WILEY Ecology of FRESHWATER FISH

Juvenile river residence and performance of Snake River fall Chinook salmon

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Abstract

An animal's performance during its early life stage can greatly influence its survival to adulthood. Therefore, understanding aspects of early life history can be informative, particularly when designing management plans to rebuild a population. For a threatened population of fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River of Idaho, we reconstructed the early life history for 124 returning wild and hatchery adults using information recorded in their otoliths. Of our sampled wild adults (*n* = 61), 43% and 49% reared within the Snake River and Clearwater/Salmon rivers. We also found that only 21% of our sampled wild adults exhibited the historically common subyearling out-migration strategy, in which juveniles exit freshwater shortly after hatching, while the remaining wild adults exhibited the yearling out-migration strategy (i.e., individuals delay their freshwater exit). As expected, yearlings had, on average, a significantly larger body size than subyearlings at ocean entry. However, 35% of wild yearlings overlapped in size with wild subyearlings suggesting that spending more time in freshwater might not necessarily result in a larger body size. Lastly, we observed that variability in fork length at Snake River egress and ocean entry were best explained by migration strategy and where it reared, followed by hatch year and sex. Results from this study highlight the utility of adult otoliths in providing details about early life history, an understanding of which is critical to the conservation of Snake River fall Chinook salmon.

KEYWORDS
otolith, rearing and overwintering location, somatic growth, yearling

1 | INTRODUCTION

Many species take part in annual or seasonal migrations that are thought to optimise fitness (Baker, 1978) and which are prompted by food and/or reproductive requirements (Lascelles et al., 2014; Ronce, Olivieri, Clobert, & Danchin, 2001). Ultimately, optimising fitness involves trade-offs between growth and survival (e.g., Gross, 1987). However, due to anthropogenic disturbances that disrupt habitat quality, quantity and connectivity (Halpern et al., 2008; Lotze et al., 2006), migratory species are being adversely affected as the habitats they rely on for all or part of their life are lost or disturbed (Fukushima, Jutagate, Grudpan, Phomikong, & Nohara, 2014; Martin et al., 2007; Robinson et al., 2009). Disturbances to habitat can lead to phenotypic changes that are presumably guided by selection (Williams, Zabel, Waples, Hutchings, & Connor, 2008).

Fall Chinook salmon, *Oncorhynchus tshawytscha*, in the Snake River Basin (a tributary of the Columbia River in the U.S. Pacific northwest) have lost about 90% of their historic spawning habitat with the creation of the Hell's Canyon dam complex in the 1960s (Ruckelshaus, Levin, Johnson, & Kareiva, 2002; Figure 1). Due to
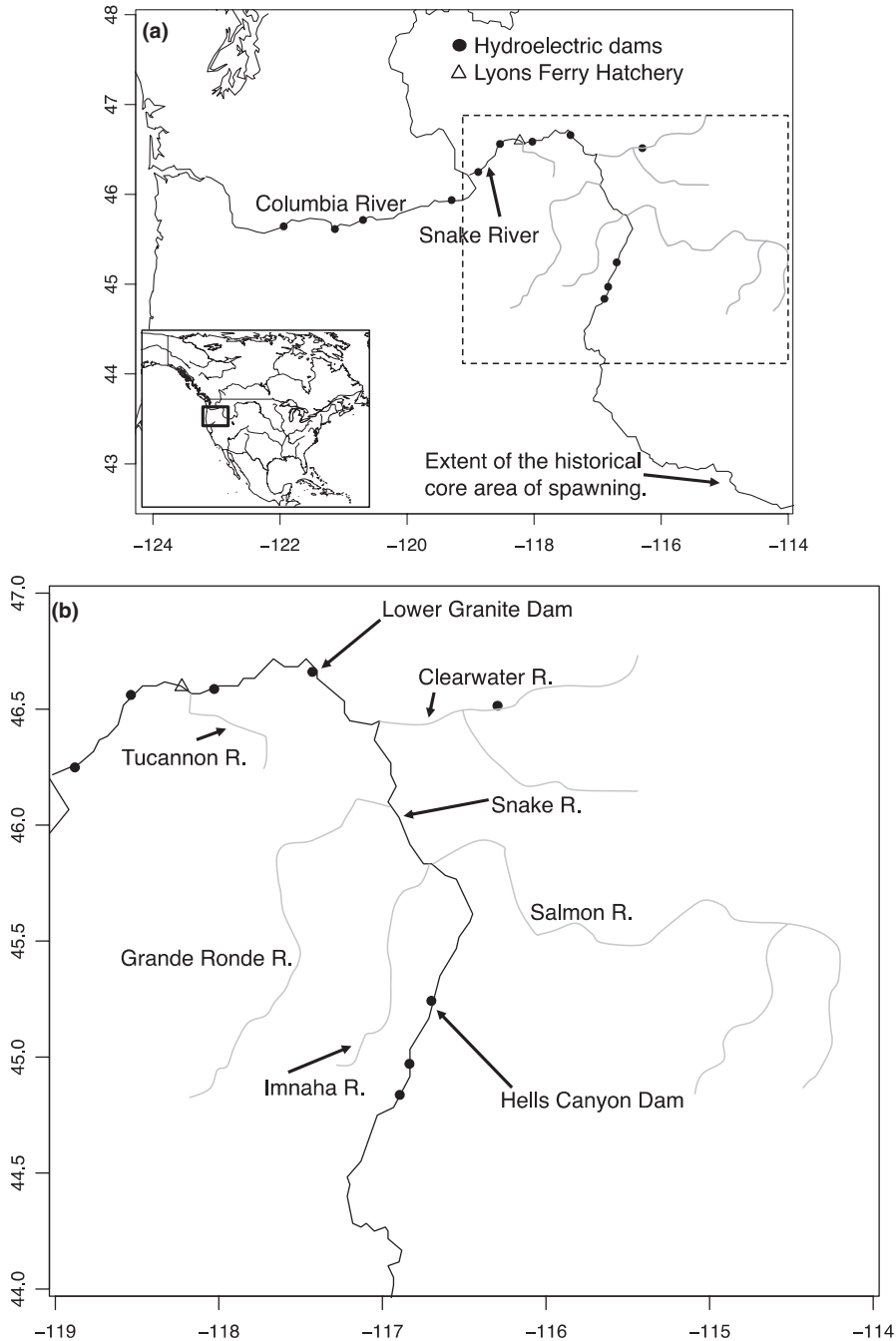
FIGURE 1 (a) Map of the Columbia and Snake rivers showing location of dams, Lyons Ferry Hatchery, and area blocked to spawning of fall Chinook salmon (*Oncorhynchus tshawytscha*). (b) Map of the Snake River watershed showing Lower Granite Dam and the three river spawning locations identified to have unique 87Sr/86Sr values (Hegg, Kennedy, Chittaro, et al., 2013): Snake River, Clearwater and Salmon rivers, and Tucannon, Grande Ronde and Imnaha rivers

dramatic declines in its abundance, Snake River fall Chinook salmon was listed as threatened under the Endangered Species Act, ESA, in 1992 (Pacific Fisheries Management Council, 2014). Several factors continue to limit its recovery including migration through eight dams (Mathur, Heisey, Euston, Skalski, & Hays, 1996; Singer et al., 2013), dam-altered hydrology and water temperature (Geist, Deng, Mueller, Brink, & Chandler, 2010; Harnish, Sharma, McMichael, Langshaw, & Pearsons, 2014; Steel & Lange, 2007), predation from invasive species (Kuehne & Olden, 2012), reduced availability and quality of rearing (Tiffan, Erhardt, & St. John, 2014; Tiffan, Garland, & Rondorf, 2006) and spawning habitat (Chapman, Weitkamp, Welsh, Dell, & Schadt, 1986; Geist et al., 2008; Hatten et al., 2009), harvest levels and hatchery practices (Ruckelshaus et al., 2002).

Notable in this population is the presence of a relatively novel juvenile out-migration strategy for which little is understood (Connor, Burge, Waitt, & Bjornn, 2002; Williams et al., 2008). Historically, the Snake River fall Chinook salmon consisted predominantly of a subyearling out-migration strategy whereby juveniles migrate to the ocean a few months after their spring emergence (i.e., first feeding; Connor et al., 2002; Williams et al., 2008). Specifically, during the 1960s, the subyearling migration strategy was observed in about 97% of adult fall Chinook salmon sampled from the Columbia River (Young & Robinson, 1974), which included Snake River fall Chinook salmon (i.e., approximately 10%–20% of all individuals; Hatten et al., 2009; Myers et al., 1998). Over the last two decades, however, an increasing incidence of

a yearling out-migration strategy has been reported in which juveniles are thought to remain in freshwater for an extended period (i.e., overwinter) prior to migrating to the ocean the following spring (Connor, Sneva, Tiffan, Steinhorst, & Ross, 2005). In fact, from 1994 to 2001, an average of 48% of adult wild-origin females from the Snake River basin exhibited the yearling strategy (Connor et al., 2005). Because migration timing has significant effects on the degree to which individuals overlap in space and time with vital resources (Crozier et al., 2008; Scheuerell, Zabel, & Sandford, 2009; Stearns, 1992), which in turn can impact population recovery, it is important that we identify the rivers and migration strategies that contribute individuals to the adult population.

Here, we examine the early life history of Snake River Chinook salmon by examining their otoliths, which are calcified structures used for balance. The chemical and structural analysis of a fish's hard parts, particularly scales and otoliths, make them a useful tool for acquiring information about an individuals' movement and performance (Campana, 1999). During the life of a fish, its otoliths grow continually by the deposition of layers of calcium carbonate and protein, and these layers form visible increments that can be used to determine age (Jones, 1992; Stevenson & Campana, 1992). This age information together with body size–age relationships means that body size and somatic growth can be estimated for earlier points in an individuals' life (Casselman, 1987). Further, as otolith layers form, ions are deposited onto the otoliths' growing surface often at concentrations that reflect those in the environment (Bath et al., 2000), and therefore, all individuals, regardless of size and age, are marked with environmentally derived ions. The combined information provided by otolith structure and chemistry allows retrospective determination of age-, size- and location-specific chemical signatures that can be used to assess habitat use, somatic growth and movement (Elsdon et al., 2008; Kennedy, Klaue, Blum, Folt, & Nislow, 2002; Walther & Thorrold, 2010).

