Migratory bottlenecks as integrators of species- and population-level diversity: the Skeena River estuary, its salmon, and industrial development

Running title: Skeena River estuary and salmon biodiversity

Charmaine Carr-Harris[1,2]

Allen S. Gottesfeld[1]

Jonathan W. Moore[2]

[1]Skeena Fisheries Commission; 3135 Barnes Crescent, Kispiox, British Columbia, CANADA V0J 1Y4.

[2]Earth to Ocean Research Group, Simon Fraser University; 8888 University Drive, Burnaby, British Columbia, CANADA V5A 1S6.

Author to whom correspondence should be addressed: Charmaine Carr-Harris; ccarrharris@gmail.com

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Abstract

We quantify how an estuarine migratory bottleneck supports population- and species- level diversity of salmon. The estuary of the Skeena River is under pressure from industrial development, with two gas liquefaction terminals and a potash loading facility in various stages of environmental review processes at the same time as recent changes to Canadian environmental laws have reduced the timeframe for federal environmental assessments. We conducted a juvenile salmonid sampling program throughout the Skeena River estuary in 2007 and 2013. We captured all species of juvenile salmonids throughout the estuary in both years, and found that areas proposed for development support some of the highest abundances of some species of salmonids. Specifically, the highest abundances of sockeye (both years) Chinook in 2007, and coho salmon in 2013 were captured in areas proposed for development. For example, juvenile sockeye salmon were 2-8 times more abundant in the proposed development areas. Genetic stock assignment demonstrated that the Chinook salmon and most of the sockeye salmon that were captured originated from throughout the Skeena watershed, while some sockeye salmon came from the Nass, Stikine, Southeast Alaska, and coastal systems on the northern and central coasts of British Columbia. These fish support extensive commercial, recreational, and First Nations fisheries throughout the Skeena River and beyond. Our results demonstrate that estuary habitats integrate species and population diversity of salmon, and that proposed development in these areas will threaten the fisheries that depend on these fishes.

Keywords: biodiversity, Canada, corridor, habitat, migration, nursery, smolt, watershed

Introduction

Animal migrations connect diverse habitats across space and time, but these migrations are globally threatened (Wilcove & Wikelski, 2008). Migratory species not only rely on the key habitats for feeding, breeding, or other life history processes, but also need connectivity among those habitats. While some migratory populations move over broad swaths of land, others move through migratory bottlenecks (Berger, Young & Berger, 2008). Migratory bottlenecks are areas along migratory routes where migration is constrained, leading to aggregation. For example, the oasis at Eilat (Elat), Israel is an important resting stop used by many species of Old World bird species during flights between Europe and sub-Saharan Africa (Safriel, 1968). Degradation of these key habitats could adversely affect multiple species or populations that rely on these migratory bottlenecks. For instance, human encroachment further threatens already depleted Saiga populations in Mongolia (Berger, Young & Berger, 2008), while road and residential development near a migratory bottleneck at Trappers' Point in western Wyoming, USA, threatens several populations of pronghorn and mule deer (Sawyer, Lindzey & McWhirter, 2005). Thus, identifying migratory bottlenecks is a critical step in the management and conservation of migratory species and populations.

Estuaries link freshwater and marine habitats for diadromous species such as Pacific salmon (*Oncorhynchus* spp.). Thus, estuaries may serve as bottlenecks during two transitions of salmon life history—first, in the spring when juvenile salmon leave freshwater rearing habitats and undertake their seaward migration and then again in the summer and fall when adult salmon return to freshwater to spawn. Estuaries are staging areas and transition zones where juvenile salmonids physiologically adapt to saltwater environments (Heard, 1991). The early marine life

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history stages, including estuarine residence, are among the most critical life history stages for juvenile salmon (Parker, 1968; Simenstad & Cordell, 2000; Kareiva, Marvier & McClure, 2010) and the growth attained during this period can determine whether they survive to reproduce (Mortensen, Wertheimer & Landingham, 1999; Beamish & Mahnken, 2001; Farley, Moss & Beamish, 2007). Some species, such as pink (*Oncorhynchus gorbuscha*), chum (*O. keta*) and Chinook (*O. tshawytscha*) salmon may remain in estuaries for weeks or months during their downstream migration (Kareiva, Marvier & McClure, 2010). For large watersheds that contain several salmon species and potentially hundreds of locally adapted salmon populations, estuaries may thus represent key migration bottlenecks that support high salmon biodiversity.

The Skeena River of British Columbia, Canada, is an example of a large watershed with high salmon biodiversity. All species of Pacific salmon and steelhead (*O. mykiss*) spawn throughout this 55,000 km^2 watershed, representing hundreds of populations (Morrell, 2005). The life-histories of these various species and populations are different, ranging from pink and chum salmon, which enter marine waters immediately after emergence as planktivores less than 30 mm in length, to coho salmon (*O. kisutch*) which spend one or two years in freshwater prior to their downstream migration, and are partially piscivorous when they arrive at sea, sometimes preying on juvenile pink and chum salmon (Parker, 1971). Within the different populations of each species there is considerable genetic, phenotypic and life-history diversity, encompassing variation in run timing, age structure, and preferred spawning habitats (Gottesfeld & Rabnett, 2008). These fishes support numerous commercial, recreational and First Nations food, social and ceremonial (FSC) fisheries throughout the watershed. During the peak of the commercial fishing industry in the early 1900s, millions of salmon of all species were captured annually by

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seine and gillnet fleets that supported dozens of fish canneries in the Skeena estuary (Blyth, 1991; Gottesfeld & Rabnett, 2005). Variability of these salmon populations now threatens fisheries; for instance low sockeye (*O. nerka*) returns in 2013 led to the unprecedented closure of Skeena commercial, recreational, and First Nations fisheries due to conservation concerns (Pacific Salmon Commission, 2014).

There are currently several large-scale industrial development projects pending in the Skeena River estuary, including a bulk potash loading facility, expanded rail, road, and utility corridor, and two liquefied natural gas (LNG) terminals (Stantec Consulting 2011, 2013; AECOM 2013; Figs. 1, 2). While previous understanding of estuaries in general (Simenstad & Cordell, 2000) and the Skeena River estuary in particular (Manzer, 1956; Higgins & Shouwenburg, 1973) suggest that these habitats support juvenile salmon, consulting agencies on behalf of the project proponents have failed to identify potentially significant impacts to juvenile salmonids and their habitat (Stantec Consulting, 2011, 2013; AECOM 2013). For example, the causeway and berth for one of the proposed LNG terminals is situated between Lelu and Kitson Islands on Flora Bank, which represents 50-60% of tidal and subtidal eelgrass habitat in the Skeena estuary, and was previously found to be among the most important early marine habitats for pink salmon from the Skeena watershed (Hoos, 1975). Nevertheless the project description that was submitted to the Canadian Environmental Assessment (CEA) Agency for assessment of this project (Stantec Consulting, 2013) was based on reports that did not include any field studies of juvenile salmon.

