Migration and Spawning Affect the Stable Isotope Values of Multiple Tissues in Pacific Salmon

Kathryn S. Peiman[1,*]
David A. Patterson[2]
Scott G. Hinch[3]
Michael Power[4]
Steven J. Cooke[1]
[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario K1S 5B6, Canada; [2]Fisheries and Oceans Canada, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada; [3]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; [4]Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada

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ABSTRACT

Migration can be energetically demanding for animals, especially when individuals have only one chance to reproduce and rely on stored energy to complete both tasks. We investigated whether protein and fat catabolism, measured by stable isotope values, predicted successful migration and reproduction in semelparous sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, British Columbia. We used stable isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) from adipose fins, blood, and scales sampled upon initial capture to assess an individual's oceanic habitat use; used passive integrated transponders to measure migration timing and success; and then collected isotope samples from the same individuals upon death to assess the level of protein and fat catabolism. We also assessed catabolism in pink salmon (*Oncorhynchus gorbuscha*) using stable isotope values from scales and adipose fins collected at death. We found consistent increases in δ^{13}C over time across sockeye salmon tissues, showing that δ^{13}C values collected from dead fish no longer represent ocean conditions. In contrast, δ^{15}N increased only in adipose tissue of sockeye males and was particularly high in large male pink salmon, likely because of their extreme morphological changes for spawning. Migration time through lakes was related to δ^{13}C, suggesting that males with lower energy reserves spent less time in lakes before spawning, and successful female sockeye spawners had higher δ^{13}C values, suggesting that they catabolized more fat than unsuccessful females. Even though we were unable to link ocean habitat use to migration or reproductive success, we found several patterns of isotopic increases due to protein and lipid catabolism. These findings have implications for reinterpreting past and future studies using stable isotope values collected from migrating or dead salmon and, by extension, other animals.

Keywords: tissue, habitat use, catabolism, morphology, spawning.

Introduction

Carryover effects occur when an individual's previous history affects their current performance (O'Connor et al. 2014). This can occur across different timescales, including across annual cycles (Norris and Taylor 2006), although research linking seasons (e.g., nonbreeding to breeding) and on some taxa (i.e., fishes) is lacking (Marra et al. 2015). While most carryover studies have been carried out at the population level (e.g., birds [Ockendon et al. 2013; Paxton et al. 2014], amphibians [reviewed in Cayuela et al. 2020], insects [Salis et al. 2018], fish [Gosselin et al. 2021]), there is a small but growing literature showing carryover effects at the individual level in fishes (O'Connor et al. 2010; Midwood et al. 2014; Birnie-Gauvin et al. 2021). Carryover effects are important because they mean that the performance of an animal in one situation depends on the conditions it experienced earlier in life (O'Connor and Cooke 2015). However, to accurately interpret these effects, one needs to measure conditions at two points in time by either capturing the same individual in two environments or sampling a tissue that reflects conditions in the previous environment. The latter may be accomplished through the use of stable isotope values.

Pacific salmon (*Oncorhynchus* spp.) are anadromous, with adults migrating to freshwater to spawn and juveniles migrating to sea where they mature. They are also semelparous, with death following their one spawning migration regardless of whether they reproduce. Sockeye salmon (*Oncorhynchus nerka*) typically spend 2 yr in freshwater lakes and 2 yr at sea

*Corresponding author; email: kathryn.peiman@carleton.ca.

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before returning to freshwater to spawn, while pink salmon (*Oncorhynchus gorbuscha*) migrate to sea in their first summer and spend one additional year maturing in the marine environment. While both juvenile freshwater and adult oceanic environments affect body condition and survival of salmon (Bradford 1995; Donaldson et al. 2012; Gosselin and Anderson 2017; Gosselin et al. 2018, 2021; Chasco et al. 2021; Wilson et al. 2021), the nonbreeding ocean environment can exert a major effect on survival for some populations (Gosselin et al. 2021). However, little is known about how ocean conditions carry over to affect the migration timing and reproduction of individuals that survive. The Fraser River system (British Columbia) supports all five North American Pacific salmon species and supports the greatest abundance of these salmon of any river globally (Northcote and Atagi 1997). However, female sockeye salmon in this river have been experiencing abnormally high levels of en route and prespawn mortality over the past few decades under stressful conditions such as low flows and high temperatures (Hinch et al. 2021). While mortalities have been linked to coastal conditions (Hinch et al. 2012), linkages to earlier open-water oceanic conditions in survivors have proved challenging to establish.

Stable isotopes are natural chemical tags in animal tissues primarily accumulated from diet at the time of tissue formation, with carbon stable isotope ($\delta^{13}C$) values being reflective of habitat and nitrogen stable isotope ($\delta^{15}N$) values being reflective of diet (Fry 2006). Tissues with different turnover rates (i.e., metabolically active vs. inert) reflect different past time points, making stable isotopes ideal to use in studies of carryover effects, as sampling the appropriate tissue can give you information about the conditions in earlier environments (Kelly et al. 2008). In marine systems, sea surface temperature is one of the major controllers of dissolved CO_2 concentration, which affects the processes that fractionate carbon isotopes (Espinasse et al. 2022), so that higher sea surface temperatures result in higher $\delta^{13}C$ values (Espinasse et al. 2020). Warmer temperatures in the open ocean have been implicated in reducing body condition in salmon, likely due to reduced ocean productivity (Wells et al. 2006; Burke et al. 2013), so lower $\delta^{13}C$ values should be associated with better body condition. Although $\delta^{13}C$ values can marginally increase across trophic levels, $\delta^{15}N$ values predictably increase much more with each trophic level (Kelly 2000; Fry 2006). High-caloric prey (crustaceans, squid, and fish) have higher $\delta^{15}N$ values than lower-quality prey (Karpenko et al. 2007; Ménard et al. 2014; Espinasse et al. 2020); thus, $\delta^{15}N$ can also be used as a proxy of diet quality. Combined, the two stable isotope values provide an indication of the ecological niche occupied by individuals during the time of tissue formation (Johnson and Schindler 2012; Trueman et al. 2012).

When individuals cease feeding and rely on endogenous energy stores, tissue is catabolized (Navarro and Gutierrez 1995; Vander Zanden and Rasmussen 2001; Vander Zanden et al. 2015), which is essentially an internally driven trophic shift that affects the interpretation of isotope values (Gaye-Siessegger et al. 2004; Hatch 2012; Hertz et al. 2015). Specifically, increases in $\delta^{13}C$ occur when lipids (which are depleted of ^{13}C compared to proteins and carbohydrates) have been used up or when the amino acid substrates for new fatty acids are depleted of ^{12}C. Increases in $\delta^{15}N$ occur when protein is catabolized (as ^{14}N is preferentially excreted over ^{15}N) or when ^{15}N is used for newly built amino acids and proteins (DeNiro and Epstein 1977; Gaye-Siessegger et al. 2004; Hatch 2012; Hertz et al. 2015). Literature reviews suggest that $\delta^{15}N$ increases on average about 0.5‰ as a result of starvation across taxa (Hertz et al. 2015; Doi et al. 2017) while changes in $\delta^{13}C$ are inconsistent in direction and magnitude (Hatch 2012; Hertz et al. 2015; Doi et al. 2017). However, semelparous salmon that migrate long distances use the majority of their energy for migration and spawning (7%–20% of their protein and 60%–86% of their lipids are used during migration alone; Crossin et al. 2004), so we predict that both protein and lipid catabolism will be detectable through isotopic increases in the more metabolically active tissues of salmon during upriver migration. Despite variation among populations in initial somatic energy (8.3–9.8 MJ/kg) and lipids (6.3%–13.6%) for migration, salmon die when they have 3–4 MJ/kg of energy or 2%–3% of lipids remaining (Crossin et al. 2004), suggesting that early or excessive catabolism should affect en route survival or ability to spawn. However, this catabolism may affect our ability to use metabolically active tissues to interpret the conditions at past time points and thus assess carryover effects.

Species- and sex-specific effects can also affect stable isotope ratios. During their spawning migration, adult sockeye salmon cease feeding before reaching the coastal shelf (Morash et al. 2013), but pink salmon continue feeding while in the coastal region (Bower et al. 2011; Sturdevant et al. 2013). Female sockeye salmon also undergo most of their gonadal development in freshwater, while pink salmon are mature upon river entry (Dye et al. 1986; McBride et al. 1986); some pink salmon populations even spawn in intertidal areas (Rousenfell 1958; Helle 1970). Additionally, in both species, males exhibit more extensive changes in secondary sexual traits than females, but the changes in pink salmon are more extreme than those in sockeye salmon. In fact, male pink salmon undergo perhaps the most extreme morphological change of any species of fish, which has even been termed a metamorphosis (Davidson 1935). This morphological development is predicted to be associated with higher levels of protein catabolism (Hendry and Berg 1999). The difference between these two species and between the sexes, therefore, makes an ideal contrast for examining how tissue stable isotope ratios change during the migration and spawning phases because of differences in maturation schedules and morphological changes.