In this study, we used otolith chemistry and structure as a means to investigate early life-history movement and performance of Snake River fall Chinook salmon. This population is an ideal study species because they have predictable spawning times and locations allowing adults to be readily collected, and an early life history in which they occupy chemically distinct freshwater, estuarine and ocean habitats, which can facilitate otolith-derived reconstruction of their movement and habitat use (Hegg, Kennedy, & Fremier, 2013). The purpose of our project was threefold. First, we wanted to identify where returning adults reared as juveniles, and which juvenile out-migration strategy they exhibited (subyearling vs. yearling). Second, using somatic growth as an indicator of performance, we sought to determine whether performance varied with respect to rearing location and migration strategy. Last, we wanted to investigate the extent to which growth and size at Snake River egress and ocean entry were explained by a suite of independent variables. Results from this study are intended to help inform recovery planning for Snake River fall Chinook salmon including future habitat restoration and conservation efforts in the Snake River Basin and Columbia River.

2 | MATERIAL AND METHODS

2.1 | Study species

The ESA listed Snake River fall Chinook salmon, an evolutionary significant unit (ESU) of Chinook salmon (*Oncorhynchus tshawytscha*), includes wild-origin individuals from the mainstem Snake River below the impassable Hells Canyon Dam (at river kilometre 400) and from the Tucannon, Grande Ronde, Imnaha, Salmon and Clearwater rivers (NOAA NMFSC, 2017; Figure 1). Also considered part of the ESU are individuals from four hatchery programmes, Lyons Ferry Hatchery Program, Fall Chinook Acclimation Ponds Program, Nez Perce Tribal Hatchery Program and the Oxbow Hatchery Program.

Spawning of Snake River fall Chinook salmon occurs in gravel beds primarily located within Snake and Clearwater rivers (Zabel, Haught, & Chittaro, 2010) with peak spawning occurring in November (Connor et al., 2002; Harnish et al., 2014). Individuals hatch and remain in the interstitial spaces of the gravel until spring when their yolk-sac is depleted, after which they leave the gravel and become free-swimming juveniles (referred to as emergence; Quinn, 2005). Juveniles will then rear in freshwater habitats as they make their way downstream towards the ocean. Those juveniles that successfully migrate downstream will spend 1–4 years in the ocean before returning to the Columbia River estuary and migrating upriver to spawn in freshwater.

2.2 | Fish collection and otolith preparation

In 2011, approximately 11% of presumed wild returning adults (28,216 individuals) were randomly sampled across the run at Lower Granite Dam (Milks, Grider, & Schuck, 2013). Specifically, at Lower Granite Dam, a trap built into the fish ladder was systematically operated 10% each hour from 18 August to 20 November 2011. Trapped fish without a tag and with an intact adipose fin were considered wild and transported to Lyons Ferry Hatchery, Washington, and the other hatcheries in the basin for the purpose of maintaining genetic diversity in the hatchery broodstock (Milks et al., 2013). We randomly subsampled 124 adult fall Chinook salmon (830 mm average fork length; 72 mm standard deviation), representing approximately 0.4% of the total return, from Lyons Ferry Hatchery spawning operations, November 2011.

Although these sampled adults lacked an internal or external artificial tag, such as an acoustic or radio tag, and had an intact adipose fin (injecting/attaching tags and fin clipping are procedures used in hatcheries to identify hatchery-produced individuals), we refer to them as presumed wild since not all hatchery-produced fish are tagged and/or clipped. For the purpose of this study, we determined whether a fish was hatchery- or wild-produced using otolith microchemistry (described below).

Juvenile fall Chinook salmon (*n* = 21; 90 mm average fork length; 17 mm standard deviation) were collected during the summer of 2011 at Lower Granite Dam, the first dam fish encounter on their

path downstream, and used to evaluate the accuracy of our classification of adults to rearing location (see *Classification of adults and juveniles to rearing location*). This test of classification accuracy was possible because rearing location was known for these juveniles. Specifically, these juveniles were previously implanted with passive integrated transponder tags (PIT tags) upriver of Lower Granite Dam (located on the portion of the Snake River downstream of the Clearwater River).

We measured the fork length (mm) of each fish, removed their sagittal otoliths and placed these otoliths into dry storage. Left sagittal otoliths were mounted on glass microscope slides using thermoplastic cement (Crystal Bond, http://www.crystalbond.com; reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.). Each otolith from juvenile and adult Chinook salmon was polished on both sides in a sagittal plane using slurries (600-grit silicon carbide, 5.0 alumina oxide and 1.0 micropolish; http://www.buehler.com) and a grinding wheel with Buehler© 1500 micropolishing pads. Polishing ceased when the core was visible. We photographed polished otoliths using a digital camera (Leica DFC450) mounted on a compound microscope

(Zeiss©). To back-calculate brood year of each adult, age was provided by Washington Department of Fish and Wildlife Fish Ageing Laboratory and was based on scale analysis of three scales taken dorsal to the lateral line and posterior to the dorsal fin as described in Connor et al. (2005).

2.3 | Otolith microstructure

To reconstruct the juvenile size at Snake River egress and ocean entry from adult otoliths, we used a quadratic relationship between fork length and otolith radius that was developed for Snake River fall Chinook salmon (Zabel et al., 2010). For this relationship, Zabel et al. (2010) reported deviations between observed and predicted (from back-calculations) fish lengths had a mean of −0.9 mm and a standard deviation of 3.5 mm. To use this relationship to estimate size at Snake River egress and ocean entry, we needed the otolith radius at Snake River egress and ocean entry. First, we determined the location on the otolith of Snake River egress and ocean entry using otolith microchemistry. Then, we measured otolith radius to Snake River egress and ocean entry as the distance from the otolith core
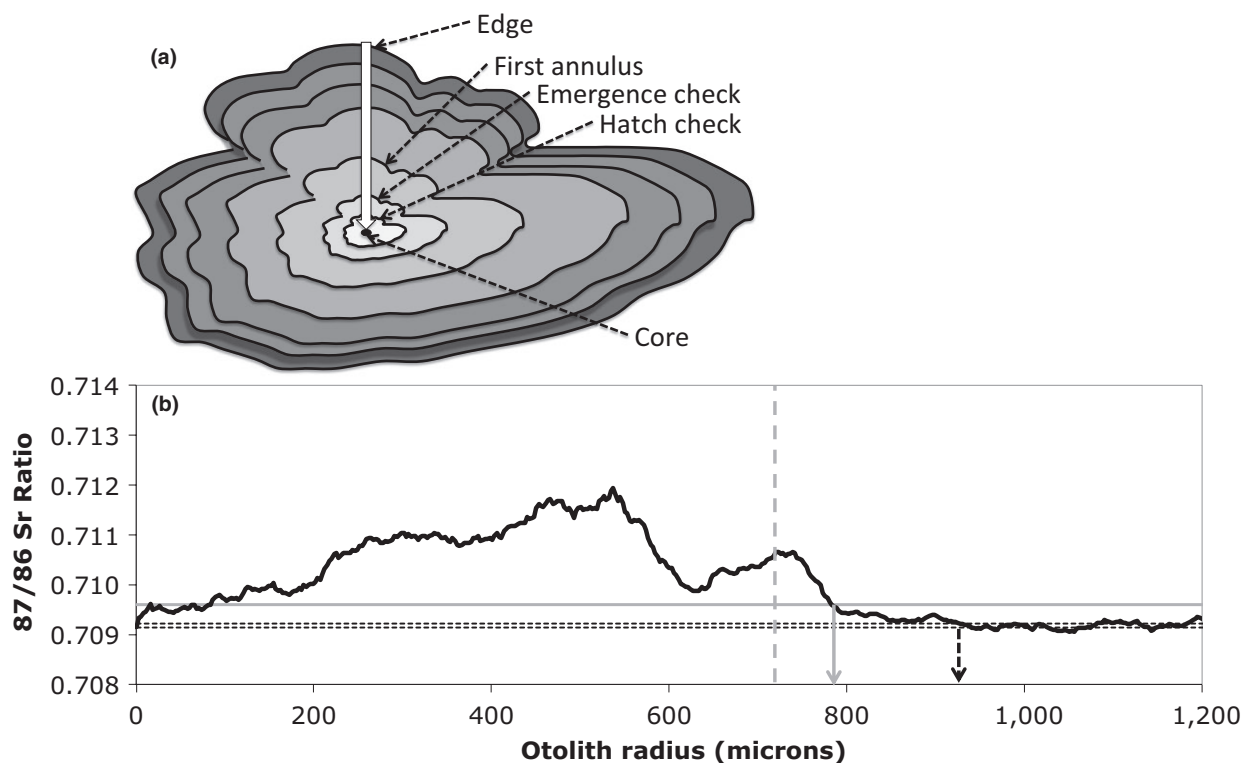

FIGURE 2 (a) Illustration of an adult otolith showing hatch, emergence and first annulus marks and the path of laser ablation (white arrow). (b) Representation showing how changes in $^{87}Sr/^{86}Sr$ ratio of an adult Chinook salmon otolith were used to identify the otolith radius at Snake River egress and ocean entry, and whether the fish exhibited the yearling or subyearling migration strategy. Laser ablation inductively coupled plasma mass spectrometry from otolith edge to core was used to produce a time series of $^{87}Sr/^{86}Sr$ ratio (black line). We used visual inspection of the $^{87}Sr/^{86}Sr$ ratio to determine the otolith radius when an individual exited Snake River (Snake River is indicated by the horizontal grey line at 0.70960; the grey arrow corresponds to Snake River egress). We used the merging of $^{87}Sr/^{86}Sr$ ratio onto the range of 0.70914–0.70922 (represented as two dashed black lines), which is centred on the global marine signature of 0.70918, to identify the otolith radius when an individual entered the ocean (indicated by a black arrow). Lastly, we determined migration strategy by comparing otolith radius at first annulus to otolith radius at ocean entry. If otolith radius to the first annulus (indicated as the vertical dashed grey line) is less than otolith radius at ocean entry, then the fish is categorised as exhibiting the yearling migration strategy; otherwise, the fish is categorised as exhibiting the subyearling strategy

to the location on the otolith of Snake River egress and ocean entry, respectively, along a transect perpendicular to the longitudinal axis on the dorsal side of the otolith. Along this same transect, we also measured the otolith radius to the outside margin of the first annual mark (Murray, 1994). We used the otolith radius to the first annual mark to classify individuals to a migration strategy. Otolith radius was measured from digital photographs using Image Pro software (version 7.0; MediaCybernetics©).

