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Assessing estuaries as stopover habitats for juvenile Pacific salmon

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ABSTRACT: Habitats along migratory routes may provide key resources for migratory species (e.g. stopover habitat). For example, migratory juvenile salmon transit through estuaries on their way from freshwaters out to the ocean, but they may also reside and feed in these habitats. Here we examined the amount of time that juvenile salmon feed and reside in the estuary of the Skeena River (British Columbia, Canada), the second-largest salmon-bearing watershed in Canada. We implemented a novel application of stable isotopes of sulfur, carbon, and nitrogen as clocks to estimate the days since estuary entry. Salmon estuary residency varied across species; 25% of individuals spent at least 33, 22, 30, and 5 d in the estuary for Chinook *Oncorhynchus tshawytscha*, coho *O. kisutch*, pink *O. gorbuscha*, and sockeye salmon *O. nerka*, respectively. Larger pink and Chinook salmon resided in the estuary for longer durations, growing at an estimated 0.2 and 0.5 mm d^{-1}, respectively, evidence that estuary residency provides growth opportunities. A negative relationship between size and estuary residency in coho salmon suggests the potential existence of an estuary fry life history. Genetic stock assignment indicated that different populations of sockeye salmon may reside in the estuary for different amounts of time. Collectively, these results reveal that estuaries can represent stopover habitats for salmon, and that the extent varies across salmon species and populations. These data address a knowledge gap in assessment of environmental risks of proposed industrial developments. This study indicates the importance of considering the fundamental nature of habitats through which migratory species move.

KEY WORDS: Anadromy · Bottleneck · Corridor · Early marine · Nursery habitat · Smolt · Stable isotope · *Oncorhynchus*

INTRODUCTION

Migratory species pose particular challenges for environmental decision making and conservation (Martin et al. 2007, Runge et al. 2014). First, migratory species rely on distant and distinct habitats, mandating management approaches that span the potentially vast range of the migration (Runge et al. 2014, Moore et al. 2015b). For example, habitat loss in the neotropics can drive declines of migratory birds that breed in temperate forests (Robbins et al. 1989), demanding international conservation efforts (Martin et al. 2007, Runge et al. 2015). Second, in order to travel between habitats, migratory species need connectivity among habitats, and there are large efforts focused on the quantification and protection of migratory corridors (Haddad et al. 2003, Shepherd & Whittington 2006, Doerr et al. 2011). Third, as they make their migration from one habitat to another, migratory species may also rely on habitats for physiological transitions or feeding (i.e. stopover habitats; Moore et al. 1995, Murray & Fuller 2015). Loss of even small amounts of stopover habitat may have disproportionately large impacts on migra-

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tory populations (Iwamura et al. 2014). Accordingly, effective management of migratory species is founded on the accurate characterization of these different components of their life cycle (Runge et al. 2014). For instance, different levels of habitat protection may be mandated for migratory corridors vs. stopover habitat. Conservation of migratory connectivity has often focused on the absence of potential anthropogenic barriers such as fences for migratory ungulates (Haddad et al. 2003, Doerr et al. 2011). However, if species are residing and growing in the habitat through which they are migrating (i.e. stopover habitat), then effective management needs to also protect various aspects of habitat quality (Murray & Fuller 2015). Thus, a key challenge in effective decision making for migratory species is the characterization of how species use the habitats that they move through.

Estuaries could represent important stopover habitats or simply migratory corridors for diadromous fishes like salmon. Anadromous salmon transit estuaries as they migrate from the freshwaters where they were born to the ocean where they will grow; thus estuaries must function as migratory corridors. Alternatively, juvenile salmon may stop over in estuaries to capitalize on refuge from predators, foraging opportunities, and a mix of salinities that may ease the challenging physiological transformation from freshwater to saltwater environments (Healey 1982, Macdonald et al. 1988, Weitkamp et al. 2014). At the foundation of understanding the relative importance of estuaries to juvenile salmon is the quantification of the amount of time they reside and feed there (Healey 1982, Thorpe 1994). For example, Chinook salmon *Oncorhynchus tshawytscha* grow rapidly and rear extensively in estuaries (Neilson et al. 1985, Levings et al. 1986, Bottom et al. 2005, Volk et al. 2010). Chinook salmon are known for their extensive life-history diversity (Bourret et al. 2016); indeed, juvenile residency in estuaries can range from 1 to 90 d (Miller & Simenstad 1997). Generally, it is thought that pink *O. gorbuscha*, coho *O. kisutch*, and sockeye salmon *O. nerka* move through estuaries in a short amount of time, while chum *O. keta* and some Chinook salmon will stop over in the estuary for weeks or months (Quinn 2005, Weitkamp et al. 2014). Most studies have observed sockeye salmon rapidly transiting estuaries (Furey et al. 2015), whereas Simmons et al. (2013) found extended occupancy of an estuary by juveniles from a population of sockeye salmon. Indeed, estuary residence patterns likely vary greatly across estuaries, species, populations, and individuals (Miller & Simenstad 1997, Bottom et al. 2005, Volk et al. 2010, Claiborne et al. 2014, Weitkamp et al. 2014, Furey et al. 2015). The estuary phase of the salmon life cycle is relatively understudied, especially for some species like pink salmon (Weitkamp et al. 2014), leaving uncertainty in this key question: Do estuaries represent stopover habitats or merely migratory corridors for juvenile salmon?

Understanding the role of estuaries for migratory species such as salmon is particularly pressing given historical and proposed development. Globally, estuaries have been heavily modified by human development. For instance, estuary seagrass ecosystems are in a 'global crisis' (Orth et al. 2006), with the total global area of seagrasses decreasing by 7% yr^{-1} since 1990 (Waycott et al. 2009). One set of timely and controversial examples of proposed industrial development in estuaries of salmon-bearing rivers are the proposed fossil fuel pipelines and terminals in the estuary of the second-largest salmon-bearing river in Canada, the Skeena River, British Columbia. For example, the Pacific Northwest Liquid Natural Gas (PNW LNG) Project has proposed a large LNG terminal for the Flora Bank/Lelu Island area of the Skeena River estuary. This portion of the estuary has particularly high densities of juvenile salmon that originate from throughout the Skeena River watershed (Higgins & Schouwenburg 1973, Carr-Harris et al. 2015, Moore et al. 2015a,b). However, estuarine residency by migratory juvenile salmon was identified as a critical data gap by an independent science team (Pickard et al. 2015). The Canadian Environmental Assessment Agency recently approved PNW LNG's environmental assessment application.

The amount of time that salmon reside in estuaries is challenging to quantify. Intensive field sampling over time can illustrate the temporal extent to which the estuary is used by juvenile salmon (e.g. Carr-Harris et al. 2015), but salmon may enter the estuary at different dates and thereby complicate interpretation. Acoustic tagging studies provide in-depth information on movements, but can only assess movements of larger individuals of larger species of juvenile salmon (e.g. Melnychuk et al. 2007, Welch et al. 2009, Furey et al. 2015). Hard structures such as scales or otoliths can provide insight into reconstructed movement patterns (Volk et al. 2010, Brennan et al. 2015, Claiborne & Campbell 2016). Perhaps due to different environmental conditions, different populations of salmon can have different otolith growth patterns (Zabel et al. 2010), and laboratory studies have found that time estimates based on otoliths are fairly accurate and precise (Freshwater et al. 2015, Claiborne & Campbell 2016). Here we used a

complementary approach—the application of known turnover rates of tissues and stable isotopes as clocks. Through studies of isotopes of tissues with known turnover rates, stable isotopes also may be used as clocks to quantify the timing of diet or habitat shifts. By comparing isotope signatures of tissues to the isotopic landscape (isoscape), studies have used isotopes to illuminate migratory connectivity (Hobson & Wassenaar 2001, Rubenstein & Hobson 2004). The shift in diet of migratory animals provides an opportunity to use stable isotopic clocks to track the arrival of a species to a new environment (Vander Zanden et al. 2015). Although previous laboratory studies have characterized turnover rates of juvenile salmonid tissues (Heady & Moore 2013), this approach has not yet been used extensively to examine estuary migration patterns in juvenile salmon.

