

# **Abiotic and biotic dimensions of habitat for juvenile salmon and other fishes in the Skeena River estuary**

by

**Ciara Elizabeth Sharpe**

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# Approval

**Name:** Ciara Elizabeth Sharpe

**Degree:** Master of Science

**Title:** Abiotic and biotic dimensions of habitat for juvenile salmon and other fishes in the Skeena River estuary

**Examining Committee:**

**Chair: Dr. Wendy Palen**  
Associate Professor

**Dr. Jonathan Moore**  
Senior Supervisor  
Associate Professor

**Dr. Isabelle Côté**  
Supervisor  
Professor

**Dr. Douglas Braun**  
Internal Examiner  
Adjunct Professor  
School of Resource and Environmental Management

**Date Defended/Approved:** December 11, 2017

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## Abstract

Estuaries are increasingly degraded globally but provide nursery services for juvenile fishes through predator protection and increased food availability. This thesis examined the abiotic and biotic factors that contributed to abundance patterns of juvenile salmon and forage fish species in the Skeena River estuary, BC. I first showed that spatial abundance patterns were heterogeneous for salmon and that the combination of variables that predicted abundance differed between species. Inclusion of these dynamic abiotic and biotic variables increased predictive power over solely using static habitat descriptors for juvenile salmon. Next, I examined the association between fish and prey abundance for two forage fish and juvenile salmon species. Overall, fish abundance was not related to prey abundance, except for herring which co-varied with a highly consumed prey species. Understanding the factors influencing estuarine habitat use by economically-important juvenile salmon and forage fish can help inform risk assessment and guide environmental planning.

**Keywords:** estuary; *Oncorhynchus* spp.; juvenile salmon; forage fish; Skeena River; zooplankton

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# Chapter 1. Introduction

Estuaries are productive transition zones between fresh water and marine environments (Simenstad 1983; Orth et al. 2006; Waycott et al. 2009). These ecosystems support many species of fish, birds and marine mammals (Simenstad et al. 1979) and are commonly referred to as nursery habitats, as they provide a safe environment for the growth and development for many species of young fish (Beck et al. 2001; Dahlgren et al. 2006). Predator refuge, favorable environmental conditions and increased food availability are thought to explain the nursery role of estuarine environments. Estuary turbidity, marine vegetation and sheltered nearshore geography can provide protection from predators (St. John et al. 1992; Gregory & Levings 1996; Fukuwaka & Suzuki 1998; Bottom et al. 2005b; Brodeur & Morgan 2016; Levings 2016), while preferable salinity and temperature regimes can promote optimal growing conditions. These conditions combined with marine and freshwater sources of nutrients create highly productive environments with high food supply and foraging opportunities for fish (Grimes & Finucane 1991; St. John et al. 1992; Grimes & Kingsford 1996; Hill & Wheeler 2002; De Robertis et al. 2005; Ware 2005; Selleslagh et al. 2012; Brodeur & Morgan 2016). By supporting high growth rates and decreased mortality from predation, estuaries are thought to be instrumental in providing higher survival rates for juvenile fish (Beck et al. 2001; Heck et al. 2003; Alofs & Polivka 2004; Sheaves et al. 2015). Despite the importance of estuary habitat to many fish species, estuaries continue to be one of the most degraded environments globally (Kennish 2002; Lotze et al. 2006; Orth et al. 2006). For example, over 65% of seagrass and wetland habitat has been destroyed since the onset of industrialization (Lotze et al. 2006). Degradation resulting from habitat alteration and destruction, pollution and overharvesting of estuarine food webs continues to be a widespread challenge (Kennish 2002).

In the northeast Pacific, estuaries support many economic and culturally important species. Pacific salmon and forage fish, such as Pacific herring (*Clupea pallasii*) sustain indigenous fisheries and cultures (Thornton et al. 2010; DFO 2016; Nesbitt & Moore 2016), along with commercial and recreational fisheries which significantly contribute to North American economies annually (Kristianson & Strongitharm 2006; BCMOE 2008; Schindler et al. 2010; DFO 2016). Although

restoration efforts are occurring in degraded estuaries along the northeast Pacific (Levings & Nishimura 1997; Williams & Orr 2002; Simenstad et al. 2006), continued development and industrialization of estuaries highlights the need to further understand what makes different locations in estuaries particularly important habitat for juvenile salmon and forage fish.

Defined simply as the locality, site and particular type of local environment occupied by an organism (Lincoln et al. 1987), habitat provides the resources and the conditions that are needed by species for occupancy and survival (Fretwell 1972; Hall et al. 1997). Thus, “the favorableness of the habitat will depend on the level of resources... the number of natural enemies... and the density of the organism” (Southwood 1977). Estuary habitats in the NE Pacific can be broken into three main descriptors: beaches (e.g., sandy, cobble, boulder), channels (e.g., tidal channels, riverine) and vegetative (e.g., eelgrass, saltmarsh, macroalgae) habitat. These estuary habitats are known to contribute different types and levels of resources along with varying degrees of predator refuge. For example, vegetation such as salt-marsh or eelgrass contributes to the detrital food web and provides habitat for many secondary producers (i.e., invertebrates such as harpacticoid copepods) (Stanhope & Levings 1985; Sherwood et al. 1990), while sand and cobble beaches support tube-dwelling amphipods (*Corophium spp.*) and algal primary production (Reimers 1971; Levings & McDaniel 1976; Pomeroy & Levings 1980). Other environmental or physical conditions such as water quality (e.g., temperature and salinity), habitat connectivity and tidal dynamics can influence the relative use and importance of habitats in estuaries (Levings 2016).

Estuaries provide habitat to Pacific salmon during their ocean migration as juveniles, providing a transition zone for juvenile salmon to physiologically adapt to the marine environment. This critical stopover habitat for juvenile salmon is where increased foraging opportunities can lead to higher growth rates for juveniles (Naiman & Sibert 1979; Sobczak et al. 2002). Given that predation in marine environments is often size selective (Sogard 1997), elevated growth rates during estuarine residence has been linked to increased survival during the subsequent early-marine phase (Reimers 1971; Pearcy 1992; Bond et al. 2008; Duffy & Beauchamp 2011).

Estuarine dependence and residence time for juvenile fish varies across salmon species, populations and watersheds. In general, Chinook (*Oncorhynchus tshawytscha*)

and chum (*O. keta*) salmon are the most estuary dependent, as they spend the most amount of time in estuarine environments and are often found in association with specific estuary habitats, such as salt-marsh habitat (Healey 1980, 1982; Levy & Northcote 1982; Bottom et al. 2005a; Hering et al. 2010). Juvenile pink (*O. gorbuscha*), sockeye (*O. nerka*) and coho (*O. kisutch*) salmon migrate through the estuary at a faster rate (Simenstad et al. 1982; Simenstad 1983; Pearcy 1992; Thorpe 1994; Moore et al. 2016). Although less research has been conducted on steelhead (*O. mykiss*), in some systems juvenile steelhead have been observed migrating rapidly through estuaries (Moore et al. 2010) while in other systems they remain in estuary habitat for longer time periods (Bond et al. 2008). Salmon populations within watersheds utilize different habitat over varying time-scales. For example, 13 types of estuarine rearing strategies were identified for Chinook salmon utilizing freshwater, estuarine and marine food resources in the Columbia River estuary (Bottom et al. 2008). Last, degree of estuary dependency can vary from estuary to estuary. For example, Chinook salmon were found residing in estuaries across the Pacific Northwest for a range of 1 - 90 days (Miller & Simenstad 1997). Thus, it is generally understood that estuaries support juvenile salmon during migration and that importance of estuaries to salmon populations likely varies across species and watersheds. However, in general this life phase is understudied. For example, Weitkamp et al. (2014) identified 15 times more research on freshwater life-history stages of salmon compared with estuarine life-history.

Forage fish of the NE Pacific also depend on estuarine and nearshore environments during several life-history stages. Pacific herring and surf smelt (*Hypomesus pretiosus*) support commercial, traditional and recreational fisheries in British Columbia (Therriault & Hay 2003; DFO 2014, 2016), and generally make up a large portion of the forage fish community (Bottom & Jones 1990). Herring and smelt are crucial components of the broader marine food web (Therriault et al. 2009). Herring spawn in inter-tidal nearshore environments including estuaries in February and March (Haegele & Schweigert 1985; Lassuy & Moran 1989). Next, larvae are distributed according to water circulation patterns for two to three months, where highest survival rates are thought to occur in nearshore environments (Stevenson 1962). Juvenile herring begin aggregating in estuarine environments at lengths of 25-40mm (Lassuy & Moran 1989), where warmer temperatures, refuge from adverse weather and high food availability provide nursery services (Hourston 1959; Abookire et al. 2000). Immature

herring can often be found in higher abundances within estuarine environments compared to surrounding freshwater or nearshore marine environments (Bottom & Jones 1990; St. John et al. 1992). Juvenile herring may migrate offshore after their first summer or remain in nearshore until maturity (2-5 years). Generally, adults migrate from offshore environments to spawn in the spring, however, many resident populations remain in coastal inlets and bays. In contrast, adult surf smelt spawn on beaches including within estuaries and remain in nearshore coastal habitat year-round (Therriault & Hay 2003; DFO 2014), however, data on the distribution and general biology of surf smelt is sparse. It is unclear how juvenile or adult life-history stages of surf smelt utilize estuarine environments. Similar to herring smelt can be found in high abundances in estuaries along the eastern Pacific during spring and summer months (Bottom & Jones 1990). Although both herring and smelt can be found in high abundances in estuaries, many knowledge gaps remain regarding the use and importance of estuarine habitats for these forage fish species.

Estuaries are dynamic environments where fish distributions can be influenced by a suite of biological and physical factors. Daily changes (i.e. tidal fluctuations) and seasonal changes in physio-chemical characteristics such as turbidity and salinity can influence distribution and abundance of estuarine fishes (Marshall & Elliott 1998; Wagner & Austin 1999; Harrison & Whitfield 2006). For many estuary-dependant species, environmental variables, such as salinity and turbidity, primarily drive fish assemblage spatio-temporal dynamics. However, biotic factors like presence of marine vegetation, such as eelgrass or tidal marshes, can influence estuary use patterns for many species, including juvenile salmon (Semmens 2008; Waycott et al. 2009). Thus, suitability of different estuary regions to fish can be influenced by a dynamic suite of abiotic (e.g., water quality and tide) and biotic (e.g., food-web dynamics, marine vegetation) factors. Models aimed at defining the relationships between abundance of a species with environmental predictors are widely used to explain abundance patterns of fish across estuaries (Maravelias & Reid 1997; Guisan & Zimmerman 2000). For example, França et al. (2012) assessed the variation of fish abundance across habitat types saltmarsh, mudflat and subtidal along with environmental attributes in estuaries along the Portuguese coast. Understanding the relationships between metrics of fish habitat usage (such as by relative abundance) and specific habitat features can result in

prioritization of habitat protection, guide restoration activities, or inform decision-making on proposed industrial developments.

Fish distribution and estuarine use may also be influenced by food-web dynamics. Prey availability and identity in estuaries can limit production in estuaries for juvenile salmon (Healey 1979) and forage fish (Nobriga & Rosenfield 2016). For example, loss of salt-marsh habitat leading to lower productivity of vegetation-associated gammarid amphipod was linked to decreased salmon survival in the Squamish River estuary (Stanhope & Levings 1985). Lower densities of preferred prey results in lower growth rates in laboratory conditions (Volk et al. 1984) and increased risky behavior such as leaving shallow nearshore environments to forage in open-water habitats with higher predation risk (Willette 2001). In addition, changes to food availability and composition were related to declining survival for juvenile long-fin smelt (*Spirinchus thaleichthys*) in the San Francisco estuary (Nobriga & Rosenfield 2016). Food-webs in marine (Ji et al. 2010) and estuarine environments (Nobriga & Rosenfield 2016), are being impacted through anthropogenic and climate mechanisms, thus there is a need to understand the connections between fish and prey dynamics.

This thesis focuses on the estuary of the Skeena River. The Skeena River estuary is fed by the Skeena River watershed (55,000 km<sup>2</sup>), which is the second largest river in British Columbia and supports all species of eastern Pacific salmon, including sockeye, coho, Chinook, pink, chum and steelhead. Juvenile salmon from all species migrate during spring and summer from freshwater to marine environments, through the estuary, where all species have been captured historically (Higgins & Schouwenburg 1973) and in recent years (Carr-Harris et al. 2015; Moore et al. 2015b, 2016; Stantec 2016). High abundances of herring and smelt in the Skeena River estuary have been captured during spring and summer (Higgins & Schouwenburg 1973; Moore et al. 2015a), however many uncertainties exist surrounding their distribution and use of estuary habitats. Recent research has demonstrated the widespread use of estuary habitat by juvenile salmon and laid the foundations for understanding the role of estuary habitat for Skeena River salmon. Population-level identification of juvenile Chinook and sockeye salmon found over 40 populations from the Skeena watershed utilizing the estuary (Carr-Harris et al. 2015; Moore et al. 2015b). Estuarine residence in the Skeena River was found to follow similar trends from other estuaries, with 25% of individuals Chinook, coho, pink and sockeye salmon residing at least 33, 22, 30, 5 days in the

estuary respectively (50% of individuals spent 27, 14, 6, 2 days respectively) (Moore et al. 2016). Lastly, certain regions in the Skeena River estuary were found to contain particularly high abundances of most juvenile salmon species. However, knowledge of the factors contributing to the abundance of juvenile salmon in highly used regions are needed to begin to understand the importance of certain habitats or locations in the estuary.

The aim of this thesis was to examine what contributes to the utilization of estuary habitat by juvenile salmon and forage fish. To accomplish this, I sampled fish populations in the Skeena River estuary in 2015 and 2016 alongside sampling of nine abiotic (e.g., salinity, temperature) and two biotic (e.g., marine vegetation, prey abundance) variables. This sampling was part of a long-term research collaboration with the North Coast Juvenile Salmon Monitoring Program, involving Simon Fraser University, Skeena Fisheries Commission (SFC) and Lax Kw'alaams First Nation. As several large-scale industrial developments had been proposed for the Skeena River estuary, this research aimed to provide further clarity about how juvenile salmon use estuary habitat in the Skeena River estuary during a vulnerable life history stage. More generally, this study advanced our understanding about the different dimensions of fish habitat in large-river estuaries.

In Chapter 2, I investigated spatial distribution patterns of juvenile sockeye, coho and Chinook salmon, discovering that salmon abundance is heterogeneous across the estuary. I found that specific locations within the estuary consistently supported higher abundances of juvenile salmon compared with others. I modeled juvenile salmon abundance patterns across the estuary using two approaches. The first approach examined how abiotic variables and marine vegetation explained abundance patterns in the estuary. The second approach used static habitat type descriptors (e.g., eelgrass bed, rocky shore) to model juvenile salmon abundance. By comparing modeling approaches, I demonstrated that models including abiotic and biotic variables better predicted juvenile salmon abundance over solely using habitat type. I also found that different combinations of abiotic and biotic variables explain abundance patterns for each species of salmon. My findings highlight the dynamic and complex nature of estuaries and provide insight into the challenges of characterization of estuary habitat for salmon during environmental assessment and management planning.

In Chapter 3, I examined the potential role of zooplankton abundance in contributing to spatial patterns of abundance for sockeye salmon, coho salmon, herring and smelt in the estuary. I first applied methods from Chapter 2 to model forage fish (herring and smelt) abundance with abiotic and biotic variables using multi-modal inference. I then determined if prey abundance explained abundance patterns of juvenile sockeye, coho salmon, herring and smelt. Specifically, I investigated if general prey abundance along with abundance of highly consumed prey or less consumed prey taxa were associated with fish abundance across the estuary. I predicted that fish distributions would be positively related to highly consumed prey taxa over lesser consumed prey taxa. I found that herring abundance was related to highly consumed prey abundance and less consumed prey abundance. However, sockeye salmon, coho salmon or smelt abundance were not associated with prey abundance in the estuary.

In my concluding chapter (Chapter 4), I discuss the implications of key findings and several challenges while working in dynamic estuary environments. Overall, my research contributes to the growing body of research identifying the factors influencing estuary habitat use for juvenile salmon and forage fish. I outline future research directions to advance our understanding about the potentially key nursery role estuaries play during young life-history stages of fish.

# Chapter 2. The multi-faceted and species-specific determinants of key salmon habitat in a major estuary<sup>1</sup>

## 2.1. Abstract

Assessment of risk to animal populations from human developments often relies on simple habitat descriptions for focal species, yet simple metrics of habitat may not accurately capture a species' true requirements. Understanding the nature of habitat is particularly pressing for estuaries as they are among the most degraded ecosystems globally, but provide critical rearing habitat for many species, including Pacific salmon. While current approaches use simple habitat-type models to assess risk to salmon in estuaries and assume that different species of salmon rely on the same habitat, here we ask – what combination of habitat type and variable abiotic or biotic factors best explain juvenile salmon usage of estuary habitat? We conducted juvenile salmon sampling throughout the Skeena River estuary (British Columbia, Canada) for two years across different habitat types (eelgrass beds, open-water, sandy banks and rocky shores). We compared simple habitat type models to models with more complex abiotic and biotic variables to explain the variability of Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*) and sockeye (*O. nerka*) salmon abundance in the estuary. The combination of variables that best predicted salmon abundance differed across salmon species and models with these variables had greater predictive power than those using habitat type alone. For example, coho and sockeye salmon were more abundant when water was more turbid, but this was not the case for Chinook salmon. Chinook and sockeye salmon used eelgrass habitat more frequently than other habitat types, whereas coho salmon were more abundant in sites with high macroalgae cover. Thus, current approaches of simple classification of estuary habitat used in environmental risk assessment do not reflect the complex nature of salmon habitat preference and the dynamic nature of estuaries. By understanding which abiotic and biotic factors are linked to juvenile salmon abundance, we can better protect and manage those aspects of habitat critical for salmon.

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<sup>1</sup> A version of Chapter 2 is in preparation for journal submission, with coauthors Charmaine Carr-Harris, Michael Arbeider, Samantha Wilson and Jonathan W. Moore

## 2.2. Introduction

Understanding of the nature of habitats that support species of conservation concern and economic importance is a foundation of management and conservation. Many conservation efforts, such as the International Union for Conservation of Nature (IUCN) Red List and Convention of Biological Diversity (CBD), base their mandates on defining and managing for important habitat (CBD 2008; IUCN 2017). However, identifying the specific habitat attributes that support species can be challenging. Recent assessment of Canadian Species At Risk Act (SARA) has revealed that 62.9% of SARA species lack “Critical Habitat” designation (Bird & Hodges 2017). Thus, for the majority of Canadian species at risk, there is no formal definition of important habitat. This lack of definition is in part due to insufficient knowledge of species biology, distribution and habitat use along with limited expertise and funding capacity (Bird & Hodges 2017). Aquatic habitats exemplify this challenge with fluid boundaries and habitat supporting mobile and migratory species utilizing interconnected habitats across rivers, estuaries, watersheds and oceans (Murphy et al. 1989; Fausch et al. 2002; Naiman & Latterell 2005; Nagelkerken et al. 2015; Bird & Hodges 2017).

Given their importance as nursery habitat for fish as well as rapid on-going degradation, estuaries are an ecosystem where understanding habitat is particularly urgent (Kennish 2002; Levin & Stunz 2005). Estuaries are among the most altered habitats in the world (Lotze et al. 2006). For instance, seagrass, a potentially important biogenic habitat that can be found in estuaries, have declined in area by 7% per year over the last two decades (Waycott et al. 2008). This rapid anthropogenic change is concerning given that estuaries may provide nursery habitat for a diversity of fish species (Beck et al. 2001; Able 2005; Nagelkerken et al. 2015). As nursery habitats, estuaries can provide predator refugia and feeding opportunities to larval and juvenile stages of many species (Beck et al. 2001; Able 2005). Accordingly, there is a time-sensitive need to further understand the nature of habitat for species of conservation or management concern to enable prioritization or protection of essential estuary habitats.

One group of fish that rely on habitats in estuaries are Pacific salmon (*Oncorhynchus spp.*) as they migrate from freshwater to the ocean (Weitkamp et al.

2014). As estuaries provide habitat for physiological transition and feeding of juvenile salmon during migration, degradation of this ecosystem may have disproportionately large impacts on salmon populations (Moore et al. 1995; Iwamura et al. 2014; Murray & Fuller 2015). High estuarine productivity supports rapid growth of juvenile salmon, which can increase early marine survival (Beamish et al. 2004; Cross et al. 2008; Duffy & Beauchamp 2011; Weitkamp et al. 2015). Estuary habitat degradation has been associated with decreased survival of salmon and can therefore have population-level consequences for these species (Magnusson & Hilborn 2003; Meador & MacLatchy 2014). Understanding and identifying juvenile salmon estuary habitat is particularly relevant given their enormous economic and cultural importance. Salmon support commercial and recreational fisheries contributing hundreds of millions of dollars to North American economies annually (Kristianson & Strongitharm 2006; BCMOE 2008; Schindler et al. 2010) and sustain indigenous fisheries and cultures (Nesbitt & Moore 2016).

The suitability of different estuary habitats to juvenile salmon is influenced by a suite of factors (Simenstad et al. 2006). These include water quality (salinity, turbidity and temperature), spatial habitat distribution, temporal factors, tidal influences and food web dynamics (Bacheler et al. 2009). Nearshore estuarine vegetation such as eelgrass beds, macroalgae, marshes and riparian vegetation are commonly cited as being preferred habitat for species of juvenile salmon (Levy & Northcote 1982; Shaffer 2004; Quiñones & Mulligan 2005; Hering et al. 2010; McNatt et al. 2016). For example, both Chinook (*O. tshawytscha*) and chum (*O. keta*) salmon distribution is disproportionately associated with eelgrass habitat when other habitats are available (Bayer 1981; Macdonald 1984; Harris et al. 2008; Semmens 2008). Vegetation is hypothesized to provide shelter from predators and supports increased secondary production and increased diversity of prey (plankton and epiphytic fish) (Duggins et al. 1989, 1990; Semmens 2008). Other habitat types such as sand flats (including sand and cobble) also can contribute to food sources for juvenile salmon. Microalgae and trapped detritus found in the interstices support important invertebrate prey such as gammarid amphipods and tube-dwelling amphipods (Levings & McDaniel 1976; Pomeroy & Levings 1980; Levings 1982; Thom et al. 1989). Salmon also use different habitats in estuaries over changing tidal scales and daylight hours (Levy & Northcote 1982; Hering

et al. 2010; Thedinga et al. 2011; McNatt et al. 2016). Thus, the nature of important estuary salmon habitat is complicated and multifaceted.

Different salmon species, size classes, and populations may use estuaries differently (Simenstad et al. 1982; Weitkamp et al. 2014). Juvenile Chinook and chum salmon are generally considered to be the most estuary-dependent species, spending the most time rearing in the estuary, whereas pink (*O. gorbuscha*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon generally migrate through the estuary at a faster rate (Healey 1980; Simenstad 1983; Thorpe 1994; Moore et al. 2016). Along with varying estuary residence times, different species of juvenile salmon have varying habitat and food requirements in the estuary. Juvenile Chinook salmon use a variety of habitats depending on size and population, with subyearling Chinook often spending considerable time in nearshore environments like marshes and sandflats (Dawley et al. 1986; Bottom et al. 2005b; McNatt et al. 2016) while yearling Chinook are known to depend less on nearshore areas, moving into deeper neritic regions (Simenstad et al. 1982). Juvenile chum and pink salmon occupy shallow nearshore habitats within estuaries such as saltmarshes, tidal creeks and intertidal flats, where they feed on small zooplankton like calanoid copepods before moving further offshore (Manzer 1969; Healey 1982; Levy & Northcote 1982; Simenstad et al. 1982). Sockeye and coho salmon generally move directly into deeper neritic habitats upon arrival in the estuary, acting as planktivores and piscivores, respectively (Manzer 1969; Higgs et al. 1995). Thus, there is growing appreciation for different habitat requirements by salmon across species, populations, and locations.

