



Intra- and inter-population variation in sensitivity of migratory sockeye salmon smolts to phenological mismatch

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ABSTRACT: Certain consumer traits may influence sensitivity to phenological mismatches between consumers and their prey, and understanding the variation in these traits across or within populations could be helpful in predicting if and how a consumer population will respond to climate change. Here, we quantify intra- and inter-population variation in traits of sockeye salmon (*Oncorhynchus nerka*) smolts that may influence sensitivity to starvation associated with phenological mismatch. We asked 2 questions: (1) What is the magnitude of intra- and inter-population variation in physical and energetic condition at different stages of emigration? (2) How would this trait influence survival during periods of starvation? We collected sockeye salmon smolts from 3 populations before and 8 populations after riverine migration within the Skeena River watershed, BC, and measured condition-specific traits such as size and energetic condition. We discovered among-population variation was lower after migration: before migration traits differed between populations, but after-migration traits were more similar across populations. We estimated starvation resistance, the number of days until predicted death, using a previously developed model. Mean starvation resistance varied between 18 and 33 d across populations and varied within each population to as low as 6 d. These results reveal substantial within- and across-population sensitivity to starvation which may be associated with phenological mismatch. Thus, factors other than phenology (e.g. freshwater ecosystem dynamics that influence smolt condition) have the potential to influence sensitivity to phenological mismatch and, potentially, marine survival.

KEY WORDS: Match–mismatch hypothesis · Sensitivity · Migration · Phenology · Salmon · Trait variation

1. INTRODUCTION

Global climate change is shifting the phenology of species at different rates, changing how and when species interact, potentially decoupling species interactions (e.g. predator–prey, parasite–host; Parmesan & Yohe 2003, Root et al. 2003, Parmesan 2006, Thackeray et al. 2010). While some mismatches may have survival or fitness consequences (Durant et al. 2005, Pearce-Higgins et al. 2009, Ozgul et al. 2010), not all phenological mismatches with prey resources

result in changes in survival. For example, predator–prey phenological mismatches between hatching of great tits *Parus major* and peak caterpillar abundance have led to a decrease in great tit fledgling survival (Visser et al. 2006). Alternatively, phenological mismatches between Soay sheep *Ovies aries* and peak spring vegetation did not influence lamb survival, possibly because lactating mothers could offset the energetic deficit using endogenous energy stored from previous seasons (Durant et al. 2005, Kerby & Post 2013, Paoli et al. 2020). Thus, certain

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traits, such as energy stores or body condition, may influence if and how survival and fitness are affected by food limitation resulting from a phenological mismatch (i.e. the length of time until starvation) and therefore influence how sensitive that population or species is to a phenological mismatch. However, empirical evidence of differential sensitivity to phenological mismatch is sparse (Miller-Rushing et al. 2010, Thackeray et al. 2016).

Sensitivity to phenological mismatches is likely influenced by species-, population-, and individual-level traits (Cushing 1990, Miller-Rushing et al. 2010). For example, species that have a single seasonal life history event (i.e. univoltine organisms that reproduce once annually; Knell & Thackeray 2016), have a simplified population structure (age or size at age; Ohlberger et al. 2014), rely heavily on a single prey type (specialist predators; Tucker et al. 2019), or are less plastic (regarding both phenology and prey type) are more likely to be sensitive to phenological mismatches (Cushing 1990, Durant et al. 2007, Miller-Rushing et al. 2010). However, the population and individual traits that may influence sensitivity to phenological mismatch have received much less attention. For instance, perhaps different individuals or populations have traits (e.g. body size or energy stores) that render them more or less sensitive to the potential consequences of phenological mismatch. A clearer understanding of how intra- and inter-population variation in traits can mediate sensitivity to phenological mismatch could help predict vulnerability to climate-driven changes in phenology.

Pacific salmon *Oncorhynchus* spp. are renowned for their locally adapted migratory traits (e.g. migration timing, body shape, aerobic scope) (Crossin et al. 2004, Eliason et al. 2011) that could potentially influence their sensitivity to phenological mismatch. Juvenile salmon rear in freshwater lakes and streams for up to several years (Groot & Margolis 1991, Quinn 2018a) before completing a freshwater migration that may be energetically expensive, extend over hundreds of kilometers, and take up to several weeks to complete (Brett 1995, Hinch et al. 2006). During this migration, it is believed that Pacific salmon smolts feed only minimally, if at all, and generally rely on endogenous energy stores, although direct empirical evidence in the literature is lacking (Stefansson et al. 2003, Quinn 2005, Hinch et al. 2006, Larsson et al. 2011). They then spend up to several months in the estuary before transitioning to open ocean feeding grounds (Pearcy 1992, Preikshot et al. 2012, Moore et al. 2016). Parts of the early marine migration may also be food limited (Utne et al. 2021). For example,

juvenile salmon from the Fraser River and Salish Sea pass through the prey-scarce Johnstone Strait region prior to reaching the more prey-abundant open coastal waters (McKinnell et al. 2014, James 2019). Survival during this early marine period has been linked to size and growth (Ward et al. 1989, Henderson & Cass 1991, Beamish & Mahnken 2001). Timing of the juvenile outmigration can also impact survival, where mistimed arrival in the estuary can result in phenological asynchrony between juvenile salmon and prey availability. Phenological mismatch can lead to a decrease in individual and cohort survival of Pacific salmon (Ryding & Skalski 1999, Chittenden et al. 2010, Satterthwaite et al. 2014, Malick et al. 2015, Wilson et al. 2021a), but this is not universally the case (Scheuerell et al. 2009, Irvine et al. 2013, Evans et al. 2014, Gosselin et al. 2018). Thus, it is possible that some traits such as migration timing, size, or energetic condition could influence the sensitivity of some species, populations, or individual salmon to phenological mismatches.

Freshwater rearing conditions and their varying impacts across individuals and populations of juvenile salmon traits could influence salmon sensitivity to challenging early marine rearing conditions associated with phenological mismatch (Sturrock et al. 2020, Wilson et al. 2021a), a form of carryover effects. Carryover effects are performance effects that become apparent at later life stages but that are caused by experiences during earlier life stages (O'Connor et al. 2014). Juvenile salmon exhibit high intra- and inter-population variability in traits (e.g. size, condition factor, migration timing; Bradford et al. 1997, Beacham et al. 2014a, Carr-Harris et al. 2018) which likely depend on freshwater factors such as density dependence, rearing habitat productivity, and environmental conditions (Freshwater 2017, Jones et al. 2020) as well as population-specific genetic differences (Pon et al. 2007). These differences may become important because juvenile salmon fuel their downstream migration predominantly on endogenous energy reserves. Indeed, experimental evidence demonstrates that juvenile salmon with better body condition are more likely to survive long periods of starvation (Fergusson et al. 2010, Persson et al. 2018, Wilson et al. 2021b). Therefore, individuals and populations with better body condition may be more likely to survive (i.e. less sensitive) to periods of poor estuary or marine growth conditions associated with phenological mismatch (Saloniemi et al. 2004) (Fig. 1). Accordingly, individuals or populations of salmon of better body condition may be more robust to poor ocean entry conditions (Fig. 1).

