RESEARCH ARTICLE

Estuary habitat associations for juvenile Pacific salmon and pelagic fish: Implications for coastal planning processes

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Abstract

1. Assessment of risk from industrial developments often relies on simple habitat descriptions for focal species. However, simple habitat metrics may not be accurate predictors of locations that species actually use. 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.

2. Canadian environmental impact assessment approaches use simple habitat-type models to assess risk from developments and assume that different species of salmon rely on the same habitat. This study asked what combination of habitat type and biophysical covariates best predicted use of estuary habitat by juvenile salmon and two dominant small pelagic fish.

3. Fish were sampled via purse seine throughout the Skeena River estuary (British Columbia, Canada) for 2 years across different habitat types (eelgrass, open water, sandy banks, and rocky shores). Simple habitat-type models were compared with models with more complex biophysical variables to predict the variability in relative abundance of juvenile Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), and sockeye (*Oncorhynchus nerka*) salmon, along with pelagic fish species Pacific herring (*Clupea pallasii*) and surf smelt (*Hypomesus pretiosus*).

4. The combination of variables that best predicted abundance differed across fish species. Pelagic fish were associated with near-shore sites, increased temperature (herring), and increased salinity (smelt). Juvenile coho and sockeye salmon (but not Chinook), were more abundant in higher turbid waters. Chinook and sockeye salmon used eelgrass habitat more frequently than other habitat types, whereas coho salmon were more abundant in areas with high macroalgae cover. Models with

these variables had greater predictive power than those using habitat type alone for juvenile salmon.

5. Simple classifications of estuary habitat currently used in environmental risk assessment may not reflect the complex nature of fish–habitat associations. Understanding biophysical factors associated with estuary fish abundance can inform management of estuary habitat to support their nursery function for important fish.

1 | INTRODUCTION

Understanding of the nature of habitats that support species of conservation concern and economic importance is a key scientific foundation of management and conservation. Many conservation efforts, such as the International Union for Conservation of Nature Red List and Convention of Biological Diversity, base their mandates on defining and managing for important habitat (Secretariat of the Convention on Biological Diversity, 2008; International Union for Conservation of Nature, 2017). However, identifying the specific habitat attributes that support species can be challenging. Recent assessment of the 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 such as estuaries exemplify this challenge with fluid boundaries and habitat supporting mobile and migratory species utilizing interconnected habitats (Bird & Hodges, 2017; Fausch, Torgersen, Baxter, & Li, 2002; Murphy, Heifetz, Thedinga, Johnson, & Koski, 1989; Nagelkerken, Sheaves, Baker, & Connolly, 2015; Naiman & Latterell, 2005).

Given the importance of estuaries as nursery habitat for fish as well as their rapid ongoing degradation, understanding habitat use by species of importance 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, has declined in area by 7% per year over the last two decades (Waycott et al., 2009). Wetland and marsh habitats are also projected to decline by 83% in some north-eastern Pacific estuaries by 2110 due to sea-level rise (Thorne et al., 2018). Given that estuaries may provide nursery habitat for a diversity of fish species (Able, 2005; Beck et al., 2001; Nagelkerken et al., 2015), 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.

Estuaries act as nurseries for fish that support fisheries through two main mechanisms: providing refuge from predators, and elevated prey resources relative to adjacent marine or freshwater environments. Estuaries provide refuge to young fishes through turbid waters and nearshore structural complexity (Bottom et al., 2005; Brodeur & Morgan, 2016; Fukuwaka & Suzuki, 1998; Levings, 2016; St. John, Macdonald, Harrison, Beamish, & Choromanski, 1992) and thus decrease predation risk to small and young fishes (Alofs & Polivka, 2004; Beck et al., 2001; Heck, Hays, & Orth, 2003; Sheaves, Baker, Nagelkerken, & Connolly, 2015). The nursery function of estuaries can also be supported by higher food availability than surrounding marine or freshwater ecosystems (Brodeur & Morgan, 2016; De Robertis et al., 2005; Grimes & Finucane, 1991; Grimes & Kingsford, 1996; Hill & Wheeler, 2002; Selleslagh, Lesourd, & Amara, 2012; St. John et al., 1992; Ware, 2005). Estuaries that border the north-east Pacific Ocean support many species of economic and cultural importance, including Pacific salmon (*Oncorhynchus* spp.) and small pelagic fish such as Pacific herring (*Clupea pallasii*) and surf smelt (*Hypomesus pretiosus*) (Abookire, Piatt, & Robards, 2000; Bottom & Jones, 1990; Toft et al., 2018; Weitkamp, Bentley, & Litz, 2012). In these estuaries during spring and summer, resident pelagic fishes present in high abundances (St. John et al., 1992) are joined by juvenile salmon of multiple species as they move through and stopover in the estuary during their migration from the fresh water to the ocean.

As estuaries provide habitat for juvenile salmon during the outmigration process (Healey, 1980; Iwata & Komatsu, 1984; Munsch, Cordell, & Toft, 2016), degradation of this ecosystem may have impacts on salmon populations. High estuarine productivity supports rapid growth of juvenile salmon, which can increase early marine survival (Beamish, Mahnken, & Neville, 2004; A. D. Cross, Beauchamp, Myers, & Moss, 2008; Duffy & Beauchamp, 2011; Weitkamp et al., 2015). Estuary habitat degradation is associated with decreased survival of salmon and can have population-level consequences for these species (Magnusson & Hilborn, 2003; Meador & MacLatchy, 2014; Toft et al., 2018). Estuaries at the base of large watersheds may support juvenile salmon from many different populations that are originating from across vast areas (Carr-Harris et al., 2018; Moore et al., 2015). 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 (tfgtBritish Columbia Ministry of Environment, 2008; Kristianson & Strongitharm, 2006; Schindler et al., 2010) and sustain indigenous fisheries (Nesbitt & Moore, 2016).

The suitability of different estuary habitats to juvenile salmon is thought to be influenced by a suite of factors (Simenstad, Reed, & Ford, 2006). These include water quality (salinity, turbidity, and temperature), spatial habitat distribution, temporal factors, tidal influences, and food web dynamics (Bacheler, Paramore, Buckel, & Hightower, 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 (Hering, Bottom, Prentice, Jones, & Fleming, 2010; Levy & Northcote, 1982; McNatt, Bottom, & Hinton, 2016; Quiñones & Mulligan, 2005; Shaffer, 2004). For example, both Chinook (*Oncorhynchus tshawytscha*) and chum (*Oncorhynchus keta*) salmon distributions are disproportionately associated with eelgrass habitat when other habitats are available (Harris, Neff, Johnson, & Thedinga, 2008; Kennedy, Juanes, & El-Sabaawi, 2018; A. L. Macdonald, 1984; Rubin, Hayes, & Grossman, 2018; Semmens, 2008). Vegetation is hypothesized to provide shelter from predators and support increased secondary production and increased diversity of prey (plankton and epiphytic fish) (Bottom & Jones, 1990; Duggins, Simenstad, & Estes, 1989; Semmens, 2008). Other habitat types, such as sand flats (including sand and cobble), can also contribute to food sources for juvenile salmon (Levings & McDaniel, 1976). Microalgae and trapped detritus found in the interstices of sand and cobble can support important invertebrate prey such as gammarid amphipods and tube-dwelling amphipods (Levings, 1982; Levings & McDaniel, 1976; Pomeroy & Levings, 1980; Thom, Simenstad, Cordell, & Salo, 1989). Salmon also use different habitats in estuaries over changing tidal scales and daylight hours (Hering et al., 2010; Levy & Northcote, 1982; McNatt et al., 2016; Thedinga, Johnson, & Neff, 2011). Thus, though there is a substantial body of work on salmon in estuaries, this phase of their life cycle is generally understudied (Weitkamp, Goulette, Hawkes, O'Malley, & Lipsky, 2014) and there is need to build understanding of salmon usage of complicated estuary habitats.