Here, we assess carryover effects from ocean conditions on migration and reproductive success in single populations of sockeye and pink salmon by using $\delta^{13}C$ and $\delta^{15}N$ values derived from less metabolically active scales as a proxy for ocean conditions and those derived from more metabolically active adipose tissue and blood as a proxy for catabolism. We employed a repeated-measures sampling protocol for sockeye salmon, where we sampled individually tagged fish twice (an initial sample near the end of migration and a final sample upon

death), while we sampled pink salmon only upon death. This gave us data on en route survival and migration timing for sockeye and on spawning success and secondary sexual traits for both species. We predicted that sockeye experiencing en route mortality would have higher initial $\delta^{13}C$ values in the less metabolically active tissue (scale) reflective of warmer ocean conditions than successful migrants. We also predicted that sockeye experiencing en route mortality would have higher initial $\delta^{13}C$ and $\delta^{15}N$ values in more metabolically active tissues (adipose fin and blood) driven by early or excessive fat and protein catabolism to fuel migration than successful migrants. For sockeye, we further predicted that individuals with higher energy reserves (reflected in lower initial $\delta^{13}C$ values, higher initial $\delta^{15}N$ values, and larger changes in isotope values) should arrive at spawning grounds earlier (Mathes et al. 2010), pass faster through lakes (Roscoe et al. 2010), and have more time to spawn before death. For both species, we predicted that lower spawning success would be associated with higher initial $\delta^{13}C$ values in less active tissue (scale) and higher initial $\delta^{13}C$ and $\delta^{15}N$ values in more active tissues (adipose fin and blood). For sockeye, we also predicted that only more active tissue (i.e., adipose fin and blood) $\delta^{13}C$ and $\delta^{15}N$ values would increase from the initial to final repeated time points because of the fractionation associated with lipid and protein catabolism, resulting in a mean increase and a positive correlation among individuals for both isotope values. Finally, for both species, we predicted that larger secondary sexual traits (body length, hump depth, upper jaw [hooknose] length) would be associated with higher final $\delta^{15}N$ values and larger changes in isotope values in the more active tissues of males. Because of some unexpected results (see below), we also compiled stable isotope values from the literature for sockeye and pink salmon (table S1, available online) as a thought experiment for exploring the many causes of variation in stable isotopes.

Methods

The Seton River is located 312 km upstream of the mouth of the Fraser River, and the 18-m-high Seton Dam is located approximately 4 km upstream of the confluence of the two rivers (fig. 1). Sockeye salmon were initially trapped from August 19 to 31, 2016, by a fence below the dam and then individually captured using dip nets and transferred to a water-filled V-shaped trough at the edge of the river where tissue samples were collected (for full details, see Bass et al. 2018; Kanigan et al. 2019). We collected initial samples, which consisted of scales (from the upper body below the dorsal fin), a biopsy from the adipose fin (using a hole punch), and blood (from the caudal vasculature with a 21-G needle and 3-mL vacutainer), from a subsample of fish that were then tagged with a passive integrated transponder (PIT) tag and an external spaghetti tag inserted through the musculature behind the dorsal fin. We did not collect muscle samples, as we were interested in repeatable samples and did not want to cause tissue damage that could impact survival. All applicable institutional and national guidelines for the care and use of animals were followed.

Fish had to then pass the dam using the fishway and migrate through Seton and Anderson Lakes, a distance of approximately 45 km, before either entering a closed side channel engineered for spawning (50.547486, −122.483250) or continuing upstream to Gates Creek. PIT arrays detected tagged fish as they exited the fish ladder, exited Anderson Lake, and entered the spawning channel. Only fish that entered the spawning channel were used, as we could not be sure of the fate of fish that ascended the creek. PIT array data were used to calculate en route survival (successful if detected leaving Anderson Lake) and migration time (duration in the lakes and in the spawning channel). We searched the spawning channel each day, collected tagged fish within 24 h of death, collected final samples (scales from the upper body below the dorsal fin, adipose tissue, and blood in a few cases), and took a photograph of each fish to calculate the linear measurements of secondary sexual characteristics (upper jaw length and hump height). Female body cavities were opened to determine spawning success and were recorded as successful (<50% of eggs retained) or unsuccessful (Burnett et al. 2017).

We also collected additional dead fish that had been tagged at Seton Dam for a concurrent study (for those results, see Bass et al. 2018), and these were handled the same way as above except that no initial tissue samples were collected. As they were PIT tagged, migration timing data were available. Other fish that we collected at death were not tagged, and these were used only for determining the relationship between final isotope values and secondary sexual trait size or spawning success. Death and final sample collection of fish occurred from August 31 to September 21, 2016.

Pink salmon were sampled at death only from September 25 to October 6, 2017. They were collected within 24 h of death from an artificial spawning channel (50.670329, −121.972412) just below Seton Dam. As the vast majority of pink salmon do not migrate past the dam or through lakes, this location represented their natural terminal spawning area. The fish were not captured or tagged upon river entry, so we obtained only final tissue and therefore isotope samples at death. We collected scales and an adipose sample and took a photograph to calculate linear measurements as above. Spawning success for females was calculated as above. Stable isotope values for pink salmon scales reported here are the same data as those reported for day 0 in Peiman et al. (2022).

Stable Isotopes

In fish, isotopic turnover rates for whole blood vary widely. Half-lives of 22–200 d have been reported for $\delta^{13}C$ (MacAvoy et al. 2001; Buchheister and Latour 2010; Boecklen et al. 2011; Ankjærø et al. 2012), but turnover seems to be faster (38 d) for $\delta^{15}N$ (Buchheister and Latour 2010). There are no studies on turnover time in adipose fin specifically, but the fatty acid profile of adipose fin is similar to muscle (Young et al. 2014); in general, fin tissue has a $\delta^{13}C$ half-life (~1 mo) that is similar to that of muscle (2–8 wk; Boecklen et al. 2011). However, half-lives of $\delta^{15}N$ values in fin tissue (95 d) and muscle (84 d) may be longer (Busst and Britton 2018). Adipose fins in male sockeye also increase in size during migration (Hendry and Berg 1999), suggesting that adipose may have the faster turnover for $\delta^{13}C$ while blood may have the faster turnover for $\delta^{15}N$. As salmon stop feeding before river entry,

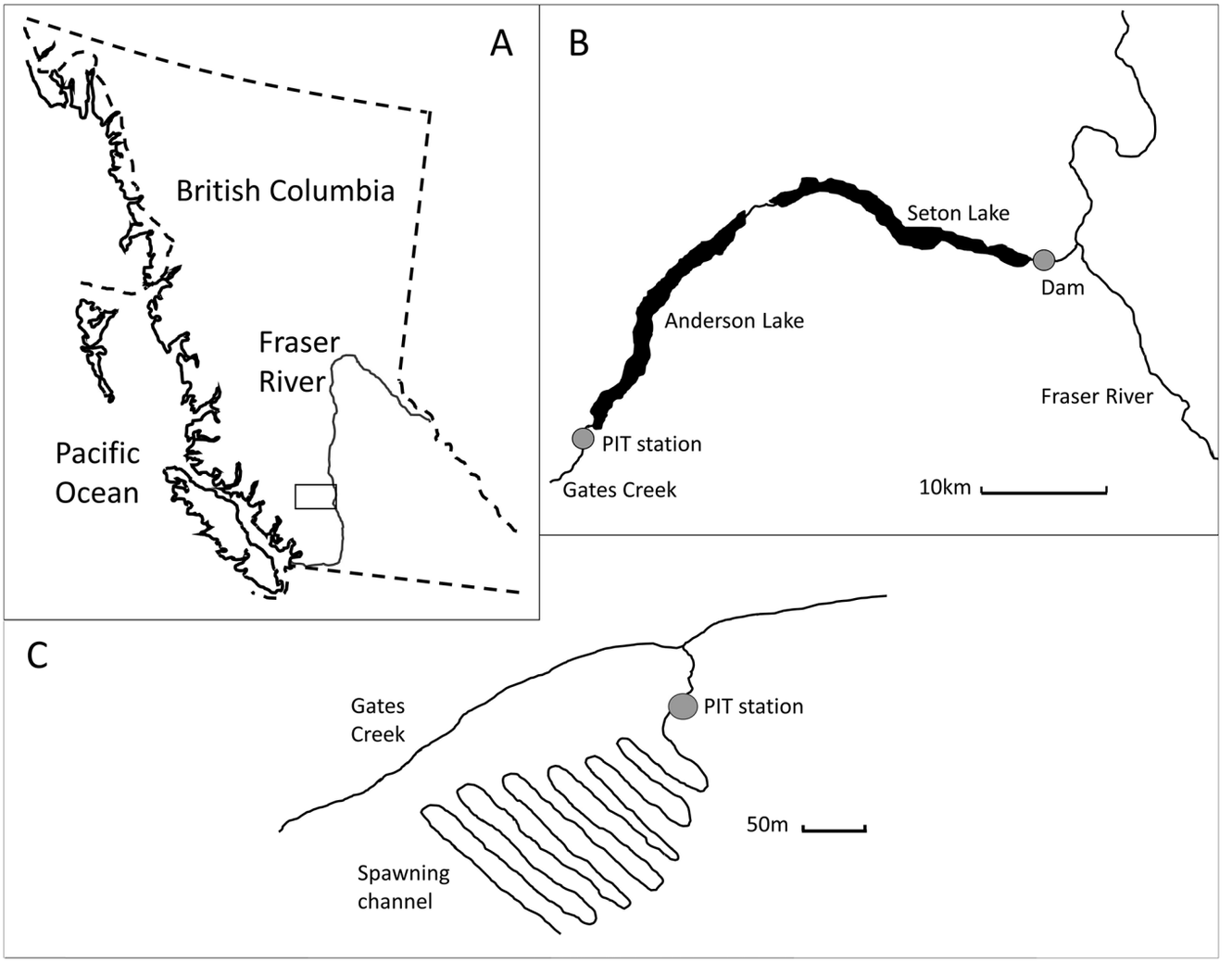

Figure 1. *A*, Box outlines the location of the Anderson-Seton watershed in the Fraser River system, British Columbia. *B*, Seton Dam ("Dam"; where initial sockeye samples were taken) and station for detecting passive integrated transponder (PIT) tags exiting the lake. *C*, Gates Creek spawning channel (where sockeye were collected upon death) and station for detecting tags entering the channel. The distance from exiting Anderson Lake to the spawning channel is approximately 800 m.

scales do not grow (somatic growth has ceased; Tzadik et al. 2017), but they may be chemically altered or physically eroded during migration and spawning (Kacem et al. 2013; Tzadik et al. 2017). Nevertheless, they are still assumed to be less metabolically active and therefore more reflective of ocean conditions than other tissues (adipose fin and blood).