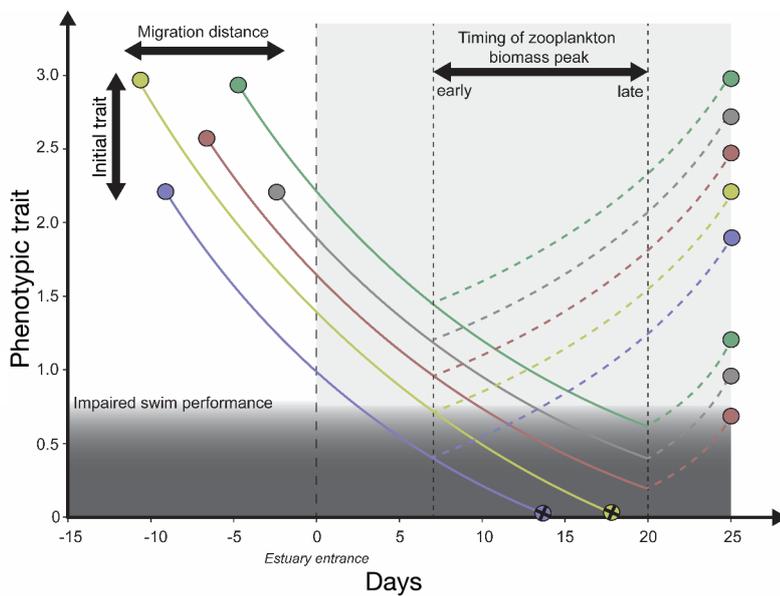


Fig. 1. Concept of how a phenotypic trait associated with physical or energetic condition (such as condition factor) could impact the sensitivity of different populations to phenological mismatch. Five populations (as denoted by the different colours) originate in freshwater and exhibit variation in condition and migration length. As fish begin the energetically expensive freshwater migration, condition continues to decrease until zooplankton biomass peaks. If zooplankton peak abundance occurs close to the time of estuary entrance, all populations persist (phenological match). However, if zooplankton peak abundance is shifted too long after estuary entrance (phenological mismatch), populations of lower condition cannot persist. Thus, condition could determine sensitivity. When the interaction with ocean arrival and zooplankton phenology (exposure) is also considered, sensitivity and exposure show population-specific vulnerability to phenological mismatch

Here, we examine how variation in individual- and population-specific traits can influence sensitivity to starvation associated with downstream migration and potential phenological mismatch. Specifically, we asked the questions (1) What is the magnitude of intra- and inter-population variation in physical and energetic condition at different stages of emigration? and (2) How would these differences influence survival during periods of starvation (i.e. conditions associated with or exacerbated by a phenological mismatch)? Using wild sockeye salmon (*O. nerka*) smolts from 3 populations captured at the initiation of downstream migration at lake outlets and from 8 populations captured in the Skeena River estuary after freshwater migration, we compared physical and energetic condition within and across populations. We hypothesized that different rearing lakes and freshwater migration durations would produce smolts with differing body condition across populations but also that there would be substantial within-population variation (MacDonald et al. 2019). We

explored how this variation could translate into sensitivity to phenological mismatch using a bioenergetics model and a previously developed model linking prolonged swim performance, a proxy for survival, with condition factor. We expected that variation in modelled time to starvation would be higher across populations than within populations based on differences in population-specific condition and size, estuary arrival timing, and migration duration. This means that populations of sockeye salmon could exhibit a range of physiological sensitivity to starvation that could influence their vulnerability to phenological mismatch in the early marine environment (Fig. 1).

2. MATERIALS AND METHODS

The Skeena River drains approximately 55 000 km² of northwestern British Columbia and hosts the second largest sockeye salmon run in Canada. There are >30 genetically distinct Skeena River sockeye salmon populations; the majority of sockeye salmon (>90% in some years) are produced from the Babine Lake system (Gottesfeld & Rabnett 2008). The Babine Lake system is assessed as a single stock and is composed of multiple spawning populations that share common rearing lake habitats. In this large and complex system, smolts emigrate from Babine Lake over a 4 to 6 wk period, much longer than other small lake systems within the Skeena River (Table S1 in the Supplement at www.int-res.com/articles/suppl/m692p119_supp.pdf).

Lake-type juvenile Skeena River sockeye salmon rear for 1 to 2 yr in natal lakes and rivers before they migrate to the Skeena River estuary in the spring. Lakes in the Skeena River basin range in primary productivity, size, and elevation, producing smolts across a range of sizes and conditions (Groot & Margolis 1991, Gottesfeld & Rabnett 2008). Depending on the population, smolts may migrate over 500 km before reaching the estuary and typically arrive in the estuary in an ordered sequence based on migration distance and rearing location elevation (Carr-Harris et al. 2018). Most populations arrive in the estuary over a period of ~2 to 3 wk; however, due to the staggered nature of their arrival, sockeye salmon

smolts are continuously arriving in the estuary over an 8 to 10 wk period starting in early May and ending in mid-July (Carr-Harris et al. 2018). The Skeena River estuary is ~1500 km², extending 75 km upstream of Port Edward to 50 km southwest through Ogden Channel and over 85 km northwest through Chatham Sound at peak river discharge (Fig. 2). Skeena River sockeye salmon smolts spend between 2 and 18 d in the estuary before moving on to more northern coastal feeding grounds (Moore et al. 2016).

2.1. Collection

Sockeye smolts were collected from 3 freshwater lakes upon lake exit as well as in the Skeena River estuary (Fig. 2). Sockeye salmon smolts were collected from Babine Lake every third day between May 4 and June 8, 2015 (n = 85), and between April 30 and June 9, 2016 (n = 103), using the Babine Lake smolt enumeration facility located at the Nilkitkwa Lake outlet (see Tiley et al. 2017 for more details on collection). Smolts were collected every other day from the outlet of Kitwanga (Gitanyow) Lake between April 21 and May 11, 2016 (n = 36), and from the Slamgeesh Lake outlet between April 26 and May 5, 2016 (n = 35), using permanent full fence weirs. In the estuary, sockeye salmon smolts were captured between May 5 and June 8, 2015 (n = 77), and between May 13 and June 21, 2016 (n = 165), as part of the North Coast Juvenile Salmon Monitoring Program (see Carr-Harris et al. 2018 and Sharpe et al. 2019 for methodological details). Briefly, juvenile salmon were captured weekly using a purse seine (9.1 m deep, 73.2 m long, 51 mm mesh at tow end, 13 mm mesh at the bunt) towed for 5 min per set at 25 sites. A subset of sockeye salmon were collected, and a fin clip was taken for genetic stock identification and stored in 95% ethanol until analysis (Beacham et al. 2005). Seven of the sockeye salmon smolts that were caught had external tags from Babine Lake. No genetic analyses were completed for these 7 fish, and they were assigned to Babine Lake. All fish were randomly selected, euthanized with an overdose of tricaine methanesulfonate (MS222), frozen at -20°C for approximately 1 mo, then transferred on dry ice to where they were stored at -80°C until analysis. All fish handling and sampling procedures were performed in accordance with the animal care protocol (1158B-11) from the University Animal Care Committee at Simon Fraser University.

Genetic analyses were completed using microsatellite DNA analysis at Fisheries and Oceans Can-

ada's Molecular Genetics Laboratory (Pacific Biological Station, Nanaimo, British Columbia) (Beacham et al. 2005). Each fish was assigned to a population probabilistically using allele frequencies from known samples collected from 20 regions throughout the Pacific Northwest (Beacham et al. 2014a). Only fish with a percent certainty greater than 75% were included in this analysis. There are multiple spawning sites within the Babine Lake system, but they are difficult to genetically isolate and generally have less than 75% certainty, so all populations assigned from Babine and Nilkitkwa lakes were assigned to a generic Babine Lake population (Beacham et al. 2014b). These populations almost all rear in Babine Lake and so share rearing conditions. Of the 242 samples run for DNA, 24 had less than 75% certainty in population assignment and were removed from analysis, and 7 did not have enough DNA to test.

2.2. Condition determination

We determined the physical and energetic condition of fish by measuring fork length (FL) and wet weight of thawed fish as well as determining proximate body constituents (percent lipid, percent water, and percent ash). All fish captured in 2015 were run for proximate body condition analyses; however, for logistical reasons, we ran only a random subset of 81 of the 110 Babine Lake sockeye salmon smolts captured in the estuary in 2016. Fulton's condition factor (*K*) was determined by:

$$K = \frac{W_t}{FL^3} \times 100 \quad (1)$$

where W_t is wet weight in grams, and FL is in centimeters.

