

## RESEARCH ARTICLE

# Individual variation, population-specific behaviours and stochastic processes shape marine migration phenologies

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## Abstract

1. The phenology of long-distance migrations can influence individual fitness, moderate population dynamics and regulate the availability of ecosystem services to other trophic levels. Phenology varies within and among populations, and can be influenced by conditions individuals experience both prior to departure and encounter en route.
2. Assessing how intrinsic and extrinsic factors (e.g., individual physical condition vs. environmental conditions) interact to influence variation in migratory phenologies across ecological scales is often limited due to logistical constraints associated with tracking large numbers of individuals from multiple populations simultaneously.
3. We used two natural tags, DNA and otolith microstructure analysis, to estimate the relative influence of individual traits (life-history strategy, body size at departure and growth during migration), population-specific behaviours and interannual variability on the phenology of marine migrations in juvenile sockeye salmon *Oncorhynchus nerka*.
4. We show that the timing and duration of juvenile sockeye salmon migrations were correlated with both life-history strategy and body size, while migration duration was also correlated with departure timing and growth rates during migration. Even after accounting for the effect of individual traits, several populations exhibited distinct migration phenologies. Finally, we observed substantial interannual and residual variation, suggesting stochastic environmental conditions moderate the influence of carry-over effects that develop prior to departure, as well as population-specific strategies.
5. Migratory phenologies are shaped by complex interactions between drivers acting at multiple ecological and temporal scales. Given evidence that intraspecific diversity can stabilize ecological systems, conservation efforts should seek to maintain migratory variation among populations and preserve locally adapted phenotypes; however, variation within populations, which may buffer systems from environmental stochasticity, should also be regularly assessed and preserved.

## KEYWORDS

body size, carry-over effects, life history, migration, otolith, Pacific salmon, phenology

## 1 | INTRODUCTION

Long-distance migrations are taxonomically widespread and have profound ecological impacts by linking distinct communities or habitats (Bauer & Hoyer, 2014). During long-distance migrations, individuals often encounter variable environmental conditions and increased predation risk, as well as expend considerable energy reserves. As a result, mortality rates during migrations are often high and can have a disproportionately large effect on population dynamics (Newton, 2006; Sillett & Holmes, 2002). As mechanisms of mortality are rarely static in time or space, variation in the phenology of migrations may alter individual fitness costs and influence population dynamics (Cooke et al., 2004; Newton, 2006).

Processes occurring at multiple ecological scales can shape differences in migratory phenology. If migratory traits are strongly heritable, local selective pressures may lead to population-specific strategies that minimize travel costs. For example, sockeye salmon (*Oncorhynchus nerka*) populations exhibit distinct adult spawning phenologies associated with thermal regimes in freshwater habitats (Hilborn, Quinn, Schindler, & Rogers, 2003). Similarly, black-tailed godwit (*Limosa limosa*) migrations reflect population-specific differences in overwintering habitat quality (Gunnarsson et al., 2006). Yet, individuals also exhibit considerable plasticity in phenology, often due to strong carry-over effects from earlier life-history stages (Norris & Taylor, 2006). Physical condition (Marra, Hobson, & Holmes, 1998), body size (Freshwater et al., 2016b) or age (McKinnon, Fraser, Stanley, & Stutchbury, 2014; Tibblin, Forsman, Borger, & Larsson, 2015) can influence the timing or duration of migrations. Finally, severe environmental conditions or local stochastic processes can alter individual migration schedules (Schaub, Liechti, & Jenni, 2004; Senner et al., 2015). Ultimately, both carry-over effects and stochastic events may reduce apparent differences among comigrating populations by increasing variation among individuals.

The extent and scale of phenological variation within metapopulations may have distinct ecological, and ultimately conservation, implications. Greater diversity in the timing or duration of migrations can increase the availability of the ecosystem services that mobile populations provide, for example, by increasing higher trophic levels' access to prey (Deacy, Leacock, Armstrong, & Stanford, 2016; Kovach, Joyce, Echave, Lindberg, & Tallmon, 2013; Schindler et al., 2010). Given that periods of peak survival during migration vary interannually (Scheuerell, Zabel, & Sandford, 2009), phenological diversity may also improve the likelihood that migratory species persist, by decreasing a metapopulation's exposure to poor environmental conditions and the risk of mass mortality events (Morris et al., 2007). These portfolio effects may become increasingly valuable in the face of future environmental change (Anderson, Moore, McClure, Dulvy, & Cooper, 2015). In such a scenario, whether variation is predominantly expressed within or between populations may determine whether management actions focus on maintaining specific component populations or diversity within the aggregate as a whole. Furthermore, as migration phenologies advance and become more compressed (Kovach et al., 2013), the likelihood of

management interventions increases, creating an additional incentive to quantify intraspecific diversity at multiple scales.

Despite their ecological consequences, our understanding of how phenologies vary across such scales is often limited by the logistical challenge of estimating traits among and within comigrating populations. Many common techniques, such as surveys of species abundance during migratory periods, confound sympatric populations and provide little data on individual traits that may influence variation in phenology (Forrest & Miller-Rushing, 2010). Marking a large number of individuals with low-cost tags (e.g., passive integrated transponder tags) can counteract some of these issues and has provided evidence of phenology-specific survival rates (Scheuerell et al., 2009; Zabel & Achord, 2004). However, individual data can generally be collected only at the time of tagging and these efforts are often only effective in specific habitats (e.g., rivers with hydropower development). Larger tags have greater transmission frequency and data storage capacity that can provide movement data on an individual scale (Furey et al., 2016), but are infrequently used to compare multiple populations simultaneously due to high costs per sampling unit (but see Lacroix, 2008). Such tags may also be too large to apply to the entire size range of a population due to tag burden concerns (Clark et al., 2016). As an alternative to artificial tags, natural markers such as DNA, parasites, stable isotopes or calcareous structures can provide migration or connectivity data at individual scales (Gillanders, 2010).