Here we quantified the degree to which migratory salmon reside and feed in the estuary habitat through which they migrate on their way to the ocean. Through a novel application of stable isotopes as clocks, we assessed the amount of time that 5 species of juvenile salmon feed and reside in the estuary of the Skeena River. We asked the question: Do estuaries represent stopover habitats or migratory corridors for juvenile salmon? We were further interested in whether these patterns varied across species, regions within the estuary, and populations within species. If salmon are not feeding and residing in estuary habitat, then the estuary may simply represent a migratory corridor. Alternatively, if individuals are feeding and residing in the estuary, this represents evidence that salmon use estuaries as stopover habitats. This information addresses identified data gaps relevant to ongoing environmental decision making.

MATERIALS AND METHODS

Study design

We used stable isotopes to estimate the amount of time that juvenile salmon were feeding and residing in the estuary of the Skeena River. This isotope study was a component of a larger multiyear sampling program on the ecology of juvenile salmon and their food webs in the estuary of the Skeena River (Carr-Harris et al. 2015, Moore et al. 2015b). One of the core components of this program is using standardized fish collections at different sites across the spring and summer season to describe the spatiotemporal patterns of the estuarine fish community.

Fish were collected by standardized purse seining from different sites within the Skeena River Estuary throughout the spring–summer season of 2014. The purse seine was 9.14 m deep and 73 m long, with 5.1 cm webbing at the tow end and 1.3 cm webbing at the bunt, and was deployed between a 3 m boat and a larger vessel. Sites were sampled approximately every 10 d between 9 April and 7 July. We collected fish for stable isotope analyses from 2 regions of the estuary, which we hereafter refer to as the 'inner' region and the 'middle' region. The inner region represents estuary habitat closer to where the north arm of the Skeena River (Inverness Passage) enters the estuary and includes sites on or adjacent to Flora Bank. Inner sites included: several sites on and near Flora Bank, Inside Coast Island, Kitson Island, several sites around Lelu Island, Porpoise Channel, Ridley Island (SW), and Tsum Tsadai (Fig. 1). The middle region was located approximately 5 km from the inner region and sites there were at Kinahan Islands and to the north (Fig. 1).

Juvenile salmon smolt swim approximately 15 to 20 km d^{-1} when they are performing directed movement in nearshore marine environments (Welch et al. 2009) and thus have the potential to transit through the study region within 1 d. It should be noted that these estimates are derived from large sockeye salmon smolts; swim speeds of smaller outmigrating salmon such as pink salmon fry are likely substantially slower. Regardless, estimates of estuary residence of approximately 1 d or less (and several days or less for smaller-bodied species) would support the possibility that juvenile salmon are only transiting through the estuary habitat. Alternatively, estuary residence for longer periods of time would provide evidence of the degree to which estuaries serve as stopover habitat for juvenile salmon.

A subsample of the total fish collected was retained for stable isotope analyses from each region from each time period for each species. Fish were euthanized with a lethal dose of tricaine methanesulfonate (MS-222), stored on ice, and transferred to a −20°C freezer for future laboratory processing. Fork length was measured for each individual.

To explore the possibility that different populations of salmon within a species may have different patterns of estuary residency, we used genetic stock assignment to identify the population of origin of estuary-collected juvenile sockeye and Chinook salmon (Carr-Harris et al. 2015). Salmon can exhibit fine-scale genetic differentiation among spawning locations; for example, there are dozens of locally adapted salmon populations that spawn throughout the Skeena River watershed (e.g. Chinook and sockeye

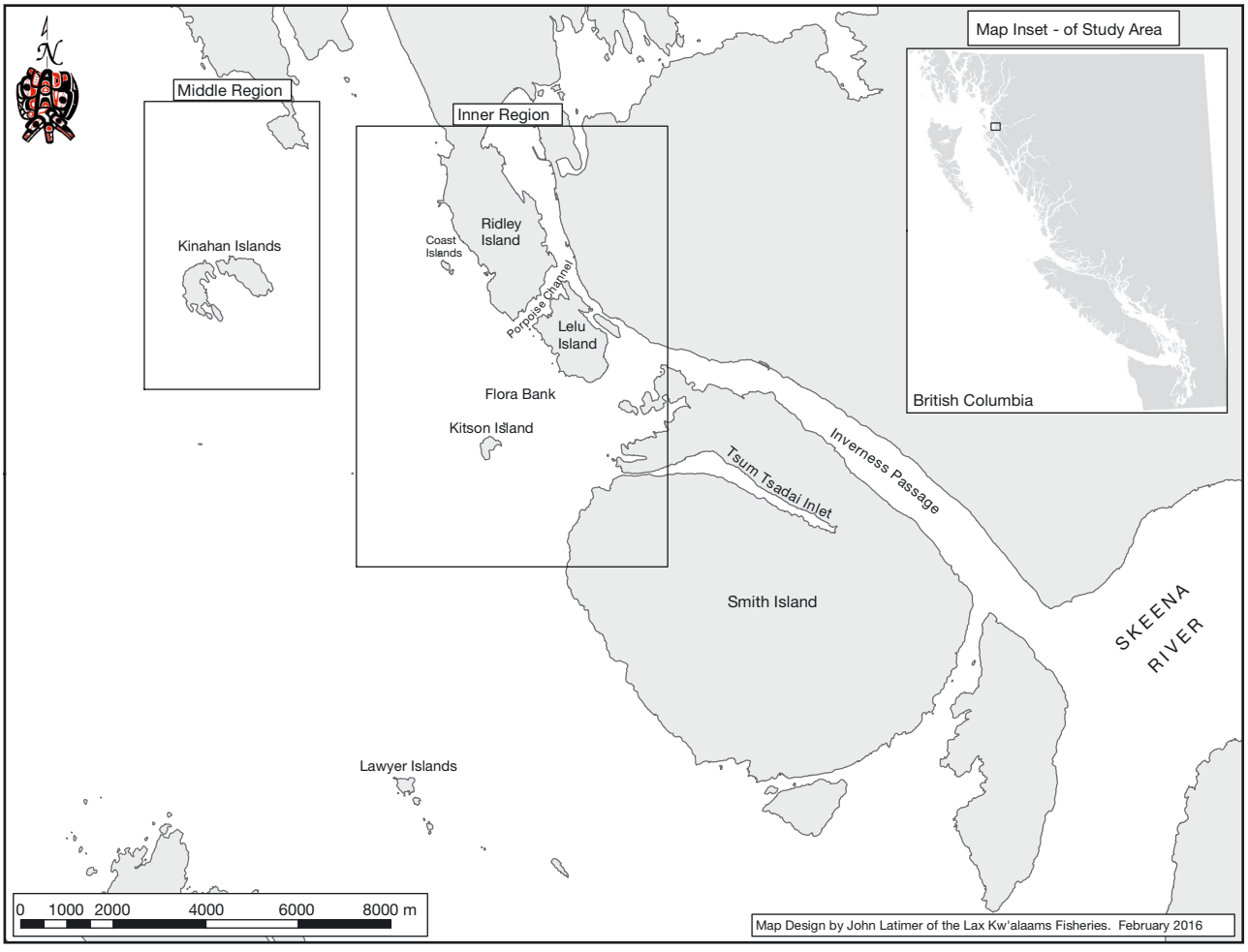

Fig. 1. Study area. Stable isotopes of juvenile salmon *Oncorhynchus* spp. were collected from the inner and middle regions of the Skeena River Estuary, British Columbia, Canada. Flora Bank is a shallow sandy area that supports the majority of the eelgrass in the greater Skeena River Estuary