Canadian environmental law has been recently revised by significant changes to the CEA Act and the Fisheries Act (Favaro, Reynolds & Cote, 2012; Hutchings & Post, 2013). While supporters of the new laws maintain that they will strengthen environmental protection while reducing the regulatory burden for industrial development, there is concern about decreased regulatory oversight, environmental protection, and accountability in industrial development (Hutchings & Post, 2013). Regional offices have closed and staffing levels have been reduced as a result of budget cuts and restructuring of the Department of Fisheries and Oceans (DFO) Fisheries Protection (formerly Habitat Protection) branch. The scope and time frames of environmental reviews, as well as the number of projects that must complete a federal environmental assessment, have been reduced by the new CEA Act (Gibson, 2012), while the responsibility for significant aspects of the environmental review process have shifted away from the federal DFO to other jurisdictions (Doelle, 2012). For example, a Memorandum of Understanding between the DFO and the National Energy Board, which regulates and promotes oil and gas development in Canada, assigned to the latter the responsibility for determining whether a fisheries assessment is required for pipeline stream crossings (National Energy Board, 2013). Following changes to the Fisheries Act in 2012, only fish that support commercial, recreational, or Aboriginal fisheries remain protected (Government of Canada, 2012), meaning that in order to deny a proposed project on the basis of potential damage to fish habitat, it must first be demonstrated that fisheries are supported by the habitats in question. At the time of writing, the proposed potash terminal had completed the CEA Agency's review process under the old legislation and was approved to proceed to the permitting stages. The two LNG terminals entered the environmental assessment process under the new regulations.

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Here we examine a potential migratory bottleneck as a key integrator of population- and species-level diversity. Specifically, we investigated whether the estuary of the Skeena River acts a key migratory bottleneck for anadromous salmon that support fisheries, with implications for impending industrial development. We undertook a sampling program in order to examine the geographic and temporal habitat utilization of five species of Pacific salmon in the greater Skeena estuary and how these relate to the footprints of the proposed development projects. These data can help quantify which species and populations are at risk of being affected by habitat loss in these areas. If the estuary of the Skeena River is significant habitat for salmon that support fisheries, the proposed new developments will test Canada's new environmental laws.

Methods

Study area

The main stem of the Skeena River, which drains approximately 55,000 km^2, is approximately 570 km long with a mean discharge of about 1,750 m^3/s. The Skeena River enters the ocean near the village of Port Edward on the north-west coast of British Columbia, where it divides into three channels at a group of islands near the mouth of the river. All of the proposed developments fall within the jurisdiction of the Prince Rupert Port Authority near the exit of the northernmost and central channels, both of which flow northward. At peak flood, the zone of freshwater influence extends approximately 50 km southwest through Ogden Channel, and northwest through Chatham Sound and out Dixon Entrance (Figs. 1 and 2).

Diversity of Skeena River salmon

Salmon escapements to the Skeena River included approximately 668,000 sockeye, 2.5 million pink, 88,000 coho, and 36,000 Chinook salmon in 2009 (Pacific Salmon Commission, 2014). The total returns are much higher when the various fisheries are taken into account. The Northern Boundary Technical Committee of the Pacific Salmon Commission estimate an average run size of nearly 3,000,000 sockeye salmon (1985-2012) with an average exploitation rate of 41% (Pacific Salmon Commission, 2014), and an average exploitation rate of about 50% for Chinook salmon (Pacific Salmon Commission, 2014). Chum salmon are the least numerous of the commercially exploited anadromous species, with estimated escapements of several thousand in recent years (English, 2012), considerably less than historical abundances (Price, Gayeski & Standford, 2013). Steelhead salmon returns to the Skeena during the past decade have been between 20,000 and 50,000 (Hooton, 2011).

Salmon populations, or stocks, may be defined geographically, genetically, or by other means (Waples, 1998). Within the Skeena watershed, there are up to 70 sockeye, 55 Chinook, 133 coho, 75 even-year pink, 81 odd-year pink, and 34 chum salmon stocks associated with specific spawning areas (Morrell, 2000). In addition to the Skeena River, salmon from other watersheds such as the Nass River and several smaller coastal systems in the region may also utilize the Skeena River estuary. Populations may also be separated by their degree of genetic differentiation, which varies according to gene flow; the rate of migration between populations (Waples, 1998). Thus the genetic structures of the different pink, chum and coho salmon populations, which have higher straying rates, are less well defined than for Chinook and sockeye salmon populations (Quinn, 2004). At present, there are 29 Skeena Chinook salmon and 29 Skeena sockeye salmon populations for which baseline genetic data are available that can be reliably separated using microsatellite variation (Beacham et al., 2005, 2006). These populations represent geographically and genetically distinct spawning stocks throughout the Skeena watershed, and the baselines are continually modified as new populations are added (Beacham et al., *In press*). The 29 Skeena sockeye salmon populations of the genetic baseline includes populations from 15 different lakes and four river-type populations. Some lakes contain more than one population. For example, Babine Lake, the largest sockeye salmon rearing lake in British Columbia, accounts for up to 90 percent of Skeena River sockeye salmon production and contains ten known populations. Populations are spatially related, such that multiple populations from a single lake are more closely related than populations from different lakes. Thus the overall population structure groups the different populations into reporting units that roughly cluster the populations within the different rearing lakes (Beacham et al., *In press*).

Fish sampling

We collected juvenile salmonids by trawl between May 26 and July 5, 2007, and from May 5 to July 1, 2013. Trawl sampling was conducted using a midwater trawl which was fished from an 11 m ex-gillnet vessel, HMV Pacific Coast. The trawl net was 18 m long with an opening 5 m wide and 4.6 m deep, with a rigid, baffled holding box designed for live capture (Gottesfeld et al., 2009). The trawl net was deployed for a targeted duration of at least 15 min and up to 20 min for an approximate tow length of 1 km, depending on the velocity of prevailing currents. Trawl sites were aggregated into generalized regions according to their relative proximity to the northern or southern exit of the Skeena River (Fig. 1). The 2007 trawl sampling program was more extensive than in 2013, and encompassed five regions (Inside North (IN), Outside North (ON), Middle (MID), Inside South (IS), and Outside South (OS)), while the 2013 program encompassed only three regions (IN, IS, and OS) (Fig. 1). Hereafter we refer to these as "regions". The IN region contains the proposed industrial development footprints.

Beach seine sampling was carried out from April 29 to June 13, 2013 in order to sample the nearshore fish community. Beach seining occurred weekly at shoreline sites close to proposed industrial activities near the northern entrance to the Skeena River (Fig. 2). The beach seine net was 35 m long and 3 m deep, with 13 mm mesh at the tow ends and 6 mm mesh at the bunt. Each beach seine sampling event consisted of a single set, during which the seine net was deployed down-current from an anchor point on the beach using a 3 m vessel. The beach seine sites were all located within the IN region, and were grouped according to the island or inlet where each site was located (Fig. 2). Hereafter we refer to these as "groups". The Ridley Island and Lelu Island groups are within proposed industrial development footprints.

