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ARTICLE

Chinook salmon exhibit long-term rearing and early marine growth in the Fraser River, British Columbia, a large urban estuary

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Abstract: Estuaries represent a transition zone for salmon migrating from fresh water to marine waters, yet their contribution to juvenile growth is poorly quantified. Here, we use genetic stock identification and otolith analyses to quantify estuarine habitat use by Chinook salmon (*Oncorhynchus tshawytscha*) — the Pacific salmon species considered most reliant on this habitat — in Canada's most productive salmon river, the Fraser River. Two years of sampling revealed subyearling migrant (ocean-type) Chinook from the Harrison River to be the estuary's dominant salmon population throughout the emigration period. These Chinook salmon were caught predominantly in the estuary's brackish marshes but shifted to more saline habitats as they grew. Otolith analyses indicated that these Chinook salmon have wide-ranging entry timing (from February to May) and longer estuarine residency (weeks to months, mean 41.8 days) than estimated by prior studies, but similar daily growth rates (mean ± SD: 0.57 ± 0.13 mm) across entry dates and residency periods, implying sufficient foraging opportunities throughout the emigration period and habitats. Together, these results suggest that estuarine habitat is more important for early marine growth of subyearling migrant Chinook salmon than previously recognized.

Résumé : Si les estuaires constituent des zones de transition pour les saumons migrants de l'eau douce vers la mer, leur contribution à la croissance des juvéniles n'est pas bien quantifiée. Nous utilisons l'identification génétique au stock et des analyses d'otolites pour quantifier l'utilisation de l'habitat estuarien par le saumon chinook (*Oncorhynchus tshawytscha*) — l'espèce de saumon du Pacifique considérée comme dépendant le plus de cet habitat — dans la rivière à saumons la plus productive du Canada, le fleuve Fraser. Deux années d'échantillonnage révèlent que des saumons chinooks migrants (type océanique) de moins d'un an issus de la rivière Harrison constituaient la population dominante de saumons dans l'estuaire durant toute la période d'émigration. Ces saumons chinooks ont été capturés principalement dans les marais saumâtres de l'estuaire, mais se déplaçaient vers des habitats plus salins au fil de leur croissance. Les analyses d'otolites indiquent que ces saumons chinooks présentent une grande fourchette de dates d'entrée en mer (de février en mai) et de plus longues durées de résidence dans l'estuaire (de plusieurs semaines à plusieurs mois, pour une moyenne 41,8 jours) que ce qu'estimaient des études antérieures, mais des taux de croissance quotidiens semblables (moyenne ± ET: 0,57 ± 0,13 mm) peu importe la date d'entrée ou la durée de résidence, ce qui indiquerait des occasions d'approvisionnement suffisantes durant toute la période et dans tous les habitats d'émigration. Collectivement, ces résultats donnent à penser que l'habitat estuarien est plus important pour le début de la croissance en mer de saumons chinooks migrants de moins d'un an que ce qui était reconnu auparavant. [Traduit par la Rédaction]

Introduction

Chinook salmon display high plasticity in their life history strategies, including the extent of rearing time in fresh water before downstream migration (Bourret et al. 2016; COSEWIC 2018). Subyearling migrant (i.e., ocean-type) Chinook salmon (*Oncorhynchus tshawytscha*) emigrate within their first year, sometimes shortly after hatching at sizes as small as 20 mm (Healey 1991; Weitkamp et al. 2014). These fish are smaller than their yearling migrant counterparts, which remain in fresh water for at least their first winter and may be more than 100 mm long before they migrate downriver. Conversely, subyearling migrants rely more heavily on estuarine and nearshore marine environments as they grow to smolt sizes (>60 mm fork length on average; Healey 1991; Weitkamp et al. 2014). Size-selective mortality influences Chinook salmon at multiple life stages, and there has been particular interest in how growth during emigration may

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influence survival (Beamish et al. 2003; Duffy and Beauchamp 2011). The critical-size critical-period hypothesis proposes that juvenile salmon must reach a minimum size threshold to survive their first winter and predicts that individuals that grow faster during the early marine phase, which begins in estuaries, will be better able to avoid predation and more resilient to periods of starvation if food becomes scarce (Beamish and Mahnken 2001).

Estuaries provide a gradual transition for juvenile salmon from fresh to saline water conditions. This transition comes with metabolic costs and may cause physiological stress, but this stress generally decreases with increasing body size (Quinn 2018). This may partially explain why subyearling migrant Chinook salmon spend more time in estuaries than do larger yearling migrants (Weitkamp et al. 2014). Estuaries also provide an increase in food availability relative to freshwater habitat (Quinn 2018), while still offering high energy density insect prey (Levings et al. 1991; Davis et al. 2019).

The Fraser River estuary sits at the mouth of Canada's most productive salmon river, which supports 17 genetically and ecologically distinct Chinook salmon populations (Northcote and Atagi 1997; COSEWIC 2018). Most of these populations are now considered to be Endangered or Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Fisheries and Oceans Canada 2019), and the estuary itself has been highly modified and continues to face multiple cumulative threats, including urban, agricultural, and industrial developments (Schaefer 2004; Kehoe et al. 2020). Yet, few studies have examined the abundance or growth of juvenile salmon in the estuary, and none employed modern technologies such as genetic stock identification (GSI) or otolith analysis (i.e., Greer et al. 1980; Levy and Northcote 1982; Levings et al. 1991), such that its current importance for these populations is unknown. Studying the use of estuarine habitat by juvenile salmon can, however, be difficult, with low mark–recapture success rates and hazardous sampling conditions, particularly in large delta systems such as the Fraser River (Levings et al. 1983; Sutherland et al. 2013). Otolith analysis from fish captured postmigration can provide a detailed picture of the life history of individual fish, including quantitative measures of residency in different water bodies (Miller et al. 2010; Volk et al. 2010).

Here, we present the first study to apply modern otolith and GSI technology to quantify estuarine emigration timing, residency, and growth of wild Chinook salmon in the Fraser River estuary. Our objectives were to determine whether (*i*) Chinook salmon display a wide range of entry timing and residency period, capitalizing on early estuarine entry to distribute density between freshwater and estuarine habitats, and (*ii*) estuarine residency is positively correlated with growth and size at capture.

Methods

Study system

The Harrison River, a tributary of the Fraser River, once produced the highest proportion of fall subyearling migrant Chinook salmon in the Salish Sea (Fraser et al. 1982; Murray and Rosenau 1989). Declines in this population have led to its recent designation as Threatened by COSEWIC (Fisheries and Oceans Canada 2019). The juvenile emigration in 2016 followed the strongest return of Harrison Chinook salmon in the previous decade, presenting an important opportunity to study the natural rearing dynamics of this population. The Harrison River is a continuation from the glacier-fed Lillooet River, which feeds into Harrison Lake. Harrison River drains the lake for 18 km and is joined by the small Chehalis River just before it meets the Fraser. Here, pockets of freshwater riparian habitat may provide rearing habitat for juvenile salmon. From the Harrison River confluence, the Fraser River extends another ~30 km to the tidal wedge near Mission, British Columbia, after which off-channel habitat loss has been extensive, with little remaining in the final 80 km of river until the Woodward Island marsh complex near the mouth (M5, Fig. 1). Extending from the mouth of the river are large tidal flats (Roberts and Sturgeon banks), which were formed from thousands of years of fluvial deposits and are characterized by shallow slopes and low to moderate salinity (Balke 2017). Much of the river has been channelized such that the majority of the flow exits via the Main (southern) arm and (a small proportion via) Canoe Pass (Dashtgard et al. 2012), which together host small islets and channels that represent some of the last intact brackish marsh habitat in the estuary (Fig. 1). The majority of the Fraser delta has been permanently cut off to salmon or altered by industrial, agricultural, and urban development (Waldichuk 1985; Levings et al. 1991). While the exact boundaries of the Fraser estuary are subjective (e.g., influence of fresh water in the surface layer extends beyond the Strait of Georgia; however, man-made barriers along the northern and southern ends of the delta create local high-salinity gradients by restricting the river flow), we define the estuary as the area spanning the maximum upstream saltwater intrusion (just after the splitting of the river into the North and Main arms ~30 km from the delta front; orange bar, Fig. 1 (see colour version online)) to the point of shelf drop-off into the Strait of Georgia at the seaward edge of Roberts and Sturgeon banks (edge of habitat polygons, Fig. 1).

