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Disentangling individual- and population-scale processes within a latitudinal size-gradient in Sockeye Salmon

Cameron Freshwater[1], Marc Trudel[1,2], Terry D. Beacham[2], Lyse Godbout[2], Chrys-Ellen M. Neville[2], Strahan Tucker[2], and Francis Juanes[1]

[1]Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5, Canada.

[2]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, V9T 6N7, Canada.

Running Header – Multi-scale Processes Within A Size-Gradient

Abstract

We examined how individual processes contribute to a latitudinal gradient in body size within populations of migrating juvenile Sockeye Salmon (*Oncorhynchus nerka*) while simultaneously testing for size-selective mortality, a potentially confounding population scale process. Using otolith microstructure techniques and structural equation modeling, we determined that ocean entry size and phenology had strong, direct effects on size at capture. Population identity and freshwater age also had strong indirect effects, moderated by size at entry. Conversely, marine growth rates immediately after entry or before capture were relatively weak predictors of size during migration. We next tested for shifts in size distribution indicative of selective mortality, but detected no evidence of smaller individuals experiencing lower survival during early marine migrations. These results indicate that the migratory distributions of juvenile Sockeye Salmon are influenced by body size and that this variation is predominantly driven by traits present prior to freshwater outmigration, rather than marine growth or differential survival. We suggest integrating individual variation in migratory characteristics with the effects of environmental conditions experienced en route to provide an improved understanding of migratory species.

Key Words: body size; migration; size-selective mortality; structural equation modeling

Introduction

Due to the strong link between body size and a wide range of ecological patterns, quantifying and interpreting variation in size within populations is often a critical step to understanding their dynamics (Peters 1983, Brown et al. 2004). This is particularly true in migratory species where body size is positively correlated with both travel speed (Ware 1978) and energy stores (Huss et al. 2008). Although differences in body size are strongly influenced by genetics and life-history strategy, from a proximal perspective they are a function of an individual's previous size, growth rate, and age. However the frequency of size classes within a group can also be strongly influenced by size-dependent mechanisms, such as selective mortality, that act on the population as a whole (Sogard 1997). As a result, the size distribution of a migrating population may be predominantly static and driven by individual traits that are present prior to departure or moderated by the conditions the population experiences during its long distance movement.

Sockeye Salmon (*Oncorhynchus nerka*, Walbaum) is an anadromous species with a broad geographic distribution, distinct life history strategies at several biological scales (Burgner 1991), and evidence of differential migration between and within populations (Beacham et al. 2014a, Beacham et al. 2014b). After rearing in freshwater systems, juvenile Sockeye Salmon migrate from coastal rivers to maturation grounds in the North Pacific Ocean and Bering Sea over a period of several months (Burgner 1991). Juveniles travelling along the coastal migration corridor exhibit a consistent latitudinal gradient in body size. Individuals captured in northern regions are significantly larger and in better condition than those captured at approximately the same time further south (Tucker et al. 2009, Beacham et al. 2014b). Furthermore, this pattern persists from May through the following March each year, across more than a decade of survey data (Tucker et al. 2009, Beacham et al. 2014b). Since this gradient persists within a given population aggregate, differences in body size are not an artifact of northern regions simply producing larger fish *sensu* Bergmann's rule (Tucker et al. 2009, Beacham et al. 2014b).

Instead, larger body size in northern regions is expected to be correlated with individual traits influenced by both freshwater and marine rearing environments. Specifically, greater size at ocean entry (smolt size), a longer period of time at sea, more years spent rearing in freshwater, faster growth at key points during migration, or a combination of several of these traits could create a latitudinal gradient in body size (Tucker et al. 2009). Populations that produce larger smolts are typically distributed further north and earlier in the year, which supports the hypothesis that size at ocean entry can shape spatial variation in size (Beacham *et al.* 2014b). Yet it is unknown whether there is sufficient variation in smolt size to create a latitudinal gradient within populations and the effects of ocean entry timing, age, and marine growth are untested altogether.

