the estuary for at least 50 days, with peak emigration for different populations varying by over five weeks. The outmigration timing of specific populations was related to

geographic factors including elevation of the rearing lake and the river distance between individual rearing lakes and the estuary, with different populations arriving approximately two days later for every 100 m of elevation, or four days later for every 100 km of river distance. We concurrently quantified the estuarine prey of juvenile sockeye salmon and discovered that (i) zooplankton species composition and abundance varied throughout smolt migration period and (ii) the different salmon subpopulations encountered different prey abundances upon ocean entry. Furthermore, this marine ecosystem has warmed by more than 0.7 °C during the last 50 years. Together these results indicate under-appreciated phenological diversity in this harvested metapopulation, and suggest potential population-level response diversity and metapopulation-level resilience to climate change.

3.2. Introduction

Worldwide increases in temperatures observed during the present century have driven shifts in phenology, the timing of seasonal biological events, for many species (Parmesan & Yohe, 2003; Parmesan, 2006). Global temperature increases of 0.13 degrees per decade since 1950 (IPCC 2013) correspond with mean documented phenological advances of 5.1 days per decade during the past 50 years for terrestrial and marine species (Root *et al.*, 2003). Earlier springs and longer growing seasons have been observed in temperate regions (Menzel *et al.*, 2006), resulting in earlier leaf unfolding and flowering in many plant species, and earlier breeding and migration dates for butterflies, amphibians, and birds (Walther *et al.*, 2002). Phenological responses to thermal change are not synchronous between species (CaraDonna *et al.*, 2014), and vary by habitat (Thackeray *et al.*, 2010), life-history (Winder & Schindler, 2004; Adrian *et al.*, 2006), trophic level (Thackeray *et al.*, 2010; Poloczanska *et al.*, 2013) and functional group (Edwards & Richardson, 2004). These phenological responses likely differ because different environmental cues, including photoperiod and temperature change, initiate biological events for different species (Robinson *et al.*, 2009; Ovaskainen *et al.*, 2013). There is emerging evidence that climate change can decouple phenologies of predators and their prey species (e.g., Winder & Schindler, 2004; Penuelas & Filella, 2013), resulting in a temporal mismatch causing reduced fitness, recruitment, and abundance (Cushing, 1990). In aquatic systems, where phytoplankton (Winder & Schindler, 2004) and some species of zooplankton (Edwards & Richardson, 2004) are particularly sensitive to thermal change, increasing temporal distances between higher and lower trophic levels may result in cascading mismatches that affect secondary and tertiary consumers such as seabirds (Bertram *et al.*, 2001) and piscivorous fishes

(Trudel *et al.*, 2007). The magnitude of temporal mismatches between species is increasing with climate change (Gordo & Sanz, 2005), and productivity of Atlantic cod (*Gadus morhua*; Beaugrand *et al.*, 2003), Atlantic salmon (*Salmo salar*; Beaugrand & Reid, 2003), and Cassin's auklet (*Ptychoramphus aleuticus*; Bertram *et al.*, 2001) have been related to the timing and seasonal abundance of zooplankton biomass, which is related to increasing sea surface temperatures. Thus, the phenological advance of key life-history events is not only a major signal of climate change, but also a potentially important driver of ecosystem change (Post & Inouye, 2008).

Within- and among- species phenological variation may attenuate ecosystem responses to asynchronous temporal shifts. Phenological diversity is expressed at both species- and population-levels. For example, different plant species have different timing of flowering (Iler *et al.*, 2013), but diversity within-species also influences phenology--phenological variation increased with genetic diversity, with lower phenological variation observed for cloned plants than for cultivars with higher genetic diversity or wild plants (Doi *et al.*, 2010). This within- and among-species phenological diversity may provide resilience to communities or metapopulations faced with climate change. In plant communities, spatiotemporal partitioning, or phenological complementarity, can increase with species richness (McKane *et al.*, 1990) and enable efficient uptake of resources such as light and nitrogen within the community (Stevens & Carson, 2001). Phenological variation may also conserve ecosystem function in the face of climate change by reducing phenological mismatch between interacting species at different trophic levels (Bartomeus *et al.*, 2013; Burkle *et al.*, 2013; Iler *et al.*, 2013). For example, increased species richness reduced the probability of asynchrony between apple trees and their bee pollinators (Bartomeus *et al.*, 2013). While within-species population diversity may increase ecosystem function (Luck *et al.*, 2003), there have been few studies of population-level phenological diversity and its potential importance for climate change resilience.

The downstream migration of juvenile diadromous salmonids to the marine ecosystem is one important example of a critical migration period that may be vulnerable to climate-induced mismatch. For migrating populations of all species, the timing of migrations has presumably evolved to coincide with the availability of specific resources, such as feeding opportunities, at their destination habitats (Both & Visser, 2001). Temporal and geographic shifts in the availability of the resources at the destination may occur independently from changes in the phenology of the migration itself, and the effects of climate change, which are not uniform across space, may affect species differently (Stenseth & Mysterud, 2002). Diadromous salmonids, which spawn and rear in freshwater before migrating downstream to marine feeding areas are exposed to the effects of thermal warming in both environments. While feeding success for post smolts depends on the timing of the transition between freshwater and marine habitats (Crozier *et al.*, 2008), the cues that initiate downstream migration for juvenile salmon are not directly connected to the conditions in the marine environments that receive the smolts. The timing and abundance of juvenile salmonid prey, such as zooplankton, can control the marine survival of salmon (Beaugrand & Reid, 2003) and salmon survival is improved when their outmigration coincides with peak prey abundance (Chittenden *et al.*, 2010; Satterthwaite *et al.*, 2014). Increasing evidence suggests that the early marine phase of their life-history can control their annual productivity (Macdonald *et al.*, 1987); for example, marine conditions in the first year at sea determine adult returns for steelhead salmon (*Oncorhynchus mykiss*; Moore *et al.*, 2014) and synchronous year-class failures have been observed for different species of salmon and herring which entered the same region of coastal waters in the same year (Beamish *et al.*, 2012). The abundance of their zooplankton prey is highly pulsed and is shifting rapidly with climate change (Edwards & Richardson, 2004). For example, peak abundances for marine plankton have advanced by an average of 7.6 days per decade (Richardson, 2008). The timing of peak abundance of *Neocalanus plumchrus*, the most abundant species of large calanoid copepod in the Strait of Georgia, British Columbia and an important prey item for juvenile salmonids, advanced by 14 days per decade since 1956 (Mackas *et al.*, 1998). The timing of salmon migration is likely responding differently than zooplankton to climate change, although there is limited evidence that salmon outmigration timing may also be advancing earlier. Specifically, Atlantic salmon outmigration timing has advanced 2.5 days per decade across the North Atlantic basin (Otero *et al.*, 2013). However, phenological traits such as migration timing are highly heritable (Carlson & Seamons, 2008) and controlled primarily by photoperiod and secondarily by freshwater temperature (Mccormick *et al.*, 2002). The timing of salmon migration may therefore be less plastic than that of their zooplankton prey. In addition, the climate conditions that juvenile salmon experience in freshwater that influence the plastic component of phenology will likely be different than the marine climate conditions that control marine zooplankton. Thus, given continuing climatic change, understanding the phenology of outmigrating salmon and their prey is increasingly important.

Here we quantify the potential for intra-specific diversity in downstream migration timing for salmon, a key phenological trait at the nexus of climate change and salmon resilience. Specifically, we examined population-level phenological diversity of downstream migration within a meta-population of sockeye salmon (*Oncorhynchus* *nerka*) using two years of genetic data collected from the Skeena River estuary, British Columbia. The Skeena River sockeye salmon meta-population contains at least 30 genetically distinct sub-populations with limited recent hatchery enhancement for only a few small populations of conservation concern. Smolt fence data from several Skeena River sockeye salmon rearing systems suggests that the total duration of the sockeye smolt migration period exceeds six weeks (Wood *et al.*, 1998). With the brief life cycles and likelihood of rapidly shifting temporal patterns of abundance for zooplankton prey, juvenile salmon entering the ocean at different times may encounter different prey assemblages. Consistent differences in the timing of downstream migration and ocean entry between the different sub-populations across years could result in different feeding opportunities for individual populations upon ocean entry. Our study objectives were to quantify phenological diversity of smolt migration timing across sub-populations, examine geographical factors that are associated with migration timing for the different sub-populations, and assess how migration timing for the different sub-populations relates to the timing of food availability (zooplankton abundance) in the estuary. Together these results indicate remarkable phenological diversity within this large salmon watershed that can influence the response and resilience of these harvested fish to climate change.

3.3. Methods

3.3.1. Study system

The Skeena River (Figure 3.1) drains a catchment area of nearly 55,000 km^2 and supports the second largest sockeye salmon return in British Columbia after the Fraser River. The average aggregate sockeye salmon return to the Skeena River was approximately three million from 1985 to 2013 (Pacific Salmon Commission 2014 Northern Boundary Technical Committee report available at: http://www.psc.org/pubs/TCNB14-1.pdf) and is comprised of at least 30 genetically distinct sub-populations (Morrell, 2000), which spawn throughout the Skeena watershed. Most of the known populations are lake-type sockeye salmon, which generally spawn in tributaries upstream of the rearing lakes where they usually rear for one year prior to initiating the seaward migration in the spring of their second year (Gottesfeld & Rabnett, 2008). Life history variations between populations include a wild Upper Babine population, which spawns downstream of their rearing lake, and Nanika sockeye, which rear in Morice Lake for two years prior to downstream migration (Gottesfeld & Rabnett, 2008). Approximately 87 percent of Skeena River sockeye salmon originate from Babine Lake. The proportion of the Babine sockeye salmon component was increased by artificial spawning channels that were constructed at Fulton and Pinkut Rivers in the 1970s (Wood *et al.*, 1998). Productivity varies among the different Skeena River sockeye salmon sub-populations, and several small populations have seen stable or increasing returns during the past decade when major populations have followed a general trend of declining productivity (Skeena Salmon Program, datasets: extended time series of catch and escapement estimates for Skeena sockeye, pink, chum and coho salmon populations, available at: http://skeenasalmonprogram.ca/library/lib_263/).