Despite the potential species-specificity and complexity of salmon estuary habitat, juvenile salmon habitat in estuaries is often assessed and designated in terms of coarse categories such as beaches, channels, vegetation, and artificial or ecosystem-engineered habitat (Levings 1985; Murphy et al. 1989; Hosack et al. 2006; Thedinga et al. 2011; Dumbauld et al. 2015; Levings 2016). In Canada, current practices in assessment of potential risks from proposed developments to salmon often rely on classifying habitat importance based on dominant vegetation type (i.e. eelgrass and kelp forests are considered important salmon habitat while open-water habitats are not, (Pacific Northwest LNG, PNW LNG) (Stantec 2015)). This habitat classification enables decision-makers to quantify the risks of a potential development through considering the areal extent of habitat destruction and associated proposed habitat compensation.

Under this 'no net loss' policy, destruction of habitat should be associated with creation of equivalent habitat elsewhere (*Fisheries Act* R.S.C. 1985 c. F-14, s. 35)(Williams 1990). However, analyses have revealed that habitat offsetting efforts, including estuarine compensation efforts, often do not meet stated objectives and that the majority of projects fail to achieve no net loss (Kistritz 1996; Levings & Nishimura 1997; Harper & Quigley 2005; Quigley & Harper 2006; Favaro & Olszynski 2017). Moreover, there is great scientific uncertainty as to whether the classification of habitat truly captures the biological importance of a given area.

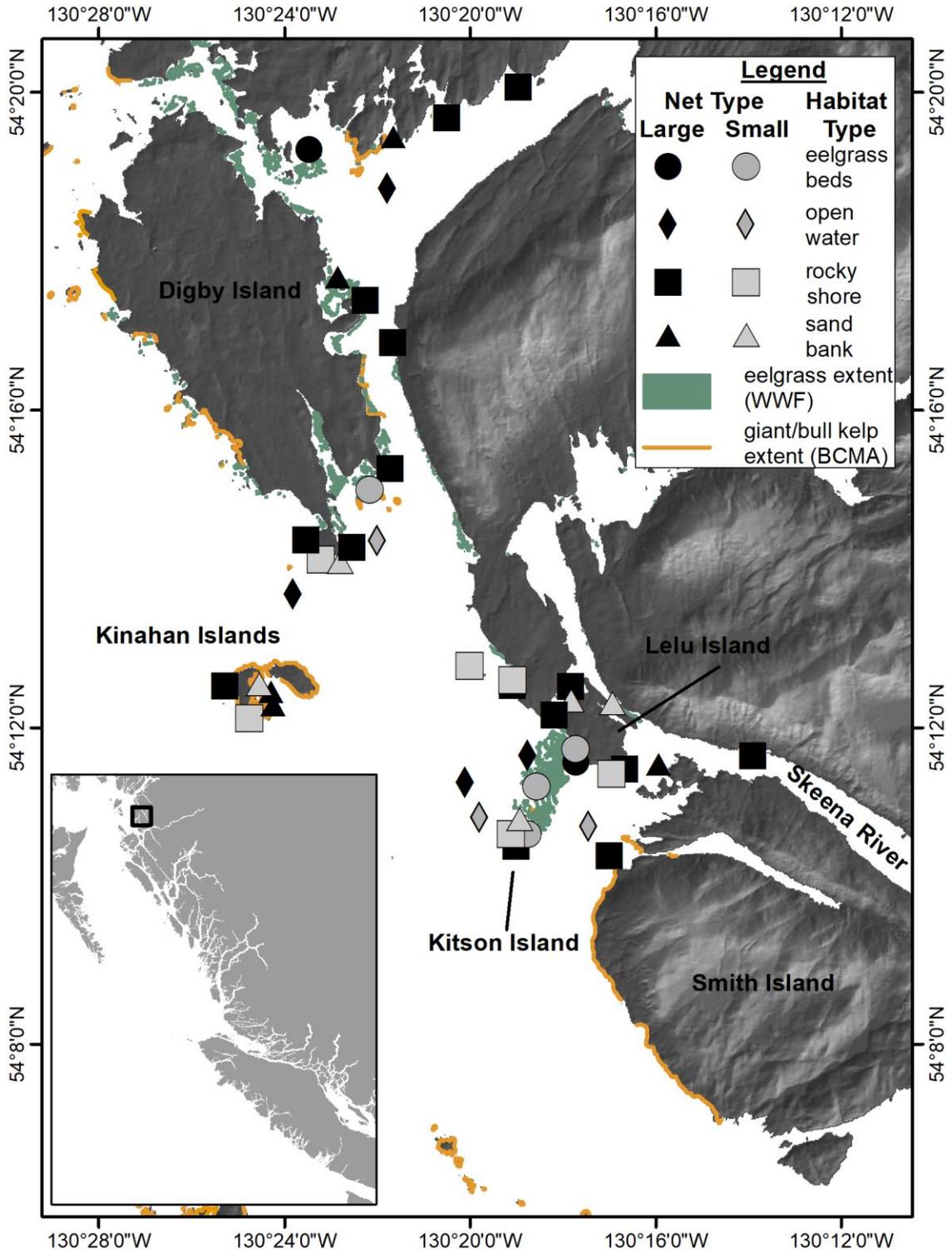
The Skeena River estuary (British Columbia, Canada) is an example of a region where coarse habitat categorizations are used to assess potential environmental risks of development to juvenile salmon. The Skeena River supports all species of eastern Pacific Salmon and is the second-largest salmon-producing watershed in British Columbia. Compared to other major salmon estuaries that have been well studied (i.e. Columbia River and Fraser River estuaries), the Skeena River estuary is relatively pristine with most development contained in one region 15-30km north of the river mouth. Similarly, the extensive network of salmon-producing rivers upstream flow freely, devoid of dams and other impoundments. The Skeena River estuary is currently the proposed location of six Liquefied Natural Gas (LNG) terminals (Province of British Columbia 2014, 2015; Exxon Mobil 2015; Woodside Energy Holdings Pty Ltd. 2015; Pacific Northwest LNG 2016; Pembina Pipeline 2017) at various stages of the provincial and federal environmental assessment processes. Although Petronas recently terminated their investment in the PNW LNG project (Pacific Northwest LNG 2016), the proposed project received both federal and provincial approval and can still be constructed at a later date. PNW LNG provides a timely and relevant example of how the environmental assessment process deals with salmon habitat. The environmental assessments of these industrial projects have relied on coarse habitat classification for their consideration of environmental risks, with eelgrass identified as key salmon habitat. Accordingly, potential risk to salmon is quantified by the areal extent of alteration of eelgrass habitat. Further, habitat mitigation efforts would create new eelgrass habitat to compensate for the eelgrass habitat that will be damaged by the project (Pacific Northwest LNG 2016). The efficacy of such restoration is based on the assumption that eelgrass habitat is an accurate predictor of significant juvenile salmon habitat. An

improved understanding of habitat use by juvenile salmon could clarify the degree of certainty in these current risk assessment approaches.

Here, we aim to quantify estuary habitat use by juvenile salmon in the Skeena River estuary and determine if salmon abundance can be explained by coarse habitat type description, along with other abiotic and biotic factors. In this paper, we address the following questions: a) How are salmon spatially distributed across Skeena River estuary habitats? b) Can juvenile salmon abundance patterns be better explained by simple habitat classifications or by using a more complex suite of abiotic and biotic variables? and c) How do these patterns vary across Chinook, coho, and sockeye salmon? Our study reveals disconnects between current approaches in assessing risk to salmon in estuaries like the Skeena River estuary and scientific understanding of their habitat use.

### **2.3. Methods**

We performed an extensive two-year field study of juvenile salmon and their habitats in the Skeena River estuary in 2015 and 2016. This research is part of a collaborative research program with the Lax Kw'alaams Fisheries Program, Skeena Fisheries Commission and Simon Fraser University examining the estuary phase of juvenile salmon migration in the Skeena River (Carr-Harris et al. 2015; Moore et al. 2015b, 2016). Previous research mapping juvenile salmon use of estuary regions found particularly high abundances of juvenile sockeye, Chinook and coho salmon near the Skeena River mouth, around the Lelu Island and Flora Bank region. This area supports more than 40 populations of sockeye and Chinook from throughout the Skeena River watershed (Higgins & Schouwenburg 1973; Carr-Harris et al. 2015; Moore et al. 2015b) (Figure 2.1). This region also encompasses the location of five of the six LNG developments that have been proposed for the greater Skeena River estuary (Province of British Columbia 2014, 2015; Exxon Mobil 2015; Pacific Northwest LNG 2016; Pembina Pipeline 2017). Our study builds on these previous findings, and addresses finer-scale questions relating to how salmon are using specific estuary habitat within the proposed region.



**Figure 2.1.** Map of sampling locations according to habitat type and net type used across the Skeena River estuary. Extent of kelp (British Columbia Marine Conservation Analysis Project Team 2011) and eelgrass (Forsyth et al. 1998; WWF- Canada 2009; Ambach & Casey 2011; Ocean Ecology 2013) habitat shown.

### 2.3.1. Study System

Our study area in the Skeena River estuary is within the traditional territories of the Coast Tsimshian First Nations. The Skeena River is approximately 570 km long with a drainage area of 55,000 km<sup>2</sup> meeting the ocean near Prince Rupert, British Columbia (54.13°N, -130.10°N), where six species of Pacific salmon transition through the estuary on their way from freshwater rearing habitats out to the ocean phase of their life cycle (Gottesfeld & Rabnett 2008). The estuary extends from approximately 75 km upstream of the river mouth into Chatham Sound. Peak abundances of juvenile pink and chum salmon are observed in the Skeena River estuary in early spring (March - May), while the peak migration for juvenile sockeye, coho and Chinook salmon occurs between mid-May and mid-June. Some individuals of all species have been captured in the estuary as late as July (Carr-Harris et al. 2015). The spring freshet, a period with elevated river discharge and turbidity, generally occurs annually between May 19 - June 29 (Hoos 1975), but timing and discharge vary according to yearly temperatures, snowpack and spring flooding events (Hoos 1975).

The mouth of the Skeena River is divided into three channels, extending south to Ogden and Grenville Channels and northwest through Chatham Sound, where it meets freshwater from the Nass River. Our sampling region is near the river mouth in the northern-most channel, Inverness Passage, extending north past Prince Rupert, and west to Kinahan Islands (Figure 2.1). This region is characterized by a mesohaline to polyhaline salinity gradient. Although there are narrow bands of salt grass, intertidal macroalgae and kelp beds (Figure 2.1), the primary habitat types are mud and sand banks, rocky shores and eelgrass beds (Table 2.1). Most of the eelgrass in the Skeena River estuary (50-60%) is located on Flora Bank, which is a sandy area approximately 2.3 km by 1.7 km (Hoos 1975).

**Table 2.1 Physical and biological description of habitat types sampled. Adapted from Levings 2016.**

Habitat	General geomorphological or biological features
Eelgrass beds	Gently sloping shorelines, mid to lower tidal elevation. Floating blade length ranges to about 1m above the substrate at high tide. Species present: <i>Zostera marina</i> (dominant) and <i>Zostera latifolia</i>
Rocky shore	Shoreline steep and linear along fjords and ice-scoured estuaries, sometimes solid rock boulders >26 cm in diameter. Microalgae often present.
Sand banks	Combination of sand and mud flats, shoreline typically developed into banks with grain size between 0.062-2.00 mm. Gravel and cobble with deltaic or sometimes curved shorelines can occur, grain size 0.2-26 cm.
Open water	Neritic habitat located >200m from shore

### 2.3.2. Fish Sampling

We sampled fish in the Skeena River estuary during the peak smolt migration period from April to mid-July 2015 and 2016. In 2015, we sampled 25 sites with a large purse seine every two weeks, of which a subset of eight sites were sampled every week. In 2016, the same subset of eight sites were sampled every week, while a smaller purse seine was used to survey habitat closer to shore every two weeks at an additional 18 sites (Figure 2.1). Sites were selected to represent the four most available habitat types: eelgrass beds, rocky shores, sand banks and open-water habitat (Table 2.1). We employed a stratified sampling design to select sites with varying vegetative cover (eelgrass or not), exposure, proximity to shore (nearshore and open-water habitat) and distance from the river mouth (salinity gradient across the estuary). Although we collected all species of juvenile salmon, different early-season sampling dates between years resulted in inconsistent sampling for chum and pink salmon. Therefore, we focused on sockeye, coho and Chinook salmon for analysis.

We deployed the larger purse seine (9.1 m deep by 73.2 m long, 5.1 cm webbing at the tow end, 1.3 cm webbing at the bunt) using a 3 m skiff to tow the bunt end away from a larger vessel, holding the net open into the tidal current for 5 min per set. The smaller purse seine net (5.5 m deep by 15.2 m long, 1.3 cm webbing at the tow end,

0.64 cm webbing at the bunt end) was deployed using two 3 m skiffs with the net held open for 2.5 min per set. The mesh sizes from both nets were small enough to retain coho, Chinook, and sockeye salmon smolts.

### **2.3.3. Measuring Abiotic and Biotic Variables**

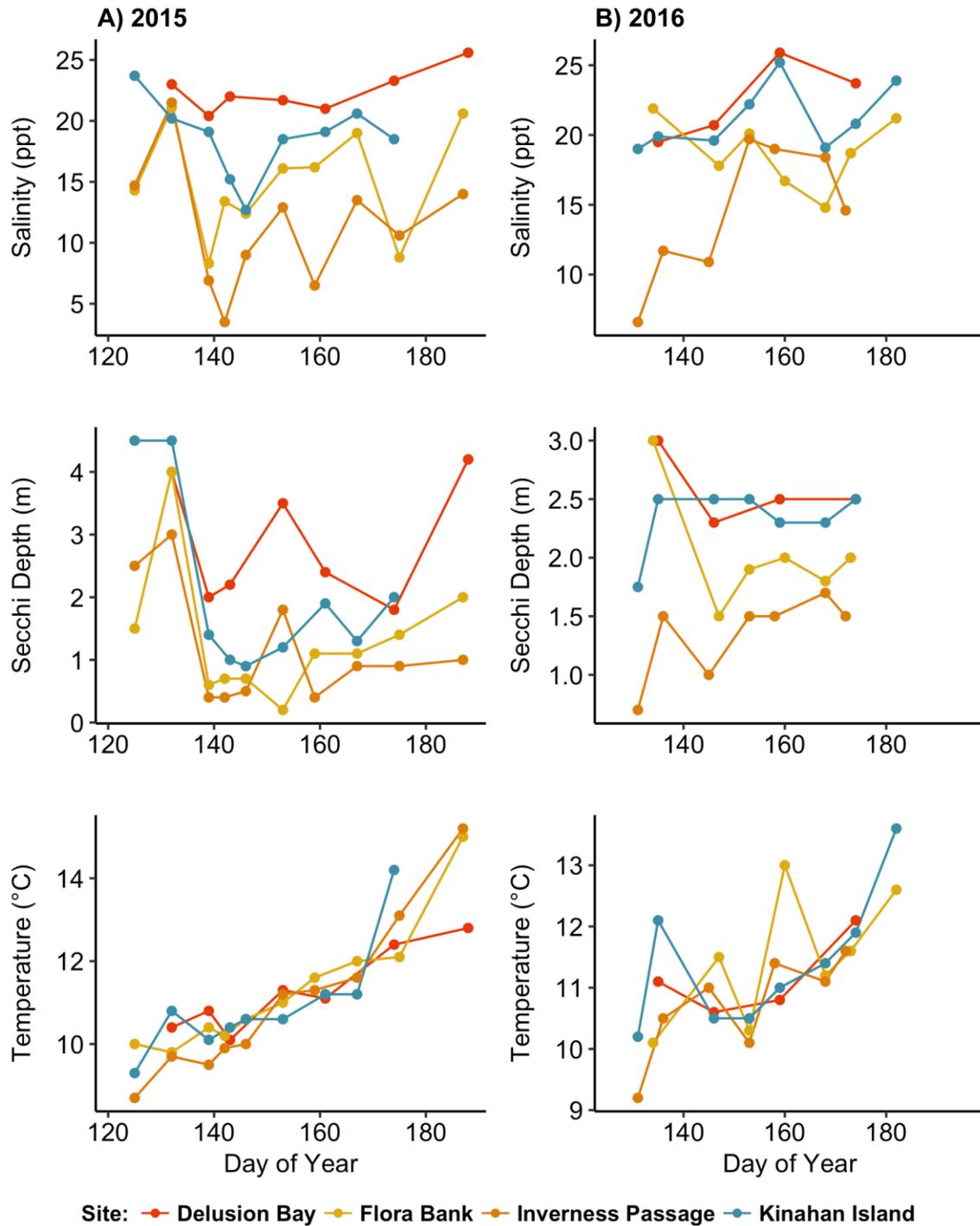
We collected data from various habitat and environmental variables known to influence estuarine fish habitat utilization such as water quality, and tidal variables along with vegetative and spatial attributes (Bacheler et al. 2009). We measured salinity, temperature, turbidity and depth after each set (see Table 2.2 for collection details). At each sampling location, salinity and temperature were recorded at a depth of one meter. Water quality attributes (salinity, temperature and turbidity) were variable across sites and time between and within sampling years (Figure 2.2). For each site, we determined the distance from the river (measured from a fixed point at the river mouth, 54.137945° N 130.116621° W, to the site coordinates) and proximity to shore (measured from site center to the nearest point on shore). Although all sites in the study area are located within a relatively unexposed part of the coast line, exposure was assigned a categorical variable (high, moderate or low) based on exposure to Chatham Sound given the predominant westerly wind-direction during the sampling period. We used data collected at the Prince Rupert, BC (Station Number 9354, 54.317° N 130.324° W) tide station located within our study area to generate tide height and tide phase. To capture both tidal phase (incoming and outgoing) and relative strength of the tide phase, the slope of a line tangent to the daily tide curve at the time of sampling was used to represent tide stage. This slope represents the rate of tidal rise or fall at the time of sampling.

We surveyed benthic substrate along three parallel 20 m transects at each site with an underwater camera (HD Sea-Drop 1080p Sea-Viewer Inc.). Camera surveys were conducted in July during the period of highest water visibility. The camera was submerged at the start of each transect and slowly drifted with the current. A metal weight suspended from the camera ensured that the camera drifted approximately 0.3 m off the ocean floor. We analyzed video footage using Coral Point Count with Excel extensions (CPCe) to determine percent cover of substrate: sediment, rock, invertebrate, eelgrass and macroalgae (Leonard & Clark 1993; Ninio et al. 2003; Kohler & Gill 2006; Guinan et al. 2009). From each of three video transects, 20 still frames were randomly selected at a minimum time of two seconds apart, ensuring that frames did not overlap.

To estimate benthic composition, we randomly overlaid 30 points on each frame (1800 points per site) and identified the substrate type under each point, and calculated the percent cover (number of points with a given substrate type/total number of points) of the different bottom substrate types at each site. We determined 30 points to be a suitable characterization of the substrate by taking the mean number of points used to calculate percent cover of benthic substrate in similar studies (Miller & Müller 1999; Ninio et al. 2003; Stevens & Connolly 2005; Lam et al. 2006; Guinan et al. 2009).

**Table 2.2 Abiotic and biotic attributes used to model salmon abundance in the estuary, given with units and method of measurement.**

Attribute	Unit	Method of measurement	Range (Mean)
<u>Water quality</u>			
salinity	ppt	YSI (Pro 2030)	3.5 - 25.9 (19.1)
temperature	°C	YSI (Pro 2030)	8.7 - 15.9 (11.6)
turbidity	meters	secchi disk depth	0.2 - 7.0 (2.1)
<u>Tidal attributes</u>			
tide height	meters	tide height at station 9354	0.5 - 6.5 (3.9)
tide stage	n/a	slope of tangent line at sampling event during daily tidal cycle	-0.02 - 0.02 (NA)
<u>Spatial attributes</u>			
distance from river mouth	kilometers	measured from the river mouth to site coordinates (shortest swimming route)	9.2 - 33.2 (18.2)
distance to shore	meters	measured from the site to closest point of shore contact	17.3 - 1192.1 (205.0)
exposure	n/a	categorical variable	1, 2, 3
depth	meters	depth sounder	2.9 - 63.1 (11.2)
<u>Vegetative variables</u>			
eelgrass percent cover	mean % cover	point count analysis of video	0 - 70.0 (5.9)
macroalgae percent cover	mean % cover	point count analysis of video	0 - 87.2 (5.9)



**Figure 2.2.** Water quality variables (salinity, secchi depth, temperature) across sampling date (April 30 = day of year (DOY) of 120, May 20 = DOY 140, June 9 = DOY 160, July 19 = DOY 180) in A) 2015 and B) 2016 from four sites in the Skeena River estuary. Sites Delusion Bay and Kinahan Island are more distal to the river outflow, while Flora Bank and Inverness Passage are more proximal to the river outflow.

### 2.3.4. Modeling Salmon Abundance

We modelled sockeye, coho and Chinook salmon abundance patterns across the estuary as a function of various habitat features and environmental attributes. We described estuary habitat for juvenile salmon using both a fine-scale and coarse-scale approaches. Our fine-scale approach (A) modeled salmon abundance patterns for each species separately, with various abiotic and biotic variables. We used information theoretic criterion (AIC) to choose the combination of abiotic and biotic variables that had the most support for each species. Our coarse-scale approach (B) modeled salmon abundance for each species separately, using four basic habitat types available to juvenile salmon: eelgrass beds, sandy banks, rocky shores and open-water habitat. Finally, we compared top models from approach A with models from approach B using AIC. Below we describe our quantitative approach in more detail.

To develop predictive models for both approaches, we used (CPUE) as a measurement of salmon abundance. While the CPUE values of the large seine net remained equal to the original catch data, relative abundance from the smaller seine net was standardized to the larger purse seine. We calculated CPUE for small net by multiplying catches by the large net area (length by width) and net tow duration, and then dividing by the area and tow duration of small net.

All modeling was performed using the R package `glmmTMB` (Magnusson et al. 2016), which estimates parameters by maximizing likelihood. All models included site and sampling period as random effects to account for any spatial and temporal covariation (Table A.2.). Including these random effects accounts for extraneous variation that may have influenced the associations we were actually testing. Collinearity of all variables was low with variance inflation factors (VIF) less than three (Zuur et al. 2009, 2010). Global models for each species were fit with commonly used distributions for count data (Poisson, Negative Binomial (NB1) and Negative Binomial 2 (NB2) parameterizations (Guisan & Zimmerman 2000)) and assessed with Akaike's Information Criterion corrected for small sample size (AICc) to affirm the most suitable parameterization (NB2 for sockeye salmon and NB1 for coho and Chinook salmon) (Akaike 1973). All continuous predictors were centered and scaled (subtracted the mean

from each observation and divided by two standard deviations) to facilitate meaningful comparisons of effect sizes among predictors (Grueber et al. 2011).