In this study, we used genetic stock identification techniques to identify comigrating populations of juvenile sockeye salmon originating from the Fraser River watershed, a 220,000 km<sup>2</sup> region extending from southern to north-central British Columbia. We then used a second natural marker, otolith microstructure, to estimate a suite of individual characteristics, including the timing and duration of early marine migrations within a proposed critical habitat (Beamish, Neville, Sweeting, & Lange, 2012). We next constructed hierarchical models to examine how diversity in the phenology (timing and duration) of marine migrations varied across ecological scales. Specifically we explored whether (a) the timing of nearshore migrations was influenced by individual traits (life-history strategy and body size) and rearing habitat (nursery lake latitude and downstream migration distance); (b) the duration of nearshore migrations was influenced by individual traits fixed prior to emigration (life-history strategy, body size and ocean entry date) and traits moderated by conditions encountered en route (growth); (c) CUs exhibited differences in migratory phenology after accounting for these effects; and (d) if the relationships between individual traits and phenology were stable among CUs and between years.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

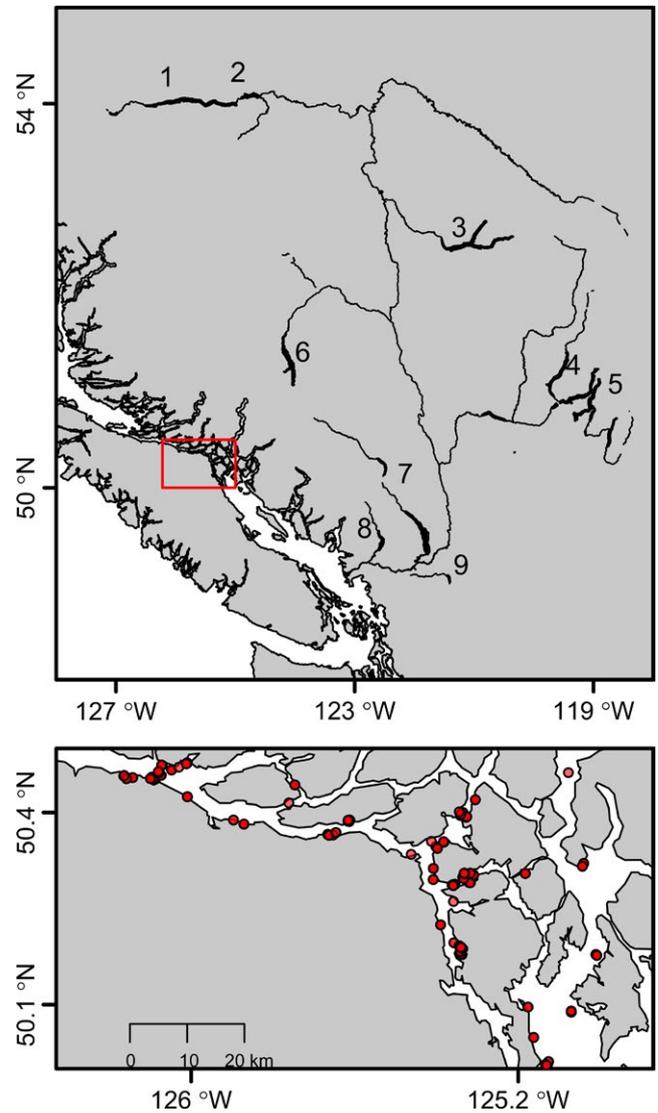
Sockeye salmon is an anadromous, semelparous fish distributed throughout the North Pacific Ocean. Adults spawn in natal

freshwater systems in late summer and autumn, with juveniles emerging from redds the following spring. The majority of juvenile sockeye salmon rear in nearby nursery lakes for one-two years before emigrating to marine environments; however, a minority of individuals have an alternative, “sea-type” life history, migrating to estuarine habitats shortly after emergence (i.e., at age-0) (Birtwell, Nassichuk, & Buene, 1987). After foraging offshore for one-three years, sockeye salmon return to spawn (Burgner, 1991).

Canada’s most abundant sockeye salmon metapopulation spawns in the Fraser River watershed in southern British Columbia. These populations initially enter the ocean in the Strait of Georgia, where juveniles rear for weeks to months before migrating along the continental shelf to mature in the Gulf of Alaska (Burgner, 1991; Tucker et al., 2009). Mortality rates shortly after ocean entry are typically high and are thought to regulate future adult abundance (Percy, 1992). As a result, the interaction between migratory phenology and rearing conditions in the Strait of Georgia may strongly influence juvenile sockeye salmon survival (Beamish et al., 2012, 2016). Estimates of migration timing are available for a small number of indicator populations (Freshwater et al., 2016b; Furey, Vincent, Hinch, & Welch, 2015) and the population aggregate as a whole (Neville et al., 2016; Preikshot, Beamish, Sweeting, Neville, & Beacham, 2012). However, differences in early marine life histories among Fraser River sockeye salmon populations are poorly resolved and have been identified as a substantial knowledge gap in sustainable management (Cohen, 2012).

## 2.2 | Field sampling

We sampled juvenile sockeye salmon weekly in the Discovery Islands and Johnstone Strait (a region approximately 200 km northwest of the Fraser River; Figure 1), covering the peak migratory period (mid-May to mid-July) in 2014–2016. Fish were collected with a modified purse seine, fished from the *F/V Nordic Queen* during daylight hours. We randomly selected up to 30 juvenile sockeye salmon per set to retain for sampling, which were then euthanized with MS-222. After capture, we recorded fork lengths and preserved tissue samples for genetic stock identification. Individuals were assigned to populations within the Fraser River using 14 microsatellite loci, with a 50% lower probability limit and an estimated 5% false assignment rate (Beacham et al., 2005). We aggregated samples at the level of conservation units (CUs), often the focal unit for management, to ensure sufficient year-specific sample sizes. CUs may contain multiple populations, but individuals within these populations are genetically similar, rear in the same nursery lakes and share spawning migration phenologies (Holtby & Ciruna, 2007). Preliminary analyses indicated that our results were not strongly influenced by aggregating individuals at this level, suggesting these shared traits result in similar juvenile ecologies. Note that a CU’s name refers to the lake(s) where the majority of juveniles rear and is followed by a letter that references the CU’s run timing: early summer (ES), summer (S) or late summer (L).