salmon). For Chinook and sockeye salmon, for which the genetic baselines are well developed, fin clips were collected and sent to the Fisheries and Oceans Canada Molecular Genetics Laboratory of the Pacific Biological Station for genetic stock identification. Genetics were performed on a subset of sockeye and Chinook salmon. Sampling was approved by the University Animal Care Committee at Simon Fraser University (protocol number 1158B-11) and by a scientific collection permit from Fisheries and Oceans Canada.

Stable isotopes

Stable isotopes are naturally occurring isotopes that can provide insight into both ecological processes and patterns (Peterson et al. 1985, Peterson & Fry 1987, Moore & Semmens 2008). For example, nitrogen isotopes are frequently used as an indicator of trophic processes and nutrient cycling dynamics, or as a tracer of food web interactions. On the other hand, carbon isotopes change minimally upon assimilation, so they are a powerful indicator of the source of energy for consumers. Further, sulfur isotopes can be an effective tracer of different habitats or energy sources, especially in estuaries.

Here we used stable isotopes as 'clocks' to estimate the timing of a habitat shift, namely the number of days that any given juvenile salmon that we collected had resided in the estuary. Laboratory experiments have revealed that stable isotope signatures change in a predictable fashion following a diet or habitat switch (Vander Zanden et al. 2015). In this application, isotope signatures of juvenile salmon will start to shift when they change habitats and begin feeding on prey with different isotope signatures. Because

it takes time for the tissues to come to a new equilibrium, the degree to which the stable isotopes approach the new baseline can be used to estimate the timing of when the diet shift happened. Specifically, stable isotope turnover is thought to exponentially approach saturation. In our application, where juvenile salmon migrate from freshwater to estuary habitats, isotope values of juvenile salmon (δX_t) are predicted to be:

$$\delta X_t = \delta X_{\text{estuary}} - (\delta X_{\text{estuary}} - \delta X_{\text{freshwater}})e^{-t/\tau} \quad (1)$$

a function of the estuary baseline signature ($\delta X_{\text{estuary}}$), the freshwater baseline signature ($\delta X_{\text{freshwater}}$), and exponential decay governed by the turnover rate of the tissue of interest (τ) and the time (t) since habitat shift. This equation can be rearranged to estimate the time of diet switch. In our application, we estimated the time since estuary entry (t_{est}) as:

$$t_{est} = -\tau \cdot \ln\left(\frac{\delta X_{\text{estuary}} - \delta X_t}{\delta X_{\text{estuary}} - \delta X_{\text{freshwater}}}\right) \quad (2)$$

t_{est} represents an estimate of the number of days that the individual had resided and fed in the estuary prior to being sampled. Some fish that we sampled would have, in all likelihood, resided in the estuary for longer periods if they had not been sampled. Thus, these represent conservative estimates of estuary residence; in other words, t_{est} represents the minimum number of days that the individual would have fed and resided in the estuary.

Turnover rates (τ) of liver and muscle of juvenile salmonids have previously been estimated as 16 ± 4.8 and 39 ± 3.2 d (mean ± SE) in laboratory studies of steelhead *O. mykiss* (Heady & Moore 2013). Accordingly, liver tissues should more rapidly shift towards estuary baselines than muscle tissues. We averaged time estimates from multiple tissues to improve estimates of time since diet shifts, as recommended by Heady & Moore (2013) and described in more detail below.

We took the robust approach of characterizing species- and tissue-specific isotopic baselines. To characterize the freshwater baseline for juvenile salmon, we collected salmon of each different species within the freshwater environment. Specifically, we collected young salmon in freshwater rearing habitat in the Skeena River to characterize the freshwater isotope baseline for C, S, and N for liver and muscle tissues. Individuals were pooled for analyses when they were too small to provide enough sample material for analyses (for pink and chum salmon). Freshwater baseline samples were collected for all species: Chinook (N = 8; this and following represents the numbers of samples run for baselines for each isotope and tissue type; pooled individuals were considered single data points), chum (N = 13), coho (N = 5), pink (N = 19), and sockeye salmon (N = 5). Given that there were 2 tissues and 3 isotopes per sample, the total number of values used to characterize each species' baseline was 6 times the sample sizes listed above. Given logistical challenges of sampling young salmon in the spring as the snowmelt occurs, freshwater baselines were obtained from a single location for each species and assumed to approximate the watershed-wide baseline. We examine this assumption with simulations, as described below. Sockeye salmon freshwater baseline samples were collected from Babine Lake, the location of 95% of Skeena's sockeye (Gottesfeld & Rabnett 2008). Coho salmon freshwater baseline samples were collected from the Slamgeesh River, and pink, chum, and Chinook salmon juveniles were collected from the Kispiox River. We characterized the estuary isotope baseline by collecting liver and muscle tissues from fish species that reside in the estuary and fill a similar trophic niche as juvenile salmon. Specifically, we collected surf smelt *Hypomesus pretiosus* (5 from each of 2 regions) and Pacific herring *Clupea pallasii* (5 from 1 region) to characterize the estuary isotope baseline. We are confident that these species represent the estuary baseline and are resident; our on-going research finds all life stages of these 2 species in the study region (Moore et al. 2015a). While we present data from both species, we used smelt as the appropriate estuary baseline, as this species and juvenile salmon feed on similar zooplankton prey (McCabe et al. 1983). Thus, the isotope values of this species represent the approximate isotope values that salmon would approach as they enter and feed in the estuary.

In order to improve the ease of interpretation of stable isotope graphs, we estimated correction factors among the different tissues. Turnover models did not demand any correction factors because we compared muscle to muscle and liver to liver. Previous research has found that different tissues have different diet discrimination factors (McCutchan et al. 2003). We compared liver and muscle isotope signatures of individuals from the baseline sampling (e.g. freshwater samples of juvenile salmon as well as estuary fishes) to quantify the background difference between liver and muscle isotope signatures. We used these correction factors for graphically presenting the results. We performed these calculations on the averages for the 8 different fish species we examined. Liver isotope signatures were generally more

depleted than muscle isotope signatures for $\delta^{13}C$ (mean ± SE difference = −0.63 ± 0.22). Liver $\delta^{15}N$ was slightly more depleted than muscle $\delta^{15}N$ (−0.40 ± 0.25), while there was no substantial pattern for $\delta^{34}S$ (0.14 ± 0.39).