Model approach A investigated which combination of abiotic and biotic variables (Table 2.2) was most important in explaining salmon abundance across the estuary using multi-model inference. Since all abiotic and biotic variables were selected based on *a priori* hypotheses as outlined by previous studies (Straty & Jaenicke 1980; Pearcy 1992; Semmens 2008; McNatt et al. 2016; Roegner et al. 2016), they were included in the modeling selection process. Due to inconsistent depth sampling resulting from technical problems, we removed depth from the final variable list as it substantially reduced the number of sampling events with complete covariate sets. We fit models with all possible combinations of variables, including net type and sampling year as fixed effects (4096 models total per species), ranked them using AICc and performed model averaging on a  $\Delta$ AICc less than two candidate model set. We quantified the importance of each predictor variable based on cumulative Akaike weight of the model candidate set (AICc less than two), creating a measure of Relative Variable Importance (RVI) (Burnham & Anderson 2002). RVI values across variables range from 0 to 1 as Akaike weights sum to one within a candidate model set. A top model(s) for each species was identified as the model with the fewest predictor variables chosen from the set of models with a  $\Delta$ AICc less than two (Burnham & Anderson 2002; Bolker 2008). We used model averaged coefficients and RVI values to make inferences about abiotic and biotic variables described salmon abundance patterns. Top models (most parsimonious models with  $\Delta$ AICc less than two) were used to compare modeling approaches (A or B) with AICc.

In approach B, we examined the degree to which coarse-scale habitat types explained the abundance of each salmon species in the estuary. Salmon abundance was modeled with a categorical variable representing habitat type (eelgrass beds, sandy banks, rocky shores and open water) and we tested the inclusion of net type and sampling year as fixed effects with AICc model selection. This approach is analogous to common practices in environmental impact assessment and mitigation. For each species, a top model (most parsimonious within  $\Delta$ AICc less than 2) was identified.

We determined which approach (A or B) was more suitable to explain juvenile salmon abundance by ranking top models from each approach with AICc for each

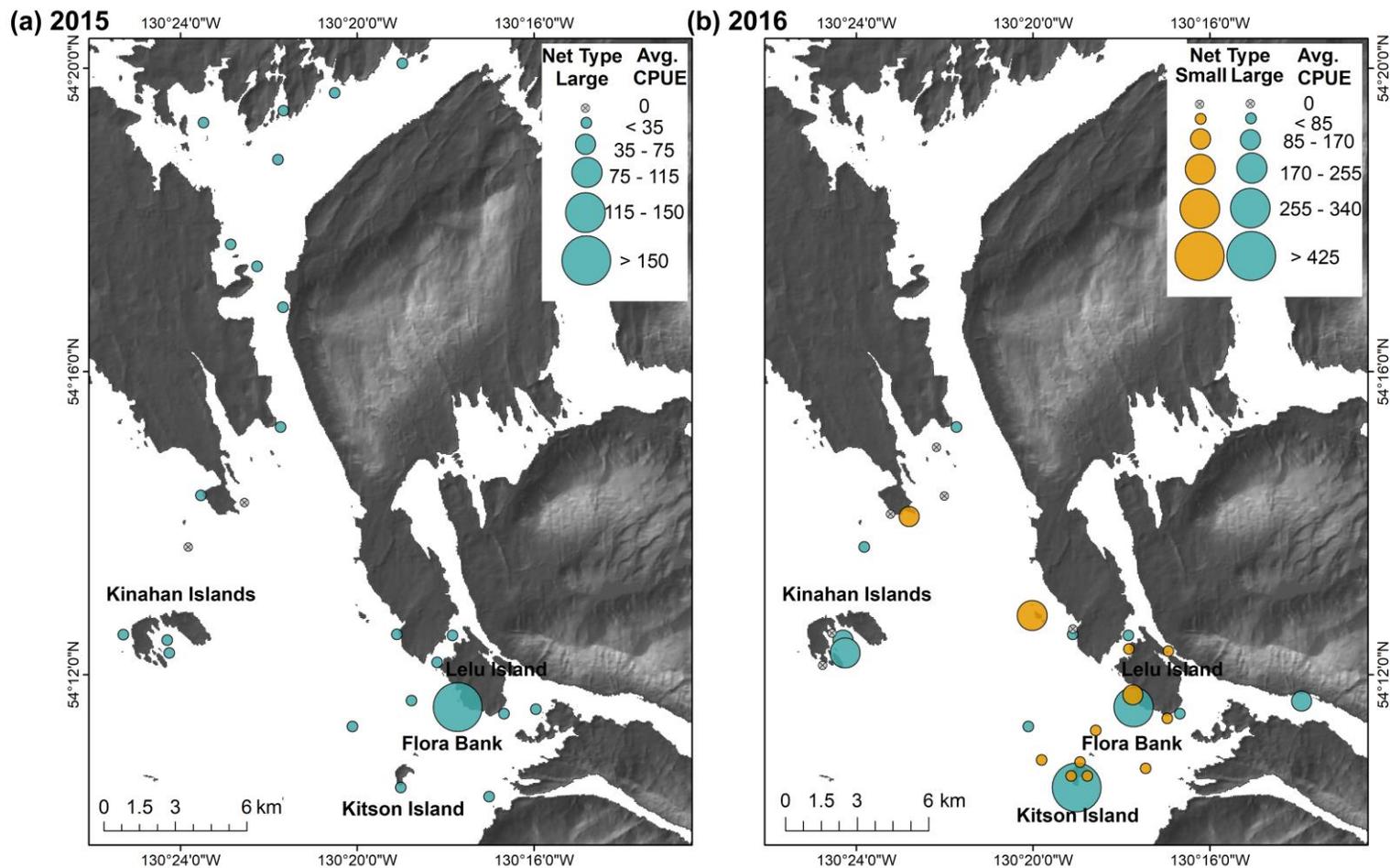
salmon species. Given the uncertainty surrounding the use of  $R^2$  (coefficient of determination values) in GLMM modeling, we visually assessed the predicted versus observed CPUE relationships of top models for each species separately and used a Pearson correlation coefficient to determine the predictive capability of our models. We performed all statistical analysis using R 3.3.1 (R Core Team 2016).

## **2.4. Results**

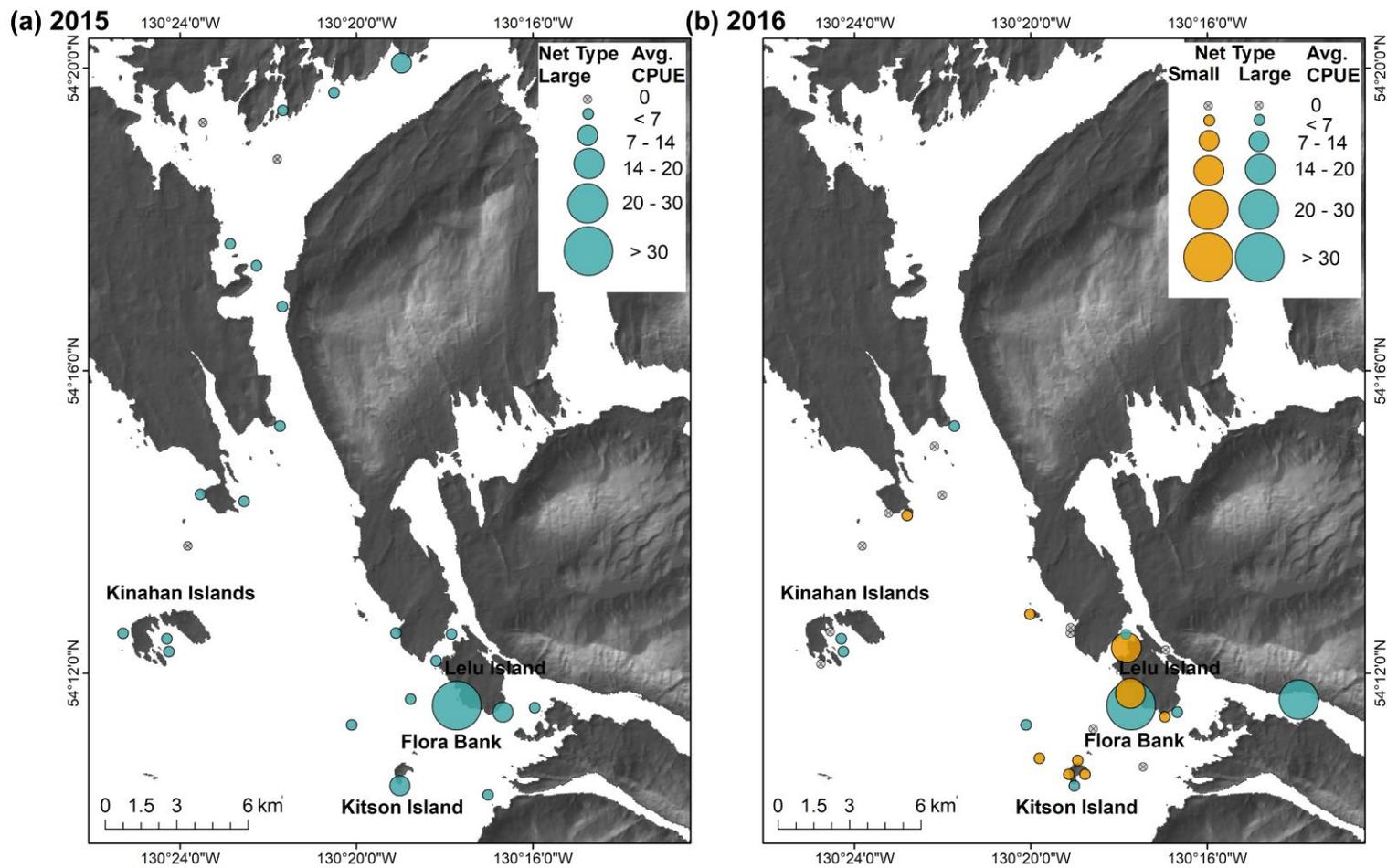
### **2.4.1. Patterns of Spatial Distribution**

We caught 1746 sockeye, 683 coho and 58 Chinook salmon in 2015, and 8621 sockeye, 723 coho and 51 Chinook salmon in 2016. The larger catch of juvenile sockeye in 2016 is not surprising due to higher numbers of sockeye smolts out-migrating from major Skeena River sockeye salmon populations because of higher spawner recruitment two years before (parent generation). The peak catches of sockeye, coho and Chinook salmon occurred during the six-week period between May 8 and June 5 in both 2015 and 2016 (Figure A.1).

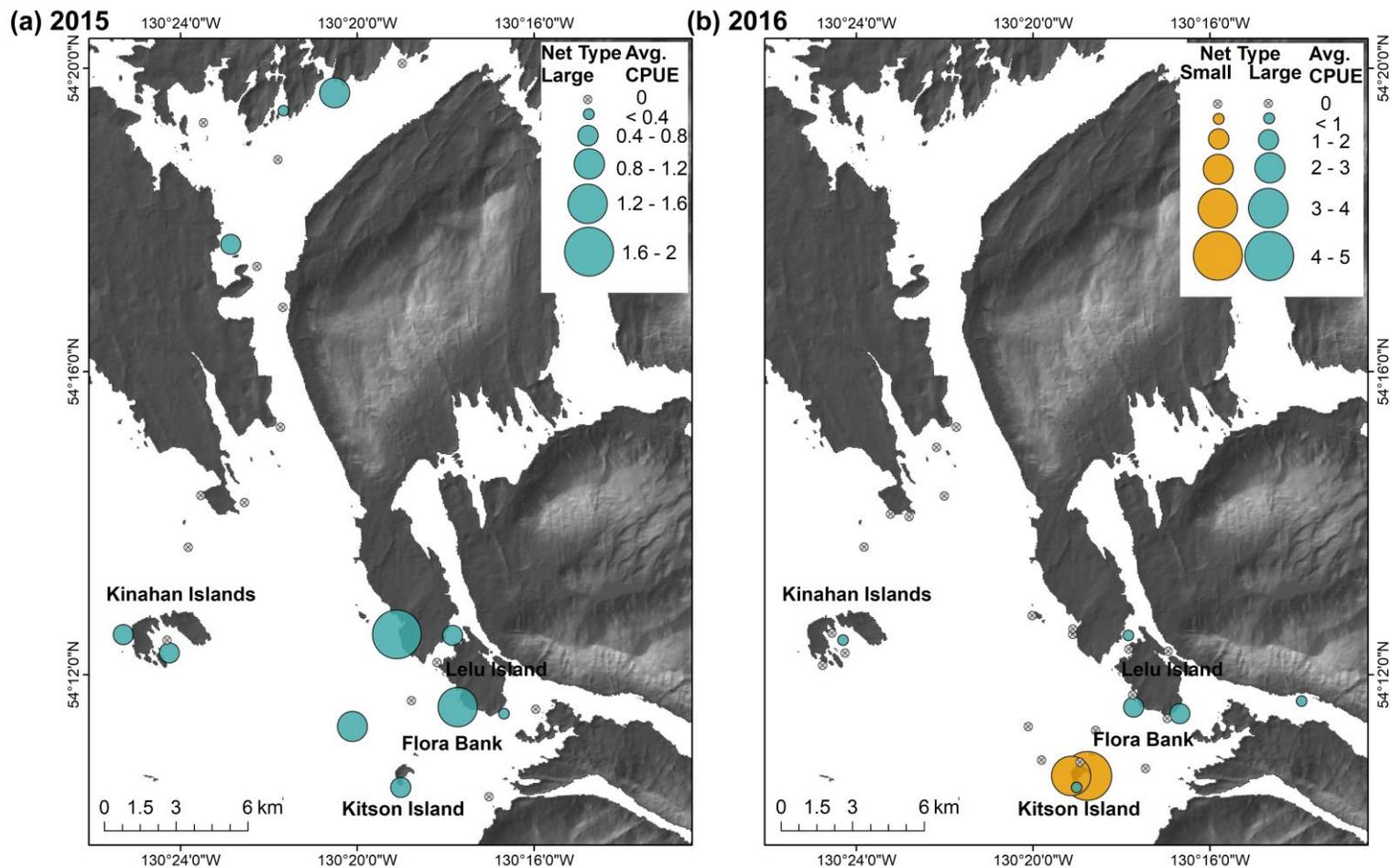
Within sampling years, fish were unevenly distributed across the estuary with higher catches (CPUE) of salmon consistently found at some sites compared to others (Figure 2.3 - 2.5). Specifically, the relative abundance of all salmon species during the peak smolt out-migration (May 8 - June 5) was highest at sites surrounding Lelu Island including Flora Bank and Kitson Island. Comparing the grouped mean CPUE of sites around Flora Bank and Kitson Island (including Porpoise Harbour, Inverness Passage and Agnew Bank) to elsewhere in the estuary illustrates these differences in salmon abundances across space. In 2015, CPUEs for sockeye, coho and Chinook salmon were 8, 5 and 3 times higher, respectively, for the Flora Bank region compared to other sites on average, and 2, 3 and 19 times higher, respectively, in 2016. At the site level, we found the highest abundances of salmon at Flora Bank in both years using the big purse seine. On average, the CPUE of sockeye, coho and Chinook salmon in 2015 were 38, 8 and 5 times higher, respectively, at the Flora Bank big purse seine site alone compared to other sites during peak migration. Higher abundances were also found at the Flora Bank big purse seine site in 2016, where we collected 5, 9, and 2 times more sockeye, coho and Chinook salmon, respectively, on average compared to other big purse seine sites in the estuary.



**Figure 2.3.** Mean sockeye salmon abundance during peak migration (May 8 - June 5) at sampling locations in the Skeena River estuary in a) 2015 and b) 2016. Colours indicate the different net types (orange = small purse seine, blue = large purse seine). Legend showing point area representative for average sockeye salmon CPUE abundance. Point area represents different average sockeye salmon CPUE in 2015 and 2016.



**Figure 2.4.** Mean coho salmon abundance during six week peak migration (May 8 - June 5) at sampling locations in the Skeena estuary in a) 2015 and b) 2016. Colours indicate the different net types (orange = small purse seine, blue = big purse seine). Legend showing point area representative for average coho CPUE abundance.



**Figure 2.5.** Mean Chinook salmon abundance during six week peak migration (May 8 - June 5) at sampling locations in the Skeena estuary in a) 2015 and b) 2016. Colours indicate the different net types (orange = small purse seine, blue = big purse seine). Legend showing point area representative for average Chinook CPUE abundance. Point area represents different average Chinook salmon CPUE in 2015 and 2016.

## 2.4.2. Linking Salmon Abundance with Abiotic and Biotic Variables (Approach A)

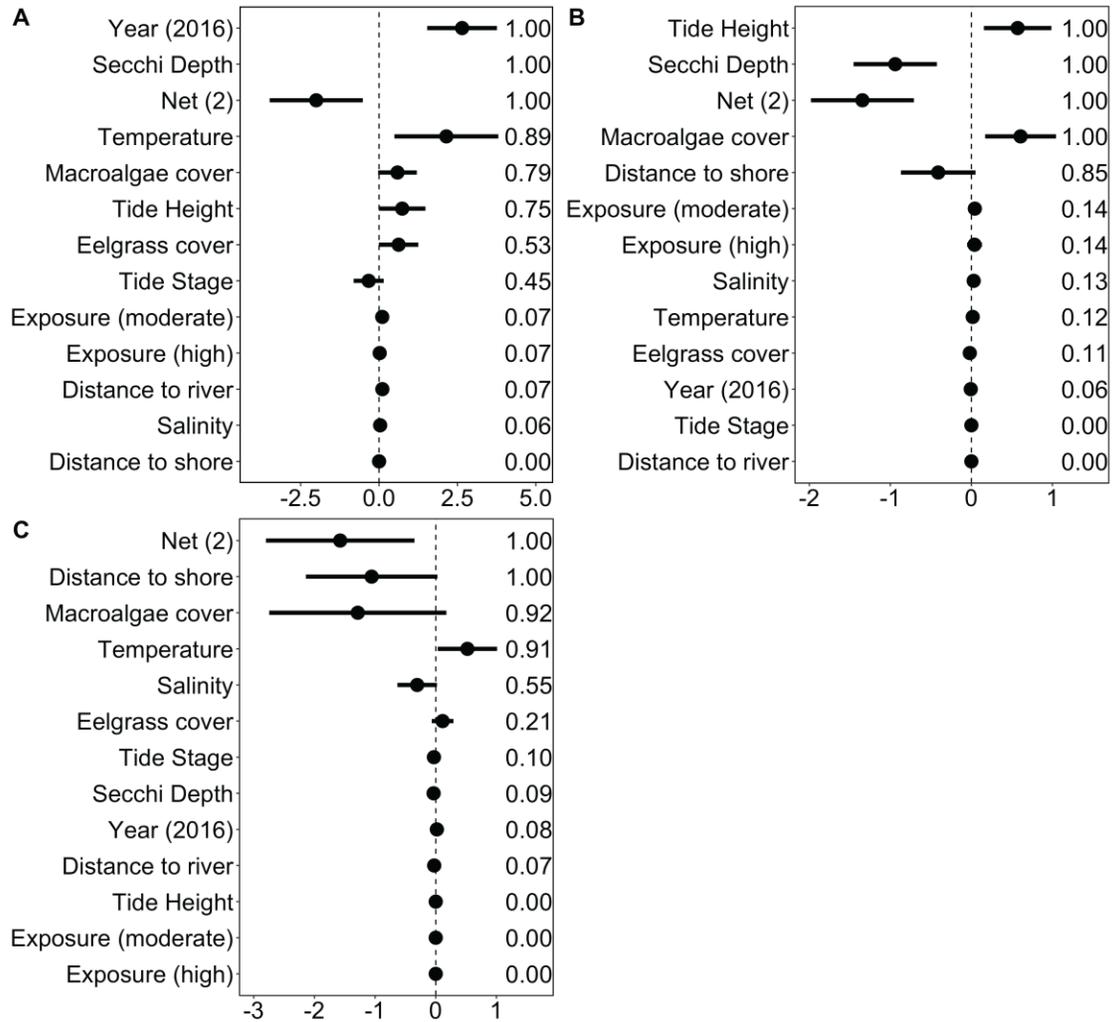
Different combinations of abiotic and biotic variables best explain the abundance of each salmon species (Figure 2.6, Table A.1). Net type (large or small purse seine) had the highest RVI score (Figure 2.6) and was present in every top model (Table A.1) for sockeye, coho and Chinook salmon, indicating we caught fewer salmon with the smaller purse seine net than the larger purse seine net.

Model-averaged coefficients suggests that increased turbidity and temperature increased sockeye salmon abundance (95% confidence interval (CI) does not cross zero) (Figure 2.6a) We also caught more sockeye salmon in 2016 than in 2015. Year (1.00), turbidity (1.00) and net (1.00) ranked highest in relative variable importance (RVI) and were included in every model within  $\Delta\text{AICc} < 2$  candidate set (Table A.1). Temperature (0.89), macroalgae cover (0.79), and tide height (0.75) had relatively high RVI scores, indicating their importance in explaining sockeye abundance. Eelgrass cover was also present in six of the 11 models within the 2  $\Delta\text{AICc}$  candidate set and had an RVI of 0.53. Although tide height, macroalgae and eelgrass cover appear to have positive relationships with sockeye salmon abundance, these relationships are uncertain (Figure 2.6a). Other abiotic variables had lower RVI scores (tide stage (0.45), exposure (0.07), distance to river (0.07), salinity (0.06), distance to shore (0.00)) and were not present or common within the 2  $\Delta\text{AICc}$  candidate set for sockeye salmon.

Higher abundances of juvenile coho salmon were associated with higher tide height, turbidity and macroalgae cover (Figure 2.6b). Tide Height (1.00), secchi depth (1.00), net type (1.00) and macroalgae cover (1.00), had the highest RVI scores. We found distance to shore to be another important predictor for coho salmon as it was present in all models within  $\Delta\text{AICc} < 2$  (except the top model) (Table A.1) and had a relatively high RVI score (0.85). Although proximity to shore appears to be associated with higher abundances of coho salmon, this relationship is uncertain. Exposure (.14), salinity (0.13), temperature (0.12) and eelgrass cover (0.11), tidal stage (0.00) and distance to river mouth (0.00) had lower RVI scores and were uncommon or absent from

the  $\Delta AICc < 2$  candidate set, thus appear to be less important in explaining juvenile coho salmon abundance.