**FIGURE 1** Location of nursery lakes for Fraser River CUs (top panel) and sampling locations for individual fish within Johnstone Strait and the Discovery Islands (bottom panel). CU’s lakes are numbered: (1) Nadina-Francois, (2) Francois-Fraser, (3) Quesnel, (4) Shuswap-ES, (5) Shuswap-L, (6) Chilko, (7) Lillooet-Harrison, (8) Pitt and (9) Chilliwack

## 2.3 | Otolith microstructure analysis

For each year of sampling, we selected CUs with at least five individuals for further analyses (sensitivity analyses indicated parameter estimates and model rankings were similar when CUs with <20 individuals were excluded; online supplement). For each CU, otoliths were removed from up to 60 individuals spanning that year’s sampling period. We used otolith microstructure techniques to estimate age at out-migration, size at ocean entry, ocean entry date, duration of residence in the Strait of Georgia (i.e., number of daily increments) and marine growth rates (see Freshwater et al., 2015 for validation and details on sample preparation). We made all measurements dorsal and perpendicular to the otolith’s anterior–posterior centerline and used the average of three sequential measurements, per otolith

metric, for analysis. If an otolith was vateritic or damaged, if all measurements could not be completed, or if individual counts differed by more than five increments, that individual was excluded from subsequent analyses.

The relationship between otolith and somatic growth can vary strongly during development, rendering estimates based on simple regressions inaccurate (Campana, 1990). Therefore, to estimate fork length at ocean entry, we used a biological intercept model following Campana (1990).

$$FL_{e,i} = FL_{c,i} + ((OR_{e,i} - OR_{c,i}) \times (FL_{c,i} - FL_h) \times (OR_{c,i} - OR_h)^{-1})$$

where FL is fork length and OR otolith radius for individual  $i$  at ocean entry  $e$ , at capture  $c$  or at hatch  $h$  (the biological intercept). We assumed  $FL_h$  was 19.8 mm, the mean value for intermediate temperature treatments from a published, laboratory-based study on multiple Fraser River sockeye salmon populations (Beacham & Murray, 1988). We also used a mean value calculated from a subset of otoliths ( $0.226 \text{ mm} \pm 0.019 \text{ SD}$ ,  $n = 31$ ) for the  $OR_h$  parameter because this measurement could not be reliably estimated for all samples. We note that the accuracy of biological intercept models is robust to normal variation around the intercept because the values are small relative to variance in later life stages (Campana, 1990).

We estimated marine growth rates as

$$G_i = (FL_{c,i} - FL_{e,i}) \times D_i^{-1}$$

where  $G$  is the mean daily growth rate for individual  $i$  and  $D$  is the number of daily increments formed between marine entry and the otolith edge.

## 2.4 | Statistical analyses

We constructed two sets of hierarchical, linear models to estimate individual variation in two phenological traits: the start date of marine migrations (i.e., ocean entry date) and the duration of the initial marine migration (i.e., number of days from ocean entry date to capture). We included life-history type, represented by freshwater age, as categorical, fixed effects in both models because migratory behaviour appears to be correlated with life-history strategy in juvenile sockeye salmon (Beamish et al., 2016; Freshwater et al., 2016b; Tucker et al., 2009). In the ocean entry date models, we also included size at ocean entry and two proxies for freshwater habitat quality as covariates. The first freshwater habitat covariate, nursery lake latitude, was included to serve as a proxy for photoperiod and temperature, both of which may influence migration timing (Achord, Zabel, & Sandford, 2007; Clarke, Shelbourn, & Brett, 1978). We also tested for effects of downstream migration distance, a proxy for migration difficulty (Weitkamp et al., 2015). These variables were strongly correlated with one another ( $r = 0.96$ ) and were not included in the same model, but compared using an information theoretic approach (details below).

In the migration duration models, we included ocean entry size, ocean entry date and marine growth rate as covariates. We did not include lake latitude or downstream migration distance as covariates because we had no a priori reason to believe they would influence migratory behaviour after juveniles had entered the marine environment. Before fitting models, we confirmed that explanatory variables were not collinear using variance inflation factors (the VIF of all explanatory variables was less <2; VIF <3 indicates minimal collinearity). We centred and scaled continuous predictor variables to better compare models that included covariates measured in different units (Schielzeth, 2010).

To account for nonindependence and estimate variation at different ecological scales, we fit CU, nested within year, as random effects. We included both random intercepts and random slopes to account for CU- and year-specific deviations in mean values, as well as relationships between explanatory and response variables. We did not include CU-specific random effects on latitude or river distance covariates as these variables were already CU-specific. To assess the importance of different predictor variables, we compared models with varying numbers of fixed effects. We compared competing models using differences in the Widely Applicable Information Criterion,  $\Delta\text{WAIC}$ , an alternative to AIC when comparing models with nonflat priors (McElreath, 2016). Details of model structure are provided in Table 1.

## 2.5 | Parameter estimation

We fit models within a Bayesian framework using weakly informative priors (Table 1). We sampled from the posterior distribution using Markov chain Monte Carlo (MCMC) techniques implemented in Stan using the *rethinking* package (McElreath, 2016) in the program R (R Core Team 2017). We ran three MCMC chains of 9,000 iterations each, with a warm-up of 1,000 iterations. To confirm the models converged appropriately, we inspected chain coherence and stability with trace plots, ensured at least 1,000 effective samples were produced, and confirmed each parameter's Gelman–Rubin convergence diagnostic was <1.01 (diagnostics in Supporting Information Tables S1 and S2).

## 3 | RESULTS

We examined otoliths from 679 juvenile sockeye salmon. After excluding vateritic or otherwise damaged samples ( $n = 58$  individuals), we incorporated data from 621 juveniles belonging to nine CUs collected during three years of sampling (Supporting Information Table S3). Based on otolith characteristics, we observed substantial variability among individuals in both the timing and duration of their nearshore migration. Within a given year, sockeye salmon entered the Strait of Georgia over a 40- to 50-day period and resided in the Strait between six and 69 days.