Propagating uncertainty

We used bootstrapping to propagate multiple sources of uncertainty into estimates of estuary entry. For each fish/isotope/tissue, we drew 10 000 estimates from normal distributions of the observed mean and standard deviation of τ, $\delta X_{estuary}$, and $\delta X_{freshwater}$, resulting in a distribution of t_{est}. We also included measurement error in these calculations by including a normally distributed error term with standard deviation of 0.4, the stated measurement uncertainty of stable isotope laboratory analyses of known standards. Thus, for each isotope and each tissue of every fish, we generated distributions of t_{est}. The joint posterior probability distribution for each fish was calculated as the product of the probability distributions of the different isotopes and tissues. Isotope clocks become less accurate and precise when estuary residency exceeds 100 d (see simulation results); we therefore cut off all estimates at this threshold.

Fish/isotopes/tissues were excluded from the analyses if their isotope signatures were outside of the mixing space (defined as the range between the appropriate mean freshwater and estuary baseline ±1 SD). This resulted in the exclusion of 5.2% of individuals. We hypothesize that these juvenile salmon originated from freshwater habitats that differed in their isotope baselines.

Model sensitivity

We used a simulation to examine the precision and accuracy of the isotope clock model, based on our data and parameters, to estimate estuary residency. As noted above, we used bootstrapping to propagate the measured variability in turnover rate, estuary baseline, and freshwater baselines. However, a potential additional unknown source of uncertainty is from potential geographic variation in the freshwater baselines. While we obtained species-specific freshwater baselines, these were only from 1 location per species due to logistical constraints. While the variation across individuals was relatively low (see below), it is possible that salmon from different locations within the large Skeena watershed had different freshwater baselines. Thus, we performed a simulation to explore how unknown additional variation in the freshwater baseline ($\delta X_{freshwater}$) would influence the precision of estimates of estuary residency. To this end, we simulated a series of 'true' estuary residency times (N = 1000) and used Eq. (1) to predict juvenile salmon isotope signatures across this range of estuary residency, propagating measured variation in baselines and turnover rates. We then used Eq. (2) to predict estuary residency for each simulated fish and compared the predicted to the 'true' estuary residency. This base simulation represents the precision of the approach used in this paper. We performed 2 additional simulations to explore how potential additional geographic variation in freshwater baselines could influence model precision. For the first scenario, we quantified the variation in freshwater baselines among species (Chinook, sockeye, and coho; collected from different locations) and added this variation (normally distributed around 0) to the $\delta X_{freshwater}$. This scenario represents the possibility that observed among-species differences in freshwater baselines translate into similar magnitude differences among geographies within a species. For the second scenario, we doubled this variation as an extreme case. We performed these analyses based on Chinook salmon muscle and liver tissues for sulfur isotopes.

Statistical analyses

We examined whether estuary residence was related to region of capture ('inner' vs. 'middle'), date of capture, and length of fish at time of sampling. We fit generalized linear models (GLMs) with all 3 terms, with the Gaussian family distribution with a log-link function to reduce heteroscedasticity. To assess the degree to which different factors were related to estuary residence, we examined the model coefficients of the different factors and their significance. Given the lack of *a priori* hypotheses, we did not include interaction terms in the model. We also ran separate analyses for sockeye and Chinook salmon where we examined whether population of origin was correlated with estuary residence. Given that genetics were run on only a subsample of the fish, these needed to be separate analyses. The population analyses used the same error structure as above. All analyses were conducted in R (R Core Team 2014).

RESULTS

We found a substantial difference in the isotope values of estuary and freshwater baselines for carbon (C) and sulfur (S; Fig. 2), but not for nitrogen (N; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m559p201_supp.pdf). The freshwater baselines were different for different salmon species. Chinook, coho, and sockeye salmon baselines all exhibited depleted $\delta^{34}S$ and $\delta^{13}C$ values well-differentiated from the estuary baseline. There was less isotopic differentiation between estuary and freshwater baselines for chum and pink salmon. Chum and pink salmon fry, which emigrate from freshwater immediately upon emergence and thus may retain the isotope signature of their mother, had baseline $\delta^{34}S$ and $\delta^{13}C$ values that appeared oceanic. There was still sufficient differentiation among estuary and freshwater baselines for isotope clock analyses for pink salmon. However, many chum salmon individuals sampled in the estuary were not located in the predicted isotope mixing space between their freshwater and estuary baseline (Fig. 2B). This pattern suggested that chum salmon juveniles did not con-