2.4 | Otolith microchemistry

To reconstruct where adults resided as juveniles, we used the chemistry of their otoliths. Polished otoliths from adults and juveniles were analysed for $^{87}Sr/^{86}Sr$ at the GeoAnalytical Lab at Washington State University (Pullman, WA, USA), using a Finnigan Neptune (Thermo Scientific) multicollector inductively coupled plasma mass spectrometer with helium as the carrier gas. The mass spectrometer was coupled with a New Wave UP-213 laser ablation sampling system (frequency of 20 Hz, 40 μm spot size; LA-MC-ICPMS). Using an automated microscope stage, the laser beam moved at a speed of 10 μm/s and ablated the polished otolith along a transect from the otolith edge to its core (the transect was perpendicular to the longitudinal axis on the dorsal side of the otolith). This edge-to-core scan line on the otolith corresponds to the entire life of the fish (Figure 2a).

Data acquisition of the LA-MC-ICPMS lasted 250 s, 14 s of which were designated for instrument calibration and gas background counts prior to the start of each ablation. Data were recorded with a 0.262 s integration time. Measurement of $^{87}Sr/^{86}Sr$ was calculated and corrected through simultaneous measurement of 83Kr, 84Sr, 85Rb, 86Sr, 87Sr and 88Sr. Measurements were mass-bias corrected and corrected for interferences in 86Kr, 87Rb and Ca dimers using natural ratios, similar to Woodhead, Swearer, Hergt, and Maas (2005) and Barnett-Johnson, Ramos, Grimes, and MacFarlane (2005). To evaluate measurement error, we analysed a marine shell standard that was assumed to be in equilibrium with the global marine value of $^{87}Sr/^{86}Sr$ (0.70918) (Faure & Mensing, 2004). The marine shell standard was analysed 3–4 times every 15–20 otolith samples. During the course of this study, the average $^{87}Sr/^{86}Sr$ ratio for the marine shell was 0.709197 (*SD* = 0.000036, *n* = 21). Values of otolith $^{87}Sr/^{86}Sr$ ratio were adjusted daily using a correction factor calculated each analysis day from the average deviation of the shell standard to the marine value (Hegg, Kennedy, Chittaro et al., 2013).

To estimate whether an individual was wild- or hatchery-produced, we relied upon otolith microchemistry. Work by Hegg (2017) and Hegg, Kennedy, and Chittaro (2018) differentiated juvenile Snake River fall chinook salmon of known-origin based on unique $^{87}Sr/^{86}Sr$ ratio and trace element ratios (25Mg:43Ca, 55Mn:43Ca, 66Zn:43Ca, 86Sr:43Ca, 138Ba:43Ca and 208Pb:43Ca). They reported that with this multielement approach, on average, 92.6% of their 302 juveniles of known-origin were correctly classified among six locations in the Snake River basin, including the Lyons Ferry and Nez Perce hatcheries (Heggs, 2017). We applied this multielement technique to the 124 presumed wild adults of this study to identify

hatchery- and wild-produced individuals and thereby incorporate this hatchery-wild classification into our analyses of early life-history residence, size and growth.

Trace elemental ratios were measured using a Finnigan Element 2 (Thermo Scientific) high-resolution ICP–MS (with helium as the carrier gas), coupled with the New Wave laser ablation system (New Wave UP-213) at the GeoAnalytical Facility of Washington State University. The laser beam moved from otolith edge to core at a speed of 10 μm/s and had a 30 μm spot size. Data were recorded with a 1 s integration time (Hegg et al., 2018). Trace element counts were corrected to the SRM 610 standard and corrected to calcium using a ten second, within-run blank. Limits of detection for each element were calculated as 3 X standard deviation from the mean of the blank. Expressed as a ratio of elements to calcium resulted in detection limits of Sr/Ca 0.029 mm/mol, Ba/Ca 0.023 mm/mol, Mn/Ca 0.031 mm/mol and Mg/Ca 0.022 mm/mol (Hegg et al., 2018).

2.5 | Life stage determination

One of our goals was to reconstruct juvenile river residence for each adult during two early life-history stages: rearing and overwintering. To reconstruct where fish resided during both of these stages, we calculated average $^{87}Sr/^{86}Sr$, across 20 μm, for rearing and overwintering sections within the juvenile portion of adult otoliths.

The rearing and overwintering sections of the otolith were defined as the portions of the otolith between 250 and 500 μm from the otolith core and between 500 μm and the radius from the core corresponding to when a fish exited the Snake River respectively. These rearing and overwintering portions of each otolith were based on findings from our study of otolith radius at Snake River egress. In particular, most of our sampled adults (~60%) showed evidence of egress from Snake River (i.e., $^{87}Sr/^{86}Sr$ ratio that fell below 0.70960) between a radius of 500 and 800 μm. Therefore, we targeted a rearing $^{87}Sr/^{86}Sr$ ratio to be between 250 and 500 μm and an overwintering $^{87}Sr/^{86}Sr$ ratio beyond 500 μm.

Because rearing location was known for the 21 juveniles collected at Lower Granite Dam, we quantified the $^{87}Sr/^{86}Sr$ ratio associated with rearing location so as to evaluate our classification accuracy. To determine the rearing $^{87}Sr/^{86}Sr$ ratio for otoliths from juveniles, we used the same procedure for determining the rearing $^{87}Sr/^{86}Sr$ ratio for otoliths from adults; that is, we targeted the portion of otolith between a radius of 250 and 500 μm from the core.

2.6 | Classification of adults and juveniles to rearing location

Results from Hegg, Kennedy, Chittaro, et al. (2013) indicated that $^{87}Sr/^{86}Sr$ ratio for water samples (taken across seasons and years in the Snake River basin) was significantly different among major spawning locations, (a) Clearwater and Salmon rivers; (b) Snake River; and (b) Tucannon, Grande Ronde and Imnaha rivers. For the purpose of this study, Snake River was defined as the section of Snake River upstream of the reservoir created by dams near the confluence

between the Snake and Clearwater rivers and downstream of Hells Canyon Dams (Figure 1).

Because there is a direct relationship between ^{87}Sr/^{86}Sr ratio in otoliths and water (Kennedy, Folt, Blum, & Chamberlain, 1997), we used the ^{87}Sr/^{86}Sr ratio in water to represent the chemical signatures for each of the three locations (taken from Hegg, 2017; Hegg et al., 2018). We then classified the rearing and overwintering ^{87}Sr/^{86}Sr ratio from otoliths of our collected adults to the three locations (for details about the overwintering classification see *Identification of migration strategy and overwintering location*). This classification of otolith ^{87}Sr/^{86}Sr ratio, representing the rearing and overwintering portion of an individuals' life history, to water ^{87}Sr/^{86}Sr ratio from the three locations was done through the use of the {mixtools} package for R. {mixtools} is an expectation-maximisation algorithm that uses an iterative method to maximise posteriori probability estimates of, in our study, location assignments for each fish (Benaglia, Chauveau, Hunter, & Young, 2009). For an individual to be classified to one of the three locations, we required the posterior probability to be greater than or equal to 0.66 (i.e., two times greater than random chance of 0.33).

We also classified the rearing ^{87}Sr/^{86}Sr ratio from the otoliths of juveniles to which their rearing location was known. The purpose of classifying juveniles to their rearing location was to evaluate the ability of {mixtools} to correctly classify juveniles when rearing location was known: all 21 juveniles reared in Snake River. Lastly, to investigate the rearing and overwintering assignments of hatchery- and wild-produced fish, we performed separate classifications with {mixtool} on fish categorised as hatchery- or wild-produced.

2.7 | Identifying migration strategy and overwintering location

For each adult, we assigned a migration strategy (i.e., yearling or subyearling) using a combination of otolith radius to the first annual mark and otolith radius at ocean entry (Figure 2b). A fish was categorised as exhibiting a subyearling strategy if its otolith radius at ocean entry was less than its radius to the first annulus. Alternatively, a fish was categorised as exhibiting a yearling strategy if its otolith radius at ocean entry was greater than or equal to its radius to the first annulus. This classification is comparable to that used by Connor et al. (2005) on scales from fall Chinook salmon. Otolith radius corresponding to ocean entry was measured at the convergence of ^{87}Sr/^{86}Sr ratio, from the edge-to-core scan, onto the range of 0.70914–0.70922, which is centred on the global marine signature of 0.70918 (Figure 2b).

For those individuals that we categorised as exhibiting the yearling migration strategy, we also determined where they overwintered. Our assessment of overwintering location used the same statistical approach (i.e., {mixtools} package for R) outlined in the *Classification of adults and juveniles to rearing location*.

2.8 | Body size and growth

To estimate fork length at Snake River egress and ocean entry from adult otoliths, we first determined where on each otolith these two

points in time occurred by using data of ^{87}Sr/^{86}Sr ratio from the otolith edge-to-core scans. As previously mentioned, otolith radius at ocean entry was measured at the point on the edge-to-core scan where the ^{87}Sr/^{86}Sr ratio converged with the range of 0.70914–0.70922, which is centred on the global marine signature of 0.70918 (Figure 2b). In contrast, otolith radius at Snake River egress was measured at the point on the edge-to-core scan where ^{87}Sr/^{86}Sr ratio was 0.70960 (Snake River ^{87}Sr/^{86}Sr ratio). Next, we input these values of otolith radius at Snake River egress and ocean entry into the quadratic relationship between fork length and otolith radius developed for Snake River fall Chinook salmon (Zabel et al., 2010) and calculated fork length at Snake River egress and ocean entry. From these estimates of fork length, we then calculated the amount of somatic growth (mm) each fish experienced during the interval of time between Snake River egress and ocean entry (i.e., fork length at Snake River egress subtracted from fork length at ocean entry). Finally, we used one-way ANOVA to evaluate whether fork length and growth varied significantly among fish classified to different rearing and overwintering locations, migration strategies and hatchery- or wild-produced.