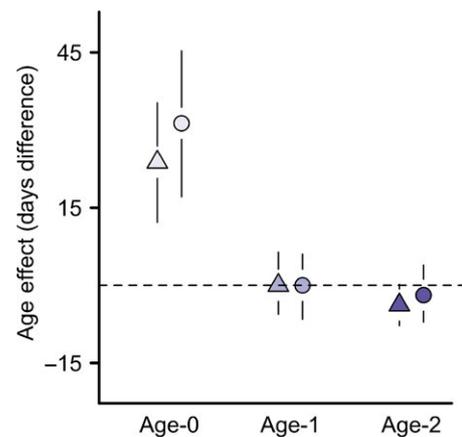
We used hierarchical linear models to clarify how variation in migratory phenology was partitioned among individuals, CUs and sampling years. Model selection indicated strong support for including life-history type and entry size as predictors of entry date, as well as moderate support for including in-river migration distance

**TABLE 1** Model for duration of migration through the Strait of Georgia of individual sockeye salmon  $i$  belonging to conservation unit  $c$  in year  $t$ . The migration timing (i.e., ocean entry date) model was identical except that entry date and marine growth were replaced as covariates by river distance

Data model	$Y_{tci} \sim \text{Normal}(\mu, \sigma)$
Process model	$\mu_{tci} = A_{tc} + B_{\text{date},tc} D_i + B_{\text{growth},tc} G_i + B_{\text{size},tc} S_i + B_{\text{age0},tc} Y_{0,i} + B_{\text{age2},tc} Y_{2,i}$ $A_{tc} = \alpha + \alpha_c + \alpha_t$ $B_{\text{date},tc} = \beta_{\text{date}} + \beta_{\text{date},c} + \beta_{\text{date},t}$ $B_{\text{growth},tc} = \beta_{\text{growth}} + \beta_{\text{growth},c} + \beta_{\text{growth},t}$ $B_{\text{size},tc} = \beta_{\text{size}} + \beta_{\text{size},c} + \beta_{\text{size},t}$ $B_{\text{age0},tc} = \beta_{\text{age0}} + \beta_{\text{age0},c} + \beta_{\text{age0},t}$ $B_{\text{age2},tc} = \beta_{\text{age2}} + \beta_{\text{age2},c} + \beta_{\text{age2},t}$ <p>where <math>D</math>, <math>G</math>, <math>S</math>, <math>Y_0</math>, and <math>Y_1</math> are the entry date, growth rate, entry size and age-0 and age-1 dummy variables, respectively, for individual <math>i</math></p>
Multivariate priors	$\begin{bmatrix} \alpha_c \\ \beta_{\text{date},c} \\ \beta_{\text{growth},c} \\ \beta_{\text{size},c} \\ \beta_{\text{age0},c} \\ \beta_{\text{age2},c} \end{bmatrix} \sim \text{MVN}(0, S_c)$ $\begin{bmatrix} \alpha_t \\ \beta_{\text{date},t} \\ \beta_{\text{growth},t} \\ \beta_{\text{size},t} \\ \beta_{\text{age0},t} \\ \beta_{\text{age2},t} \end{bmatrix} \sim \text{MVN}(0, S_t)$
Adaptive priors	$S_c = \begin{bmatrix} \phi_{\alpha_c}^2 & \dots & \phi_{\alpha_c} \phi_{\beta_{\text{age2},c}} \rho_{\alpha_c, \beta_{\text{age2},c}} \\ \vdots & \ddots & \vdots \\ \phi_{\alpha_c} \phi_{\beta_{\text{age2},c}} \rho_{\alpha_c, \beta_{\text{age2},c}} & \dots & \phi_{\beta_{\text{age2},c}}^2 \end{bmatrix}$ $S_t = \begin{bmatrix} \phi_{\alpha_t}^2 & \dots & \phi_{\alpha_t} \phi_{\beta_{\text{age2},t}} \rho_{\alpha_t, \beta_{\text{age2},t}} \\ \vdots & \ddots & \vdots \\ \phi_{\alpha_t} \phi_{\beta_{\text{age2},t}} \rho_{\alpha_t, \beta_{\text{age2},t}} & \dots & \phi_{\beta_{\text{age2},t}}^2 \end{bmatrix}$
Fixed priors	$\alpha \sim \text{Normal}(15,30)$ $\beta_{\text{age0}} \sim \text{Normal}(5,30)$ $\beta_{\text{age2}} \sim \text{Normal}(0,30)$ $(\beta_{\text{date}}, \beta_{\text{growth}}, \beta_{\text{size}}) \sim \text{Normal}(0,3)$ $(\sigma, \phi_{x_c}, \phi_{x_t}) \sim \text{Cauchy}(0,2)$ $(\rho_{x_c}, \rho_{x_t}) \sim \text{LKJcorr}(4)$

or latitude (top-ranked model had three fixed covariates, including river distance, and 0.71 of WAIC weight; Supporting Information Table S4). Similarly, life-history type, entry size, entry date and marine growth rates were supported as predictors of migration duration (top-ranked model had >0.99 of model weight; Supporting Information Table S5).

Life-history type, represented by freshwater age, had a particularly strong effect on the timing and duration of migration. Although we did not sample any Harrison River individuals, the Fraser River's most abundant sea-type CU, we observed age-0 (i.e., sea-type) migrants in two CUs that are typically dominated by lake-type individuals. Age-0 individuals made up a relatively small fraction of the total catch (1.5% across all years); however, these juveniles consistently entered the marine environment approximately three weeks later in the year and resided in the Strait for approximately 30 days longer than individuals that had reared in nursery lakes for one or two years (Figure 2). Although age-2 juveniles (3.7% of sampled individuals across all years) entered the marine environment earlier in the year



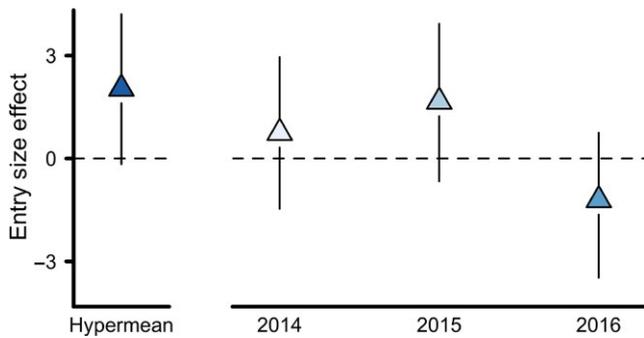
**FIGURE 2** Posterior estimates of entry date (triangles) and duration of migration (circles) for each age class. Whiskers represent 90% highest posterior density interval (HPDI). Y-axis labelled to represent deviations from age-1 individuals so that horizontal line represents mean phenology of age-1 fish

and moved through the Strait more quickly on average, these posterior parameter estimates overlapped zero, suggesting differences were moderate after accounting for the effect of other covariates (Figure 2).