3.3.2 Diversity of sockeye rearing lakes

Geographic characteristics of the different rearing lakes affect life history stage timing for different Skeena sockeye salmon sub-populations. The timing of fry emergence, length of the growing season, and freshwater zooplankton availability are influenced by water temperature and clarity and the timing of onset of thermal stratification, ice formation and breakup (Quinn, 2005). These abiotic factors are influenced by the elevation, depth, latitude and proximity to the coast of each rearing lake. Sockeye salmon rearing lakes in the Skeena watershed range from low-elevation coastal lakes (<100 m elevation) such as Johnston and Alastair Lakes, less than 100 km (network river distance) from the estuary which rarely freeze during the winter, to Sustut and Johansen Lakes in the high interior, which are over 1300 m in elevation and over 575 km from the coast, and covered by ice for more than 6 months of the year (Table 3.1; Figure 3.1). Water clarity, which influences primary production and therefore food availability, ranges from turbid glacial lakes such as Motase Lake in the upper Skeena and Kitsumkalum Lake in the lower Skeena, which support low densities of sockeye fry and produce relatively small smolts, whereas better growing conditions in the relatively warm, clear lakes such as Lakelse and Kitwanga support higher densities and produce larger smolts (Table 3.1). Sockeye salmon fall fry densities observed in hydroacoustic surveys throughout the Skeena watershed range by two orders of magnitude, from 50 juvenile sockeye salmon per hectare at Motase Lake to 7,500 juvenile sockeye salmon per hectare at Johnston Lake in 2010 (Skeena Fisheries Commission hydroacoustic reports available at: http://www.skeenafisheries.ca/?page_id=410). The relative productivity and carrying capacity of most of the Skeena sockeye salmon rearing lakes have been quantified using the PR (photosynthetic rate) model, which estimates the optimal number and biomass of fry, and adult spawners required to produce that biomass based on total annual carbon production at each lake (Shortreed *et al.*, 1998; Shortreed & Morton, 2000). Thus, these different rearing lakes that support the population diversity of sockeye salmon have fundamentally different geographic and biologic attributes that may be linked to smolt outmigration timing.

3.3.3 Fish sampling

Juvenile sockeye salmon were captured in the Skeena River estuary using trawl and purse seine sampling. Several juvenile sockeye salmon were also collected during beach seine sampling targeting juvenile pink salmon early in the 2014 season. Weekly trawl samples were collected at six sites in the proximal northern Skeena River estuary from the beginning of May until the beginning of July in both years (Figure 3-1). The trawl, which was 18 m long with a 5 x 4.6 m opening was fished from a chartered gillnet vessel, HMV Pacific Coast, and towed for a targeted duration of approximately 15 minutes for each set. In 2014 we used a purse seine as a secondary gear weekly at six sites between May 7 and July 23 in order to increase our sample numbers (Figure 3-1). The purse seine, which was 9m deep and 73m long, with 50 mm mesh webbing at the tow end and 12 mm webbing at the bunt, was deployed using a 3 m skiff to tow the bunt end away from a larger vessel, and hold net open into the tidal current for a targeted duration of five minutes per set. At the end of each set, the purse seine was closed and bagged by simultaneously pulling a purse line while hauling the web into the larger vessel. Once the net was closed, fish were transferred from the seine net into buckets using dip nets. Captured fish were counted to species and all non-salmonids were released after each trawl or purse seine set. A subsample of sockeye salmon from each sampling event (up to 50 individuals) was lightly anesthetized with tricaine methanesulfonate (MS-222). Sockeye salmon lengths were recorded to the nearest mm, and a small piece of caudal fin removed for genetic analysis. These fish were released following a recovery period in aerated buckets.

3.3.4 Genetic analysis

Microsatellite DNA analysis was used to determine the populations of origin for juvenile sockeye salmon captured in 2013 and 2014. DNA was extracted from dessicated tissue samples and amplified by polymerase chain reaction (PCR) at 14 microsatellite loci for sockeye salmon (Beacham *et al.*, 2005). The PCR products were size-fractionated, and allele sizes were determined with an ABI 3730 capillary DNA sequencer. Genotypes were scored with GeneMapper software v3.0 (Applied Biosystems) using an internal lane sizing standard (Withler *et al.*, 2007). Allele frequencies were compared with coastwide baselines of 245 sockeye salmon populations from 20 regions (Beacham *et al.*, 2014a) in which individual probabilities and population proportions were assigned using a modified, C-based version of the program BAYES (Pella & Masuda, 2001; Neaves *et al.*, 2005). Genetic analyses were performed at Fishery and Oceans Canada Molecular Genetics Laboratory at the Pacific Biological Station in Nanaimo, British Columbia.

3.3.5 Statistical analyses

Trawl capture data which were collected in both years were used to compare the overall temporal distribution of the sockeye smolt migration in 2013 and 2014. We estimated the normalized catch per unit effort (CPUE) for a 20-minute set by dividing the number of sockeye salmon captured by the duration of the trawl in minutes, and multiplying by 20. We constructed a generalized additive model (GAM) to predict CPUE for each year by applying a nonparametric smoothing function to the date of capture to account for the time signal in the data, and a parametric factor for the different years. To account for the non-normal distribution of CPUE data as a result of the high proportion of zero catches, we used a negative binomial distribution with a log link to run the GAM. To determine whether year of capture had an effect on CPUE, we used analysis of variance (ANOVA) to compare a model that included terms for day and year of capture with a model that excluded year.

Linear models were used to test whether sockeye smolt migration timing varied by year, population, or both. Using only specimens whose genetic determination exceeded a threshold of 90% probability of correct assignment for individual determination, we compared a series of models using year of capture, population of origin, and both year of capture and population of origin as predictors for the date of capture in the estuary with a null, intercept-only model. We used a nested model framework, with data from the two sample years nested within the different populations to determine whether year of capture, population of origin, or both were significant predictors for date of capture in the estuary.

Linear mixed-effects modeling was used to test whether physical and biotic characteristics of sockeye salmon rearing lakes affect timing of migration for the different Skeena River sockeye salmon populations. We included random terms for the different populations and fixed terms for the river distance, elevation and latitude, and productivity. Elevation and latitude affect temperature, timing of ice breakup, and photoperiod (latitude only), which might influence the timing of onset of downstream migration, while river distance, the network distance from each natal lake to the estuary, will influence the duration of the migration to the estuary following smolt departure. Productivity may affect the size and density of smolts in a given lake. For the productivity term, we used S_{max}, the optimal spawner escapement derived from the PR (Photosynthetic rate) model divided by the surface area of each lake (Shortreed *et al.*, 1998, 2007; Shortreed & Morton, 2000). We constructed a series of models including every combination of random and fixed terms which were fitted using maximum likelihood, and used Akaike's Information Criterion (AIC) to select the model with the most support. Data from a single population, Johnston Lake, which were found to have considerable leverage on model fit, were excluded from linear mixed effects model analyses. All statistical analyses were conducted within the R programming environment (R Core Team, 2013).

We estimated the expected duration of downstream migration from the different rearing lakes to determine whether it explained the variation in downstream migration timing for the different populations. The duration of the downstream migration from Babine Lake to the estuary was estimated using tags from an existing smolt weir at the outlet of Nilkitkwa Lake, immediately downstream of Babine Lake, where a mark and recapture project was carried out by Skeena Fisheries Commission and Lake Babine Nation to enumerate out-migrating smolts in 2013 and 2014 (Skeena Fisheries Commission reports available at: http://www.skeenafisheries.ca/?page_id=1259). Smolts from Babine Lake were trapped at the weir and marked by applying coloured staples posterior to the dorsal fins, and returned to Nilkitwka Lake (Macdonald & Smith, 1980). Approximately one million tags were applied to an estimated migration of 60 million smolts between May 5 and June 7 in each year. Ten different colour patterns were used to differentiate between smolts trapped on different days. We captured several tagged sockeye smolts bearing colored staples during the estuary sampling project, and by knowing which colors were applied on which days, we were able to estimate the number of days that these marked smolts swam in transit between Babine Lake and our estuarine capture sites. The average distance travelled per day was estimated as the quotient of the network distance between the smolt weir and a reference point in the estuary, and the number of days elapsed following release into Nilkitwka Lake. The duration of the downstream migration for non-Babine populations was estimated as the quotient of the distance from each natal lake to the estuary and the average distance travelled per day. We did not account for sources of potential bias in the tag data including the effect of the staples, or tag burden on the swimming speed of juvenile sockeye, or higher potential mortality of these slower-migrating tagged sockeye.

3.3.6 Zooplankton sampling

We collected zooplankton samples in 2013 and 2014 to compare food availability for out-migrating juvenile sockeye salmon during their outmigration period. Zooplankton samples were collected biweekly from the middle of April until the middle of July in 2013 and 2014 from a station located in the Skeena River estuary between the Kinahan Islands, approximately 10 km from the northern exit of the Skeena River (54° 13.4' N 130° 22.3' W) (Figure 3-1), where juvenile salmon have been observed feeding in past years (unpublished data). In both years, vertical plankton tows were conducted during daylight hours using a simple conical plankton net with 250 µm mesh and a mouth diameter of 57 cm which was deployed and hauled by hand. Samples were collected to a depth of 20 m, where juvenile salmon are known to feed (Straty & Jaenicke, 1980).

Zooplankton samples were preserved in 5% formalin buffered with seawater. The samples were later rinsed through a 150 um sieve, and subsamples were drawn from each sample using a Folsom plankton splitter. Subsamples were enumerated under a Leica M70 dissecting microscope into broad taxonomic categories. The relative abundances of zooplankton taxa were determined by dividing the number of individuals in each category for each sample by the maximum number of individuals encountered during the sampling period.