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

Statistical analysis

We analyzed trawl CPUE for sockeye, coho and Chinook salmon with generalized additive models (Hastie & Tibshirani, 1990). Specifically, generalized additive models were constructed to estimate the overall mean CPUE for each species in each region in each year by applying a non-parametric smooth function to day-of-year and treating the different regions as parametric factors. The resulting model is of the form

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

where Y is the CPUE (mean normalized catch per 20 min set) for a given species, f is a thin-plate regression spline smoother (Wood, 2003) for day of year d, and the β coefficient is the mean abundance for each region x. In essence, these models examine the relative effect of each region on catch rate, after controlling for time. We ran a separate model for each species and each year using a negative binomial distribution with a log link. β is thus an estimate of the relative CPUE of a region, and is on a log-scale. We used the fitted models to predict the relative abundances of each species at regular intervals in each region during the sampling period, which were backtransformed to produce estimates of the CPUE at each region for each prediction interval. Generalized additive models were constructed using the mgcv package (Wood, 2006) in the R programming environment (R Core Team, 2013).

Genetic analysis

Tissue samples were collected for DNA analysis from a subsample of Chinook and sockeye salmon specimens. Small pieces of the upper caudal fins were preserved by desiccation on filter paper. DNA was extracted and amplified by polymerase chain reaction (Withler et al., 2002) at 13 microsatellite loci for Chinook salmon (*Ots2, Ots9, Ots100, Ots101, Ots102, Ots104, Ots107, Ssa197, Ogo2, Ogo4, Oke4, Oki100, Omy325*; Beacham et al., 2006) and 14 microsatellite loci for sockeye salmon (*Ots2, Ots3, Ots100, Ots103, Ots107, Ots108, Ok1a, Oki1b, Oki6, Oki10,*

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Oki16, Oki29, One8, Omy77; Beacham et al., 2005). The polymerase chain reaction products were size-fractionated on denaturing polyacrylamide gels, and allele sizes were determined with an ABI 3730 capillary DNA sequencer. Genotypes were scored with GeneMapper software v3.0 (Applied Biosystems) using an internal lane sizing standard (Beacham et al., 2005). Allele frequencies were compared with coastwide baselines of 243 sockeye populations from 20 regions, and 207 Chinook populations from 39 regions using a Bayesian procedure (Pella & Masuda, 2001), in which individual probabilities and stock proportions were assigned using a modified, C-based version of the program BAYES (Neaves et al., 2005). Genetic analyses were performed at DFO's Molecular Genetics Laboratory at the Pacific Biological Station.

The population of origin for each specimen was determined based on the geographic distribution of the most likely genetic assignments. We accepted individual assignments above a probability threshold of 90%. Where the probability of assignment to a specific population was less than 90%, we assigned populations to coarser resolution groups of lake, sub-basin, basin, or larger areas depending on the geographic distribution of the five most likely population assignments.

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

Results

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Spatial and temporal distribution of juvenile salmonids

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

Different species of salmon had different patterns of temporal abundance in the Skeena River estuary. High abundances of juvenile pink salmon were observed during early-season beach seine sets, and were captured in diminishing abundance from the first day of sampling until the second week of May 2013. The highest abundances of juvenile chum salmon were captured by beach seine between the second and fourth weeks of May. Smaller numbers of pink and chum salmon were captured by trawl in 2007, and pink but not chum salmon in 2013. Juvenile coho salmon were observed in trawls from the middle of May onward in both years, and in high abundances in beach seine sets in the third and fourth weeks of May 2013. Juvenile Chinook salmon were captured throughout the sampling period in both years and by both gear in 2013, and in much higher abundances in 2007 than in 2013. Juvenile sockeye salmon, which were only captured by trawl, were the most abundant species captured by trawl in both 2007 and 2013. Sockeye salmon were continually present in the study area from May 26 (the first day of sampling) to July 5 in 2007, and from May 13 until July 1 (the last day of sampling) in 2013, with peak abundances observed between the last week of May and the first week of June in both years (Fig. 3).

The different species of juvenile salmon were differently prevalent at the four groups of sites sampled by beach seine (Fig. 4). Sockeye salmon were not caught in beach seine sets but were abundant in nearshore trawls, in some cases within 20 m of shore. Pink salmon were most abundant in beach seine sets, especially at Kinahan Islands and at Ridley Island close to the proposed industrial developments (Fig. 4a). Most chum salmon were captured in the Tsum Tsadai Inlet area, outside of the proposed development footprint. The highest beach seine catches for coho and Chinook salmon were at the Lelu Island and Ridley Island groups (Fig. 4c and d), both of which are in proposed development areas.

The different species of juvenile salmon were also differently distributed among the trawl sampling regions. The highest abundances of juvenile sockeye salmon in trawl sets were captured in the IN region in both years (Fig. 5a), the region with the proposed industrial developments. For regions that were sampled in both years, the abundances of juvenile sockeye and coho salmon captured by trawl were similar within regions across years (Fig. 5). The highest abundances of juvenile Chinook salmon were captured by trawl in the IN region in 2007, and evenly distributed between the IN and IS regions in 2013 (Fig. 5). In 2007, the highest abundances (mean normalized trawl catches for all weeks) of both pink and chum salmon were captured in the ON region (not sampled in 2013) at two of the northernmost sites close to Portland Inlet, which drains the Nass River, and empties into Chatham Sound (Fig. 5c and e). In

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2013, the highest abundances of pink salmon captured by trawl were found in the OS region (Fig. 5c).

These observations were supported by general additive modeling which accounted for seasonal variation. Specifically, the GAMs statistically indicated that juvenile sockeye salmon were most abundant in the IN region in both years, and juvenile coho salmon were most abundant in the IN region in 2013 (Fig. 6). The β coefficient for sockeye in the IN region ranged was 1.74 + 0.36 ($p < 0.0001$, this and the following represent the best estimate of the coefficient + 1 SE and P-value of the coefficient) in 2007 and 1.56 + 0.34 ($p < 0.0001$) in 2013 (Fig. 6). The predicted abundances for sockeye in the IN region were 2-8 x higher than in the other regions in both years. For example, the predicted abundances of sockeye on May 28 were 24 sockeye (per 20 minute set) in the IN, 11 in the IS, and 7 in the OS region in 2013, and 27 in the IN, 13 in the IS, 9 in the OS, 3 in the MID and 4 in the ON in 2007. The β coefficients for coho salmon in the IN region were 0.63 + 0.28 ($p = 0.0262$) in 2007 and 0.45 + 0.19 ($p = 0.022$) in 2013 (Fig. 6). The backtransformed predicted abundances of coho were 2-7x higher in the IN than in other regions in 2013, and 2-7x higher in the IN and MID regions than in other regions in 2007. Chinook salmon appeared to be most abundant in the IN region in 2007 and in the IS region in 2013, however neither of these values were significant ($p > 0.05$).