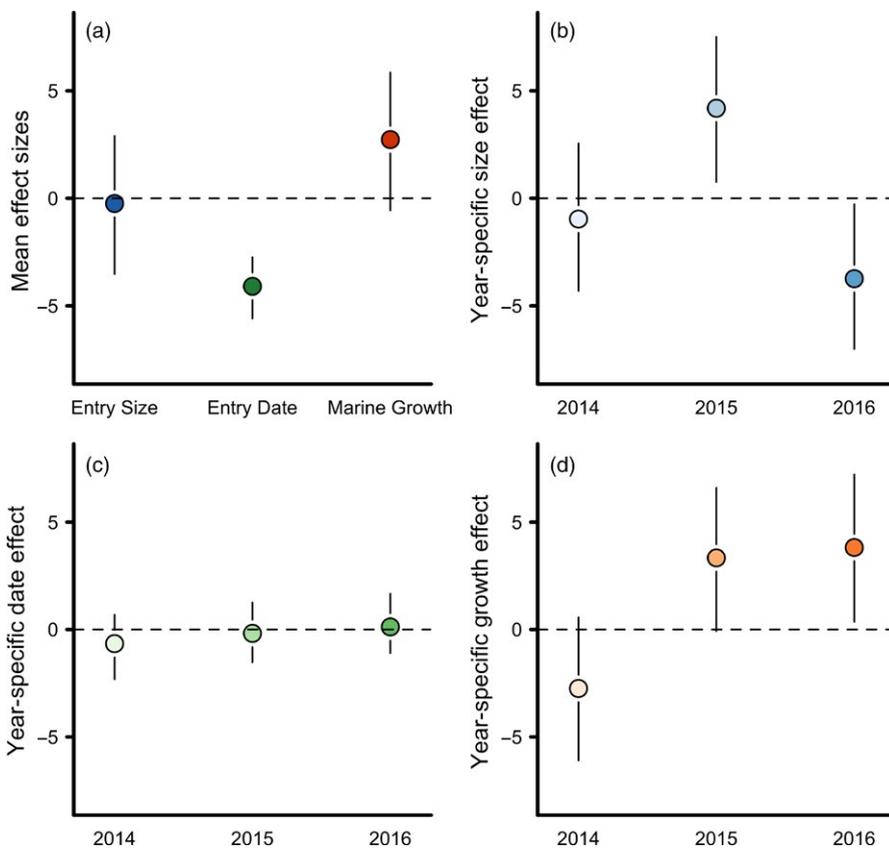
Model selection indicated strong support for including all individual traits as fixed covariates (Supporting Information Tables S2 and S3); however, the overall mean effects of entry size, and marine growth on migratory traits were moderated by interannual differences in the magnitude, and even direction, of these effects (Figures 3 and 4). Body size was generally positively correlated with entry date and negatively correlated with number of days spent migrating (i.e., larger individuals entered later in the year

and migrated more quickly on average); however, these patterns reversed in certain years (Figures 3 and 4b). Entry date and marine growth had more consistent effects on migration duration—individuals that entered late in the year and grew quickly moved through the Strait in a shorter period of time (Figure 4c,d). Unlike the considerable interannual variability in covariate effects, posterior means of CU-specific estimates were nearly always centred on zero (Supporting Information Figure S1), suggesting the effect of individual traits on migration timing and duration is relatively stable among CUs.