Proximate body composition was determined using protocols of Wilson et al. (2021a) and Crossin & Hinch (2005) adapted from Bligh & Dyer (1959) and Higgs et al. (1979). Briefly, lipid percent was determined from a subsample of 0.3 ± 0.015 g of a homogenate of whole fish which was mixed with methanol, chloroform, and water in a ratio of 1:1:0.48, homogenized, and decanted. Upon formation of biphasic layers, the chloroform layer was removed, measured, and evaporated on pre-weighed aluminium dishes, leaving only lipid remaining, which could be weighed. Moisture content was determined by drying 0.3 ± 0.015 g of homogenate at 100°C for 16 to 20 h. Ash was determined by combusting the 0.3 ± 0.015 g of homogenate to 600°C in a muffle furnace for 2.5 h.

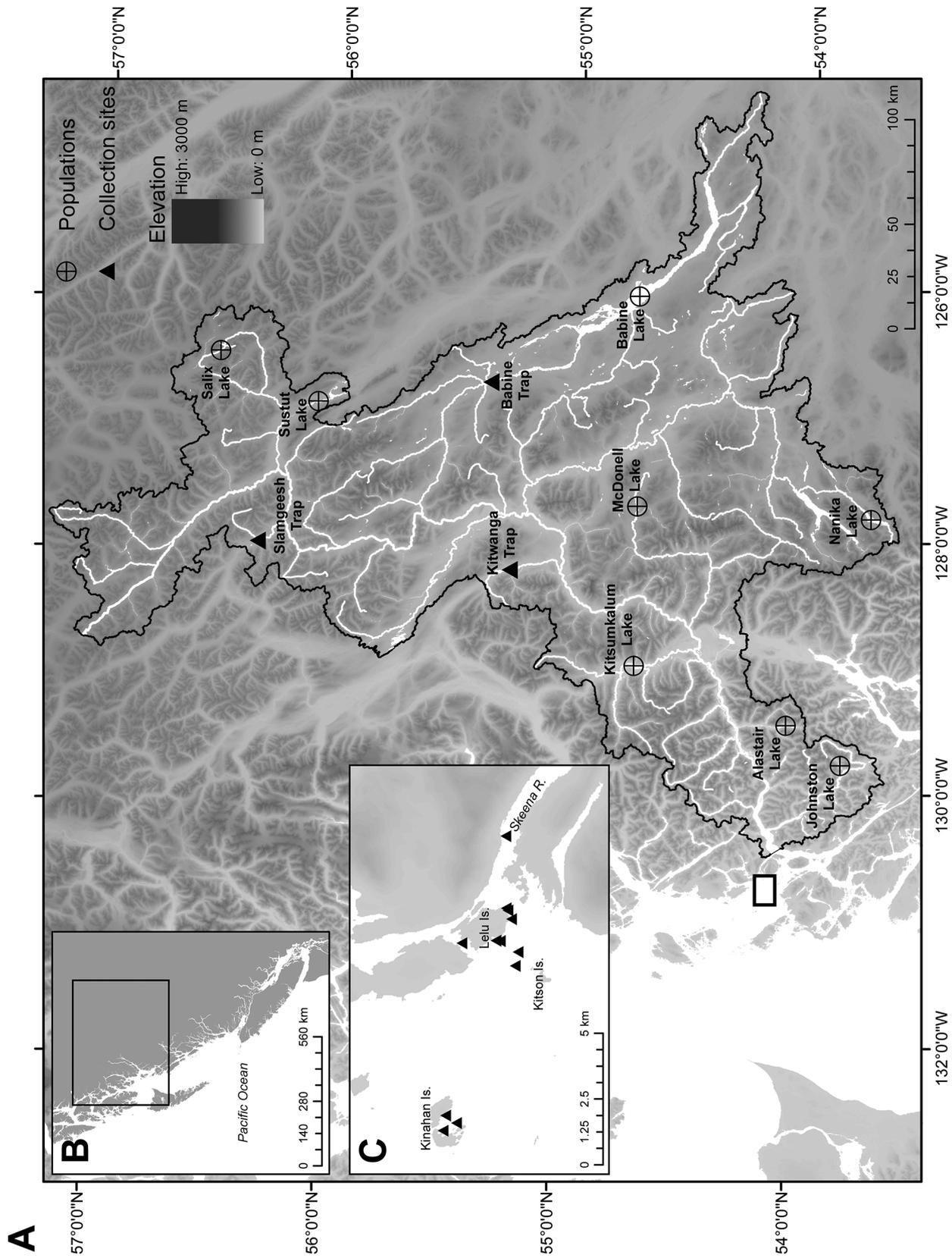


Fig. 2. (A) Skeena River with fence sites (black triangles), (B) coastal British Columbia, and (C) estuary capture locations (black triangles). Originating locations of populations captured in the Skeena River estuary are denoted by circles with crosses through them

Percent whole body protein (P) was determined from percent water (W), percent lipid (L), and percent ash (A) (Brett & Groves 1979, Breck 2008):

$$P = 100 - (W + L + A) \quad (2)$$

Energy density was determined from the amount of lipid per fish multiplied by the energy density of lipid (0.0362) added to the amount of protein multiplied by the energy density of protein (0.0201) (Brett & Groves 1979).

2.3 Bioenergetic modelling

2.3.1. Estimating change in condition

To estimate the change in fish condition through time, we used a modified version of the Wisconsin bioenergetics model parameterized for juvenile rainbow trout *O. mykiss* (Hanson et al. 1997, Tyler & Bolduc 2008, Deslauriers et al. 2017), as juvenile sockeye salmon values were not available. We fit the model with 0 g consumption to simulate starvation conditions and used initial fish weight and regional water temperatures (corresponding to regions of the Skeena River system experienced during downstream migration) to model weight change over 45 d of migration (see Text S1). Bioenergetics simulations were started in similar temperature conditions in which fish were captured. For example, fish captured at the Babine Lake trap were modelled as experiencing Babine River temperatures for 9 d and mainstem conditions for 4 d, reflecting current estimates of migration timing (C. Carr-Harris pers. comm.). After the 13 d freshwater migration, fish were modelled with estuary water temperatures. Fish captured in the estuary were modelled with only estuary water temperatures. Intra-population variation in migration timing ranges was ~30 d for Babine Lake smolts and <14 d for Slamgeesh Lake and Kitwanga Lake smolts. Temperatures vary during the emigration period. As a result, we compared different water temperature scenarios to determine the sensitivity of our results to water temperature; see Section 2.3.2 for water temperature profiles assigned to migrants from each capture site (Fig. S1).

Using estimated daily weight from the Wisconsin bioenergetics model, we calculated the change in condition factor using initial FL (Eq. 1). This produced a daily estimate of condition factor which decreased throughout the 45 d modelling period.

This modelling depends on a variety of assumptions. (1) Metabolic processes use the same amount

of energy in freshwater compared to saltwater. It is possible that energy use in saltwater is higher due to the need to osmoregulate; however, this has not been robustly quantified for juvenile salmon (Wagner et al. 2006). The Wisconsin bioenergetics model does not have parameters for salmon in the ocean, so we used the data available and recognize that estimated energy use in the ocean is likely conservative. (2) Metabolic rate remains the same for starving and fed fish. This is also likely a conservative estimate, as starving fish have decreased activity and likely have decreased metabolic rate (see Text S1 for more details). Again, these parameters are not available. However, Wilson et al. (2021a) held sockeye salmon without food for 61 d and measured weekly change in weight. We compared the observed change in weight of those fish to the predicted change in weight using the Wisconsin bioenergetics model and found the results were similar for the first 3 wk (mean starvation resistance [i.e. days to 30% probability of death] was usually between 3 and 4 wk, such that most starvation resistance estimates did not extend far beyond times that predicted and observed weights began to vary substantially; Fig. S2). (3) Bioenergetic models for juvenile rainbow trout can be used to predict weight change in juvenile sockeye salmon. Though there may be some differences, we believe that the model performs well for this study (see previous point). Therefore, model estimates did correspond to observed patterns, but it should be noted that bioenergetics models make assumptions and are a simple way to explore energy use.