Alternatively, changes in the size distribution of a migrating population may be the result of processes acting on that population as a whole, rather than the differential migration of individuals. Mortality is estimated to be especially high among juvenile Pacific salmon at sea (Beamish and Mahnken 2001) and appears to be size-selective in several populations (Holtby et al. 1990, Henderson and Cass 1991, Bond et al. 2008, Claiborne et al. 2011, Duffy and Beauchamp 2011); however, it remains unclear whether this mortality is greatest during juvenile migrations, during the first winter at sea, or is stable throughout ocean residency. If mortality rates of Sockeye Salmon are particularly high during northward migrations, an increase in the mean size of the population with latitude could occur due to the selective removal of the smallest individuals independently of individual variation in migratory characteristics.

Tucker et al. (2009) and Beacham et al. (2014b) observed an increase in juvenile Sockeye Salmon body size with latitude; however, the nature of their data prevented them from examining individual populations in a given year. Therefore, our first objective was to test the hypothesis that body size of Sockeye Salmon varies consistently with latitude while controlling for inter-annual and population effects. Next, we tested the relative importance of size at ocean entry, length of ocean residency, marine growth, and age in creating a body size gradient. Since migratory phenology and size often vary between years (Kovach et al. 2013) and populations (Beacham et al. 2014b), we also tested for inter-annual and population effects. Finally, we tested for the presence of size-selective mortality (SSM) to determine whether population scale processes could be interacting with or masking individual differences.

Methods

At the level of the individual, the final body size of an organism (L_t) is a function of its previous size (L_0), growth (G), and time (t) where:

(1) $$L_t = L_0 + G*t$$

To gauge the relative importance of variation among individuals, each of these parameters must be estimated during the period of interest. In this study, L_0 represented size at the beginning of migration (i.e. ocean entry) and G represented growth during a time period of days (t). We examined growth during two distinct periods. First, we estimated growth during the initial week after ocean entry because of its association with the duration of nearshore residency and migratory rate of other salmonids (Healey 1980). The second period represented growth in the week immediately prior to capture and was chosen to encompass potential spatial variation in growing conditions that could result in divergent body sizes developing en route (Tucker et al.

2009, Ferriss et al. 2014). Depending on population and growth history, Sockeye Salmon can enter the marine environment as sub-yearlings or after a variable number of years of freshwater rearing. Since freshwater age may be correlated with body size and phenology (Bugayev 2000), we also estimated its indirect effect on capture fork length via size at ocean entry and length of marine residency.

Conversely, tests of size-selective mortality (SSM) require repeated sampling of a population over time or space so that size distributions before and after potential mortality events can be compared. In juvenile fishes SSM is generally directional so that larger individuals have higher survival rates (Sogard 1997). As smaller individuals are removed via SSM, the size distribution of the population should exhibit decreased variance, increased kurtosis, and negative skewness (indicative of a rightward shift), as well as an increase in mean size (Gagliano et al. 2007).

Data Collection

We collected juvenile Sockeye Salmon in 2007 (June 22 – July 5) and 2008 (June 21 – July 3) from seven sampling regions along a south-north gradient from southern British Columbia to the Alaskan border (Fig. 1; Table S1). Fish were captured with a mid-water rope trawl hauled at the surface for 15-30 minutes at 5 knots (~9.8 km/h) by *CCGS W.E. Ricker* and *F/V Viking Storm*. Up to 30 juvenile Sockeye Salmon were randomly selected from each net tow for sampling. We recorded fish length and mass and removed both sagittal otoliths at time of capture. Tissue samples were removed from the operculum and preserved for population identification. Individuals were identified to the population level using 14 microsatellite loci

(Beacham et al. 2005). A 50% probability was used as a lower limit when assigning individuals to populations and the false assignment rate was estimated to be 5% (Beacham et al. 2005).