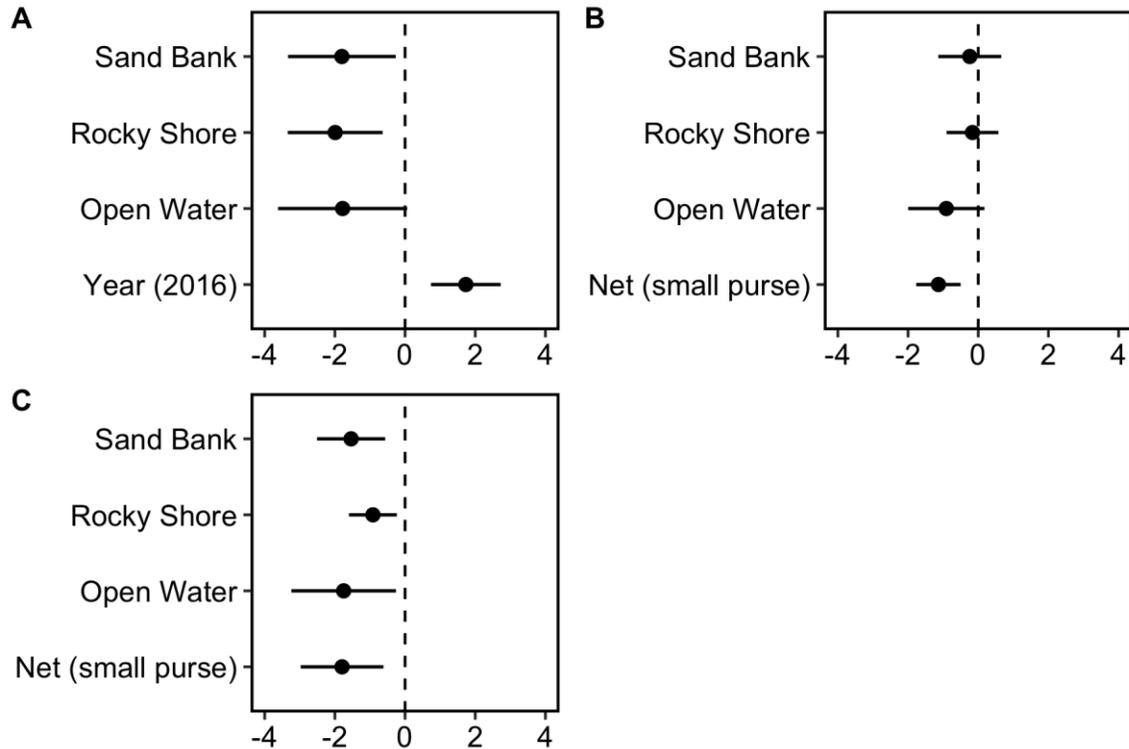
Increased temperature was associated with higher abundances of Chinook salmon (Figure 2.6c). Although it appears we caught less Chinook salmon with increasing distance to shore and macroalgae cover, these results are uncertain. Net (1.00), distance to shore (1.00), macroalgae cover (0.92) and temperature (0.91) ranked highest in RVI. Given its high RVI score (0.55) and appearance in five out of ten models within  $\Delta AICc < 2$  (except the top model) (Table A.1), salinity may be an important variable in explaining Chinook salmon abundance. The variables eelgrass cover (0.21), tidal stage (0.10), secchi depth (0.9), year (0.8), distance to river mouth (0.7), tide height (0.00) and exposure (0.00) had lower RVI scores and were not found frequently in  $\Delta AICc < 2$  candidate set, thus are likely less important variables in predicting juvenile Chinook salmon.



**Figure 2.6.** Standardized model-averaged coefficients (points) and 95 % confidence intervals (bars) used to describe salmon abundance (A) sockeye, B) coho and C) Chinook) presented in decreased order of relative variable importance (RVI). RVI values shown on rightmost of each panel. Coefficients are related to the (log) mean of normalized CPUE. Parameter year (2016) compares catches to the sampling year 2015 as a baseline, the small purse seine net is being compared to the large purse seine net, and low exposure is used as a reference to compare moderate and high exposed sites.

### 2.4.3. Linking Salmon Abundance with Habitat Type (Approach B)

We consistently found higher abundances (CPUE) of juvenile sockeye and Chinook salmon in eelgrass beds compared to other habitat types (Figure 2.7a and 2.7c). Coho salmon were caught in all habitat types equally (Figure 2.7b).



**Figure 2.7.** Standardized parameter estimates (dots) and 95% confidence intervals (bars) from top models (most parsimonious within  $\Delta AICc$  less than 2) for modeling approach B – habitat type top models for A) sockeye, B) coho and C) Chinook salmon. Open-water, sand banks and rocky shores habitat types are compared to the eelgrass bed habitat type as a baseline (dashed line). Coefficients are related to the (log) mean of normalized CPUE.

### 2.4.4. Comparing Modeling Approaches

Model selection in approach A produced one top model for coho and Chinook salmon along with two equally supported top models for sockeye salmon (Table A.1, Figure A.2). Comparison of models from approach A (fine-scale) and approach B (coarse scale) shows that top models (most parsimonious model within a  $\Delta AICc < 2$ ) from modeling approach A had more support for all species (Table 2.3). The same results

were found when comparing habitat type models from approach B across two candidate sets from approach A – 1)  $\Delta\text{AICc} < 2$  and 2) models representing all possible model combinations of the global model (Table A.2). Top habitat-type models (approach B) for sockeye, coho and Chinook salmon had a  $\Delta\text{AICc}$  score of 12.5, 30.5 and 3.8, respectively when compared to all models from both  $\Delta\text{AICc} < 2$  and all possible model combinations candidate sets. When compared to all possible combinations of models, habitat-type models (approach B) ranked 481, 3084, and 72 out of 4096 models total for sockeye, coho and Chinook salmon respectively. Furthermore, predicted versus observed CPUE values were more correlated for model approach A across all species (Table 2.3, Figure A.3). Correlation coefficients from predicted versus observed values from sockeye models were 0.3 and 0.43 from approach A compared with 0.13 from approach B. For coho, correlation coefficients were 0.46 and 0.34 and Chinook coefficients were 0.23 and 0.18 for approach A and B, respectively. This suggests that the modeling approach using abiotic and biotic variables have a higher predictive capability.

Predicted versus observed relationships for both approaches show significant amounts of scatter and deviation away from a 1:1 linear relationship for all species, particularly around low predicted CPUE values (Figure A.3). These findings suggest that although our more complex habitat approach fit the abundance data better, there remains substantial unexplained variance in salmon abundance.

**Table 2.3. AICc summary for comparison of top models (most parsimonious within  $\Delta\text{AICc}$  less than 2) from modeling salmon abundance across both approaches A) abiotic and biotic variable modeling and B) habitat type modeling. All models contain year and sampling period as random effects.**

Salmon Species	Model Approach	Model Parameters (Fixed Effects Only)	<sup>a</sup> k	<sup>b</sup> $\Delta\text{AICc}$	<sup>c</sup> r
Sockeye	A	year + net + secchi depth + temperature + tide height	7	0	0.30
	A	year + net + secchi depth + tide height + macroalgae cover	7	0.4	0.43
	B	year + site type	4	10.9	0.13
Coho	A	net + secchi depth + macroalgae cover + tide height	6	0	0.46
	B	net + site type	4	29.2	0.34
Chinook	A	net + distance to shore + macroalgae cover	5	0	0.23
	B	net + site type	4	2.3	0.18

<sup>a</sup> k = number of model parameters. <sup>b</sup>  $\Delta\text{AICc}$  = change in AICc score from top model. <sup>c</sup> r = pearson correlation coefficient of predicted versus observed CPUE.

## **2.5. Discussion**

### **2.5.1. Linking Juvenile Salmon Abundance with Estuary Habitats and Processes**

Spatial distributions of juvenile salmon in the estuary illustrate that some regions of the estuary are more highly used than others. All species of salmon were found in higher abundances on the Flora Bank region around Lelu Island during juvenile salmon migration (Figure 2.3 - 2.5). For example, sockeye and coho salmon were found to be on average 8 and 5 times more abundant in 2015 in this region, and 2 and 3 times more abundant in 2016, compared to other sites in the estuary. This trend was observed across two years and for all three species of juvenile salmon.

We found that different combinations of abiotic and biotic variables were important descriptors of estuary habitat for the different species of salmon. Environmental attributes such as turbidity are known to influence juvenile salmon distribution across estuaries (Straty & Jaenicke 1980). In the Skeena River estuary, coho and sockeye salmon tended to be caught in higher numbers in more turbid water; however, turbidity did not explain Chinook abundance patterns. During the peak salmon migration period in May and June, estuary turbidity is heavily influenced by river discharge, as colder snow-melt freshets bring high concentrations of suspended sediments to create a large river plume (Hoos 1975; Levy & Northcote 1982; Simenstad et al. 1982). Although extreme turbidity may have negative effects on foraging success of fish in freshwater (Sigler et al. 1984; Berg & Northcote 1985; Breitburg 1988), high turbidity waters are also a refuge from predators. Most of the fish and birds that prey on juvenile salmon are visual predators, and highly turbid estuary waters provide refuge to juvenile salmon by decreasing sight distance, thus reducing the chance of being seen and eaten (Blaber & Blaber 1980; Simenstad et al. 1982; Gregory & Levings 1996, 1998; Phillips et al. 2017). Juvenile fish, including salmon, sometimes increase risky behaviour in turbid conditions by increased feeding activity, migration rate and use of higher-risk offshore habitat (Ginetz & Larkin 1976; Gradall & Swenson 1982; Gregory 1993; Gregory & Northcote 1993; Miner & Stein 1996). As seaward migration for juvenile salmon represents a period of elevated vulnerability to predators, our study contributes to the notion that turbidity in estuaries is likely a key component of habitat for juvenile salmon (Groot & Margolis 1990).

We found temperature to be an important variable in explaining sockeye and Chinook abundances – higher juvenile sockeye and Chinook salmon abundance was associated with higher temperatures. Water temperature affects metabolism and regulatory processes such as activity, growth and sexual maturation (Javaid & Anderson 1967; Straty & Jaenicke 1980). Fish can detect temperature gradients as small as 0.03°C (Murray 1971) and have been observed distributing within preferred temperature ranges (Garside & Tait 1958; Javaid & Anderson 1967; Armstrong et al. 2013). For example, Chinook, coho and chum salmon orientate towards warmer surface water during downstream migration (Birtwell & Kruzynski 1989; Levings 2016). Selecting for warmer temperatures (within a temperature optimum) may allow fish to capitalize on the productive food supply in estuaries by increasing scope for growth (Javaid & Anderson 1967; Murray 1971; Straty & Jaenicke 1980). Similar behavioral thermoregulation has been shown to increase the growth rate of juvenile coho salmon in freshwater (Armstrong et al. 2013). Increased growth rates during estuary rearing produce larger fish with an increased chance of survival in marine environments (Foerster 1954; Beamish et al. 2004; Duffy & Beauchamp 2011). Excessively high water temperatures are associated with decreased juvenile salmon survival (Bottom et al. 2008), however, the range of temperatures (9 - 15 °C) experienced in the Skeena River estuary from May to July are well within the tolerance range of salmon (Brett 1952). During this time, freshwater from the Skeena River is colder than the marine environment, creating a temperature gradient across our study region (strongest during snow-melt freshet in May, ranging from 9.1°C - 12.6 °C). As juvenile salmon did not show distribution patterns in relation to distance to the river, sockeye and coho salmon may have an affinity for temperature at a site level as opposed to a larger geographical gradient across the estuary.

Estuary tidal dynamics can heavily influence the habitat use of juvenile salmon. In the Skeena River estuary, more coho salmon were caught at higher tides. Sockeye salmon may also have been associated with higher tide but this result is uncertain. Juvenile salmon are often found moving into estuaries during ebb tides (Lacroix et al. 2005; Perry et al. 2010; Hasler & Scholz 2012) and can be found concentrating in certain habitats during different tidal stages (Pearcy 1992). Tides can control the accessibility of salmon habitat like salt marshes and tidal channels following ebb and flow cycles (Levings et al. 1991). Juvenile Chinook, chum and pink salmon often move in and out of

tidal channels daily and into slough habitat during flood and ebb tides (Levings 1982; Macdonald et al. 1987; Levings et al. 1991; Hering et al. 2010; McNatt et al. 2016). In the Fraser River estuary, Chinook salmon move out of tidal channels on ebb tides and concentrate in river channels and sand flats where high densities of prey have been found (Alldredge & Hamner 1980; Levings 1982; Levings et al. 1991). Similarly, sites in the Skeena River estuary, such as the Flora Bank eelgrass beds, dewater at lower tides. Although we found coho salmon more frequently during higher tides in the estuary, this result may be confounded by our inability to sample all sites across a range of tide heights. Alternative research approaches, such as using tags to track individual salmon (Semmens 2008), could provide more insight into distribution of salmon across finer temporal scales.

Our research contributes to the ongoing conversation on the importance of vegetative cover such as eelgrass for juvenile salmon in estuaries (Simenstad et al. 1982). Sockeye and Chinook salmon utilized eelgrass habitats over other available habitat types (open-water, rocky shores and sandy banks) in the Skeena River estuary, while coho salmon did not have an obvious preferred habitat type. However, for all three species, eelgrass cover was not a strong predictor of salmon abundance when more dimensions of habitat were modeled (approach A). This suggests that the presence of eelgrass is important for sockeye and Chinook but increased eelgrass cover did not contribute to habitat use – i.e. higher abundances were not associated with denser eelgrass beds compared to less dense eelgrass beds. We also found a positive association with coho and potentially sockeye salmon and macroalgae cover in the Skeena River estuary. For sockeye and coho salmon, which are known to be rapid migrators (Thorpe 1994; Weitkamp et al. 2014), an association with nearshore vegetation such as eelgrass or macroalgae habitat has not been previously documented (Murphy et al. 2000; Hosack et al. 2006). Juvenile Chinook salmon have demonstrated variable eelgrass association with strong association in some cases (Semmens 2008) and not in others (Healey 1980; Hosack et al. 2006; Dumbauld et al. 2015). In addition, juvenile Chinook salmon have also been found in high abundances on sand and mudflat habitat types (Levings 1982; Thom et al. 1989). We found more juvenile Chinook salmon in eelgrass beds compared to other habitat types sampled in the Skeena River estuary. Eelgrass and microalgae beds can provide predator refuge and increase secondary production and diversity of plankton and epiphytic fish prey in estuaries (Duggins et al.

1989, 1990; Semmens 2008). Vegetative cover increases structural complexity that has been associated with increased survival of small fish and juvenile salmon in the presence of predators (Gotceitas 1990; Gregory & Levings 1996). A finer-scale study of eelgrass habitat that quantifies eelgrass density, quality and community in the Skeena River estuary would supplement these results. Our study supports the idea that eelgrass habitats can be more heavily used by some species of salmon compared to other habitat types but eelgrass habitat alone was clearly only one dimension of salmon habitat. Local conditions, including the spatial arrangement of habitats, environmental gradients, prey distribution and tides and currents, likely contribute to the differential use of habitats across estuaries and species.

Juvenile salmon are known to distribute according to geospatial factors such as proximity to land (Bottom et al. 2005a; Roegner et al. 2016) and freshwater outflow (Macdonald et al. 1987). In our study, distance from the river mouth was not an important factor in describing the spatial distribution of juvenile salmon in the Skeena River estuary. If all individuals are dispersing randomly upon reaching the estuary, we would expect to catch more salmon at sites closer to the river because they have a smaller area to disperse over. We did not see any relationship between juvenile sockeye, coho or Chinook salmon abundance and proximity to the mouth of the Skeena River. This suggests that salmon are actively selecting locations in the estuary and are influenced by other factors such as tides, current, prey distribution, habitat availability and environmental gradients. Shaffer (2004) found no relationship between distance from the river or shoreline for juvenile Chinook and coho in Puget Sound, WA. In the Skeena River estuary, however, proximity to shore appears to be an important predictor of juvenile coho and Chinook salmon abundance, although we found uncertainty surrounding this relationship. In contrast to previous studies documenting the use of nearshore habitats by fry and sub-yearling Chinook salmon (Simenstad et al. 1982; Bottom et al. 2005a; Hering et al. 2010; Roegner et al. 2016), we discovered yearling Chinook salmon (85 mm - 185 mm) with an affinity for nearshore habitat. Although a small percentage of Chinook salmon from the Skeena River Watershed leave freshwater in their first summer (Gottesfeld & Rabnett 2007), we did not find fry or sub-yearling in the estuary during two years of sampling. Perhaps this life-history of Chinook might depend more on the lower Skeena River/upper estuary. In the Skeena River, nearshore

habitat appears to be an important habitat for juvenile Chinook and possibly for coho salmon.

### **2.5.2. Comparing Modeling Approaches**

Models using a detailed description of estuary habitat by incorporating various abiotic and biotic attributes fit abundance data better and had a higher predictive capability than models based on coarse habitats. Simple habitat classification did not capture the dynamic nature of habitats in estuaries (Simenstad et al. 2006) as habitat boundaries in aquatic systems are rarely fixed and gradients of environmental conditions commonly occur in estuaries (Pardo & Armitage 1997). Research in the Fraser River estuary, concluded that habitats (including mudflats) surrounding vegetative marsh “are inseparable because of water flow patterns”, as juvenile salmon move into unvegetated sand flats during lower tides (Levings 1982). Furthermore, detrital carbon from different habitat types across the estuary support salmon prey in adjacent areas (Levings et al. 1991). A spectrum of habitat types and conditions is likely needed to satisfy the feeding and refuge requirements of juvenile salmon during their migration (Naiman & Latterell 2005). For example, stable isotope evidence in the Columbia River estuary has identified 13 types of estuarine rearing strategies for Chinook salmon, including utilization of food webs from freshwater wetland, fluvial, estuarine wetland and marine food resources (Bottom et al. 2008). In addition, habitat sequences at a landscape scale may be important for gathering necessary olfactory cues during smolt transformations from environmental gradients (Dittman et al. 1996; Bottom et al. 2005b). Thus, in addition to specific habitat requirements, the spatial arrangements and habitat distribution within estuaries are likely important to juvenile salmon during downstream migrations. Juvenile salmon are using a mosaic of interconnected habitats and we find that a simple classification system is missing important elements.

### **2.5.3. Limitations**

Our approach to assess estuary habitat utilization used CPUE as an indicator of the relative usage of different habitats. This captures one metric of habitat “importance”, but does not capture other aspects such as residency, growth, and survival during the estuarine life-history stage. We also recognize that capture efficiency of purse seine nets could be influenced by tide, turbidity and current. For example, fish catches may be

lower in less turbid waters as fish may be able to avoid nets more effectively. Another challenge we encountered was low number of Chinook salmon compared to sockeye and coho salmon. Although all the models for Chinook salmon converged, it would be important to conduct further sampling before using these results to directly inform management decisions about Chinook salmon use of estuary habitat. As previous sampling with beach seine or trawl did not have a higher capture rate (Carr-Harris et al. 2015), sampling with the larger purse seine more frequently in future would likely provide increased sample sizes. In addition, while it examined a suite of environmental variables to model salmon abundance across the estuary, our study did not account for all potentially important variables such as current magnitude and direction, spatial connectivity of habitats, distribution of preferred prey, and predation risk. This likely contributed to low predictive capability of models from both coarse and fine scale approaches. However, in complex and dynamic estuarine environments, such as the Skeena River estuary, where it is difficult to capture all metrics possibly influencing estuary use by juvenile salmon, we are uncertain how sampling more variables or even more frequently would contribute to increased predictive power. Although our research findings contribute to the growing body of evidence on factors that influence juvenile salmon estuary habitat use, it also demonstrates that a high degree of scientific uncertainty remains regarding the use of estuary habitat by young salmon.

#### **2.5.4. Management Implications**

Our study illuminates that the fundamental aspect of identifying important habitat remains a key challenge when assessing environmental risks. Coarse habitat categorizations, currently used by Canadian provincial and federal environmental risk assessment, explain relatively little variation in salmon abundance. For instance, we found juvenile salmon unevenly distributed across the estuary, using some eelgrass beds and not others. The highest abundances of all species of juvenile salmon were consistently observed within the Lelu Island and Flora Bank region but it is still not clear why this is. It is possibly the combination of preferred turbidity, temperatures, and spatial arrangement of the Flora Bank eelgrass bed, in addition to other factors such as currents or prey abundance, which makes this habitat highly used. Our results thus suggest that replacement of lost or damaged eelgrass habitat, mitigation policies proposed by current industrial development environmental assessment in the Skeena River estuary (Pacific

Northwest LNG 2016), may not be able to achieve no net loss of important habitat for salmon. In general, habitat mitigation policy used in Canada rarely achieves adequate habitat compensation because restored habitat patches are smaller and have lower habitat productivity and ecosystem function (Harper & Quigley 2005; Quigley & Harper 2006; Favaro & Olszynski 2017). Habitat compensation projects on salt marsh habitat on the Fraser River estuary have had mixed success, with many projects failing to achieve no net loss in both areal extent and restored habitat utilization by juvenile salmon (Kistritz 1996; Levings & Nishimura 1997). Habitat compensation for highway expansion along the tidal extent of lower Skeena River resulted in net gain of salt-marsh habitat 23 years after project completion (White 2011); however, the function and utilization of these habitat by fish and invertebrates was never evaluated. No net loss habitat compensation is currently an integral part of assessing and mitigating environmental risk for developments but our results indicate that this simplifying framework is challenged in dynamic and complicated estuary habitat, such as the Flora Bank region. In addition, we found eelgrass habitat was used more frequently than other habitat types for juvenile sockeye and Chinook salmon but not for juvenile coho salmon. Blanket habitat prescriptions for “salmon” will inadequately integrate the species-specific use of estuary habitat. Planning processes for consideration of salmon habitat in some jurisdictions are shifting towards a more inclusive landscape-process-based approach such as in the Columbia River estuary (Bottom et al. 2005b; Beechie et al. 2010; Hanski 2011; Nagelkerken et al. 2015).

While our more complex consideration of habitat provided greater predictive power than a more typical coarse-grained approach, it is important to emphasize that even with extensive research, we still found a large degree of uncertainty associated with predicting the abundance of salmon across space and time. Aside from incorporating scientific uncertainty into management decisions and planning, our results can contribute to understanding environmental risk assessment — industrial projects situated in regions supporting the highest abundances of salmon are likely to pose a higher risk to salmon populations compared to estuary regions with little or no salmon use. Instead of coarse habitat-based approaches, one option might be to use field studies of salmon themselves (such as this) to identify regions where projects may pose particularly high risks.

Designating and managing key habitat for mobile and aquatic species, such as salmon, are particularly challenging because they require a continuous corridor of habitats arranged in particular distributions over their journey (Murphy et al. 1997; Naiman & Latterell 2005; Runge et al. 2014; Moore et al. 2016). For example, marine and freshwater SARA-listed species had significantly lower rates of “Critical Habitat” designation (0% and 9.3% respectively), compared with species using terrestrial (12.2%) or riparian habitat (38.9%) (Bird & Hodges 2017). While many factors likely explain this discrepancy, it indicates the potential challenge of identification of important habitat and management of risks to mobile aquatic species, species at risk or otherwise. Our study supports the growing body of work identifying the contributing factors of estuary habitat for juvenile salmon and illuminates that current approaches to assessing risks to salmon in estuaries are based on oversimplification of their habitat.

## Chapter 3. Linking estuarine fish and prey dynamics for forage fish and juvenile salmon species<sup>2</sup>

### 3.1. Abstract

High productivity and lower predation risk in estuarine environments create favorable conditions that contribute to increased growth and survival for a range of species. Elevated food supply in estuaries supports economically important fish species such as migrating juvenile salmon and Pacific herring (*Clupea pallasii*) in temperate estuaries during spring and summer. During estuarine residence, specific prey taxa are known to be particularly important in the diet of many fish species. Linking spatio-temporal dynamics of zooplankton prey and fish abundances can provide insight into the nursery function of estuaries. We investigated if abundance patterns of two juvenile salmon species and two forage fish species were related to zooplankton distribution across the Skeena River estuary (British Columbia, Canada). We used total prey abundance, along with abundances of highly consumed and less consumed individual prey taxa to model catch-per-unit-effort (CPUE) of sockeye salmon (*Oncorhynchus nerka*), coho salmon (*O. kisutch*), Pacific herring and surf smelt (*Hypomesus pretiosus*). Increased abundances of a highly consumed prey taxon, calanoid copepods, were associated with higher herring catch. Total prey abundance was not related to abundance of herring suggesting that herring distribution patterns may be influenced by important prey taxon. In addition, juvenile salmon and smelt CPUE was not related to zooplankton abundance in the estuary. We also investigated forage fish abundance patterns in relation to abiotic (e.g., turbidity) and biotic (e.g., macroalgae cover) variables. Several abiotic factors such as, temperature, turbidity and distance to shore were also found to explain variation in forage fish abundance. Our findings advance understanding about forage fish use of estuary environments and highlight the complicated dynamics of key prey and estuary fish species.