All samples for stable isotope analysis were kept on ice in the field (<12 h), in a chest freezer (−20°C) for <1 mo, and then at −80°C until preparation. We cleaned scales under a dissecting microscope using distilled water, removing all external dirt, fungus, and skin. For sockeye salmon scales, we cut the outermost portion of the scale that represented the last spring/summer at sea (Hutchinson and Trueman 2006; Espinasse et al. 2020) using a microscalpel. However, there were some low sample weights (<0.25 mg) that reduced our sample size for the measurement of $\delta^{15}N$ values. For pink salmon scales, we used the whole scale, which included their 2 yr of life. But because fish scales grow both outwardly and by underplating, these whole-scale isotope values are biased to the last few months of oceanic feeding (Hutchinson and Trueman 2006). Regenerated scales were not used, and all scales were prepared by one person. We note that scale alteration/resorption (mentioned above) may have unknown effects on isotope values (see "Discussion"). Scales were oven-dried at 60°C for 24 h. Whole blood was also oven-dried at 60°C for 28 h.

We did not extract lipids from adipose fin tissue or blood because all C:N ratios were below 4 (Tarroux et al. 2010; for sockeye, mean initial adipose ratio: 3.18 [range: 2.94–3.66]; mean blood ratio: 3.59 [range: 3.34–3.82]) and the validity of general lipid models are still debated given the species and life history specificity of lipid dynamics (e.g., Sheridan 1994; Tocher 2003; Cloyed et al. 2020). Additionally, we were interested in using $\delta^{13}C$ as a proxy for lipid catabolism, so extracting or correcting for lipids would defeat this purpose. We cleaned adipose samples using

distilled water, removing all external dirt and fungus. Adipose samples were oven-dried at 60°C for 48 h.

Dried and homogenized tissues used for stable isotope analysis were weighed into tin capsules using an analytical balance (XP205 DeltaRange, Mettler-Toledo, Greifensee, Switzerland) and subsequently analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Environmental Isotope Laboratory, University of Waterloo, Waterloo, Ontario. Analyses were completed using a Delta Plus continuous-flow stable isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) coupled to an ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA) with a reportable analytical precision of $\pm 0.2‰$ ($\delta^{13}C$) and $\pm 0.3‰$ ($\delta^{15}N$). Machine analytical precision was verified by repeat measurement of internal laboratory standards cross-calibrated against certified International Atomic Energy Agency (IAEA) reference materials, including IAEA-N1 + N2 for $\delta^{15}N$ and IAEA-CH3 + CH6 for $\delta^{13}C$. No less than 20% of samples in any given run were comprised of internal standards or reference materials, with measurements used to assess linearity and mass spectrometer drift throughout the duration of the analytical run. Results are reported in per mill (‰) units against the primary reference scale of Vienna Pee Dee Belemnite for $\delta^{13}C$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}N$ (Mariotti 1983).

Secondary Sexual Traits

We took a photograph of each fish using a Nikon camera mounted on a tripod in the field. We used tpsDig2 (ver. 2.25) to place landmarks on each fish. For sockeye salmon, we defined hump depth as the distance from the anterior insertion point of the dorsal fin to the lateral line. For pink salmon, we defined hump depth as the distance from the maximum hump height to the lateral line (Makiguchi et al. 2017). We also measured upper jaw length from the most anterior part of the premaxilla to the posterior end of the maxilla (Makiguchi et al. 2017). We then extracted these linear measurements using CoordGen8. In addition to these raw (absolute) trait measurements, we regressed each body metric against standard length within each sex to obtain size-corrected (residual) trait values (Reist 1985).

Statistical Analysis

To test whether initial stable isotope values predicted en route mortality from Seton Dam to Gates Creek spawning channel for sockeye salmon, we used a generalized linear model (GLM) with a binomial outcome (successful vs. failed) and sex as a covariate. We included adipose and scale tissue stable isotope values and their interaction with sex. (We did not analyze blood stable isotopes in these fish.) To test whether spawning success affected adipose and scale final isotope values collected at death, we used a GLM with date of death and standard length as covariates. To test whether isotope values changed between sampling points, we used a repeated-measures ANOVA with sex as a covariate plus its interaction with time (sampling point). Using GLMs, we tested whether initial isotope values (adipose, scale, and blood) predicted migration timing (capture date, duration in lakes, and duration in spawning channel) with standard length as a covariate and the interaction of sex with tissue type. We also tested whether secondary sexual traits (standard length, absolute and residual maxilla length, and absolute and residual hump depth) predicted final isotope values (adipose and scale) with death date as a covariate and the interaction of sex with tissue type. Finally, using GLMs, we tested whether two factors predicted the change in isotope values (final value − initial value; denoted as Δadipose and Δscale, respectively): (1) migration timing, with standard length as a covariate and the interaction of sex with migration timing, and (2) secondary sexual traits, with death date as a covariate and the interaction of sex with the sexual trait.

For pink salmon, we tested whether final isotope values predicted secondary sexual traits (standard length, residual maxilla length, and residual hump depth) with death date as a covariate for adipose (as we had adipose samples only from males), but for scales, we also included sex as a covariate and the interaction of sex and scale.

For all models, analyses for $\delta^{13}C$ and $\delta^{15}N$ were run separately (for summary statistics, see table 1). All analyses were conducted in SPSS version 28.0.1.1 (14). To be conservative, we excluded one male sockeye's $\delta^{13}C$ initial scale value, as it was an outlier ($z = -3.2$).

Results

Sockeye Salmon: En Route Mortality

Of the sockeye tagged at Seton Dam for this project, nine (13.4%) failed to successfully migrate past the lakes, while the remaining 58 (86.6%) made it to Gates Creek. Successful migrators did not differ in initial scale or adipose stable isotope values (for $\delta^{13}C$, all model effects $P \geq 0.087$; for $\delta^{15}N$, all model effects $P \geq 0.11$) from those that died en route.

Sockeye and Pink Salmon: Spawning Success

Of the female sockeye that successfully migrated and for which we had initial samples, only three (12.5%) failed to spawn, leaving an insufficient sample size to test whether initial isotope values predicted spawning success. However, in female sockeye, we could test whether final scale and adipose stable isotope values (collected at death) were associated with spawning success as a result of our larger sample at this time point (table 1). Final scale $\delta^{13}C$ values were higher in successful females than in failed females ($F_{1,44} = 4.563$, $P = 0.038$; all other model effects $P \geq 0.190$), whereas the final scale $\delta^{15}N$ values did not differ (all model effects $P \geq 0.180$; table 1). Final adipose $\delta^{13}C$ values were also higher in successful females than in failed females ($F_{1,37} = 20.362$, $P < 0.001$; all other model effects $P \geq 0.064$), whereas the final adipose $\delta^{15}N$ values did not differ (all model effects $P \geq 0.714$).

For pink salmon, most spawned (23 of 26; 88%), so there were too few failed spawners to allow appropriate statistical analysis.

Table 1: Average, range, and *n* of stable isotope values for pink and sockeye salmon collected at death on the spawning ground or before passage over Seton Dam in the Seton River, British Columbia

Species sample, sex, statistic	Scale $\delta^{13}C$	Scale $\delta^{15}N$	Adipose $\delta^{13}C$	Adipose $\delta^{15}N$	Blood $\delta^{13}C$	Blood $\delta^{15}N$
Pink salmon final:						
Male:						
Average ± SD	−17.07 ± .74	11.65 ± .71	−19.14 ± .99	13.18 ± .73	NA	NA
Range	−18.13 to −14.52	10.62 to 13.78	−20.63 to −17.61	11.95 to 14.83	NA	NA
n	33	33	12	12	NA	NA
Female (spawned):						
Average ± SD	−17.17 ± .59	11.28 ± .59	NA	NA	NA	NA
Range	−18.21 to −16.06	10.15 to 12.25	NA	NA	NA	NA
n	22	22	NA	NA	NA	NA
Female (failed):						
Average ± SD	−16.26 ± 1.54	11.96 ± .72	NA	NA	NA	NA
Range	−17.07 to −14.83	11.54 to 12.79	NA	NA	NA	NA
n	3	3	NA	NA	NA	NA
Sockeye salmon initial:						
Male:						
Average ± SD	−19.15 ± .66	10.09 ± .63	−20.48 ± .48	11.00 ± .40	−22.33 ± .42	10.16 ± .51
Range	−20.27 to −18.00	8.74 to 11.26	−21.26 to −19.43	10.11 to 12.28	−22.91 to −21.35	9.05 to 11.15
n	25	21	27	27	15	15
Female:						
Average ± SD	−19.14 ± .66	9.82 ± .59	−20.38 ± .58	10.55 ± .37	−22.20 ± .38	10.32 ± .46
Range	−20.65 to −18.09	9.02 to 11.38	−21.81 to −19.31	9.99 to 11.52	−22.90 to −21.30	9.65 to 10.98
n	22	21	28	28	16	16
Sockeye salmon final:						
Male:						
Average ± SD	−18.65 ± .37	10.36 ± .66	−19.58 ± .46	11.38 ± .59	NA	NA
Range	−19.36 to −17.63	8.54 to 11.62	−20.48 to −18.65	10.51 to 12.86	NA	NA
n	24	24	17	18	NA	NA
Female (spawned):						
Average ± SD	−18.73 ± .41	9.92 ± .54	−19.20 ± .30	10.85 ± .53	−21.56 ± .47	10.23 ± .27
Range	−19.65 to −17.84	8.89 to 11.12	−19.70 to −18.57	9.83 to 11.92	−22.09 to −21.21	10.00 to 10.53
n	32	32	23	22	3	3
Female (failed):						
Average ± SD	−19.06 ± .42	9.67 ± .55	−19.84 ± .44	10.79 ± .39	−21.04	10.45
Range	−19.61 to −18.25	8.95 to 10.65	−20.88 to −18.96	10.23 to 11.59	NA	NA
n	16	16	18	18	1	1