To ensure a sufficient sample size the analysis focused on individuals belonging to four of the most abundant populations. Lower Adams River (LA) and Chilko Lake (CH) are populations that are located in the Fraser River drainage, approximately 484 km and 629 km, respectively, from their ocean entry point in the southern Strait of Georgia (Crossin et al. 2004). After ocean entry, both populations generally migrate north through Johnstone Strait (Tucker et al. 2009; Beacham et al. 2014a, 2014b). Great Central Lake (GC) and Sproat Lake (SP) populations spawn in central Vancouver Island (26 km and 8 km from the coast, respectively), enter the ocean on the west coast via Barkley Sound, and undertake a similar northward migration along the continental shelf (Wood et al. 1993, Tucker et al. 2009, Beacham et al. 2014b, Beacham et al. 2014a). North of Vancouver Island, all four populations are commonly captured together and appear to exhibit similar migratory pathways to their maturation grounds in the Gulf of Alaska (Tucker et al. 2009; Beacham et al. 2014a, 2014b; Fig. 1).

We used otolith microstructure techniques to estimate the growth and migration history of captured fish. Otoliths are calcareous structures found in many teleosts that are commonly used in age and growth studies because of their incremental formation. Otolith and somatic growth are strongly correlated in juvenile Sockeye Salmon and individuals form a distinct marine entry check mark after transitioning to saltwater (Freshwater et al. 2015). Therefore otolith size at this check can be used as a proxy for body size at ocean entry. By enumerating and measuring the spacing between otolith micro-increments that are formed daily after the marine entry check mark, it is possible to estimate length of ocean residency and marine growth rates, respectively (Neilson et al. 1985, Zhang and Beamish 2000). Finally, annual age can be inferred by counting annuli, large opaque bands that represent periods of slower, winter growth (Neilson et al. 1985, Zhang and Beamish 2000).

The otolith microstructure of approximately one third of the captured individuals (*n* = 367) was examined. Microstructure observations were made after otoliths were polished by hand following methods in Freshwater et al. (2015). cellSens Imaging Software (Olympus Scientific Solutions America) was used to measure several otolith microstructure characteristics: 1) marine entry check radius, 2) number of daily circuli after entry mark, 3) length of first marine weekly increment, 4) length of last marine weekly increment, and 5) freshwater age. We measured radii from the otolith core to the marine entry check. We enumerated increments between the marine entry check mark and the otolith periphery to estimate days at sea. To estimate weekly growth, we measured the distance between the marine entry check and the seventh daily ring after marine entry (first week of growth) and between the seventh to last daily ring and the otolith periphery (last week of growth). Individuals with one freshwater winter annulus were classified as age-1 and those with two as age-2. All measurements were made dorsal and perpendicular to the anterior-posterior centerline of the otolith (Fig. 2) and were completed three times per otolith with the average used in subsequent analysis. If measurements could not be completed due to damage or if counts differed by more than eight daily rings, the otolith was discarded (18 out of 367).

Otolith width was positively and linearly related to fork length at capture ($r^2 = 0.80$, $n = 367$, $P < 0.001$), suggesting the radius of the marine entry provides a reasonable estimate of fork length at ocean entry. However since estimates of size are necessarily calculated using fork length at capture (e.g. Neilson et al. 1985), we were concerned that using back-calculated estimates of entry size in the SEMs could falsely inflate the correlation between size at ocean entry and size at capture. Therefore, raw otolith microstructure measurements were used in model construction.

Statistical Analyses

Since tissues were not collected from juvenile Sockeye Salmon captured in the Strait of Georgia in 2007, stock identification could not be completed on these individuals. Therefore, we conducted all analyses on two distinct datasets to spatially and temporally balance the sampling design. The first dataset included Vancouver Island populations (GC and SP) sampled in both 2007 and 2008 (subsequently referred to as VI dataset), while the second included Fraser River populations (CH and LA) captured in 2008 (subsequently referred to as FR dataset).