We used a generalised linear modelling (glm) approach to investigate the extent to which body size (i.e., fork length at Snake River egress and ocean entry) and growth of juvenile Chinook salmon were explained by a suite of five independent variables. We included hatch year (n = 4 in 2007, 103 in 2008 and 17 in 2009) to account for different conditions in the freshwater habitat across years, and rearing location to account for different conditions across habitat areas (see Table 1 for sample sizes). Sex, migration strategy and hatchery- or wild-produced were included to account for phenotypic or genotypic differences among groups of fish. We ran 32 models (including a null model with no effects) representing all possible combinations of the aforementioned data set of five variables. All model parameters were estimated by maximising the likelihood function.

To compare models, we calculated four values for each model: Akaike's information criterion (AIC), delta AIC, relative likelihood and AIC weight. Smaller AIC values indicate "better" models and when comparing two models, with delta AIC being the difference in AIC between two models (Akaike, 1973; Burnham & Anderson, 2002). A delta AIC of <2 indicates little difference between competing models; a delta AIC of 2–10 indicates moderate support for a difference between the models, and a delta AIC of >10 indicates strong support (Burnham & Anderson, 2002). Relative likelihood represents the likelihood of a model given the data, whereas AIC weight is the discrete probability of each model (Burnham & Anderson, 2002). The best model was defined as having the lowest AIC, although preference was given to the simplest model if two or more models had a delta AIC of less than 2.

3 | RESULTS

3.1 | Classification of adults and juveniles to rearing location

Our rearing classification of all (n = 124) adults (i.e., pooled hatchery- and wild-produced) revealed that 74% of these fish reared in

TABLE 1 Predicted rearing and overwintering location of adult fall Chinook salmon based on maximum-likelihood estimation. The number (and percent) of hatchery- and wild-produced fish that were classified to each rearing and overwintering location is indicated, as is the respective number (and percent) of individuals that exhibited the yearling migration strategy

Classification type and area	Pooled hatchery- and wild-produced fish Number of fish (%)	Wild-produced fish Number of fish (%)	Yearling (%)	Hatchery-produced fish Number of fish (%)	Yearling (%)
Rearing					
Tucannon, Grande Ronde and Imnaha	2 (2)	2 (3)	0 (0)	3 (5)	2 (5)
Clearwater, Salmon	28 (22)	30 (49)	23 (48)	3 (5)	1 (2)
Snake	92 (74)	26 (43)	22 (46)	57 (90)	41 (93)
Unassigned	2 (2)	3 (5)			
Total sample size	124	61	48 (79[a])	63	44 (70[a])
Overwintering					
Tucannon, Grande Ronde and Imnaha	5 (5)		3 (6)		37 (84)
Clearwater, Salmon	9 (10)		7 (15)		2 (5)
Snake	75 (82)		38 (77)		0 (0)
Unassigned	3 (3)		1 (2)		5 (11)
Total sample size	92		48		44

[a]Migration strategy was not determined for one wild-produced and two hatchery-produced fish.

Snake River, 22% in Clearwater and Salmon rivers, 2% in Tucannon, Grand Ronde and Imnaha rivers, and 2% were unassigned (Table 1). Of these adults, 61 and 63 were classified as wild- and hatchery-produced, respectively. Results of our rearing classification of wild adults indicated that 49% of these individuals reared in Clearwater and Salmon rivers, 43% reared in Snake River, 3% in Tucannon, Grand Ronde and Imnaha rivers, and 5% unassigned (Table 1). In terms of hatchery adults, our rearing classification among the three locations indicated that 90% reared in Snake River; 5% in Tucannon, Grand Ronde and Imnaha rivers; and 5% in Clearwater and Salmon rivers (Table 1). Individual assignment probabilities were generally high, such that all but 4 adults were assigned to a rearing location with >70% probabilities, and 3 others were not assigned owing to probabilities <65%. The test of classification accuracy, which used rearing signatures from otoliths of collected juveniles for which rearing location was known, indicated that 17 individuals out of 21 (81%) were correctly classified to Snake River; 2 were assigned to Tucannon, Grand Ronde and Imnaha rivers; 1 was assigned to Clearwater and Salmon rivers; and 1 was unassigned.

3.2 | Identifying migration strategy and overwintering locations

Of 124 wild and hatchery adults, the majority (76%) were categorised as exhibiting a yearling strategy. Three individuals were not assigned a strategy because their otolith annual mark could not be visually identified. Our overwintering classification of all yearling adults (i.e., pooled hatchery- and wild-produced; n = 92)

revealed that 82% of these fish overwintered in Snake River; 10% in Clearwater and Salmon rivers; 5% in Tucannon, Grand Ronde and Imnaha rivers; and 3% were unassigned (Table 1). Our overwintering classification of wild-produced adults indicated that the majority (77%) of individuals overwintered in Snake River (0% of the hatchery adults), 15% in Clearwater and Salmon rivers (5% of the hatchery adults), 6% in Tucannon, Grand Ronde and Imnaha rivers (84% of the hatchery adults), and 2% were unassigned (11% of the hatchery adults; Table 1). Of our wild yearlings, 38% were assigned the same location as both their rearing and overwintering location; 31% were assigned to Snake River and 7% to Clearwater and Salmon rivers. Individual assignment probabilities were generally high, such that all but two adults were assigned to a overwintering location with >70% probabilities, and 6 others were unassigned.

3.3 | Body size and growth

Forty percent of wild returning adults that exhibited the yearling strategy overlapped in terms of fork length at Snake River egress with individuals that exhibited the subyearling strategy, while 35% of individuals overlapped in size at ocean entry. Specifically, our back-calculated estimates of fork length at Snake River egress ranged from 116–167 and 124–298 mm for wild subyearlings and yearlings, respectively, while fork length at ocean entry ranged from 128–189 and 140–323 mm for wild subyearlings and yearlings respectively (Figure 3a,b). For hatchery fish, estimates of fork length at Snake River egress ranged from 106–170 and 124–316 mm for subyearlings and yearlings, respectively, while fork length at ocean entry
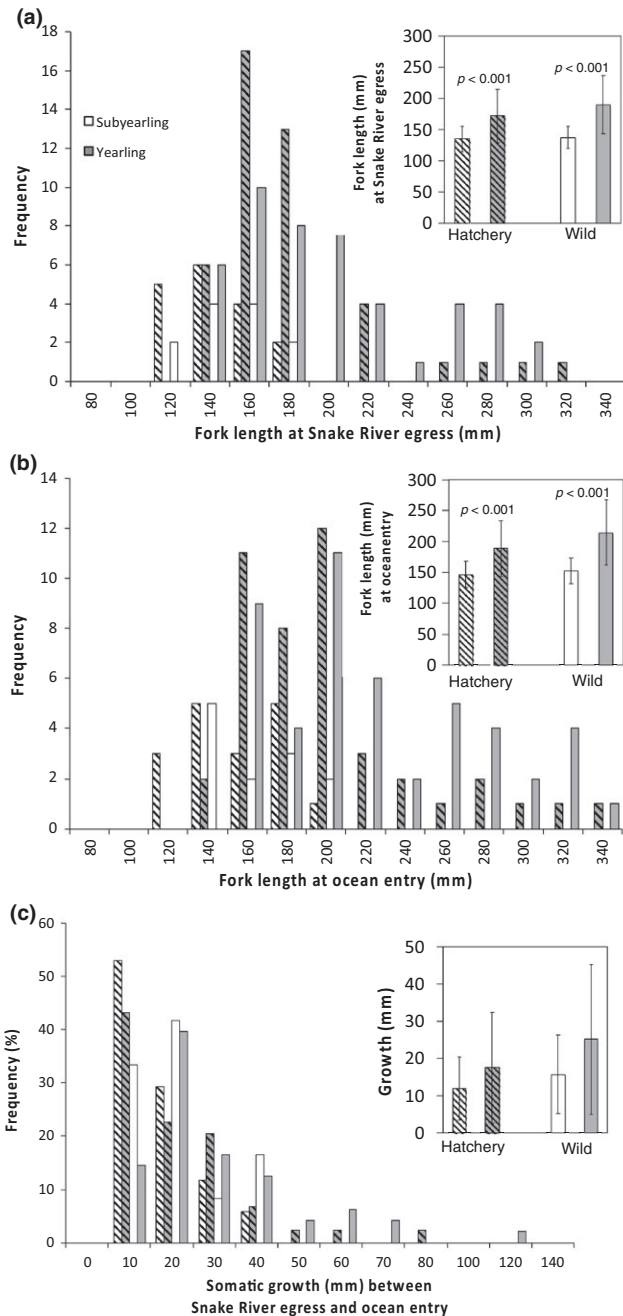
FIGURE 3 Frequency distributions of otolith-derived back-calculated estimates of fall Chinook salmon fork length at (a) Snake River egress and (b) ocean entry. Plot (c) is the percent frequency distribution of somatic growth (mm) that was accumulated between Snake River egress and ocean entry. Within each plot bars correspond to either yearling (grey bars) or subyearling (white bars) migration strategies and hatchery- (hatched bars) or wild- (solid bars) produced. Inset plots show the average (box) and standard deviation (whiskers) of hatchery- and wild-produced fish with respect to subyearling and yearling migration strategies. *p*-values from ANOVAs are indicated

ranged from 114–184 and 129–323 mm for subyearlings and yearlings respectively.

ANOVA results indicated that wild yearlings had a significantly larger fork length than wild subyearlings, by an average of 53

and 62 mm, at Snake River egress ($F_{1,58}$ = 14.5, p < 0.001; inset of Figure 3a) and ocean entry ($F_{1,58}$ = 15.9, p < 0.001; inset of Figure 3b) respectively. In terms of hatchery fish, ANOVA results indicated that yearlings had a significantly larger fork length than subyearlings, by an average of 37 and 42 mm, at Snake River egress ($F_{1,59}$ = 11.2, p < 0.001; inset of Figure 3a) and ocean entry ($F_{1,59}$ = 13.6, p < 0.001; inset of Figure 3b) respectively. We also observed significantly larger fork length of yearlings, relative to subyearlings, at both Snake River egress and ocean entry within hatchery- and wild-produced fish that had a rearing location in Snake River and for wild-produced fish that reared in Clearwater and Salmon rivers (Figure 4a,b), while the other rearing locations had insufficient sample sizes (i.e., n < 6) to permit statistical analyses. In terms of growth, 67% of all sampled fish exhibiting the subyearling and yearling strategies grew 10 mm or more during the period of time from when they exited the Snake River and entered the ocean, and no significant differences in growth were detected between migration strategies within either hatchery or wild fish (inset Figure 3c).