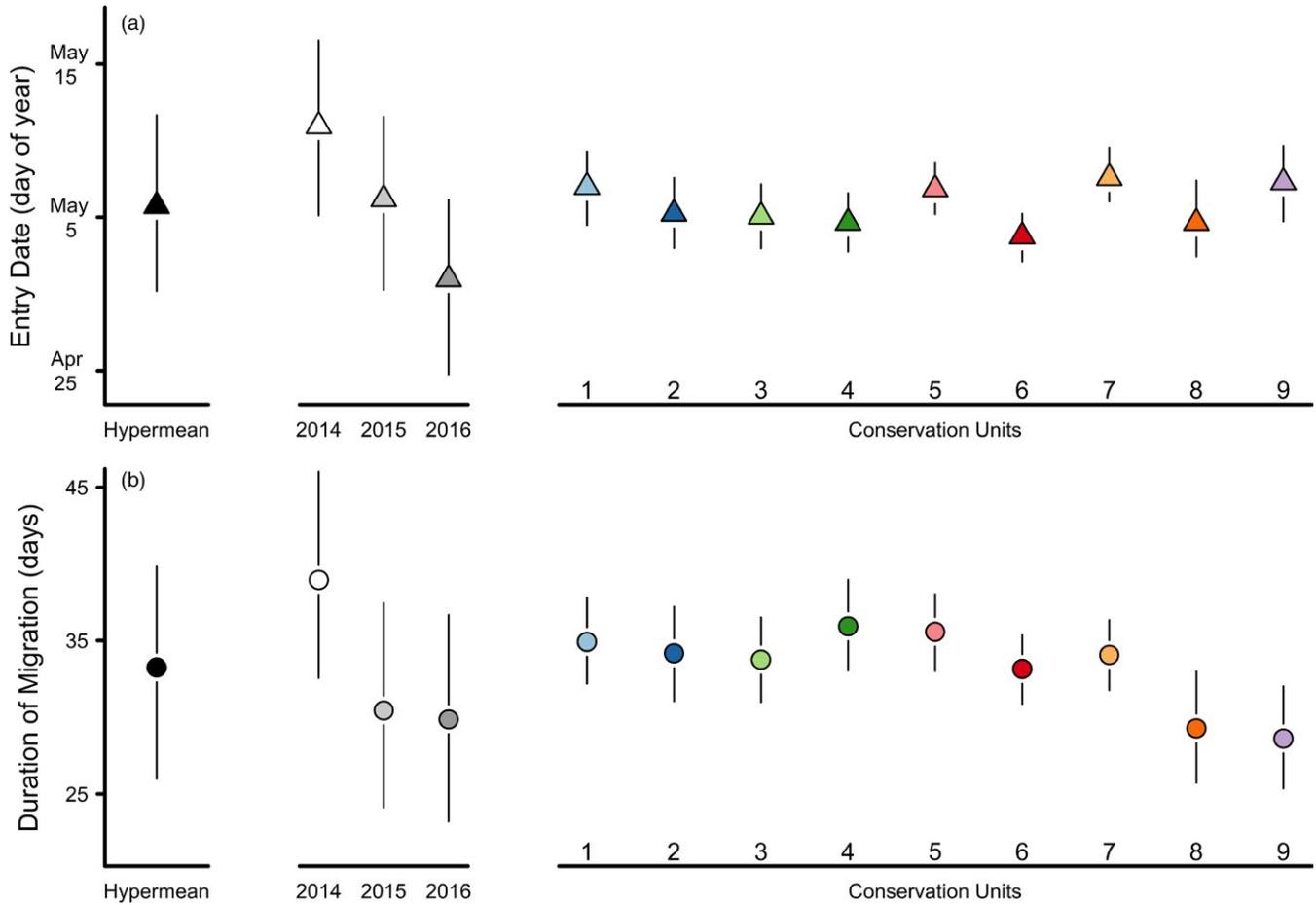
We observed considerable variation among years and CUs in mean entry date and duration of migration (Figure 5). In the case of entry date, these differences were associated with differences in downstream migration distance—CUs that reared further upriver entered the marine environment later in the year. Including migration distance as a covariate was supported by model selection (Supporting Information Table S4) and reduced variation among CUs considerably (Figure 5); however, its posterior estimates were relatively small and overlapped zero in all years ( $\beta_{\text{dist}} = 0.74$  90% HPDI =  $-0.51$  to  $1.96$ ; Supporting Information Figure S2). After accounting for the effect of river distance and individual traits, migrations began earlier in more recent years and were consistently later in certain CUs (Figure 5). Migration duration was considerably longer in 2014 and considerably shorter among individuals migrating from specific CUs such as Nadina-Francois-ES and Francois-Fraser-S (Figure 5). Overall, we observed less variation in mean migration



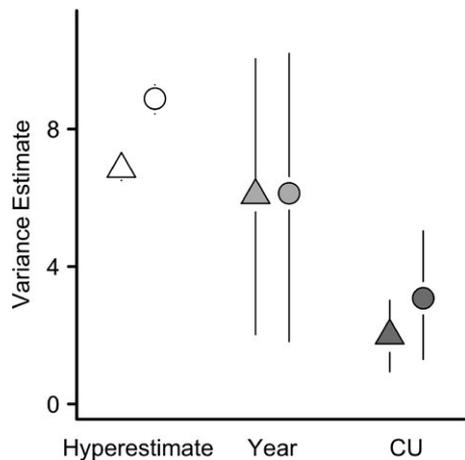
**FIGURE 3** Posterior mean estimates of entry size effects on ocean entry date. Whiskers represent 90% highest posterior density interval (HPDI)



**FIGURE 4** Posterior hyper- (a) and year-specific (b–d) mean effects for explanatory covariates in the duration of migration model. Whiskers represent 90% highest posterior density interval (HPDI)



**FIGURE 5** Posterior estimates of overall mean entry date (a) and duration of migration (b), as well as year- and CU-specific deviations from the hypermean. Whiskers represent 90% HPDI estimates. CUs ordered relative to migration distance: (1) Pitt-ES, (2) Chilliwack-ES, (3) Lillooet-Harrison-L, (4) Shuswap-ES, (5) Shuswap-L, (6) Chilko-S/Chilko-ES, (7) Quesnel-S, (8) Francois-Fraser-S, (9) Nadina-Francois-ES. Note that the entry date model (top panel) includes migration distance as a covariate



**FIGURE 6** Posterior estimates of variance parameters ( $\sigma$ ,  $\phi_{yr}$ ,  $\phi_{CU}$ ) for mean entry date (triangles) and duration of migration (circles). Whiskers represent 90% HPDI estimates

timing than mean entry date (Figure 6), as well as greater inter-annual and residual variation in these traits than between CUs (Figure 6).

#### 4 | DISCUSSION

The phenology of long-distance migrations can influence individual fitness (Dickerson, Brinck, Willson, Bentzen, & Quinn, 2005; Kokko, 1999), as well as the availability of ecosystem services provided by migratory populations (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Schindler et al., 2010). Consequently, how phenology varies among and within populations can shape the dynamics both of migratory species (Cooke et al., 2004; Newton, 2006) and the broader ecological community (Deacy et al., 2016; Ruff et al., 2011; Schindler et al., 2013). We used hierarchical models to examine how variation in the timing and duration of juvenile Fraser River sockeye salmon marine migrations was partitioned among individuals, conservation units (groupings of genetically and ecologically similar populations managed as a unit) and sampling years. Migration phenology was correlated with a suite of individual characteristics determined during residence in nursery lakes, suggesting carry-over effects of freshwater life-history stages on both the timing and duration of early marine migrations. Even after accounting for these individual effects, however, several CUs exhibited distinct migratory phenologies. Furthermore,

we observed considerable interannual variation in migration phenology, likely due to dynamic environmental processes. Years differed not only in mean migration timing and duration, but also in the relationship between individual traits and migration phenology. Our results provide evidence that migratory diversity within a metapopulation is shaped by interactions between individual characteristics, population-specific behaviours and stochastic processes occurring at multiple temporal scales.