Genetic analysis

Genetic determinations were obtained from 476 sockeye salmon captured in 2007, 361 sockeye salmon captured in 2013, and 19 Chinook salmon captured in 2013. Of these, 92% of the

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sockeye salmon captured in 2007, 96% sockeye salmon captured in 2013, and all of the Chinook salmon originated in the Skeena watershed. Ten Chinook salmon determinations exceeded 90% probability, representing five different populations, and at least seven of the remaining nine came from the more broadly defined Skeena watershed. Four of the five Chinook salmon populations that exceeded the 90% probability threshold were captured in the IN region, including representatives from Nangeese River in the Kispiox sub-basin, Morice River, and Kitsumkalum River. A total of 220 of the individual sockeye salmon determinations from both years exceeded 90% probability, representing 25 individual populations including 15 from the Skeena, two from the Nass, and several from smaller coastal systems in the north and central coasts of British Columbia.

The highest genetic diversities for sockeye salmon were observed in the IN and OS regions. Twelve of the 13 different sockeye salmon stocks that were captured in the IN region originated in the Skeena watershed, including populations from Alastair, Kalum, and Lakelse Lakes in the Lower Skeena, Morice Lake in the Bulkley system, Sustut Lake in the high interior, and four different populations of Babine Lake sockeye. Representatives of 14 different sockeye salmon populations were captured in the OS region, of which eight were Skeena populations, one was from the Kwinageese River in the Nass watershed. Several fish came from nearby coastal lakes such as Lowe Lake in Grenville Channel and Freda and Kooryet Lakes on Banks Island. At least one sockeye salmon came from Namu Lake on BC’s central coast. Most of the specimens whose first probability of assignment did not exceed the 90% threshold were from the Babine drainage (548 of 616). The others, which were grouped by lake, sub-basin, watershed or statistical area came from the other Skeena sockeye lakes, coastal systems, and the Stikine drainage.

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Discussion

Our results indicate that the Skeena River estuary, especially the proposed development footprints, support diverse and abundant juvenile salmon populations. During our two years of sampling, we found that the different species of juvenile salmon occupied areas within the footprint of the proposed development projects continually from the middle of May until at least the beginning of July. Some of the highest abundances of some species were observed in areas proposed for development. Specifically, sockeye salmon were 2-8 times more abundant in the IN region in both years. Chinook salmon were 2-6 x more abundant in the IN than in other regions, and coho salmon were 2-7x more abundant in the IN and MID than in other regions. Juvenile Chinook and sockeye salmon were genetically identified as originating from populations throughout the Skeena watershed and beyond. These data provide evidence that the Skeena River estuary in general, and the proposed development sites in particular, represent a key migratory bottleneck that aggregates high salmon biodiversity.

Adult salmon recruitment, and therefore the productivity of fisheries, is influenced by survival of juveniles during the early marine life-history stages, those we sampled in the Skeena River estuary (Parker, 1968). We captured thousands of juvenile pink salmon by beach seine within the proposed development footprints in the IN region. Pink salmon, which enter marine waters soon after emergence and return to spawn after a single year at sea, occupy littoral habitats for several weeks before moving further offshore (Manzer, 1956). For pink salmon, the earliest marine life-history stage is a critical period of high mortality (Parker, 1968). The relationship between the abundance of pink salmon smolts captured up to two months after emergence and adult returns in the following year in Southeast Alaska is stronger than the relationship between brood year abundance and adult returns (Orsi, Fergusson & Sturdevant, 2012), which implies that the magnitude of the pink salmon return to this area may be determined by survival of juveniles during the early marine life-history stages such as those that we observed in our beach seine samples. Juvenile chum salmon were also captured in high numbers in beach seine sets early in the sampling season. Several dozen larger juvenile chum salmon were captured in an experimental purse seine set in a nearby area in early August (Carr-Harris, unpublished), supporting the possibility that some populations may utilize these habitats for months (Manzer, 1956).

The region with proposed development contained the highest densities of coho and sockeye salmon in both years, and Chinook salmon in 2007. Abundances of sockeye and coho salmon were consistently high in this region in the two years sampled, suggesting that the IN region contains important feeding and holding areas for outmigrating salmon smolts. These results are supported by previous research in the estuary, conducted in the 1950s (Manzer, 1956) and 1970s (Higgins & Shouwenburg, 1973) that found the areas currently proposed for development including the waters around Flora Bank and southeast Ridley Island to be critical habitat for juvenile salmonids (Hoos, 1975). While these results are perhaps not surprising because it is well known that estuaries are critical habitat for juvenile salmon (Heard, 1991; Simenstad & Cordell, 2000; Beck et al., 2001), they contradict the recent reports by proponents' consulting groups that have not reported significant numbers of juvenile salmon in this area (Stantec Consulting 2011, 2013; AECOM, 2013) The most important capture sites for juvenile salmon were within 10 km

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of the northern entrance of the Skeena River, either within the development footprints, or in habitats where juvenile salmon would have to transit through the proposed developments to access. These migrants could be affected by habitat loss as a result of removal of foreshore habitat and dredging, reducing connectivity between freshwater and marine habitats following the installation of causeways and berths, and eventually the effects of pollution and propeller wash from tanker traffic. Cumulative degradation of estuarine habitats could erode the diversity, resilience, and productivity of salmon from the Skeena River and beyond (Bottom et al., 2009).

Our data indicate that the estuary of the Skeena River in general, and the area proposed for developments in particular, is an ecologically significant habitat that integrates diversity of all species of anadromous salmonids from the Skeena River and surrounding areas. We captured representatives of at least five different Chinook salmon populations and 25 different sockeye salmon populations from throughout the Skeena drainage and beyond, and we captured sockeye salmon from most of the Skeena River populations currently represented in the DNA baseline. Specifically, 23 of the 29 sockeye salmon populations in the genetic baseline were represented in the probability distributions for genetic assignment for the combined 2007 and 2013 trawl samples with over 90% probability for 15 different Skeena sockeye salmon populations (Fig. 7). Genetic resolution is expected to improve as the baseline is expanded (Beacham et al., *In press*). On a finer scale, the proposed development region contained particularly high salmon population diversity. Individuals were assigned to 13 sockeye salmon and four Chinook salmon populations. Some of the fish that we captured in the IN region are of conservation concern, such as sockeye salmon from Morice and Lakelse Lakes and chum salmon from throughout the Skeena River watershed, for which low escapements in recent years compared with historical abundances have prompted calls for a recovery plan (Price, Gayeski & Stanford, 2013). Our data indicate that the estuary, especially the area of the proposed development projects, represent a migratory bottleneck for multiple salmon species and populations.

Many of the salmon populations that we sampled near the proposed developments support commercial, recreational, and First Nations fisheries. For example, we captured Chinook salmon from Morice River, which are targeted by the Wet'suwe'ten First Nation in Moricetown, approximately 450 km upriver from our capture sites, and from the Kitsumkalum River, approximately 120 km upriver, which are targeted by recreational fisheries in the Lower Skeena river and in coastal waters (Gottesfeld & Rabnett, 2008). One of the sockeye salmon smolts that we collected at Kinahan Islands (IN zone) in 2013 was previously tagged 450 km upstream at the outlet of Babine Lake. Babine Lake sockeye are targeted by the Area 4 commercial gillnet fishery in Chatham Sound and the mouth of the Skeena River, a commercial terminal fishery in Babine Lake, and as well as First Nations FSC fisheries (Gottesfeld & Rabnett, 2008) which are protected by the Canadian constitution (Government of Canada, 1982). Therefore, habitat loss at as a result of proposed development at the northern exit of the Skeena River has the potential to affect salmon and fisheries throughout the Skeena Watershed. Our data indicates that these habitats, their fish, and their fisheries warrant protection under the terms of the revised Fisheries Act of 2013 (Government of Canada , 2012).