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<sup>2</sup> A version of Chapter 3 is in preparation for journal submission, with coauthors Charmaine Carr-Harris, Michael Arbeider and Jonathan W. Moore

## 3.2. Introduction

Estuaries are widely recognized to be important nursery grounds for larval and juvenile fish around the world (Beck et al. 2001; Able 2005; Dahlgren et al. 2006). For example, estuaries that border the northeast Pacific support many species of economic and cultural importance including Pacific salmon and forage fish such as herring and smelt (Bottom & Jones 1990; Abookire et al. 2000; Weitkamp et al. 2012). Compared to adjacent marine or freshwater environments, estuaries can act as nurseries through two main mechanisms: providing refuge from predators as well as elevated prey resources. Estuaries can provide refuge to young fishes through turbid waters and nearshore structural complexity (St. John et al. 1992; Fukuwaka & Suzuki 1998; Bottom et al. 2005b; Brodeur & Morgan 2016; Levings 2016) and thus decrease predation risk to young fishes (Beck et al. 2001; Heck et al. 2003; Alofs & Polivka 2004; Sheaves et al. 2015). The nursery function of estuaries can also be supported by higher food availability than surrounding marine or freshwater ecosystems (Grimes & Finucane 1991; St. John et al. 1992, 1992; Grimes & Kingsford 1996; Hill & Wheeler 2002; De Robertis et al. 2005; Ware 2005; Selleslagh et al. 2012; Brodeur & Morgan 2016). Driven by a combination of detrital production and the mixing of nutrients from marine upwelling and freshwater inputs (Hill & Wheeler 2002; Maier & Simenstad 2009), high basal production provides increased prey resources that contributes to increased growth of juvenile fish (Naiman & Sibert 1979; Sobczak et al. 2002). In turn, elevated growth can translate into increased survival and thus population productivity, particularly given that predation in marine ecosystems is often size-selective (Sogard 1997). In salmon for example, fast growth during estuarine residence is linked to subsequently increased marine survival (Pearcy 1992; Duffy & Beauchamp 2011). Thus, investigating the interrelationships between estuary-rearing fishes, physical habitat and prey resources can provide the foundation to understanding the potential for estuaries, and different locations within estuaries, to function as nursery habitat. Yet, linking prey resources to estuary-rearing fishes is challenging, entailing identification of key prey for different fishes; quantification of the spatio-temporal dynamics of prey such as zooplankton; and finally examining whether prey dynamics might be linked to fish dynamics.

There is a building understanding of key prey resources for different fish across temperate estuaries. Although juvenile salmon are typically generalist consumers, feeding on different prey in different estuaries due to differences in prey communities (Pearcy 1992; Weitkamp & Sturdevant 2008), there are some emerging generalities. For example, young coho salmon are known to be piscivorous, consuming larval fish in nearshore environments (Auburn & Ignell 2000; Brodeur et al. 2007; Pool et al. 2008). In addition, many fish species tend to consume certain zooplankton species more than expected. For example, chum salmon in the Nanaimo estuary consume harpacticoid copepods in vast numbers despite this prey's relative rarity in the environment (Healey 1979). Juvenile and adult herring have been found to be less selective feeders than juvenile salmon, consuming zooplankton in relation to their availability in the environment (St. John et al. 1992). Various prey characteristics including prey size (Feller & Kaczynski 1975; Schabetsberger et al. 2003; Moss & Beauchamp 2007), swimming speed (Drenner et al. 1978), energy richness (Trudel et al. 2007), and availability (Weitkamp & Sturdevant 2008) likely contribute to prey preference or selection.

A second step in linking estuary fishes and their resources requires quantifying prey spatio-temporal dynamics. The dynamics of estuary prey over space and time can be driven by a complicated interplay of physical and chemical conditions in estuaries. Zooplankton distribution can be strongly influenced by salinity in estuaries (Bottom & Jones 1990; David et al. 2016). Further, high zooplankton densities are often found at plume boundaries, as downwelling velocities of saltwater at leading edges of river plumes create aggregations of buoyant zooplankton in mixing zones which can stretch from hundreds of meters to kilometers (St. John et al. 1992; Phillips et al. 2017). The creation and maintenance of prey aggregations are dependent on river discharge, magnitude of tidal fluctuation and wind (St. John et al. 1992; Schlacher & Wooldridge 1995; Gómez-Erache et al. 2000; Kemp & Keister 2015). Finer-scale patterns of zooplankton distribution are contingent on water circulation patterns and tides (Peterson & Peterson 2009), creating different zooplankton communities across eddy lines (Pool et al. 2008), bays (Jones et al. 1990) and plume fronts (De Robertis et al. 2005), where water becomes trapped by physical coastline features or water currents. Zooplankton community assemblage and relative abundance can also vary across subtidal and intertidal habitat, where tidal hydrodynamics concentrate prey along shore (David et al.

2016). Further, some prey species are likely more specific in terms of their habitat, relying on specific habitat features. For example, epibenthic zooplankton prey such as harpacticoid copepods are associated with nearshore vegetation such as eelgrass and macroalgae (Thistle et al. 1984; Salo et al. 1989; Fujiwara & Highsmith 1997).

The final aspect of the relationship between fish and resources in estuaries is the explicit linkage of prey dynamics to fish dynamics. On a broad-scale, fish abundance and fish community assemblage have been shown to be influenced by prey density (Haertel & Osterberg 1967). Past research has connected prey and fish distribution patterns on a large scale for overall prey abundances across estuary zones (St. John et al. 1992; De Robertis et al. 2005; Brodeur & Morgan 2016), and on occasion for particularly important prey species (Healey 1979). Within estuaries, stomach fullness and feeding intensity of fish have been directly related to higher abundances of zooplankton in some cases (Bottom et al. 1984; Bottom & Jones 1990) and not others (De Robertis et al. 2005). Thus, while there is building appreciation for the identity and spatio-temporal dynamics of key prey resources for estuarine fishes, linking this information to the dynamics of fish can be challenging. In particular, it is relatively unknown as to whether local abundance of preferred prey may relate to the spatial patterns of abundance for different estuary fishes.

This study focuses on linkages between prey and estuary fishes in the Skeena River of British Columbia, the second most-productive salmon watershed in Canada. The Skeena River estuary supports all species of North American Pacific salmon (*Oncorhynchus kisutch*, *O. nerka*, *O. tshawytscha*, *O. keta*, *O. gorbuscha*, *O. mykiss*) and forage fish such as Pacific herring (*Clupea pallasii*) and surf smelt (*Hypomesus pretiosus*). Pacific herring and surf smelt (herein herring and smelt) are the most abundant small pelagic fishes (i.e. forage fish) in this coastal food web (Moore et al. 2015a; Stantec 2016; Carr-Harris 2017), directly support local commercial and traditional fisheries in the Skeena region (DFO 2016) and are key prey for a variety of consumers, ranging from birds to marine mammals to larger fishes (Therriault et al. 2009). Like other estuaries that border the NE Pacific Ocean, during spring and summer, these resident forage fishes are joined by juvenile salmon of multiple species as salmon migrate through the estuary from the freshwater to the ocean. Previous research has described juvenile salmon distribution patterns and residence times for different species of Pacific salmon in this estuary (Carr-Harris et al. 2015; Moore et al. 2015b, 2016) and how local

abundance patterns of sockeye, coho and Chinook salmon relate to abiotic and biotic variables (Chapter 2). In addition, recent research quantified zooplankton spatio-temporal dynamics in the estuary and discovered that different estuary fish species – sockeye salmon, coho salmon, Pacific herring and surf smelt – preferentially consumed different zooplankton species (Table 3.1) (Arbeider et al. in prep). Specifically, the relative importance of different zooplankton species to these four fish species was quantified with the Index of Relative Importance, a metric that incorporates the number of prey, their weight, and their frequency of occurrence. Whether spatial patterns of abundance for key prey taxa are linked to spatial patterns of these different estuary fishes remains unknown.

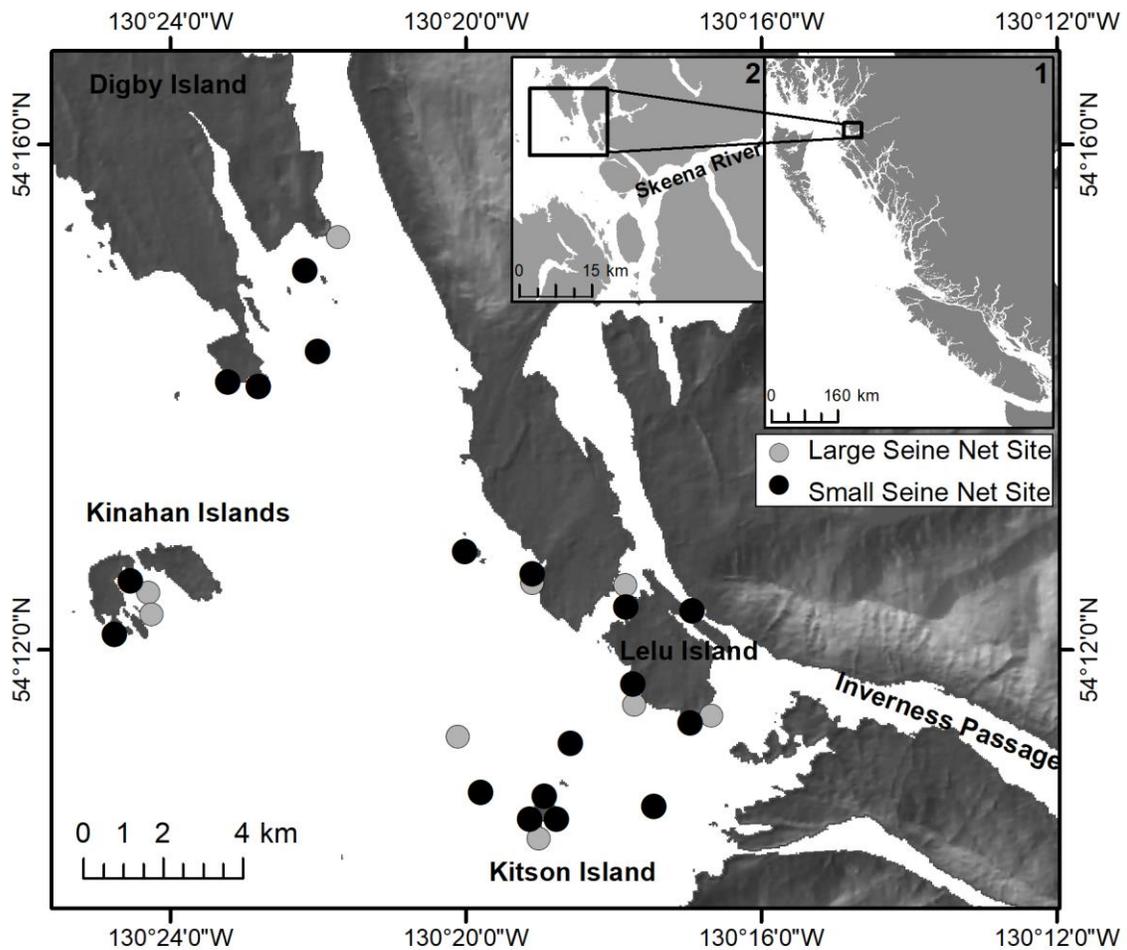
Here we seek to examine the potential role of prey in contributing to spatial patterns of estuary use of four economically and ecologically important fishes. We focus on Pacific herring, surf smelt, coho salmon, and sockeye salmon in the Skeena River estuary. We examined whether the abundance of the four fish species was linked to the abundance of key prey after considering biotic and abiotic aspects of estuary habitat. Species-specific habitat models for salmon have previously been quantified (Chapter 2), here we develop similar models for herring and surf smelt, which have been less well studied. For each of the four fish species, we then examine potential spatial associations between fish abundance and the abundance of a) total zooplankton and b) individual prey species determined to be highly consumed or less consumed in a concurrent study (Arbeider et al. in prep). We hypothesized that the abundance of different fish species would be positively associated with the abundance of their most highly consumed prey species. This information advances our understanding of the potential role of prey in contributing to estuary nursery habitat for juvenile salmon and forage fish.

### **3.3. Methods**

#### **3.3.1. Study Location**

The 55,000 km<sup>2</sup> watershed of the Skeena River drains into the estuary located near Prince Rupert, exerting freshwater influence 75 km into Chatham Sound (Trites 1956; Hoos 1975). Similar to other temperate estuaries, forage fish and juvenile salmon utilize habitat in the Skeena River estuary throughout the spring and summer months (Bottom et al. 1984; Bottom & Jones 1990; St. John et al. 1992). There is growing, but

still limited, body of research on the Skeena River estuary (Sharpe et al. in prep; Trites 1956; Manzer 1969; Higgins & Schouwenburg 1973; Hoos 1975; Levings et al. 1975; Ages 1995; Carr-Harris et al. 2015; Moore et al. 2016) leaving significant knowledge gaps about the utilization of the estuary by juvenile salmon, forage fish and the estuary food webs that support them.



**Figure 3.1.** Map of sampling locations coloured by net type (black = small seine net, grey = large seine net) used across the Skeena River estuary. Map inserts indicate location of sampling region in relation to: 1) the coastline of British Columbia, 2) the mouth of the Skeena River.

### **3.3.2. Fish Sampling**

We sampled fish in the Skeena River estuary with a purse seine from May to July in 2016 (Figure 3.1). We selected sites to be representative of the most common habitat types: eelgrass beds, rocky shores, sand banks and open-water habitat. To sample sites at varying depths, we sampled 27 sites bi-weekly across the estuary: 18 sites with a small purse seine and 9 sites with a large purse seine. We used two boats to set both the large purse seine (9.1 m deep by 73.2 m long, 5.1 cm webbing at the tow end, 1.3 cm webbing at the bunt end) and smaller purse seine (5.5 m deep by 15.2 m long, 1.3 cm webbing at the tow end, 0.64 cm webbing at the bunt end) by holding the nets open in the tidal current. The large net and small nets were towed for 5 and 2.5 minutes, respectively, before closing the seines. We measured fork-length from a maximum of 25 individuals from all fish species caught in each net set. Although we collected information on a variety of fish species, we focused our analyses on two economically important salmon species (sockeye and coho) and two common forage fish species (smelt and herring). Fish were collected from ten, small purse seine sites across the estuary (111 sockeye salmon, 57 coho salmon, 57 herring and 35 smelt) and immediately stored in 5% seawater buffered formalin solution. Stomach content analysis was performed by Biological Environmental Services where prey items were identified to lowest possible taxon.

### **3.3.3. Plankton Sampling**

At every set of the small purse seine, we sampled zooplankton communities in the water column to a depth of 5 m. We performed vertical plankton tows with a standard WP2 plankton net with 250  $\mu\text{m}$  mesh and a mouth diameter of 57 cm. Zooplankton were preserved in 5% seawater buffered formalin (within eight hours of collection) for identification and enumeration (Arbeider et al. in prep). We are using density (count per  $\text{m}^3$ ) as a measure of zooplankton abundance.

To more accurately represent the variation in fish abundance linked with zooplankton sampling, we paired zooplankton abundances from nine of the small purse seine sets with the nearest large purse seine sites by averaging fish abundance. We calculated catch-per-unit-effort (CPUE) by first multiplying small net catches by the large net area and tow duration and then dividing by the area and tow duration of the small

net, thus standardizing catches from the small seine to the large seine net. For each sampling event, a mean fish CPUE was taken for paired sites. All paired large seine samples were between 100 – 600 m away from the closest zooplankton sample and occurred within 4 days or less of the small purse seine sites. Given turbulent water mixing, we believe that the zooplankton samples will provide an effective index of the available zooplankton prey at this temporal and spatial resolution. We also ran statistical analysis on small purse seine sites only (excluding large purse seine sites) and found that the results were qualitatively similar to findings from the paired sampling design. The strength and direction of abiotic effects on fish abundance was similar when large purse seine sites were excluded.

### **3.3.4. Abiotic and Biotic Variable Sampling**

During each estuary fish sampling event, we measured the following environmental variables: salinity (range across sites: 6.6-22.8 ppt), temperature (9.2 - 12.6 °C) and turbidity (secchi depth: 0.7 - 3.0 meters). In addition, we determined tidal height, tidal stage, distance from the river mouth, distance to shore, exposure, eelgrass percent cover and macroalgae cover. Tidal height and tidal stage were calculated using data collected at Prince Rupert, BC (Station Number 9354, 54.317° N 130.324° W). Distances (from site to river mouth and from sites to shore) were obtained using line measurements in Google Earth. We assigned an exposure category to each site (high, moderate and low). We surveyed vegetative cover at each site with video captured on a towed drop camera. Point count analysis was performed on random, non-overlapping images from three parallel transects to create an average eelgrass and macroalgae percent cover estimate for each site. A more detailed description of methods for abiotic and biotic sampling is outlined in Chapter 2.

### **3.3.5. Selection of Zooplankton Species**

This study builds on a more detailed study of diet composition of sockeye salmon, coho salmon, Pacific herring and surf smelt and zooplankton communities in the Skeena River estuary (Arbeider et al. in prep). To examine if fish abundance patterns correlate with prey abundance in the estuary, we selected prey taxa known to be highly consumed and less consumed by fish species in the Skeena River estuary (Arbeider et al. in prep). Arbeider et al. (in prep.) identified highly consumed prey for sockeye salmon,

coho salmon, herring and smelt using a modified Index of Relative Importance (IRI) (Bottom & Jones 1990). By accounting for prey biomass and frequency across all diet samples (variation between individual fish), IRI standardizes prey abundance to facilitate comparison of consumption across prey species (Bottom & Jones 1990). We defined highly consumed zooplankton as those taxa with IRI scores that were greater than the mean IRI score (standard errors do not cross zero) for each of the four fish species (Table 3.1). Conversely, we selected a less-consumed zooplankton taxa for each fish species, which had a low IRI score but was ubiquitously found in the environment (zooplankton tows) (Table 3.1). Incorporating both highly consumed and less consumed zooplankton into models of fish abundance allows us to compare relationships between fish abundance and important and less important zooplankton taxa. In addition, species had to be present in both diet contents (IRI scores) and in the zooplankton tows for modeling to be possible. Thus, we excluded prey (i.e. tunicates, larval fish, insect; (Arbeider et al. in prep)) that were not effectively sampled with standard WP2 plankton nets (but that were consumed highly by some fishes).

**Table 3.1 Summary of prey taxon included in modeling and corresponding IRI value (Bottom & Jones 1990) from stomach content analysis (Arbeider et al. in prep). IRI standardizes for prey biomass and frequency across diets samples allowing for comparison of prey abundance. Highly consumed (A) and less consumed (B) prey taxa are identified based on mean IRI value.**

Fish Species	Prey Type <sup>a,b</sup>	Prey Group	Prey Taxon <sup>c</sup>	IRI Value (SE)	Mean IRI Value <sup>d</sup>
sockeye	A	harpacticoid copepod	Harpacticoida	6530 (540)	1505
	A	calanoid copepods	Calanoida	3340 (470)	
	A	barnacle cyprid	Cirripedia, cyprid	2735 (460)	
	B	barnacle nauplii	Cirripedia, nauplii	525 (150)	
coho	A	decapod zoea	Decapoda, zoea	2190 (475)	1645
	B	calanoid copepod	Calanoida	85 (30)	
herring	A	calanoid copepod	Calanoida	9355 (715)	1405
	A	barnacle cyprid	Cirripedia, cyprid	2185 (600)	
	B	oikopleurons	Oikopleura spp.	150 (140)	
smelt	A	calanoid copepod	Calanoida	12580 (1060)	1070
	A	gastropods	Limnecina sp.	2275 (795)	
	B	barnacle nauplii	Cirripedia, nauplii	220 (115)	

<sup>a</sup> Highly consumed (A) prey were selected as the prey taxon with IRI scores greater than mean IRI value.

<sup>b</sup> Less consumed (B) prey were selected as the prey taxon with the lowest IRI score found relatively ubiquitously across the estuary (limited to one prey species per fish species)

<sup>c</sup> Taxon level differs (class, order, genus) according to the level of identification in previous study, (Arbeider et al. in prep).

<sup>d</sup> Mean IRI value calculated across all consumed prey groups for each fish species. There were 14, 12, 13, 18 prey groups total for sockeye salmon, coho salmon, herring and smelt (Arbeider et al. in prep).

### 3.3.6. Statistical Analysis

To investigate if zooplankton abundance contributed to fish abundance patterns across the estuary, we modeled CPUE (as a proxy of fish abundance) as a function of zooplankton abundance with mixed-effect models after accounting for abiotic and biotic habitat variables.

In Chapter 2, models using abiotic and biotic variables to explain coho and sockeye salmon abundance in the estuary were developed using a bigger dataset from both 2015 and 2016 (Chapter 2). Multi-model inference was used to determine the abiotic and biotic variables that best explained abundance patterns and Akaike's Information Criterion corrected for small sample size (AICc) (Akaike 1973) was used to identify top models for each species (defined as the most parsimonious model(s) with a

$\Delta AIC < 2$ ) (Chapter 2). Model averaging was performed on the candidate set of models with  $\Delta AIC < 2$  after modeling all possible combinations and a measure of Relative Variable Importance (RVI) was calculated (summed Akaike weights within a candidate set) to quantify the importance of each predictor variable. Model selection from the candidate set identified one top model for coho and two models for sockeye salmon, which were equally well supported and parsimonious (Chapter 2). Here we used the same protocol, using the data from 2015 and 2016, to perform multi-model inference and model selection to identify a top model for forage fish species, herring and smelt. We use these models as “null habitat models”, to act as a baseline for examining if zooplankton abundance can further contribute to explain further variation in fish abundance.

For the 2016 dataset with paired zooplankton and fish abundance data, we statistically examined whether zooplankton abundance helped explain fish abundance patterns. By adding highly consumed and less consumed zooplankton taxon abundance independently to habitat models, we determined if highly or lesser consumed prey species improve the model fit by comparing models with AICc (Akaike 1973). We compared models including highly consumed zooplankton taxa, less consumed zooplankton taxa and total zooplankton abundance separately (Table 3.2) and highlight top model(s) (most parsimonious models with a  $\Delta AIC < 2$ ) for each fish species. We used the R package glmmTMB (Magnusson et al. 2016) for all modeling to estimate parameters by maximum likelihood. To account for spatial and temporal covariation, we include site and sampling period as random effects. To effectively compare effect sizes, we centered and scaled all predictor variables (Grueber et al. 2011). All predictor variables, habitat and prey abundance groups, were not highly correlated (i.e. low variance inflation factors (VIF)  $< 3$ , and Pearson correlation coefficients  $< 0.5$  (Zuur et al. 2009, 2010)). We performed all statistical analysis using R 3.3.1 (R Core Team 2016).

## **3.4. Results**

### **3.4.1. Temporal Abundance Dynamics of Estuary Fish and Prey in 2016**

We captured 7715 juvenile sockeye salmon individuals during purse seine sampling in 2016, ranging in size from 52mm - 168mm (Figure B.1a), with highest CPUE of sockeye salmon from May 15 - May 30 (Figure B.2a). Raw catch values for all fish species in section 3.4.1. do not include a portion of large purse seine sampling events used, thus are different values than shown in Chapter 2. Harpacticoid copepods, the most highly consumed prey group, were caught consistently throughout the season. Two other highly consumed prey groups, calanoid copepods and barnacle cyprids were found in highest abundances in June and late May, respectively (Figure B.3).

We caught 555 coho salmon across the season ranging in size from 80mm - 242mm (Figure B.1b). Coho abundance in the estuary appears to be relatively evenly distributed across time with only slightly higher catches found in June (Figure B.2b). Abundances of high consumed prey taxa, decapod zoea were highest in mid-May (Figure B.3).