2.3.2. Water temperature

Water temperature profiles (i.e. daily water temperature estimates based on migration route and estimated duration for 40 d after emigration past the freshwater smolt fence sites) were created for each capture site based on the most likely migration timing and available temperature stations in the Skeena River and Skeena River estuary. For the Skeena River estuary, we used mean daily temperature between May 15 and June 30, averaged across 1990 to 2019, from Stn 46145, Dixon Entrance (54.370° N, 132.44° W). We relied on 2 government stations for creating freshwater temperature migration profiles (<https://wateroffice.ec.gc.ca/>): data from Stn 08EB005 (55.717° N, 127.687° W) above the Babine River confluence and Stn 08EB003 (55.301° N, 127.673° W) below the Babine River confluence. For temperatures from the Babine River, we used mean daily temperature averaged across sites for 2016 and

2017, which were collected from 15 stations along the Babine River (Pitman & Moore 2021). For fish captured at the Babine fence, we modelled temperature based on a 9 d migration through the Babine River (May 9–17; using daily averaged Babine River temperature for 2016 and 2017) and 4 d migration (May 18–21) through the Skeena mainstem (Stn 08EB003); for the remaining 32 d, we used Skeena River estuary water temperature data (May 22–Jun 22; Stn 46145). For fish captured at the Slamgeesh Lake fence, we used water temperatures from Stn 08EB005 above the Babine River confluence for 9 d (May 9–17) and water temperatures from Stn 08EB003 below the Babine River confluence for 4 d (May 18–21); for the remaining days, we used data from the Skeena River estuary (May 22–Jun 22; Stn 46145). Finally, the Kitwanga population is closer to the Skeena River estuary, with likely a much shorter migration time. Therefore, we used water temperatures from the Skeena River below the Babine River confluence for 7 d (May 18–24; Stn 08EB003) and the estuary water temperature profile for the remaining 38 d (May 25–Jul 1; Stn 46145; Fig. S1). We modelled energy use of all populations using the 10th, mean, and 90th percentiles of water temperature for all migration routes (Fig. S1).

2.4. Predictive modelling

We used a previously developed model of swim performance and smolt condition to predict whether a smolt would complete or fail a prolonged swim performance test based on its condition factor (for details see Wilson et al. 2021a). Prolonged swim performance affects migratory capacity, and the ability to capture prey and escape predators, and thus is related to survival (Beamish 1978, Plaut 2001). Therefore, completion of a prolonged swim performance trial indicates that the fish is healthy and in better condition than those that cannot complete the test and can be used as a proxy for fitness and survival.

Briefly, sockeye salmon smolts were captured from Chilko Lake of the Fraser River watershed, British Columbia, and transported to a holding facility, where they were held without food. Seven days after capture, fish were transferred from freshwater to fully saline (28–30 ppt) water over a 36 h period. Every week for 6 wk, 18 fish underwent a prolonged swim performance challenge. Nine fish were placed in a swim tunnel (9 cm wide, 15 cm tall, 142 cm long) and held for 12 min at a flow rate of $\sim 0.085 \text{ m s}^{-1}$ (~ 1 body length [BL] s^{-1}); over a period of 12 min,

flow was slowly increased to 0.50 m s^{-1} ($\sim 4.5\text{--}6.4 \text{ BL s}^{-1}$) and remained at that flow rate for 90 min or until the fish could no longer swim. Fish that did not complete the 90 min swim test failed, and fish that completed the 90 min swim test passed. Fish were euthanized with an overdose of MS222 (0.5 g l^{-1}), and FL was measured (mm); fish were then weighed (g), frozen on dry ice, and stored at -80°C . Proximate body composition was determined using the methods described in Section 2.2.

We used a generalized linear model with a binomial distribution and logit link function to create models from combinations of standardized and centered independent smolt condition variables to predict the probability of a fish completing the 90 min prolonged swim test. The most parsimonious model (defined by Akaike's information criterion corrected for small sample sizes) included only condition factor. We used k -fold cross-validation to determine accuracy of the model, whereby the model was re-parameterized with 90% of the data (training dataset) and used to predict the remaining 10% of data (test dataset). To be more conservative, we ran the model with predicted probabilities of $\geq 0.3 =$ passed and $< 0.3 =$ failed, and these predictions were compared to observations to determine model predictive performance. This procedure was repeated 1000 times, with samples randomly assigned to either training or test datasets. We found that the generalized linear model using condition factor as the predictor variable could correctly predict whether a fish could complete the swim trial 78.7% of the time.

Swim performance trials were completed on fish that varied in condition factor. At the end of the trial, each fish was euthanized and measured for FL and weight, and condition factor was calculated before being stored for later analysis of constituent components (see Section 2.2). A generalized linear model was developed relating physical traits to whether the fish could complete the swim performance trial. The most parsimonious model was:

$$\text{logit}(\phi) = 1.679 \times K - 1.620 \quad (3)$$

where ϕ is the binary swim performance outcome (pass or fail), and K is Fulton's condition factor.

We used this generalized linear model (Eq. 3) to predict whether a wild-caught fish could complete the swim performance trial, where failure to complete the swim performance trial was a proxy for death (see Wilson et al. 2021a).

Using the predicted daily weight from the Wisconsin bioenergetics model for each of the temperature

scenarios, and assuming FL would not change over the period of starvation, we calculated daily condition factor for each fish captured in the estuary or at the freshwater fences and for each water temperature scenario (verified by experimental data; see Fig. S4). We used the predicted daily condition factor to estimate daily probabilities of completing the swim performance test. As fish had 0 g consumption (unfed), these daily probabilities slowly decreased as condition factor decreased until probability was less than 30% that fish could complete the swim performance test. We then estimated starvation resistance: the number of days between capture and the first day that the probability of a fish completing the swim performance test fell below the 30% threshold.

2.5. Statistical analyses

We separately compared the population means of each physical and energetic condition metric (FL; weight; Fulton's condition factor; energy density; and protein, moisture, and lipid content) for the 3 populations captured before riverine migration and the 8 populations captured in the estuary. Data from 2015 and 2016 for Babine Lake did not differ and were grouped for the remaining analyses (Figs. S3 & S6). Though data were collected throughout the migration period, there were no trends through timing and no time covariates were included in analyses (Figs. S3–S5). Data were tested for normality and homoscedasticity. We compared population means using ANOVAs. If the parameter estimates from the ANOVA were significantly different, we used post hoc pairwise Bonferroni *t*-tests to identify significantly different populations. We applied an adjusted α value of 0.00625 based on Bonferroni correction for 8 tests, to minimize the increased false positive error rates associated with multiple statistical tests (Field et al. 2012).

To quantify within- and across-population variation, we compared variance that was explained by all populations vs. total residual variance (sensu McLean et al. 2018). To accomplish this, we ran an intercept-only random effects model with a single physical or energetic metric as the dependent variable and population as a random effect. We calculated the percent of the variance absorbed by the population random intercept relative to the total variation (sum of the population intercept and individual residual variance estimate). Thus, the percent of among-population variation was calculated as the variance of the population intercept divided by the

sum of the population intercept and individual residual variance estimate, multiplied by 100. A value close to 100 indicates that among-population variation explains almost all of the total variation, such that 2 individuals from the same population are likely to be more similar than 2 individuals from different populations. A value near zero indicates that the among-population variation is relatively low, such that 2 individuals from different populations are equally likely to be similar as 2 individuals from the same population.

All statistics were performed in the R statistical computing environment (v.3.6.3) (R Core Team 2020) using the RStudio graphical user interface (GUI) (v.1.2.5033, 2019) and the following packages: 'AICcmodavg' (Mazerolle 2017), 'lme4' (Bates et al. 2015), and 'GGplot2' for graphing (Wickham 2009). The Fish Bioenergetics 4.0 GUI was used in the R statistical computing environment for the Wisconsin bioenergetics model simulations (Deslauriers et al. 2017).