Fish sampling

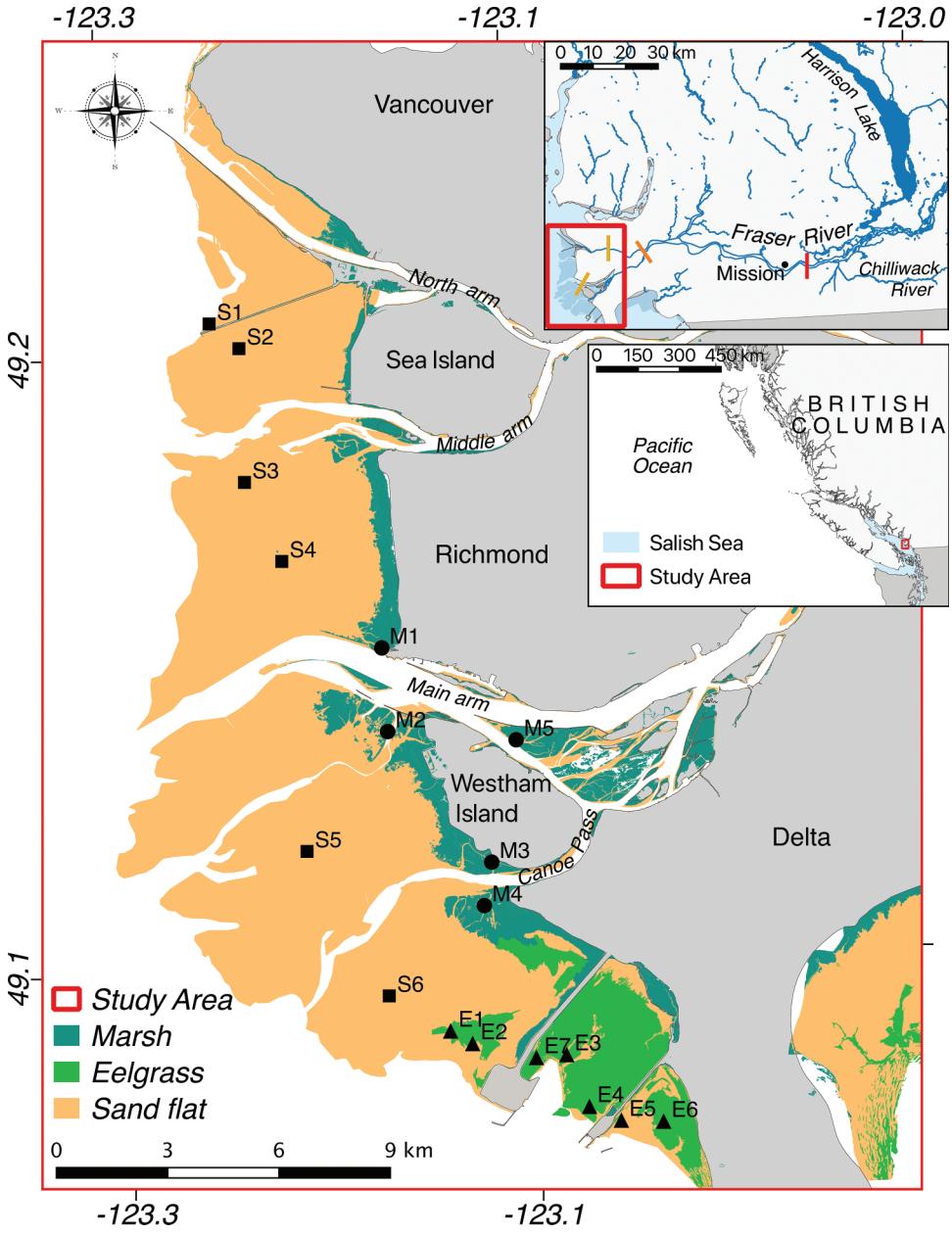
Sampling sites were selected based on historic surveys of the estuary and expanded to represent key habitat types available in the estuary — detailed description in Chalifour et al. (2019). We surveyed 17 estuarine sites approximately every 2 weeks at high tide from 29 March to 15 July in 2016, with an additional two sampling rounds (i.e., sampling all sites) between 19 September and 12 October. In 2017, we repeated these surveys from 5 March to 15 July, with 2 days of additional sampling 21–22 August. Each sampling event at a site consisted of three nonoverlapping, round-haul seine sets from a small vessel. We used a custom purse seine (40 m long × 4 m wide bunt (4 mm mesh) and 3 m wide bag (6 mm mesh)) to survey outer (eelgrass and sand flat) sites from a modified crab fishing vessel and a beach seine (20 m × 3 m with a 1.5 m × 1.5 m bag (3 mm mesh)) to survey the inner (marsh) sites from a motorized dinghy.

In each set, we identified all juvenile salmonids to species and measured fork length and body depth prior to release. From these we obtained 293 and 543 fin clips in 2016 and 2017, respectively. Fin clips were stored on Whatman sheets for subsequent genetic stock identification (GSI) via analysis of microsatellite variation (Beacham et al. 2012). We also euthanized and retained the first 10 Chinook salmon (maximum) collected per site, resulting in a total subsample of 254 juvenile Chinook salmon from 2016; no salmon were retained in 2017. All handling and sampling of fish was conducted following the guidelines set out by the Canadian Council on Animal Care (CCAC) and the approved animal use protocol 2016-010(1) with the University of Victoria. Retained fish were frozen at −20 °C for further analyses.

Otolith analyses

Based on our GSI results, we assessed the otoliths from a subsample of the retained 2016 Lower Fraser River (Harrison) Chinook salmon (final n = 91) for variations in estuarine entry date, residency period, and back-calculated estimates of body growth. Sagittal otolith pairs from frozen juvenile Harrison Chinook salmon (initial n = 153) were extracted and stored dry in plastic sample trays, with the left otolith preferentially analyzed unless lost or broken. We attempted to select otoliths from Harrison Chinook salmon that were caught throughout the season and represented all three estuarine habitat types; however, most of the retained fish were caught in May in marsh habitat, and smaller otoliths were more subject to damage during analysis

Fig. 1. Sampling locations within the marsh (M1–M5), sand flats (SF1–SF6), and eelgrass beds (E1–E6) of the Fraser River estuary, British Columbia, Canada. All sites were sampled each year, with the exception of E6, which was replaced by eelgrass site 7 (E7) in 2017. Gold lines in top inset (inside study area box) show the maximum upstream extent of saltwater intrusion during freshet (highest river flows). The dark orange line (immediately to right of box) shows the maximum upstream extent of saltwater intrusion during base river flows (i.e., earliest point of estuarine entry) at ~30 km from the delta front. The red line (right side of Mission location) marks the furthest upstream point of observable tides ~90 km from the delta front. Map data from the BC Data Catalogue's (https://catalogue.data.gov.bc.ca/dataset) Freshwater Atlas (fresh water) and Canadian Hydrographic Service (coastline), Natural Earth (British Columbia polygon), and Norman Maher (Salish Sea boundary). Habitat polygons adapted from the Habitat Inventory of the Lower Fraser River Estuary, 2002/3 (Fraser River Estuary Management Program). Saltwater intrusion points and tidal extent based on Dashtgard et al. (2012). [Colour online.]



(Table 1). Otoliths were washed in distilled water and fixed sulcus-side-up onto a glass slide using heated Crystalbond resin. To minimize external contamination and breaking, we wet-polished otoliths using distilled water and 30 μm and 3 μm aluminum oxide lapping film, finishing with 0.3 μm diamond lapping film from 3M. Otoliths were polished gradually on both sides by reheating the resin and flipping the otolith, until clear daily growth rings were visually apparent under a compound microscope at 20× magnification. Digital images were collected throughout the polishing process using a Lumix microscope-mounted camera. All otolith measurements were made using Fiji, a distribution of ImageJ (Schindelin et al. 2012).

After polishing, otoliths were fixed to petrographic slides and rewashed using distilled water for microchemical analysis using laser ablation with inductively coupled plasma mass spectrometry (LA-ICPMS). We used a New Wave UP-213 laser and Thermal X Series II ICPMS at the School of Earth and Ocean Sciences at the University of Victoria to measure otolith calcium (^{43}Ca),

Table 1. Summary of 2016 Harrison Chinook salmon otoliths analyzed by month and habitat of capture.

	April	May	June	July	Total
Marsh	9 (3)	60 (41)	36 (23)	0	105 (67)
Sand flat	1 (0)	26 (16)	8 (2)	0	35 (18)
Eelgrass	0	7 (2)	5 (3)	1 (1)	13 (6)
Total	10 (3)	93 (59)	49 (28)	1 (1)	153 (91)

Note: For each month, the number of otoliths extracted for polishing is shown with the final *n* analyzed via LA-ICPMS given in parentheses.

strontium (^{86}Sr), and barium (^{138}Ba) isotopes. The laser was set at a pulse rate of 10 Hz with a 30 μm spot size and firing rate of 5 μm·s^{-1}. Strontium and barium to calcium ratios deposited in otoliths can be used to infer migratory patterns in fish, particularly from fresh to brackish or marine environments in juvenile salmon (Miller 2011). To accurately capture these environmental transition zones for small otoliths, we ran a laser transect from the dorsal to ventral edge through the core across the widest point of the otolith (Sanborn and Telmer 2003). We scanned 100 otoliths representing 98/153 fish (two pairs run). Of these fish, seven were excluded from final analyses due to either low detectability (likely due to over-polishing or glue interference with the LA-ICPMS) or difficulty in aligning the LA-ICPMS results with the visual growth measurements postscan, leaving a final sample size of 91 fully measured otoliths (Table 1). At the beginning and end of each slide, and after every five otoliths, we ran three National Institute of Standards and Technology (NIST) glass standards to account for instrument drift (NIST 615, 613, and 611). Ion data were calibrated by subtracting background count rates and correcting for the precision of measurements of the NIST glass standards. During the course of the study, the mean percent relative standard deviations for NIST 615 glass were ^{86}Sr = 1.1%, ^{138}Ba = 3.7%; for NIST 613 were ^{86}Sr = 1.0%, ^{138}Ba = 2.8%; and for NIST 611 were ^{86}Sr = 0.3%, ^{138}Ba = 2.1%, respectively. Ion concentrations were converted to molar ratios using calcium as an internal standard.

We identified the estimated estuarine entry point (i.e., below the maximum upstream saltwater intrusion; Fig. 1) as the first inflection of Sr:Ca concentration, where Ba:Ca were simultaneously increasing, indicating a brackish environment (Volk et al. 2010; Miller 2011). This was initially done visually and then confirmed via a *z* test on the running averages of 10 values in the region including the inflection to determine when the increase was significant (Volk et al. 2010). Where growth lines were visible across the entire otolith, we further validated the dorsal inflection point against the ventral inflection point to ensure that they corresponded to the same visual growth line. Although line scans are less precise than point measures in deriving specific concentrations of isotopes, they consistently identify transition points among habitats by accurately capturing inflections in these concentrations (Sanborn and Telmer 2003). In 44% of our samples, the Sr:Ca concentrations and Ba:Ca concentrations at the otolith edge (reflecting the previous 2–14 days) were more aligned with a high Ba, low salinity condition than with any of the high salinity conditions tested in Miller (2011). However, based on the results of this study, most of these fish had been in the estuary for 3 weeks or more, including six individuals caught in the outer estuary (in sand flat and eelgrass sites), reflecting the strong freshwater signature of the Fraser River estuary (see online Supplementary material, Fig. S1[1]).