Our generalised linear modelling (GLM) revealed that the same two independent variables best-explained variability in size at Snake River egress and ocean entry, as well as growth that occurred between Snake River egress and ocean entry. Specifically, the best models consisted of migration strategy and rearing location, followed by sex and hatch year (Table 2). Size at Snake River egress and ocean entry was significantly greater for fish that were yearlings and reared in Clearwater and Salmon rivers. Growth was significantly greater for fish that were females, yearlings, and those reared in Clearwater and Salmon rivers.

4 | DISCUSSION

In this study, we investigated the early life history of Snake River fall Chinook salmon from adults returning to spawn so as to better comprehend what freshwater habitats support rearing of juveniles that return as adults. Specifically, we reconstructed where adults reared and overwintered, whether they exhibited a subyearling or yearling migration strategy, and how big they were as they entered the marine environment. Our results indicated that of our sampled adults the Snake River was important for both life-history stages, that yearlings were the prevailing migration strategy, and that considerable overlap in body size existed between yearlings and subyearlings suggesting that spending more time in freshwater (i.e., yearlings) might not result in a larger body size. These findings provide details about the early life history of Snake River fall Chinook salmon, an understanding of which is critical to aid in their management and conservation.

4.1 | Classification rearing and overwintering locations

Current estimates of the spawner abundance for wild Snake River fall Chinook salmon are approximately 2,200 individuals (Cooney
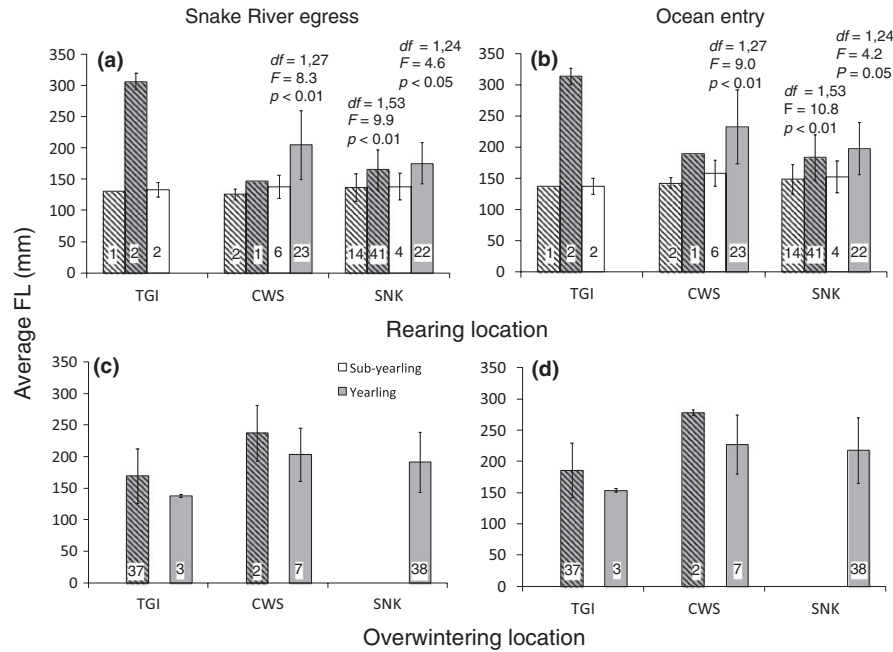
FIGURE 4 Estimates of fall Chinook salmon fork length (mm) with respect to rearing (a and b) and overwintering (c and d) locations, and Snake River egress (a and c) and ocean entry (b and d). Within each plot, fork length is further differentiated between individuals assigned as subyearling (white bars) or yearling (grey bars) migration strategy and between those that are hatchery- (hatched bars) or wild- (solid bars) produced. Classifications to rearing and overwintering locations are based on analyses of $^{87}Sr/^{86}Sr$ ratio (see Section 2). Significant ANOVA results from comparisons between migration strategies, within a location, are indicated with *p* values. Average (bar) and standard deviations (whiskers) are depicted, and sample sizes are indicated within bars. Location abbreviations: Tucannon, Grande Ronde and Imnaha rivers (TGI), Clearwater and Salmon rivers (CWS) and Snake River (SNK)

et al., 2011) with a long-term goal to achieve a population of about 14,000 individuals (Milks et al., 2013). Because of this need to expand the number of individuals returning to spawn, knowing where adults resided as juveniles is important for characterising freshwater habitat qualities that are conducive to growth and survival of viable smolts as well as where mitigation and conservation efforts could be targeted to assist population recovery. Our assessment of where adults resided as juveniles revealed that Snake River was an important location given that it was used as a rearing and overwintering location by most of our sampled returning adults (Table 1). Specifically, 74% and 82% of our adults (i.e., pooled hatchery- and wild-produced) were assigned Snake River as their rearing and overwintering location respectively. Our findings are comparable to those of Hegg, Kennedy, Chittaro, et al. (2013) who reported that 68% and 97% of their presumed wild adults (*n* = 120, consisting of fish collected in 2006, 2007 and 2008 from Lyons Ferry Hatchery in a manner similar to that of this study) reared and overwintered, respectively, in Snake River.

When we categorised our adults as hatchery- or wild-produced, our analyses indicated about half (49%) of our wild-produced fish reared in Clearwater and Salmon rivers and 43% in Snake River, while a high percentage (90%) of our hatchery-produced fish reared in Snake River (Table 1). Importantly, even though the classification success was high of known-origin juveniles as either wild- or hatchery-produced (Heggs, 2017), it was not 100% accurate, and

thus, it was possible that some of our adults were incorrectly assigned as hatchery- or wild-produced. Given the possibility of misassignment, our estimates for wild-produced fish are comparable to what we would expect if the representation of returning adults was proportional to river production. For example, estimates of available spawning habitat in the Snake River watershed indicated that Clearwater and Salmon rivers, Snake River, and Tucannon, Grande Ronde, and Imnaha rivers accounted for 44%, 41% and 15% of this total area, respectively (StreamNet Project, 2012), while spawning surveys from 1991 to 1998 showed that Snake and Clearwater rivers comprised 58% and 27% of the redds, respectively, with 15% found in other areas (Connor et al., 2002). Further, our findings that most of our hatchery-produced fish were assigned Snake River as their rearing location is in agreement with the fact that Lyons Ferry Hatchery, the primary source of hatchery fall Chinook salmon, is located within Snake River, which is reflected in the $^{87}Sr/^{86}Sr$ ratio of its water. Interestingly, Tucannon, Grande Ronde and Imnaha rivers were the overwintering location of most (84%) of our hatchery-produced fish, while none were assigned to the Snake River despite its aforementioned importance as a rearing location (Table 1).

4.2 | Identifying migration strategy

Species recovery is often a complex process that is made more difficult because of gaps in our ecological understanding (Hutchings &

TABLE 2 Top model results from the generalised linear modelling approach investigating the extent to which fork length (i.e., size) at Snake River egress and ocean entry, and somatic growth varied with respect to five variables. Delta AIC is the difference between each model and the model with the lowest AIC. Relative likelihood is the likelihood of a model given the data, and AIC weight is the discrete probability of each model. Coefficient of determination (r^2) is also indicated for each model

Model	AIC	Delta AIC	Relative likelihood	AIC weight	r^2
Size at Snake River egress ~Migration strategy +Rear + Sex [a]	1,194.5	0.00	1.00	0.33	0.31
Size at Snake River egress ~Migration strategy +Rear + Sex +Hatch year	1,195.3	0.84	0.66	0.22	0.33
Size at Snake River egress ~Migration strategy +Rear + Hatch year [a]	1,196.2	1.67	0.44	0.14	0.31
Size at Snake River egress ~Migration strategy +Rear + Sex +Hatchery/Wild	1,196.4	1.87	0.39	0.13	0.31
Size at ocean entry ~Migration strategy +Rear + Hatch year [a]	1,219.4	0.00	1.00	0.27	0.33
Size at ocean entry ~Migration strategy +Rear + Sex [a]	1,219.9	0.56	0.76	0.20	0.32
Size at ocean entry ~Migration strategy +Rear + Hatch year +Hatchery/Wild	1,220.0	0.67	0.72	0.19	0.34
Size at ocean entry ~Migration strategy +Rear + Hatch year +Sex	1,220.8	1.45	0.48	0.13	0.33
Size at ocean entry ~Migration strategy +Rear + Hatchery/Wild +Sex	1,221.2	1.79	0.41	0.11	0.32
Growth ~Migration strategy +Rear + Sex +Hatchery/Wild	985.0	0.00	1.00	0.44	0.17
Growth ~Migration strategy +Rear + Sex [a]	985.2	0.25	0.88	0.39	0.16

[a]Best model.

Reynolds, 2004; Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011). When Snake River fall Chinook salmon was listed as threatened under ESA in 1992, the subyearling migration strategy was regarded as the dominant strategy, and this understanding was reflected in management plans (Pacific Fisheries Management Council, 2014). About a decade later the discovery of the yearling strategy and its relatively high occurrence (Connor et al., 2005) emphasised that rebuilding Snake River fall Chinook salmon would likely require actions to improve survival of both subyearling and yearling migrants (Bourret, Caudill, & Keefer, 2016). Given that traits, like age of maturity, have been shown to be linked to a species' ability to handle anthropogenic effects and environmental variability (Juan-Jordá, Mosqueira, Freire, & Dulvy, 2015; Moore, Yeakel, Peard, Lough, & Beere, 2014), the subyearling and yearling migration strategies could represent an important buffer to changing environmental conditions, and ultimately recovery (Bourret et al., 2016; Moran et al., 2013).