Note. Carbon stable isotope ($\delta^{13}C$) and nitrogen stable isotope ($\delta^{15}N$) values for pink salmon are from 2017, and those for sockeye salmon are from 2016. For females, data are grouped by successful (spawned) and unsuccessful (failed) spawners. "Initial" refers to samples collected at Seton Dam; "final" refers to samples collected at death. NA = not available.

Sockeye Salmon: Migration Timing

In support of our prediction, sockeye with lower initial blood $\delta^{13}C$ values were captured earlier than those with higher initial blood $\delta^{13}C$ values ($F_{1,23} = 5.49$, $P = 0.019$; all other model effects $P \geq 0.86$; fig. 2*A*); capture date was not related to initial $\delta^{15}N$ values in either sex (all $P \geq 0.157$). In contrast to our prediction, sockeye with higher initial blood $\delta^{13}C$ values migrated through the lake faster than those with lower initial blood $\delta^{13}C$ values ($F_{1,23} = 7.90$, $P = 0.005$; fig. 2*B*). Male sockeye with higher initial scale $\delta^{13}C$ values migrated through the lake faster, while females did not exhibit such a relationship (sex × scale $\delta^{13}C$: $F_{1,31} = 6.14$, $P = 0.013$; sex: $F_{1,31} = 6.12$, $P = 0.013$; scale $\delta^{13}C$: $F_{1,31} = 5.76$, $P = 0.016$; fig. 3). Duration in the lakes was not related to initial $\delta^{15}N$ values for any tissue in either sex (all model effects $P \geq 0.15$). Duration in the spawning channel was not related to initial $\delta^{13}C$ (all model effects $P \geq 0.21$) or initial $\delta^{15}N$ (all model effects $P \geq 0.20$) values for any tissue.

Capture date was negatively related to Δscale $\delta^{13}C$ values in males but not in females (table 2; fig. 4*A*). Duration in the lakes was positively related to Δadipose $\delta^{13}C$ values, regardless of sex (table 2; fig. 4*B*). Duration in the spawning channel was positively related to Δscale $\delta^{15}N$ values in males but not in females (table 2; fig. 4*C*). No other relationships between migration timing and Δ isotope values were significant in any other tissue, although sexes differed in some Δ isotope values (table 2).

Sockeye Salmon: Sampling Time (Initial to Final Values)

Adipose stable isotope values increased over the period from initial capture until death (figs. 5, 6), but the effect depended on sex (table 3). For $\delta^{13}C$, female adipose values increased more than male adipose values; for $\delta^{15}N$, male adipose values increased, whereas female adipose values did not change. Scale and blood $\delta^{13}C$ values also increased with time, whereas $\delta^{15}N$ values for these tissues did not (table 3).

Initial and final values for scale $\delta^{15}N$ and adipose $\delta^{15}N$ and $\delta^{13}C$ were significantly positively correlated for both sexes, and blood $\delta^{15}N$ values were significantly positively correlated for females (no samples were analyzed for males; $R^2 = 0.46–0.98$), while scale $\delta^{13}C$ values in either sex and blood $\delta^{13}C$ values (in females) were not correlated (table 4).

Sockeye and Pink Salmon: Sexual Traits

Longer ($F_{1,50} = 5.17$, $P = 0.023$; fig. 7*A*) and deeper ($F_{1,43} = 5.672$, $P = 0.022$; fig. 7*B*) sockeye (no effect of sex) had lower final adipose $\delta^{13}C$ values (all other model effects $P \geq 0.11$). There were no other significant correlations between morphology and final stable isotope values in any other tissue (all model effects $P \geq 0.056$). Absolute maxilla length was negatively related to Δadipose $\delta^{13}C$ values, but this was driven by differences in sex (as males had larger maxillaries and larger changes in isotope values; fig. 8*A*). Residual maxilla length was positively related to Δadipose $\delta^{13}C$ values (table 5; fig. 8*B*). There were no other significant correlations between morphology and Δ stable isotope values in any other tissue, although sexes differed in some Δ isotope values (table 5).

Pink salmon final scale $\delta^{15}N$ and $\delta^{13}C$ values were not associated with body length, residual upper jaw, or residual hump depth in either males or females (all $P > 0.106$). In males, body length was correlated with final adipose $\delta^{15}N$ values ($F_{1,9} = 6.327$, $P = 0.033$) but not final adipose $\delta^{13}C$ values ($F_{1,9} = 0.703$, $P = 0.423$).

Discussion

Our goal was to assess carryover effects from ocean conditions on migration and reproductive success in salmon, but some surprising results led us to conclude that we could not test the hypothesis as originally intended. Instead, only a subset of our data was from tissues that had slow enough turnover rates to assess carryover effects (scale $\delta^{15}N$ and blood $\delta^{13}C$, similar to other studies; MacAvoy et al. 2001; Boecklen et al. 2011; Buss and Britton 2018). While we did not find any relationship between initial scale $\delta^{15}N$ values (reflecting oceanic diet) and survival of migrating sockeye, we did find that sockeye with lower initial blood $\delta^{13}C$ values (possibly reflecting cooler oceanic conditions) arrived earlier, although tissue catabolism also remains a possible explanation for the latter relationship. Testing carryover effects requires having tissue samples that reflect the diet and habitat of when that tissue was formed without additional confounding effects acting to alter the isotope value, and our study highlights the challenges of knowing when this requirement is met.

Scales from dead salmonids are regularly used in research (for references, see table S1) and are inert once the fish is dead (Peiman et al. 2022). As scale growth should cease at river entry (because somatic growth ceases; Tzadik et al. 2017), we predicted that final scale stable isotope values from fish on the spawning grounds would not differ from samples earlier in migration, so they would still reflect ocean conditions. Yet we found that mean scale $\delta^{13}C$ values increased between initial and final collection, a time span of less than 1 mo, indicating that scales were being altered chemically or by erosion during migration. Salmon resorb their scales during spawning, which can result in the erosion of material especially at the outer edges and/or molecular changes (Kacem et al. 2013; Tzadik et al. 2017). For example, female salmon resorb calcium from scales for the development of their ovaries and vitellogenesis (Mugiya and Watabe 1977; Carragher and Sumpter 1991; Persson et al. 1998), while males extract mineral and organic compounds for secondary trait development (Kacem et al. 2013). As scale $\delta^{13}C$ was not correlated between initial and final sockeye samples, resorption did not occur in a predictable way among individuals. In fact, some individuals had slightly lower final $\delta^{13}C$ values (by <0.5‰). Although scales have lipids (Grahl-Nielsen and Glover 2010), to the best of our knowledge it has not been shown that these are mobilized by fish, although this was the assumed mechanism when higher scale $\delta^{13}C$ values and lower C:N ratios were measured in spawned sockeye than in prespawn sockeye in Alaska (Doson Coll 2015). Yet other studies have assumed