Our study highlights the challenges of relying on proponent-funded research to assess potential environmental impacts of proposed developments. The environmental assessment studies conducted by project proponents provide an opportunity to collect information and identify important juvenile salmonid nursery habitats within the Skeena estuary; but the data collected on behalf of private industries are generally proprietary and inaccessible to independent review, and may be interpreted subjectively and selectively. For example, in 2010, the consulting organization on behalf of the proposed Canpotex potash terminal conducted trawl sampling with similar gear, timing, and site selection as the current study. The data have not been disclosed to the public, and the project's eventual approval was based on an environmental impact statement that concluded that the juvenile salmon that had been observed at those sampling stations were not likely part of the major migration (Stantec Consulting, 2011). Our data indicate the opposite. Economic co-dependency between industry and their private scientists will exert great pressure on the openness and integrity of environmental science (Moore & Moore, 2013). In addition, recent changes to Canada's environmental legislation may facilitate industrial development with potential consequences for the long-term viability and sustainability of natural resources such as salmon (Favaro, Reynolds & Cote, 2012; Hutchings & Post, 2013). The Skeena River watershed is a region where annual salmon migrations sustain the ecosystem, culture, and economies of First Nations, commercial, and recreational fishing sectors (Gottesfeld & Rabnett, 2008). Our data indicates that all surveyed parts of the estuary support salmon, especially the regions that are slated for development. This represents a critical opportunity for science to inform policy, in a region where fisheries protection is of high priority to many groups and communities.

Protection of migratory bottlenecks represent real opportunities to sustain many different populations and species (Berger, Young & Berger, 2008). The Skeena estuary funnels hundreds of millions of juvenile salmon through the transition from freshwater to marine habitats each year. An effective strategy to protect these animals would be to identify and target the most important areas for direct conservation efforts. For example, nursery habitats are specific areas within greater regions that may contribute disproportionately to adult recruitment (Beck et al., 2001). High densities of juveniles are one characteristic of nursery habitats (Beck et al., 2001), and within the greater Skeena estuary, the highest densities and highest diversity of the most ecologically and economically important species of juvenile salmonids were found in the inside north region where development is proposed. Thus, alteration of this habitat could degrade nearby and distant fish populations and their fisheries; conservation of this local habitat would support economies and cultures throughout the Skeena River watershed and beyond. Given that migratory species rely on habitats and connectivity across great distances, there is a challenge and opportunity to align the scales of environmental assessments and resource management with the natural spatial scales of migratory species.

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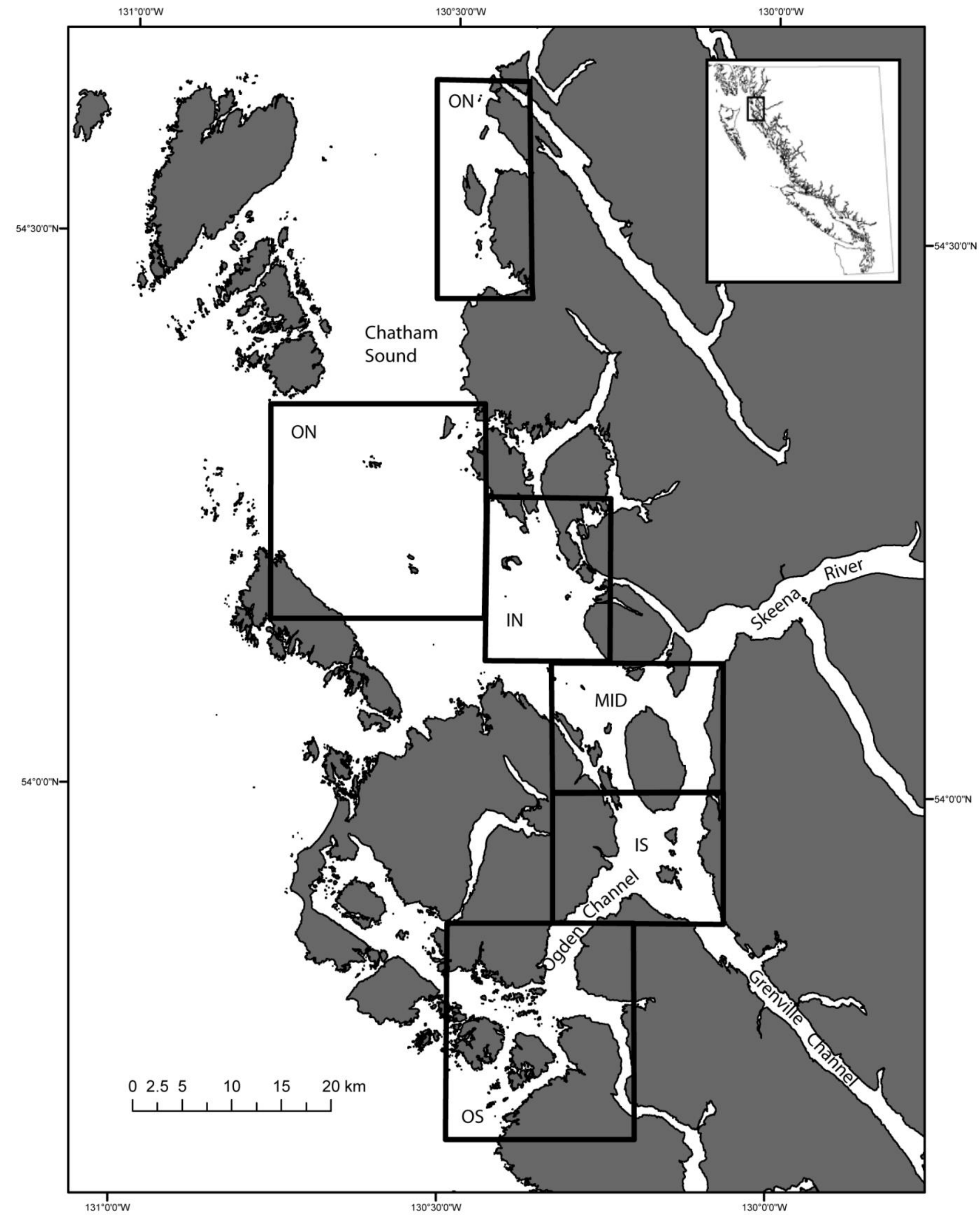

Figure 1. The Skeena River estuary, proposed development, and distribution of juvenile salmon sampling. During the period of highest flow, the zone of freshwater influence extends from the mouth of the Skeena south to Ogden and Grenville Channels, and northwest through Chatham Sound, which also receives freshwater from the Nass River. The study area is shown divided into our analysis regions indicated by the letters IN for inside North, ON for outside north, MID for middle, IS for inside south, and OS for outside south. The IN region contains the focal industrial developments. Note that the ON region includes two polygons.