Different salmon species, size classes, and populations may use estuaries differently (Simenstad, Fresh, & Salo, 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 (*Oncorhynchus gorbuscha*), sockeye (*Oncorhynchu nerka*), and coho (*Oncorhynchu kisutch*) salmon are thought to generally migrate through the estuary at a faster rate (Healey, 1980; Moore et al., 2016; Simenstad, 1983; Thorpe, 1994). 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 sub-yearling Chinook often spending considerable time in nearshore environments like marshes and sandflats (Bottom, Simenstad, et al., 2005; Dawley et al., 1986; McNatt et al.,

2016), whereas yearling Chinook are thought to depend less on nearshore areas, moving into deeper neritic regions (Simenstad et al., 1982). Juvenile chum and pink salmon have been observed to 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 (Healey, 1982; Levy & Northcote, 1982; Manzer, 1969; Simenstad et al., 1982). Sockeye and coho salmon are thought to generally move directly into deeper neritic habitats upon arrival in the estuary, acting as planktivores and piscivores respectively (Higgs, Macdonald, & Levings, 1995; Manzer, 1969). Thus, there is growing appreciation for different habitat requirements by salmon across species, populations, and locations.

Decision-making and planning processes in estuaries entail characterization of the value of different habitats to species of importance like salmon. 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 (Dumbauld, Hosack, & Bosley, 2015; Hosack, Dumbauld, Ruesink, & Armstrong, 2006; Levings, 1985, 2016; Murphy et al., 1989; Thedinga et al., 2011). 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—that is, eelgrass and kelp forests are considered important salmon habitat whereas open-water habitats are not (Pacific Northwest liquefied natural gas [LNG]; Stantec, 2015). This habitat classification enables project proponents and decision-makers to quantify the risks of a potential development through considering the areal extent of habitat destruction and associated proposed habitat compensation. Under 'no net loss' policy, destruction of habitat should be associated with creation of equivalent habitat elsewhere (*Fisheries Act* R.S.C. 1985 c. F14, s. 35) (Williams, 1990). Even if projects do achieve no net loss (which is rare—see Favaro & Olszynski, 2017; Harper & Quigley, 2005; Kistritz, 1996; Levings & Nishimura, 1997; Quigley & Harper, 2006), the efficacy of the compensation will be influenced by the degree to which habitat classifications actually do characterize the true importance to the species. Moreover, there is scientific uncertainty as to whether this approach for classification of habitat reflects that actual usage of a given area by a species of management concern.

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 proposed 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 with other major salmon estuaries that have been well studied (i.e. Columbia River and Fraser River estuaries), the Skeena River estuary is less altered by industrial development; most development is contained in one region 15–30 km north of the river mouth. Over the last 5 years, the Skeena River estuary was the proposed location for eight LNG terminals (Aurora LNG, 2014; Exxon Mobil, 2015; Pacific Northwest LNG, 2016; Pembina Pipeline, 2017;

Prince Rupert LNG Ltd, 2017; Province of British Columbia, 2014, 2015; Woodside Energy Holdings Pty Ltd, 2015), currently at various stages of the provincial and federal environmental assessment processes. For example, although Petronas recently terminated their investment in the Pacific Northwest LNG project (Pacific Northwest LNG, 2016), the proposed project received both federal and provincial approval. Pacific Northwest LNG provides a timely and relevant example of how the environmental assessment process considers salmon habitat. The environmental assessments of these industrial projects used coarse habitat classification for their consideration of environmental risks, with eelgrass identified as key salmon habitat. Accordingly, potential risk to salmon was 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 would have been damaged by the project (Pacific Northwest LNG, 2016). An improved understanding of habitat use by juvenile salmon could clarify the degree of certainty in these current risk assessment approaches.

Though they receive less attention, estuaries such as that of the Skeena River also support other fishes that are of management concern, such as Pacific herring and surf smelt. Both species directly support commercial and traditional fisheries (including in the Skeena region) (Department of Fisheries and Oceans [DFO], 2016; Therriault & Hay, 2003; Thornton, Moss, Butler, Hebert, & Funk, 2010) and are key food sources for marine mammals, birds, and fishes of commercial importance, like halibut and salmon (Best & St-Pierre, 1986; Koehn et al., 2017; Thornton et al., 2010). Herring and smelt can inhabit estuarine and nearshore environments during several life-history stages. Herring spawn in intertidal nearshore environments, including estuaries, in February and March (Haegele & Schweigert, 1985; Lassuy & Moran, 1989). Next, larvae are distributed according to water circulation patterns for 2–3 months, where highest survival rates occur in nearshore environments (Stevenson, 1962). Juvenile herring may begin aggregating in estuarine environments at lengths of 25–40 mm (Lassuy & Moran, 1989), where warmer temperatures, refuge from adverse weather, and high food availability provide nursery services (Abookire et al., 2000; Hourston, 1959). Immature herring can often be found in higher abundances within estuarine environments compared with surrounding freshwater or nearshore marine environments (Bottom & Jones, 1990; St. John et al., 1992). In contrast, adult smelt spawn on beaches and remain in nearshore coastal habitat year round (DFO, 2014; Therriault & Hay, 2003); however, data on the distribution and general biology of surf smelt are sparse. Although both herring and smelt can be found in high abundances in estuaries, including the Skeena River estuary during spring and summer (Higgins & Schouwenburg, 1973; Moore, Carr-Harris, & Gordon, 2015), many knowledge gaps remain regarding their distribution and use of estuarine habitats.

This study investigates estuary habitat use by juvenile salmon and small pelagic fishes as related to estuary planning and environmental risk assessment processes in a major estuary of western North America. This paper addresses the following questions: (a) How are fish spatially distributed across Skeena River estuary habitats? (b) Can fish abundance patterns be better explained by simple habitat classifications or by using a more complex suite of biophysical variables? (c) How do these patterns vary across salmon and pelagic fish species? This study identifies uncertainty associated with current approaches in environmental impact assessment and provides the scientific basis for progress towards a multifaceted understanding of estuary habitat classification.

2 | METHODS

A 2-year field study of juvenile salmon and pelagic species and their habitats was conducted in the Skeena River estuary in 2015 and 2016. This research is part of a collaborative research programme 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 (Arbeider, Sharpe, Carr-Harris, & Moore, 2019; Carr-Harris et al., 2018; Carr-Harris, Gottesfeld, & Moore, 2015; Moore et al., 2016; Moore, Carr-Harris, Gottesfeld, et al., 2015). 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 (Figure 1) (Carr-Harris et al., 2015). In addition, this area supports more than 40 populations of sockeye and Chinook salmon from throughout the Skeena River watershed (Carr-Harris et al., 2015, 2018; Moore, Carr-Harris, Gottesfeld, et al., 2015) and encompasses the locations of seven of the eight LNG developments that were proposed for the greater Skeena River estuary (Aurora LNG, 2014; Exxon Mobil, 2015; Pacific Northwest LNG, 2016; Pembina Pipeline, 2017; Prince Rupert LNG Ltd, 2017; Province of British Columbia, 2014, 2015). This study builds on these previous findings to examine how salmon and other pelagic fish are using specific estuary habitat types and locations.