3. RESULTS

3.1. Condition of freshwater-captured populations

Physical and energetic condition metrics varied widely both across individuals within a population and between populations captured in freshwater. For example, smolts captured at the Babine Lake outlet had variable fork length (mean FL = 79.1 mm, range = 65–98 mm, SE \pm 0.5; n = 188) that differed from smolts captured at Slamgeesh Lake (mean FL = 99.9 mm, range = 80–124 mm, SE \pm 1.4; n = 35) and Kitwanga Lake (mean FL = 107.3, range = 97–120 mm, SE \pm 1.0; n = 36) (Table 1).

Mean energetic and physical condition metrics differed significantly among populations for smolts captured at each fence site (FL *F*-value = 374.1, *df* = 2, p < 0.0001; weight *F*-value = 590.4, *df* = 2, p < 0.0001; lipid content *F*-value = 119.1, *df* = 2, p < 0.0001; water content *F*-value = 203.4, *df* = 2, p < 0.0001; protein content *F*-value = 123.5, *df* = 2, p < 0.0001; Fulton's condition factor *F*-value = 72.1, *df* = 2, p < 0.0001; and energy density *F*-value = 190.4, *df* = 2, p < 0.0001). Post hoc pairwise Bonferroni *t*-tests demonstrated that all 3 populations significantly differed from each other, with FL (p < 0.0001), weight (p < 0.0001), and energy density (p < 0.0001) all higher in Kitwanga smolts followed by Slamgeesh Lake smolts and with Babine smolts having the lowest condition metrics (Table 1). Water content was also significantly differ-

Table 1. Physical and energetic condition of sockeye salmon smolts collected at freshwater lake exit at 3 smolt fences and in the Skeena River estuary. NA: not available. Numbers in parentheses show SE

	— Freshwater fence —			Population captured in the Skeena River estuary ^a							
	Babine Lake	Slamgeesh Lake	Kitwanga Lake	Johnston Lake	Alastair Lake	Kalum Lake	McDonnell Lake	Babine Lake	Nanika Lake	Sustut Lake	Salix Lake
Sample size	188 ^b	35	36	3	5	13	2	130	5	13	10
Distance to the ocean (km)	440	459	264	67	95	158	248	440	522	575	515
Median percent stomach fullness ^c	0	0	0	NA	100	100	NA	75	NA	100	100
Fork length (mm)	79.1 (±0.5)	99.9 (±1.4)	107.4 (±1.0)	57.3 (±3.8)	76.4 (±4.4)	67.1 (±2.2)	74.0 (±2.0)	77.7 (±0.6)	74.6 (±4.1)	76.5 (±1.6)	92.3 (±2.4)
Weight (g)	4.67 (±0.08)	9.47 (±0.46)	14.06 (±0.39)	1.83 (±0.43)	4.68 (±0.82)	3.37 (±0.31)	3.59 (±0.32)	4.59 (±0.1)	4.38 (±0.50)	4.77 (±0.27)	8.54 (±0.61)
Fulton's condition factor	0.94 (±0.01)	0.93 (±0.01)	1.13 (±0.01)	0.94 (±0.05)	1.01 (±0.03)	1.09 (±0.04)	0.88 (±0.01)	0.96 (±0.01)	1.06 (±0.08)	1.06 (±0.04)	1.07 (±0.03)
Energy density (MJ kg ⁻¹)	4.43 (±0.04)	5.07 (±0.08)	6.15 (±0.08)	4.22 (±0.18)	4.46 (±0.01)	4.24 (±0.09)	4.31 (±0.10)	4.30 (±0.03)	4.53 (±0.14)	4.77 (±0.13)	5.02 (±0.09)
Water (% wet wt)	78.46 (±0.11)	76.12 (±0.05)	73.03 (±0.25)	78.17 (±0.81)	77.17 (±0.61)	78.06 (±0.42)	77.84 (±0.51)	78.24 (±0.09)	76.96 (±0.46)	76.46 (±0.41)	75.95 (±0.31)
Protein (% wet wt)	15.87 (±0.05)	17.61 (±0.26)	17.98 (±0.13)	16.85 (±0.65)	17.68 (±0.44)	17.14 (±0.38)	17.24 (±0.31)	16.47 (±0.06)	17.36 (±0.32)	17.62 (±0.18)	17.84 (±0.25)
Lipid (% wet wt)	3.42 (±0.10)	4.22 (±0.16)	7.0 (±0.20)	2.31 (±0.17)	2.51 (±0.20)	2.20 (±0.12)	2.33 (±0.12)	2.74 (±0.07)	2.87 (±0.32)	3.41 (±0.31)	3.96 (±0.18)
Estimated survivorship	25 (6–44)	26 (14–33)	33 (27–38)	20 (15–23)	25 (21–30)	27 (19–38)	18 (17–18)	22 (7–38)	27 (13–35)	27 (9–36)	29 (23–35)

^aPairwise comparisons across populations are shown in Tables S2–S10
^bSamples collected over 2 yr; n = 85 in 2015, and n = 103 in 2016
^cStomach contents analyzed for 2016 samples only

ent among groups ($p < 0.0001$) but, as expected, displayed the opposite trend, with Babine having the highest water content followed by Slamgeesh Lake smolts and Kitwanga Lake smolts (Table 1). Mean protein content differed significantly between Babine Lake and Kitwanga Lake smolts ($p < 0.0001$) and between Babine Lake and Slamgeesh Lake smolts ($p < 0.0001$) but did not differ between Slamgeesh Lake and Kitwanga Lake smolts ($p = 0.25$). Protein content was higher in Kitwanga Lake and Slamgeesh Lake smolts compared to Babine Lake smolts. Both Fulton's condition factor and mean lipid content differed significantly between Babine Lake and Kitwanga Lake smolts ($p < 0.0001$). Lipid but not Fulton's condition factor differed significantly between Babine Lake and Slamgeesh Lake (lipid $p = 0.0022$, $Kp = 1$) (Fig. 3, Table S10). Fulton's condition factor and lipid content were higher in Kitwanga Lake smolts compared to either Babine Lake or Slamgeesh Lake smolts. Generally, smolts from Kitwanga Lake were larger and had higher physical

and energetic condition than smolts from Slamgeesh or Babine lakes, and Slamgeesh smolts had higher condition metrics than Babine smolts.

3.2. Condition of estuary-captured populations

Body condition metrics varied both within and across populations sampled in the estuary. For example, smolts ranged in Fulton's condition factor between 0.67 and 1.39 across populations (Table 1). Populations varied significantly in physical and energetic condition (FL F -value = 14.46, $df = 7$, $p < 0.0001$; weight F -value = 19.59, $df = 7$, $p < 0.0001$; lipid content F -value = 5.593, $df = 7$, $p < 0.0001$; water content F -value = 9.492, $df = 7$, $p < 0.0001$; protein content F -value = 9.6, $df = 7$, $p < 0.0001$; Fulton's condition factor F -value = 5.286, $df = 7$, $p < 0.0001$; and energy density F -value = 9.369, $df = 7$, $p < 0.0001$). Note that some populations had small sample sizes and may not be representative of the population. Smolts from