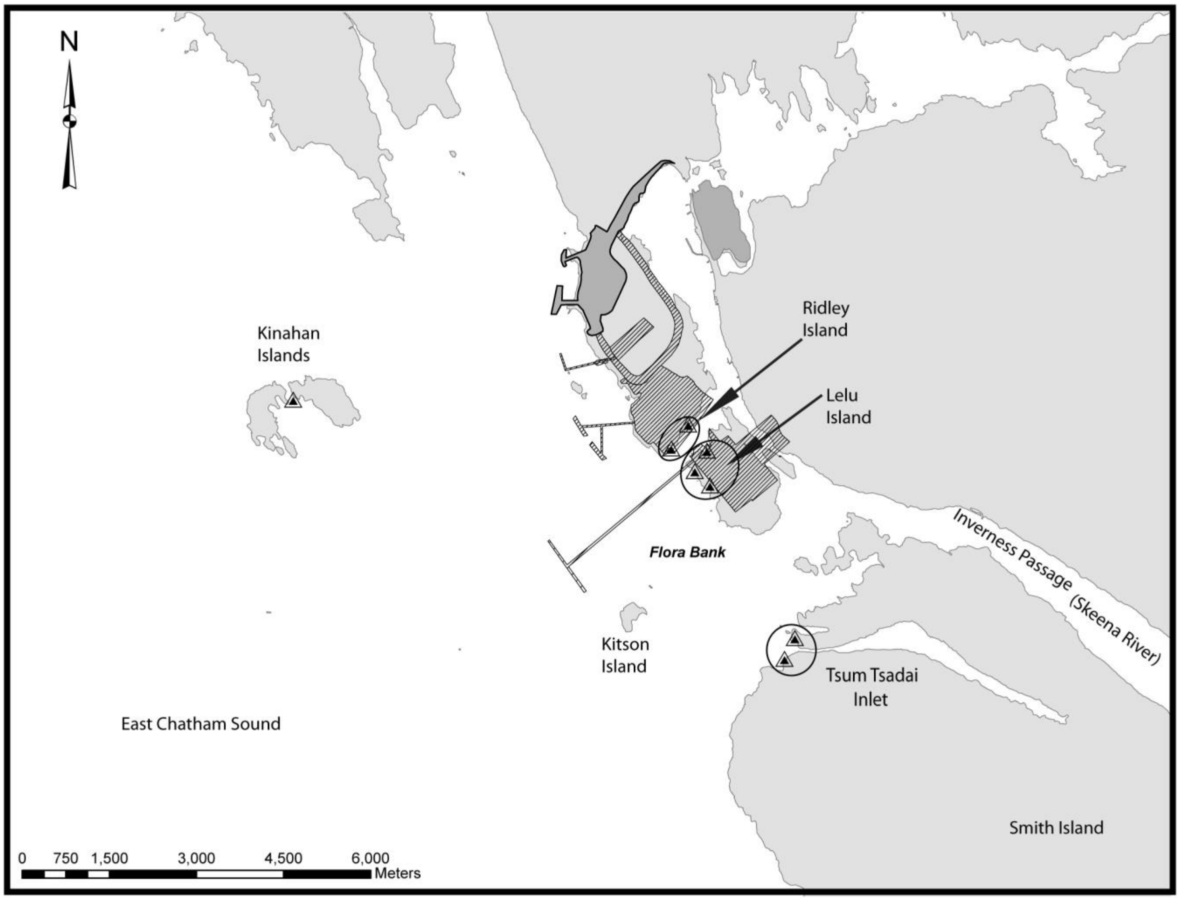

Figure 2. Beach seine sampling stations within the IN region indicated in Fig. 1. Existing developments are shown in dark grey, while proposed development areas are diagonally shaded. Beach seine sampling stations are indicated by triangles. Beach seine site groups are indicated with open circles, except at Kinahan Islands where there was only one site.

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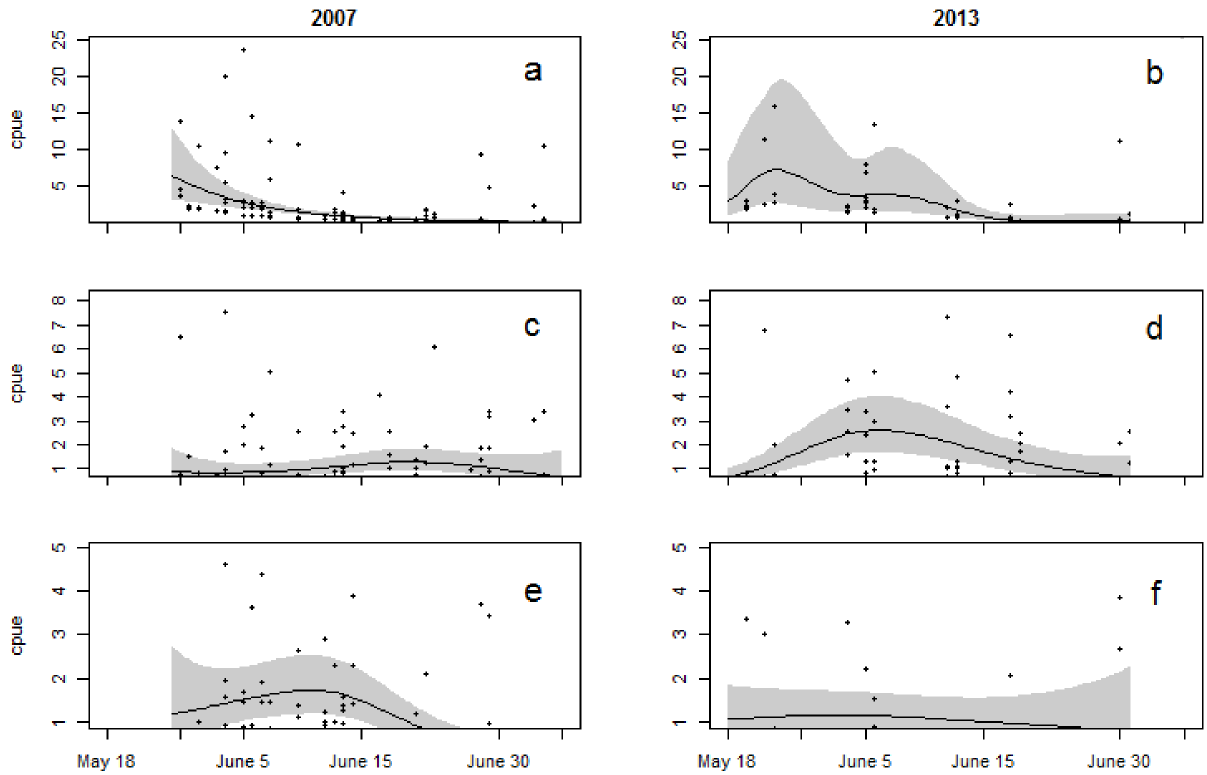

Figure 3. GAM estimates of abundance showing temporal trend for sockeye (a, b), coho (c,d) and Chinook (e,f) salmon abundance during juvenile outmigration season in 2007 and 2013. Points indicate normalized trawl catch per 20 min set, note different scales for each species. The smoothed line and shaded region indicate the temporal trend and confidence region for the GAM models.