3.3.7 Sea surface temperature

We analyzed historic sea surface temperature (SST) data to determine the presence and magnitude of a long-term trend of increasing SST in our study area. Daily SST collected from 1964 to 2013 from the nearby lighthouse station on Bonilla Island (53.300°N, 130.380°W, approximately 83 km SW of Kinahan Islands) were obtained from DFO (available at http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html). We used simple linear models to estimate the mean slope, or increase in average annual temperatures and average monthly temperatures for March, April, May and June for the period between 1964 and 2013. The mean increase in temperatures during the whole time series was estimated as the product of the slope and the duration of the time series (49 years).

3.4. Results

3.4.1 Fish sampling & genetic analysis

Juvenile sockeye salmon were captured over a period of six weeks from May 13-July 1 in 2013 and a period of seven weeks from May 7-July 4 in 2013. We captured 217 juvenile sockeye salmon by trawl in 2013, and 776 by trawl and 3,165 by purse seine in 2014. An additional eight juvenile sockeye salmon were captured opportunistically by beach seine in 2014. Successful genetic determinations were completed for 217 sockeye in 2013 and 780 in 2014. Ninety-seven percent of the genetically identified sockeye originated in the Skeena watershed. We captured sockeye salmon from 22 genetically distinct Skeena River sockeye salmon populations. Approximately 42% of juvenile sockeye salmon in 2013 and 43% in 2014 originated from the enhanced Babine Lake populations at Pinkut and Fulton Rivers. Of the total number of genetic determinations, 76 or 36% exceeded the 90% probability threshold of correct assignment in 2013, and 267 or 38 % in 2014.

3.4.2 Timing

The overall timing of the juvenile sockeye salmon outmigration was similar for both of our study years. GAMs indicated that the overall distribution of estuary residence timing for juvenile sockeye salmon was similar in both years, predicting peak abundances for juvenile sockeye salmon on May 31 for both 2013 and 2014 (Fig. 3.3a). Juvenile sockeye salmon migrate through the estuary for almost two months, and we observed sockeye salmon smolts in the estuary for at least 51 days. The generalized additive model predicted a mean CPUE of 18.0 juvenile sockeye salmon per 20 minute set on May 31, 2013, and 27.3 juvenile sockeye salmon per 20 minute set on May 31, 2014. For a model that included year of capture as a factor and a nonparametric smooth term for date, the nonparametric smooth terms for date of capture was significant ($p<0.001$) but there was no significant difference between the two years ($p=0.56$). There was no support for including a parametric term for year in comparison with a model that excluded year (ANOVA, Chi-squared test, $p=0.52$).

Different sockeye salmon populations within the Skeena River exhibited different smolt migration timing (Table 3.2, Figs. 3.2, 3.3). The peak dates of capture for different populations which we encountered in the estuary ranged from May 16 for sockeye salmon smolts from Kitwanga Lake to June 22 for sockeye salmon smolts from Sustut Lake (Table 3.1, Fig 3.3), a difference of five weeks. Linear modeling indicated that date of capture was affected by population (ANOVA, $p<0.0001$) but not by year ($p=0.2395$) for the two years of data available.

3.4.3 Factors that affect timing for different populations

There was evidence that geographic factors were linked to smolt migration timing for the different populations. The mean date of estuary residence for the different Skeena River sockeye salmon populations was correlated with river distance ($p=0.042$), elevation ($p=0.017$), but not latitude ($p=0.178$) or productivity ($p=0.945$; Fig. 3.4). Given strong support for including population but not year in the linear models (ANOVA, chi-squared test, $p=0.1178$), we used AIC to compare linear mixed effects models with random terms that allowed the intercept to vary by population using pooled data from both years of sampling. While the geographic variables accounted for less variation than population effects, AIC indicated higher support for models that included any combination of river distance, elevation, latitude, and productivity as fixed effects rather than models that included only a random term for population with no fixed effects (Table 3.3). There was considerable correlation between the geographic variables for river distance and elevation ($R^2=0.94$), river distance and latitude ($R^2=0.70$), and elevation and latitude ($R^2=0.68$). As a result, we were not able to determine which combination of these factors contributed most to estuary residence timing for the different sockeye salmon populations. AIC indicated the highest support with very little difference (ΔAIC = 0.40) for models that included a single term for river distance or elevation. While river distance, elevation and latitude were significant covariates ($p<0.05$) in models that included a single fixed effect for each, none were significant in models that included a combination of these variables. Models that included a single fixed-effect suggested that the expected timing of downstream migration was negatively correlated with river distance, latitude, and elevation. The predicted downstream migration timing was 4.4 ± 2.5 (this and the following represent mean value ± 95% confidence interval) days later for every 100 km of increasing river distance, 1.9 ± 1.1 days later for every 100 m of elevation, or 8.1 ± 6.1 days later per degree of latitude.

Opportunistic recapture of tagged smolts from the Lake Babine enumeration project enabled an estimation of travel time between the lake and estuary. We captured nine smolts bearing tags from the Lake Babine smolt enumeration project between May 5 and May 19, 2014, which had been marked at the weir between 9 and 16 days prior to capture in the estuary. Under the assumption of an extra day's travel to swim from the release site back to the lake outlet, the mean duration of the downstream migration was 10.8 days for these smolts, or an average velocity of about 40 km per day. If we assume the same downstream velocity for other Skeena River sockeye salmon populations, the expected duration of the downstream migration would range from two days for Alastair Lake smolts that migrate from 67 km upstream, to 14 days for Sustut Lake smolts migrating from 575 km upstream. The range of expected downstream migration time of 12 days is a third of the observed range of estuary residence time that we observed in our sample data of over 36 days between peak timing for the different populations.

3.4.4 Zooplankton

There was considerable within-year variability in the composition of estuary zooplankton communities throughout the smolt migration period in 2013 and 2014 (Figure 3-5). The zooplankton samples collected in both years were dominated by small calanoid copepods, mostly *Acartia longerimis* and *Pseudocalanus minutus*. The timing of peak abundance of small calanoids varied in the two years sampled, with the highest abundances observed at the beginning of July in 2013, and at the beginning of June in 2014. In both years, the highest relative abundance of decapod larvae was observed at the beginning of May, and a second peak of decapod abundance occurred in the middle of June 2014. Euphausid abundance was bimodal in both years, with peak abundance of nauplii observed in the first week of May 2013 and the second week of May 2014 followed by a peak of larger calyptopis and furciila stages at the beginning of July 2013 and towards the end of August 2014. Timing for larvaceans was bimodal in both years with peaks observed at the beginning of May and end of July 2013, and the middle of May and middle of June 2014 (Figure 3-5).

3.4.5 Sea surface temperature

There was evidence that the ocean is warming in the marine ecosystem that Skeena River sockeye salmon enter (Figure 3-6). There was considerable interannual variability between the average annual and spring monthly SST at the Bonilla Island lighthouse station, with a discernible trend of increasing spring SST in the period between 1964 and 2013. During this period, there was a significant increase in monthly SST of 0.76 ± 0.32 °C (error term represents ± 1 standard error for this and the estimates that follow) for April (p=0.0236) and 0.78 ± 0.35 °C for May (p=0.0323). Mean temperature increases of 0.37 ± 0.39 degrees March and 0.54 ± 0.33 degrees for June were not significant (p=0.344 for March and p=0.112 for June).

3.5. Discussion

Different populations of Skeena River sockeye salmon smolts had different smolt migration timing, with a 36 day difference in peak migration timing for the first and last populations to appear in the estuary. There was more variation in the timing of estuarine residence among the different sockeye salmon populations than between years. In contrast, there was little variation in the overall timing of Skeena River sockeye smolt migration between the two years sampled, and the timing for the different populations appeared to be coherent between years. The migration phenology of different Skeena River sockeye salmon populations also had a strong geographic signature within this large watershed. Specifically, we observed later timing for populations that originated from further upstream and from higher latitudes and elevations. Our observation of later migration timing with increasing elevation is consistent with a previous study of Columbia River Chinook salmon which found that juvenile migration timing was one day later for every 122 m of elevation gain (Achord *et al.*, 2011). There are plausible explanations as to why the different geographic variables might influence smolt migration timing. For example, the timing of departure may be constrained by conditions in the rearing lakes. The peak juvenile sockeye salmon migration occurs shortly after the timing of ice breakup, which occurs later at higher latitudes and elevations at Skeena River sockeye salmon rearing lakes, as demonstrated by smolt weir data collected from enumeration programs (smolt weir data, Gitanyow Fisheries Authority (available at http://www.gitanyowfisheries.com/kitwanga-smolt-fence-enumeration) and Gitskan Watershed Authorities (available at http://www.skeenafisheries.ca/?page_id=1112). Geographic constraints (Bradshaw & Holzapfel, 2008) may interact with locally adapted phenology given its high heritability (h2=0.51; Carlson & Seamons, 2008) to produce structured migration timing between different sockeye salmon populations such as those we observed in the Skeena River watershed.

The geographic pattern of smolt outmigration timing was greater than predicted based on observed downstream migration speeds. Smolt tag data from Babine Lake suggest that sockeye salmon smolts migrate at approximately the velocity of the river current. If this is true for all populations of Skeena River sockeye salmon smolts, the expected range of estuary arrival time would be 10-12 days between sockeye salmon populations from the furthest upriver and downstream systems. However, sampling in 2013 and 2014 found that the peak smolt migration timing for the different populations of juvenile sockeye salmon varies by up to five weeks during the spring migration. Furthermore, the timing of estuarine residence varies between different sockeye smolt populations that originate from the same lake. Of the different sockeye salmon populations that we captured in the estuary, at least eight populations came from Babine Lake. We observed phenological diversity among the different populations of sockeye salmon from Babine Lake, with mean timing of estuary capture ranging from May 14 to June 15, 2014. Thus, the data provide evidence for phenological variation among the populations of a single lake in addition to a geographic component to smolt migration timing.