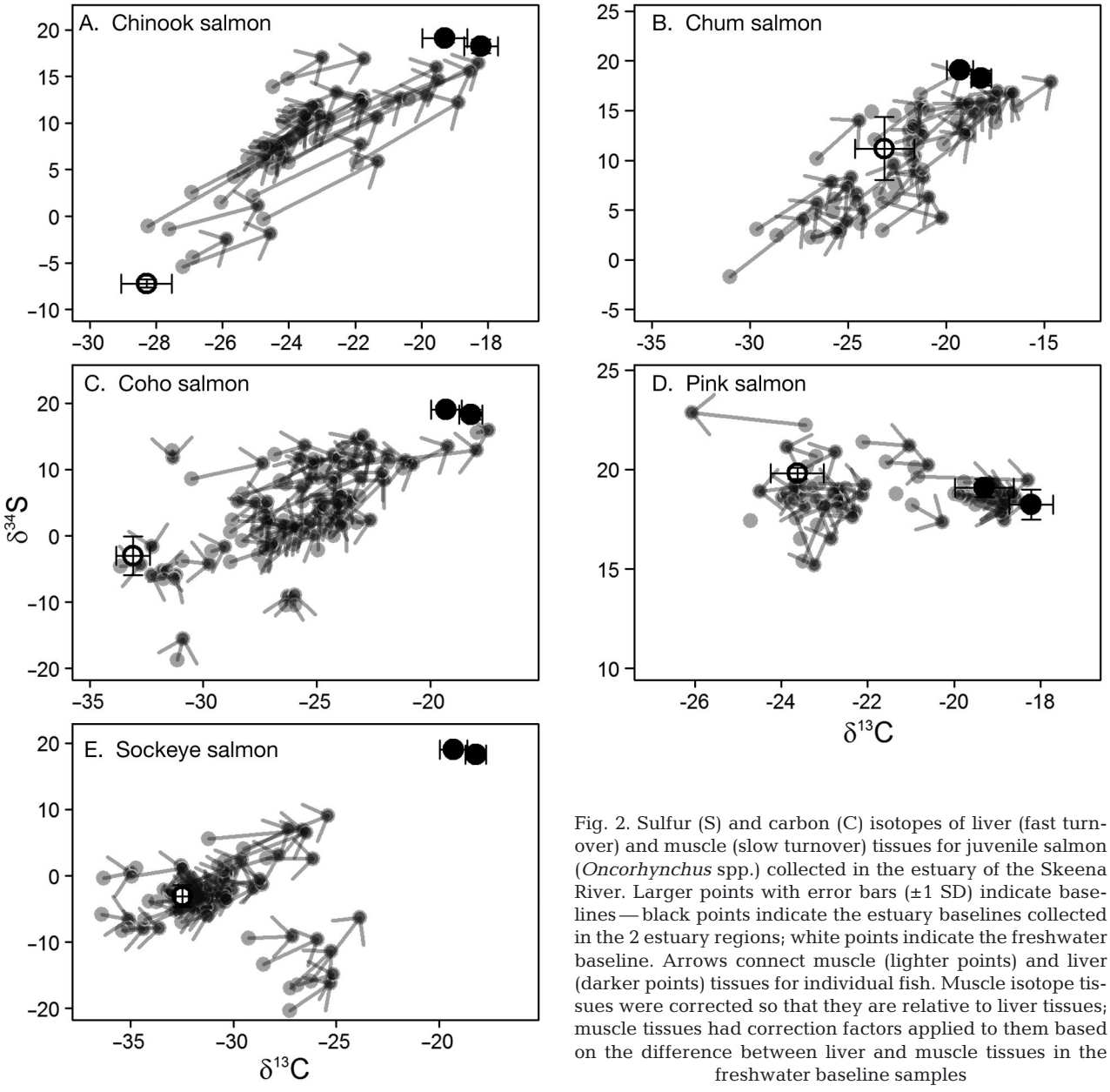

Fig. 2. Sulfur (S) and carbon (C) isotopes of liver (fast turnover) and muscle (slow turnover) tissues for juvenile salmon (*Oncorhynchus* spp.) collected in the estuary of the Skeena River. Larger points with error bars (±1 SD) indicate baselines — black points indicate the estuary baselines collected in the 2 estuary regions; white points indicate the freshwater baseline. Arrows connect muscle (lighter points) and liver (darker points) tissues for individual fish. Muscle isotope tissues were corrected so that they are relative to liver tissues; muscle tissues had correction factors applied to them based on the difference between liver and muscle tissues in the freshwater baseline samples

form to the assumptions of our stable isotope clock approach; accordingly, we did not perform clock analyses on juveniles of this species. We focused isotopic clock analyses on C and S isotopes for Chinook, coho, sockeye, and pink salmon.

Stable isotope signatures of estuarine juvenile salmon were generally between freshwater baselines and estuary baselines—evidence of various degrees of feeding and residing in the estuary ecosystem. As predicted, the isotope signatures of liver, the tissue with faster turnover rates, were more similar to estuary baselines than muscle, a slower-turnover tissue (Fig. 2). Vectors of isotopes for individuals, where the muscle isotope signature was connected to the liver isotope signature, generally pointed towards the estuary baseline (Fig. 2).

Simulations revealed that stable isotope clock models were accurate, fairly precise, and fairly robust to additional potential variation in freshwater baselines (Fig. S2), although this depended on estuary residency duration and tissue turnover rate. Estimates of estuary residency were fairly precise, and not surprisingly, became less precise as duration of estuary residency increased. Muscle isotopes were accurate for upwards of 100 d, and precision scaled with estuary residence period (Fig. S2). Liver tissues with faster turnover rates were precise for shorter estuary residence periods but became less precise at longer estuary residence periods (Fig. S3). In addition, for liver tissues, the estimated residence time started to be less accurate (underestimate) when residence time exceeded 2 mo (Fig. S3). These simulations also help to clarify the potential implications of unaccounted-for variation in freshwater baselines. For example, estimates of estuary residency based on muscle tissue and sulfur isotopes in Chinook salmon that had resided in the estuary for 3 wk (21 d) had a standard deviation of the model-predicted residence time of 2.0 (Fig. S2). Adding observed species-level variation (scenario 1) decreased the precision so that the standard deviation of the model-predicted residence time became 3.5. In the extreme case of adding 2 times the species-level variation (scenario 2), the standard deviation became 6.5. In a similar fashion, additional variation somewhat decreased the precision of estimates of estuary residency when liver tissues were used (Fig. S3). These simulations provide evidence that our application of stable isotope clocks is conservative, accurate, fairly precise, and fairly robust to possible additional variation in freshwater isotope baselines because of the large spread between estuary and freshwater isotope signatures (Fig. 2).

Different individuals of different salmon species had resided in the estuary for variable durations based on isotopic clock analyses. Propagating uncertainty yielded probability distributions of the amount of time that each individual salmon had been residing and feeding in the estuary (Fig. 3). Based on the most likely day (highest probability estimate), there was substantial variation across and among species (Table 1). Specifically, 50% of the Chinook salmon juveniles that we collected had been in the estuary for at least 26 d, 25% of individuals had been in the estuary at least 33 d, and 5% of individuals had been

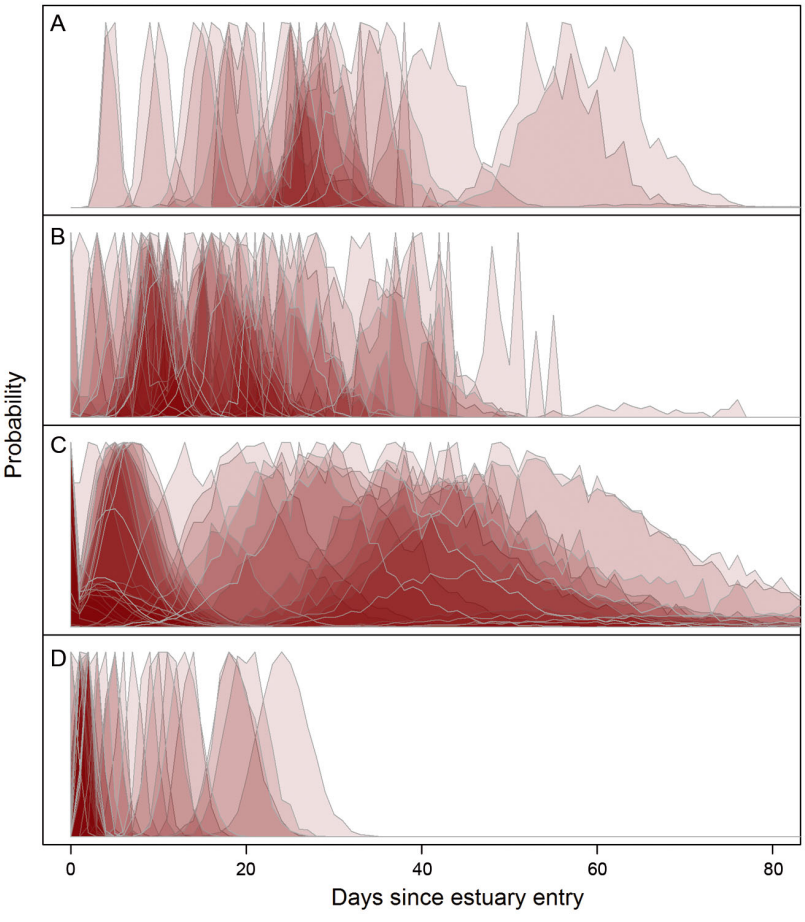

Fig. 3. Estimates of days since estuary entry (t_{est}) for (A) Chinook salmon *Oncorhynchus tshawytscha*, (B) pink salmon *O. gorbuscha*, (C) coho salmon O. *kisutch*, and (D) sockeye salmon *O. nerka*. Shown are posterior probabilities of estimated time since estuary entry for individual fish, generated based on the product of estimates from liver and muscle tissues and sulfur and carbon isotopes

Table 1. Summary of days since estuary entry of juveniles of different species of salmon (*Oncorhynchus* spp.) collected in the different sampling regions of the Skeena River estuary (see Fig. 1). Shown is the sample size for each category and the 5, 25, 50 (median), 75, and 95% value for the sampled population. For example, 25% of juvenile Chinook salmon sampled in the inner region had resided for less than 15 d in the estuary. Data shown are based on the single highest probability estimate for each individual. NA: chum salmon isotope clocks were not run as they did not reliably occur within the isotope mixing space