2.1 | Study system

The study area in the Skeena River estuary is within the traditional territories of the Coastal Tsimshian First Nations. The Skeena River is approximately 570 km long with a drainage area of 55,000 km^2 meeting the ocean near Prince Rupert, British Columbia (54.13°N, 130.10°W), 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), whereas 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 and June 29, 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 north-west
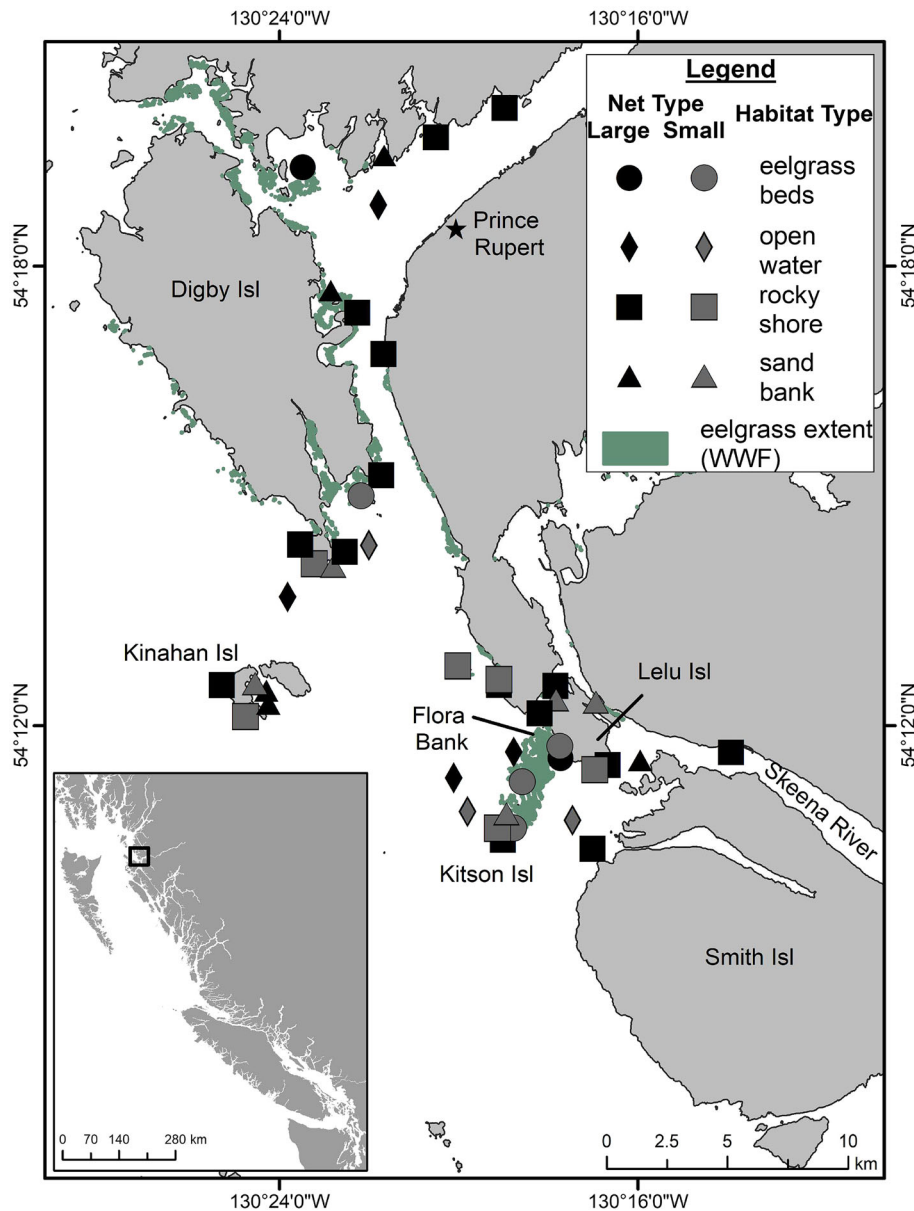
FIGURE 1 Map of sampling locations according to habitat type and net type used across the Skeena River estuary. Extent of eelgrass habitat shown (Ambach & Casey, 2011; Forsyth, Borstad, Horniak, & Brown, 1998; Ocean Ecology, 2013; WWF-Canada, 2009)

through Chatham Sound, where it meets fresh water from the Nass River. The sampling region was near the river mouth in the northern-most channel, Inverness Passage, extending north past Prince Rupert and west to Kinahan Islands (Figure 1). This region was selected for this study as it is known to be highly used by juvenile salmon compared with other regions of the estuary (Carr-Harris et al., 2015; Higgins & Schouwenburg, 1973). This region is characterized by a mesohaline to polyhaline salinity gradient. Although there are narrow bands of salt grass, intertidal macroalgae, and kelp beds, the primary habitat types are mud and sand banks, rocky shores, and eelgrass beds (Table 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).

2.2 | Fish sampling

Fish were sampled in the Skeena River estuary during the peak smolt migration period from April to mid-July 2015 and 2016. In 2015, 25 sites were sampled with a large purse seine every 2 weeks, of which a subset of eight sites were sampled every week. In 2016, the same subset of eight sites was sampled every week, whereas a smaller purse seine was used to survey habitat closer to shore every 2 weeks at an additional 18 sites (Figure 1). Purse seine nets were used in this study because it was previously determined to be the most effective method at capturing juvenile sockeye, coho, and Chinook salmon in the Skeena River estuary (North Coast Juvenile Salmon Monitoring Program, unpublished data). During this time period, beach seine sampling was

TABLE 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 1 m above the substrate at high tide. Species present: *Zostera marina* (dominant) and *Zostera latifolia*
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 and 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 >200 m from shore

also conducted but is not included in this study due to inconsistent sampling methods, locations, and dates. As both pink and chum fry can escape the mesh of the large purse seine, this study focused on sockeye, coho, and Chinook salmon, along with herring and smelt for analysis.

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) was deployed 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 set using two 3 m skiffs with the net held open for 2.5 min per set. Sites were selected to represent the four most available habitat types: eelgrass beds, rocky shores, sand banks, and open-water habitat (Table 1). A stratified sampling design was used 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). All fish sampling was performed in accordance with the animal care protocol (# 1158B-11) from the University Animal Care Committee at Simon Fraser University.

2.3 | Measuring biophysical variables

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 were collected (Bacheler et al., 2009). Salinity, temperature, turbidity, and depth were measured after each set (see Table 2 for collection details). At each sampling location, salinity and temperature were recorded at a depth of 1 m. Water quality attributes (salinity, temperature, and turbidity) were variable across sites and time between and within sampling years (Figure S1). For each site, 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 centre to the nearest point on shore) was determined. Data collected at the Prince Rupert, BC (Station Number 9354, 54.317°N 130.324°W) tide station located within our study area were used to generate tide height.

Benthic substrate was surveyed 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. Video footage using Coral Point Count with Excel extensions was analysed to determine percentage cover of substrate: sediment, rock, invertebrate, eelgrass, and macroalgae (Guinan, Grehan, Dolan, & Brown, 2009; Kohler & Gill, 2006; Leonard & Clark, 1993; Ninio, Delean, Osborne, & Sweatman, 2003). From each of three video transects, 20 still frames were

TABLE 2 Biophysical attributes used to model salmon abundance in the estuary, given with units and method of measurement

Attribute	Unit	Method of measurement	Range (mean)
Water quality			
Salinity	ppt	YSI (Pro 2030)	3.5–25.9 (19.1)
Temperature	°C	YSI (Pro 2030)	8.7–15.9 (11.6)
Turbidity	metres	Secchi disk depth	0.2–7.0 (2.1)
Tidal attributes			
Tide height	metres	Tide height at station 9354	0.5–6.5 (3.9)
Spatial attributes			
Distance from river mouth	kilometres	Measured from the river mouth to site coordinates (shortest swimming route)	9.2–33.2 (18.2)
Distance to shore	metres	Measured from the site to closest point of shore contact	17.3–1,192.1 (205.0)
Vegetative variables			
Eelgrass percentage cover	mean % cover	Point count analysis of video	0–70.0 (5.9)
Macroalgae percentage cover	mean % cover	Point count analysis of video	0–87.2 (5.9)

randomly selected at a minimum time of 2 s apart, ensuring that frames did not overlap. To estimate benthic composition, 30 points were randomly overlaid on each frame (1,800 points per site), the substrate type under each point identified, and the percentage cover (number of points with a given substrate type/total number of points) of the different bottom substrate types at each site calculated.

2.4 | Modelling fish abundance

Fish abundance patterns were modelled across the estuary as a function of various habitat features and environmental attributes. Estuary habitat for focal fish species using both a fine-scale and coarse-scale approach was described. First, a fine-scale approach (A) modelled fish abundance patterns for each species separately, with various biophysical variables. The Akaike information theoretic criterion (AIC) was used to select the combination of biophysical variables that had the most support for each species. Second, a coarse-scale approach (B) modelled abundance for each species separately, using four basic available habitat types: eelgrass beds, sandy banks, rocky shores, and open-water habitat (Table 1). Finally, the top models from approach A and approach B were compared using AIC. The quantitative approach used in this study is described in more detail in the following.