We used linear models to test the hypothesis that fork length at capture increased with latitude, while controlling for the effects of population identity and year of capture (set as fixed effects and coded as dummy binary variables). Since fork length at capture was not normally distributed, it was log transformed before constructing linear models.

Next, we used structural equation modeing (SEM) to examine the relationship between fork length at capture and the suite of early marine characteristics estimated from otolith microstructure (see methods above). In SEM, multivariate techniques are used to simultaneously model several interacting processes and provide insight on their cumulative effects (Grace and Keeley 2006). Given that variability in body size, phenology, age, and growth can have cascading effects on each other, SEM provides an ideal framework for disentangling causal pathways among these individual characteristics. We specified, evaluated, and adapted models following guidelines developed for ecological systems in Grace et al. (2010). We developed *a priori* models based on observational and theoretical evidence (Fig. 3; detailed justifications for paths provided in Table S2). Initially we did not include direct effects linking population and year to size at capture to test whether the other explanatory variables adequately accounted for inter-population and –annual effects. However, these SEMs fit poorly and direct links between population and year to capture size were included in all final models. Differences in the structure of the FR and VI datasets forced us to specify unique SEMs for each region including: a) unique focal populations, b) no year effect in the FR model since population-identified data were not available for 2007 (see above), and c) no freshwater age effects in the FR model because only two age-2 fish from these populations were captured.

To compare the relative importance of early marine characteristics that differed substantially in unit of measurement and variance, all continuous variables were centered and reduced to a mean and variance of zero and one, respectively. Although fork length at capture and marine entry check radius measurements were not normally distributed, we estimated SEMs using either weighted least-square with mean and variance corrected (WLSMV; VI dataset) or robust maximum likelihood techniques (MLR; FR dataset). Since both are robust to deviations from normality (Brown 2006, Rosseel 2012), we standardized, but did not transform all data. WLSMV was required for the VI dataset SEM since it included an endogenous categorical variable (i.e. freshwater age).

We confirmed adequate model fit with a chi-square goodness of fit index, which compares the implied model covariance structure to that of the raw data ($P > 0.05$ indicates adequate fit), and secondarily tested fit with four additional indices (Table S3): Normed Fit Index (Bentler and Bonett 1980), Non-Normed Fit Index (Hu and Bentler 1998), Root-Mean-Square Error of Approximation (MacCallum et al. 1996), and Comparative Fit Index (Bentler

1990). We calculated the indirect effects of explanatory variables on capture size by multiplying coefficients from compound significant paths (Grace and Keeley 2006).

To test for the presence of SSM, we estimated three metrics associated with size distributions: variance, Pearson's kurtosis coefficient, and Pearson's skewness coefficient. We calculated each metric for each subpopulation, i.e. a unique combination of population, sampling region, and year (regions denoted in Fig. 1; catch breakdown in Table S1). Specifically, we predicted that if SSM was the principal mechanism of a latitudinal increase in mean size, variance would decrease, kurtosis would increase, and skewness would decrease (indicating a rightward shift) with increasing latitude. To test these hypotheses, we compared the performance of a suite of hierarchical linear models testing for correlations between each SSM metric and latitude, while controlling for the effects of population identity and sampling year.

Since variance typically decreases with sample size before stabilizing, we preliminarily tested for the potential confounding effect of small sample sizes within subpopulations. We sampled with replacement from four different subpopulations, calculated the variance at sample sizes ranging from 5-150 individuals, and repeated this procedure 10,000 times. Depending on the subpopulation, variance estimates stabilized at 20 – 40 individuals (Fig. S1). We next constructed models for three different datasets that consisted of subpopulations containing at least 20, 30, or 50 individuals. Model selection indicated the results were qualitatively similar regardless of the sample size threshold and our explanatory power was increased when a larger number of subpopulations could be included (i.e. a threshold of $n = 20$). Therefore, we only present those results here.