Individuals exhibit considerable variation in traits such as body size and condition that moderate migratory performance (Gunnarsson et al., 2006; Marra et al., 1998). Previous evidence indicates that individual salmon differ in their use of nearshore stopover habitats (Moore et al., 2016) and are broadly distributed in space and time during marine migrations along the continental shelf (Beacham et al., 2014a; Tucker et al., 2009). Furthermore, such heterogeneity appears to be influenced by conditions experienced during freshwater rearing via variation in juvenile size and ocean entry timing (Freshwater et al., 2016b). The present study clarifies that individual traits shape the timing and duration of migration at finer ecological scales than previous studies, which may have important consequences for population dynamics given that juvenile survival is often associated with out-migration phenology (Scheuerell et al., 2009).

Juvenile salmon life history, represented by freshwater age, was correlated with differences in both the timing and duration of marine migrations. Sea-type individuals (freshwater age-0) entered the marine environment more than three weeks later and remained in the Strait for approximately a month longer than lake-type individuals, even after accounting for differences in traits such as size. The sea-type juveniles observed here originated from lake-type CUs, a scenario that is rarely observed in sockeye salmon in this region (Burgner, 1991). Interestingly, their phenology resembled that of the Harrison River CU, the most abundant sea-type population in the Fraser River, which enters the Strait of Georgia relatively late in the year and resides there longer than other CUs (Beacham et al., 2014a; Beamish et al., 2016; Tucker et al., 2009). Notably, Harrison River has experienced greater productivity in recent years relative to other CUs in the metapopulation (Freshwater et al., 2018; Peterman & Dorner, 2012). Thus, it seems possible that selection may currently favour a sea-type life history and that age-0 individuals could become proportionally more abundant in the future.

Conversely, differences between age-2 and age-1 individuals were more moderate. Although age-2 individuals typically migrated earlier and spent fewer days in the Strait, these differences were small (one to three days) and posterior estimates overlapped zero. These patterns suggest that differences in migration phenology among age-2 and age-1 juveniles may be driven by traits, such as body size, that covary with age.

Migrants often moderate their behaviour based on the interaction between food availability, energy deposition rate and departure timing (Jenni & Schaub, 2003). In this study, entry date was consistently negatively correlated with the duration of migration, indicating juveniles that entered late in the year migrated out of the region relatively quickly. Seasonal increases in movement

rates may reflect changes in zooplankton abundance, the primary prey for juvenile sockeye salmon, which typically peaks earlier in the Strait than further north along the migratory corridor (Mackas et al., 2012). Migration duration was also positively correlated with growth rates, suggesting individuals that were growing more rapidly, remained in the Strait for longer. The migration speeds of juvenile Chinook salmon (*O. tshawytscha*) are negatively correlated with primary productivity and zooplankton biomass (Burke, Liermann, Teel, & Anderson, 2013; Tomaro, Teel, Peterson, & Miller, 2012), and juvenile sockeye salmon may increase travel speeds when competitors are abundant (Freshwater et al., 2017). Juvenile salmon migrate long distances to exploit opportunities for rapid growth in northern habitats (Quinn, 2005). Presumably, these migrations are timed to coincide with seasonal peaks in prey availability; however, the shifts in migration speed that we observed suggest that salmon may delay their movements when local environmental conditions are relatively favourable for growth.

Although body size was negatively correlated with entry date, its effect on migratory duration varied across years. This variability contrasts with previous studies where size was consistently and positively correlated with travel speeds (Freshwater et al., 2016a,b, 2017). In particular, the effect of size on migration duration reversed in 2015, a year in which age-0 juveniles were most abundant, while the body size of lake-type individuals was smaller on average and less variable. These patterns may have altered the average relationship between size and migration duration in this year. Size effects may also have been weakened by the influence of entry date and freshwater age (although VIF did not indicate marked collinearity, entry size is correlated with both traits).

Sockeye salmon populations exhibit distinct spatial distributions (Beacham et al., 2014a; Tucker et al., 2009) and physical traits (e.g., body size; Beacham et al., 2014b) during juvenile migrations. However, it is not immediately clear how variation within populations interacts with population-specific strategies to shape migratory characteristics. In this study, we used hierarchical models to clarify how variation among CUs in early marine traits influenced migration phenology, after accounting for the effect of a suite of individual traits. Generally, CUs from interior systems (Francois-Fraser-S and Nadina-Francois-ES) were observed migrating late in the year and moving relatively rapidly through the Strait of Georgia. These trends in migration timing are consistent with evidence from the Fraser (Neville et al., 2016) and Columbia Rivers (Weitkamp et al., 2015) that interior populations tend to exit freshwater later than those located further downriver. Although the estimated effect size of in-river migration distance on ocean entry timing in this study was uncertain, the median slope estimate was positive and reduced posterior estimates of variation among CUs. We did not include in-river migration distance as a covariate in migration duration models because there is no clear mechanism linking the two after accounting for variation in entry date. Even so, after accounting for entry date and other individual traits, interior CUs migrated more rapidly through the Strait than CUs rearing in lakes closer to the coast.

This pattern, as well as the relatively weak effect of migration distance on entry timing, suggests that our model does not fully incorporate the mechanisms driving differences among CUs in migration phenology. One explanation is that traits such as body size have population-specific effects, yet the relationship between individual traits and phenology appeared to be stable among the CUs we examined. Alternatively, certain lakes may be exposed to unique drivers (e.g., longer or more frequent winter ice-over), which may create a nonlinear relationship between distance/latitude and juvenile migration phenology, as well as carry-over effects on marine migration. CU-specific differences in phenology could also be the result of varying degrees of local adaptation (Carlson & Seamons, 2008), driven by differences in connectivity among CUs. Interior populations of Pacific salmon appear to receive fewer strays than downstream populations (Keefer, Peery, Firehammer, & Moser, 2005), likely due to the high costs associated with upstream migration (Crossin, Hinch, Farrell, Higgs, & Healey, 2004). As a result, interior populations may be more likely to exhibit adaptive divergence, including distinct juvenile migratory phenologies, than coastal populations.