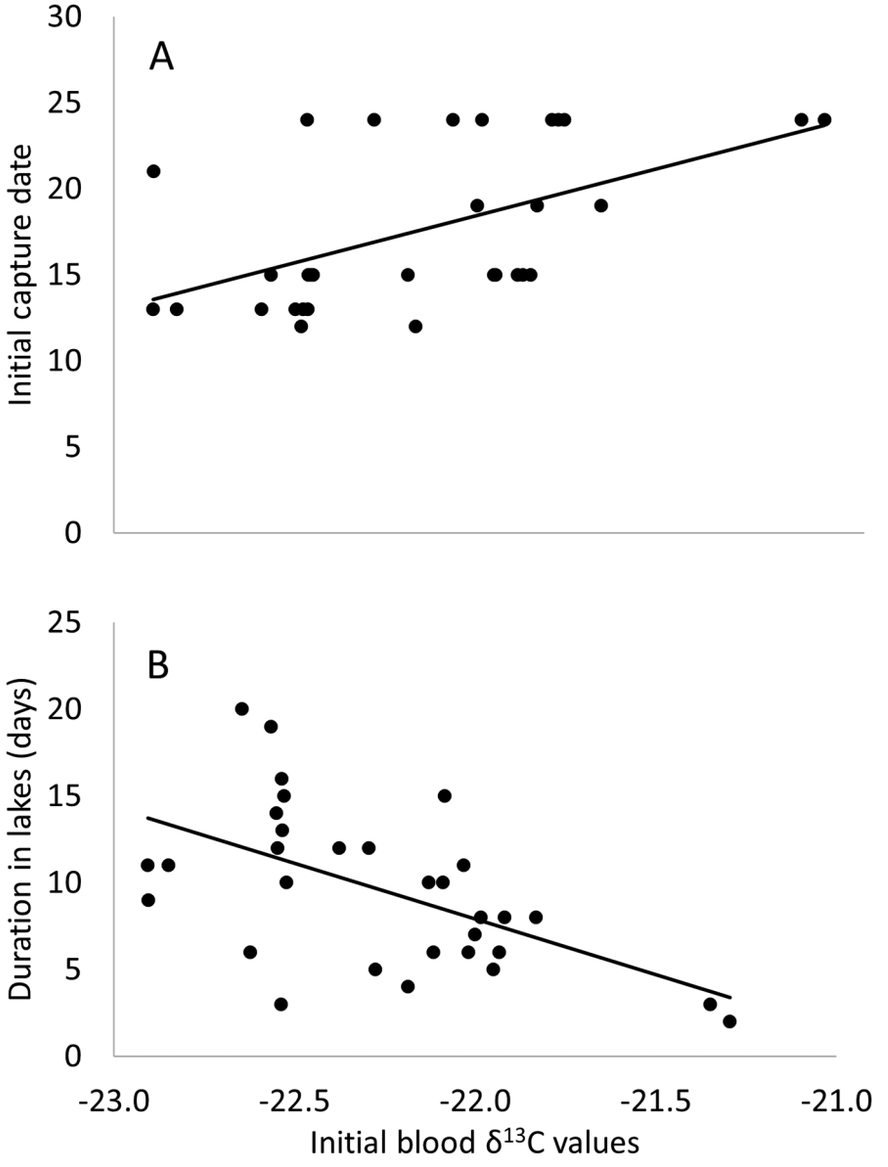

Figure 2. Initial blood carbon stable isotope ($\delta^{13}C$) values of sockeye (collected at Seton Dam) in relation to the date they were captured (i.e., when samples were taken) and released at Seton Dam (where 1 on the *y*-axis represents August 8; *A*) and the number of days they spent in the lakes (*B*). There was no effect of sex, so sexes were combined. Lines are least squares linear regressions.

(without testing) that the amount of scale lipid is too small to affect stable isotope values (Espinasse et al. 2019). However, fatty acid levels in scales can change after just 5 d of starvation (Grahl-Nielsen and Glover 2010), so it is possible that fish mobilized the small amount of fatty acids from scales (4.5–5.5 μg/mg; Grahl-Nielsen and Glover 2010) for use during the last stages of migration and/or spawning.

We also found that successful female sockeye spawners had higher final scale $\delta^{13}C$ values than those that failed to spawn, suggesting that they started with higher scale $\delta^{13}C$ values (reflecting warmer oceanic conditions), that the outside edge of the scale was resorbed and the inner portion of the annulus had a different average value, that scale lipids were mobilized for use in final egg maturation or spawning ground interactions, or that $\delta^{13}C$ values increased through the preferential removal of ^{12}C over ^{13}C from scales (although we did not find any literature showing that this occurs). As successful females also had higher adipose $\delta^{13}C$ values, we believe scale resorption is a less likely explanation. Regardless of the mechanism, our results show that scale samples collected during migration may no longer reflect the same time-averaged conditions as samples collected in the ocean and that scales collected on the spawning ground definitely do not, at least where $\delta^{13}C$ is concerned. In contrast, scale $\delta^{15}N$ values did not change over time, a result also found at the population level when comparing pre- and postspawn sockeye scales in Alaska (Doson Coll 2015). Furthermore, our

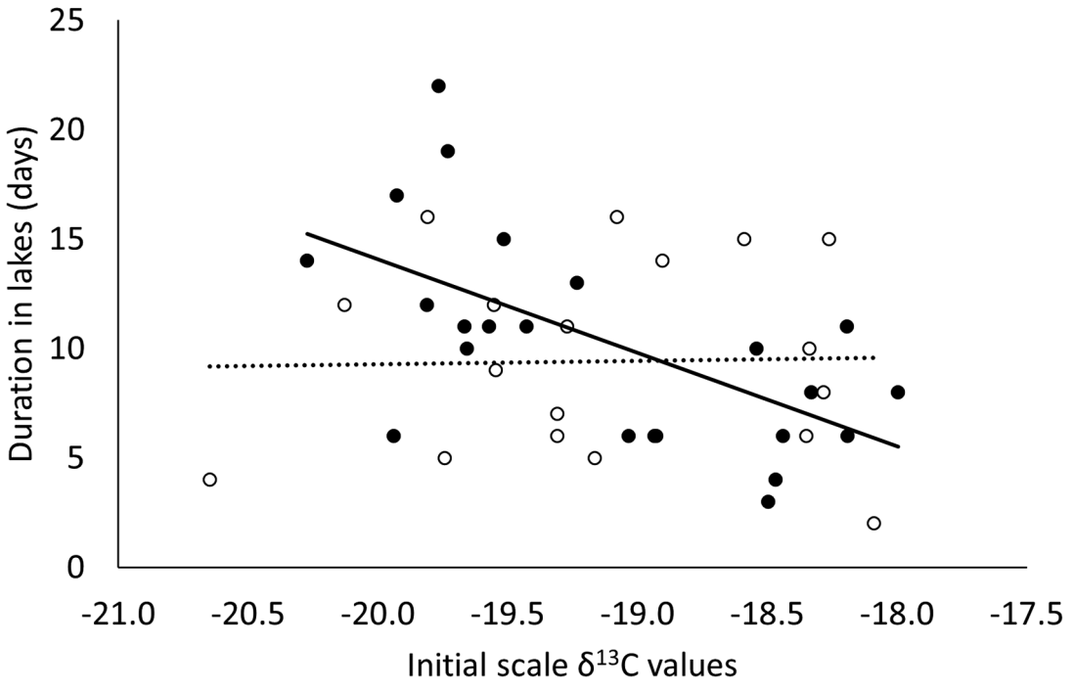

Figure 3. Number of days individual sockeye took to migrate through two lakes in relation to their initial scale carbon stable isotopes ($\delta^{13}C$) values collected at Seton Dam for males (filled circles, solid line) and females (open circles, dotted line). Lines are least squares linear regressions.

sockeye $\delta^{15}N$ values were strongly correlated between sampling points, suggesting that scale resorption does not alter $\delta^{15}N$ values through the preferential depletion of ^{14}N, as has been hypothesized by Guiry and Hunt (2020). Increases in $\delta^{13}C$ over the migration period have major implications for studies that have used archival scales from migrating or spawned-out fish to reconstruct oceanic history, as alteration of scales by biological or erosional processes could lead to erroneous conclusions about oceanic temperatures (e.g., Welch and Parsons 1993; Johnson and Schindler 2012; Espinasse et al. 2020).

En route mortality is a major concern for sockeye salmon stocks in the Fraser River (reviewed in Patterson et al. 2016). We assumed that scale $\delta^{13}C$ values would reflect ocean conditions (sea surface temperature), letting us use these values as a proxy to determine whether oceanic conditions affected migration success. As described above, however, the increase in scale $\delta^{13}C$ values in sockeye between our two sampling points means that even our initial samples (collected just after sockeye left the Fraser River and entered their natal stream) may have changed, making this prediction untestable. In contrast, scale $\delta^{15}N$ values were consistent, but we did not find any relationship between initial scale $\delta^{15}N$ values (reflecting oceanic diet) and survival of migrating sockeye. While passage over Seton Dam via the fishway requires burst swimming (Pon et al. 2009), the rest of the migration is through lakes, so it is less metabolically challenging. This may be why successful dam passage is more closely tied to other metrics, such as injury (Bass et al. 2018) and physiological capacity (Roscoe et al. 2011; Minke-Martin et al. 2018), that may affect burst swimming and anaerobic activity over the dam (Burnett et al. 2014) than to past diet (initial scale $\delta^{15}N$ values) or current levels of protein and lipid catabolism (initial adipose $\delta^{13}C$ and $\delta^{15}N$ values).

For sockeye that did survive, we found that individuals with higher initial blood $\delta^{13}C$ values were captured later. If initial blood $\delta^{13}C$ values still reflect ocean conditions (based on a ~1-wk coastal migration [Crossin et al. 2007] and average 11-d in-river migration [Eliason et al. 2011] and that blood $\delta^{13}C$ values can have a half-life of 100 d [Boecklen et al. 2011]), later-arriving individuals may have occupied a warmer location in the ocean. Alternatively, if blood turnover is faster, late individuals may have catabolized more fat during their upriver migration. We also found that late-arriving male sockeye had smaller increases in scale $\delta^{13}C$ values before death, suggesting that they were closer to their terminal energy threshold than earlier males. Other studies also show that late-arriving fish have less energy (Mathes et al. 2010), although these fish may be either less (Roscoe et al. 2010; Hinch et al. 2012) or more (Mathes et al. 2010) reproductively advanced. Regardless of capture date, we also found that all sockeye with higher initial blood $\delta^{13}C$ values and male sockeye with higher initial scale $\delta^{13}C$ values migrated through the lakes faster and that sockeye that migrated through the lakes faster had a smaller increase in their adipose $\delta^{13}C$ values before death. Since early migrants typically hold in lakes (Hinch et al. 2012; Minke-Martin et al. 2018), our results suggest that lipid-depleted sockeye (due to warmer and therefore poorer ocean conditions or to excessive catabolism) arrive later and move through lakes faster.