To develop predictive models for both approaches, catch-per-unit-effort (CPUE) was used as a measurement of fish abundance. Whereas 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. CPUE for the small net was calculated 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 the small net.

All modelling was performed using the R package glmmTMB (Magnusson et al., 2016), which estimates parameters by maximizing likelihood. All models included site and time period as random effects to account for any spatial and temporal covariation (Table S2). Sampling events were grouped into eight 2-week time intervals to create the time period variable with the following start dates March 24, April 10, April 24, May 8, May 22, June 5, June 19, and July 3 (ending July 17). Including these random effects accounts for extraneous variation that may have influenced the associations being tested. Collinearity of all variables was low with variance inflation factors VIF < 3 (Zuur, Ieno, & Elphick, 2010; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). 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 AIC corrected for small sample size (AICc) to affirm the most suitable parameterization (NB2 for sockeye salmon, herring, and smelt; NB1 for coho and Chinook salmon; Akaike, 1973). All continuous predictors were centred and scaled (subtraction of the mean from each observation and division by two standard deviations) to facilitate meaningful comparisons of effect sizes among predictors (Grueber, Nakagawa, Laws, & Jamieson, 2011).

Modelling approach A investigated which combination of biophysical variables (Table 2) was most important in explaining fish abundance

across the estuary using multimodel inference. Since all biophysical variables were selected based on a priori hypotheses as outlined by previous studies (McNatt et al., 2016; Pearcy, 1992; Roegner, Weitkamp, & Teel, 2016; Semmens, 2008; Straty & Jaenicke, 1980), they were included in the modelling selection process. Owing to inconsistent depth sampling resulting from technical problems, depth was removed from the final variable list as it substantially reduced the number of sampling events with complete covariate sets. Models were fitted with all possible combinations of variables, including net type and sampling year as fixed effects (1,024 models total per species), ranked using AICc and model averaging performed on a candidate model set of models with AICc < 2. The importance of each predictor variable was quantified based on cumulative Akaike weight of the model candidate set (AICc < 2), creating a measure of relative variable importance (RVI; Burnham & Anderson, 2002). RVI values range from 0 to 1 as Akaike weights sum to 1 within a candidate model set. A top model for each species was chosen from a set of models with a AICc < 2 and identified as the model with lowest AICc score and the fewest predictor variables (Bolker, 2008; Burnham & Anderson, 2002). Model averaged coefficients and RVI values were used to make inferences about biophysical variables that described salmon abundance patterns. Top models (most parsimonious models with AICc < 2) were used to compare modelling approaches (A or B) with AICc.

In approach B, the degree to which coarse-scale habitat types explained the abundance of each fish species in the estuary was examined. Fish abundance was modelled with a categorical variable representing habitat type (eelgrass beds, sandy banks, rocky shores, and open water) and the inclusion of net type and sampling year as fixed effects were tested with AICc model selection. This approach thus examines habitat categorizations commonly used in environmental impact assessment and mitigation. For each species, a top model (most parsimonious within AICc < 2) was identified.

Modelling approaches A and B were compared by examining the top models from each approach with AICc for each fish species. The predicted versus observed CPUE relationships of the top models for each species were assessed. By comparing predicted and observed values from each top model, the predictive capability of both modelling approaches can be evaluated. Pearson correlation coefficients of predicted and observed values and root-mean-square error (RMSE) values were used as performance measures for this comparison. RMSE values were estimated by bootstrapping randomly sampled data (with replacement) 1,000 times for each model. Bootstrapped RMSEs for the top model from each modelling approach were then compared, to determine certainty estimates of model rank. All statistical analysis was performed using R 3.3.1 (R Core Team, 2016)

3 | RESULTS

3.1 | Patterns of temporal and spatial distribution

High abundances of juvenile salmon were caught across sampling years, with 1,746 sockeye, 683 coho, and 58 Chinook salmon caught 2015, and 8,621 sockeye, 723 coho, and 51 Chinook salmon captured

in 2016. The range in fork lengths for juvenile salmon were as follows: sockeye (52–174 mm), coho (73–242 mm), and Chinook (86–185 mm) salmon. The larger catch of juvenile sockeye salmon in 2016 is not surprising due to higher numbers of smolts out-migrating from major Skeena River sockeye salmon populations because of higher spawner recruitment 2 years before (parent generation). The peak catches of

sockeye, coho, and Chinook salmon occurred during the 6-week period between May 8 and June 5 in both 2015 and 2016 (Figure S2).

Within sampling years, fish were unevenly distributed across the estuary, with higher catches (CPUE) of juvenile salmon consistently found at some sites than at others (Figure 2). Specifically, the relative abundance of all salmon species during the peak smolt out-migration
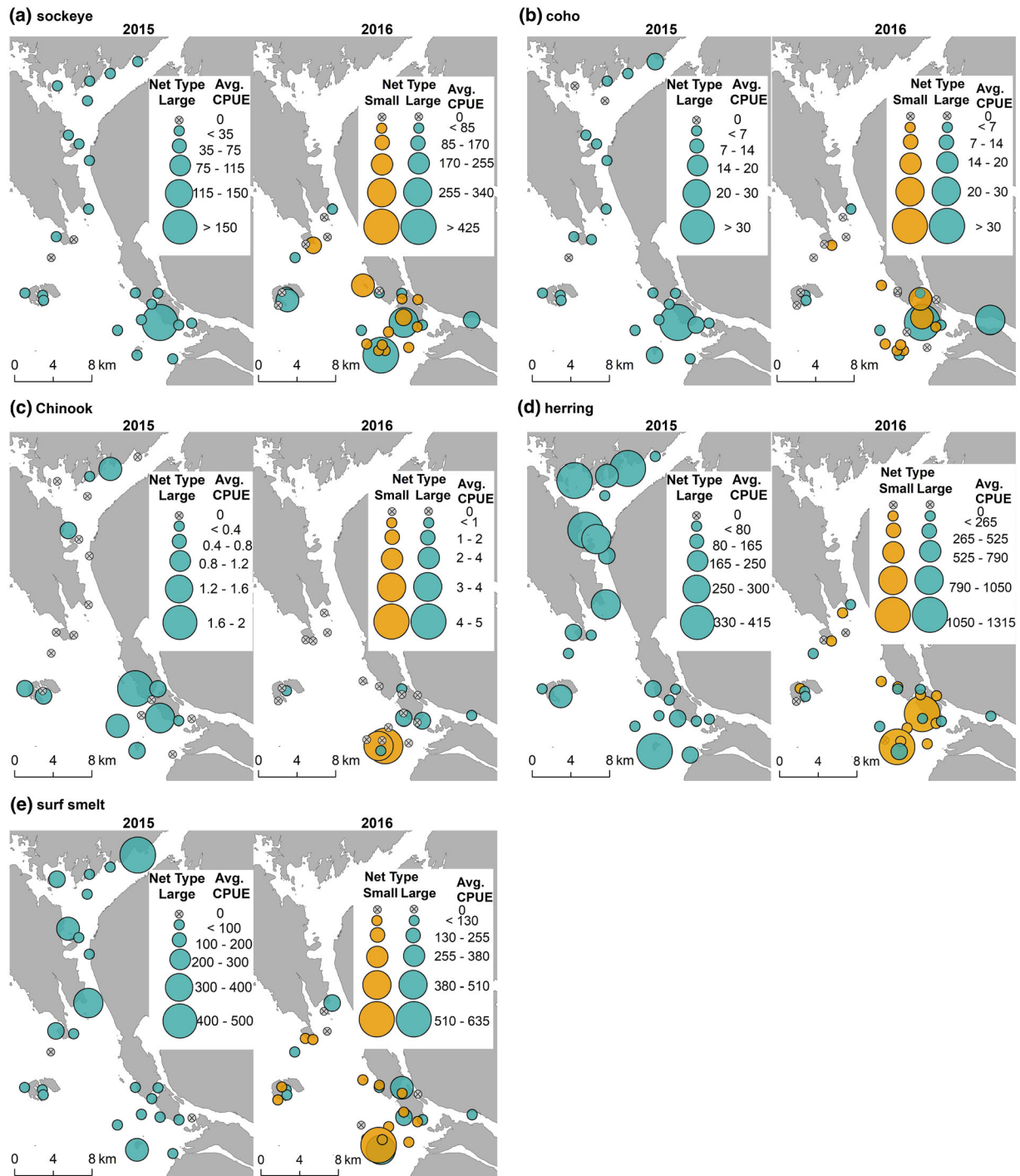