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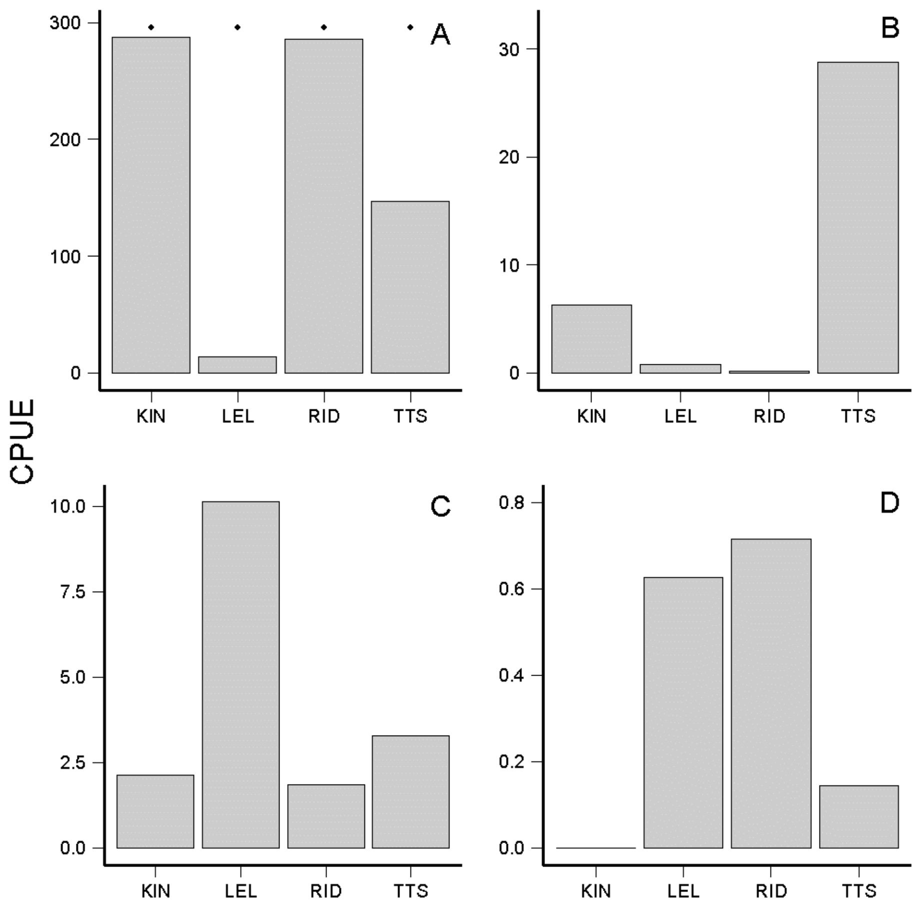

Figure 4. Average beach seine catches of juvenile pink (a), chum (b), coho (c), and Chinook (d) salmon by group, pooled across all sampling dates. No sockeye salmon were captured by beach seine. Pink salmon catches greater than 100 per location are indicated by black dots above bars. Catches greater than 100 or 1000 individuals were calculated as 100 or 1000. Note different scales of y-axes. Locations are as follows: KIN=Kinahan Islands, LEL=Lelu Island, RID=Ridley Island, TTS=Tsum Tsadai Inlet. LEL and RID sites are within footprints of proposed development.

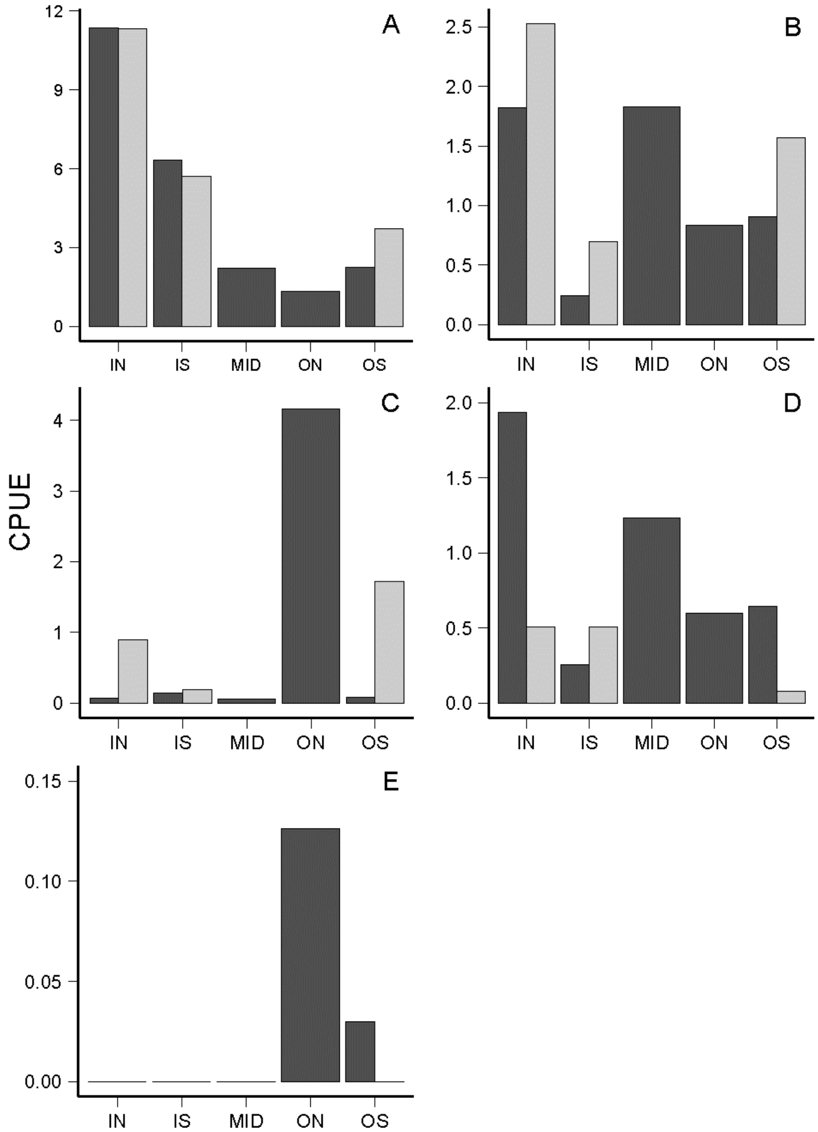

Figure 5. Average normalized trawl catch of all species of juvenile sockeye (a), coho (b), pink (c), Chinook (d) and chum (e) salmon, pooled across all locations and sampling dates and normalized for 20 min sets. Dark grey bars indicate 2007 and light grey bars indicate 2013. Note different scales for y-axes for different species. Region boundaries and abbreviations are same as for Fig.1.