Table 2: Generalized linear models analyzing the effects of migration timing on the change in stable isotope values for sockeye salmon from the Seton River, British Columbia

Model, stable isotope value change, effect	*F*	df	*P*
Duration in lakes:			
ΔAdipose δ^{13}C:			
Sex × migration timing	.91	1, 18	.34
Migration timing	**4.51**	**1, 19**	**.034**
Sex	6.8	1, 19	.009
ΔAdipose δ^{15}N:			
Sex × migration timing	.64	1, 20	.51
Migration timing	.44	1, 21	.51
Sex	5.91	1, 21	.015
ΔScale δ^{13}C:			
Sex × migration timing	3.58	1, 26	.059
Migration timing	.82	1, 27	.37
Sex	.004	1, 27	.95
ΔScale δ^{15}N:			
Sex × migration timing	.2	1, 22	.66
Migration timing	.047	1, 23	.83
Sex	.02	1, 23	.89
Duration in spawning channel:			
ΔAdipose δ^{13}C:			
Sex × migration timing	2.81	1, 18	.094
Migration timing	.34	1, 19	.53
Sex	5.02	1, 19	.025
ΔAdipose δ^{15}N:			
Sex × migration timing	.76	1, 20	.38
Migration timing	<.01	1, 21	.99
Sex	5.56	1, 21	.018
ΔScale δ^{13}C:			
Sex × migration timing	1.27	1, 26	.27
Migration timing	3.66	1, 27	.056
Sex	.42	1, 27	.87
ΔScale δ^{15}N:			
Sex × migration timing	**8.32**	**1, 22**	**.004**
Migration timing	1.74	1, 22	.19
Sex	8.34	1, 22	.004
Capture date:			
ΔAdipose δ^{13}C:			
Sex × migration timing	.66	1, 18	.42
Migration timing	2.47	1, 19	.12
Sex	5.5	1, 19	.019
ΔAdipose δ^{15}N:			
Sex × migration timing	.81	1, 20	.37
Migration timing	.82	1, 21	.37
Sex	6.44	1, 21	.011
ΔScale δ^{13}C:			
Sex × migration timing	**4.82**	**1, 26**	**.028**
Migration timing	.87	1, 26	.35
Sex	4.1	1, 26	.043
ΔScale δ^{15}N:			
Sex × migration timing	.003	1, 22	.95
Migration timing	.02	1, 23	.89
Sex	.017	1, 23	.90

Note. Change (Δ) in carbon stable isotope (δ^{13}C) and nitrogen stable isotope (δ^{15}N) values is calculated as the final value minus the initial value. The interaction effect was removed and the model was rerun if it was not significant. Significant effects of interest are shown in bold.

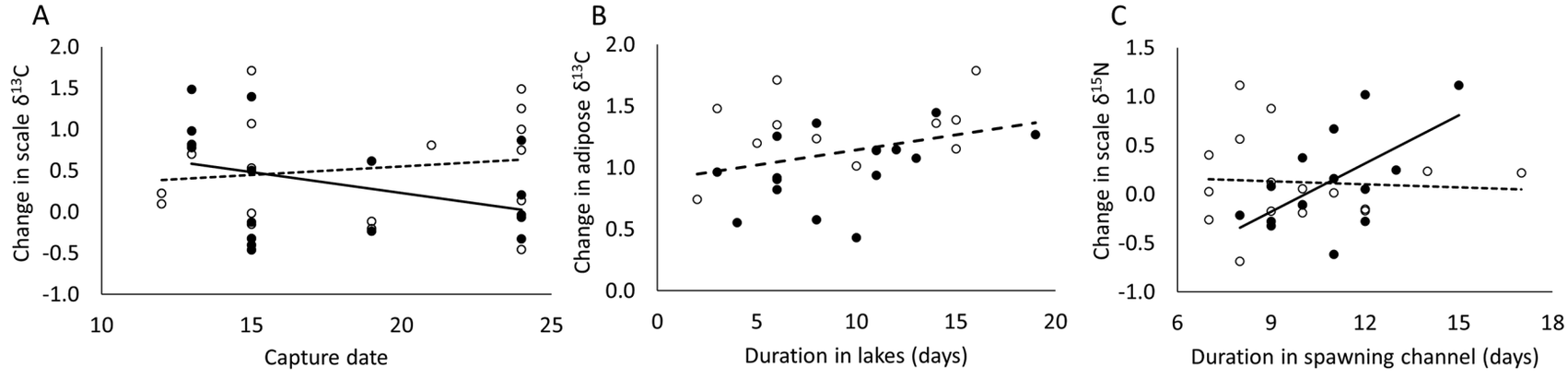

Figure 4. *A*, Capture date (where 1 on the *x*-axis represents August 8) predicts the change in scale carbon stable isotope ($\delta^{13}C$) values in male sockeye but not female sockeye. *B*, Number of days individual sockeye took to migrate through two lakes predicts the change in $\delta^{13}C$ values for adipose tissue regardless of sex. *C*, Number of days individual sockeye were in the spawning channel predicts the change in scale nitrogen stable isotope ($\delta^{15}N$) values in males but not females. Males are indicated by filled circles, and females are indicated by open circles. For *A* and *C*, males are represented by solid lines, and females are represented by dashed lines; lines are least squares linear regressions for each sex. For *B*, the least squares linear regression is for sexes combined.

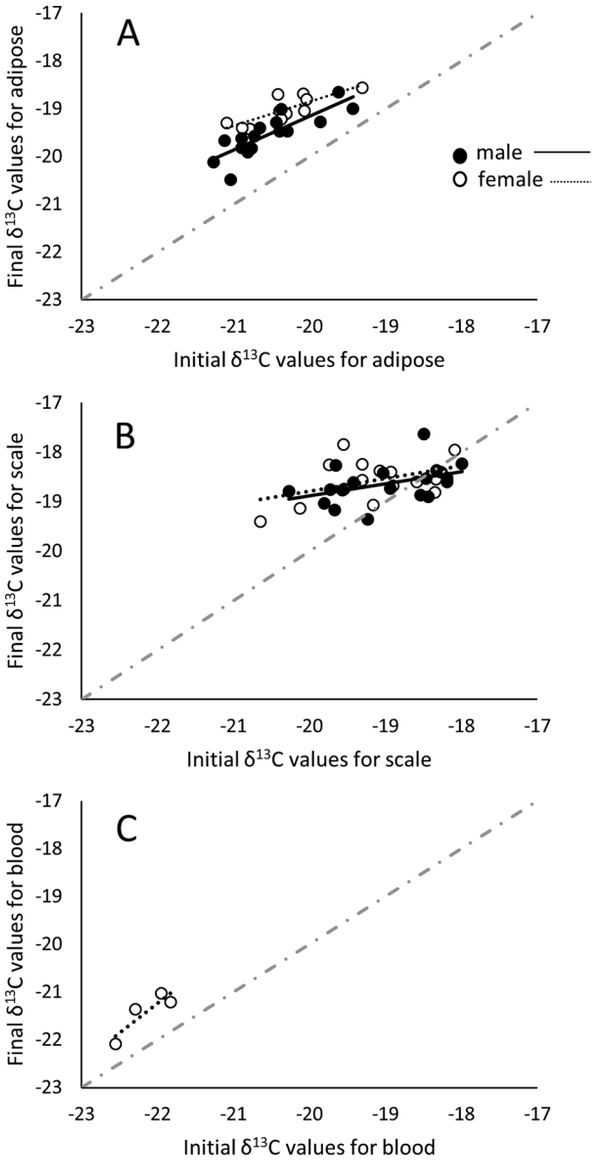

Figure 5. Initial (Seton Dam) and final (at death) paired carbon stable isotope ($\delta^{13}C$) values for sockeye salmon. *A*, Adipose samples. *B*, Scale samples. *C*, Blood samples. For each, males are indicated by filled circles and solid lines, and females are indicated by open circles and dotted lines; lines are least squares linear regressions. The *x*- and *y*-axis scales were kept the same for all panels to show tissue offsets. The 1 : 1 line of no change is represented by the dash-dot line.