The salinity of the Fraser River estuary ranges to 0‰ and declines over the emigration period with the onset of the spring freshet (La Croix et al. 2015), which limits the extent of saltwater influence on the estuary (Dashtgard et al. 2012) and may explain the postestuarine entry ratios detected in our samples. Barium and strontium concentrations are naturally low in the Harrison River system (Voss et al. 2014), so it may be possible that an increase in these isotopes would be seen after entry into the Fraser main stem. Although they increase seasonally with the spring freshet, these ion concentrations are also at their lowest values at the mouth of the Fraser, relative to its headwaters (Cameron et al. 1995; Voss et al. 2014). Although our measured otolith concentrations of Sr:Ca were low, they were still comparable to the ranges of ratios observed in the Salmon River, a much smaller system with lower freshwater influence (Volk et al. 2010). Given that the flow rates of the Fraser River are highest in the spring and peak freshet occurred in May in 2016, it is likely that saltwater intrusion was limited to the seaward edge of the brackish marsh (yellow bars, Fig. 1), resulting in a very weak marine isotopic signature in the estuary. We therefore assume that despite the relatively low Sr:Ca concentrations at the inflection point, the Sr:Ca inflection indicates entry into the estuary proper — below the maximum extent of saltwater intrusion during base river flows ~30 km from the delta front (orange bar, Fig. 1; i.e., likely maximum extent of marine isotopic signature), since the salinity measured at our marsh sites was often below 5‰ even at high tide (Hanna Instruments 9829 Multiparameter Meter; Supplementary Table S1[1]). Strontium accumulates over time in the otolith after entry into brackish waters and tends to remain near its peak concentration, such that it does not return to pre-inflection levels despite fluctuations in salinity in estuarine environments (Volk et al. 2010). The otoliths measured in this study demonstrated increasing Sr:Ca ratios at the otolith edge (post-inflection) as salmon migrated outward to habitats with increasing salinity and as salmon spent more time in the estuary (see Results), aligning with Volk et al.'s findings.

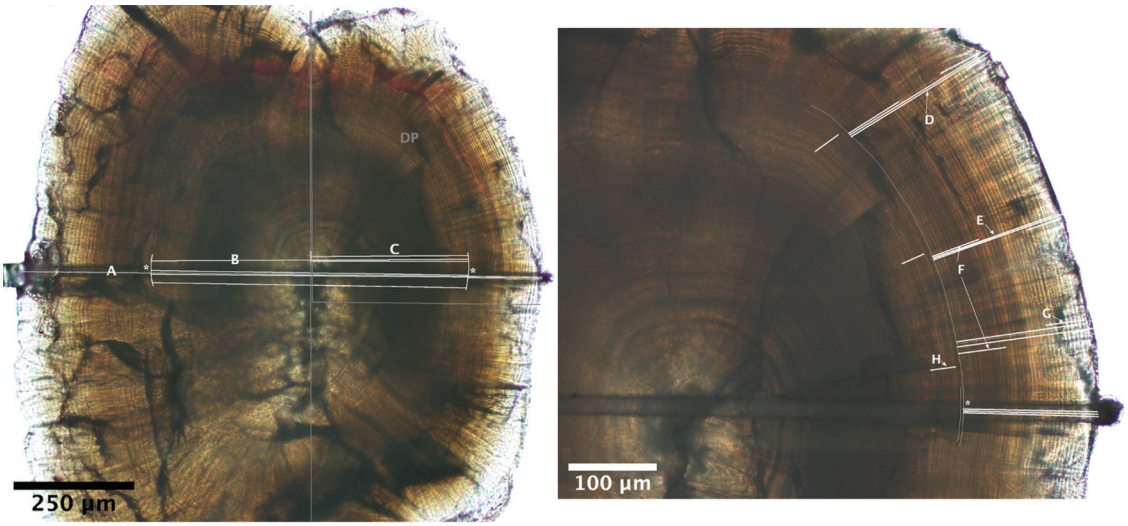
One challenge with LA-ICPMS line scans is the lack of a standardized method for aligning the microchemistry results with post-ablation visual landmarks — such as otolith daily growth rings (Danek et al. 2015). To address this, we used inflections in the Ca signatures to identify the otolith edges on the microchemistry scan and calculated the actual scan rate as the otolith scan time (using these edges) divided by the measured width of the otolith along the laser transect (Andrew Claiborne, Washington Department of Fisheries, Washington, personal communication, 2018). All otoliths were measured by the same trained reader, with each measurement taken three times and averaged (Fig. 2). A subsample of ten otoliths were re-evaluated three times in a blind precision study, with a final precision rate of over 90% for all averaged measurements (>95% for most). When counting daily growth rings, we assumed that visual otolith increments approximated daily growth and counted a minimum of seven daily rings to account for natural variability (Chittaro et al. 2015). We avoided using the width of outermost increments in our growth measurements, as these may still have been forming at capture and are prone to damage during preparation (Campana 2001). We calculated residency time as the total estuarine growth period divided by the average daily growth to give an approximate number of days in the estuary prior to capture. This is considered to be a minimum residency time, as all fish were captured within the estuary and may have remained longer had they evaded capture. We obtained estuarine entry date by subtracting the residency period from the date of capture.

Growth statistics

We back-calculated fork length at time of estuarine entry by testing a series of relationships between measured otolith radius

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0247.

Fig. 2. Diagram of otolith measurements taken. Each measurement was taken three times, and the mean result was used for subsequent analyses. A: otolith width, B: otolith width at estuarine entry, C: otolith radius at estuarine entry, D: total estuarine growth, E: mean daily estuarine growth (measurement divided by count of daily increments), F: early estuarine daily growth, G: late estuarine daily growth, H: freshwater daily growth, DP: dorso-posterior quadrant of the sagittal otolith. The asterisks (*) indicate estuarine entry inflection as identified by LA-ICPMS. [Colour online.]



and width (at entry and capture) and fork length (at capture), including linear regressions and a biological intercept model. While some studies have found a biological intercept model to best represent growth over time due to its ability to incorporate estimated size at hatching (Zabel et al. 2010), we did not see a strong discrepancy in the relationship at small sizes, the model did not fit our data as well as a linear model, and we could only measure size at hatching from a subset of our otoliths. We therefore determined that the best model for our data was a simple linear regression model using otolith width and following the Scale Proportion Hypothesis and the Body Proportion Hypothesis, taking the mean of the results from each hypothesis to minimize error (Supplementary Fig. S2[1]; Francis 1990). Based on these results, daily growth and total estuarine growth were converted into somatic growth using the calculated fork length at entry for each individual fish (e.g., mean daily growth of fish i = [fork length at capture of fish i – fork length at entry of fish i]/number of days in the estuary of fish i).

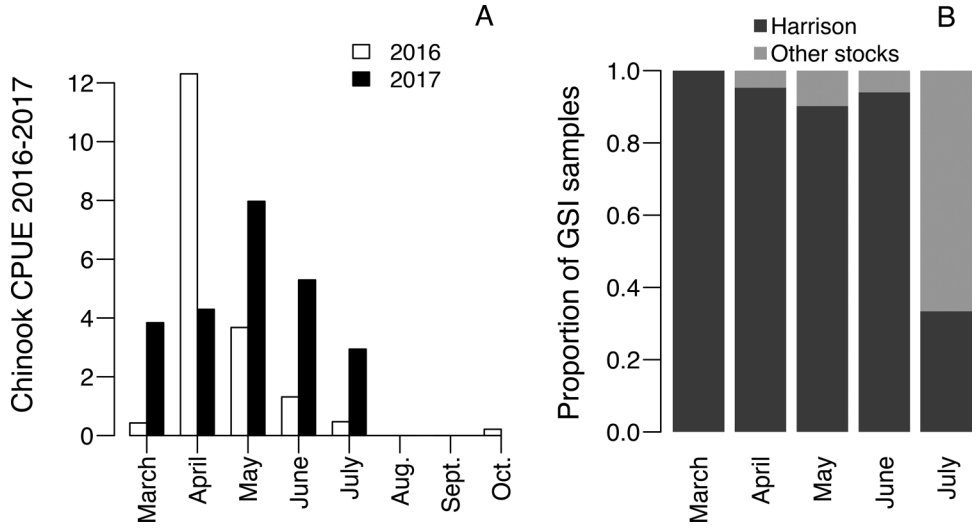
We assessed the relationship between growth and estimated entry date, and between growth and estuarine residency, using linear regression (function "lm" in R :: stats). Similarly, we assessed the relationship between size at capture and catch date. We used ANOVA (function "aov" in R :: stats) to test the differences in size among habitat types and used a Tukey's honestly significantly different (HSD) post hoc test to compare pairwise differences among groups (i.e., fork length of Harrison Chinook salmon captured in sand flat compared with marsh, fork length in eelgrass compared with marsh, and fork length in eelgrass compared with sand flat; function "TukeyHSD" in R :: stats). The range of estuarine entry timing and estuarine residency period were summarized using frequency plots. When analyzing residency period, six outlier fish that were below 45 mm fork length were removed, as they were assumed to be too small to survive migration into the ocean, thus biasing the minimum residency period. All analyses and figures were completed using R version 3.6.2 (R Core Team 2019), except for the site map (Fig. 1), which was created in QGIS version 3.6.3 (QGIS Development Team 2019), and the otolith microscope images (Fig. 2), which were assembled in Adobe Photoshop 2020.