We use date of capture of smolts in the estuary as a proxy for timing of the downstream migration. However, we note that estuary residence duration can contribute to these data. There is little information on the duration of smolt residence time in the estuary itself. If sockeye salmon smolts remain in the estuary for varying periods of time following the downstream migration, the timing of ocean entry may be overestimated. Previous research suggests that sockeye salmon spend little time in estuaries compared with other salmon species such as Chinook (*O. tshawytscha*) and chum (*O. keta*) salmon (Thorpe, 1994; Weitkamp *et al.*, 2014). Other studies have found that smaller and ocean-type sockeye salmon may inhabit estuaries for a longer period of time. For example, sockeye salmon smolts from the ultra-oligotrophic Owikeeno Lake, which are among the smallest lake-type sockeye smolts in British Columbia (Mckinnell *et al.*, 2011), remain in estuarine waters in Rivers Inlet for over a month as they traverse the inlet (Ajmani, 2012). We excluded one population from Johnston Lake from mixed effects model analyses because it appeared to exert disproportional influence on model results. Johnston Lake sockeye salmon smolts were captured in the estuary throughout the sampling period unlike all of the other sockeye salmon populations which exhibited relatively compact distributions of dates of capture in the estuary. Johnston Lake is an oligotrophic lake that drains into the lower Skeena River, and hydroacoustic surveys conducted in 2010 and 2014 have recorded the highest densities of the smallest sockeye salmon fry observed anywhere in the Skeena watershed (Skeena Fisheries Commission hydroacoustic reports available at http://www.skeenafisheries.ca). The few juvenile sockeye salmon that we captured from Johnston Lake (n=5) were substantially smaller (67.2 ± 7.3 mm) than the average length of juvenile sockeye salmon smolts captured in 2014 (87.5 ± 11.0 mm). The possibility of small smolts from Johnston Lake remaining in the estuary to rear for longer than their larger counterparts from other Skeena River sockeye salmon rearing lakes provides one feasible explanation for their unusual timing. The more compact temporal distributions of other Skeena River sockeye salmon populations that we captured in the estuary (Figure 2) support our use of date of estuarine capture as a proxy for timing of migration.

The different Skeena River sockeye salmon populations arriving at different times encountered fundamentally different zooplankton prey communities in the estuary. Juvenile sockeye salmon were captured in the Skeena River estuary over a period of six weeks in 2013 and 7 weeks in 2014. In both years, the timing of peak abundance for juvenile sockeye salmon coincided with the timing of minimum abundances of known sockeye salmon prey items, including euphausids, decapods, oikopleurans, and calanoid copepods at our zooplankton sampling station. Interestingly, the peak of the sockeye smolt outmigration, coinciding with the minimum abundance of zooplankton, is primarily dominated by a single enhanced population from Babine Lake. However, it is unlikely that the magnitude of the juvenile sockeye salmon outmigration from the Skeena River and surrounding areas was so great as to affect the standing crop of zooplankton (Walters *et al.*, 1978; Price *et al.*, 2013). Previous surveys of juvenile sockeye salmon diets have reported high variability in sockeye salmon stomach contents, and selectivity of food items respective to the available zooplankton (Price *et al.*, 2013). Juvenile sockeye salmon consume a variety of prey in the months following marine entry, with copepods, euphausids, decapods, amphipods, larvaceans, fish and terrestrial insects found in stomach contents during diet studies conducted in northern British Columbia (Manzer, 1969; Healey, 1991; Brodeur *et al.*, 2007). Calanoid copepods were a major component of sockeye salmon stomachs in previous studies, but were under-represented compared to the high proportion of calanoid copepods present in the water column. It has been suggested that the high degree of selectivity exhibited by sockeye salmon diets is related to the quality of available prey (Trudel *et al.*, 2007; Tanasichuk & Routledge, 2011), and growth and survival in juvenile coho salmon was related to the lipid content of consumed prey (Orsi *et al.*, 2004; Trudel *et al.*, 2007). Sockeye salmon returns to Alberni Inlet, British Columbia were strongly correlated with the abundance of one species of euphausid (*Thysanoessa spinifera*) during their first summer at sea (Tanasichuk & Routledge, 2011). Therefore, while small calanoids, mostly *Acartia longerimis* and *Pseudocalanus minutus,* were the most numerous species captured in our 2013 and 2014 zooplankton samples, decapods and euphausids, which were minor components of the total zooplankton biomass, may be disproportionately important for juvenile salmon growth in the early marine environment. Opportunities for feeding may benefit smolts in the period immediately following the energetically expensive downstream migration. Thus, the quantity and quality of prey available in estuarine habitats may be important for their long-term survival.

Zooplankton phenology, which is already quite variable, is likely to become more variable and advance with climate change (Rubao *et al.*, 2010). There was local evidence for long-term warming ocean temperatures, likely driving phenological changes in zooplankton, including known juvenile salmon prey. Local monthly SST in April and May have increased by more than 0.70 °C overall since 1964. While the two years of zooplankton data that we collected for the current study are obviously not sufficient to examine for trends, the timing of peak abundance for most zooplankton taxa varied between 2013 and 2014 while the timing of peak abundance for juvenile sockeye salmon in aggregate and for each population remained consistent across years. Previous research suggests that zooplankton phenology advances with increasing ocean temperatures (Edwards & Richardson, 2004; Hays *et al.*, 2005; Richardson, 2008; Poloczanska *et al.*, 2013) and zooplankton biomass variability is correlated with SST (Beaugrand & Reid, 2003; Rubao *et al.*, 2010). There is evidence that recent marine climate change is already affecting salmon populations. Salmon productivity is affected by regional abundance of phyto- and zooplankton in the marine environment (Ware & Thomson, 2005). Sea surface temperatures have been correlated with pink salmon growth and survival (Mortensen *et al.*, 1999), Atlantic salmon stock size (Friedland *et al.*, 2003), and historic sockeye salmon abundance (Finney, 2000). Thus, salmon productivity appears to be already responding to increasing ocean temperatures and the potential for mismatches between phytoplankton, zooplankton and salmon may increase as ocean temperatures continue to rise.

The diversity of outmigration timing of sockeye smolts that we observed within the Skeena River watershed has two major implications for the response of salmon to ocean climate change. First, given that different populations experience different early marine conditions, their phenological diversity is likely to contribute to different responses to earlier or later marine prey dynamics. For instance, earlier migrating populations may have better survival in years with earlier zooplankton blooms than populations that migrate later. Phenological diversity of smolt migration timing, which arises from genetic and geographic factors, may protect some populations from shifting marine conditions during ocean entry and render other populations more vulnerable. Second, migration diversity may contribute response diversity and thus stability to processes that integrate across population diversity, such as meta-population dynamics or fisheries harvests. It is possible that the diversity of smolt migration timing thus contributes to the stability of salmon meta-populations and fisheries confronted with the challenges of marine climate change. There is considerable population-level diversity within large salmon-bearing watersheds like the Skeena River that can influence the sustainable management of these fish and fisheries. Life history, or age structure diversity, buffers populations from poor marine conditions by staggering the year of ocean entry (Schindler *et al.*, 2010; Moore *et al.*, 2014). The diversity of adult run-timing for the different Skeena River sockeye salmon populations is already well established and used as a management tool to target enhanced Babine Lake populations while conserving small Skeena River sockeye salmon populations during commercial fishery openings (Beacham *et al.*, 2014b). Our research illustrates that within-population genetic and phenotypic diversity can increase species' potential to respond to shifting environmental conditions (Luck *et al.*, 2003; Doi *et al.*, 2010). Regardless of future human intervention, global temperatures are projected to rise through the next century as a result of the accumulation of anthropogenically-introduced carbon dioxide in the atmosphere (IPCC 2013). Given that the direction and magnitude of future climate shifts remain unclear, protection of habitat integrity and local adaptations can conserve evolutionary potential (Reed et al. 2011) and enable metapopulation sustainability (Anderson *et al.*, 2014).

3.6. References

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3.7. Tables

Table 3.1. Geographic variables for Skeena sockeye rearing lakes.

Lake	Drainage	Sockeye populations	River distance (km)	Elevation (m)	Latitude (degrees N)	Surface area (ha)	S^{max}
Johnston	Ecstall	Johnston	67.13	58	53.868	187	4125[1]
Alastair	Gitnadoix	Alastair	94.51	30	54.144	686	23437[2]
Lakelse	Lakelse	Williams, Schulbuckhand	129.41	76	54.366	1372	35916[1]
Kalum	Kitsumkalum	Kalum, Kalum Lake	157.78	122	54.720	1900	20531[2]
Mcdonell	Zymoetz	Mcdonell	248.17	830	54.781	227	4072[1]
Kitwanga	Kitwanga	Kitwanga	263.97	376	55.334	774	36984[1]
Morice	Morice	Nanika	522.62	939	54.107	9739	191362[1]
Stephens	Kispiox	Stephens	390.02	520	55.764	188	7069[1]
Swan	Kispiox	Swan	397.63	520	55.779	1736	21432[1]
Babine/ Nilkitkwa	Babine	Upper Babine, Lower Babine	440.66	712	55.414	46100	1808245[3]
		Four mile					
		Grizzly					
		Fulton					
		Pinkut					
		Pierre					
		Morrison					
Morrison	Babine	Tahlo	505.33	743	55.174	1300	44587[3]
Slamgeesh	Slamgeesh	Damshilgwet	459.2	618	56.400	45	423[1]
Motase	Motase	Motase	510	1021		397	1764[1]
Sustut	Sustut	Sustut	575.41	1301	56.400	250	2775[2]
Bear	Sustut	Salix	515.28	805	56.195	1884	40532[1]

[1] Smax (optimal smolt biomass produced in lake, from PR Capacity model, estimate from Shortreed et al. 2007)

[2] Shortreed et al. 1998

[3] Shortreed et al. 2001

Table 3.2. Linear model coefficients indicating mean date of estuarine capture for Skeena sockeye populations represented in 2013 and 2014 estuary sampling.