The relationships between morphology and final isotope values likely reflect the effects of catabolism and tissue reorganization. We found a negative relationship between final $\delta^{13}C$ in adipose tissue and body length in sockeye, similar to the negative relationship found between $\delta^{13}C$ in red blood cell tissue and body length in sockeye (K. Birnie-Gauvin, K. S. Peiman, D. A. Patterson, K. A. Robinson, M. Power, S. G. Hinch, and S. J. Cooke, unpublished manuscript). This could result from smaller fish being less energy efficient and relying more on anaerobic metabolism, requiring the catabolism of more lipids than larger individuals during migration and reproduction (Johnson and Schindler 2012). Larger fish also have more energy available per unit of mass during breeding than smaller fish (Hendry et al. 1999). However, Satterfield and Finney (2002) found no relationship between $\delta^{13}C$ and sockeye length, although their samples were from fish on arrival to the spawning grounds after a short river migration (50 km). Our results for pink salmon showed no relationship between $\delta^{13}C$ and body length, possibly because they are more efficient swimmers than sockeye salmon (Crossin et al. 2003). In sockeye, both hump depth and maxillary length

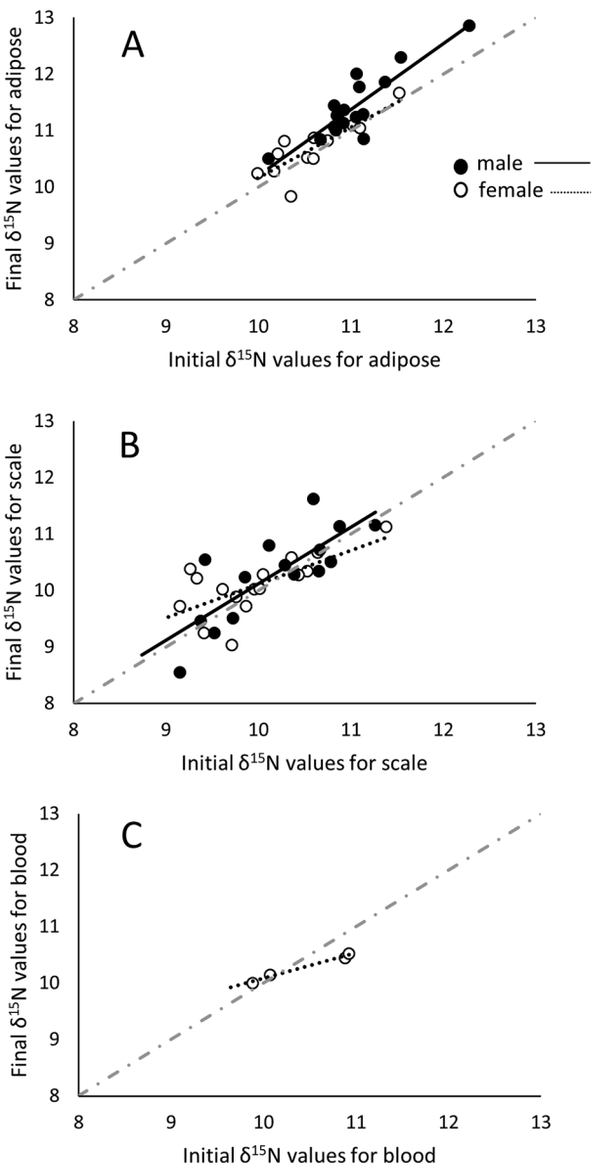

Figure 6. Initial (Seton Dam) and final (at death) paired nitrogen stable isotope ($\delta^{15}N$) values for sockeye salmon. *A*, Adipose samples. *B*, Scale samples. *C*, Blood samples. For each, males are indicated by filled circles and solid lines, and females are indicated by open circles and dotted lines; lines are least squares linear regressions. The *x*- and *y*-axis scales were kept the same for all panels to show tissue offsets. The 1 : 1 line of no change is represented by the dash-dot line.

Table 3: Results of repeated-measures ANOVAs, with sex and sampling time as covariates, of sockeye salmon from the Seton River, British Columbia

Tissue and stable isotope type, effect	F	df	P
Adipose $\delta^{13}C$:			
Time	17.36	1, 25	**<.001**
Sex	4.24	1, 25	**.05**
Sex × time	7.48	1, 25	**.011**
Adipose $\delta^{15}N$:			
Time	20.209	1, 27	**<.001**
Sex	10.12	1, 27	**.0037**
Sex × time	6.82	1, 27	**.015**
Scale $\delta^{13}C$:			
Time	16.66	1, 33	**<.001**
Sex	.002	1, 33	.96
Sex × time	.54	1, 33	.47
Scale $\delta^{15}N$:			
Time	2.1	1, 29	.16
Sex	.93	1, 29	.34
Sex × time	.0008	1, 29	.98
Blood $\delta^{13}C$:			
Time	40.628	1, 3	**.008**
Blood $\delta^{15}N$:			
Time	1.102	1, 3	.371

Note. Time had two points: initial and final. Sex and sampling point are covariates for all tissue and stable isotope types except blood. Statistically significant P values are shown in bold. $\delta^{13}C$ = carbon stable isotope; $\delta^{15}N$ = nitrogen stable isotope.

increase at the end of migration during the time fish spend in the lake (Hamon and Foote 2000). We found that individuals with deeper humps had lower final adipose $\delta^{13}C$ values and that individuals with longer maxillaries for their body size had larger increases in their adipose $\delta^{13}C$ values before death, which suggest that individuals that developed larger secondary traits had greater energy reserves. However, longer male pink salmon had higher adipose $\delta^{15}N$ values. The development of the male pink salmon hump involves formation of connective tissue (collagen) and growth of neural spines (Susuki et al. 2014), during which amine groups containing ^{15}N are preferentially retained compared to those with ^{14}N (Tibbets et al. 2008; Doronin et al. 2017). This more extreme tissue reorganization in pink salmon than in sockeye salmon may explain why only large pink salmon males showed elevated adipose $\delta^{15}N$. This is unlikely to be a size-based trophic-level effect from ocean feeding, as only the more metabolically active adipose tissue showed this relationship, not scale tissue. However, the pink salmon used in this study are some of the largest in British Columbia (e.g., Beacham et al. 1988; Hoshino et al. 2008; Sahashi and Yoshiyama 2016). To determine the generality of our finding, the relationship between stable isotope values and morphological traits should be examined across salmon populations that vary in morphology. For example, populations with on average smaller pink salmon may not show this relationship, and beach-spawning sockeye salmon ecotypes (which have deeper bodies than the stream forms we used) may show a stronger relationship than the one we found (Quinn et al. 2001; Arostegui and Quinn 2019).

Table 4: Correlations between initial and final stable isotope values analyzed separately by sex and tissue type for sockeye salmon

	Scale $\delta^{13}C$	Scale $\delta^{15}N$	Adipose $\delta^{13}C$	Adipose $\delta^{15}N$	Blood $\delta^{13}C$	Blood $\delta^{15}N$
Male:						
n	18	15	16	17	—	—
R^2	.081	.63	.69	.77	—	—
P	.18	**<.001**	**<.001**	**<.001**	—	—
Female:						
n	17	16	11	12	4	4
R^2	.21	.46	.67	.68	.78	.98
P	.068	**.004**	**.002**	**<.001**	.11	**.011**

Note. Statistically significant P values are shown in bold. Dashes indicate that there were no samples. $\delta^{13}C$ = carbon stable isotope; $\delta^{15}N$ = nitrogen stable isotope.

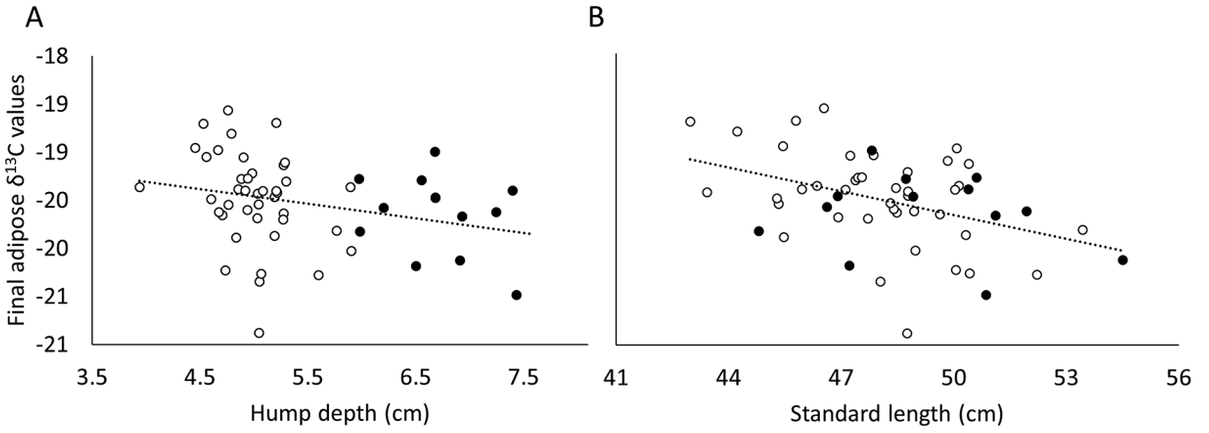

Figure 7. Negative relationship between hump depth (*A*) and standard length (*B*) in sockeye salmon and final adipose carbon stable isotope (δ^{13}C) values. Males are represented by filled circles, and females are represented by open circles. Least squares linear regression lines are for sexes combined.

We predicted that both δ^{13}C and δ^{15}N would increase between initial and final sockeye salmon samples in the more metabolically active adipose and blood tissues. Our results supported this prediction for adipose tissue; however, the relationship varied between sexes: females increased in δ^{13}C, and males increased in δ^{15}N. Thus, both sexes of sockeye continued to catabolize adipose tissue during their last month before death, with females mobilizing more fats, presumably for final egg maturation, and males utilizing more proteins, presumably for reorganization of tissues for secondary sexual trait development (Hendry and Berg 1999). These final changes likely happened mainly in the lakes, as on the spawning grounds male secondary sexual traits no longer increase in size (Hendry and Berg 1999). Similarly, Doson Coll (2015) found that postspawn sockeye had higher muscle δ^{13}C than samples collected downstream but did not test for sex effects. Since we found that both δ^{13}C and δ^{15}N from adipose tissue were also correlated between sampling time points within each sockeye sex, individuals were likely consistent in their level of catabolism. We had limited blood samples ($n = 4$), but they showed a pattern similar to that of adipose tissue, with both δ^{13}C and δ^{15}N correlated over time (significant for δ^{15}N). We acknowledge that in carnivores such as salmon that have high lipid diets, the lipid carbon from the diet can be used to build tissue proteins, which should mainly affect trophic discrimination factors among tissue types (Newsome et al. 2014; Wolf et al. 2015).