We used an information theoretic approach to test for the effect of latitude on fork length at capture and on the three SSM metrics (Burnham and Anderson 2002). Akaike Information Criteria adjusted for small sample sizes (AICc) were used to assess model performance with different combinations of predictor variables, beginning with a null model containing no explanatory variables (Zuur et al. 2009). Since AIC selection often ranks complex models with little additional explanatory power as equivalent to simpler, nested models, we selected the most parsimonious model (i.e. fewest explanatory variables) with a ΔAICc < 2 (Burnham and Anderson 2002, Richards 2008). We used histograms of residuals, Shapiro-Wilks tests, and QQ plots to verify models met normality and homoscedasticity assumptions.

All statistical analyses were performed with the statistical software R (R Core Team 2012) using the moments (Komsta and Novometsky 2012) and lavaan (Rosseel 2012) packages.

Results

Latitudinal size-gradient

We examined variation in fork length at capture in 1011 juvenile Sockeye Salmon (n_{VI} = 684; n_{FR} = 327). As previously observed (Tucker et al. 2009, Beacham et al. 2014b), the mean fork length of individuals captured increased with latitude across all sampled populations and years (Fig. 4, Table 1). AICc model selection indicated saturated models incorporating latitude, population, and year effects had the greatest support in both datasets (ΔAICc of next best model > 2; Table S4). Among VI individuals, juveniles from Great Central Lake were smaller than those from Sproat Lake (mean ± SD: $\mathrm{FL}_{\mathrm{GC}}$ = 117 ± 19.5 mm; $\mathrm{FL}_{\mathrm{SP}}$ = 140 ± 23.1 mm), and individuals were smaller in 2007 than 2008 (FL_{2007} = 120 ± 20.5 mm, FL_{2008} = 140 ± 23.8 mm). In the FR dataset, Lower Adams River individuals tended to be smaller than juveniles originating from Chilko Lake ($FL_{LA} = 112 \pm 10.8$ mm, $FL_{CH} = 123 \pm 14.4$ mm). Finally, capture size increased more quickly with latitude among VI individuals than FR individuals (Table 1).

Individual-scale processes

We analyzed the otoliths of 367 of the 1011 juvenile Sockeye Salmon captured in 2007 and 2008 ($n_{VI} = 262$; $n_{FR} = 105$; Table S5). The range of values observed across otolith metrics was similar for both datasets, although VI juveniles exhibited greater variation in ocean entry size and duration of marine residency. Subpopulation-specific estimates of freshwater age, marine entry check radius, duration of marine residency, and weekly growth data are presented in Table S5 and Fig. S2-S5. In general, fish captured in northern regions were larger at ocean entry and had been at sea for a greater number of days. These individuals typically also had larger weekly increments, but this trend appeared weaker than the relationship between latitude, entry size, and phenology.

Chi-square goodness of fit tests indicated the SEMs fit the observed data well (VI dataset: $\chi^2 = 8.48$, DF = 5, $P = 0.13$; FR dataset: $\chi^2 = 0.92$, DF = 2, $P = 0.61$; additional indices also suggested good fit (Table S3). Both SEMs explained a substantial proportion of the variation observed in body size during the juvenile migration of Sockeye Salmon ($r_{VI}^2 = 0.86$; $r_{FR}^2 = 0.51$). In both models juvenile body size was directly and indirectly affected by multiple individual characteristics; however, the importance of different traits, as well as how individual traits interacted with one another, differed between VI and FR individuals (Fig. 5, Table S6-S7).

Among VI juveniles otolith radius at the entry check, a proxy for ocean entry size, had the greatest direct effect on size at capture (Fig. 5a, Table 2). Since size at ocean entry was significantly correlated with freshwater age, age also had strong positive, but indirect, effects on body size at capture (Fig. 5a, Table 2). The model identified strong, positive correlations between duration of marine residency and size at capture; however, there was no significant relationship between size at ocean entry and the timing of ocean entry (Fig. 5a). Although Great Central Lake individuals were typically smaller during migration than Sproat Lake juveniles, population identity did not influence size at capture directly. Rather, Great Central Lake individuals exhibited significant differences in entry size, age structure, and ocean entry timing (Fig. 5a) and, as a result, the total effect of population identity on body size was considerable (Table 2). The VI SEM indicated strong inter-annual effects on body size at capture and population age structure, as well as correlations with growth immediately prior to capture and the timing of ocean entry (Fig. 5a, Table 2). Finally, early marine growth was a weak, but significant predictor of final body size, while marine growth immediately prior to capture was not significantly correlated with final body size (Fig. 5a, Table 2).