FIGURE 2 Mean fish abundance of (a) sockeye salmon, (b) coho salmon, (c) Chinook salmon, (d) Pacific herring, and (e) surf smelt at sampling locations in the Skeena River estuary in 2015 and 2016. Fish abundance plotted during peak migration in the estuary: early May–late June for salmon (a–c) and early May–mid-July for herring and smelt (d,e). Colours indicate the different net types (orange: small purse seine; blue: large purse seine). Legend showing point area representative for average fish catch-per-unit-effort (CPUE) abundance. Point area represents different average fish CPUE in 2015 and 2016

(May 8–June 5) was highest at sites surrounding Lelu Island, including Flora Bank and Kitson Island (refer to Figure 1 for location names). Comparing the grouped mean CPUE of sites around Flora Bank and Kitson Island (including Porpoise Harbour, Inverness Passage, and Agnew Bank) with elsewhere in the estuary illustrates these differences in salmon abundances across space. In 2015, CPUEs for sockeye, coho, and Chinook salmon were eight, five, and three times higher respectively for the Flora Bank region than for other sites on average, and 2, 3 and 19 times higher respectively in 2016. At the site level, the highest abundances of salmon were found at the Flora Bank site 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 than at other sites during peak migration. Higher abundances were also found at the Flora Bank big purse seine site in 2016, where five, nine, and two times more sockeye, coho, and Chinook salmon respectively were collected, on average, than at other big purse seine sites in the estuary.

High densities of herring were caught across the season, representing diverse age classes, including young-of-the-year and adult herring, ranging in size from 36 mm to 270 mm (Figure S3). More herring were caught in 2015 (19,262) than in 2016 (11,862); and abundances of herring increased over time, with the highest abundances found at the end of the June (Figure S2). Smelt caught in the estuary ranged in size from 61 mm to 199 mm and represent several age classes with a bimodal size distribution (Figure S3). Fewer smelt were caught in 2016 (4,533) than in 2015 (13,631). Compared with salmon spatial distribution of abundance, herring and smelt were more ubiquitously distributed across study sites (Figure 2). Similar to the trends for juvenile salmon already mentioned, certain sites around Kitson Island had high abundances of herring and smelt for 2015 and 2016. For example, in 2016, four times more herring were caught on average around Kitson Island than at the other sites combined. However, sites further north, in Prince Rupert Harbour, sampled in 2015 had high abundances of both species of pelagic fish, which was different than observed for juvenile salmon.

3.2 | Linking fish abundance with biophysical variables (approach A)

Different combinations of biophysical variables best explain the relative abundance of each fish species (Figure 3). Net type (large or small purse seine) had the highest RVI score (Figure 3) and was present in every top model (Table S1) for sockeye, coho, and Chinook salmon,
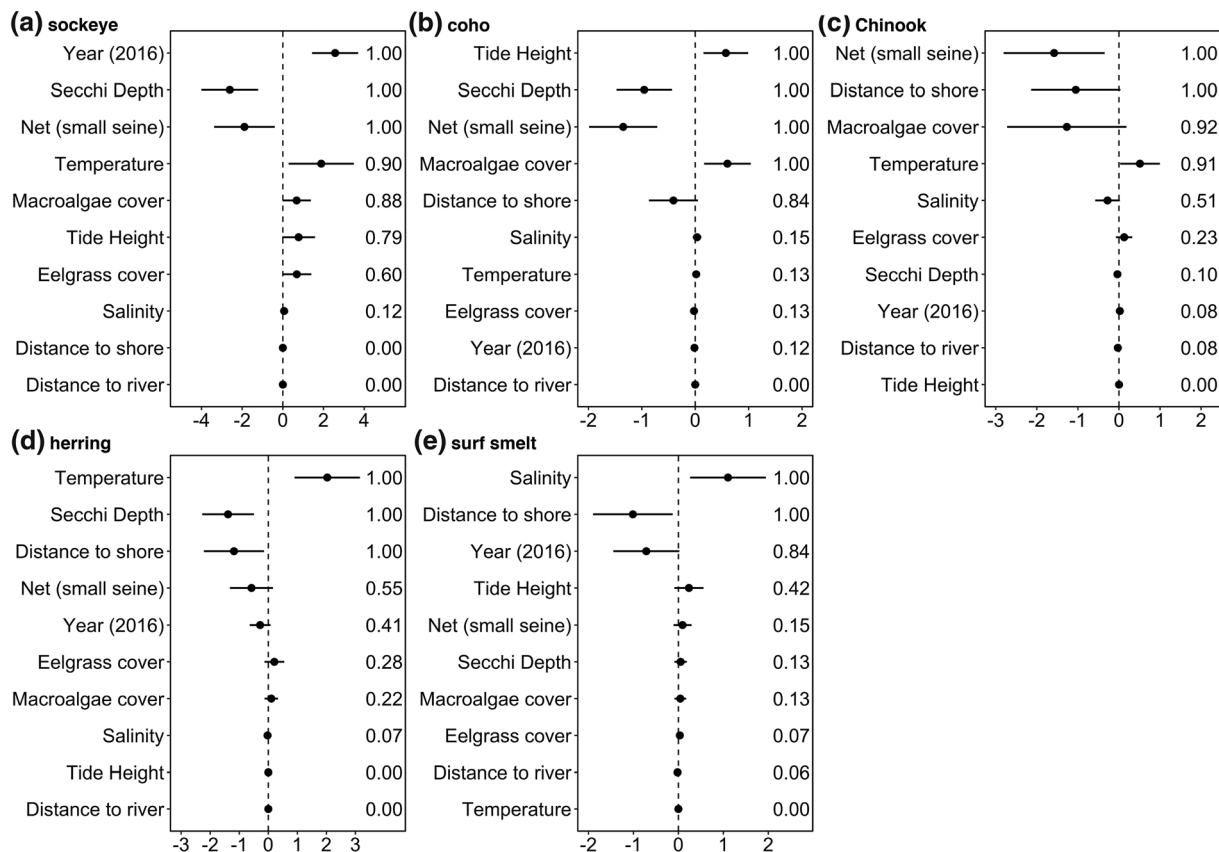

FIGURE 3 Standardized model-averaged coefficients (points) and 95% confidence intervals (bars) used to describe fish abundance of (a) sockeye salmon, (b) coho salmon, (c) Chinook salmon, (d) Pacific herring, and (e) surf smelt presented in decreasing order of relative variable importance (RVI). RVI values shown on rightmost of each panel. Coefficients are related to the (log) mean of normalized catch-per-unit-effort. Parameter year (2016) compares catches with the sampling year 2015 as a baseline and the small purse seine net is being compared with the large purse seine net

indicating we caught relatively fewer salmon with the smaller purse seine net than the larger purse seine net.