High densities of herring were caught across the season, representing diverse age classes, including young-of-the-year and adult herring, ranging in size 36 mm - 270mm (Figure B.1c). We caught 9210 herring in purse nets throughout the season, with the highest abundances in June (Figure B.2c). The highest abundances of preferred prey taxa, barnacle cyprids and calanoid copepods, occurred in late-May and June, respectively, overlapping with the highest abundances of herring captured in the estuary (Figure B.3).

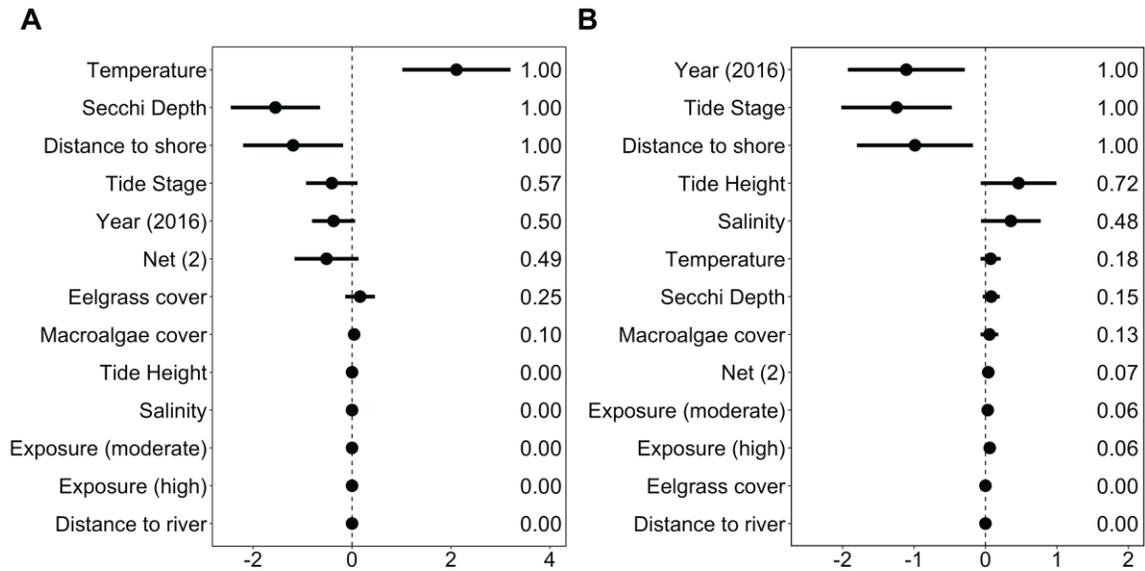
Smelt caught in the estuary ranged in size from 61 mm - 199mm, representing several age classes (Figure B.1d). We caught high densities of smelt across all sampling events, with the highest abundance of smelt caught on June 18 (Figure B.2d). Calanoid copepod, the most highly consumed prey taxa for smelt, were most abundant in June, while gastropods (the second most highly consumed prey taxa) were consistently present across sampling periods (Figure B.3).

### 3.4.2. Factors Contributing to Estuary Utilization by Forage Fish

Higher catches of herring were associated with increasing turbidity (decreasing secchi depth), warmer temperatures, and at sampling locations closer to shore (Figure 3.2a). Temperature (1.00), secchi depth (1.00) and distance to shore (1.00) ranked highest in RVI score and were included in all candidate set models. Other variables tidal stage (0.57), year (0.50) and net (0.49) had relatively high RVI score indicating their potential importance in explaining herring abundance. Although these trends were uncertain, they could indicate that we caught lower abundances of herring at lower rates of tidal rise and fall, in 2016 compared to 2015 and with the small purse seine net compared to the large purse seine net. The variables eelgrass cover (0.25), macroalgae cover (0.10), tide height (0.00), salinity (0.00), exposure (0.00) and distance to river (0.00) had low RVI scores and were uncommon or absent from  $\Delta AICc < 2$  candidate set.

Smelt were found in higher abundances closer to shore and had a negative association with tidal stage (Figure 3.2b). As tidal stage represents the rate of tidal rise or fall at the time of sampling, a negative association suggests that we caught smelt during dropping tides and periods around slack tide. In addition, we caught less smelt in 2016 compared to 2015. Tidal stage, distance to shore, and year were found in every model from the candidate set, thus had the highest RVI scores (1.00). Other variables tide height (0.72) and salinity (0.48) had relatively high RVI suggesting that there may be a trend towards higher catches associated with higher tides and salinities. Temperature (0.18), secchi depth (0.15), macroalgae cover (0.13), net type (0.07), exposure (0.6), eelgrass cover (0.00) and distance to river (0.00) had low RVI scores indicating that they did not explain fish abundance in the estuary.

Using data from multiple years (2015 and 2016) (Chapter 2), we identified one top model for herring and one top model for smelt (most parsimonious model(s) with a  $\Delta AIC < 2$ ) (Table B.1, Figure B.4). These habitat models were used as “null habitat models” to determine if prey abundance contributed to explaining spatial patterns across the estuary.



**Figure 3.2.** Standardized parameter estimates (dots) with 95% (bars) confidence intervals for A) herring and B) smelt presented in decreasing order of relative importance (RVI) using larger multi-year data set. RVI values shown on the rightmost panel. Coefficients are related to the (log) mean of normalized CPUE. Parameter year (2016) compares catches to the sampling year 2015 as a baseline, the small purse seine net is being compared to the large purse seine net, and low exposure is used as a reference to compare moderate and high exposed sites.

### 3.4.3. Linking Fish and Prey Abundance Patterns Across the Estuary

The inclusion of each of the two highly consumed prey taxa and one less consumed prey taxa improved the fit of the null habitat model for herring and were similarly supported (Table 3.2). We found a positive association between herring CPUE and calanoid copepod abundance, the prey group most highly consumed (Figure 3.3a). Herring CPUE was negatively correlated with barnacle cyprid and oikopleuran abundance, a moderately consumed prey taxon and the least consumed prey group respectively (Figure 3.3b and Figure 3.3c).

Abundance patterns of sockeye salmon, coho salmon and smelt were not associated with the abundance of highly consumed or less consumed prey groups (Table 3.2). Inclusion of prey groups did not improve the fit of the null habitat model for these fish species. Total prey abundance was not associated with increased catch of sockeye salmon, coho salmon, herring and smelt.

**Table 3.2 Comparison of models containing habitat variables only (A-E models, listed below) from Chapter 2, with models containing abundance of highly consumed prey, less consumed and total prey abundance using AICc. Models where prey abundance improved model fit ( $2 \Delta AICc < 2$ ) compared to null models or models with only habitat variables are identified (\*). All models contain year and sampling period as random effects.**

Species	Model Type	Model Parameters (fixed effects only)	<sup>a</sup> k	<sup>b</sup> $\Delta AICc$	<sup>c</sup> weight
sockeye	highly consumed prey	B + harpacticoid copepod abund.	6	0	0.288
salmon	habitat model	B	5	0.6	0.209
	highly consumed prey	B + barnacle cyprid abund.	6	2	0.106
	habitat model	A	5	2.9	0.068
	less consumed prey	B + barnacle nauplii abund.	6	2.9	0.067
	highly consumed prey	A + calanoid copepod abund.	6	3	0.065
	total prey abundance	B + total prey abund.	6	3.1	0.06
	highly consumed prey	A + harpacticoid copepod abund.	6	3.6	0.048
	total prey abundance	A + total prey abund.	6	4.5	0.03
	less consumed prey	A + barnacle nauplii abund.	6	5.3	0.021
	highly consumed prey	A + calanoid copepod abund.	6	5.4	0.019
	highly consumed prey	A + barnacle cyprid abund.	6	5.4	0.019
coho	habitat model	C	5	0	0.5
salmon	highly consumed prey	C + decapod zoaea abund.	6	1.7	0.21
	total prey abundance	C + total prey abund.	6	2.4	0.15
	less consumed prey	C + calanoid copepod abund.	6	2.5	0.14
herring	highly consumed prey*	D + barnacle cyprid abund.	6	0	0.355
	highly consumed prey*	D + calanoid copepod abund.	6	0.6	0.257
	less consumed prey*	D + oikopleuran abund.	6	1	0.22
	total prey abundance	D + total prey abund.	6	2.5	0.101
	habitat model	D	5	3.3	0.067
smelt	habitat model	E	4	0	0.481
	less consumed prey	E + barnacle nauplii abund.	5	1.5	0.4
	highly consumed prey	E + gastropod abund.	5	3.5	0.18
	total prey abundance	E + total prey abund.	5	3.6	0.16
	highly consumed prey	E + calanoid copepod abund.	5	3.9	0.13

<sup>a</sup> k = number of model parameters.

<sup>b</sup>  $\Delta AICc$  = change in AICc score from top model.

<sup>c</sup> weight = AICc model weight

<sup>1</sup>Parameters included in habitat model(s) for each species:

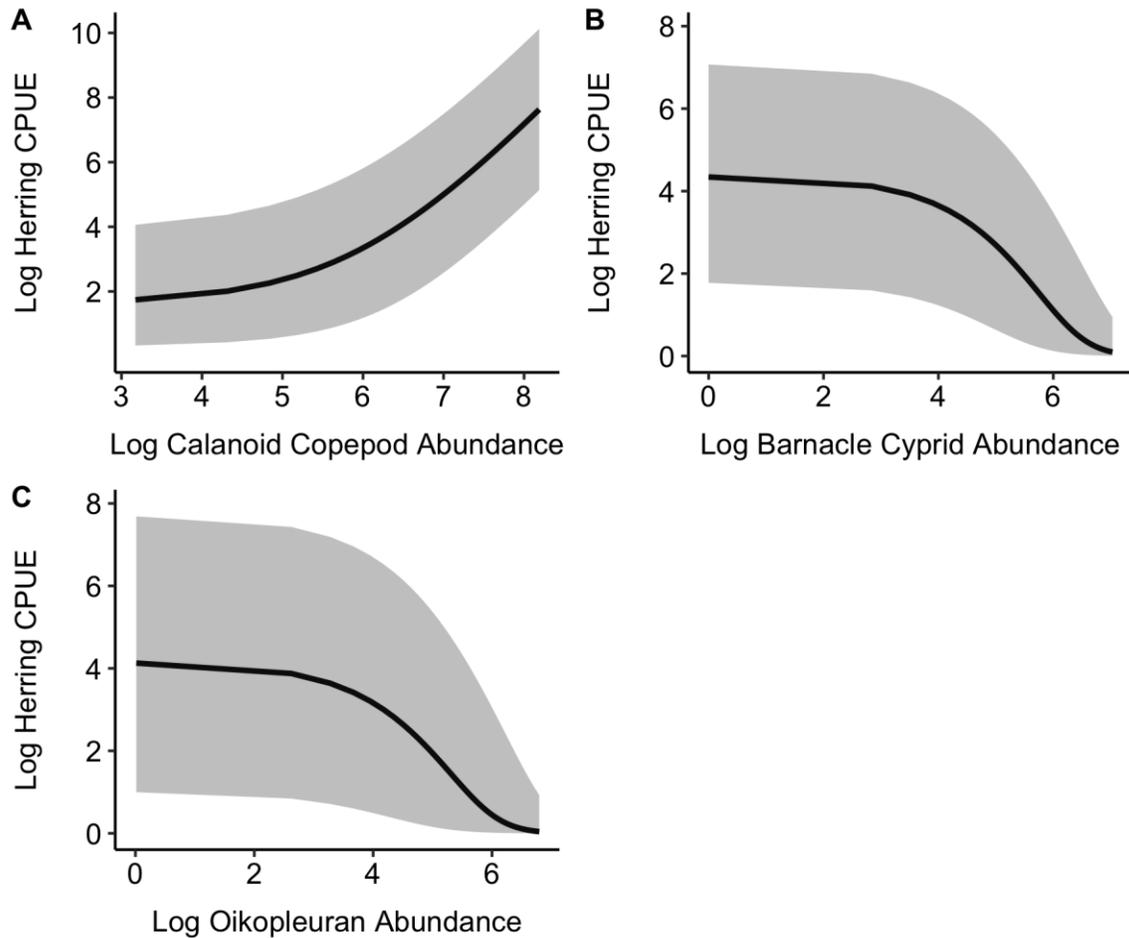
A) sockeye top model (a): secchi depth + tide height + temperature

B) sockeye top model (b): secchi depth + tide height + macroalgae cover

C) coho top model: secchi depth + tide height + macroalgae cover

D) herring top model: secchi depth + temperature + distance to shore

E) smelt top model: distance to shore + tidal stage



**Figure 3.3.** The effects of prey abundance (as estimated by density, count per  $m^3$ ) for taxa known to be highly consumed by herring, A) calanoid copepod, B) barnacle cyprid, and taxa less consumed, C) oikopleuran, on herring catch-per-unit-effort (CPUE) with 95% confidence interval banded in grey. The trend line represents prediction of fish CPUE across varying prey abundances (plotted on the x-axis), whilst holding other explanatory variables at their mean.

### 3.5. Discussion

Here we examined whether preferred prey abundance was linked to abundance of four estuary fish after accounting for other abiotic and biotic predictors in the Skeena River estuary. As predicted, the abundance of herring was positively associated with the abundance of the highest-consumed prey taxa, calanoid copepods; barnacle cyprids (a lesser consumed prey taxa) and oikopleurans (consumed the least) were negative correlated. In contrast, abundances of different prey groups did not improve

understanding of juvenile salmon and forage fish species abundances. Abiotic or biotic predictors such as turbidity, temperature and distance from shore were associated with estuary fish distribution for juvenile sockeye and coho salmon along with forage fish species herring and smelt. Our findings highlight the complicated dynamics of key prey and estuary fish species in conjunction with abiotic and biotic estuarine characteristics.

### **3.5.1. Linking Spatial Dynamics of Fish and Prey Taxa**

Higher abundance of herring was found in conjunction with higher availability of calanoid copepod, the most highly consumed prey item of herring, after accounting for habitat variables (Figure 3.3). Calanoid copepods were four times more important to herring diet based on IRI scores than the next highest consumed prey, barnacle cyprids (Arbeider et al. in prep). In contrast, herring spatial distribution patterns were negatively associated with their least consumed prey, oikopleurans, and not associated with total prey abundance. The positive correlation with specific, highly consumed prey taxa, instead of overall prey abundance or lesser consumed species suggests that herring may be tracking key zooplankton taxa in the estuary. Thus, the spatial dynamics of prey within estuaries may influence the function of particular locations as nursery grounds for some fish species.

Environmental gradients that simultaneously influence fish and zooplankton spatial distributions in the estuary can create opposite or overlapping distributions between fish and their prey. For example, abundance of barnacle cyprids, highly consumed prey for herring, had a negative relationship with temperature (Arbeider et al. in prep), while we found higher abundances of herring at higher temperatures in the estuary. The opposite affinity of fish and prey across a temperature gradient could explain why barnacle cyprid abundance was negatively associated with herring abundance across the estuary. A different case can be made for herring and highly consumed taxon, calanoid copepods, which covaried positively. While calanoid copepods were more abundant in higher salinity environments (Arbeider et al. in prep), we found herring in more turbid regions of the estuary associated to lower salinity environments closer to river outflow. Despite differences in broad-scale distribution patterns resulting from environmental variation across the estuary, a strong correlation between herring and calanoid copepod abundances exists. This further suggests that prey dynamics may structure estuary fish abundance patterns at a finer-spatial scale.

The distribution of estuary fish and their prey is likely driven by a combination of broader-scale environmental gradients as well as finer-scale processes. Both Arbeider et al. (in prep.) and Chapter 2 of this thesis found a patchy distribution of prey and salmon abundance, respectively, with higher abundances found at some locations and not others across the Skeena River estuary. Zooplankton distribution patterns are known to be influenced at finer-scale by estuary hydrodynamics. Prey aggregations can be found along converging water currents such as river plumes and tide lines (De Robertis et al. 2005), within bays which provide a physical barrier to water circulation (Jones et al. 1990) and concentrating along nearshore environments (David et al. 2016). In addition, tides and winds can contribute further to these more fine-scale water circulation patterns (Schlacher & Wooldridge 1995; Gómez-Erache et al. 2000; De Robertis et al. 2005; Peterson & Peterson 2009). However, we found no evidence that fish distribution patterns were influenced by general zooplankton abundance and it is unclear how these hydrodynamic processes could be influencing individual prey taxa. Although the abundance of calanoid copepods can explain aspects of herring distribution in the estuary, we must recognize that as a large-scale field study, our analyses are correlative. We cannot rule out the possibility that herring are utilizing certain nearshore locations for other purposes such as predator refuge, while consuming calanoid copepods (simultaneously concentrated in nearshore environments) or if they are selecting certain estuary locations due to higher abundances of prey.

Potential positive relationships between fish abundances and their prey may be obscured by predation and depletion. Coastal ecosystems are generally thought to be driven by bottom-up dynamics, with the abundance of basal resources being an effective predictor of higher trophic levels (Ware 2005). However, predation, especially by mass migrations of transient predators like salmon, can deplete prey abundances (Healey 1979; Fulton 1985; Salo et al. 1989; Shiimoto et al. 1997; Springer & van Vliet 2014). For example, the feeding intensity of chum fry in Puget Sound and Nanaimo estuary was linked to decreased abundance of a relatively rare but preferred prey species of harpacticoid copepod (Feller & Kaczynski 1975; Healey 1979). Thus, it is possible that preferred prey could have explained the spatial distributions of their predators if we could have accounted for prey depletion or quantified local prey production (rather than abundance).

We found no evidence of associations between abundances of coho salmon, sockeye salmon and smelt abundance and prey abundance across the estuary. For coho salmon, we used decapod zoaea as a preferred prey (Arbeider et al. in prep); however, both larval fish and insects were found to be more than twice as important to diet composition than decapod larvae based on IRI scores. We were not able to include these prey taxa in our analysis as our plankton sampling method did not capture larval fish or zooplankton effectively (Arbeider et al. in prep). Interestingly, harpacticoid copepods and calanoid copepods were by far the most highly consumed species by sockeye salmon and smelt respectively, but did not contribute to explaining their abundance patterns. As discussed above, intensive feeding could mask fish-prey correlations patterns across the estuary, especially for rare taxa such as harpacticoid copepods (Healey 1979; Fujiwara & Highsmith 1997). In addition, other factors such as distance from shore, or factors unaccounted for (e.g., currents and interspecific competition) may be more important to smelt distribution patterns than prey abundance. Zooplankton and fish abundance were also highly dynamic and variable, perhaps more in-depth sampling might have detected more relationships between fish abundance and their prey.

### **3.5.2. Estuary Utilization by Forage Fish Species**

Using a broader dataset from two years, we examined which abiotic and biotic factors explained the spatial abundances of smelt and herring across the Skeena River estuary. Previously we found that water characteristics (e.g., turbidity), spatial distribution, tidal and vegetative habitat characteristics influence juvenile salmon abundance patterns in the estuary (Chapter 2). Here we developed similar models for smelt and herring, which were highly abundant during the spring/summer in this region, and discovered that their abundances are primarily related to abiotic variables. Specifically, we discovered that herring abundances were higher in locations with higher temperatures, lower secchi depths (higher turbidity), and lower distances to shore (Figure 3.2). Warmer temperature and low visibility are hypothesized to contribute to the nursery function of estuaries. In general, turbidity from river plumes are thought to provide increased cover from predation (Blaber & Blaber 1980; Simenstad et al. 1982; Gregory & Levings 1998), but may also may enhance visual contrast of prey resulting in higher feeding success for juvenile herring (Boehlert & Morgan 1985). Increased

biomass of forage fish species, including herring, is positively associated with warmer temperatures in other estuaries (Marshall & Elliott 1998; Abookire et al. 2000) and nearshore environments (Cross et al. 1980). Fish have been observed distributing towards preferred temperatures in fresh and marine water environments to increase metabolism and support increase growth rates (Garside & Tait 1958; Javaid & Anderson 1967; Straty & Jaenicke 1980; Armstrong et al. 2013). The optimal temperature for juvenile herring was reported as 12.2 °C in one study (Haist & Stocker 1985), which is on the warm end of the range of temperatures we observed in the Skeena River estuary (9.2 – 12.6 °C). Interestingly, temperature and turbidity did not generally co-vary with each other; except during spring freshet when colder river waters create a temperature gradient across the estuary. Collectively these findings suggest that temperature and turbidity are two major environmental gradients that structure herring distribution patterns across the estuary.

Abiotic variables such as turbidity and temperature did not explain variation in smelt abundance. Smelt were negative associated with tidal stages indicating that smelt tended to be caught more when the tide was dropping and periods around slack tide. However, there is some evidence that we caught higher smelt abundances at higher tide heights; although this trend is uncertain it may suggest that the highest abundances of smelt were caught during periods of high slack tides. Similarly smelt may be found more abundantly related to more saline conditions but there is high uncertainty surrounding this finding. Higher abundances of surf smelt have been found at lower salinities on a similar geographic scale in the Skagit River estuary (Reum et al. 2011) and in lower saline conditions related to the estuarine mixing zone of the Columbia River estuary (Bottom & Jones 1990). The region sampled in this study only represents a portion of the estuary, thus it is possible that surf smelt may be associated on an estuary-wide scale to salinity gradients (estuarine mixing zone vs. tidal-fluvial zone). Further research investigating smelt distribution across the estuary is needed to understand broad-scale distributions of smelt abundance.

Our analyses reveal that there tended to be higher abundances of both herring and smelt close to shore in the Skeena River estuary. Previous work has documented that juvenile herring concentrate in shallow sheltered regions and hypothesized that shelter provided by nearshore environments was likely driving this trend (Hourston 1959). Nearshore environments provide shelter for forage fish species from adverse wind and

wave activity, and shoreline complexity creates refuges from strong currents, such as back eddies (Hourston 1959). Additionally, nearshore environments can have higher habitat complexity, including intertidal vegetation, which provides more shelter from predation (Heck et al. 2003; Alofs & Polivka 2004). Our results support the importance of nearshore habitat for both herring and smelt.

We found high densities of both juvenile and adult herring and surf smelt using the Skeena River estuary during the spring and early summer. Thus, these species use estuaries throughout their life-cycle, in contrast with salmon which use the estuary as they move through it as out-migrating juveniles and again as returning adults. Herring and other forage fish can be found in low numbers in estuaries during winter months but use temperate estuaries in high densities in spring and summer months presumably due to high food availability, warm water temperatures and potentially even shelter from adverse weather (Abookire et al. 2000). While most herring and smelt individuals collected were of the smaller size classes indicative of being juveniles, we also observed some large adult individuals. Large spawning events for herring typically occur in outer regions of the Skeena River estuary during March-April (DFO 2016), although mature adult herring and associated spawning events have been found in May and June (Stantec 2016). Spawning behavior of smelt has not been researched in the estuary but a spawning event in June was documented within our study area (Carr-Harris 2017). As this is the second study (Higgins & Schouwenburg 1973) examining how forage fish are using the Skeena River estuary, there remains significant knowledge gaps regarding the larger estuary fish community. Other ecologically and traditionally important forage fish species such as long-fin smelt (*Spirinchus thaleichthys*), sandlance (*Ammodytes hexapterus*) and eulachon (*Thaleichthys pacificus*) are found in the estuary. Given the key role forage fish play in supporting many species in the coastal food web (Therriault et al. 2009), further research targeting the patterns of estuarine use by these species is needed.