Population	Estimate[1]	SE	t value	Pr(>|t|)		Mean date[1]
Alastair	55.3	1.56	35.424	< 2e-16	***	25-May
Damshilgwet	51.0	8.82	-0.483	0.629714		21-May
Four mile	71.2	3.87	4.107	4.99E-05	***	10-Jun
Fulton	63.3	1.73	4.686	3.98E-06	***	02-Jun
Grizzly	60.0	8.82	0.537	0.591339		30-May
Johnston Lake	68.7	3.63	3.702	0.000248	***	07-Jun
Kalum	55.2	3.87	-0.024	0.981189		25-May
Kalum Lake	48.9	3.16	-2.013	0.044876	*	19-May
Kitwanga	44.0	6.34	-1.777	0.07647	.	14-May
Lower Babine R	57.3	2.31	0.887	0.375456		27-May
Mcdonnel	51.2	3.87	-1.056	0.291592		21-May
Morrison	72.0	5.25	3.188	0.00156	**	11-Jun
Nanika	57.1	2.57	0.698	0.48538		27-May
Pierre	68.8	2.49	5.416	1.13E-07	***	08-Jun
Pinkut	73.0	8.82	2.011	0.045125	*	12-Jun
Salix (Bear)	80.0	6.34	3.905	0.000113	***	19-Jun
Stephens	48.6	2.67	-2.504	0.012716	*	19-May
Sustut	80.5	2.36	10.672	< 2e-16	***	19-Jun
Swan	64.0	6.34	1.38	0.168565		03-Jun
Tahlo	63.5	4.61	1.786	0.074924	.	03-Jun
Upper Babine R	48.5	2.09	-3.215	0.001423	**	19-May
Williams	49.8	2.95	-1.865	0.062961	.	20-May

[1] Linear model predictions for mean day of estuary residence for each population (day of year after April 1). Estimates for each population of genetically identified Skeena sockeye represent sum of linear model coefficient for each population (factor) and coefficient for baseline population. P-value indicates likelihood that the mean day of estuary residence for a given population differs from the mean value.

***indicates significance at $p<0.0001$; **significant at $p<0.01$; *significant at $p<0.05$

Table 3.3. **Delta-AIC values for mixed-effects models fitted to genetic data collected from juvenile sockeye captured in the Skeena estuary in 2013 and 2014.**

Fixed effects	df	delta AIC
river distance	4	0.000
elevation	4	0.402
elevation + latitude	5	1.109
river distance + latitude	5	1.374
river distance + productivity	5	1.392
river distance + elevation	5	1.561
elevation + productivity	5	2.330
river distance + latitude + productivity	6	2.835
river distance + elevation + latitude	6	2.838
elevation + latitude + productivity	6	3.003
river distance + elevation + productivity	6	3.179
latitude	4	3.653
river distance + elevation + latitude + productivity	7	4.542
latitude + productivity	5	5.582
productivity	4	9.453
none	2	79.230

Note. All models are fitted to pooled data from both years and include population as a random effect.

3.8. Figures

Figure 3.1. Map of 2013 and 2014 study area showing purse seine (circles) and trawl capture sites triangles) in Skeena estuary

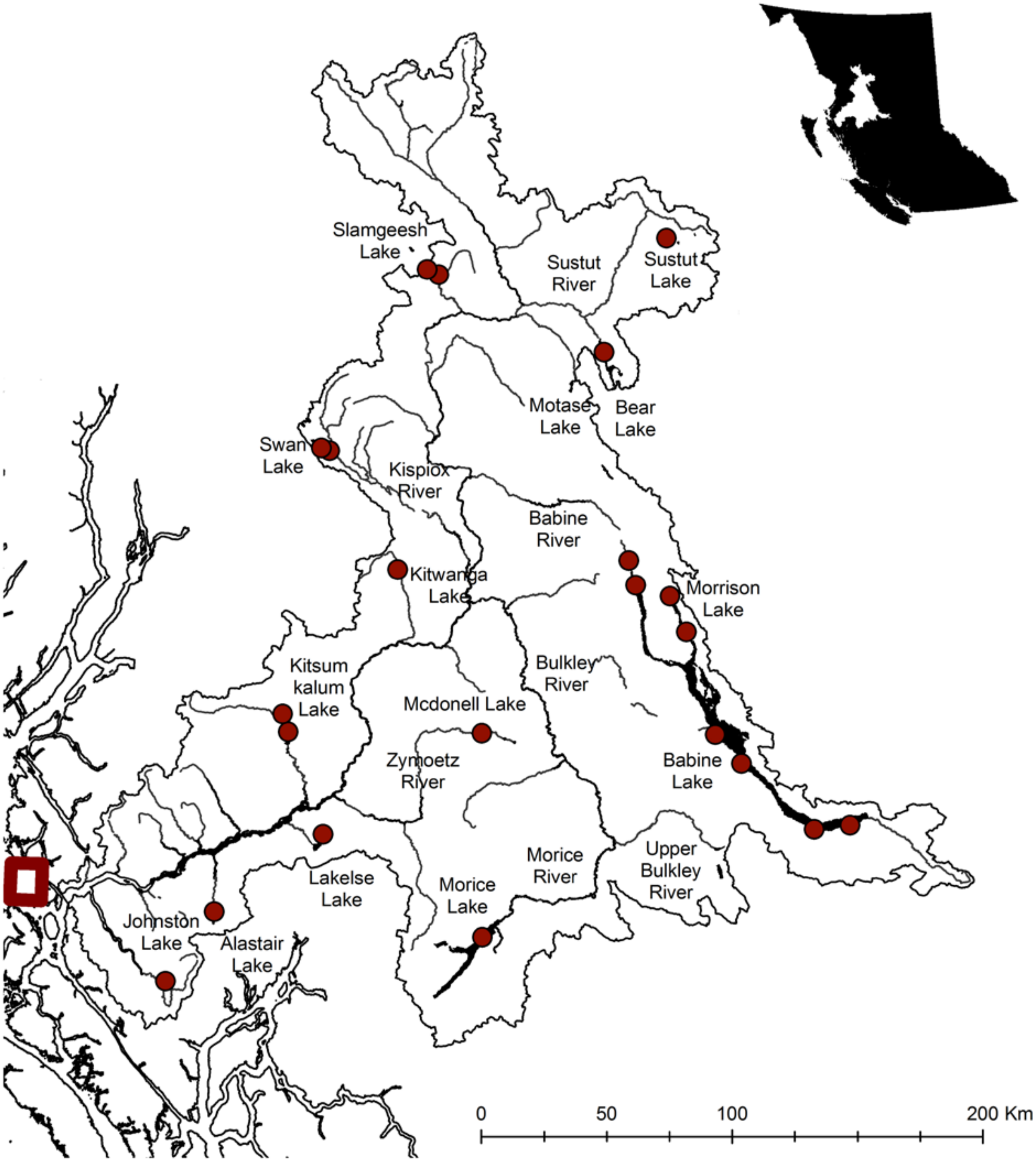

Figure 3.2. Skeena River and watershed boundary, with major tributaries and sockeye rearing lakes labelled.

Note. Red points indicate spawning areas for genetically identified juvenile sockeye captured in the estuary in 2013 and 2014, some sockeye rearing lakes contain multiple populations. Estuary sampling area is contained in red polygon.

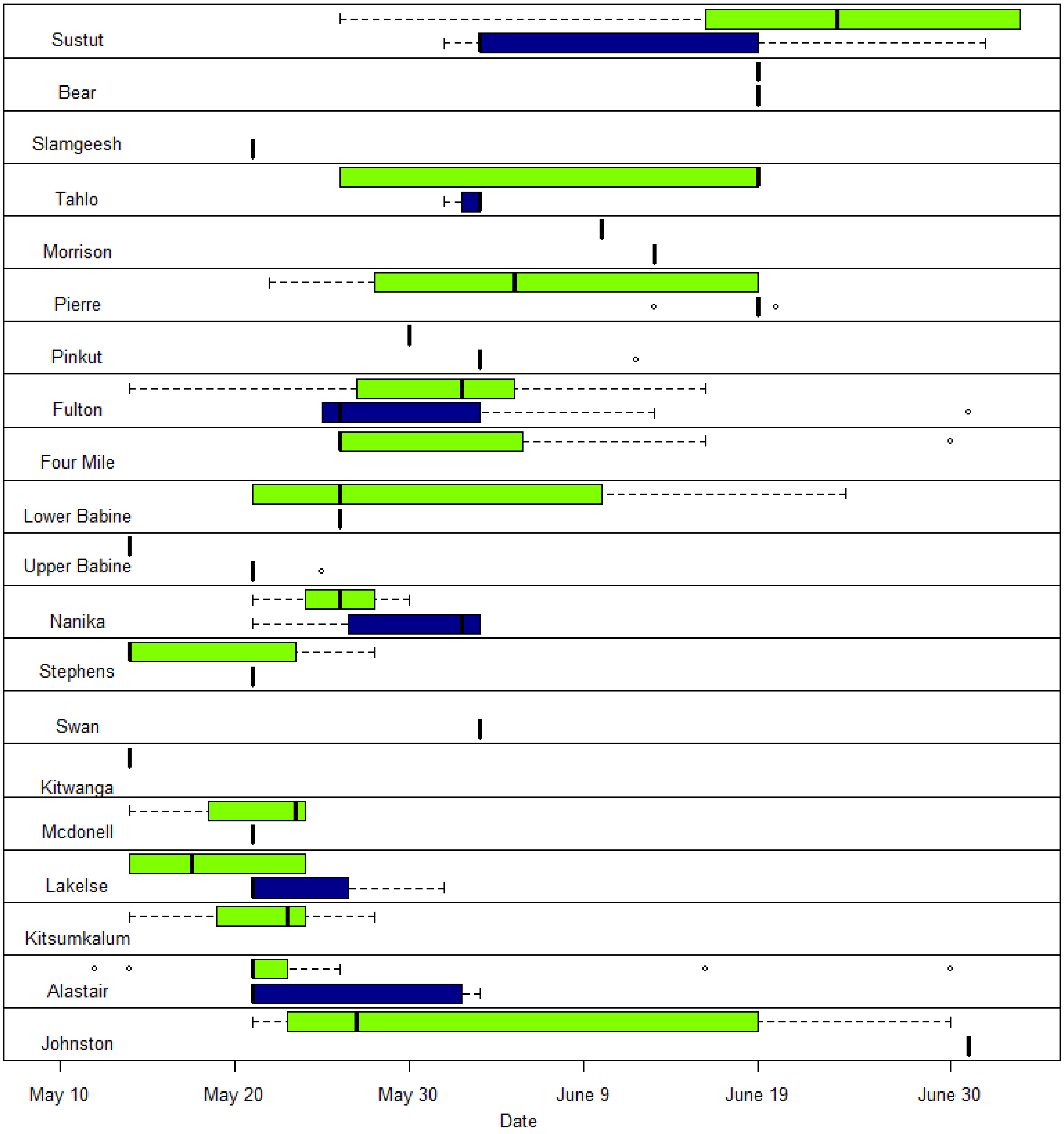

Figure 3.3. Boxplots of estuary capture dates for Skeena sockeye smolts by population and year of capture.