Salmon	Region	N	Days since estuary entry				
			5%	25%	50%	75%	95%
Chinook	All	32	7.2	17.8	26.5	32.5	56.8
Chinook	Inner	25	5.8	15.0	26.0	32.0	56.8
Chinook	Middle	7	17.6	22.5	27.0	31.5	48.7
Chum	All	48	NA				
Chum	Inner	33	NA				
Chum	Middle	15	NA				
Coho	All	62	0.1	9.0	14.0	21.8	42.9
Coho	Inner	39	0.0	9.0	14.0	20.5	32.7
Coho	Middle	23	3.1	8.5	14.0	31.0	46.6
Pink	All	57	0.0	0.0	6.0	31.0	101.0
Pink	Inner	24	0.0	0.0	4.5	32.0	50.8
Pink	Middle	33	0.0	0.0	6.0	31.0	101.0
Sockeye	All	54	0.7	1.0	2.0	5.0	18.0
Sockeye	Inner	31	0.5	1.0	2.0	3.0	10.5
Sockeye	Middle	23	1.0	1.0	2.0	10.0	8.9

in the estuary at least 54 d (Table 1). Juvenile coho salmon apparently resided in the estuary for somewhat shorter amounts of time: 50% of individuals had been in the estuary for at least 15 d, 25% of individuals had been in the estuary for at least 22 d, and 5% of individuals had been in the estuary for at least 43 d. In contrast, 50% of juvenile pink salmon had been in the estuary for at least 6 d, evidence that most pink salmon were recent immigrants to the estuary. However, a substantial portion of the pink salmon population was identified as having reared in the estuary for several weeks or more; 25% of individuals had been in the estuary for at least 30 d. The majority of juvenile sockeye salmon were characterized as having entered the estuary within a few days of being sampled; 50% of individuals had been the estuary for 2 d or less. However, many juvenile sockeye salmon were residing and feeding in the estuary for upwards of 1 wk; 25% of individuals had been rearing for at least 5 d and 5% had been rearing for 18 d or more.

Estuary residence of the different species of salmon was explained by different factors (Fig. 4). For Chinook salmon (Fig. 4A), individuals that were larger had resided longer in the estuary than those that were shorter (length = 0.03 ±0.005, $p < 0.00001$; this and the following represent the coefficient estimate in $\log_e$ parameter space ± 1 SE and its significance based on the GLM that also includes region and date). Coefficients for neither region nor date were significantly different from 0 ($p = 0.45$ and 0.52, respectively).

Estuary residence in pink salmon was related to all 3 factors: length, region, and date. Fish that were sampled later in the season had resided longer in the estuary than those that were sampled earlier in the season (date = 0.09 ± 0.02, $p < 0.0001$). In addition, fish that were collected in the middle region of the estuary had resided for a longer period than those collected in the inner region (region = 0.45 ± 0.21, $p = 0.03$). Further, length was a significant predictor of estuary residence (length = −0.047 ± 0.013, $p = 0.001$). Intriguingly, this parameter value was negative, implying that longer fish had resided for shorter periods, even though data inspection clearly reveals that larger fish had resided in the estuary for a longer time period (Fig. 4B). We thus fit a model post hoc that included an interaction term between length and date, and in this model there was a significantly negative interaction term (length × date = −0.006 ± 0.009, $p = 0.000001$), and in this model the relationship between length and estuary residence was estimated to be significant and positive (length = 0.36 ± 0.06, $p = 0.000001$). Thus, pink salmon individuals that were larger had resided longer in the estuary than those that were shorter, but this relationship was weaker for individuals that were collected later in the season.

Estuary residence in coho salmon was not significantly related to region or date of collection ($p = 0.29$ and 0.26, respectively). Intriguingly, smaller coho salmon tended to have resided in the estuary for more days than larger individuals (Fig. 4C; length = −0.018 ± 0.005, $p = 0.007$).

For sockeye salmon, individuals that were collected later in the season (towards June/July) had resided longer in the estuary than those that were collected early in the season (towards April) (date = 0.03 ± 0.006, $p = 0.00001$; Fig. 4D). In addition, juvenile sockeye salmon collected in the 'middle' region had resided in the estuary longer than those collected in the 'inner' region (region = 0.69 ± 0.20, $p = 0.001$). In sockeye salmon, individual length was not a significant predictor of estuary residence ($p = 0.14$).

Genetic stock assignment of juvenile sockeye and Chinook salmon collected in the estuary allowed us to uncover potential population-specific patterns of estuary residency. Estuary-collected sockeye salmon were identified as coming from 14 different popula-

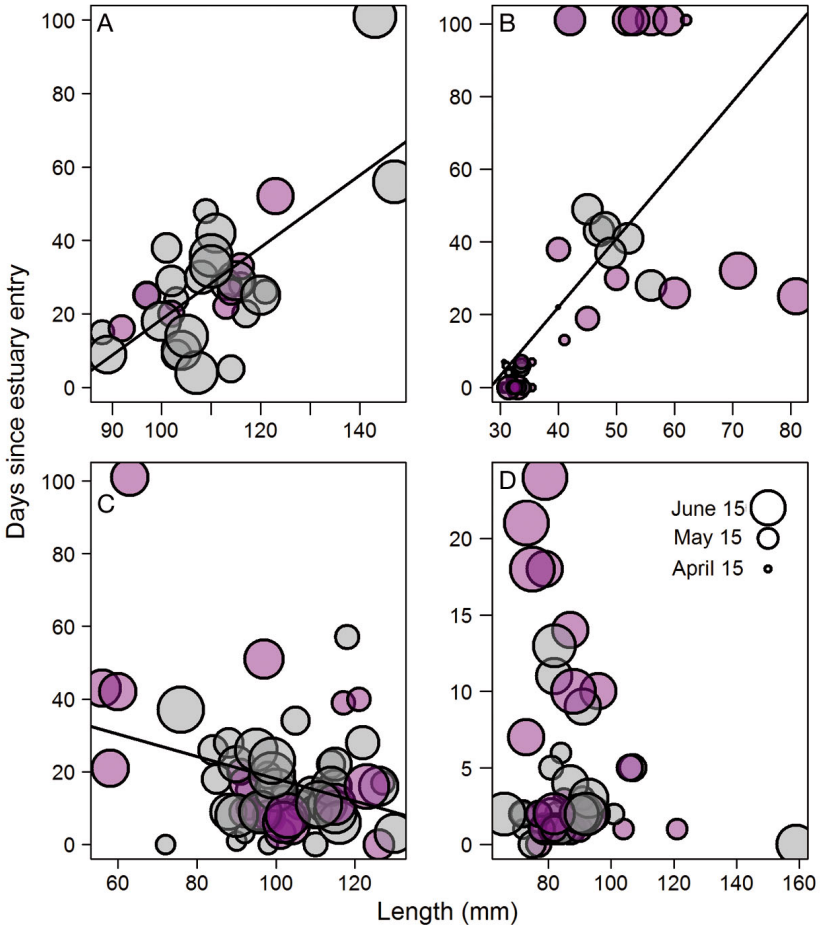

Fig. 4. Correlation between individual salmon size and estuary residence for (A) Chinook salmon *O. tshawytscha*, (B) pink salmon *O. gorbuscha*, (C) coho salmon *O. kisutch*, and (D) sockeye salmon *O. nerka*. Each point represents a different individual collected in the estuary, with their most likely estimate of days since estuary entry (t_{est}) as a function of their observed length. For visualization, shown is a line with the best fit linear model. The size of the point is related to the date of capture, which ranged from April to July; larger (smaller) points represent individuals that were captured later (earlier) in the season, as shown by the text and white circles in panel D. Point color indicates location of capture, where grey is the 'inner' region and purple is the 'middle' region (see Fig. 1)

tions. Six populations of sockeye salmon included at least 3 genetically identified individuals for which we also obtained stable isotope clock estimates of days since estuary entry (Fig. 5), and these populations exhibited different ranges of estuary residency (GLM, p-values for population-specific coefficients range from 0.001 to 0.94). Juvenile sockeye salmon from the Sustut River in the upper Skeena River watershed were estimated to have resided approximately 2 wk in the estuary. Sockeye salmon from Alastair Lake were estimated to have spent several days to 12 d. In contrast, sockeye salmon from various populations in the Babine Lake catchment, such as Fulton River, were estimated to have spent less time in the estuary, with the median fish having spent 1 or 2 d in the estuary (Fig. 5). Our sample collection also included Chinook salmon from 7 different populations. Sample sizes and replication within different populations of Chinook salmon were insufficient to characterize population-specific patterns.