### **3.5.3. Conclusions**

We found evidence linking the abundances of a forage fish species to the distribution of a highly consumed prey taxon in the Skeena River estuary in one of the four fish species that we examined. Specifically, our results indicate that herring may be tracking preferred prey abundances across the estuary but did not observe any such

associations for juvenile sockeye salmon, coho salmon, or surf smelt. We also developed habitat models for herring and smelt—herring were more abundant in warmer and more turbid waters that were closer to shore. Smelt were also more abundant closer to shore. Understanding connections between trophic levels in estuary food webs will advance understanding of changes to estuary environments over time, including potential risks from degradation of estuary habitat (Kennish 2002; Lotze et al. 2006) or climate-induced changes (Stewart et al. 2005; Ji et al. 2010), but remain challenging.

## Chapter 4. General Discussion

The aim of this thesis was to examine what abiotic and biotic factors contributed to distribution of juvenile salmon and forage fish in the Skeena River estuary. I found that various combinations of abiotic and biotic variables explained distribution for juvenile salmon and forage fish species in the estuary (Chapter 2 and 3).

Environmental variables, such as temperature and turbidity have been strongly associated with structuring abundance and distribution of estuary fish communities, as shown in the Skeena River estuary (Marshall & Elliott 1998; Wagner & Austin 1999; Harrison & Whitfield 2006). Water temperature was positively related to abundances of sockeye salmon, Chinook salmon and herring abundance distributions in the estuary, while turbidity was a determining factor for sockeye salmon and herring. Selecting for higher temperature and turbidity have been linked to increased growth rate (through higher metabolic capacity) (Straty & Jaenicke 1980) and increased cover from predators (Blaber & Blaber 1980), respectively. Distance from shore was another variable structuring abundance patterns for all fish species except sockeye salmon. As sockeye salmon are generally associated with neritic habitats this trend is not surprising (Straty & Jaenicke 1980; Simenstad et al. 1982). Nearshore habitats provide increased structural complexity associated with decreasing predation (Heck et al. 2003) and may provide higher concentrations of zooplankton trapped along the shoreline (David et al. 2016). Interestingly, sockeye and herring shared the greatest overlap of abiotic contributors, although it is unclear what contributes to this similarity. Overall, I demonstrate that abiotic variables, which may be linked to high growth rates and lower predation, are associated with fish abundance distributions in the estuary.

Biotic variables such as marine vegetation and prey abundance were found to also be associated with fish distribution in the estuary. I found higher abundances of sockeye and Chinook salmon in eelgrass locations than in other habitat types in the estuary. However, eelgrass percent cover was not related to salmon abundances, suggesting that sockeye and Chinook may prefer eelgrass habitat overall, but there was no difference between eelgrass patches of varying densities. Eelgrass is commonly cited as being an important habitat for estuary fish as it contributes high prey diversity and has been shown to reduce predation rate (Gregory & Levings 1996; Heck et al. 2003;

Semmens 2008). Epibenthic zooplankton, such as harpacticoid copepods, associated with benthic substrate such as eelgrass and macroalgae are important prey for many fish species, including sockeye salmon in the Skeena estuary (Arbeider et al. in prep; Healey 1979; Thistle et al. 1984; Salo et al. 1989; Fujiwara & Highsmith 1997). However, other types of habitat complexity, including macroalgae vegetation have been shown to be equally important for some fish species (Heck et al. 2003). Higher abundances of coho salmon and sockeye salmon were found at sites with higher macroalgae cover. Further research using stable isotope technology to investigate food web linkages and tagging studies could be used to further quantify the importance of vegetative habitats for juvenile salmon.

This thesis determined whether prey abundance distributions were linked to estuary fish distribution across the estuary, and found that prey abundance was only related to fish abundance for herring. Herring abundance was positively associated with the highest consumed prey taxon (calanoid copepods) – previously determined to be the most important contributor to diet for herring in the Skeena River estuary (Arbeider et al. in prep). As herring abundance was not related to total prey abundance, these results may indicate that herring are selecting habitat based on specific prey dynamics. High predation rates can strongly influence prey populations in estuarine environment (Healey 1979), which could be masking prey distributions in the estuary. To better understand the connection between fish and prey dynamics, future studies could quantify zooplankton production and predation rates and increase zooplankton sampled sizes.

I demonstrated that several environmental variables contribute the abundance of herring and smelt distributions in the estuary (Chapter 3). Various age classes of herring and smelt (adult and juvenile) were found using the estuary during spring and summer months. Further analysis is required to determine if juvenile and adult herring are distributed according to distributed according to different environmental variable. Juvenile herring may rear in nearshore and estuary environments until maturation before heading offshore, while some populations may be resident (Lassuy & Moran 1989). It is unclear what proportions of these fish are migratory or reside in estuary habitat year-round, although the presence of mature adults and small spawning events may be indicative of a resident population (DFO 2012). Further work examining the broad scale abundance patterns in the region could illuminate the role of estuaries on forage fish populations in British Columbia. In addition, herring distribution can be related to

daylight, as herring undertake diel migrations and are found feeding in surface waters during night at higher abundances than during the day (Emmett et al. 2004). Thus, sampling at night may provide further insight into the regions and habitats herring are utilizing in the Skeena River estuary.

For estuaries to be defined as nursery regions for juvenile salmon or forage fish, the positive influence of particular estuary habitat on juvenile fish density, growth, survival must be demonstrated according to one study (Beck et al. 2001). For example, juvenile steelhead utilization of salt-marsh habitat has been linked to increased growth rates and higher overall survival (Bond et al. 2008). In the Skeena River estuary, there is evidence of growth and prolonged estuary residence for many juvenile salmon species (Carr-Harris et al. 2015; Moore et al. 2015a, 2016). Although this research demonstrates the potential importance of the Skeena River estuary as a whole, nursery function is assessed as the relative contribution of juveniles to adult populations from discrete spatial units (Beck et al. 2001; Dahlgren et al. 2006). Recent research has begun to expand the nursery hypothesis to incorporate more complex dynamics such as migration pathways, resource dynamics (e.g., nutrients and food from adjacent habitats) and physical factors (e.g., salinity and dissolved oxygen) (Nagelkerken et al. 2015; Sheaves et al. 2015), however, the aim of understanding the role of nursery habitats in estuaries is to prioritize conservation of certain habitats (Beck et al. 2001) or spatial arrangements of habitats (Nagelkerken et al. 2015). In Chapter 2, I advanced this knowledge in the Skeena River estuary by mapping the spatial abundance patterns for juvenile sockeye, coho and Chinook salmon on a finer-scale. I found higher abundances consistently at some locations over others, including the Flora Bank eelgrass bed. These results complement historical findings, where highest catches of all species of Pacific salmon, excluding chum salmon (Higgins & Schouwenburg 1973), were also found in this region. We acknowledge that we are using relative abundance as one indicator of habitat value, which previous studies generally support (Dahlgren et al. 2006; Nagelkerken et al. 2015). Other metrics such as growth rate, foraging success and mortality could provide further insight into the relative roles of different regions (e.g., Flora Bank) or specific habitats (e.g., eelgrass beds). For example, comparing growth and foraging success in eelgrass versus non-eelgrass locations could illuminate the nursery function of specific habitats in the Skeena River estuary. Other techniques including stable isotope analysis (Bottom et al. 2008) and tagging (Semmens 2008) would provide finer-scale information

to determine if fish are utilizing certain habits preferentially. Understanding the importance of certain habitats or regions may allow for prioritization for future conservation and management planning.

This thesis assessed fish abundance patterns of five species within one region of the Skeena River estuary during late-spring and summer. Further research investigating the utilization of estuary habitat by fish communities across seasons, similar to Bottom & Jones 1990, would be beneficial for future conservation and development planning. In addition, examining how fish are using estuarine habitat in inner and outer regions would allow comparisons across broader environmental gradients, exposure levels and different habitats. For example, investigating the juvenile salmon use of salt-marsh habitat located in the tidal region of the lower Skeena River (upper extent of the estuary) may elucidate where a small percentage of Chinook salmon in the Skeena River go upon emergence as fry (Gottesfeld & Rabnett 2007). Chinook, chum and steelhead salmon fry have been found heavily utilizing salt-mash habitat in other estuaries and it has been linked to higher growth rates and survival for these salmon species (Levy & Northcote 1982; Macdonald et al. 1987; Levings et al. 1991; Fukuwaka & Suzuki 1998; Bond et al. 2008; Hering et al. 2010). Salt-marsh habitat along the Skeena River experienced degradation from historic highway and railway construction; although some restoration activity has been completed (White 2011), the importance of salt-marsh habitat for juvenile salmon in the Skeena River estuary is unknown.

#### **4.1. Management Implications**

Environmental decision making for aquatic environments in Canada is based on policies from the Canadian Environmental Assessment Act (S.C. 2012, c.19, s.52) and the Fisheries Act (R.S.C. 1985 c. F-14, s. 35). Risk to aquatic habitats from proposed development and potential impacts are quantified through the environmental assessment (EA) process. Under the EA process, risks to aquatic habitat are reduced through mitigation towards the aim of achieving no net loss of habitat, a main tenure of the Fisheries Act. Habitat degradation or destruction are mitigated through rebuilding or restoring equivalent habitat elsewhere. These policies are based on several assumptions – habitat compensation is effective and is actually performed, habitats are equivalent and that importance of certain habitats can be quantified accurately. In practice, no net loss habitat compensation rarely achieves ecosystem function and

productivity (Quigley & Harper 2006). Although there are some cases where habitat productivity and function were restored, such as salt-marsh habitat in the Fraser River estuary (Levings & Nishimura 1997), it is clear that no net loss habitat conservation goals are not being reached (Kistritz 1996; Quigley & Harper 2006; Favaro & Olszynski 2017). Further, my research suggests that understanding the importance of specific habitats in complex and dynamic environments such as estuaries remains a challenge. Certain habitat types such as salt-marsh habitat have been successfully linked to estuarine use by juvenile chum and Chinook salmon, however the contributions of other habitat types (e.g., eelgrass and mudflats) (Levings 1982; Kistritz 1996) to other fish and estuary food-webs remain poorly understood.

The findings of this thesis advance understanding about the contributing factors of estuarine habitat use for juvenile salmon and highlight a high level of uncertainty with explaining abundance patterns. Using simple habitat classifiers to explain abundance, I found that sockeye and Chinook salmon were more abundant in eelgrass habitat compared to other habitat types. However, the predictive capability of using this modeling approach was low. We consistently found high abundances of juvenile salmon at the Flora Bank eelgrass region but not abundantly at other eelgrass sites. I also determined that other environmental and physical factors such as temperature, turbidity and distance to shore explained abundance salmon abundance for certain species of salmon. While predictive capacity was higher when using abiotic and biotic variables to predict abundance patterns for juvenile salmon, high uncertainty remained. These findings highlight the complex nature of describing estuary use by a mobile species in a dynamic environment. It is difficult to have high confidence in the ability to achieve no net loss of habitat given major project developments if there is not high understanding in the identity of important habitat.

My results suggest that there is great scientific uncertainty in the efficacy of mitigation of environmental risk through habitat compensation of eelgrass habitat. Replacing damaged eelgrass habitat, such as the proposed damage of eelgrass on Flora Bank, with eelgrass elsewhere may not result in equivalent habitat productivity or to the same high degree of use by marine organisms when compared to original eelgrass habitat. Spatial arrangement of habitats, environmental variables, biotic interactions (competition and predation), food availability and local hydrology could limit utilization of one habitat or region over another.

One of the foundational questions that my project raises is: how much do we need to understand about the importance of certain habitats to make informed decisions for development? In other words, how much risk are we willing to take? The level of acceptable risk that people are willing to take is a value-based decision, not a science-based decision. What science can do, as I have done here, is quantify the scientific uncertainty and thus the risk associated with different approaches. Based on my experiences, environmental decision-making processes in Canada such as performed by the Canadian Environmental Assessment Agency (CEAA) do not generally state what level of risk they are willing to take and quantify how decisions are made. This lack of scientific transparency in decision-making criteria is a major flaw in current environmental assessment, according to leading Canadian scientists (Westwood et al. 2017).

While current approaches for assessing risk often rely exclusively on habitat-based approaches such as mapping exercises or remote sensing, it can also be possible to directly quantify the importance of habitat through field programs such as this thesis. Simple habitat classification and mitigation may be logistically easier, but our results demonstrate that they have great scientific uncertainty and pose risks of loss of important habitat. Although abundance is not a direct measure of habitat importance, locations with higher abundances are likely to have a higher habitat value (Dahlgren et al. 2006; Nagelkerken et al. 2015). This is not a novel concept, abundance was historically used to quantify environmental risk posed by industrial development in Canada. In 1973, Department of Fisheries and Oceans used abundance along with presence of eelgrass in the Skeena River estuary to inform decision making on a superport development proposed for Kitson Island and Flora Bank (Higgins & Schouwenburg 1973). They concluded that “the mouth of the shallow estuarine areas between Porpoise Channel and the mouth of the Skeena River are of high biological significant as a fish rearing habitat”. In situations where the potential risks are high, such as locations like the Skeena with important salmon populations that support economies and cultures, perhaps the bar for the degree of acceptable uncertainty should be higher. These cases may call for larger field studies such as ours and the historical studies of Flora Bank.

Currently, the Skeena River estuary remains relatively pristine compared to other large estuaries such as the Fraser and the Columbia River estuaries. Over the timeline

of this research (2015 - 2017), it was the proposed location for eight Liquefied Natural Gas (LNG) shipping terminals (Aurora LNG 2014; Prince Rupert LNG Ltd. 2017), of which six proposals currently remain at various stages of the environmental assessment process (Province of British Columbia 2014, 2015; Exxon Mobil 2015; Woodside Energy Holdings Pty Ltd. 2015; Pacific Northwest LNG 2016; Pembina Pipeline 2017). Given the sheltered location of the study area, nearby large-scale port development (Prince Rupert) along with railroad and highway accessibility, further proposed development in the future remains a high probability. I am hopeful that this thesis contributed to understanding how and why estuarine environments support economically, ecologically and traditionally important salmon and forage fish resources and contributes to on-going decision-making and planning processes.

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## Appendix A. Supporting material for Chapter 2

**Table A.1. Candidate model set (those from the global model set with a  $\Delta\text{AICc} < 2$ ) used for multi-modal inference of sockeye, coho and Chinook salmon abundance in the Skeena River estuary. Top models (most parsimonious with  $\Delta\text{AICc} < 2$ ) used to compare model approach A and B are highlighted in bold. All models contain site and time period as random effects.**

Species	Model Parameters (fixed effects only)	<sup>a</sup> k	<sup>b</sup> $\Delta\text{AICc}$	<sup>c</sup> weight
sockeye	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover + tide height	9	0	0.166
	salmon			
	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover	8	0.5	0.132
	net + year + secchi depth+ temperature + macroalgae cover + tide height	8	0.8	0.11
	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover + tide height + tide stage	10	1.4	0.081
	<b>net + year + secchi depth+ temperature + tide height</b>	7	1.5	0.08
	net + year + secchi depth+ temperature + macroalgae cover + tide height + tide stage	9	1.5	0.077
	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover + tide height + distance to river	12	1.6	0.076
	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover + tide height + salinity	10	1.6	0.074
	net + year + secchi depth+ temperature + macroalgae cover + eelgrass cover + tide stage	9	1.6	0.074
net + year + secchi depth+ temperature + tide height + tide stage	8	1.8	0.066	
net + year + secchi depth+ tide height + macroalgae cover	7	1.9	0.063	
coho	net + secchi depth+ distance to shore + macroalgae cover + tide height	7	0	0.289
salmon	<b>net + secchi depth+ macroalgae cover + tide height</b>	6	1.3	0.152
	net + secchi depth+ distance to shore + macroalgae cover + tide height + exposure	8	1.3	0.138
	net + secchi depth+ distance to shore + macroalgae cover + tide height + salinity	8	1.5	0.126
	net + secchi depth+ distance to shore + macroalgae cover + tide height + temperature	8	1.7	0.119
	net + secchi depth+ distance to shore + macroalgae cover + tide height + eelgrass cover	8	1.8	0.112
	net + secchi depth+ distance to shore + macroalgae cover + tide height + year	8	1.9	0.063
Chinook	net + distance to shore + macroalgae cover + temperature + salinity	7	0	0.18

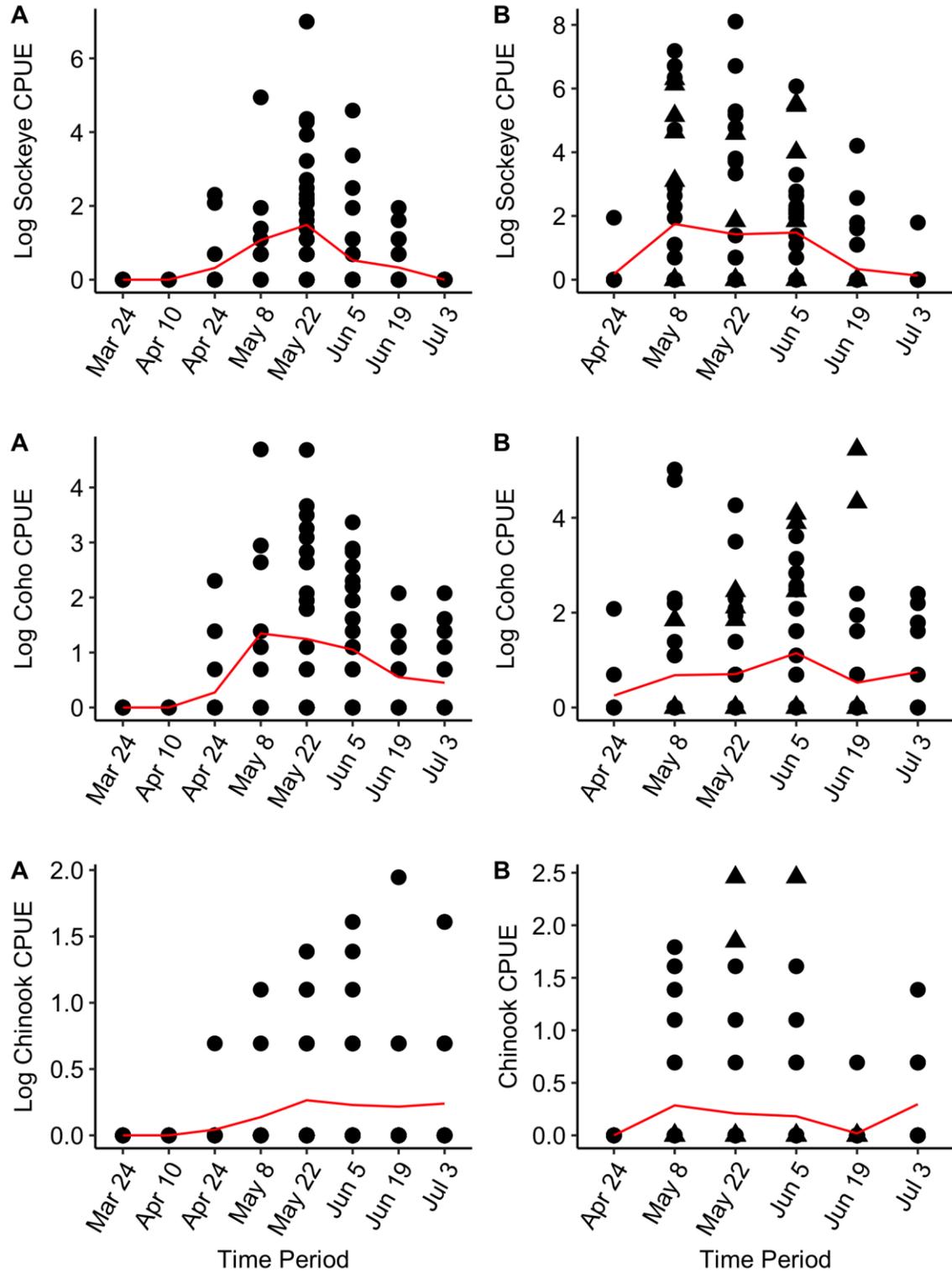
salmon	net + distance to shore + macroalgae cover + temperature + salinity + eelgrass cover	8	0.7	0.127
	net + distance to shore + macroalgae cover + temperature	6	0.8	0.12
	net + distance to shore + macroalgae cover + temperature + salinity + tide stage	8	1.3	0.095
	net + distance to shore + macroalgae cover + temperature + secchi	7	1.4	0.089
	<b>net + distance to shore + macroalgae cover</b>	5	1.5	0.085
	net + distance to shore + macroalgae cover + temperature + eelgrass cover	7	1.6	0.082
	net + distance to shore + temperature + salinity	6	1.7	0.076
	net + distance to shore + macroalgae cover + temperature + salinity + year	8	1.7	0.075
	net + distance to shore + macroalgae cover + temperature + distance to river	7	1.9	0.069

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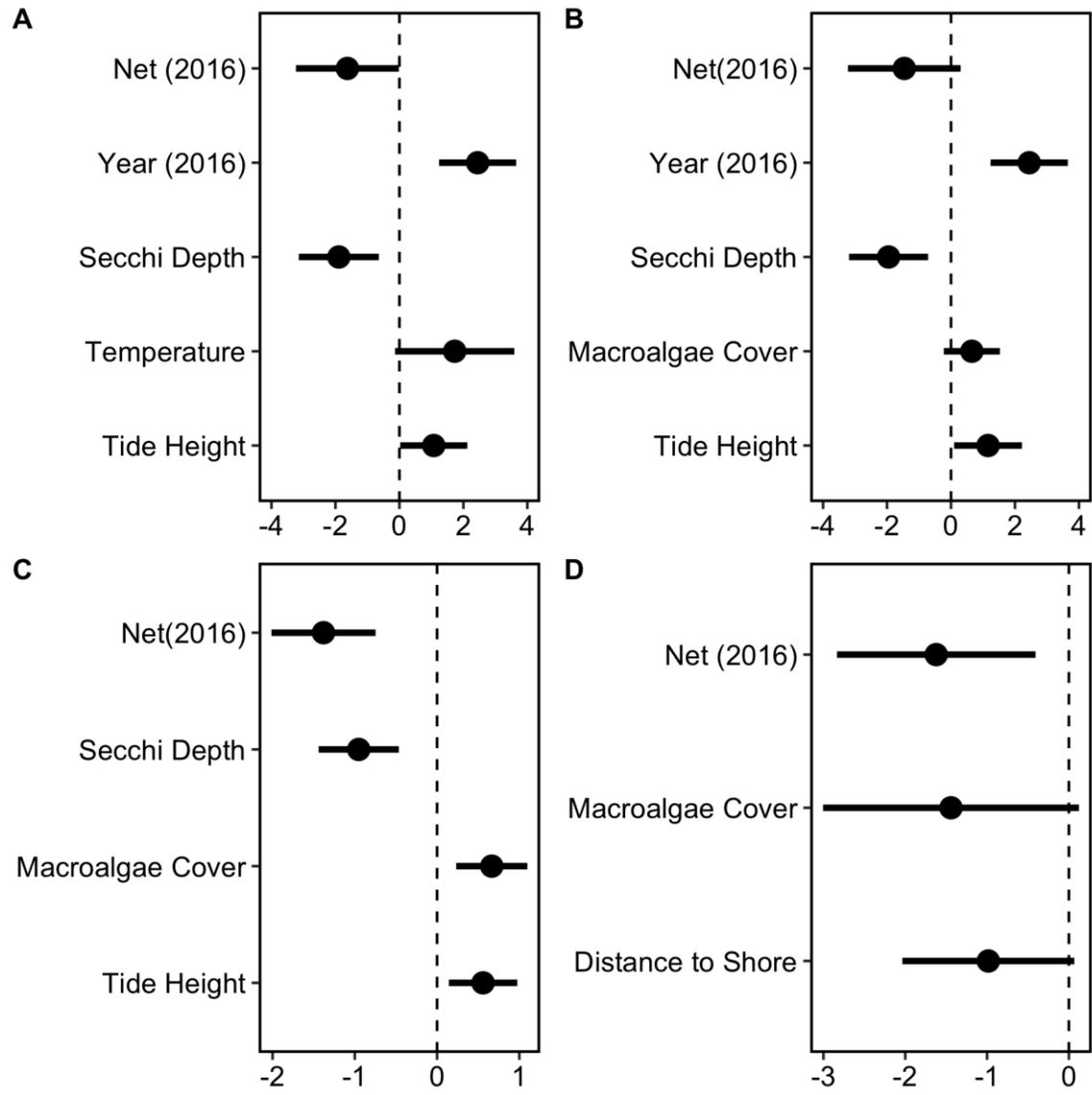
<sup>a</sup> k = number of model parameters. <sup>b</sup>  $\Delta$ AICc = change in AICc score from top model. <sup>c</sup> weight = AICc model weigh