To test whether age-2 juveniles were disproportionately influencing the model we also constructed an SEM including only age-1 VI individuals. Although the overall fit of this model was moderately weaker ($r^2 = 0.74$), the pathways identified as significant were similar (Fig. S6), indicating that entry size and timing are strong drivers of body size variation during migration independent of age structure.

Variation in fork length at capture of Fraser River juveniles was also strongly correlated with size at ocean entry and inter-population differences (Fig. 5b, Table 2). Unlike the VI dataset, there was support for a direct effect of population identity on final body size and this effect was magnified by indirect effects via differences in marine growth (Fig. 5b, Table 2). Growth immediately prior to capture and duration of marine residency were also significantly correlated with size during migration, albeit more weakly (Fig. 5b, Table 2). As in the VI dataset there was no significant correlation between duration of marine residency and size at entry (Fig. 5b).

Population-scale processes

After restricting our analysis to subpopulations with at least 20 individuals, we examined changes in variance, kurtosis and skewness across a latitudinal gradient with 17 unique combinations of population, capture region, and year. Based on AICc model selection, none of the proposed explanatory variables improved model fit relative to a null model including only an intercept term (Fig. 6, Table 3; all models shown in Table S8). Therefore, variance, kurtosis, and skewness did not consistently varied with latitude.

Discussion

In this study, we predicted latitudinal shifts in the size distribution of juvenile Sockeye Salmon would be correlated with variation in individual characteristics, as well as ecological processes that act upon populations as a whole. We tested these hypotheses using four populations of juvenile Sockeye Salmon captured at different locations along their marine migratory pathway. Specifically, we examined the relative importance of different early marine characteristics (smolt size, phenology, age, and marine growth) on the formation of a strong latitudinal gradient in body size, while controlling for inter-population and inter-annual effects. We simultaneously tested for the presence of size-selective mortality (SSM) during this period, which could independently create an apparent increase in mean size. We determined that the size of migrating individuals is more strongly related to individual traits present prior to long distance movements than growth en route. Similarly, there was no evidence that the latitudinal gradient in size we observed was driven by SSM.

Latitudinal size-gradient

Previous studies have used catch data pooled across years to demonstrate that the fork length and energy density of juvenile Sockeye Salmon increases with latitude within a population (Beacham *et al.* 2014b) or population aggregate (Tucker *et al*. 2009). Ours is the first study, however, to confirm consistent increases in fork length with latitude while controlling for both population and year effects. The presence of a latitudinal gradient across several populations and years indicates juvenile Sockeye Salmon do not move north as a homogeneous group. Instead migratory rate, phenology, or both appear to be influenced by body size.

Individual-scale processes

The Vancouver Island (VI) and Fraser River (FR) structural equation models (SEMs) indicated that size during migration was directly and indirectly related to several ecological characteristics. In both VI and FR individuals, otolith radius to the marine entry check (a proxy for size at ocean entry) had the greatest direct effect on variation in size at capture. The importance of initial size to migration is supported by previous work where Sockeye Salmon populations with a larger mean smolt size were captured further north, earlier in the year (Beacham et al. 2014a). While it is intuitive that initial fork length will influence subsequent length, at some point during development body size becomes more dependent on growth than previous size (Thanassekos et al. 2012). Our findings suggest that most of the juveniles in these populations are able to maintain their initial size differences for several weeks after ocean entry, despite the accelerating growth rates of other individuals (next paragraph). Furthermore, these size differences are strongly correlated with the spatial distribution of individuals. While it is likely that larger juveniles are able to migrate more rapidly due to the direct effect of body size on optimal swimming speeds (Ware 1978), movement rates at sea may also be influenced by size-specific behavioral differences, for example foraging activity and predator avoidance (Mittelbach 1981).