Note. Smolts captured in 2013 are shown in dark blue, and smolts captured in 2014 are shown in green. Boxes represent the first and third quartiles, with solid black lines indicating median capture date for each population/year. Upper and lower whiskers represent 10th and 90th percentiles respectively.

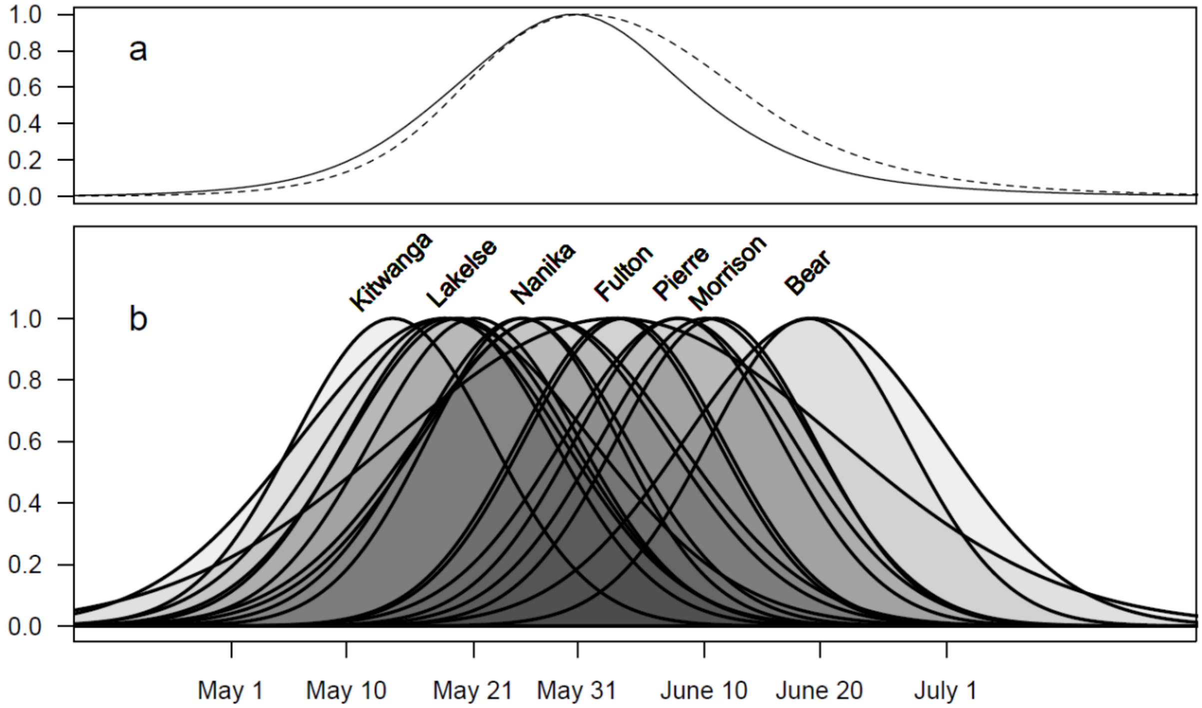

Figure 3.4. **a. Fitted GAM model predictions for trawl catch per unit effort (sockeye per 20 minute set) from May – July. b. Probability distribution of estuarine residence timing for different Skeena sockeye populations.**

Note (a) 2013 and 2014 values are indicated by dashed lines and solid lines respectively. Values were normalized by dividing predicted values by the maximum predicted value for each year so that the highest value is 1 for both years. (b) Individual probability curves depict a normal distribution using the mean and standard deviation from linear model coefficients (Table 2) of estimated peak dates of estuarine capture for Skeena sockeye populations captured in 2013 and 2014 sampling. Probability curves are normalized such that the maximum mean value for all populations is 1.

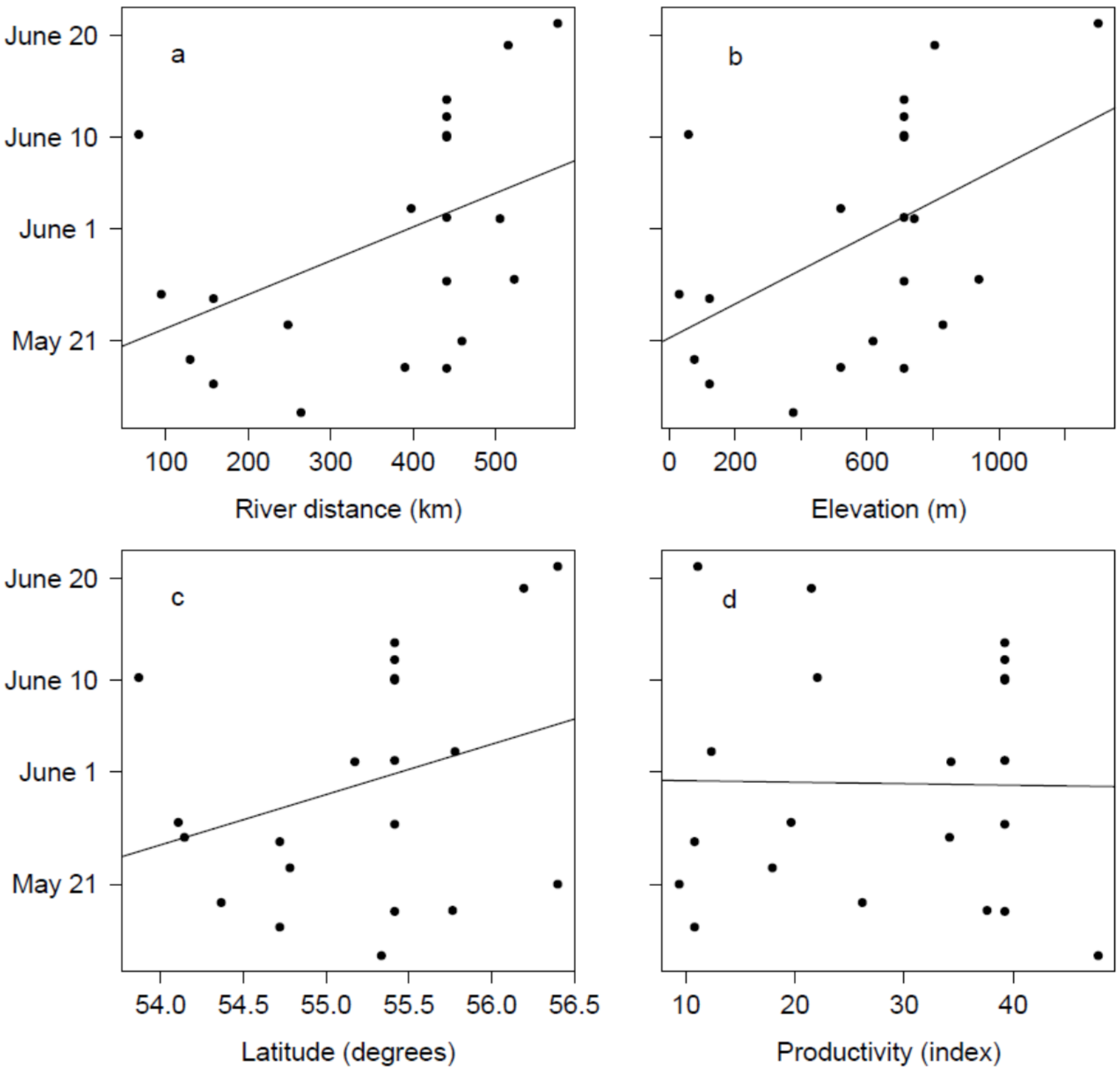

Figure 3.5. **Bivariate plots of linear model coefficients estimating mean estuarine capture date for all Skeena sockeye populations that were encountered in the estuary.**

Note. Lines indicate fitted linear models predictions for linear regressions of (a) river distance (slope=0.0331 days/km, p=0.042), (b) elevation (slope=0.0167 days/m, p=0.0281), (c) latitude (slope=4.931 days/degree, p=0.178), and (d) productivity (slope=-0.0147, p=0.945).