Given that both biotic (e.g., prey availability) and abiotic (e.g., inclement weather) drivers can lead to interannual variation in animal migrations (Jenni & Schaub, 2003), it was unsurprising that sockeye salmon phenologies varied across years. Too few years were sampled here to test specific hypotheses; however, abiotic factors such as temperature (Jonsson & Jonsson, 2014), river flow velocity (Connor, Tiffan, Plumb, & Moffitt, 2013) and current strength (Burke, Anderson, & Baptista, 2014) have been shown to constrain juvenile migrations in salmon populations. The effect of these physical factors on the timing and speed of migrations may also be moderated by biological variables such as zooplankton biomass (Tomaro et al., 2012), primary productivity (Burke et al., 2013) or density-dependent increases in migration rate (Freshwater et al., 2017). For instance, the slower migration out of the Strait in 2014 could have been related to conditions broadly favourable for growth, including relatively cool temperatures (Chandler, 2015) and late phytoplankton bloom (Allen & Latornell, 2015). Given that sea surface temperatures throughout coastal British Columbia were anomalously warm in 2015 and 2016 (Chandler, King, & Boldt, 2017), it is possible that 2014 is more representative of juvenile migration phenologies in recent decades.

The relatively large posterior estimates for residual variance ( $\phi_x$ ,  $\phi_y$ ) indicate migration phenology within a given CU and year is heterogeneous, even after accounting for variation in traits such as body size. Sockeye salmon can exhibit phenological variation within population aggregates that is associated with differences in spawning habitat at relatively small spatial scales (McGlaufflin et al., 2011). By aggregating individuals at the scale of CUs, it is possible we obscured such population-specific strategies. Additionally, juvenile salmon marine migrations appear to be influenced by hydrographic features within large river plumes (Burke et al., 2014), as well as wind-induced surface currents (Peterman et al., 1994). Given the relatively small size of juvenile sockeye salmon, they may be particularly vulnerable to such stochastic processes. Consistent with previous tagging studies (Clark et al., 2016), variance in the duration of migration was

consistently greater than variance in entry date, suggesting that individuals moving downriver in high densities become more dispersed as they migrate through marine habitats. Intrapopulation variation in ocean entry phenology and duration of nearshore residence may be adaptive given that the optimal timing of juvenile migratory events can shift year to year (Scheuerell et al., 2009).

A complementary project conducted within the Fraser River also estimated the ocean entry phenology of sockeye salmon and sampled several of the same CUs as this study (Neville et al., 2016; C. Neville, unpublished data). Most CUs common to both studies had similar estimates of entry timing, but several diverged and in-river estimates were approximately one week earlier. Although differences in entry timing between the two surveys may be due to back-calculation errors associated with otolith microstructure techniques, it is unclear why it would occur only in a subset of CUs. Alternatively, the two survey designs may have sampled different portions of each population. Juvenile sockeye salmon were scarce or absent during sampling events at the beginning and end of the marine surveys, suggesting the protocol sampled the overall migratory period. Yet, catch data provide only a snapshot of the spatial distribution of migrating fishes and our sampling may have produced incomplete estimates of migration phenology. For example, individuals that move more rapidly through a sampling location are less likely to be collected and the purse seine survey may have missed large schools of comigrating individuals that were more easily captured in-river. Assuming that both surveys sampled a representative portion of the population, it is also possible that differences are driven by the selective mortality of early migrants.

The variation in migration phenologies that we observed may be used to inform management strategies. For example, indicator populations are often used as proxies for the status of multiple salmon populations within an aggregate. Although a sampling period of three years is too brief to determine conclusively that Fraser River CUs do or do not comigrate with one another, the majority of the CUs we examined exhibited relatively similar behaviours. If these sampling years are representative, individuals from the Chilko CU (currently the Fraser River's principal indicator population) may serve as a reasonable proxy for many CUs that are less intensively sampled. Conversely, interior CUs that migrated late in the year and moved through the Strait of Georgia relatively rapidly may be less vulnerable to nearshore stressors. Additionally, individual traits that have consistent impacts on phenology and are relatively easily observed at the population level may be useful for predicting environmental interactions. For instance, when ocean entry occurs earlier in the year, juvenile salmon appear to utilize nearshore habitats for longer periods. If nearshore residence co-occurs with adverse conditions, then certain year classes may be more likely to exhibit poor early marine survival. Because individual traits will be shaped by freshwater environmental conditions, management actions should develop strategies that conserve or enhance linkages between disparate habitats. As the benefits of intraspecific diversity to ecological resilience become increasingly recognized (Schindler et al., 2010), our results indicate that managers should seek to conserve diversity both within and between sockeye salmon CUs.

This study clarifies how processes acting across multiple ecological scales, as well as occurring both before and after the initiation of migration, moderate phenology. We observed evidence of carry-over effects from freshwater residence on the timing and duration of juvenile sockeye salmon migrations. Furthermore, conditions experienced en route appeared to alter migratory behaviour via changes in growth. Yet, these individual traits do not fully account for variation in phenology among populations, suggesting local adaptation may constrain individual migratory plasticity. Finally, stochastic processes at interannual and finer scales introduced additional variability and moderated the effect of traits such as body size. The cumulative effect of these drivers is to increase the duration over which migratory populations are present in specific habitats. Such increases in phenological diversity may act to stabilize the productivity of population aggregates and increase the availability of ecosystem services provided by migratory species (Ruff et al., 2011; Schindler et al., 2010, 2013).

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## AUTHORS' CONTRIBUTIONS

C.F., M.T., S.G., S.J. and F.J. developed hypotheses and methodology; C.F., C.N. and T.B. collected data; C.F. led the analysis and writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.25v2429> (Freshwater et al., 2018b). Data, as well as the R code used to fit the hierarchical models, are also available from Zenodo <https://doi.org/10.5281/zenodo.1243958> (Freshwater et al., 2018a).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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