We do not know at what point scale alteration starts to occur, but our initial sockeye samples were collected shortly after fish left the Fraser River (4 km into the Seton River), and the amount of carbon catabolized was already predictive of sex-specific migration timing through the lakes, suggesting that alteration occurred before Seton River entry. During ocean residency, male and female salmon are morphologically identical and there are no differences in stable isotope values between the sexes (Kaeriyama

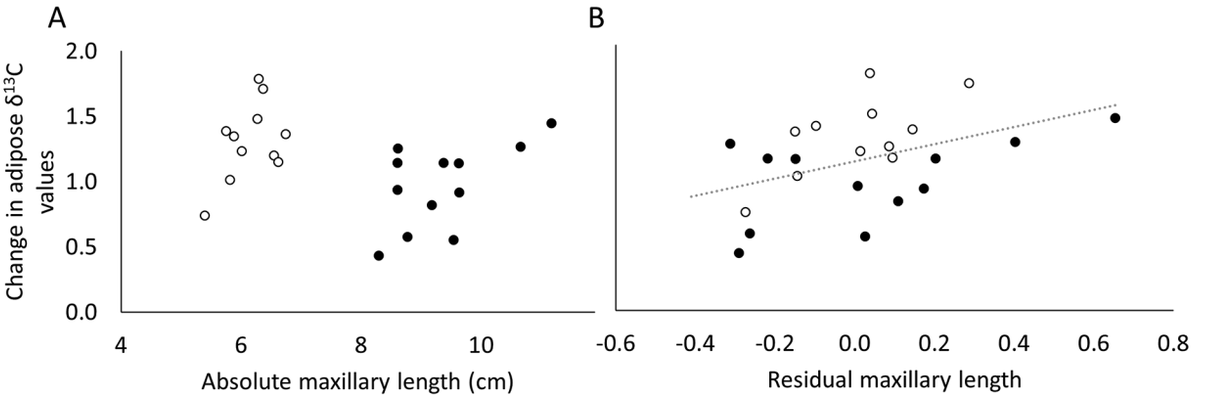

Figure 8. Change in adipose carbon stable isotope (δ^{13}C) values was negatively related to absolute maxillary length (*A*) and positively related to the residual (size-corrected) maxillary length (*B*) in sockeye salmon. Although the relationship in *A* was significant, it was clearly driven by males having longer maxillaries and smaller changes in adipose δ^{13}C values; within each sex, there appears to be a positive relationship. Males are represented by filled circles, and females are represented by open circles. The least squares linear regression line in *B* is for sexes combined.

Table 5: Generalized linear models analyzing the effects of migration timing on the change in stable isotope values for sockeye salmon

Model	*F*	df	*P*
Absolute maxilla length:			
ΔScale $\delta^{13}C$:			
Sex × trait	.98	1, 22	.32
Trait	1.44	1, 23	.23
Sex	1.00	1, 23	.31
ΔScale $\delta^{15}N$:			
Sex × trait	.16	1, 18	.69
Trait	.067	1, 19	.80
Sex	.42	1, 19	.52
ΔAdipose $\delta^{13}C$:			
Sex × trait	.41	1, 18	.52
Trait	**6.96**	**1, 19**	**.008**
Sex	11.39	1, 19	<.001
ΔAdipose $\delta^{15}N$:			
Sex × trait	.25	1, 18	.62
Trait	.61	1, 19	.44
Sex	.61	1, 19	.43
Residual maxilla length:			
ΔScale $\delta^{13}C$:			
Sex × trait	3.1	1, 22	.078
Trait	1.36	1, 23	.24
Sex	.044	1, 23	.83
ΔScale $\delta^{15}N$:			
Sex × trait	<.01	1, 18	.99
Trait	1.62	1, 19	.20
Sex	1.3	1, 19	.26
ΔAdipose $\delta^{13}C$:			
Sex × trait	1.65	1, 18	.20
Trait	**7.75**	**1, 19**	**.005**
Sex	8.67	1, 19	.003
ΔAdipose $\delta^{15}N$:			
Sex × trait	.057	1, 18	.81
Trait	.083	1, 19	.77
Sex	10.65	1, 19	.001
Absolute depth:			
ΔScale $\delta^{13}C$:			
Sex × trait	3.0	1, 26	.084
Trait	.001	1, 27	.99
Sex	.022	1, 27	.88
ΔScale $\delta^{15}N$:			
Sex × trait	.48	1, 22	.49
Trait	.067	1, 23	.8
Sex	.10	1, 23	.75
ΔAdipose $\delta^{13}C$:			
Sex × trait	.007	1, 18	.93
Trait	1.07	1, 19	.30
Sex	4.06	1, 19	.044
ΔAdipose $\delta^{15}N$:			
Sex × trait	.086	1, 20	.77
Trait	.044	1, 21	.83
Sex	1.36	1, 21	.24

Table 5 (*Continued*)

Model	*F*	df	*P*
Residual depth:			
ΔScale δ^{13}C:			
Sex × trait	2.18	1, 26	.14
Trait	.001	1, 27	.99
Sex	.096	1, 27	.76
ΔScale δ^{15}N:			
Sex × trait	.20	1, 22	.66
Trait	.83	1, 23	.36
Sex	.024	1, 23	.88
ΔAdipose δ^{13}C:			
Sex × trait	1.07	1, 18	.30
Trait	.69	1, 19	.41
Sex	5.99	1, 19	.014
ΔAdipose δ^{15}N:			
Sex × trait	.45	1, 20	.50
Trait	.29	1, 21	.59
Sex	8.63	1, 21	.003
Length:			
ΔScale δ^{13}C:			
Sex × trait	1.03	1, 26	.31
Trait	.037	1, 27	.85
Sex	.14	1, 27	.71
ΔScale δ^{15}N:			
Sex × trait	.25	1, 22	.62
Trait	1.13	1, 23	.29
Sex	.041	1, 23	.84
ΔAdipose δ^{13}C:			
Sex × trait	2.08	1, 18	.15
Trait	.079	1, 19	.78
Sex	5.28	1, 19	.022
ΔAdipose δ^{15}N:			
Sex × trait	.21	1, 20	.65
Trait	.91	1, 21	.34
Sex	4.59	1, 21	.032

Note. Change (Δ) in carbon stable isotope (δ^{13}C) and nitrogen stable isotope (δ^{15}N) values is calculated as the final value minus the initial value. The interaction effect was removed and the model was rerun if it was not significant. Significant effects of interest are shown in bold.

et al. 2004). Although we cannot rule out oceanic diet or location-based causes for our result, we suggest that the pattern of sex-related differences in migration timing related to δ^{13}C suggests that scales had already undergone some isotopic alteration during migration.

The unexpected increase in sockeye scale δ^{13}C values and evidence of sex-specific isotopic alteration led us to explore whether our scale stable isotope values had changed from oceanic values at our first Seton River sampling point for sockeye salmon or our sampling point at death for pink salmon. To do this, we compiled stable isotope values from the literature (table S1). We found that our sockeye salmon values were always lower for δ^{13}C and mostly higher for δ^{15}N than those in the literature, whereas our pink salmon values were always higher for δ^{13}C and mostly lower for δ^{15}N than those in the literature. For pink salmon, this table also revealed a strong increase in δ^{15}N from oceanic values to arrival in freshwater to spawning grounds. One explanation for this pattern is that pink salmon experience protein catabolism even before entering freshwater, possibly due to their advanced gonadal maturation before river entry (Dye et al. 1986; McBride et al. 1986). This means that δ^{15}N values collected from individuals still in the marine environment may already reflect catabolism in addition to diet, which has implications for dietary reconstructions using mature pink salmon at sea that are actively migrating toward freshwater. We fully acknowledge that many assumptions went into the supplemental comparison and encourage its interpretation primarily as a thought experiment for exploring the many causes of variation in stable isotopes and as a basis for future hypothesis testing rather than as any definite explanation for why our study values differ from previously reported literature values. There are many factors controlling yearly variation in average stable isotope values, including changes in food availability, small-scale

temperature variation, and regional differences in primary production (Satterfield and Finney 2002; Espinasse et al. 2020), to which we now add the possibility of sampling location affecting protein (especially in pink salmon) and fat (especially in sockeye salmon) catabolism related to migration and spawning—a pattern that remains to be causally tested.

Individual variation early in life experiences can have consequences for adult performance (Saboret and Ingram 2019), with freshwater conditions, ocean conditions, or migration affecting reproduction in taxa ranging from birds (Sorensen et al. 2009; Crossin et al. 2010) to fish (Henderson and Cass 1991; Gregory et al. 2019). While we found no effect of ocean $\delta^{15}N$ values on individual migration timing or survival, we were unable to assess carryover effects using scale $\delta^{13}C$ values, as these changed at some unknown point during migration. While natural tags such as stable isotopes are useful, we caution in regard to their usage in migrating salmon without further study into the effects of catabolism. More research into carryover effects, including the effects of even earlier events, such as juvenile habitat use, smolting age or timing, or energetic condition on subsequent oceanic habitat use, are other necessary avenues of investigation to pursue. Here, as elsewhere, a more holistic view across all life stages and across generations (e.g., Burton and Metcalfe 2014) is recommended for Fraser River sockeye salmon (Martins et al. 2012).

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