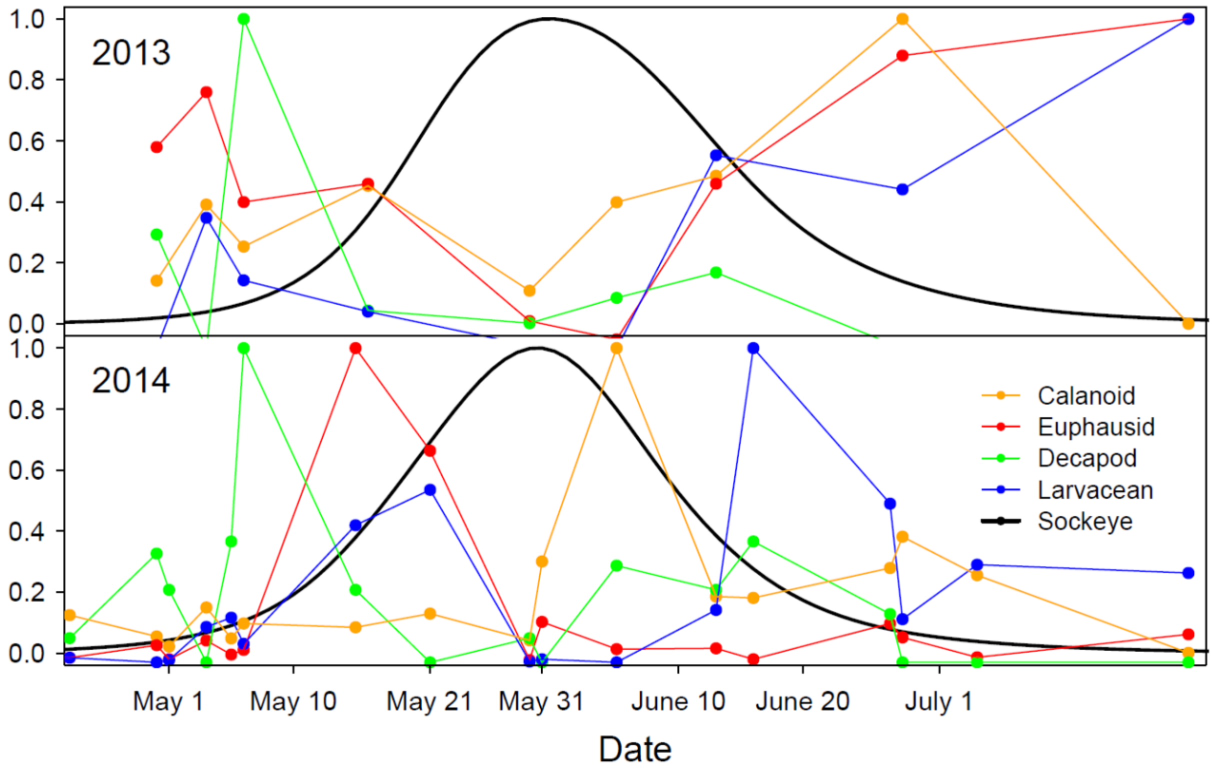

Figure 3.6. **Temporal trend for relative abundance of juvenile sockeye (black lines) and known sockeye zooplankton prey taxa (coloured lines).**

Note. Coloured points indicated abundance of each zooplankton taxon during each sampling event relative to the maximum abundance observed during the sampling period. The smoothed sockeye abundance values were generated from predicted GAM output values for each day during the time series. All values for zooplankton and sockeye are normalized so that the maximum value for each taxon is 1.

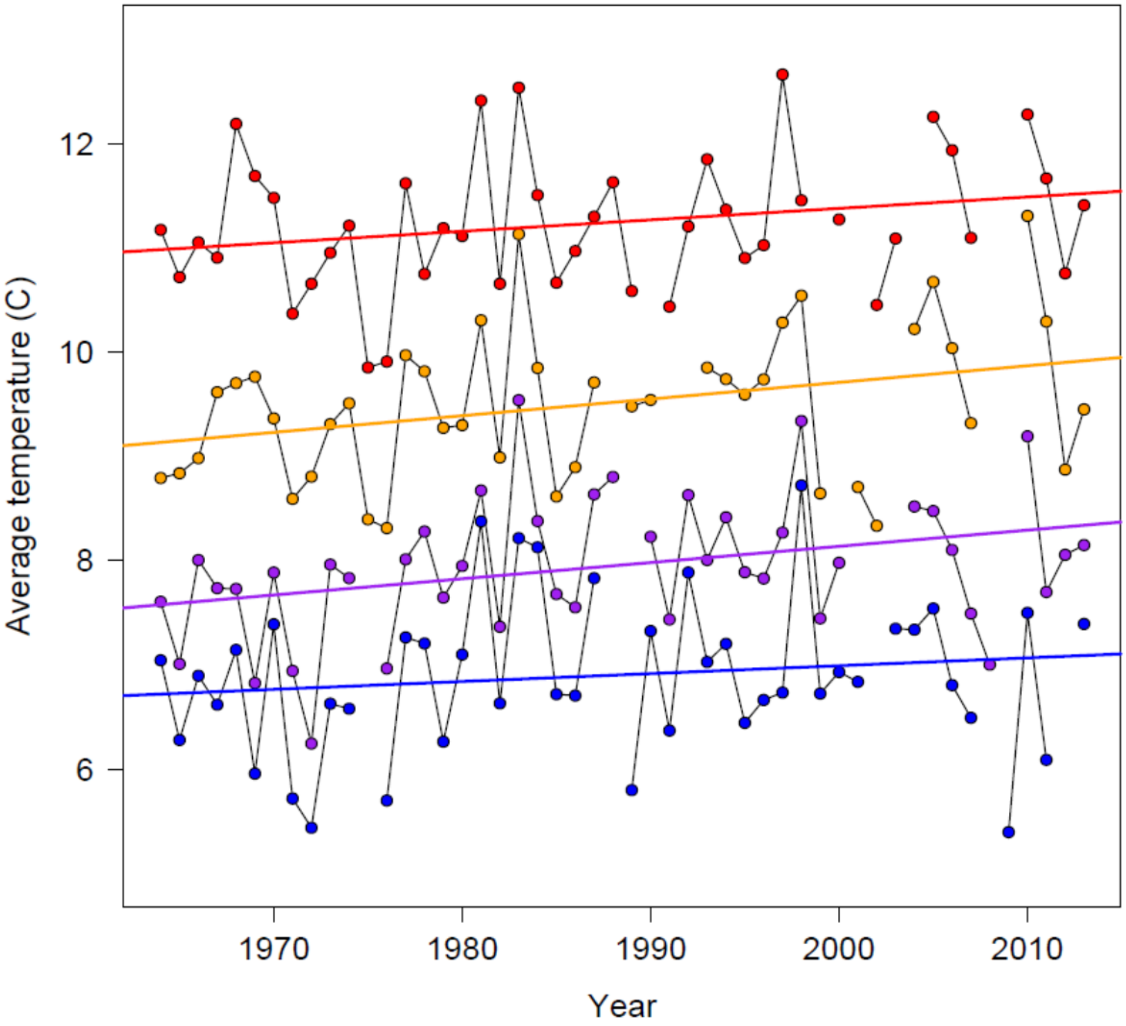

Figure 3.7. **Average monthly sea surface temperature at Bonilla Island lighthouse for March (blue), April (purple), May (gold), and June (red) from 1962-2013 with corresponding linear regression lines.**

Chapter 4. General Discussion

4.1 Overview

This thesis examined how juvenile salmon use estuaries. Estuaries are key habitats for juvenile salmon transitioning between freshwater and marine environments. For juvenile salmon, the downstream migration and early marine life history phases are critical life history stages which may determine whether they survive to reproduce (Mortensen *et al.*, 1999; Beamish & Mahnken, 2001; Farley *et al.*, 2007). I studied juvenile salmon in the estuary of the Skeena River which produces robust returns of all six species of northeast Pacific salmon and steelhead (Gottesfeld & Rabnett, 2008). This research was timely, because with several major development projects proposed for this relatively undeveloped estuary (Stantec, 2011, 2014a; AECOM, 2013), it is important to understand how these habitat alterations salmon usage of this ecosystem. My thesis consisted of an extensive field sampling of juvenile salmon and their ecosystem over two spring-summers in the Skeena estuary. For my first chapter, I compared abundances of different species of juvenile salmon in different locations over time and used genetics to identify their origin population. Next, I quantified the diversity of a key phenotypic trait, smolt migration timing for the different sub-populations of Skeena sockeye salmon. Here, I discuss the key findings of my thesis research and outline recommendations for future directions for estuary research based on these findings.

4.2 Juvenile salmonid estuary habitat utilization

In Chapter 1, I found that the different species of juvenile salmon were heterogeneously distributed throughout the Skeena estuary. The relative abundances of different species varied by capture gear, timing, and region sampled, indicating that different species occupied different parts of the estuary at different times. While the geographic extent of the Skeena estuary is hundreds of km^2 at peak discharge, our results and past research suggest that juvenile salmon aggregate in different “hotspots” within the wider estuary (Manzer, 1956; Higgins & Shouwenberg, 1973). Trawl abundance data from 2007 and 2013 indicated that the relative importance of different regions in the estuary to different species of juvenile salmon is consistent across years. In both years of my sampling, the highest abundances of salmon were captured in the areas closest to the mouth of the Skeena River. All species of juvenile salmon, and the highest abundances of some species of salmon, including juvenile sockeye and Chinook salmon, were captured in the footprints of proposed development projects. Genetic analysis revealed that juvenile Chinook and sockeye salmon captured in this area came from tributaries throughout the Skeena watershed and beyond. Taken together, the results from this chapter suggest that the proposed industrial developments in the Skeena estuary have the potential to affect fish populations throughout the Skeena watershed. These results support the findings of historic environmental assessments commissioned by various regulatory agencies in the 1970s and 1980s which examined the effects of proposed seaport developments in areas adjacent to Flora Bank, and concluded that the potential adverse effects to juvenile salmon habitat rendered this area unsuitable for development (Wright Engineers 1972; Fisheries Service 1972; Paish and Associates 1973; Higgins & Shouwenberg 1973; Hoos, 1975, Hinton 1975). I found that certain regions within the Skeena estuary had higher abundances of some species of juvenile salmon, and gained a better understanding about where different species of juvenile salmon are more likely to be found. We now know that the proposed development area has particularly high abundances of most salmon species. However, we have little understanding of what makes specific habitats more important for different species of juvenile salmon. Further work is necessary in order to determine the importance of specific habitats within these regions. While estuaries are generally considered to be important habitats for juvenile salmon (Healey, 1982; Simenstad *et al.*, 1982), for specific habitats to be considered nursery areas, it must be demonstrated these areas ultimately contribute to adult recruitment in addition to supporting high densities of juvenile salmon (Beck *et al.*, 2001). In the Skeena estuary, some attention has been paid to the utilization of the extensive eelgrass beds at Flora Bank by juvenile salmon (Hoos, 1975), but the relative importance of these habitats to different species of juvenile salmon remain unstudied, and the specific factors that support juvenile salmon in other habitat types such as rocky reefs and shallow bays are even less well understood. Furthermore, estuary habitats are dynamic, with shifting zones of low salinity and high turbidity as the river plume advances and recedes during the spring freshet, so the spatial distribution of significant juvenile rearing habitats likely changes during the smolt migration period. More information about the duration of estuarine residence time for the different species of juvenile salmon and a better understanding of the juvenile salmon resource utilization within estuary micro-habitats will allow us to quantify the effects of developing these habitats and proposed mitigation measures on salmon productivity.