Size at capture was also positively associated with the length of marine residency in all four populations. Such a pattern is likely driven by the rapid acceleration in growth that typically occurs in Sockeye Salmon after ocean entry (Burgner 1991). In several salmonids entry timing appears to be earlier among individuals that are larger at ocean entry (Irvine and Ward 1989, Weitkamp et al. 2012); however, in this study marine entry check radius was not correlated with the number of days individuals had been at sea. Since migration phenology (i.e. the timing of ocean entry) was significantly correlated with capture size, independently of size at entry, early ocean entry may be an alternative strategy that allows smaller individuals to compensate for poor growth in freshwater and reach a relatively large size during migration.

The spacing of weekly increments, which served as indicators of marine growth, was a less consistent predictor of size during migration than other otolith metrics. Among VI individuals capture size was significantly, although weakly, correlated with early marine growth, but was not linked to growth prior to capture. Conversely, the capture size of FR juveniles was directly correlated with growth in the week prior to capture, but not growth immediately after entry. The relatively weak effect of increment spacing on capture size observed here contrasts with previous work that identified strong spatial variability in salmonid marine growth rates (Ferriss et al. 2014). This discrepancy may have been caused by differences in the specific locations, years, or populations that were sampled. Alternatively, residual variation associated with the otolith-body size relationship may result in weekly increments providing a relatively weak signal compared to other otolith metrics; however, these weak relationships do not appear to be limited to weekly estimates of growth. Preliminary analyses indicated that overall marine growth rate (i.e. the average spacing of daily increments) was also a relatively poor predictor of size at capture. After accounting for the effects of capture year and population identity, the overall growth rate model had similar performance relative to a model containing either the first or the first and last weekly increments as explanatory variables (Table S9).

Size or growth advantages present in early developmental stages can have cascading impacts on subsequent life history stages, particularly in gape-limited taxa such as many fishes (Fuiman and Higgs 1997, Post 2003). Therefore, it was unsurprising that we observed indirect effects of freshwater traits on size during migration in all four populations. VI juveniles that were larger at ocean entry grew more rapidly immediately after river out-migration and this early marine growth had significant effects on marine growth prior to capture, as well as size at capture. Similarly, although no direct path between freshwater age and size at capture existed, its total effect was large because of the close correlation between age and entry size. In some cases traits also moderated one another – in the FR dataset greater early marine growth was correlated with later ocean entry, ultimately weakening the normally positive direct effect of marine residency on migration size.

Indirect effects between traits such as entry size, which are shaped by freshwater rearing, and marine characteristics are broadly consistent with previously identified linkages between life stages in Pacific salmon. For example, over multi-decadal time series freshwater growth, first year marine growth, and survival appear to be correlated (Ruggerone et al. 2009). Similarly individuals that are larger at ocean entry are typically more likely to recruit to the population (Koenings et al. 1993, Claiborne et al. 2011, Woodson et al. 2013). The results of this study are a first step towards highlighting subtle mechanisms that link freshwater productivity and marine survival.

Despite many structural similarities, the effect size of paths in the VI and FR SEMs differed. Some of these differences may be a result of the smaller, one-year sample size of the FR dataset. Others, however, may be due to the unique freshwater rearing habitats, marine entry environments, and initial migratory routes used by these distinct population groups. For example, VI individuals displayed greater variation in entry size and phenology than FR populations – characteristics that appear to be correlated with shorter downstream migrations, as well as lower migrant densities (Connor et al. 2013).