Validation of wild versus hatchery fish

The Harrison Chinook salmon population had an estimated wild spawner return of 91 906 in the fall of 2015 (adjusted for hatchery influence (pNOS); NuSEDS database, Fisheries and Oceans Canada Pacific, Vancouver, British Columbia, unpublished data), which is the highest return since 2012. Based on estimated fecundity and egg to fry survival rates, this would have produced between 9.6 and 325 million fry in 2016 (Healey and Heard 1984; Healey 1991; Fisheries and Oceans Canada 2019). This population has very low enhancement from hatcheries (~300 000 juvenile fish annually, all visually marked and released in June) within the spawning boundaries of the Harrison at the Chehalis River hatchery (Shaun Spenard, Chehalis River hatchery, British Columbia, personal communication, 2020). However, genetically similar Harrison-origin fish are produced in large numbers at the Chilliwack River hatchery, located 35 km from the confluence of the Chilliwack–Vedder river with the Fraser main stem above Mission (~1.5 million fry released annually, increased to 2.5 million in 2020; brood stock from the Chilliwack supplied to the Capilano hatchery beginning in 2013), and it is likely that straying between these two populations occurs. Microsatellite-based methods could not distinguish between natural-origin Harrison and hatchery-origin Chilliwack Chinook salmon in 2016, but this is now possible with the application of single nucleotide polymorphism (SNP) technology coupled with parentage-based tagging of hatchery fish (Beacham et al. 2018; SNP not used in this study).

In 2016 we caught 16 Harrison Chinook salmon that were adipose fin-clipped (only two in 2017), indicating that they were hatchery-produced and implanted with a coded-wire tag (CWT). In addition, we identified potential thermal marks in five of the 153 otoliths originally selected as 2016 Harrison fish and removed these from further otolith analyses. By comparing the size at release and the release date of the Chilliwack hatchery fish in 2016 (5.6 g, 15–16 May, 1 004 219 smolts age 0+ with 194 702 marked by adipose fin clip and CWT; Jeremy Mothus, Chilliwack Hatchery, British Columbia, personal communication, 2018) with the fork length (mean = 57.5 mm, range = 34.0–128.0 mm) and mass (mean = 2.64 g, range = 0.51–14.82 g) at capture and estimated fork length (mean = 37.7, range = 18.5–67.6 mm) and mass (mean = 0.76 g, range = 0.26–2.86 g) at entry of the Harrison Chinook salmon retained in

Fig. 3. Chinook salmon emigration patterns in the Fraser River estuary. (A) Catch per unit effort (CPUE; site × day sampling event) summarized by month for all Chinook salmon at 17 sites in the Fraser River estuary in 2016 (white bars) and 2017 (black bars). Effort was comparable between years, with the exception of lower sampling effort in March in 2016 (n = 14) versus 2017 (n = 31), higher effort in June 2016 (n = 35) versus 2017 (n = 17), and no sampling in September or October in 2017. Note the single Chinook salmon in October 2016 has been inflated for visual purposes. (B) Proportion of genetic stock identification (GSI) samples that were identified as lower Fraser fall Chinook (Harrison) or other stocks.



the otolith analyses, we concluded a very low likelihood that any of the 91 analyzed fish were of hatchery origin.

In addition to the thermally marked fry releases, the Chilliwack hatchery also supplies eggs and (in some years) thermally marked fry to small community hatcheries in other Lower Fraser tributaries. In 2016, there were 120 000 unmarked eggs exported to the Alouette River hatchery and 70 000 to Chapman Creek. There were no additional thermally marked fry released to other locations in 2016 (Jeremy Mothus, Chilliwack Hatchery, British Columbia, personal communication, 2018). Thus, although it is possible that fish hatched from these eggs were included in our samples, it is unlikely given that the ratio of enhanced to wild fish was so low.

Results

Over 2 years of sampling, we caught 1515 juvenile salmon in 288 sampling events, of which the majority (1155) were Chinook salmon (n = 23 were determined as hatchery-origin and removed from following results). Based on 564 genetic samples over both years, 490 (87%) were identified as lower Fraser River fall Chinook salmon from the Harrison or West Chilliwack tributaries (hereinafter referred to as "Harrison").

Emigration timing

Peak Chinook salmon catch per unit effort (CPUE) differed between the 2 sampling years (Fig. 3A). In 2016 the highest Chinook salmon catch was in April (CPUE = 12, n = 320), of which an estimated 94% were identified as Harrison (n = 88/94 GSI samples; Fig. 3B), followed by a mean of four Chinook salmon per sampling event in May (n = 114), and only one in June (n = 46; Fig. 3A). In 2017, sampling began 3 weeks earlier and Chinook salmon CPUE was four in March and April (n = 119 and 146, respectively), with peak abundance in May (CPUE = 8, n = 255).

Harrison fish were the first Chinook salmon to arrive in the estuary in both years (Fig. 3B). These fish were caught on our earliest sampling days in March, having entered the estuary as early as February. Based on otolith back-calculated entry points, more than 80% (n = 74/91) of Harrison Chinook salmon entered the estuary in March and April of 2016, with fish entering earlier residing for longer in the estuary prior to capture (Fig. 4). Compared with upriver Chinook salmon populations, Harrison Chinook were caught consistently in the estuary from March through July, after which all salmon catches rapidly declined to zero (Fig. 3B). In October 2016, a single Chinook salmon (210 mm fork length) was caught in the outer sand flats, and no other salmonids were seen in the fall.

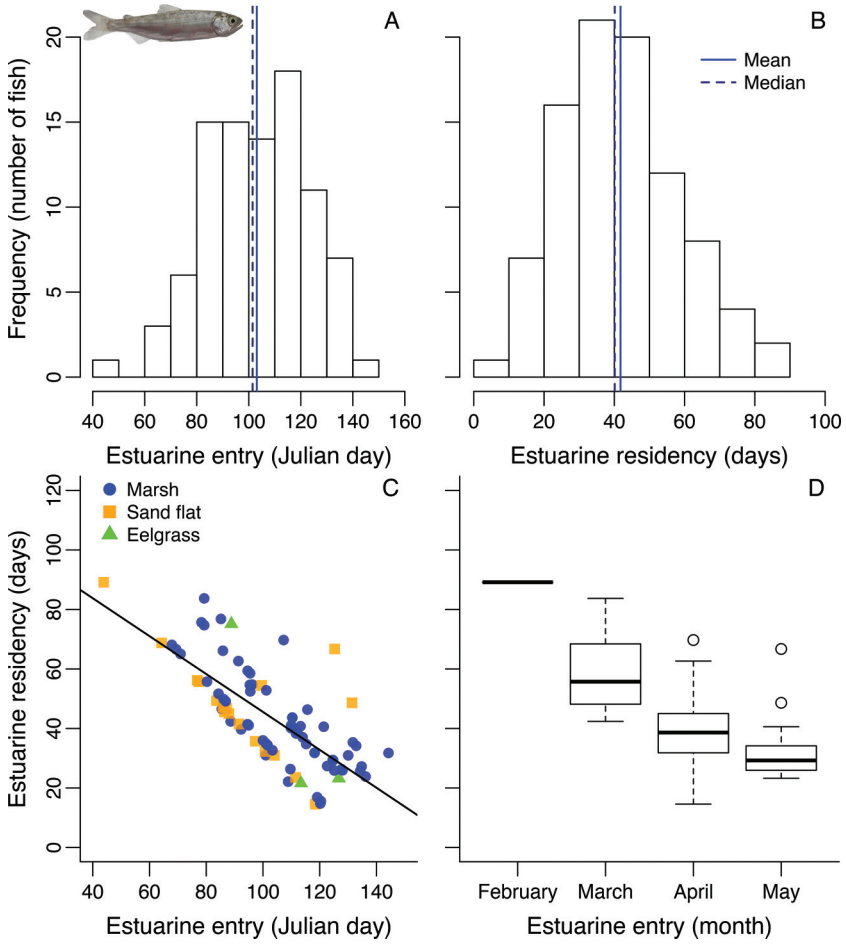
Harrison Chinook salmon estuarine residency

Otolith analyses confirmed that Harrison Chinook salmon enter the estuary at different times throughout the emigration period, with most entering before May in 2016. Estuarine residency varied across the season among the captured fish (mean ± SD: 41.8 ± 17.7 days; Fig. 4) and was negatively correlated to estuarine entry (R^2 = 0.55, $P = 6.1 \times 10^{-16}$; Fig. 4C), such that the earliest fish to enter the estuary resided the longest. The majority of fish appeared to reside in the estuary for 30–50 days (n = 41/91), with some captured after fewer than 20 days (n = 8/91, of which for were smaller than 45 mm, indicating their minimal age and underestimation of the total residency calculation), and one fish 89 days after estuarine entry. Although there appeared to be a tendency for residency of fish caught in the sand flats to be lower than those caught in the marsh (Fig. 4C), the difference between the two was not statistically different. There also appeared to be two clusters of marsh fish (Fig. 4C), with one set of data points slightly higher than the other. This pattern was explained by catch date, with fish caught earlier (before Julian date 145; 26 May 2016) also entering the estuary earlier than those that were caught later (after Julian date 144). However, these two groups of marsh fish, based on their catch date, did not experience different total residency periods.

Estuarine habitat use

Of the salmon caught in the three estuarine habitats surveyed, 78% of salmon were caught in the brackish marsh, which is the first estuarine habitat encountered and the one with the lowest salinity (Supplementary Table S1[1]). This pattern was strong enough to suggest a true difference in abundance among habitats, despite the different gear types used in the marsh and outer habitats (Chalifour et al. 2019). Concentrations of Sr:Ca

Fig. 4. Juvenile Harrison Chinook salmon estuarine entry timing and residency prior to capture, based on otolith-derived estimates. Panel A shows the range of entry timing, and panel B shows minimum residency. Panels C and D show the relationship between residency and entry timing. Entry day (C) explained 54.7% of the variation in residency period ($P = 6.1 \times 10^{-16}$). Julian day 100 corresponds to 9 April 2016 (leap year). [Colour online.]



at the otolith edge (i.e., the most recent bone deposition prior to capture) indicate that the marine signature increased both as Chinook salmon moved outward to more saline habitats and as they spent more days in the estuary, regardless of habitat (Fig. 5).