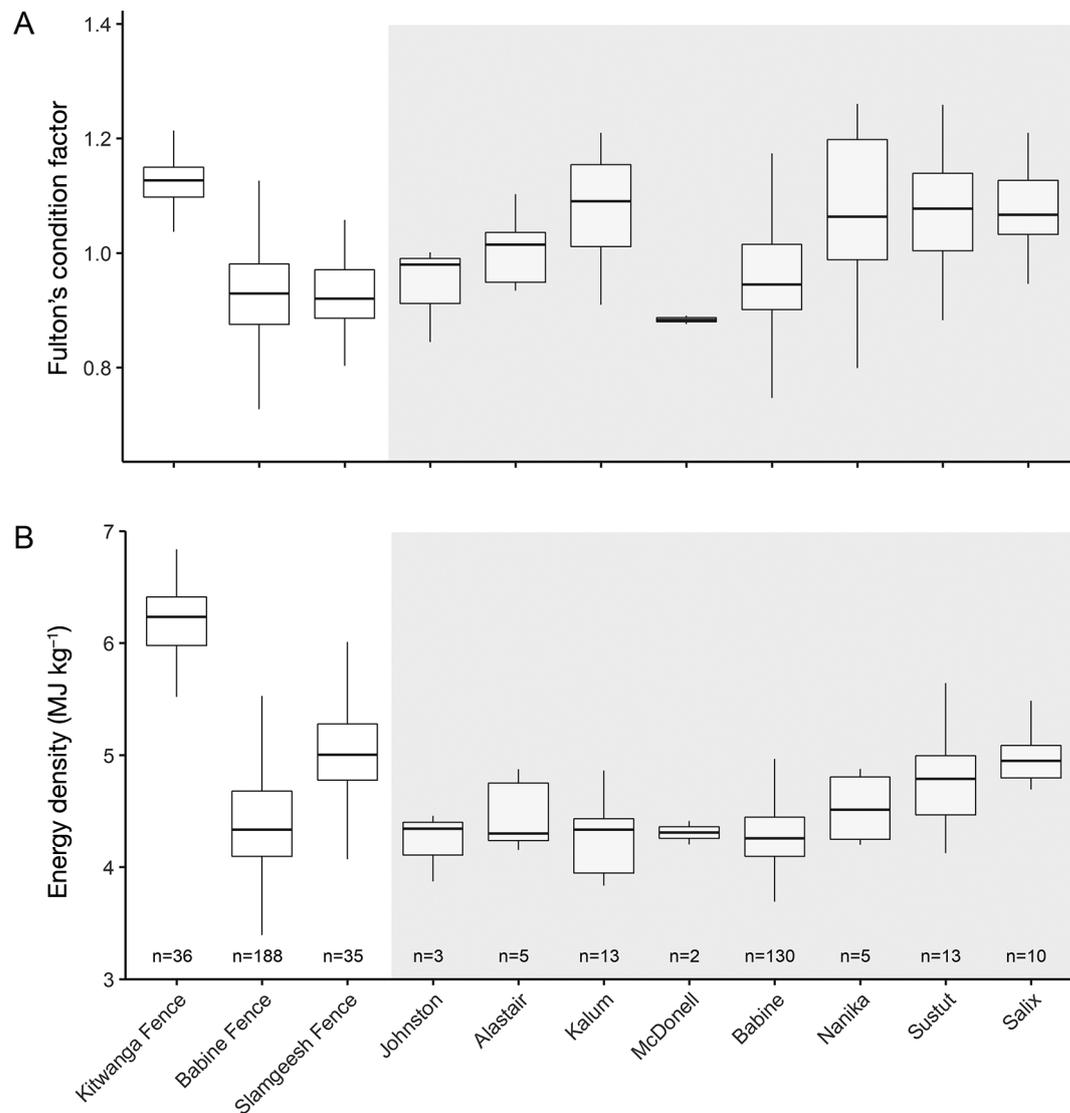


Fig. 3. (A) Fulton's condition factor and (B) energy density of sockeye salmon smolts from 3 different populations captured from freshwater (white background) and 8 different populations captured in the estuary (grey background). Boxplots show the 25th, median, and 75th percentiles; whiskers extend to $1.5 \times$ interquartile range

Johnston and Alastair lakes were generally smaller and had the lowest condition metrics compared to Sustut Lake and Salix Lake smolts, which were much larger and of better condition (Fig. 3; see Tables S2–S9 for pairwise comparisons).

3.3. Within- and among-population variation in condition

For salmon captured at the 3 freshwater fences prior to riverine migration, variation among populations was higher than within populations (percent of variability explained by population was $>60\%$) for all

metrics of physical and energetic condition (Table 2). However, among-population variance was lower for estuary samples than among-population variance for freshwater sites, with the percent of variation explained by population being $<40\%$ for all physical and energetic condition metrics, with the exception of FL and weight (Table 2). Thus, at lake exit, smolts leaving from the same lake were more similar to each other than to smolts leaving from different lakes. However, by the time the smolts had reached the estuary, the population-level variability decreased, such that in the estuary, smolts from different populations were more similar to each other than they were at lake exit.

Table 2. Percent of the total variability in physical and energetic condition explained by among-population variability for populations captured in freshwater and the Skeena River estuary

	Freshwater-captured	Estuary-captured
Sample size of individuals (populations)	259 (3)	181 (8)
Fork length (mm)*	83.3%	64.6%
Weight (g)*	89.7%	70.2%
Fulton's condition factor*	61.0%	19.4%
Energy density (MJ kg ⁻¹)*	75.4%	39.1%
Water (% wet wt)*	75.9%	33.4%
Protein (% wet wt)*	61.7%	25.9%
Lipid (% wet wt)*	68.1%	32.9%
Estimated survivorship*	43.3%	19.4%

*Values above 50 % suggest that among-population variation explains more of the total variation, such that 2 individuals from the same population are likely to be more similar than 2 individuals from different populations. Values below 50 % indicate that the among-population variation is relatively low, such that 2 individuals from different populations are equally likely to be similar as 2 individuals from the same population.

3.4. Variability in modelled starvation resistance

Bioenergetic models estimated a decrease in weight and decrease in condition factor of individual smolts captured at lake exit and in the estuary (Fig. 4). For example, the average condition factor of Babine Lake smolts captured at the Babine Lake fence was 0.94; after modelling food deprivation for 45 d using the bioenergetic model, the estimated average condition factor was 0.43—well below the estimated threshold for 30 % probability of survival (Fig. 4).

Populations had variable mean modelled starvation resistance. By integrating observed patterns in traits with previous experimental relationships between traits and survival, we estimated that starvation resistance was significantly longer by ~3 d for smolts captured in freshwater (average = 26, range = 6–44 d) vs. those captured in the estuary (average =