Model-averaged coefficients suggests that increased turbidity and temperature were associated with higher sockeye salmon relative abundance (95% confidence interval does not cross zero) (Figure 3a). More sockeye salmon were caught in 2016 than in 2015. Year (1.00), turbidity (1.00), and net (1.00) ranked highest in RVI and were included in every model within the AICc < 2 candidate set (Table S1). Temperature (0.90), macroalgae cover (0.88), and tide height (0.79) had relatively high RVI scores, indicating their importance in explaining sockeye salmon CPUE. Eelgrass cover was also present in three of the six models within the AICc < 2 candidate set and had an RVI of 0.60. Although tide height, macroalgae, and eelgrass cover appear to have positive relationships with sockeye salmon CPUE, these relationships are uncertain (95% confidence intervals cross zero; Figure 3a). Other abiotic variables had lower RVI scores (salinity, 0.12; distance to river, 0.00; distance to shore,(0.00) and were not present or common within the AICc < 2 candidate set for sockeye salmon.

Higher relative abundances of juvenile coho salmon were associated with higher tide height, turbidity, and macroalgae cover (Figure 3b). Tide height (1.00), secchi depth (1.00), net type (1.00), and macroalgae cover (1.00) had the highest RVI scores. Coho CPUE tended to be higher closer to shore, and distance to shore was another important predictor for coho salmon as it was present in all models within AICc < 2 (except the top model; Table S1) and had a relatively high RVI score (0.84). Salinity (0.15), temperature (0.13), eelgrass cover (0.13), and distance to river mouth (0.00) had lower RVI scores and were uncommon or absent from the AICc < 2 candidate set, and thus appear to be less important in explaining juvenile coho salmon relative abundance.

Increased temperature was associated with higher CPUE of Chinook salmon (Figure 3c). More Chinook salmon tended to be caught closer to shore and in locations with higher macroalgae cover, but these results have large variation (95% confidence intervals cross zero). 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 (0.51) and appearance in four out of nine models within AICc < 2

(Table S1), salinity may be an important variable in explaining Chinook salmon abundance. The variables eelgrass cover (0.23), secchi depth (0.10), year (0.08), distance to river mouth (0.08), and tide height (0.00) had lower RVI scores and were not found frequently in the AICc < 2 candidate set, and thus are likely less important variables in predicting juvenile Chinook salmon.

Higher herring CPUEs were related to higher temperatures along with decreased turbidity and smaller distances to shore (Figure 3d). Temperature (1.00), secchi (1.00), and distance to shore (1.00) had the highest RVI values. Net type (0.55) had a moderately high RVI value and was present in six of the 10 models within AICc < 2 (Table S1), suggesting that fewer herring may have been caught with the smaller purse seine. However, this relationship is likely not as important a factor for herring abundance as it is for abundances of sockeye, coho, and Chinook salmon. Year (0.41), eelgrass cover (0.28), macroalgae cover (0.22), salinity (0.07), tide height (0.00), and distance to the river mouth (0.00) had low RVI scores and were common in the AICc < 2 candidate set.

Increased salinity and locations closer to shore were associated with the relative abundance of smelt, since both had RVI values of 1.00 (Figure 3e). With a high RVI value of 0.84 for year, modelling suggests that less smelt were caught in 2016 than in 2015. Each of the following seven variables had low RVI scores and were not frequently found within the AICc < 2 candidate set (Table S1): tide height (0.42), net type (0.15), secchi depth (0.13), macroalgae cover (0.13), eelgrass cover (0.07), distance to river (0.06), and temperature (0.00). These variables are less likely to be important factors when predicting smelt CPUE.

3.3 | Linking fish abundance with habitat type (approach B)

The relative abundance of each fish species was associated with varying habitat types (Figure 4). Higher abundances (CPUE) of juvenile sockeye and Chinook salmon were consistently found over eelgrass beds than for other habitat types (Figure 4a,c). Coho salmon were
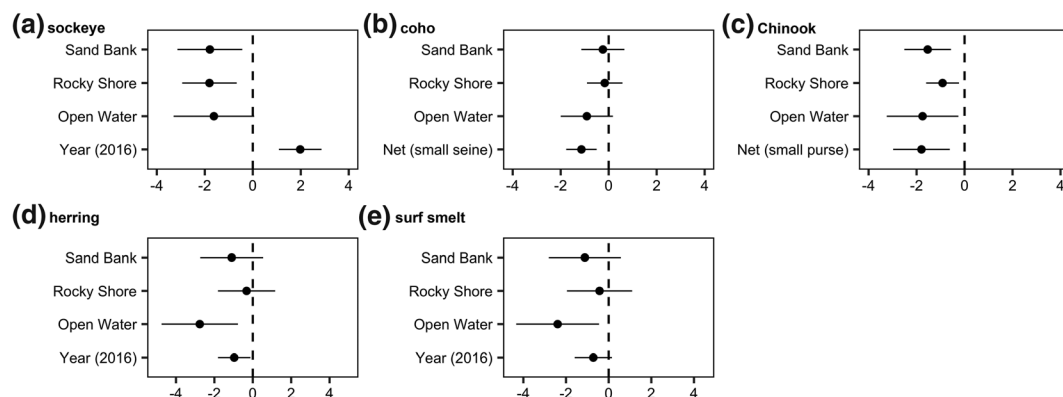

FIGURE 4 Standardized parameter estimates (dots) and 95% confidence intervals (bars) from top models (most parsimonious within AICc < 2) for modelling approach B – habitat type top models for (a) sockeye salmon, (b) coho salmon, (c) Chinook salmon, (d) Pacific herring, and (e) surf smelt. Open-water, sand banks, and rocky shores habitat types are compared with the eelgrass bed habitat type as a baseline (dashed line). Parameter year (2016) compares catches with the sampling year 2015 as a baseline and the small purse seine net is being compared with the large purse seine net. Coefficients are related to the (log) mean of normalized catch-per-unit-effort

caught in all habitat types equally (Figure 4b). Lastly, pelagic fish species herring and smelt were found less in open-water habitat than in the other three habitat types (Figure 4d,e).

3.4 | Comparing modelling approaches

Comparison of models from approach A (fine scale) and approach B (coarse scale) shows that top models (most parsimonious model within a AICc < 2) from modelling approach A had more support via AICc for all salmon species (Table 3). In addition, approach A had higher predictive capability with lower RMSE values and higher correlation between predicted and observed values than approach B did (Figure S4). Top habitat-type models (approach B) for sockeye, coho and Chinook salmon had AICc scores of 13.1, 30.5, and 3.8 respectively when compared with the best model from approach A. Approach A top models for sockeye and coho salmon had lower RMSE values for 85.6% and 79.5% of bootstrap iterations respectively compared with models from approach B. The correlation coefficient for sockeye salmon was 0.3 (approach A) compared with 0.13 (approach B), and 0.46 and 0.34 for coho salmon. The top Chinook salmon model from approach A had lower RMSE values for 50.0% of bootstrap iterations and a correlation coefficient of 0.23 compared with 0.18 (approach B). This suggests that the modelling approach using biophysical variables has a higher predictive capability for coho and sockeye salmon. However, there were convergence problems for many of the Chinook salmon bootstrap modelling iterations due to lowered sample size of bootstrap models (random sampling of data). This limits the strength of inferences that can be made about Chinook salmon.

Herring and smelt models from approach A (fine scale) had more support via AICc than models from approach B (coarse habitat approach). Specifically, herring and smelt top-habitat-type models (approach B) had AICc scores of 7.7 and 6.2. RMSE values from approach A top models were lower for herring and smelt models with 75.3% and 55.3% of bootstrap iterations respectively. However,

correlation coefficients for herring for approach A were 0.31 and 0.40, and smelt had coefficients of 0.43 and 0.50 respectively (Table 3).

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 (Figures S4 and S5). These findings suggest that, although the more complex habitat approach fits the abundance data better for salmon, there remains substantial unexplained variance in salmon abundance.

4 | DISCUSSION

4.1 | Linking juvenile salmon abundance with estuary habitats and processes

Two years of extensive field sampling during juvenile salmon migration revealed that juvenile salmon utilize some regions of the estuary more 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). For example, sockeye and coho salmon were found to be on average eight and five times more abundant in 2015 in this region, and two and three times more abundant in 2016, compared with other sites in the estuary. This trend was observed across 2 years and for all three species of juvenile salmon. Different factors predicted the abundance of juvenile salmon and small pelagic fishes that ranged from turbidity to temperature to macroalgal coverage. Collectively, this study helps improve understanding of habitat associations for important fishes in the estuary of a major salmon-producing watershed.