Harrison Chinook salmon were predominantly caught in the marsh at small sizes, after which they migrated out to the flats into more saline environments, as indicated by the larger size composition of Harrison fish in eelgrass and sand flat (Fig. 6) and the increase in catch in these outer habitats later in the season (Fig. 6B; $R^2 = 0.46$, 0.38, and 0.15; $P = 2.2 \times 10^{-16}$, 6.1×10^{-09}, and 1.6×10^{-04} for fork length versus catch date in marsh, sand flat, and eelgrass sites, respectively). All size–habitat comparisons were statistically significant (ANOVA, $F_{[2,487]} = 173$, $P < 2.2 \times 10^{-16}$).

Estuarine growth

Harrison Chinook salmon exhibited a mean (±SD) daily growth rate of 0.57 ± 0.13 mm fork length in the estuary. We did not find a significant difference in daily growth rates among fish based on estuarine entry timing (Supplementary Fig. S3A[1]). Daily growth rate was not significantly related to estuarine residency time (Supplementary Fig. S3B[1]). Daily growth rate did increase over time and with greater fork length at capture (Figs. 7A, 7B). However, when growth is converted to a proportion of fork length at capture, we found that smaller fish that were caught earlier also appear to grow faster (Supplementary Fig. S4[1]), indicating that this increase is allometric (Davis et al. 2019). These interactions appear to be compensatory such that, overall, daily growth is similar among individuals regardless of entry or residency times. When comparing total estuarine growth, fish that entered the estuary smaller and resided longer experienced the greatest proportional increase in body size (Figs. 7C, 7D).

Within individual otoliths, growth during the freshwater period (mean ± SD: 2.60 ± 0.51 μm·day^{-1} was lower than the early estuarine period (3.07 ± 0.53 μm·day^{-1}), which was in turn lower than the late estuarine period (4.00 ± 0.64 μm·day^{-1}; Supplementary Fig. S4[1]). However, this trend corresponds to differences between growth periods of less than 1 mm·day^{-1} when converted to fork length, which are no longer statistically significant. Four individuals displayed mean daily growth rates during the late estuarine period (7–14 days prior to capture) that were more than 5% lower than the early estuarine period (7–14 days after entry), and one showed lower growth during the early estuarine period than the freshwater period (Supplementary Table S2[1]), which may indicate a period of starvation. However, only one of these fish had a corresponding low estimated somatic growth rate (0.4 mm·day^{-1}).

Discussion

Using modern scientific techniques, we have confirmed the extent and variability in residency times and quantified estuarine

Fig. 5. Validation of estuarine signature in juvenile salmon otoliths. Otolith edge Sr:Ca stable isotope concentrations for Harrison Chinook salmon caught in 2016 increase with increasing salinity (A) and time in the estuary (B) in three habitat types: marsh (blue circles, $n = 67$), sand flat (orange squares, $n = 18$), and eelgrass (green triangles, $n = 6$). Estuarine residency (B) explained 24% of the variation in Sr:Ca across all habitats ($P = 1.5 \times 10^{-07}$), showing the accumulation of strontium over time despite fluctuating salinity in the estuary. [Colour online.]

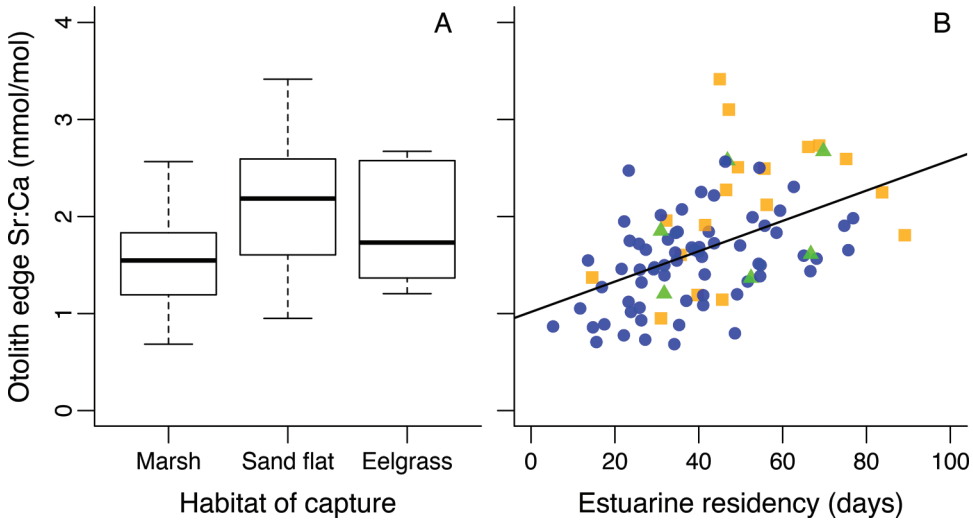
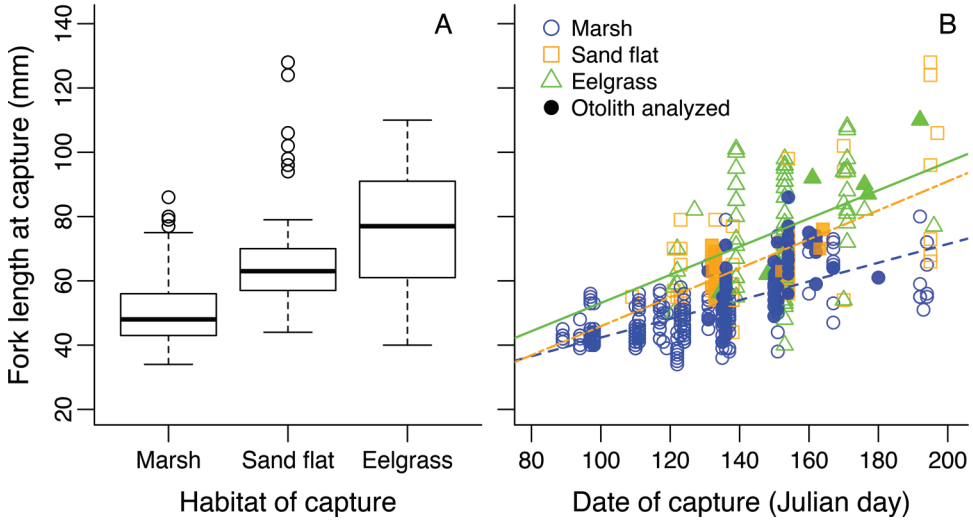


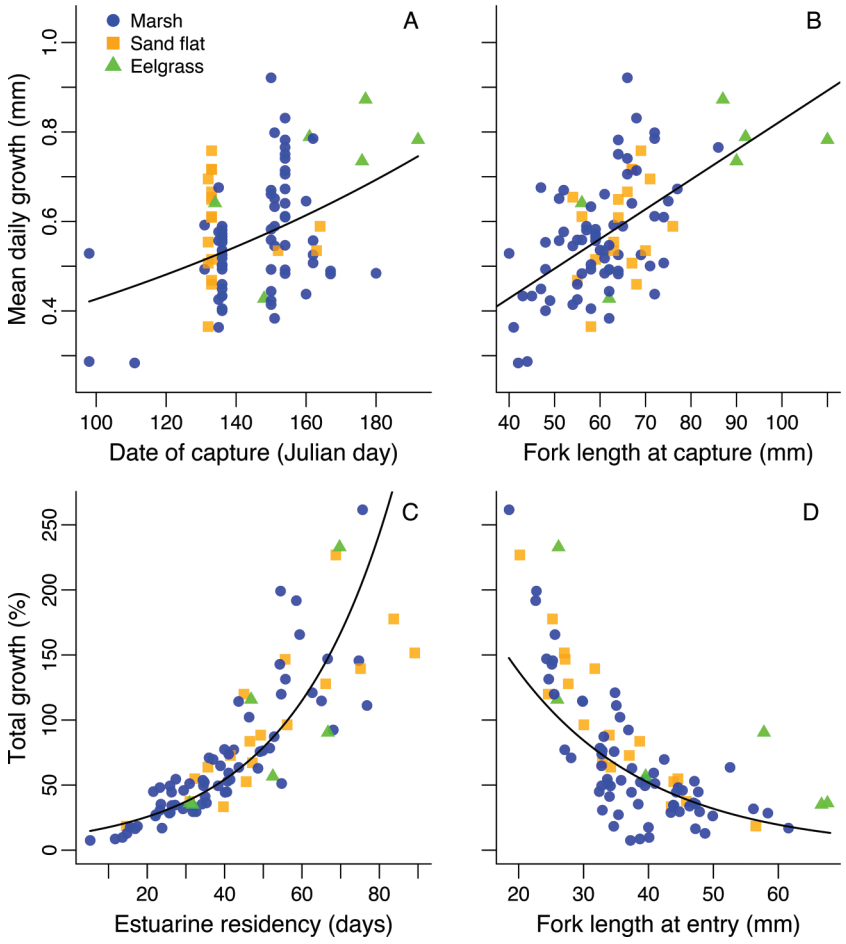
Fig. 6. Size of Harrison Chinook salmon at capture in relationship to habitat: (A) boxplot showing 2016 and 2017 Harrison Chinook salmon catch by habitat; (B) Harrison Chinook salmon size at capture in three habitat types: marsh (blue circles, $n = 328$), sand flat (orange squares, $n = 73$), and eelgrass (green triangles, $n = 89$), with the linear regression between fork length and catch date depicted for each habitat. Solid symbols indicate fish with otoliths analyzed. [Colour online.]



daily growth for Harrison Chinook, one of the dominant populations of wild Chinook salmon in Canada's largest salmon-bearing river. We provide further support for the importance of estuarine habitat for early growth of subyearling migrant Chinook salmon and report residency periods and growth rates that are comparable to populations throughout the Pacific Northwest.