In our study, 79% of the sampled wild adults exhibited the yearling strategy while Hegg, Kennedy, Chittaro, et al. (2013) and Connor et al. (2005) reported 62% and 41% respectively. The large proportion of yearlings reported here and elsewhere confirms the importance of this life-history strategy to the population. It is possible that individuals exhibiting the yearling strategy are taking advantage of large pools of relatively still water (dam-created reservoirs) that provide resources such as prey and shelter, which results in a fitness benefit (Connor et al., 2005). Despite these potential resource advantages, the prevalence of yearlings in our sampled adults is still surprising given that dam operations that improve juvenile passage survival are in operation during the period of time when subyearlings, not yearlings, are migrating. For example, juvenile bypass facilities route fish downstream, away from the dam's powerhouse, and dam operations are modified (e.g., an increase in the release of reservoir water) to facilitate fish passage around dams (Connor et al., 2005). Contrary to the subyearling migration strategy, fish exhibiting the yearling strategy are believed to move downstream in the winter, a time when bypass systems and dam operations that improve passage survival are not in operation (Buchanan, Skalski, & McMichael, 2009; Connor et al., 2005). Does our observation of a relatively large number of fish exhibiting the yearling strategy mean that the seasonal passage improvements for subyearlings are relatively minor when compared to the advantage of overwintering in freshwater? It is possible that these seasonal passage improvements are less important during cooler years assuming that the yearling life history is expressed by a larger proportion of the population during these years. Specifically, Connor et al. (2002) reported that timing of emergence and migration and the percentage of fall Chinook salmon that overwintered were all inversely related to spring water temperature.

We speculate that the cooler water temperatures experienced throughout the region in 2007–2008 might be linked to the higher incidence of yearling fish in our study. From the summer of 2007 until the summer of 2008, a moderate La Nina event occurred

whereby sea surface temperatures were 1–1.5°C lower than average (from monthly ERSST.v4 SST in 5°N-5°S, 120°-170°W; http://www.cpc.ncep.noaa.gov/data/indices/). During this period of time, 85% of our sampled adults hatched (i.e., 4, 103 and 17 fish hatched in 2007, 2008 and 2009 respectively) and these fish experienced water temperatures that were 0.6–2.2°C lower relative to other years (spanning at most from 1994–2016, http://waterdata.usgs.gov/nwis) in the Snake and Clearwater rivers. In contrast, 62% of the fish used in the study by Hegg, Kennedy, Chittaro, et al. (2013) exhibited the yearling migration strategy and hatched from 2002 to 2006, a period that was characterised by weak and moderate El Nino events (defined as 0.5–0.9°C and 1–1.5°C warmer sea surface temperatures respectively). The degree of annual variability in the proportion of adults exhibiting the yearling strategy suggests that the life-history expression and survival are sensitive to water temperature and that more work is needed to better understand the interaction between life-history traits and the environment (Kindsvater, Mangel, Reynolds, & Dulvy, 2016).

4.3 | Body size and growth

Our analysis of body size revealed that wild and hatchery juveniles that went on to exhibit the yearling strategy were 37–62 mm larger at Snake River egress and ocean entry than those that would exhibit the subyearling strategy (Figure 3a,b insets). This finding of larger yearling fish is not surprising if we assume that they overwintered within the Snake River watershed, in which case they would be older than their subyearling counter-parts by the time they exit the Snake River and enter the ocean. But what explains the overlap in size between migration strategies such that 40% of wild yearlings overlapped with subyearlings at Snake River egress, and 35% of individuals overlapped at ocean entry (Figure 3a,b insets)? Further, hatchery fish showed even greater overlap in size, whereby 68% of yearlings overlapped with subyearlings at Snake River egress and 52% of individuals at ocean entry (Figure 3a,b insets). How much of this size overlap is the result of temperature and prey resources not being conducive to growth in the time between when subyearlings and yearlings emigrate (see Connor, Marshall, Bjornn, & Burge, 2001)? Our observation of some subyearlings being larger than yearlings could be explained by the fact that larger juvenile Chinook salmon tend to migrate earlier (Achord, Zabel, & Sandford, 2007; Zabel & Achord, 2004) and/or that some yearlings hatched and emerged later and thus are unable to achieve the same level of growth relative to subyearlings. Further, does this degree of size overlap suggest that, for many yearlings, there may not be a size-related advantage to overwintering in freshwater?

Some of the observed overlap in size between migration strategies could be explained if fish overwintered in the Columbia River downstream of its confluence with Snake River instead of within the Snake River watershed. If fish overwintered below the Snake River, then they would be expected to be about the same size (and age) at Snake River egress relative to subyearlings, yet larger (and older) at ocean entry. Indeed, we observed a decrease in the number of fish

(hatchery or wild) that overlap in size between Snake River egress and ocean entry, but only for a few fish (i.e., 2 and 7 fish respectively). Regardless, the larger body size and the positive relationships between body size and fitness (Kingsolver & Huey, 2008) and survival (Duffy & Beauchamp, 2011; Sogard, 1997; Zabel & Achord, 2004) suggest a mechanism that explains why a substantial proportion of our returning adults exhibited the yearling strategy. In fact, a higher survival probability was estimated for yearlings rather than subyearlings (0.78 vs. 0.64 respectively) during the portion of their juvenile migration between Bonneville Dam, the most downstream impoundment and the mouth of the Columbia River (McMichael et al., 2010).

For many anadromous Pacific salmon, estuarine habitats are viewed as important areas where juveniles rear and grow before completing their physiological transition to a saltwater existence (Fresh, Casillas, Johnson, & Bottom, 2005; Limm & Marchetti, 2009; Sagar et al., 2013; Thorpe, 1994). But several studies have highlighted that some salmonids spend little time in the estuary (e.g., <5 days), and thus, little somatic growth is attributed to estuarine residency (Harnish, Johnson, McMichael, Hughes, & Ebberts, 2012; Hearn et al., 2014; MacFarlane, 2010; MacFarlane & Norton, 2002; Thom, Sather, Roegner, & Bottom, 2013). Moreover, yearlings are thought to be less dependent on the estuarine environment than subyearlings (Thorpe, 1994). Our reconstruction of somatic growth, which occurred between Snake River egress and ocean entry, indicated that both strategies grew similar amounts, with yearlings showing slightly more growth than subyearlings and with wild fish growing slightly more than hatchery fish (Figure 3c inset). Pooling our adults indicated a median growth of 14 mm with a range from 3 to 114 mm (Figure 3c). If we assume a median somatic growth rate of 0.57 mm/day (derived from otoliths of 12 juvenile Snake River fall Chinook salmon collected in the Columbia River estuary; Chittaro et al., 2018), then our adults would have resided approximately 25 days (median; a range of 5–200 days) within the portion of the Columbia River from its confluence with the Snake River downstream to the ocean. Therefore, these estimates of residence time suggest that some fish rapidly move through the Columbia River and estuary in days while others spend weeks to months.

It is important to note that our data are only from individuals that survived to adulthood, and thus may be skewed towards faster growers if there exists such selective pressure (Zabel & Williams, 2002). Another caveat is that size at ocean entry might represent different geographic locations among individuals. Specifically, we calculated size at ocean entry using the otolith radius that related to when an individual entered the ocean (i.e., convergence of $^{87}Sr/^{86}Sr$ ratio from the otolith scan onto the global marine signature of 0.70918; Figure 2). But the geographic location of the isotopic transition from brackish water to ocean water (i.e., 0.70918) will vary temporally depending on tidal height, wind-driven waves, ocean currents, bathymetry, freshwater from land drainage and precipitation (Simenstad et al., 2011). Therefore, depending on where the isotopic transition from brackish water to ocean water occurred as a fish migrated to the ocean, the otolith radius at ocean entry could represent

a different geographic location among fish, which will influence our estimate of size. For example, if two juvenile fish of identical age and somatic growth rate differed only in that one moved through the estuary at high tide versus low tide, then the otolith radius (and thus estimated fish size) at ocean entry of the former would be smaller because of salt water intrusion upriver than the fish moving to the ocean at low tide. Clearly, additional research is required to resolve these issues that limit the use of otoliths from surviving adults as a tool to reconstruct their estuarine residence time and growth.

According to our generalised linear modelling (GLM) approach, variability in both size at Snake River egress and ocean entry was explained by a shared suite of variables (migration strategy and rearing location) with alternative models also including the independent variables of hatch year and sex (Table 2). Ideally, results from the GLM approach would highlight potential mitigation actions that benefit juvenile size and growth in freshwater and estuarine habitats with the goal of improving survival to adulthood. Unfortunately, the results of this study provide little guidance for such actions given that factors identified to be strongly correlated with size and growth were factors for which managers have little control (e.g., migration strategy, hatch year and sex) with the exception of rearing location. And overall the r-squared values were low (0.16–0.34) for the top models (Table 2) suggesting there is a considerable amount of unexplained variability in terms of size and growth.

Because most of our sampled fish were assigned to the Snake River as their rearing or overwintering location, low sample sizes limited our ability to statistically examine patterns of size and growth among rearing and overwintering locations. That being said, wild yearlings that reared and overwintered in Clearwater and Salmon rivers tended to be larger, on average, than those in Snake River (Figure 4a–d). It is possible that the observed larger size of fish that reared and overwintered in the Clearwater and Salmon rivers is related to the cooler water temperatures (average water temperature, in 2008, from 3 sites within the Clearwater River and 2 sites within the Snake River was 9.6°C and 11.1°C, respectively; http://waterdata.usgs.gov/nwis) and resultant lower metabolic demands (Brett, Clarke, & Shelbourn, 1982) or potentially, a combination of factors such as temperature, Chinook density and prey availability (Chittaro, Zabel, Haught, Sanderson, & Kennedy, 2014; Crozier, Zabel, Hockersmith, & Achord, 2010).