DISCUSSION

We discovered that all juvenile salmon species exhibited evidence of some degree of estuary rearing and feeding. Specifically, 25% of individuals spent at least 33, 22, 30, and 5 d in the estuary for Chinook, coho, pink, and sockeye salmon, respectively. These data represent conservative estimates of estuary residency; our approach provides estimates of how many days individuals had resided in the estuary prior to their capture. In addition, juvenile salmon collected in the inner region of the estuary had been residing in the estuary as long as fish in the more distant middle region of the estuary (Table 1) for Chinook and coho, but not sockeye and pink salmon. Individuals that were larger had resided in the estuary longer for Chinook, coho, and pink salmon. Individuals that were collected later in the season had resided longer for pink and sockeye salmon. Collectively, these data are generally consistent with the hypothesis that estuaries represent stopover habitats for juvenile salmon where individuals are residing and growing, and are not just migratory corridors, but that usage patterns vary across salmon species.

Our findings indicate that juvenile Chinook salmon extensively use the Skeena River estuary for rearing and growing. We observed juvenile Chinook salmon rearing for over 1 mo in the estuary; previous research has observed that young Chinook salmon can rear in estuaries for several months, but there is a large range in the duration of rearing within and across populations (Miller & Simenstad 1997, Bottom et al. 2005, Volk et al. 2010, Claiborne et al. 2014). In

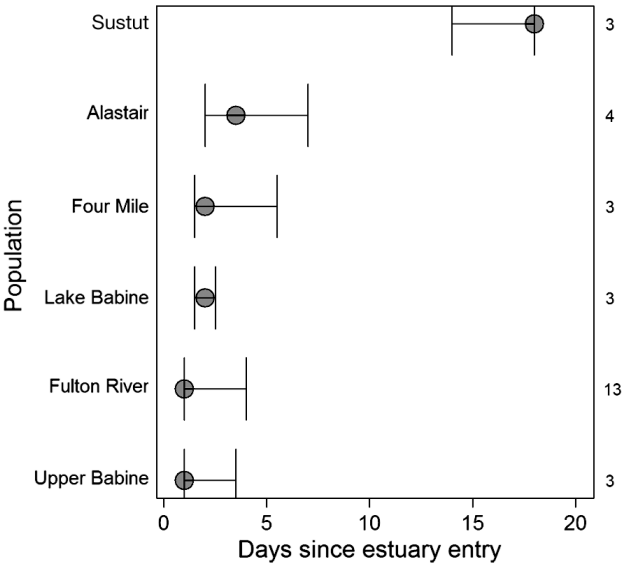

Fig. 5. Variation among sockeye salmon *Oncorhynchus nerka* populations in time since estuary entry. Shown are the median values and inner quartiles (25 and 75%). Corresponding sample sizes are shown to the right of the panel. These salmon populations are located upriver from the estuary; Alastair is approximately 60 km upstream, while the other populations are approximately 500 km upstream

our study, date of collection was not significantly related to estimates of estuary residence. This lack of a relationship is perhaps not surprising given that Chinook salmon have a high degree of diversity of outmigration timing (Bottom et al. 2005, Friesen et al. 2007, Weitkamp et al. 2015, Bourret et al. 2016, Schroeder et al. 2016). Based on stable isotope derived calculations of estuary residence, we estimate that Chinook salmon grew 0.48 ± 0.09 (SE) mm d^{-1} (Fig. 4A). These calculations are based on the population-level relationship between size and estuary residence, not tracking individuals, and thereby assume that growth is the only process determining size, not other feasible processes like size-selective survival or emigration. Nevertheless, these estimates of growth are consistent with estimates of daily growth rates of juvenile salmon from other estuaries (Miller & Simenstad 1997). Size of young salmon is critical to their future survival in the ocean, with previous studies repeatedly finding that larger fish survive better in the ocean (Holtby et al. 1990, Beamish et al. 2004, Moss et al. 2005). Thus, our study provides evidence that estuary residency provides key growth opportunities for Chinook salmon, and previous work illustrates that this estuary growth can carry over to ocean survival (Duffy & Beauchamp 2011). Indeed, previous comparative studies have found that juvenile Chinook salmon that migrate through more pristine estuaries have higher marine survival than those that migrate through more degraded estuaries (Magnusson & Hilborn 2003, Meador 2014). Collectively, our results add to the growing scientific appreciation that estuaries are critical habitat for juvenile Chinook salmon.

Our study provides evidence that pink salmon rely more on estuaries than previously thought. Pink salmon migrate to estuaries upon emergence as fry, and previous studies suggested that they move rapidly through estuaries (Levy & Northcote 1982, Weitkamp et al. 2014); however, there are relatively few studies of this topic given that outmigrating pink salmon fry are too small to tag with typical approaches. Through our novel application of stable isotope clocks, we discovered that many pink salmon were rearing in the estuary for over 1 mo (Table 1). In addition, larger individuals had reared in the estuary for a longer period than smaller individuals, showing evidence of growth. Based on these data (with caveats noted above), we estimate that young pink salmon grew 0.22 ± 0.035 (SE) mm d^{-1} in the estuary. Individuals that were sampled later in the season had resided in the estuary for a longer period than those sampled earlier in the season, further evidence of extended residency following a contracted migration downstream. Our findings collectively indicate that pink salmon migrate en masse to the Skeena River estuary in the early spring but that a substantial part of the population feeds and rears for extended periods of time, staging in the inner estuary before progressing to more distant regions in the estuary.

Sockeye salmon appeared to move through the estuary the most rapidly of the salmon species, but there were some individuals that were rearing for >1 wk. This variability in estuary residency appeared to be at least somewhat linked to population identity—genetic stock assignment of estuary juveniles revealed that different populations of sockeye salmon had resided in the estuary for different amounts of time, although sample sizes were small (Fig. 5). Similarly, a study on the Alaska peninsula found a population of sockeye salmon with extended estuary residence (Simmons et al. 2013), different than most studies of sockeye salmon in estuaries (Weitkamp et al. 2014). We did not observe a relationship between size and estuary residence for sockeye salmon, perhaps not surprising given that Skeena River sockeye salmon smolts emigrate at variable ages and sizes (Gottesfeld & Rabnett 2008), and found that they did not rear for as long in the estuary as the other species. Individuals that were sampled later in the season tended to have reared in the estuary for a longer period. Further, estuary resi-

dence was longer in the middle region compared to the inner region, suggesting that they are sequentially progressing through the estuary. Since these sockeye salmon could have traveled through both regions in less than a day, given their potential swim speeds as observed in other estuaries (Furey et al. 2015), our data illustrate that sockeye salmon are residing and feeding in the Skeena River estuary, but transiting more rapidly than other salmon species.