Our research builds from early field studies that quantified juvenile salmonid habitat use in the Fraser River estuary in the late 1970s and early 1980s (e.g., Levy and Northcote 1979, 1982; Greer et al. 1980; Levings et al. 1983). The methodologies available at the time of those studies did not include modern genetic stock identification or LA-ICPMS otolith analysis, so the authors were limited in the inferences they could make, and there has been a lack of salmon research in the estuary since. Our mean otolith-based estimate of minimum residency of 41.8 days is more than 16× the mean (of 3 days) and 39% greater than the maximum recorded residency (of 30 days) from mark–recapture studies conducted by Levy and Northcote in 1978 in the Woodward Island marsh complex (M5, Fig. 1) of the Fraser estuary (Levy and Northcote 1982). The authors' subsequent study, including channels overlapping with our site M3, yielded even lower recapture rates and shorter observed residency (Levy and Northcote 1979). Recapture rates from juvenile salmon marking experiments on the outer flats of the Fraser estuary (Sturgeon and Roberts banks, near sites S1, S2, S4, E7, E3, and E4) were even lower than recapture rates in the tidal channels (Levings et al. 1983). Although Levy and Northcote's (1982) study primarily aimed to examine whether various Pacific salmon had some residency in the estuary, such that most of their recapture efforts were made in the first week after release of marked fish, our longer-running study using otolith analysis demonstrates that mark–recapture approaches can vastly underestimate estuarine habitat use by Chinook

Fig. 7. Estuarine growth as a function of time and body size, categorized by habitat (marsh = blue circles, $n = 67$; sand flat = orange squares, $n = 18$; eelgrass = green triangles, $n = 6$). (A) Mean daily growth in fork length over time (exponential regression, $R^2 = 0.16$, $P = 8.3 \times 10^{-05}$), (B) mean daily growth in fork length as a function of body size (linear, $R^2 = 0.34$, $P = 1.1 \times 10^{-09}$), (C) total estuarine growth (proportional to entry size) over residency period (exponential, $R^2 = 0.78$, $P = 2.2 \times 10^{-16}$), and (D) total estuarine growth as a function of size at entry (exponential, $R^2 = 0.43$, $P = 1.1 \times 10^{-12}$). [Colour online.]



salmon. While the authors speculated that the actual residency of Chinook salmon was on the order of weeks to months (Levy and Northcote 1979), our study is the first to confirm their prediction quantitatively. In contrast with the findings of Levy and Northcote (1979, 1982), our results are similar to the more recent otolith study by Volk et al. (2010) for subyearling Chinook salmon in Oregon (mean minimum residency of 43.5 days, median 41.5 days), suggesting a potential pattern among early estuarine-rearing populations. We demonstrate the utility of otolith analysis in linking juvenile presence with estuarine use and recommend that these methods be used in place of mark–recapture studies in large systems where recapture rates are typically very low.

Emigration timing and residency

We found that Harrison Chinook were among the first salmon to enter the Fraser River estuary in 2016 and 2017, similar to findings from Levy and Northcote (1979). However, peak emigration to the estuary in 2016 occurred about a month earlier than in 2017 and the historical records, which measured peak Chinook abundance in the second half of May (Levy and Northcote 1979). We derived estuarine entry date from the otolith microchemistry as the fish grew, following Volk et al. (2010), who demonstrated that Sr:Ca concentrations increase asymptotically at salinities 0‰–5‰, and that despite variation in individual otoliths, the sudden increase in Sr:Ca is an accurate indicator of migration from fresh to brackish waters. These values align with the pattern of migration timing for juvenile Chinook salmon in the Fraser, which reach peak abundance at a rotary screw trap at Mission (~75 km from the river mouth, near the tidal limit) 1–3 weeks prior to the peak in the marshes at the mouth of the Main arm (Levy and Northcote 1979). Historical records have demonstrated that the migration timing of Harrison Chinook fry coincides closely with catches downstream at Mission, suggesting rapid downstream movement (Fraser et al. 1982). Given that little rearing habitat is available between Mission and the beginning of the estuary, and that saltwater influence is limited to the point where the river splits into the North and Main arms, we therefore believe that the otolith signatures that we recorded in fish captured in the Fraser River estuary reflect entry into brackish waters below the maximum extent of saltwater intrusion. While our otolith data are limited to 2016, we expect that aside from entry timing, the otolith results are likely representative of other years for two reasons. First, entry timing was seen to be a continuum, such that even though our peak catch occurred in March in 2016, Harrison Chinook entered the estuary between February and May. Second, Chinook achieved smolt sizes at similar times in both years (May–July), so we expect that the average minimum residency period would be similar to our 2016 results, if not slightly lower, in a given year.

Growth and implications for survival

The estuarine-rearing phase for Chinook salmon involves multiple trade-offs among habitat availability, predation, physiological stress from temperature and salinity, and food quality and quantity (Quinn 2018; Davis et al. 2019). Harrison Chinook salmon displayed similar daily growth rates regardless of entry date, indicating that the broad range of emigration timing to the estuary may still result in similar early marine growth. Growth rates were similar to the otolith-derived rates reported by Volk et al. (2010) (0.35–0.65 mm·day^{-1}; 2010) and Campbell (2010) (mean 0.41 mm·day^{-1}, range 0.11–0.67 mm·day^{-1}; 2010), to marsh channel mark–recapture rates in the Columbia River estuary (mean 0.49 mm·day^{-1} for fish tagged at ≥55 mm fork length, 0.58 mm·day^{-1} for fish tagged at ≥60 mm; McNatt et al. 2016), and to population estimates based on stable isotope analyses in the Skeena River estuary (mean ± SE: 0.48 ± 0.09 mm; Moore et al. 2016). Overall, we saw a benefit of early entry and long residency times for total proportional growth for subyearling migrant Chinook salmon.

Daily proportional growth rate decreased with increasing fork length (Supplementary Fig. S4[1]) — reflective of typical allometric patterns in juvenile Chinook salmon (Davis et al. 2019). The importance of estuarine rearing in brackish marsh habitat may be higher for small individuals, which also tend to be wild fish. Davis et al. (2019) demonstrated increased growth rates of wild versus hatchery fish in tidal marshes, particularly for those below 100 mm fork length. There is also likely a shift in food quality and quantity as Chinook salmon make the ontogenetic migration outward from the marsh to sand flat and eelgrass habitats in the estuary. In the tidal marshes they likely access insects as well as some amphipods and copepods (Levings et al. 1991). In contrast, subyearling juvenile Chinook salmon in eelgrass and sand flats would be more restricted to crustaceans, which may be in high abundance but have lower energy density than terrestrial insects (Levings 1985; Davis et al. 2019). Further to this, the lingering marine heatwave effects in 2016 decreased the abundance of subarctic copepods in the Salish Sea, which were replaced by low-energy-density southern copepods (Chandler et al. 2017).

A few individuals in this study demonstrated periods of decreasing mean daily growth in otolith increments, which may represent declines in somatic growth due to starvation (Bradford and Geen 1992). However, it is difficult to discern variation in otolith increment width due to environmental variations (e.g., fluctuating temperature) from actual starvation (Bradford and Geen 1992; Walker and Sutton 2016), and mean daily growth was still within one standard deviation of the population mean for all but a single small individual. Combined with the high projected density of Harrison fish in 2016, it is therefore reasonable to assume that some fish were not able to find sufficient ration to survive in the estuary, of which these few may be an example. Overall, however, it appears that the fish that we caught throughout the season were able to achieve reasonable growth rates comparable to other studies.

While we did not find a statistically significant difference in growth rate among habitats, our otolith sample size for salmon caught in eelgrass was low. We did find that juvenile Chinook were larger at capture in the sand flats than they were in marsh and were largest in eelgrass. The growth trajectory based solely on fork length over time also suggests that fish caught in eelgrass and sand flats were growing faster than those in the marsh. However, the otolith data does not support this, which could be either due to the low sample size or could simply reflect the continued influx of small migrants and potential efflux of larger individuals to and from the marsh throughout the migration period. While growth rate was not different among habitats, there were strong patterns indicating an ontogenetic shift in habitat use over the migration period.

Estuarine habitat use

Small fry entering the Fraser estuary likely require a period of transition before being physiologically adapted to life in the ocean. We found that Chinook salmon below 54 mm fork length were exclusively caught in the low-salinity marsh, suggesting that fish below this size may not be optimized to transition to higher salinities. Morgan and Iwama (1991) conducted a growth trial on subyearling migrant Chinook salmon and found that even with gradual acclimation of 1‰–2‰·day^{-1}, fish less than 50 mm fork length reared in 28‰ salinity had a mortality rate of 24%, suggesting that this salinity level was stressful for Chinook salmon of this size. Similarly, Volk et al. (2010) found that all fish less than 45 mm that were caught in the Salmon River system spent at least 30 days in the estuary prior to migrating to the river mouth. Previous studies in the Fraser estuary have suggested that Chinook salmon prefer the marsh to more open habitat or eelgrass and found that Chinook salmon caught in Roberts Bank eelgrass were larger and possibly near smolting (Greer et al. 1980; Levings et al. 1983). Combined with the increase in residency time and total estuarine growth for smaller fish, this study supports the idea that the brackish marsh of the Fraser estuary represents a critical habitat for subyearling migrant Harrison Chinook salmon.