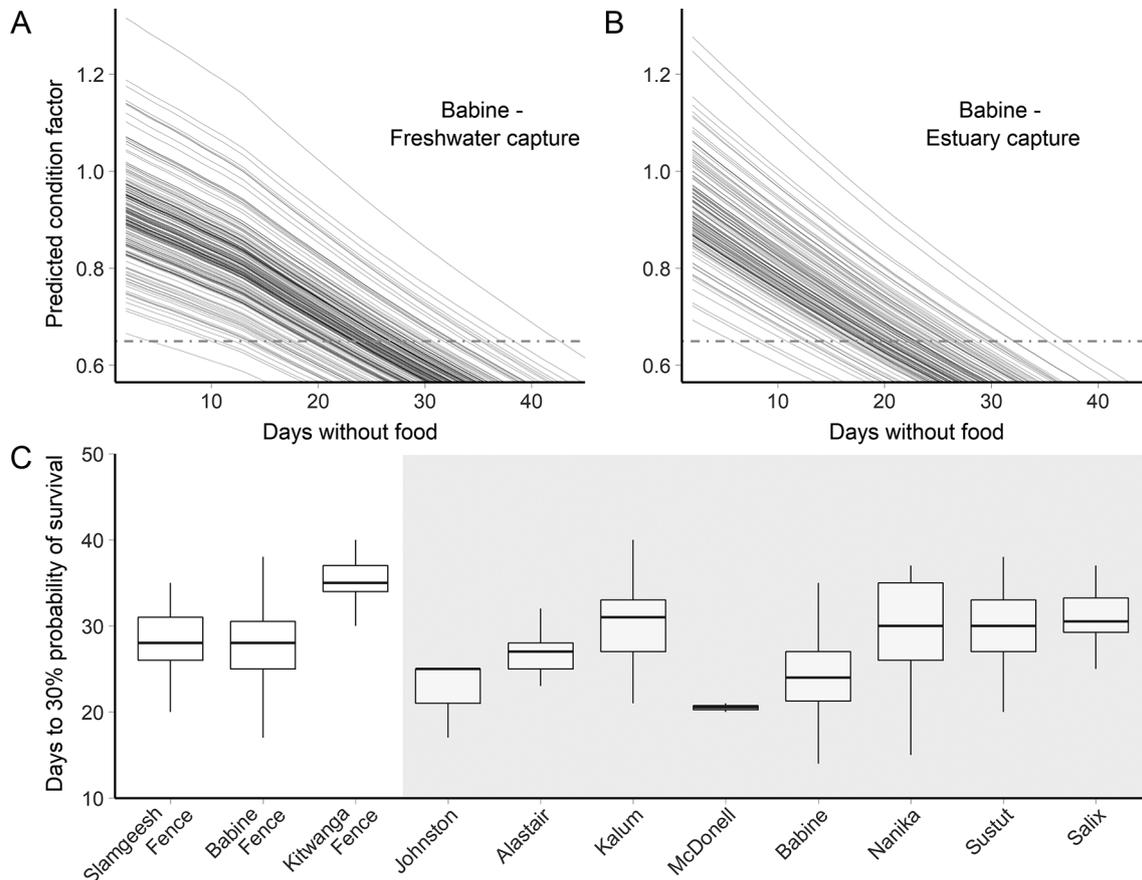


Fig. 4. (A,B) Predictions of condition factor through time without food for fish captured (A) at fence sites and (B) in the estuary. Predicted condition factor was calculated from predicted weights, which were determined using the Wisconsin bioenergetic model. The dashed line represents the critical value 0.65, when fish had <30 % probability of completing the swim trial according to Eq. (3). (C) Number of days to 30 % probability of survival using swim performance model, for fish captured at fence sites or in the estuary. Grey shaded region represents estuary residence. See Fig. 3 for boxplot definitions

23, range = 7–38 d) (F -value = 32.22, $df = 1$, $p < 0.0001$). Populations captured at lake outlets also varied in mean modelled starvation resistance (F -value = 97.52, $df = 2$, $p < 0.0001$; Table 1), with Kitwanga having significantly longer modelled starvation resistance (33 d, range = 25–43 d) compared to Slamgeesh (26 d, range = 14–36 d; $p < 0.0001$) or Babine (25 d, range = 5–45 d; $p < 0.0001$) smolts (Fig. 4, Fig. S7). Similarly, populations captured in the estuary varied significantly in mean modelled starvation resistance (F -value = 12.18, $df = 7$, $p < 0.0001$), with the mean for most populations between 18 and 29 d, but with substantial intra-population variability (Table 1). Indeed, among-individual variability was higher in modelled starvation resistance such that population explained less variance in either freshwater or the marine environment (Table 2). Bonferroni post hoc pairwise comparisons demonstrate that starvation resistance varied significantly between Babine Lake and Salix (Bear) Lake ($p < 0.0001$), Sustut Lake ($p < 0.0001$), and Kalum Lake ($p < 0.0001$) populations, between Kalum Lake and McDonnell Lake smolts ($p < 0.0001$), and between Salix/Bear Lake and Johnston Lake ($p < 0.0001$) and McDonnell Lake ($p < 0.0001$) populations (Table S8). In sum, modelled starvation resistance varied based on migration stage (lake outlet or estuary) as well as within and across populations.

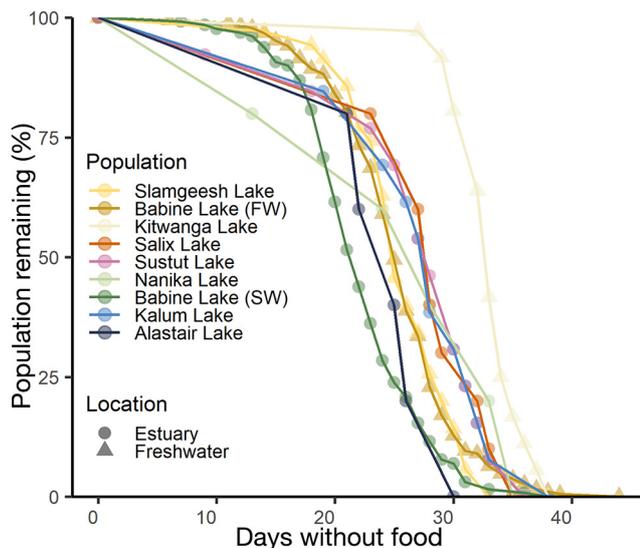


Fig. 5. Proportion of population remaining based on days to 30% survival probability using swim performance model and estimated Fulton's condition factor for each population. Babine FW were fish captured at the lake outlet, while Babine SW were fish captured in the Skeena River estuary. Triangles represent populations sampled in freshwater, before freshwater migration, and circles represent populations sampled in the estuary, after freshwater migration

Populations across both sample locations varied somewhat in the modelled time it takes for 50% of the population to die (Fig. 5). The days to 50% mortality of freshwater-captured populations from Babine and Slamgeesh lakes was 25 d and from Kitwanga Lake was 33 d. Similarly, the Kalum Lake, Nanika Lake, Salix/Bear Lake, and Sustut Lake populations captured in the estuary had 28 d to 50% mortality, while the Alastair Lake population had 25 d and the Babine Lake population had 22 d to 50% mortality.

4. DISCUSSION

Here, we show that juvenile sockeye salmon exhibit a high degree of within- and across-population variation in traits related to body condition; this trait variability indicates differential sensitivity to food deprivation (Wilson et al. 2021b), which can occur during phenological mismatches. Thus, body condition could be useful in estimating sensitivity and predicting vulnerability to future phenological shifts and mismatch. As climate change shifts the phenology of species, understanding which species and populations could be most vulnerable to changes in food availability associated with phenological mismatches is of increasing importance, especially for species of cultural or commercial importance (Cushing 1990, Miller-Rushing et al. 2010, Thackeray et al. 2016).

Observed variation in Skeena River sockeye salmon body condition translates into substantial intra- and inter-population variation in sensitivity to poor feeding conditions or timing of prey abundance relative to predator demand. For example, smolts sampled from the Babine Lake outlet have an average Fulton's condition factor of 0.94 (range = 0.68–1.34), corresponding to a starvation resistance of 25 d but ranging to as low as 6 d. Given that down-river migration of Babine Lake sockeye smolts is thought to be 7 to 12 d (C. Carr-Harris pers. comm.), smolts at the low range of the condition factor likely do not survive even the freshwater migration. Smolts from the Slamgeesh Lake population had similar mean Fulton's condition factor and modelled starvation resistance compared to smolts from the Babine Lake population but had fewer lower-conditioned individuals, possibly a trait selected for due to the increased energy requirements of a longer freshwater migration or to lake-specific differences in primary productivity. We expected that populations with longer migrations may have higher energetic condition, but Kit-

wanga Lake sockeye had the highest condition, suggesting that lake-specific factors contribute to smolt condition (Fig. 1). Indeed, the lowest Fulton's condition factor observed for Slamgeesh Lake smolts was 0.76, corresponding to 14 d survivorship. In contrast, smolts from the Kitwanga Lake population had a significantly higher Fulton's condition factor (mean = 1.13, range = 0.76–1.06) and increased predicted starvation resistance (mean = 33 d, range = 27–38 d), despite a much shorter freshwater migration than either the Babine Lake or Slamgeesh Lake populations. The larger size and condition of Kitwanga Lake sockeye smolts could make them more resilient to climate change impacts during the early marine period. Interestingly, Kitwanga Lake is a relatively shallow mesotrophic lake which produces much fewer smolts per female spawner than expected based on carrying capacity estimates derived from primary productivity (Shortreed et al. 1998). It is thought that predation or high over-winter mortality possibly due to decreased dissolved oxygen under the ice leads to decreased competition and larger, more energetically dense smolts. Therefore, decreases in freshwater survival could actually lead to shifts in freshwater traits that increase early marine survival and resilience to changes to marine prey phenology. Thus, the carryover effects of released density dependence at low abundances could contribute to the compensatory capacity of salmon. Yearly differences in freshwater growing conditions such as changes in juvenile salmon density or primary productivity could lead to differences in the physical and energetic condition of juvenile salmon populations and thus differences in predicted starvation resistance across years. Differences in freshwater growing and migrating conditions likely also influence the intra- and inter-population variability in condition and thus sensitivity to phenological mismatch.