Different combinations of biophysical variables were important descriptors of estuary habitat for the different species of salmon in the Skeena River estuary. Environmental attributes, such as turbidity, are known to influence juvenile salmon distribution across estuaries (Straty & Jaenicke, 1980). In the Skeena River estuary, coho and

TABLE 3 Akaike information theoretic criterion (AIC) corrected for small sample size (AICc) summary for comparison of top models (most parsimonious within AICc < 2) from modelling fish abundance across both approaches (A: biophysical variable modelling; B: habitat type modelling). All models contain site and sampling period as random effects

Salmon species	Model approach	Model parameters (fixed effects only)	k^a	$AICc^b$	r^c
Sockeye	A	year + net + secchi depth + temperature + tide height	7	0.0	0.30
	B	year + site type	6	11.7	0.13
Coho	A	net + secchi depth + macroalgae cover + tide height	6	0.0	0.46
	B	net + site type	6	29.2	0.34
Chinook	A	net + distance to shore + macroalgae cover	5	0.0	0.23
	B	net + site type	6	2.3	0.18
Herring	A	distance to shore + secchi depth + temperature	5	0.0	0.31
	B	year + site type	6	7.0	0.40
Smelt	A	distance to shore + salinity	4	0.0	0.43
	B	year + site type	6	5.0	0.50

[a]Number of model parameters;

[b]Change in AICc score from top model.

[c]Pearson correlation coefficient of predicted versus observed catch-per-unit-effort.

sockeye salmon tended to be caught in higher numbers in more turbid water; however, turbidity did not explain Chinook salmon abundance patterns. During the peak salmon migration period in May and June, estuary turbidity is heavily influenced by river discharge, as colder snowmelt 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 fresh water (Berg & Northcote, 1985; Breitburg, 1988; Sigler, Bjornn, & Everest, 1984) and estuaries (Gregory & Northcote, 1993), high-turbidity waters may provide refuge to juvenile salmon 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; Gregory & Levings, 1996, 1998; Phillips, Horne, & Zamon, 2017; Simenstad et al., 1982). Juvenile fish, including salmon, sometimes increase risky behaviour in turbid conditions by increasing 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 quality for juvenile salmon (Groot & Margolis, 1990).

Temperature was also an important variable in explaining sockeye and Chinook salmon abundances, with higher juvenile salmon abundances associated with higher temperatures. Water temperature affects metabolism and regulatory processes, such as activity and growth (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 (Armstrong et al., 2013; Garside & Tait, 1958; Javaid & Anderson, 1967). 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 behavioural thermoregulation has been shown to increase the growth rate of juvenile coho salmon in fresh water (Armstrong et al., 2013). Increased growth rates during estuary rearing produce larger fish with an increased chance of survival in marine environments (Beamish et al., 2004; Duffy & Beauchamp, 2011; Foerster, 1954). 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, fresh water from the Skeena River is colder than the marine environment, creating a temperature gradient across our study region (strongest during snowmelt freshet in May, ranging from 9.1°C to 12.6°C). As juvenile salmon did not show distribution patterns in relation to distance to the river, sockeye and coho salmon may be responding to the complex thermal landscape of the Skeena River estuary. Given the mixing of freshwater and marine temperature dynamics, estuaries may provide a complicated and important thermal landscape (Sheaves et al., 2015) that juvenile salmon can benefit from.

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 (95% confidence intervals cross zero). Juvenile salmon are often found moving into estuaries during ebb tides (Hasler & Scholz, 2012; Lacroix, Knox, & Stokesbury, 2005; Perry et al., 2010) 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, Conlin, & Raymond, 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 (Hering et al., 2010; Levings, 1982; Levings et al., 1991; J. S. Macdonald, Birtwell, & Kruzynski, 1987; 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, drain on lower tides. Although coho salmon were found more frequently during higher tides in the estuary, this result may be confounded by the 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.

This 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, whereas coho salmon did not have an obvious trend with regard to habitat type. However, for all three salmon species, eelgrass cover was not a strong predictor of salmon abundance when more dimensions of habitat were modelled (approach A). This suggests that the presence of eelgrass may be important for sockeye and Chinook, but increased eelgrass cover may not contribute to habitat use; that is, higher abundances were not associated with denser eelgrass beds compared with less dense eelgrass beds. A positive association was found with Chinook, coho, and potentially sockeye salmon for increasing macroalgae cover in the Skeena River estuary. For sockeye and coho salmon an association with nearshore vegetation such as eelgrass or macroalgae habitat has not been previously documented (Hosack et al., 2006; Murphy, Johnson, & Csepp, 2000). Juvenile Chinook salmon have demonstrated variable eelgrass association, with strong association in some cases (Rubin et al., 2018; Semmens, 2008) and not in others (Dumbauld et al., 2015; Healey, 1980; Hosack et al., 2006). In addition, juvenile Chinook salmon have also been found in high abundances on sand and mudflat habitat types (Levings, 1982; Thom et al., 1989). Juvenile Chinook salmon were found more frequently in eelgrass beds than in 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; Duggins, Eckman, & Sewell, 1990; Kennedy et al., 2018; 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. This study supports the idea that eelgrass habitats can be more heavily used by some species of salmon than other habitat types can, 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, Jones, Cornwell, Gray, & Simenstad, 2005; Roegner et al., 2016) and freshwater outflow (J. S. Macdonald et al., 1987). In this 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, one would expect to catch more salmon at sites closer to the river because they have a smaller area to disperse over. However, no relationships between juvenile sockeye, coho, or Chinook salmon abundance and proximity to the mouth of the Skeena River were found. This suggests that salmon are actively selecting locations in the estuary and that different locations are not created equally. 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 high variation associated with this relationship. Because much of the habitat closer to shore (within <5 m) is subtidal and can be sampled with the 9 m or 5 m deep purse seines, an association with locations closer to shore suggests that fish were found in higher abundances in subtidal nearshore habitat on channel margins compared with open water between landforms. In other estuaries, larger sub-yearlings and yearling Chinook and coho salmon are associated with deeper channel or channel margin habitats (10–15 m deep; (Gamble et al., 2018; Pinnix, Nelson, Stutzer, & Wright, 2013; Roegner et al., 2016), whereas smaller fry or sub-yearling Chinook are associated with shallow nearshore habitat (<3 m deep; Bottom, Jones, et al., 2005; Hering et al., 2010; Roegner et al., 2016; Simenstad et al., 1982). As both, coho (73–242 mm) and Chinook (85–185 mm) salmon found in the Skeena River estuary are primarily larger age classes (subyearling or ≥1 age class—using designations from Roegner et al., 2016 and Weitkamp et al., 2015), results from this study are comparable to findings from other estuaries. Although a small percentage of Chinook salmon from the Skeena River watershed leave fresh water in their first summer (Gottesfeld & Rabnett, 2007), fry age class was not found in the estuary during 2 years of sampling. Perhaps this life history of Chinook might depend more on the lower Skeena River/upper estuary. The results of this study suggest that nearshore habitat may be generally important habitat for yearling juvenile Chinook and possibly for coho salmon in the Skeena River.