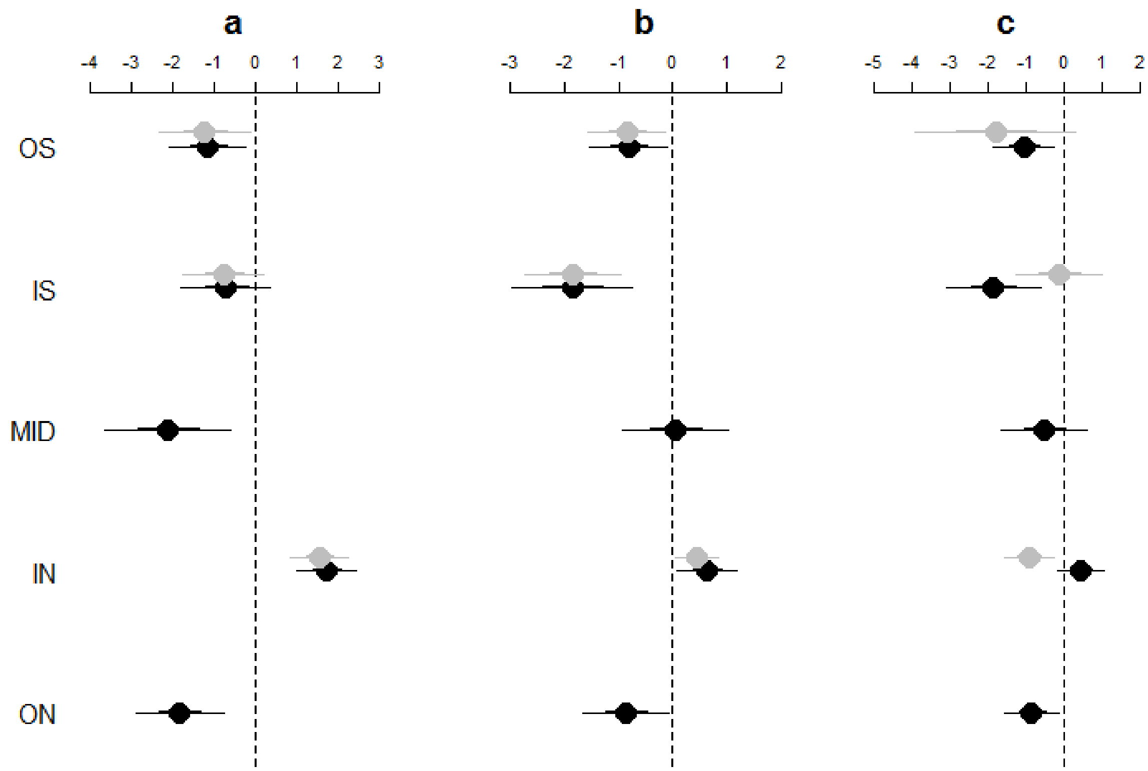

Figure 6. GAM coefficients for parametric region covariates for sockeye (a), coho (b) and Chinook (c) salmon. Coefficients are related to the (log) mean normalized catch per trawl set for each region in 2007 (black) and 2013 (grey). Thus, a value of 0 indicates a mean normalized trawl catch of 1, and a value of 1 indicates a value of 10. Error bars indicate ± 2 standard errors .

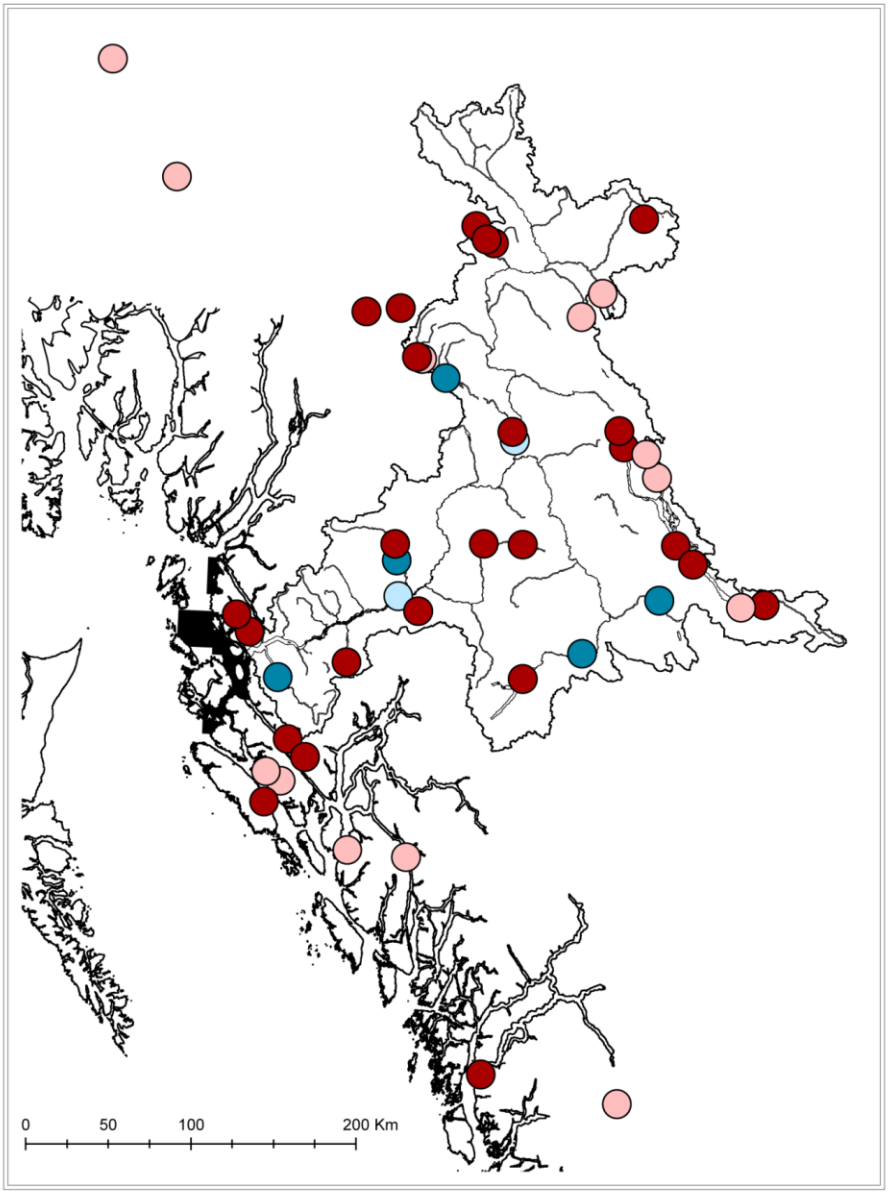

Figure 7. Map of the north coast of British Columbia and the Skeena watershed showing locations of origin for genetically identified sockeye and Chinook salmon smolts captured in the Skeena estuary in 2007 and 2013. Red and pink dots indicate the most likely location of origin for sockeye salmon, with locations that scored above (red) and below (pink) a 90% probability threshold for at least one specimen. Blue dots indicate the highest probability location of origin above (dark blue) and below (light blue) the 90% probability threshold for Chinook salmon. The sampling areas in the estuary of the Skeena River, where all fish were captured, are shown in black.

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