Trait variability of sockeye salmon captured in the estuary further demonstrates variability in sensitivity to phenological mismatch. Average Fulton's condition factor for fish captured in the estuary varied between 0.68 and 1.39 (mean = 0.99), corresponding to a predicted starvation resistance between 3 and 38 d (mean 23 d). Modelled starvation resistance for fish captured in the estuary was similar to that for fish captured before freshwater migration, even though the fish captured in freshwater had yet to complete their freshwater migration that may last up to 2 wk (C. Carr-Harris pers. comm.). Modelled starvation resistance was 3 d longer for freshwater populations than for estuary populations. While the difference in

modelled starvation resistance was statistically significant, it may not be biologically significant, given freshwater migrations are thought to take longer than a week in the Skeena watershed. We anticipated that condition-selective mortality would occur during the migration (Rondorf et al. 1985, Tucker et al. 2016) and that migrating fish would use energy stores during the downstream journey, leading to lower intra-population variation of fish captured in the estuary compared to lake outlets. However, we observed the opposite trend. Within-population variation was higher for fish captured in the estuary compared to those captured at lake outlets. The increase in intra-population variation was possibly due to differences in the timing of re-initiation of foraging and migration behaviour (e.g. migration duration), with some smolts beginning to feed in the estuary sooner than others, which may have masked observations of any possible effects of condition-selective survival in the riverine migration. In fact, many smolt stomachs were near full despite capturing them at the river mouth, highlighting the importance of upper estuary habitats for energetic recovery of migrating salmon. Indeed, estuaries are important nursery grounds for some salmon species, providing enriched feeding and growing opportunities (Healey 1982, Thorpe 1994, Quinn 2018b, Seitz et al. 2020). Future work examining condition-selective mortality should examine smolts prior to the re-initiation of feeding and/or could use telemetry techniques to examine individual survival (*sensu* Clark et al. 2016), though both approaches have significant logistical challenges associated with them.

Freshwater conditions influence smolt body condition and thus could influence sensitivity to phenological mismatch, early marine survival, and climate change sensitivity (Reed et al. 2010). Alteration to the historic migration schedule (e.g. barriers such as dams) or changes to freshwater habitat (e.g. from decreased habitat availability and/or quality) that decrease fish condition at marine entry could negatively impact early marine survival. Similarly, increased competition (through stocking or natural variation in spawners) could result in decreased average body condition for smolts (Bjornn et al. 1968, Einum et al. 2006, 2011, Grossman & Simon 2020), which could increase sensitivity to phenological mismatch. Reciprocally, if population densities decrease and relax competition, the potential increase in body condition could provide a mechanism supporting the high compensatory capacity and resilience of salmon (Healey 2009). These effects may not be immediately evident, as phenological mismatches do not occur in

every year (Cushing 1969, 1990, Chittenden et al. 2010, Wilson et al. 2021a). While freshwater carry-over effects can present a challenge for salmon conservation, they also mean that freshwater habitat improvements that improve smolt condition (Railsback et al. 2013) might foster climate resilience in some circumstances.

Starvation resistance may not be entirely reflective of sensitivity. Starvation resistance and thus predicted survival are likely underestimates given that predictions of weight loss were based on laboratory studies where fish would use less energy than in natural settings. Despite this conservative approach, these estimates show that smolts have only a few weeks of energy stores. Apart from starvation resistance, even a modest delay in marine growth could increase future predation risk (Beamish & Mahnken 2001, Duffy & Beauchamp 2011, Friedland et al. 2014). Indeed, enhanced growth can help smolts escape gap-limited predation and expand the prey base (Pope et al. 1994). Predators can also preferentially select low-condition smolts (Furey et al. 2016, Tucker et al. 2016). Therefore, starvation resistance is not necessarily indicative of mortality rates, which may be higher due to delayed marine growth.

Understanding species and population sensitivity to mismatch is the first step to identifying vulnerability and predicting impacts of climate-driven phenological mismatch. Two factors work together to determine vulnerability: sensitivity and exposure (Williams et al. 2008). Here, we have demonstrated within- and across-population differences in body condition, which could influence sensitivity to phenological mismatch. Other traits in addition to body condition such as diversity of life history expression (e.g. life span, age at maturity, migration timing), physiology (e.g. disease resistance, metabolic scope), and plasticity could further predict individual- or population-level sensitivity to phenological mismatch (Ohlberger et al. 2014, Knell & Thackeray 2016, Tucker et al. 2019). For example, populations with complex age structure may be better able to buffer total or partial loss of a cohort due to mismatch (Ohlberger et al. 2014). Current phenotypic diversity and future climate warming could influence frequency of exposure of salmon smolts to phenological mismatch. For example, Carr-Harris et al. (2018) found that Skeena River sockeye salmon smolts entered the estuary in a consistent order over a 6 wk period, and estuary conditions varied widely over that time period. Therefore, populations migrating at different times of the year experience different levels of food availability and are likely to experience dif-

ferent levels of phenological mismatch (Fig. 1). Exposure to phenological mismatch also likely varies across regions, as climate change is shifting the timing of spring primary productivity and peak zooplankton abundance to be earlier in some locations or more variable in others (Mackas et al. 1998, 2013, Edwards & Richardson 2004, Allen & Wolfe 2013, Poloczanska et al. 2013). These changes in salmon prey availability are not always accompanied by equal changes in juvenile salmon outmigration timing. For example, while regionally peak zooplankton biomass is advancing at 14 d per decade, Kovach et al. (2013) found that juvenile pink salmon *Oncorhynchus gorbuscha* in the northeastern Pacific were advancing at only 5 d per decade, and sockeye salmon and coho salmon *O. kisutch* from the same watershed were not altering their outmigration phenology. Thus, risks of phenological mismatches, predicted to increase in frequency and severity under future climate warming scenarios (Kharouba et al. 2018), are influenced by both intrinsic sensitivity and exposure that varies within and across watersheds.

Several studies have examined survival or population dynamics as a result of phenological mismatch (Scheuerell et al. 2009, Chittenden et al. 2010, Satterthwaite et al. 2014), but few have examined mitigating traits, such as condition factor, which could alter the strength of the effect of phenological mismatch. For salmon, the early marine period is thought to be one of the major determining periods of recruitment. When more fish, on average, survive this period, marine survival is higher, and more fish are recruited to the fishery (Pearcy 1992). Ours is an important theoretical step towards understanding how factors, such as sensitivity to mismatch, could influence the relationship between phenological mismatch and survival. Here, we provide a rare example of a study that translates variability of traits into variability in sensitivity to phenological mismatch.

Determining trait-based vulnerability to phenological mismatch among species and populations is imperative to predicting if and how species will be impacted by climate change and informing conservation efforts (Foden et al. 2013, Pearson et al. 2014, McLean et al. 2016). Identifying relationships between species- and population-level traits and sensitivity to change is one avenue that has been used to identify sentinel species and prioritize species of conservation concern (Williams et al. 2008, Butchart et al. 2010). Here, we reveal that condition and energy status are traits that vary across and within populations and that condition can inform starvation resistance and thus sensitivity to mismatch. Populations

with higher predicted mean starvation resistance should be less sensitive to climate change-driven phenological mismatches. Thus, phenotypic traits can be useful in understanding how species and populations will respond to oncoming change through identifying population sensitivity to phenological mismatch.

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