Historical habitat loss

Historically, the Lower Fraser region including all tributaries south and west of Lytton, British Columbia, supported 6118–8361 km of linear stream habitat and 659 km^2 of additional floodplain (Finn et al., in press). Today, ~64% of the accessible stream habitat and 85% of the floodplain in the Lower Fraser River has been lost due to human development (Finn et al., in press), particularly in the Fraser Valley (below the Harrison River confluence) and in the estuary where most of the river has been dyked (Dashtgard et al. 2012; Balke 2017). The dyking and filling of estuarine habitat has been particularly concentrated, with the areal extent of wetland habitat in the estuary reduced by over 70% since European settlement (Schaefer 2004). While much of this loss occurred between the early 1800s to 1980 (Balke 2017), an expansion of the Roberts Bank coal port in 1984 further altered more than 200 ha of estuarine habitat, which had documented impacts on juvenile Chinook salmon rearing habitat (Levings 1985). Indeed, our catch rates of Chinook in this area (sites E3, E4, and E7) have consistently been lower than those reported by Levings (1985). Despite management efforts, there have been continuous struggles to achieve "no net loss" of salmon habitat in the estuary (Levings et al. 1991; Lievesley et al. 2017). Ongoing small-scale projects including urban development and conversion of farmlands continue to degrade the remaining habitat, and several large-scale industrial developments are under current review, including a further expansion of the container terminal for the coal port and an expansion of the Vancouver International Airport, which pose major threats to the estuary. Restoration of historical wetlands may facilitate the expansion of estuarine habitat use and diversify the range of life history strategies of existing fall ocean-type Chinook salmon populations (Bottom et al. 2005; Volk et al. 2010). Removal of barriers and restoration of marsh and estuarine habitats could further enhance the rearing capacity of the Fraser estuary for salmon and would be of particular benefit to the subyearling migrant Harrison Chinook population. Previous studies have suggested very high in-river mortality of early fry migrants (e.g., Healey 1982; Bottom et al. 2005), indicating that this may not be a winning life history strategy in most years. However, this strategy may provide a buffer against increasingly variable marine conditions. Expanding the estuarine habitat available, and the quality of that habitat, is therefore likely to benefit wild Chinook salmon populations — both by bolstering diversity of emigration phenotypes (Bourret et al. 2016) and by increasing early marine survival (Magnusson and Hilborn 2003).

Productivity of Harrison Chinook salmon has generally declined since the 1980s, with more severe declines observed over the last three generations. This has been broadly attributed to conditions encountered during the early marine stage (COSEWIC 2018). This study suggests that the lack of estuarine habitat available for rearing may also be a contributor to that decline. Levy and Northcote (1982) documented high densities of juvenile salmonids in some of the last remaining brackish marsh channels in the Fraser River estuary and found that Chinook salmon had the highest density at a maximum of 0.18 fish·m^{-2}. This is approaching the high-density scenario (0.20–0.25 fish·m^{-2}) that led to substantially shorter residency times and decreased growth rates when food was scarce in the Nisqually delta (Davis et al. 2018). If we assume that this approaches a minimum habitat requirement for each fish and extrapolate to the entire population, Harrison Chinook fry in 2016 required a minimum of 1620 to 59 400 km^2 of rearing habitat for maximum survival, which would be reduced by the staggered migration of fish across the emigration period. Given the clear reliance of this Chinook salmon population on estuarine habitat for early rearing, it is highly likely that the estuarine carrying capacity for Harrison River Chinook has been diminished. In addition to this decline in available habitat, there continues to be an increase in hatchery fish production, potentially exacerbating this loss by increasing density-dependent effects in the remaining habitat (David et al. 2016).

The pattern of Chinook salmon catch between years suggests the potential for density-dependent effects to be occurring in this system. We caught fewer Chinook salmon in 2016 than in 2017, despite the higher spawner returns in 2015. Examining the seasonal breakdown of this emigration, it appears that an initial high volume of fry emigrated in the spring, as indicated by our higher catch of Chinook salmon in April in 2016 versus 2017. However, this was followed by a steep decline in May 2016 (the peak of the emigration in 2017) followed by consistently low catch throughout 2016 that resulted in the overall lower catch for that year. In 2016, the spring was anomalously dry and warm, likely due to El Niño and marine heatwave conditions, and the Fraser River freshet occurred more than a month early and was the lowest freshet on record (Chandler et al. 2017). The high density of Chinook fry emigrating in 2016, a mild winter, and anomalously low flow conditions may have therefore increased early emigration to the estuary beyond the capacity of the remaining habitat, potentially resulting in large mortality for many of these fry. These patterns should be interpreted with caution, however, as our study was not designed to assess density or natural mortality in the estuary.

Given the dynamic nature of estuarine ecosystems and the regular movement of juvenile salmon throughout them, we recommend that otolith or isotope studies be used to estimate residency as opposed to mark–recapture methods, which may consistently underestimate the use of these habitats in large systems. We also suggest that sampling juvenile salmon throughout the emigration period is an important means of quantifying individual residency and growth across the population. Although catching fish before they are ready to leave the estuary may underestimate the total residency time and growth rate of the population, it also means some fish are caught that may not have survived to ocean entry — as indicated by the few individuals that showed evidence of starvation after estuarine entry. Based upon the strong brood year of Harrison Chinook salmon in 2015 and the overall similarity of daily growth rates for the majority of fish captured in this study, we propose that the remaining habitat in the Fraser estuary provides high-quality rearing opportunity and that further protection and restoration of these habitats could boost productivity for this population. Important areas for future studies include directly linking early estuarine salmon growth to adult returns to elucidate the impacts of estuarine residency on survival.

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References

Balke, E. 2017. Investigating the role of elevated salinity in the recession of a large brackish marsh in the Fraser River estuary. M.Sc. thesis, Simon Fraser University and British Columbia Institute of Technology, Vancouver, B.C.

Beacham, T.D., Jonsen, K., and Wallace, C. 2012. A comparison of stock and individual identification for Chinook salmon in British Columbia provided by microsatellites and single-nucleotide polymorphisms. Mar. Coast. Fish. **4**(1): 1–22. doi:10.1080/19425120.2011.649391.

Beacham, T.D., Wallace, C., Macconnachie, C., Jonsen, K., McIntosh, B., Candy, J.R., and Withler, R.E. 2018. Population and individual identification of Chinook salmon in British Columbia through parentage-based tagging and genetic stock identification with single nucleotide polymorphisms. Can. J. Fish. Aquat. Sci. **75**(7): 1096–1105. doi:10.1139/cjfas-2017-0168.

Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. **49**: 423–437. doi:10.1016/S0079-6611(01)00034-9.

Beamish, R.J., Pearsall, I.A., and Healey, M.C. 2003. A history of the research on the early marine life of Pacific salmon off Canada's Pacific Coast. North Pacific Anadromous Fish Community Bull. **3**: 40.

Bottom, D.L., Jones, K.K., Cornwell, T.J., Gray, A., and Simenstad, C.A. 2005. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuar. Coast. Shelf Sci. **64**(1): 79–93. doi:10.1016/j.ecss.2005.02.008.

Bourret, S.L., Caudill, C.C., and Keefer, M.L. 2016. Diversity of juvenile Chinook salmon life history pathways. Rev. Fish Biol. Fish. **26**(3): 375–403. doi:10.1007/s11160-016-9432-3.

Bradford, M.J., and Geen, G.H. 1992. Growth estimates from otolith increment widths of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. J. Fish Biol. **41**(5): 825–832. doi:10.1111/j.1095-8649.1992.tb02710.x.

Cameron, E.M., Hall, G.E.M., Veizer, J., and Krouse, H.R. 1995. Isotopic and elemental hydrogeochemistry of a major river system: Fraser River, British Columbia, Canada. Chem. Geol. **122**(1–4): 149–169. doi:10.1016/0009-2541(95)00007-9.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**(2): 197–242. doi:10.1111/j.1095-8649.2001.tb00127.x.

Campbell, L.A. 2010. Life histories of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary as inferred from scale and otolith microchemistry. Master's thesis, Oregon State University, Corvallis.

Chalifour, L., Scott, D.C., MacDuffee, M., Iacarella, J.C., Martin, T.G., and Baum, J.K. 2019. Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics. Mar. Ecol. Prog. Ser. **625**: 145–162. doi:10.3354/meps13064.

Chandler, P.C., King, S.A., and Boldt, J. (Editors). 2017. State of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems in 2016. Can. Tech. Rep. Fish. Aquat. Sci. 3225. Available from http://waves-vagues.dfo-mpo.gc.ca/Library/40617944.pdf.

Chittaro, P.M., Zabel, R.W., Beckman, B., Larsen, D.A., and Tillotson, A. 2015. Validation of daily increment formation in otoliths from spring Chinook salmon. Northwest Sci. **89**(1): 93–98. doi:10.3955/046.089.0107.

COSEWIC. 2018. COSEWIC assessment and status report on the Chinook Salmon (*Oncorhynchus tshawytscha*) in Canada. Designatable Units in Southern British Columbia (Part One — Designatable Units with no or low levels of artificial releases in the last 12 years), in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont. Available from https://species-registry.canada.ca/index-en.html#/documents/3544.

Danek, M., Bell, T., and Laroque, C.P. 2015. Some considerations in the reconstruction of lead levels using laser ablation: lessons from the design

stage of an urban dendrochemistry study, St. John's, Canada. Geochronometria, **42**(1): 1733–8387. doi:10.1515/geochr-2015-0024.

Dashtgard, S.E., Venditti, J.G., Hill, P.R., Sisulak, C.F., Johnson, S.M., and La Croix, A.D. 2012. Sedimentation Across the Tidal–Fluvial Transition in the Lower Fraser River. Sed Record, **10**(4): 4–9. doi:10.2110/sedred.2012.4.4.