Coho salmon juveniles appear to be rearing in the estuary for up to several weeks and potentially even months. One of the intriguing results of our study was that smaller coho salmon tended to have resided in the estuary longer than larger individuals. One possible explanation for this pattern is that some of these small individuals represent a life-history strategy of coho salmon whereby some individuals go to the estuary as fry (in their first year of life) and rear there for an extended period of time. To our knowledge, this life-history strategy has not been described for coho salmon in the Skeena River (Gottesfeld & Rabnett 2008), but it has been described for coho populations in other watersheds (Miller & Sadro 2003, Koski 2009, Craig et al. 2014, Rebenack et al. 2015). In addition, some juvenile coho from other watersheds migrate during the fall and winter to marine ecosystems, and substantial numbers of these fish survive to adulthood (Bennett et al. 2015). Koski (2009) suggested that the estuarine fry life-history strategy may increase coho population productivity and adaptive capacity. Thus, somewhat similar to Chinook salmon, there is growing evidence that coho salmon exhibit a diversity of estuary life-history strategies that contribute to population dynamics (Miller & Sadro 2003, Craig et al. 2014, Jones et al. 2014, Rebenack et al. 2015).

Isotopes of juvenile chum salmon from the estuary did not follow our expectations of falling between freshwater baselines and estuary baselines, but are nonetheless revealing. A substantial proportion of estuary chum salmon were more depleted in $\delta^{13}C$ and $\delta^{34}S$ than the freshwater baseline, falling outside of the mixing space and scope of the models. It is tempting to attribute this pattern to high levels of isotopic variation across different freshwater populations and thus the lack of accurate characterization of freshwater baseline. However, chum salmon emigrate from freshwater as fry, so the isotope signature of their tissues should reflect the signature of their mothers and thus be similar across populations assuming similar ocean usage patterns, regardless of spawning location. Indeed, the isotope signatures of chum fry that we collected from freshwater are closely aligned with a meta-analysis of previously published studies of adult chum salmon isotopes (Johnson & Schindler 2009). We hypothesize that some chum fry are feeding in the lower portion of the Skeena River and are incorporating a different isotopic signature on their way to the estuary. Chum salmon populations in the Skeena River are of conservation concern and their life histories are poorly understood (Gottesfeld & Rabnett 2008).

Our approach of stable isotopes as clocks entails assumptions and uncertainties that are important to examine. Estimates of estuary residence represent snapshots of estuary residence from juvenile salmon collected in the estuary. If they had not been sampled, estuary salmon may have resided in the estuary for longer periods; our analyses thus provide conservative estimates of minimum estuary residence at the individual level. At the population level, individuals that transit through the estuary more rapidly would be less likely to be sampled; our analyses thus would be more likely to sample individuals with longer estuary residence times. In addition, our analyses utilized baselines characterized for the freshwater and estuary habitats. The estuary baseline appears to not vary substantially across the 2 sites and also across 2 species of resident zooplanktivorous fish (herring and smelt), lending confidence that this baseline was characterized accurately, although we cannot rule out the possibility that temporal variation in estuary isotopes contributed some unexplained uncertainty. For the freshwater baseline, we obtained species-specific samples for all of the different salmon species. There was minimal variation in isotope values across freshwater baseline individuals within a species. However, it is important to note that these freshwater baselines, while statistically precise for at least one major freshwater salmon population per species, may not be representative for all populations within each species. Accordingly, we ran simulations to explore the potential influence of additional geographic variation in freshwater baselines; these revealed that model estimates are relatively robust to this uncertainty (Figs. S2 & S3). These simulations reveal that our method may underestimate estuary residency when the true residency period is long (greater than 60 d), emphasizing the conservative nature of our estimates. Further, it is possible that fish are assimilating isotope signatures from habitats between estuary and freshwater rearing habitats, as we hypothesize for chum salmon. Extensive feeding during the downstream migration, coupled with a different isotope signature of this habitat, could alter expression of the freshwater baseline. Previous research suggests that salmon do not generally forage exten-

sively while they migrate downstream, although data are not extensive on this topic (Rondorf et al. 1985, Stefansson et al. 2003). We took the approach of excluding samples if they did not fall within the isotope mixing zone, as these likely represent individuals for which the baseline was not appropriate. Future work can characterize the 'isoscape' of the freshwater environment. The use of stable isotopes as clocks is also predicated on tissue turnover rates that have been accurately characterized for the appropriate study taxa and life stage (Vander Zanden et al. 2015). Our study used estimates from previous laboratory research that performed a diet-switching experiment for the same life stage for a similar species from the same genus of Pacific salmon (steelhead smolts *Oncorhynchus mykiss*; Heady & Moore 2013), suggesting that these turnover estimates are transferable to our study. Our estimates of timing were generated by combining estimates from multiple tissues and multiple isotopes; these estimates tended to agree qualitatively, although we note that muscle estimates tended to be longer than liver estimates (Fig. S4). Accordingly, our analytical approach propagated uncertainty in parameter estimates and data variability in order to generate the most robust estimates possible.

These findings fill a knowledge gap that has been previously identified as being critical to on-going environmental decision making in the Skeena River Estuary (Pickard et al. 2015). A series of large industrial projects have been proposed for the estuary that are assessing their potential environmental risks to salmon, such as the recently-approved PNW LNG terminal in the Flora Bank region. Reports for the environmental assessment application from PNW LNG terminal have stated that young salmon observed in this inner region of the estuary are involved in 'characteristic downstream migration behaviour' (Stantec 2015). In contrast, our results demonstrate that some individuals of all species are feeding and residing for days to weeks and for pink, coho, and Chinook salmon, some individuals are residing for over a month. Thus, this region of the Skeena River Estuary serves as an extended stopover habitat for migratory salmon. Alteration of this habitat has greater risks to salmon populations than assumed in the environmental assessment. These findings add to previous research that discovered that this region is a migratory bottleneck that supports all species of eastern Pacific salmon and populations from throughout the vast Skeena River watershed (Carr-Harris et al. 2015, Moore et al. 2015b).

There are increasing efforts to link understanding of migration with environmental decision making, especially for birds and ungulates (Sawyer et al. 2009, Sheehy et al. 2011, Iwamura et al. 2013, 2014, Murray & Fuller 2015, Runge et al. 2015, 2016). For example, studies of mule deer *Odocoileus hemionus* migration discovered that this species links a series of stopover habitats; these stopover habitats were given higher conservation priority and this information was used to inform land-use decision regarding natural gas development (Sawyer et al. 2009, Sawyer & Kauffman 2011). However, environmental decision making and conservation planning for migratory species is still in its infancy (Martin et al. 2007, Iwamura et al. 2013, Runge et al. 2014), and many of the Earth's great migrations have disappeared or are disappearing (Wilcove & Wikelski 2008). For example, migrations of Rocky Mountain locusts *Malanoplus spretus* once blackened the skies above North American grasslands, but this species is thought to have been accidentally driven to extinction through the destruction of a small bottleneck habitat (Lockwood 2001). While this extirpation of locusts may have benefited farmers, it is a cautionary example of how small habitats can underpin vast populations (Iwamura et al. 2013). Studies such as ours fill key knowledge gaps in identifying the fundamental nature of habitats through which migratory species move.

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