4.3 Environmental assessments in the Skeena estuary

Few direct field studies of juvenile salmon have been undertaken by proponents of development projects in the Skeena estuary, who have instead relied on desktop literature reviews to conclude that with appropriate mitigation measures including habitat offsets, salmon populations would not be affected by the proposed developments (Stantec, 2014a). The juvenile salmon and forage fish data produced by some proponent field studies were of poor quality. For example, one consulting company used a remotely-operated vehicle (ROV) to survey transects on Flora Bank in May 2013 (Stantec, 2014a), when visibility was compromised by high turbidity from the annual spring freshet. Our data indicate that the ROV survey was conducted near the peak of the juvenile sockeye salmon migration from the Skeena River in areas where we captured juvenile salmon, yet no juvenile salmon were observed by ROV (Stantec, 2014a). However, these “data” formed the basis of the environmental assessment of the biggest LNG plant proposal undertaken to date in British Columbia.

The proponents of recently proposed projects for the same region maintain that the new proposed developments will have no negative effects on fish populations because losses to fish habitat from development can be mitigated using habitat offset measures, including the construction of new habitats(Stantec, 2014b). The risks and benefits of installing some of the proposed habitat creation measures to different species of juvenile salmon are not well understood. For example, the construction of artificial rock reefs (Stantec, 2011) and shoreline benches (Stantec, 2014b), both of which have been proposed as habitat offset measures for estuary development projects, could become suitable habitats to predators of juvenile salmon, causing increased mortality, the opposite of the intended effect, to some species of juvenile salmonids (Bulleri &

Chapman, 2010). The proposed developments would alter estuary habitats at the northern exit of the Skeena River (Inverness Passage and Marcus Passage), affecting salmon entering the estuary from this route. Even if suitable offset habitat is constructed, it may not benefit juvenile salmon affected by these habitat alterations, because with swimming speeds proportional to their body lengths (Brett, 1986), they might not be able to access artificial habitats created elsewhere. For example, juvenile pink and chum salmon which migrate to sea immediately after emergence enter the estuary at 30 – 40 mm length (Healey, 1982) and are essentially planktonic at this stage. Habitat offsets would not benefit weak-swimming juvenile salmon that are unable to swim upstream against river currents or change direction if they encountered unsuitable habitats when they arrived in the estuary. Further research into the net benefits of the construction of the proposed artificial habitat for different species of juvenile salmon is necessary to support the assumption that existing levels of fisheries productivity can be achieved by habitat offset measures.

Project proponents and environmental consulting companies would benefit from meaningful collaboration with local organizations that are familiar with local fish species, geography, and environmental conditions. My field sampling program was conducted in partnership with the Lax Kw'alaams and Metlakatla First Nations, whose traditional territories include the Skeena estuary, and proposed LNG terminals. My thesis research project would not have been successful without the participation of dedicated, knowledgeable and professional fisheries resource stewards who are familiar with the area and have fished in these waters for generations. Not involving First Nations or other local experts in study design or data analysis represents a lost opportunity to improve the quality of fisheries data collected during environmental assessments.

The pace of environmental assessment review and project development has accelerated since the start of my thesis research. The British Columbia Environmental Assessment Office (BCEAO) recently granted environmental certificates to one LNG terminal and two pipelines that would supply natural gas to both of the proposed LNG terminals in Skeena estuary (Government of British Columbia, http://www.newsroom.gov.bc.ca/2014/11/three-lng-projects-granted-environmental-assessment-approval.html). The environmental certificate for the LNG terminal was granted three weeks prior to the proponent's submission of their habitat offset plan to the regulatory body. The habitat offset plan has not yet been reviewed or approved by stakeholder groups, including local First Nations. One pipeline application, which will entail significant dredging in the estuary in addition to hundreds of water crossing along its 1,300 km route from northeast British Columbia (BCEAO, 2014), was approved following a review period of only 13 days (Government of British Columbia, 2014). These pipelines do not require federal review and may now proceed to the permitting stages. Construction of a road, rail and utility corridor on Ridley Island to support new industrial development was completed in 2014 (Fig 4.1).

Figure 4.1. **Foreshore modifications including shoreline armouring and removal of riparian habitat on Ridley Island during construction of a road, rail and utility corridor.**

Note. Ridley Island is in the Skeena River estuary, and this is an example of the rapid pace of industrial development in the area. I watched this development occur over the last two years.

4.4. Phenological diversity of sockeye smolt migration

In Chapter 2, I quantified the phenological diversity of smolt migration timing for Skeena River sockeye salmon. This study uncovered a previously unappreciated aspect of diversity that may influence how these different populations experience estuary habitats. Previous studies have found that the timing of ocean entry affects marine survival for Chinook salmon (Satterthwaite *et al.*, 2014), and that earlier timing of ocean entry is associated with higher survival (Scheuerell *et al.*, 2009). Most prior studies on migration phenology have focused on enhanced populations, and populations in anthropogenically altered systems that require human intervention such as hatchery releases into estuaries or transport past dams to complete their downstream migration

(Achord *et al.*, 2011). The current study of the timing of downstream migration for Skeena River sockeye salmon described remarkable diversity in the migration phenology of wild populations in a natural system. We found considerable variation in migration timing among these sub-populations, and hypothesize that natural variation in timing of ocean entry allows different populations to access different prey resources in the estuarine environment. Previous research suggests that phenological traits such as smolt migration timing are highly hereditary (Carlson & Seamons, 2008). Our data suggest that there is also a strong geographic component to smolt migration timing. Geographic constraints may maintain the diversity of smolt migration timing among the different Skeena River sockeye salmon populations.

4.5. Genetic diversity of Skeena River sockeye salmon

Skeena River sockeye salmon are genetically diverse with at least 28 different sockeye salmon rearing lakes in the watershed. While 90% of all sockeye salmon originate from Babine Lake, which is the largest natural freshwater lake in British Columbia, the many smaller lake sockeye salmon populations contribute most of the genetic diversity of Skeena River sockeye salmon (Beacham *et al.*, 2014). While there are no significant hatchery-reared sockeye salmon populations in the Skeena River, spawning channel enhancement at two Babine Lake tributaries has resulted in a decrease in the proportion of non-Babine sockeye salmon returning to the Skeena River because of increased fishing pressure on mixed-stock fisheries targeting the enhanced populations. The proportion of non-Babine Skeena River sockeye salmon has decreased from approximately 25% prior to the inception of the spawning channels to between 10 and 15 percent of the aggregate return, and enhanced Babine sockeye salmon populations now account for approximately 50 percent of the aggregate Skeena River sockeye salmon return (Beacham *et al.*, 2014). Juvenile sockeye salmon from the enhanced Fulton River population comprised over 40% of the juvenile sockeye salmon captured in our 2013 and 2014 sampling. Higher proportions of enhanced populations result in more smolts arriving in the estuary at the same time, thus increasing the risk of a phenological mismatch between smolts and their zooplankton prey. We found that the peak migration timing for juvenile Skeena River sockeye salmon, driven by the peak sockeye smolt migration from Fulton River, coincided with minimum abundances of zooplankton prey. We observed more variability in the timing of different zooplankton prey taxa than for different sockeye salmon populations in both years. Conserving estuary habitats where we have observed high species and population diversity will increase the potential for juvenile salmon populations to coincide with estuarine resource availability. Maintaining upstream watershed habitat and salmon biodiversity will enable the Skeena River sockeye salmon meta-population to respond dynamically to marine climate change.

4.6. Conclusions

The Skeena River estuary integrates multiple scales of salmon diversity, including species, population, genetic, and phenotypical diversity. While this is not surprising given the enormous size of the Skeena watershed and the anadromous life-histories of salmon, it highlights that the estuaries of large watersheds may be a critical component of the integrity of the whole watershed and its socio-ecological system. The estuary of the Skeena River may be considered a migratory bottleneck, representing an area of high conservation priority, and protecting the Skeena River watershed can have enormous upstream benefits that reach as far as salmon can swim (Carr-Harris *et al., in press*). However, massive-scale industrial development for the Skeena River estuary is proceeding with alacrity. During our two years of sampling, we captured all six species of juvenile Pacific salmon and steelhead in areas where development is proposed, confirming previous research that suggests that all species of salmon use the estuary for some period of time (Healey, 1982; Simenstad *et al.*, 1982). However, the duration of estuary residence, and degree to which juvenile salmon rely on estuary habitats varies by species and life-history types within species (Thorpe, 1994; Weitkamp *et al.*, 2014). Thus, different species and populations may be differently affected by habitat degradation, and populations that rear in estuaries for longer periods of time may be more affected by proposed developments. Phenotypical diversity, including diversity of phenological traits such as smolt migration timing may increase the resilience of some species and metapopulations to environmental change, including anthropogenic changes caused by the developments themselves. Developing key habitats that contain high species and population-level diversity could threaten some populations of Skeena River salmon, thus limiting their potential to respond to ecological change. However, none of the environmental assessments that have been submitted to regulatory agencies for major projects in the Skeena River estuary have included population level assessments of the fish that will be affected by development, let alone comprehensive fish sampling in the areas proposed for development. This is of particular concern for communities upstream of proposed developments which depend on specific populations for sustenance, commercial or recreational fisheries. The effects of proposed industrial development on the different species and populations of juvenile salmon need to be quantified to properly assess the effects of proposed habitat alterations on salmon productivity. Together, this thesis illuminates fundamental questions in salmon biology, estuary ecology, and has application for the conservation and management of the second-largest salmon producing watershed in Canada.

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