Overall, our study highlights some interesting aspects of fall Chinook salmon early life history revealed through the use of microstructural and microchemical analyses of adult otoliths. In particular, because Snake River was used as a rearing and overwintering location by a large proportion of surviving adults, this location appears to be a critical component to population viability. However, a more thorough analysis of the contribution of fish by hatch year will likely provide a greater understanding of the importance of Snake River relative to the Clearwater and Salmon rivers and the importance of climatic events such as La Nina and El Nino. Further, despite fish that exhibited the yearling strategy spending more time in freshwater than subyearlings, both strategies overlapped in size, suggesting that there might not be

a size-related advantage by overwintering. Although, given that our study focused on individuals that survived to return to spawn and that the yearling migration strategy was exhibited by most of our sampled adults, there appears to be a survival advantage for individuals that exhibit the yearling migration strategy. What does the prevalence of yearlings mean for the recovery of wild fall Chinook salmon in the Snake River basin? For example, should hatchery practices release yearlings and subyearlings to ensure adequate representation of both strategies (Connor et al., 2005) or should only subyearlings be cultured given their historical predominance? Future work is needed to better comprehend the factors (e.g., water temperature) and processes (e.g., competition and predation) that influence juvenile size and growth, and to identify the survival advantages of rearing in different habitats and migrating at different times and body sizes for the different life-history strategies.

AUTHORS' CONTRIBUTION

PC, JCH, BPK and RZ conceived and designed the investigation. PC, JCH, LAW, LLJ and CB performed field and/or laboratory work. PC and JCH analysed the data. LAW, LLJ and CB contributed materials, reagents and/or analysis tools. PC, JCH and RZ wrote the paper.

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REFERENCES

Achord, S., Zabel, R. W., & Sandford, B. P. (2007). Migration timing, growth, and estimated parr-to-smolt survival rates of wild snake river spring-summer Chinook salmon from the salmon river basin, Idaho, to the Lower Snake River. *Transactions of the American Fisheries Society*, *136*, 142–154. https://doi.org/10.1577/T05-308.1

Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In B. N. Petrov & F. Csaki (Eds.), *Second international symposium on information theory* (pp. 267–281). Budapest, Hungary: Akademiai Kiado.

Baker, R. R. (1978). *The evolutionary ecology of animal migration.* New York, NY: Holmes & Meier.

Barnett-Johnson, R., Ramos, R. C., Grimes, C. B., & MacFarlane, R. B. (2005). Validation of Sr isotopes in otoliths by laser ablation

multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): Opening avenues in fisheries science applications. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2425–2430.

Bath, G. E., Thorrold, S. R., Jones, C. M., Campana, S. E., McLaren, J. W., & Lam, J. W. H. (2000). Strontium and barium uptake in aragonitic otoliths of marine fish. *Geochimica Et Cosmochimica Acta*, 64, 1705–1714. https://doi.org/10.1016/S0016-7037(99)00419-6

Benaglia, T., Chauveau, D., Hunter, D. A., & Young, D. S. (2009). mixtools: An R package for analyzing finite mixture models. *Journal of Statistical Software*, 32, 1–30.

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

Brett, J. R., Clarke, W. C., & Shelbourn, J. E. (1982). Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 1127, 28.

Buchanan, R. A., Skalski, J. R., & McMichael, G. A. (2009). Differentiating mortality from delayed migration in subyearling fall Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 2243–2255. https://doi.org/10.1139/F09-154

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag.

Campana, S. E. (1999). Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Marine Ecology Progress Series*, 188, 263–297. https://doi.org/10.3354/meps188263

Casselman, J. M. (1987). Determination of age and growth. In A. H. Weatherley & H. S. Gill (Eds.), *The biology of fish growth* (pp. 209–242). London, UK: Academic Press.

Chapman, D. W., Weitkamp, D. E., Welsh, T. L., Dell, M. B., & Schadt, T. H. (1986). Effects of river flow on the distribution of Chinook salmon redds. *Transactions of the American Fisheries Society*, 115, 537–547. https://doi.org/10.1577/1548-8659(1986)115<537:EORFOT>2.0.CO;2

Chittaro, P., Johnson, L., Teel, D., Moran, P., Sol, S., Macneale, K., & Zabel, R. (2018). Variability in the performance of juvenile Chinook salmon is explained primarily by when and where they resided in estuarine habitats. *Ecology of Freshwater Fish*, 27, 857–873.

Chittaro, P. M., Zabel, R. W., Haught, K., Sanderson, B. L., & Kennedy, B. P. (2014). Spatial and temporal patterns of growth and consumption by juvenile spring/summer Chinook salmon *Oncorhynchus tshawytscha*. *Environmental Biology of Fishes*, 97, 1397–1409. https://doi.org/10.1007/s10641-014-0230-2

Connor, W. P., Burge, H. L., Waitt, R., & Bjornn, T. C. (2002). Juvenile life history of wild fall Chinook salmon in the Snake and Clearwater rivers. *North American Journal of Fisheries Management*, 22, 703–712. https://doi.org/10.1577/1548-8675(2002)022<0703:JLHOWF>2.0.CO;2

Connor, W. P., Marshall, A. R., Bjornn, T. C., & Burge, H. L. (2001). Growth and long-range dispersal by wild subyearling spring and summer Chinook salmon in the Snake River basin. *Transactions of the American Fisheries Society*, 130, 1070–1076. https://doi.org/10.1577/1548-8659(2001)130<1070:GALRDB>2.0.CO;2

Connor, W. P., Sneva, J. G., Tiffan, K. F., Steinhorst, R. K., & Ross, D. (2005). Two alternative juvenile life history types for fall Chinook salmon in the Snake River Basin. *Transactions of the American Fisheries Society*, 134, 291–304. https://doi.org/10.1577/T03-131.1

Cooney, R. T., Ford, M. J., Bambrick, D., Berge, D., Chilcote, M. W., Clapp, R., …Tweten, R. (2011). 5 year review: Summary & evaluation of Snake River sockeye, Snake River spring-summer chinook, Snake River fall-run chinook, and Snake River Basin steelhead (P. 65). NOAA Fisheries Report. U.S. Department of Commerce

Crozier, L. G., Hendry, A. P., Lawson, P. W., Quinn, T. P., Mantua, N. J., Battin, J., … Huey, R. B. (2008). Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications*, 1, 252–270.

Crozier, L. G., Zabel, R. W., Hockersmith, E. E., & Achord, S. (2010). Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *Journal of Animal Ecology*, 79, 342–349. https://doi.org/10.1111/j.1365-2656.2009.01641.x

Duffy, J., & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 232–240.

Elsdon, T. S., Wells, B. K., Campana, S. E., Gillanders, B. M., Jones, C. M., Limburg, K. E., … Walther, B. D. (2008). Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions, limitations and inferences. *Oceanography and Marine Biology: An Annual Review*, 46, 297–330.

Faure, G., & Mensing, T. M. (2004). *Isotopes: Principles and applications* (p. 928). Hoboken, NJ: John Wiley & Sons Inc .

Fresh, K. L., Casillas, E., Johnson, L. L., & Bottom, D. L. (2005). Role of the estuary in the recovery of Columbia River basin salmon and steelhead: An evaluation of the effects of selected factors on salmonid population viability. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-69, 105 p.

Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P., & Nohara, S. (2014). Potential effects of hydroelectric dam development in the Mekong River Basin on the migration of siamese mud carp (*Henicorhynchus siamensis* and *H. lobatus*) elucidated by otolith microchemistry. *PLoS ONE*, 9, e103722.

Geist, D. R., Arntzen, E. V., Murray, C. J., McGrath, K. E., Bott, Y. J., & Hanrahan, T. P. (2008). Influence of river level on temperature and hydraulic gradients in chum and fall Chinook salmon spawning areas downstream of Bonneville Dam, Columbia River. *North American Journal of Fisheries Management*, 28, 30–41. https://doi.org/10.1577/M07-009.1

Geist, D. R., Deng, Z., Mueller, R. P., Brink, S. R., & Chandler, J. A. (2010). Survival and growth of juvenile Snake River fall Chinook salmon exposed to constant and fluctuating temperatures. *Transactions of the American Fisheries Society*, 139, 92–107. https://doi.org/10.1577/T09-003.1

Gross, M. R. (1987). Evolution of diadromy in fishes. *American Fisheries Society Symposium*, 1, 14–25.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., … Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319, 948–952. https://doi.org/10.1126/science.1149345

Harnish, R. A., Johnson, G. E., McMichael, G. A., Hughes, M. S., & Ebberts, B. D. (2012). Effect of migration pathway on travel time and survival of acoustic-tagged juvenile salmonids in the Columbia River Estuary. *Transactions of the American Fisheries Society*, 141, 507–519. https://doi.org/10.1080/00028487.2012.670576

Harnish, R. A., Sharma, R., McMichael, G. A., Langshaw, R. B., & Pearsons, T. N. (2014). Effect of hydroelectric dam operations on the freshwater productivity of a Columbia River fall Chinook salmon population. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 602–615. https://doi.org/10.1139/cjfas-2013-0276

Hatten, J. R., Tiffan, K. F., Anglin, D. R., Haeseker, S. L., Skalicky, J. J., & Schaller, H. (2009). A spatial model to assess the effects of hydropower operations on Columbia River fall Chinook Salmon spawning habitat. *North American Journal of Fisheries Management*, 29, 1379–1405. https://doi.org/10.1577/M08-053.1

Hearn, A., Chapman, E., Singer, G., Brostoff, W., LaCivita, P., & Klimley, A. P. (2014). Movements of out-migrating late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts through the San Francisco Bay

Estuary. *Environmental Biology of Fishes*, 97, 851–863. https://doi.org/10.1007/s10641-013-0184-9

Hegg, J. C. (2017). *Movement, migration, and melody: An interdisciplinary study of juvenile salmon ecology through otolith chemistry*. Ph.D. in Water Resources Science and Management, University of Idaho, Idaho, USA. 205 p.

Hegg, J. C., Kennedy, B. P., & Chittaro, P. M. (2018). What did you say about my mother? The complexities of maternally derived chemical signatures in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, in press. https://doi.org/10.1139/cjfas-2017-0341

Hegg, J. C., Kennedy, B. P., Chittaro, P. M., & Zabel, R. W. (2013). Spatial structuring of an evolving life-history strategy under altered environmental conditions. *Oecologia*, 172, 1017–1029.

Hegg, J. C., Kennedy, B. P., & Fremier, A. K. (2013). Predicting strontium isotope variation and fish location with bedrock geology: Understanding the effects of geologic heterogeneity. *Chemical Geology*, 360–361, 89–98.