4.2 | Linking pelagic fish abundance with estuary habitats and processes

Small pelagic fish were associated with several abiotic and spatial variables in the Skeena River estuary. Higher abundances of both herring and smelt were found close to shore in the Skeena River estuary. Juvenile herring have been previously found concentrating in shallow sheltered regions (Hourston, 1959), with researchers suggesting that shelter (from adverse wind and wave activity) and increased shoreline complexity provided by nearshore environments were likely driving this trend (Hourston, 1959). Nearshore environments can have higher habitat complexity, including intertidal vegetation, which provides more shelter from predation (Alofs & Polivka, 2004; Heck et al., 2003). Our results support the importance of nearshore habitat for both herring and smelt. Additionally, herring abundances were higher in locations with higher temperatures and higher turbidity. Increased biomass of pelagic fish species, including herring, is positively associated with warmer temperatures in other estuaries (Abookire et al., 2000; Marshall & Elliott, 1998) and nearshore environments (J. N. Cross, Steinfort, Fresh, Miller, & Simenstad, 1980; Reum et al., 2013). This supports the findings of this study that herring may be distributing in locations with increased temperatures. Furthermore, smelt tended to be more abundant in areas with higher salinity. Higher abundances of surf smelt have been found at lower salinities on a similar geographic scale in the Skagit River estuary (Reum, Essington, Greene, Rice, & Fresh, 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 with salinity gradients (estuarine mixing zone vs. tidal–fluvial zone). Research investigating smelt distribution across the estuary is needed to understand broad-scale distributions of smelt abundance.

High densities of both juvenile and adult herring and surf smelt were caught in the Skeena River estuary during the spring and early summer. These species are using estuaries throughout their life cycle, in contrast to salmon, which primarily use the estuary as they move through it as out-migrating juveniles and again as returning adults. Herring and other pelagic fish can be found in low numbers in temperate estuaries during winter months but use them in high densities in spring and summer months presumably due to high food availability, warm water temperatures, and potentially shelter from adverse weather (Abookire et al., 2000). Whereas most herring and over half the smelt individuals collected were of the smaller size classes indicative of being juveniles (Lassuy & Moran, 1989; Therriault & Hay, 2003), we also observed some large adult individuals (Figure S3). 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). It is unclear what proportions of these fish are migratory or reside in estuary habitat year round, although the presence of mature adults and separate small spawning events may be indicative of a resident population (DFO, 2012). Spawning behaviour of smelt has not been researched in the

estuary, but a spawning event in June was documented within the study area (Carr-Harris, 2017). As both herring and smelt caught during this study included multiple age classes, warm ocean conditions during the study may have impacted overall abundances. From 2013 to 2016, the warm water anomaly off the north-east Pacific Ocean caused widespread impacts to pelagic communities (Bond, Cronin, Freeland, & Mantua, 2015; Cornwall, 2019). Documented impacts include lowered phytoplankton and zooplankton biomass (Gómez-Ocampo, Gaxiola-Castro, Durazo, & Beier, 2018; Yang, Emerson, & Peña, 2018), changes to available zooplankton prey (McKinstry & Campbell, 2018), and significant declines in abundance and condition of fish and marine mammals higher up the food web, including several forage fish species in the Gulf of Alaska (Osmeridae and *Ammodytes hexapterus*; Cornwall, 2019; Daly, Brodeur, & Auth, 2017). Given the widespread effects of the warm water anomaly on marine food webs in the north-east Pacific, it is likely that pelagic species residing in this region were impacted to some degree during the time of this study. Results from eight sites in the Skeena River estuary occurring from 2014 to 2016 and in 2018 have demonstrated a declining trend in surf smelt since 2014 that may be evidence of lower survival during the warm water anomaly (North Coast Juvenile Salmon Monitoring Program, unpublished data). In contrast, herring abundance at monitoring sites was similar for all sampling years, and spawner biomass in Prince Rupert and Central Coast herring populations has increased during this time period but decreased for the Haida Gwaii population (DFO, 2018). Further research is required to understand the future impacts of warming ocean conditions on pelagic fish communities in this region.

As this is only the second study (Higgins & Schouwenburg, 1973) examining how small pelagic fish are using the Skeena River estuary, there remains significant knowledge gaps regarding the larger estuary fish community. Other ecologically and traditionally important pelagic 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 pelagic fish play in supporting many species in the coastal food web (Therriault, Hay, & Schweigert, 2009), further research targeting the patterns of estuarine use by these species is needed.

4.3 | Comparing modelling approaches

Models using a detailed description of estuary habitat by incorporating various biophysical attributes fit juvenile salmon abundance data better and had a higher predictive capability than models based on coarse habitats. Simple habitat classification may not capture the dynamic nature of habitats in estuaries (Simenstad et al., 2006) as habitat boundaries in aquatic systems are rarely fixed (migration routes connecting highly used habitats) and environmental conditions are dynamic (Nagelkerken et al., 2015; Pardo & Armitage, 1997; Sheaves, 2009; Sheaves et al., 2015). 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 supports 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 (Bottom, Simenstad, et al., 2005; Dittman, Quinn, & Nevitt, 1996). 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. Given that habitats in an estuary do not provide ecosystem function to target species independently, accounting for estuary connectivity, ecophysical factors, and resource dynamics along with spatial and temporal variation can be important in prioritization of certain habitats for management (Nagelkerken et al., 2015; Sheaves et al., 2015)

4.4 | Limitations

This study assessed estuary habitat utilization using 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 with 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, though it examined a suite of environmental variables to model salmon abundance across the estuary, this 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, sampling more variables or even more frequently may not increase 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.

4.5 | Management implications

This study has three key implications for estuary planning and decision-making processes. First, current approaches employed in Canadian provincial and federal environmental risk assessment that use coarse habitat characteristics to identify important 'salmon' habitat did not explain very much of the observed variance in salmon abundance. For instance, juvenile salmon were found unevenly distributed across the estuary, using some eelgrass beds and not others. Unequal use of eelgrass meadows by species of juvenile salmon has also been found in other estuaries (Hodgson, Ellings, Rubin, Hayes, & Grossman, 2016; Rubin et al., 2018). In addition, different salmon species had different habitat associations. Eelgrass habitat in the Skeena River estuary 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 capture only a limited portion of what defines habitat importance to different salmon species.

Second, whereas 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 there was still a large degree of uncertainty associated with predicting the abundance of salmon across space and time. 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 unmeasured factors such as currents or prey abundance, that makes this habitat highly used. Industrial projects situated in regions supporting the highest abundances of salmon pose a higher risk to salmon populations compared with estuary regions with little or no salmon use. Instead of coarse habitat-based approaches that have high scientific uncertainty, one option might be to use field studies of salmon themselves (such as this) to identify regions where projects may pose particularly high risks.

Third, the findings of this study are also relevant to current practices in habitat mitigation. Given that habitat type (e.g. eelgrass) was only a weak proxy for the use of the location by juvenile salmon, there is great scientific uncertainty whether creation of the same habitat type in a different location will provide similar function. Thus, replacement of lost or damaged eelgrass habitat, mitigation policies proposed by industrial development environmental assessment in the Skeena River estuary (Pacific Northwest LNG, 2016), may not be able to achieve no net loss of nursery function for salmon. In general, habitat mitigation policy used in Canada rarely achieves adequate habitat compensation (Favaro & Olszynski, 2017; Harper & Quigley, 2005). Although habitat compensation projects can be successful (White, 2011), overall they are resulting in restored habitats with reduced areal extent (Kistritz, 1996), less utilization by target species (Levings

& Nishimura, 1997), and have lower habitat productivity (Quigley & Harper, 2006). No net loss habitat compensation is currently an integral part of assessing and mitigating environmental risk for developments, but our results indicate that this overly simplistic framework is challenged in dynamic and complicated estuary habitat.

Designating and managing key habitat for mobile and aquatic species, such as salmon, is particularly challenging because these animals require linked habitats arranged in particular distributions over their journey (Moore et al., 2016; Murphy, Koski, Lorenz, & Thedinga, 1997; Naiman & Latterell, 2005; Runge, Martin, Possingham, Willis, & Fuller, 2014). 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). Though many factors likely explain this discrepancy, it indicates the potential challenge of identification of important habitat and management of risks to mobile aquatic species, whether species are at risk or otherwise. This study supports the growing body of work identifying the contributing factors of estuary habitat for fishes of management and conservation concern and illuminates that current approaches to assessing risks to salmon in estuaries are based on oversimplification of their 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 (Beechie et al., 2010; Bottom, Simenstad, et al., 2005; Hanski, 2011; Nagelkerken et al., 2015). Understanding complex processes involved in dynamic habitat mosaics such as estuaries can further support conservation and management objectives of important fisheries.

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