**Table A.2. Global models for modeling approaches A) abiotic and biotic variable modeling and B) habitat type modeling. Site and time period are modeled as crossed random effects. All modeling was performed in R package, glmmTMB (Magnusson et al 2016).**

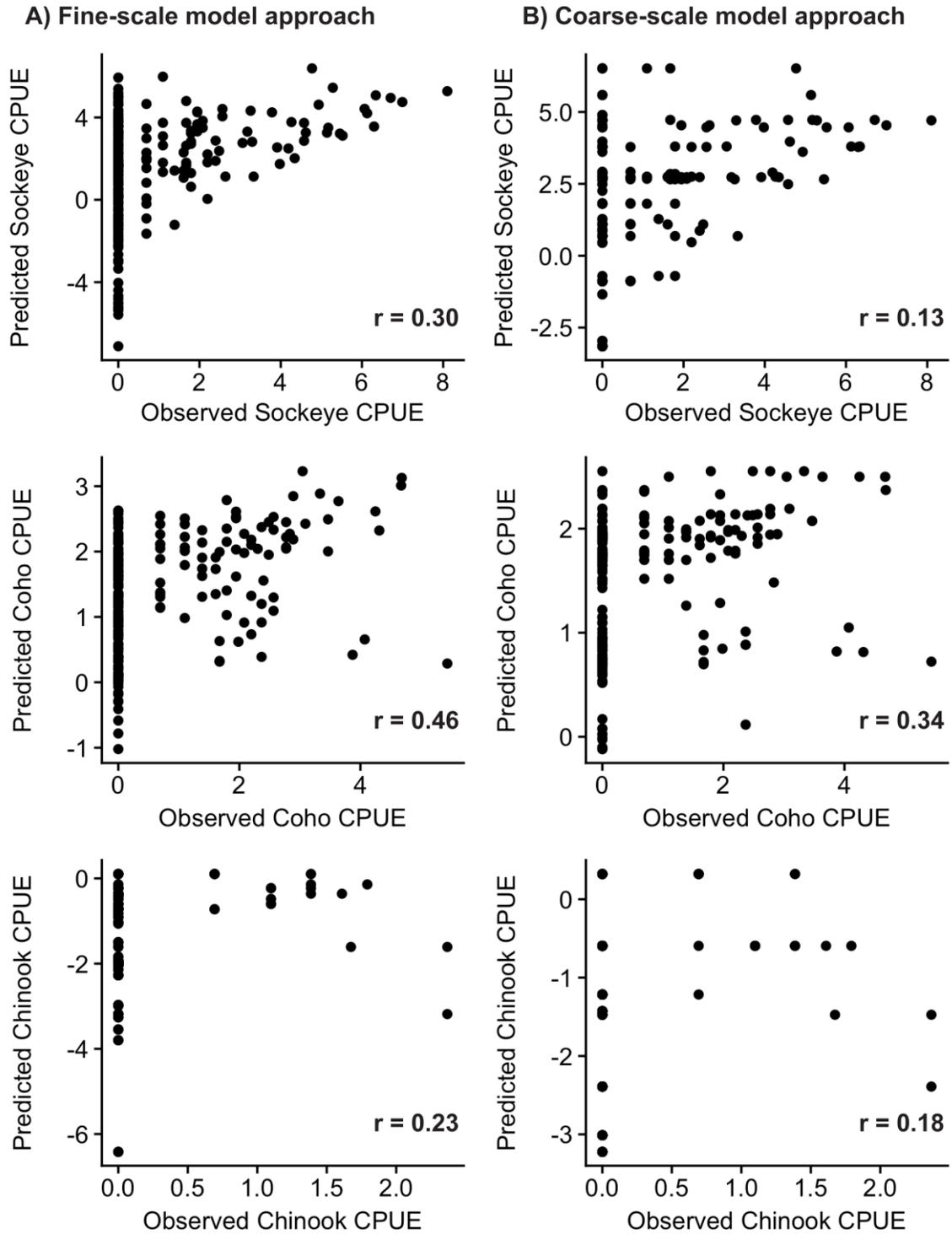
<b>Modeling Approach</b>	<b>Global Model</b>
A	(1   time period) + (1   site) + net type + year + eelgrass cover + macroalgae cover + distance to river + distance to shore + secchi depth + salinity + temperature + tide height + tide stage + exposure
B	(1   time period) + (1   site) + net type + year + site type



**Figure A.1. Temporal pattern of CPUE (grouped by period) for sockeye , coho and chinook in the estuary for A) 2015 and B) 2016 for big purse seine net (●) and small purse seine nets (▲). Mean CPUE across time periods illustrated in red.**



**Figure A.2** . Standardized parameter estimates (dots) and 95% confidence intervals (bars) from top models (most parsimonious within  $\Delta AICc$  less than 2) for modeling approach A – abiotic and biotic variables for sockeye (a, b represent both top models), c) coho and d) Chinook salmon. Top models from modeling approach A were used to compare with top models from modeling approach B (Chapter 2) and determine if prey abundance further explained fish abundance (Chapter 3). Coefficients are related to the (log) mean of normalized CPUE.



**Figure A.3.** Log observed versus log predicted juvenile sockeye, coho and Chinook abundance (CPUE) for top models from model approach A) fine-scale and B) coarse scale approaches for assessing habitat.  $r$  = Pearson correlation coefficient of predicted and observed CPUE.

## Appendix B. Supporting material for Chapter 3

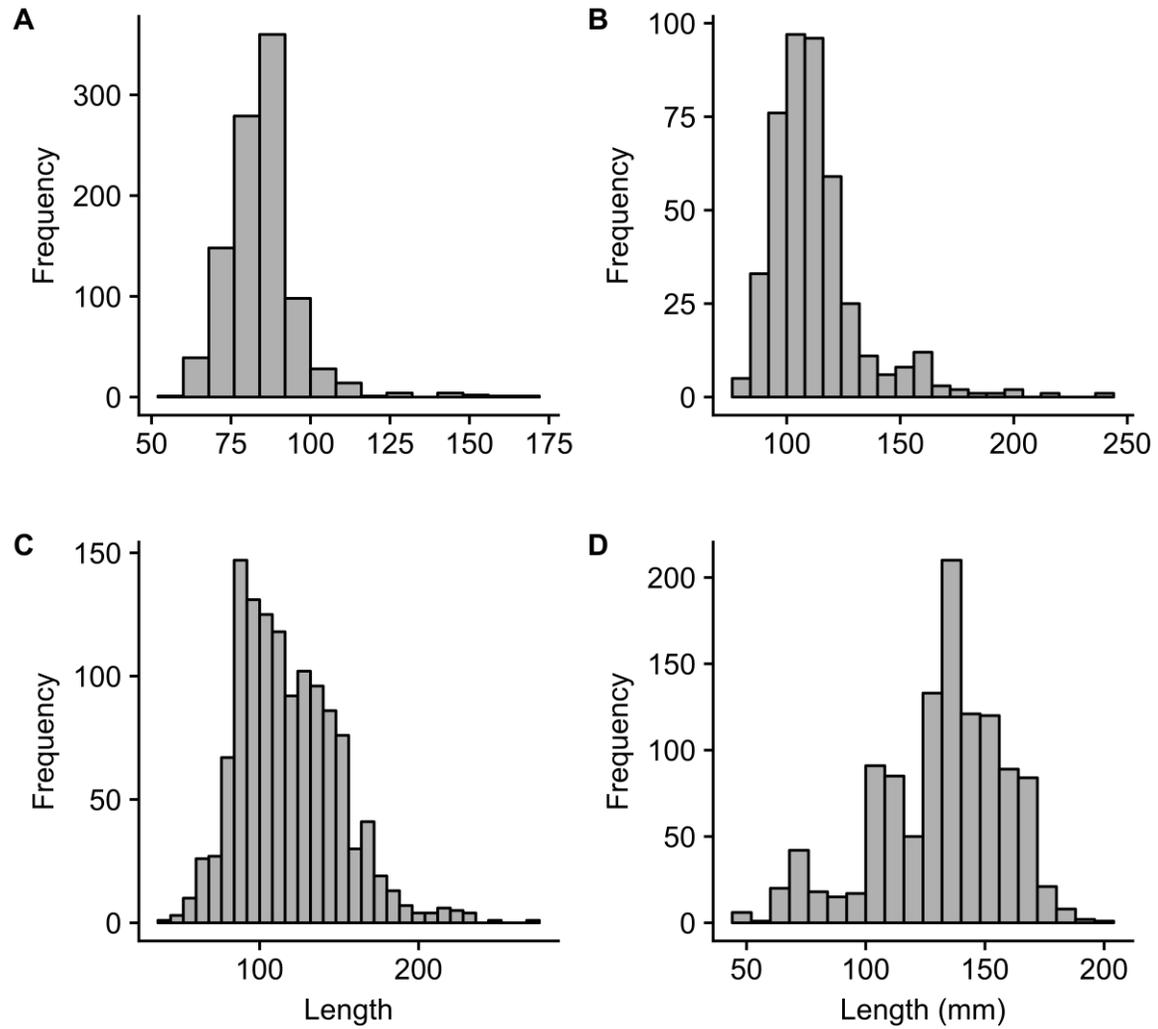
**Table B.1. Candidate model set (those from the global model set with a  $\Delta\text{AICc} < 2$ ) used for multi-modal inference of herring and smelt abundance in the Skeena River estuary. Top models (most parsimonious with  $\Delta\text{AICc} < 2$ ) used as “null habitat models” to model prey abundance are highlighted in bold. All models contain site and time period as random effects.**

Species	Model Parameters (fixed effects only)	<sup>a</sup> k	<sup>b</sup> $\Delta\text{AICc}$	<sup>c</sup> weight
herring	year + distance to shore + tidal stage + secchi depth + temperature	7	0	0.122
	distance to shore + tidal stage + secchi depth + temperature + net type	7	0.3	0.104
	year + distance to shore + secchi depth + temperature	6	0.5	0.097
	distance to shore + secchi depth + temperature + net type	6	0.6	0.09
	<b>distance to shore + secchi depth + temperature</b>	<b>5</b>	<b>1.1</b>	<b>0.069</b>
	distance to shore + secchi depth + temperature + net type + eelgrass cover	7	1.2	0.068
	year + distance to shore + tidal stage + secchi depth + temperature + net type	8	1.2	0.065
	distance to shore + tidal stage + secchi depth + temperature + net type + eelgrass cover	8	1.3	0.064
	year + distance to shore + tidal stage + secchi depth + temperature	8	1.4	0.061
	year + secchi depth + temperature + tide height + exposure + net type	7	1.5	0.059
	distance to shore + tidal stage + secchi depth + temperature	6	1.7	0.052
	year + distance to shore + tidal stage + secchi depth + temperature + macroalgae cover	8	1.7	0.052
	distance to shore + tidal stage + secchi depth + temperature + net type + algae cover	8	1.7	0.051
	year + distance to shore + secchi depth + temperature + net type	7	1.9	0.046
smelt	year + distance to shore + tidal stage + tide height + salinity	7	0	0.143
	year + distance to shore + tidal stage + tide height	6	0.6	0.105
	year + distance to shore + tidal stage + salinity	6	1	0.089
	year + distance to shore + tidal stage + tide height + secchi depth	7	1	0.088
	<b>year + distance to shore + tidal stage</b>	<b>5</b>	<b>1.3</b>	<b>0.073</b>

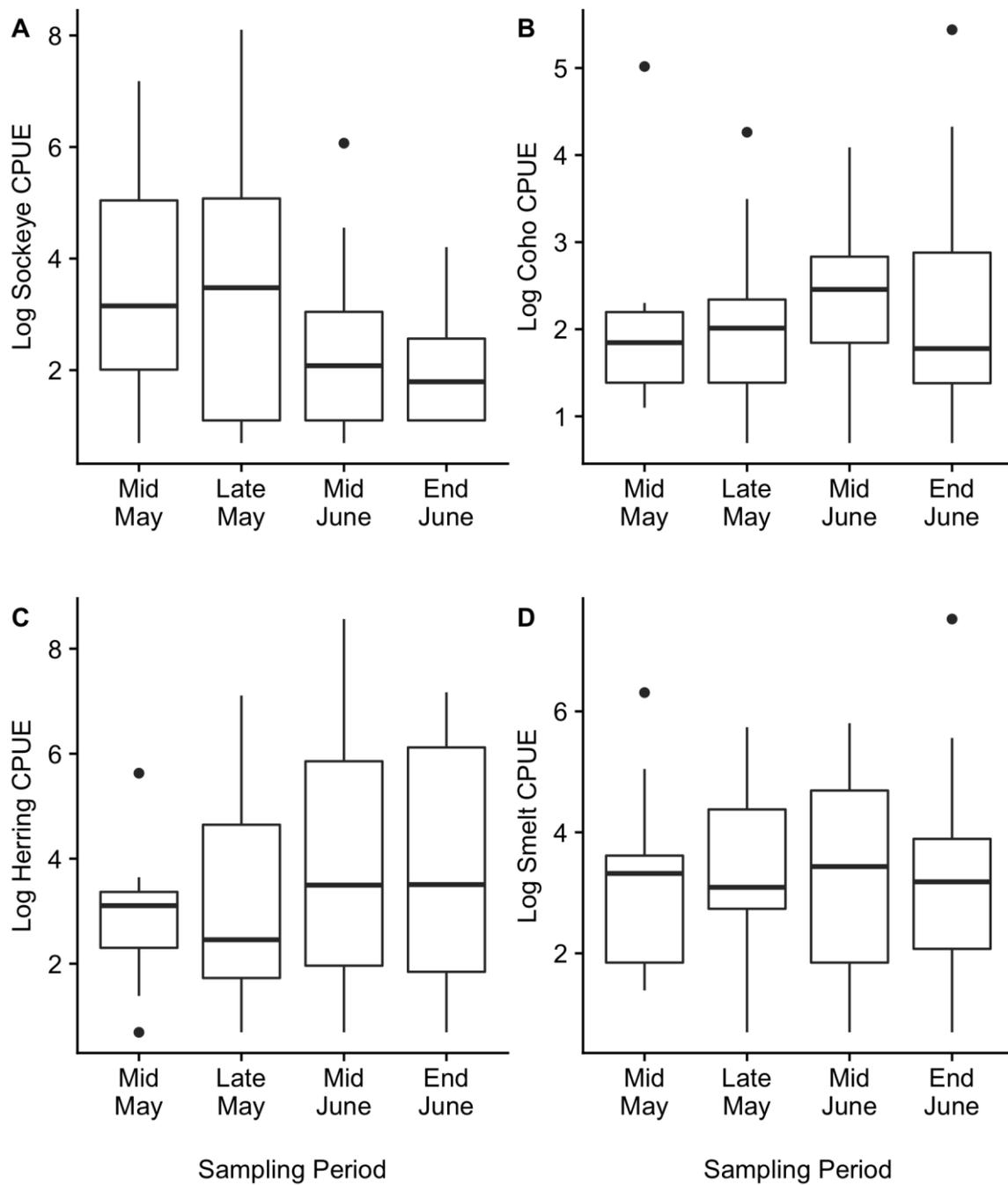
year + distance to shore + tidal stage + tide height + salinity + net type	8	1.4	0.07
year + distance to shore + tidal stage + tide height + macroalgae cover	7	1.6	0.065
year + distance to shore + tidal stage + tide height + salinity + macroalgae cover	8	1.6	0.064
year + distance to shore + tidal stage + tide height + temperature	7	1.6	0.063
year + distance to shore + tidal stage + temperature	6	1.6	0.063
year + distance to shore + tidal stage + tide height + salinity + exposure	9	1.8	0.059
year + distance to shore + tidal stage + secchi depth	6	1.8	0.059
year + distance to shore + tidal stage + tide height + salinity + temperature	8	1.8	0.059

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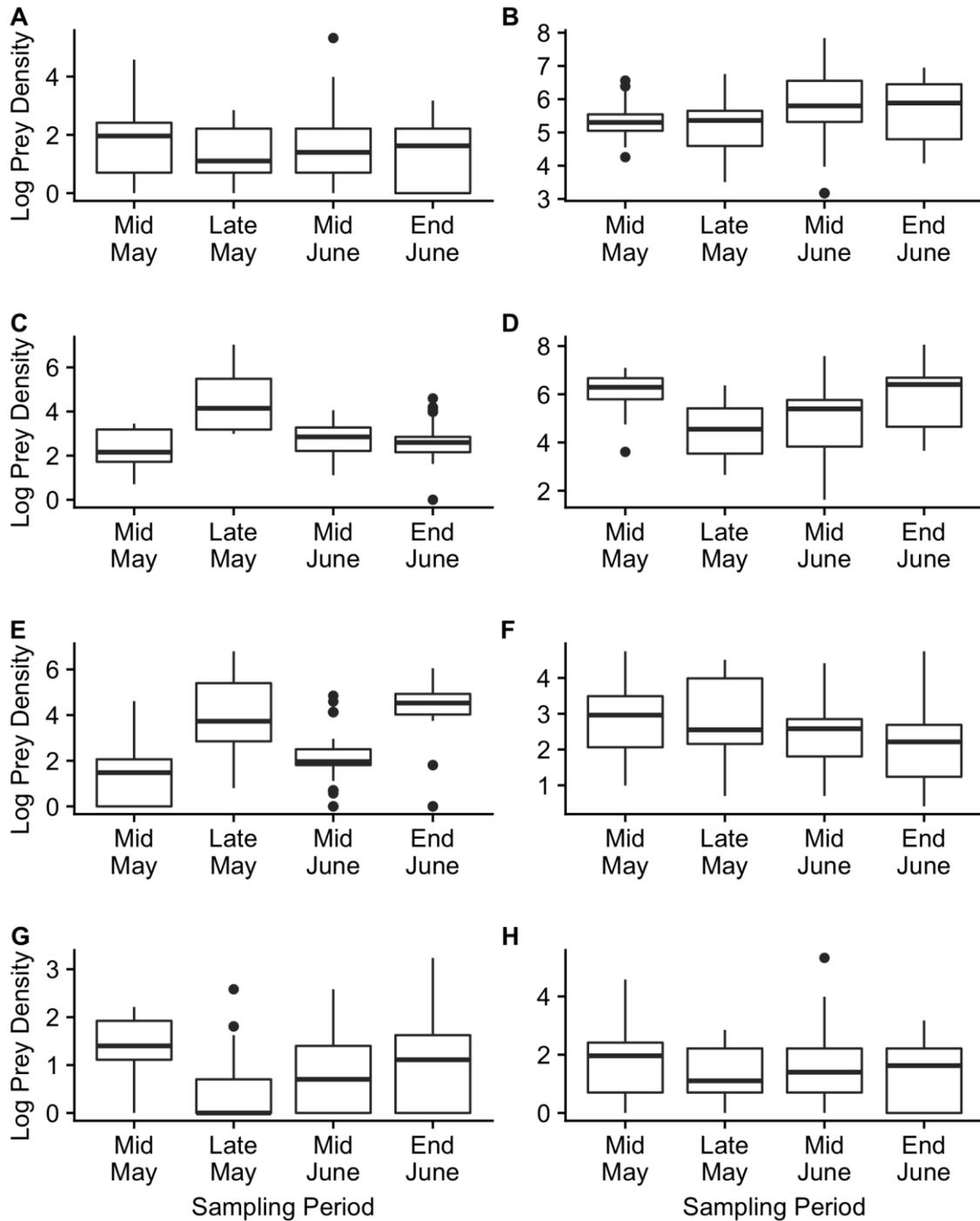
<sup>a</sup> k = number of model parameters. <sup>b</sup>  $\Delta$ AICc = change in AICc score from top model. <sup>c</sup> weight = AICc model weight



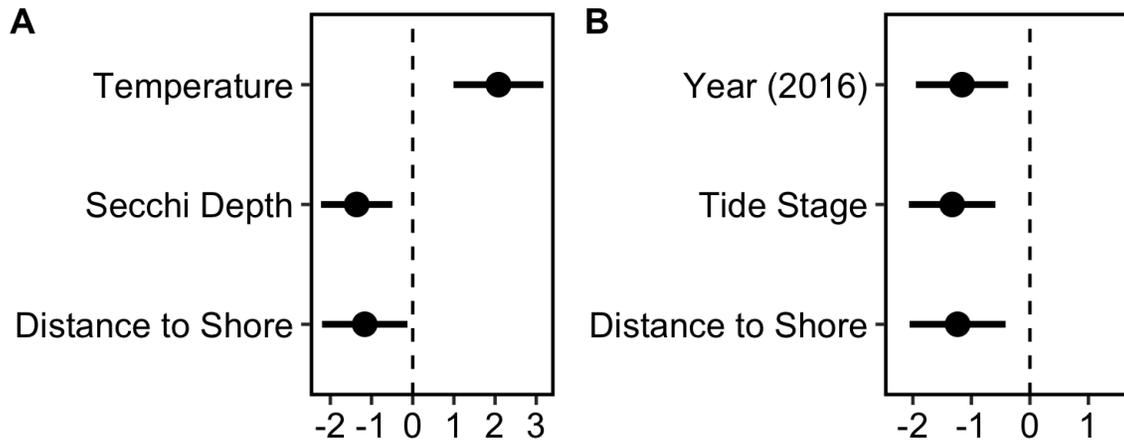
**Figure B.1. Length distribution for A) sockeye salmon, B) coho salmon, C) herring and D) smelt captured in seine nets in the Skeena River estuary.**



**Figure B.2.** Abundance (as estimated by CPUE) of A) sockeye, B) coho, C) herring and D) smelt in the estuary across sampling periods. The solid black lines indicate median CPUE for each sampling period, while box boundaries indicate first and third quartiles and whiskers indicate the highest and lowest values of fish CPUE.



**Figure B.3.** Abundance (as estimated by density; count per m<sup>3</sup>) of selected prey taxa, A) harpacticoid copepod, B) calanoid copepod, C) barnacle cyprid, D) barnacle nauplii, E) oikopleuran, F) gastropod, G) decapod zoea and H) total prey abundance, across sampling period in the estuary. The solid black lines indicate median prey abundance for each sampling period, while box boundaries indicate first and third quartiles, and whiskers indicate the highest and lowest values of prey abundance.



**Figure B.4.** Standardized parameter estimates (dots) and 95% confidence intervals (bars) from top models (most parsimonious within  $\Delta AICc$  less than 2) for A) herring and B) smelt salmon. Top models were used as “null habitat models” to determine if prey abundance further contributed to fish abundance across the estuary. Coefficients are related to the (log) mean of normalized CPUE.