Hutchings, J. A., & Reynolds, J. D. (2004). Marine fish population collapses: Consequences for recovery and extinction risk. *BioScience*, 54, 297–309. https://doi.org/10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2

Jones, C. M. (1992). Development and application of the otolith increment technique. In D. K. Stevenson & S. E. Campana (Eds.), *Otolith microstructure examination and analysis* (vol. 117, pp. 1–12), *Department of Fisheries and Oceans*. Ottawa, Canada: Canadian Special Publication of Fisheries and Aquatic Sciences.

Juan-Jordá, M. J., Mosqueira, I., Freire, J., & Dulvy, N. K. (2015). Population declines of tuna and relatives depend on their speed of life. *Proceedings of the Royal Society of London B: Biological Sciences*, 282, 1–7. https://doi.org/10.1098/rspb.2015.0322

Kennedy, B. P., Folt, C., Blum, J., & Chamberlain, C. (1997). Natural isotope markers in salmon. *Nature*, 387, 766–767. https://doi.org/10.1038/42835

Kennedy, B. P., Klaue, A., Blum, J. D., Folt, C. L., & Nislow, K. H. (2002). Reconstructing the lives of fish using Sr isotopes in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 925–929. https://doi.org/10.1139/f02-070

Kindsvater, H. K., Mangel, M., Reynolds, J. D., & Dulvy, N. K. (2016). Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution*, 6, 2125–2138. https://doi.org/10.1002/ece3.2012

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, 10, 251–268.

Kuehne, L. M., & Olden, J. D. (2012). Prey naivety in the behavioural responses of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) to an invasive predator. *Freshwater Biology*, 57, 1126–1137. https://doi.org/10.1111/j.1365-2427.2012.02776.x

Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., ... Tetley, M. J. (2014). Migratory marine species: Their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24, 111–127. https://doi.org/10.1002/aqc.2512

Limm, M., & Marchetti, M. (2009). Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. *Environmental Biology of Fishes*, 85, 141–151. https://doi.org/10.1007/s10641-009-9473-8

Lotze, H. K., Coll, M., Magera, A. M., Ward-Paige, C., & Airoldi, L. (2011). Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution*, 26, 595–605. https://doi.org/10.1016/j.tree.2011.07.008

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., ... Jackson, J. B. C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, 312, 1806–1809. https://doi.org/10.1126/science.1128035

MacFarlane, R. B. (2010). Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1549–1565. https://doi.org/10.1139/F10-080

MacFarlane, R. B., & Norton, E. C. (2002). Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. *Fishery Bulletin*, 100, 244–257.

Martin, T. G., Chadès, I., Arcese, P., Marra, P. P., Possingham, H. P., & Norris, D. R. (2007). Optimal conservation of migratory species. *PLoS ONE*, 2, e751.

Mathur, D., Heisey, P. G., Euston, E. T., Skalski, J. R., & Hays, S. (1996). Turbine passage survival estimation for chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 542–549.

McMichael, G. A., Harnish, R. A., Bellgraph, B. J., Carter, J. A., Ham, K. D., Titzler, P. S., & Hughes, S. (2010). *Survival and migratory behavior of juvenile salmonids in the lower Columbia River Estuary in 2009*. Richland, WA: Pacific Northwest National Laboratory.

Milks, D., Grider, A., & Schuck, M. (2013). *Lyons Ferry Hatchery evaluation fall Chinook salmon annual report: 2011* (p. 139). Olympia, WA: Washington Department of Fish and Wildlife.

Moore, J. W., Yeakel, J. D., Peard, D., Lough, J., & Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: Steelhead in two large North American watersheds. *Journal of Animal Ecology*, 83, 1035–1046. https://doi.org/10.1111/1365-2656.12212

Moran, P., Teel, D. J., Banks, M. A., Beacham, T. D., Bellinger, M. R., Blankenship, S. M., ... Smith, C. T. (2013). Divergent life-history races do not represent Chinook salmon coast-wide: The importance of scale in Quaternary biogeography. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 415–435. https://doi.org/10.1139/cjfas-2012-0135

Murray, C. B. (1994). A method for preparing Chinook salmon otoliths for age determination, and evidence of its validity. *Transactions of the American Fisheries Society*, 123, 358–367. https://doi.org/10.1577/1548-8659(1994)123<0358:AMFPCS>2.3.CO;2

Myers, J. M., Kope, R. G., Bryant, G. J., Teel, D., Lierheimer, L. J., Wainwright, T. C., ... Waples, R. (1998). Status review of Chinook salmon from Washington, Idaho, Oregon, and California. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-35, 443 p.

NOAA National Marine Fisheries Service (2017). ESA recovery plan for Snake River fall Chinook salmon (*Oncorhynchus tshawytscha*). (p. 366). West Coast Region, Portland, OR.

Pacific Fisheries Management Council (2014). Review of 2013 ocean salmon fisheries: Stock assessment and fishery evaluation document for the Pacific coast salmon fishery management plan. In *Document prepared for the council and its advisory entities* (p. 381). Portland, OR: Pacific Fishery Management Council

Quinn, T. P. (2005). *The behavior and ecology of Pacific salmon and trout* (p. 378). Seattle, WA: American Fisheries Society and University of Washington Press.

Robinson, R. A., Crick, H. Q. P., Learmonth, J. A., Maclean, I. M. D., Thomas, C. D., Bairlein, F., ... Visser, M. E. (2009). Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, 7, 87–99. https://doi.org/10.3354/esr00095

Ronce, O., Olivieri, I., Clobert, J., & Danchin, E. (2001). Perspectives on the study of dispersal evolution. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 341–357). Oxford, UK: Oxford University Press.

Ruckelshaus, M. H., Levin, P., Johnson, J. B., & Kareiva, P. M. (2002). The Pacific salmon wars: What science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics*, 33, 665–706. https://doi.org/10.1146/annurev.ecolsys.33.010802.150504

Sagar, J. P., Borde, A. B., Johnson, L. L., Corbett, C. A., Morace, J. L., Macneale, K. H., …Jahns, N. D. (2013). Juvenile salmon ecology in tidal freshwater wetlands of the lower Columbia river and estuary: Synthesis of the ecosystem monitoring program, 2005–2010. Prepared by the Lower Columbia Estuary Partnership for the Bonneville Power Administration, April, 2013, Available from the Lower Columbia Estuary Partnership, Portland, OR.

Scheuerell, M. D., Zabel, R. W., & Sandford, B. P. (2009). Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (Oncorhynchus spp.). Journal of Applied Ecology, 46, 983–990.

Simenstad, C. A., Burke, J. L., O'Connor, J. E., Cannon, C., Heatwole, D. W., Ramirez, M. F., … Jones, K. L. (2011). Columbia River estuary ecosystem classification: Concept and application. U.S. Geological Survey Open-File Report 2011-1228, 54 p.

Singer, G., Hearn, A., Chapman, E., Peterson, M., LaCivita, P., Brostoff, W., … Klimley, A. P. (2013). Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss). Environmental Biology of Fishes, 96, 363–379. https://doi.org/10.1007/s10641-012-0037-y

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science, 60, 1129–1157.

Stearns, S. C. (1992). The evolution of life histories. Oxford, UK: Oxford University Press.

Steel, E. A., & Lange, I. A. (2007). Using wavelet analysis to detect changes in water temperature regimes at multiple scales: Effects of multi-purpose dams in the Willamette River basin. River Research and Applications, 23, 351–359. https://doi.org/10.1002/rra.985

Stevenson, D. K., & Campana, S. E. (1992). Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences No. 117, 126 p.

StreamNet Project (2012). Streamnet Generalized Fish Distribution, Fall Chinook. Retrieved from ftp://ftp.streamnet.org/pub/streamnet/gisdata/map_data_biological/StreamNet_FishDist_July2010.zip

Thom, R. M., Sather, N. K., Roegner, G. C., & Bottom, D. L. (2013). Columbia estuary ecosystem restoration program. 2012 synthesis memorandum. Prepared by PNNL and NOAA Fisheries for the Portland District Army Corps of Engineers. 117 p.

Thorpe, J. E. (1994). Salmonid fishes and the estuarine environment. Estuaries, 17, 76–93. https://doi.org/10.2307/1352336

Tiffan, K. F., Erhardt, J. M., & St. John, S. J. (2014). Prey availability, consumption, and quality contribute to variation in growth of subyearling Chinook salmon rearing in riverine and reservoir habitats. Transactions of the American Fisheries Society, 143, 219–229. https://doi.org/10.1080/00028487.2013.839958

Tiffan, K. F., Garland, R. D., & Rondorf, D. W. (2006). Predicted changes in subyearling fall Chinook salmon rearing and migratory habitat under two drawdown scenarios for John Day Reservoir, Columbia River. North American Journal of Fisheries Management, 26, 894–907. https://doi.org/10.1577/M06-018.1

Walther, B. D., & Thorrold, S. R. (2010). Limited diversity in natal origins of immature anadromous fish during ocean residency. Canadian Journal of Fisheries and Aquatic Sciences, 67, 1699–1707. https://doi.org/10.1139/F10-086

Williams, J. G., Zabel, R. W., Waples, R. S., Hutchings, J. A., & Connor, W. P. (2008). Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. Evolutionary Applications, 1, 271–285.

Woodhead, J., Swearer, S., Hergt, J., & Maas, R. (2005). In situ Sr-isotope analysis of carbonates by LA-MC-ICP-MS: Interference corrections, high spatial resolution and an example from otolith studies. Journal of Analytical Atomic Spectrometry, 20, 22–27. https://doi.org/10.1039/b412730g

Young, F. R., & Robinson, W. L. (1974). Age, size, and sex of Columbia River chinook, 1960-69. Fish Commission of Oregon, Data Report Series, report number 4, Clackamas, OR.

Zabel, R. W., & Achord, S. (2004). Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology, 85, 795–806. https://doi.org/10.1890/02-0719

Zabel, R. W., Haught, K., & Chittaro, P. M. (2010). Variability in fish size/otolith radius relationships among populations of Chinook salmon. Environmental Biology of Fishes, 89, 267–278. https://doi.org/10.1007/s10641-010-9678-x

Zabel, R. W., & Williams, J. G. (2002). Selective mortality in Chinook salmon: What is the role of human disturbance? Ecological Applications, 12, 173–183. https://doi.org/10.1890/1051-0761(2002)012[0173:SMICSW]2.0.CO;2