David, A.T., Simenstad, C.A., Cordell, J.R., Toft, J.D., Ellings, C.S., Gray, A., and Berge, H.B. 2016. Wetland Loss, Juvenile Salmon Foraging Performance, and Density Dependence in Pacific Northwest Estuaries. Estuaries and Coasts, **39**(3): 767–780. doi:10.1007/s12237-015-0041-5.

Davis, M.J., Ellings, C.S., Woo, I., Hodgson, S., Larsen, K., and Nakai, G. 2018. Gauging resource exploitation by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in restoring estuarine habitat. Restor. Ecol. **26**(5): 976–986. doi:10.1111/rec.12643.

Davis, M.J., Woo, I., Ellings, C.S., Hodgson, S., Beauchamp, D.A., Nakai, G., and De La Cruz, S.E.W. 2019. Freshwater tidal forests and estuarine wetlands may confer early life growth advantages for delta-reared Chinook salmon. Trans. Am. Fish. Soc. **148**(2): 289–307. doi:10.1002/tafs.10134.

Duffy, E.J., and Beauchamp, D.A. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Can. J. Fish. Aquat. Sci. **68**(2): 232–240. doi:10.1139/F10-144.

Finn, R.J.R., Chalifour, L., Gergel, S.E., Hinch, S.G., Scott, D.C., and Martin, T.G. Quantifying lost and inaccessible habitat for Pacific salmon in Canada's Lower Fraser River. Ecosphere. [In press.]

Fisheries and Oceans Canada. 2019. 2019/2020 Pacific Region Salmon Integrated Fisheries Management Plan — Southern BC. Available from https://waves-vagues.dfo-mpo.gc.ca/Library/40799104.pdf.

Francis, R. 1990. Back-calculation of fish length: a critical review. J. Fish Biol. **36**: 883–902. doi:10.1111/j.1095-8649.1990.tb05636.x.

Fraser, F.J., Starr, P.J., and Fedorenko, A.Y. 1982. A review of the Chinook and coho salmon of the Fraser River. Can. Tech. Rep. Fish. Aquat. Sci. 1126.

Greer, G.L., Levings, C.D., Harbo, R., Hillaby, B., Brown, T., and Sibert, J. 1980. Distribution of fish species on Robert's and Sturgeon Banks recorded in seine and trawl surveys. Can. Manuscr. Rep. Fish. Aquat. Sci. 1596.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. *In* Estuarine Comparisons. *Edited by* V.S. Kennedy. Academic Press. pp. 315–341. doi:10.1016/B978-0-12-404070-0.50025-9.

Healey, M.C. 1991. Life History of Chinook Salmon. *In* Pacific Salmon Life Histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver, B.C. pp. 311–393.

Healey, M.C., and Heard, W.R. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Can. J. Fish. Aquat. Sci. **41**(3): 476–483. doi:10.1139/f84-057.

Kehoe, L.J., Lund, J., Chalifour, L., Asadian, Y., Balke, E., Carlson, D., et al. 2020. Conservation in heavily urbanized biodiverse regions requires urgent management action and attention to governance. Conserv. Sci. Pract. [In press]. e310. doi:10.1111/csp2.310.

La Croix, A.D., Dashtgard, S.E., Gingras, M.K., Hauck, T.E., and MacEachern, J.A. 2015. Bioturbation trends across the freshwater to brackish-water transition in rivers. Palaeogeogr. Palaeoclimatol. Palaeoecol. **440**: 66–77. doi:10.1016/j.palaeo.2015.08.030.

Levings, C.D. 1985. Juvenile salmonid use of habitats altered by a coal port in the Fraser River estuary, British Columbia. Mar. Pollut. Bull. **16**(6): 248–254. doi:10.1016/0025-326X(85)90510-7.

Levings, C.D., Conlin, K., and Raymond, B. 1991. Intertidal habitats used by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) rearing in the North Arm of the Fraser River estuary, British Columbia, Canada. Mar. Pollut. Bull. **22**(1): 20–26. doi:10.1016/0025-326X(91)90440-4.

Levings, C.D., Greer, G.L., and Miller, P. 1983. Results of preliminary mark–recapture experiments with juvenile salmonids on Sturgeon and Robert's Bank, Fraser River estuary. Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 1684.

Levy, D.A., and Northcote, T.G. 1979. The distribution and abundance of juvenile salmon in marsh habitats of the Fraser River Estuary. Technical Report No. 25. Westwater Research Centre, Vancouver, B.C.

Levy, D.A., and Northcote, T.G. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Can. J. Fish. Aquat. Sci. **39**(2): 270–276. doi:10.1139/f82-038.

Lievesley, M., Stewart, D., Knight, R., and Mason, B. 2017. Marsh and riparian habitat compensation in the Fraser River estuary: a guide for managers and practitioners. The Community Mapping Network, Vancouver, B.C.

Magnusson, A., and Hilborn, R. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries, **26**(4B): 1094–1103. doi:10.1007/BF02803366.

McNatt, R.A., Bottom, D.L., and Hinton, S.A. 2016. Residency and movement of juvenile Chinook salmon at multiple spatial scales in a tidal marsh of the Columbia River estuary. Trans. Am. Fish. Soc. **145**(4): 774–785. doi:10.1080/00028487.2016.1172509.

Miller, J.A. 2011. Effects of water temperature and barium concentration on otolith composition along a salinity gradient: Implications for migratory reconstructions. J. Exp. Mar. Biol. Ecol. **405**(1–2): 42–52. doi:10.1016/j.jembe.2011.05.017.

Miller, J.A., Gray, A., and Merz, J. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Mar. Ecol. Prog. Ser. **408**: 227–240. doi:10.3354/meps08613.

Moore, J.W., Gordon, J., Carr-Harris, C., Gottesfeld, A.S., Wilson, S.M., and Russell, J.H. 2016. Assessing estuaries as stopover habitats for juvenile Pacific salmon. Mar. Ecol. Prog. Ser. **559**: 201–215. doi:10.3354/meps11933.

Morgan, J.D., and Iwama, G.K. 1991. Effects of salinity on growth, metabolism, and ion regulation in juvenile rainbow and steelhead trout (*Oncorhynchus mykiss*) and fall Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **48**(11): 2083–2094. doi:10.1139/f91-247.

Murray, C.B., and Rosenau, M.L. 1989. Rearing of juvenile Chinook salmon in nonnatal tributaries of the lower Fraser River, British Columbia. Trans. Am. Fish. Soc. **118**: 284–289. doi:10.1577/1548-8659(1989)118<0284:ROJCSI>2.3.CO;2.

Northcote, T.G., and Atagi, D.Y. 1997. Pacific salmon abundance trends in the Fraser River watershed compared with other British Columbia systems. *In* Pacific Salmon & Their Ecosystems. *Edited by* D.J. Stouder, P.A. Bisson, and R.J. Naiman. Springer US, Boston, Mass. pp. 199–219. doi:10.1007/978-1-4615-6375-4_14.

QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from http://qgis.osgeo.org.

Quinn, T.P. 2018. The behavior and ecology of pacific salmon and trout. Second Edition. UBC Press, Vancouver, B.C.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Sanborn, M., and Telmer, K. 2003. The spatial resolution of LA-ICP-MS line scans across heterogeneous materials such as fish otoliths and zoned minerals. J. Anal. At. Spectrom. **18**(10): 1231–1237. doi:10.1039/b302513f.

Schaefer, V. 2004. Ecological setting of the Fraser River delta and its urban estuary. *In* Fraser River Delta, British Columbia: Issues of an Urban Estuary. *Edited by* B.J. Groulx, D.C. Mosher, J.L. Luternauer, and D.E. Bilderback. Geological Survey of Canada Bulletin 567. pp. 35–47.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., et al. 2012. Fiji: An open-source platform for biological-image analysis. Nat. Methods, **9**(7): 676–682. doi:10.1038/nmeth.2019.

Sutherland, T.F., Elner, R.W., and O'Neill, J.D. 2013. Robert's Bank: ecological crucible of the Fraser River estuary. Prog. Oceanogr. **115**: 171–180. doi:10.1016/j.pocean.2013.05.018.

Volk, E.C., Bottom, D.L., Jones, K.K., and Simenstad, C.A. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. Trans. Am. Fish. Soc. **139**(2): 535–549. doi:10.1577/T08-163.1.

Voss, B.M., Peucker-Ehrenbrink, B., Eglinton, T.I., Fiske, G., Wang, Z.A., Hoering, K.A., et al. 2014. Tracing river chemistry in space and time: Dissolved inorganic constituents of the Fraser River, Canada. Geochim. Cosmochim. Acta, **124**: 283–308. doi:10.1016/j.gca.2013.09.006.

Waldichuk, M. 1985. Robert's Bank coal port, British Columbia: how did the environmental impact assessment fare? Mar. Pollut. Bull. **16**(5): 179–185. doi:10.1016/0025-326X(85)90477-1.

Walker, B.M., and Sutton, T.M. 2016. Growth-increment formation using otoliths and scales for age-0 Chinook Salmon. North Am. J. Fish. Manage. **36**(5): 995–999. doi:10.1080/02755947.2016.1184202.

Weitkamp, L.A., Goulette, G., Hawkes, J., O'Malley, M., and Lipsky, C. 2014. Juvenile salmon in estuaries: Comparisons between North American Atlantic and Pacific salmon populations. Rev. Fish Biol. Fish. **24**(3): 713–736. doi:10.1007/s11160-014-9345-y.

Zabel, R.W., Haught, K., and Chittaro, P.M. 2010. Variability in fish size/otolith radius relationships among populations of Chinook salmon. Environ. Biol. Fishes, **89**(3): 267–278. doi:10.1007/s10641-010-9678-x.