Inter-population and –annual effects

Population identity had strong effects on size at capture via intervening freshwater and marine variables. Such effects are broadly supported by previous observations of substantial variation among salmonid populations in migratory patterns at sea (Trudel et al. 2011, Lacroix 2013, Beacham et al. 2014a, Beacham et al. 2014b). Consistent with findings in Beacham et al. (2014b), migrating Great Central Lake juveniles were typically smaller than other VI populations; however, this study clarifies that these size differences are likely residual effects due to growth during freshwater rearing and the timing of marine entry. Conversely, differences in size at capture between FR populations were not strongly correlated with entry size or phenology, but were related to population-specific marine growth rates. Therefore, while inter-population variation is likely common in many salmonid populations, the influence of distinct freshwater rearing habitats relative to differences in early marine distributions may vary.

Although we could not evaluate temporal differences in the FR dataset, we observed significant inter-annual effects among VI individuals. Inter-annual differences in size and phenology are likely a function of several biological processes that can influence growth in both freshwater rearing grounds and en route to overwintering regions including: primary production and prey community composition (Bi et al. 2011, Tomaro et al. 2012), density-dependent interactions (Peterman 1984), and temperature (Welch et al. 1998).

Direct effects of sampling year (VI dataset) and population (FR dataset) on size at capture were not included during initial construction of SEMs, but were added to achieve adequate model fit. These variables may represent differences not captured by other metrics. One potential gap is growth during the intermediate period between the first and last weeks of marine residency (generally a 1-7 week span). As previously noted however, preliminary analyses indicated that the relationship between overall marine growth and size at capture was similar to the patterns observed with weekly increments. Thus, it seems unlikely that direct effects of year or population account for spatial or temporal variation that was unexplained in the SEMs by excluding this intermediate period. We suggest that a more likely explanation is that year and population identity account for residual variation unexplained by the otolith-body size relationship.

Size-selective mortality

Selective mortality can strongly influence the size distribution of fish populations in general (Sogard 1997) and such shifts been observed during the marine period in several populations of Pacific salmon using hard structures (*O. kisutch*, Holtby et al. 1990; O. *nerka*, Henderson and Cass 1991, Farley *et al.* 2007; *O. tshawytscha*, Claiborne *et al.* 2011; *O.*

gorbuscha, Cross *et al.* 2011; *O. mykiss*, Bond *et al*. 2008). Yet identifying when and where selective mortality occurs during marine residency is not possible using hard structures from returning adults alone. As a result, a precise understanding of when and where bottlenecks in Pacific salmon recruitment occur remains unclear.

We did not detect any evidence of size-selective mortality in juvenile Sockeye Salmon during their initial offshore migration. Although kurtosis was weakly correlated with latitude, the relationship was negative indicating the size distribution was becoming less peaked as migration progressed – the opposite of what would be expected if smaller individuals were selectively removed. We stress that our study was not intended to rigorously explore whether or not differential survival occurs during the marine residency of Sockeye Salmon, but rather to determine if it co-occurred with the formation of a latitudinal size gradient. Therefore, we cannot reject the possibility that these populations are strongly influenced by SSM, but it is unlikely that the increase in mean size with latitude that we observed is driven by differential survival.

Several caveats limit our ability to apply our findings regarding patterns in SSM more broadly. First, we would not detect SSM if mortality is episodic and a variety of sizes are selected against at different periods. For example, while Rhinoceros Auklets preferentially target smaller juvenile Sockeye Salmon in poorer condition (Tucker et al. 2015), these predation events are spatially restricted and may not be representative of mortality during migration overall. Instead mortality during migration, a period of several months, will be a function of a wide range of predators (Christensen and Trites 2011) and pathogens (Miller et al. 2014). If various predators and pathogens target distinct size ranges of juvenile salmon during their migration, the selective effects of any one source of mortality may be masked. Similarly, we would not detect SSM if it is most severe overwinter (i.e. after our final sampling event in mid-July), after juvenile Sockeye Salmon have moved offshore to maturation grounds and are thought to be energetically stressed (Farley et al. 2011). Finally, the impact of SSM on salmon populations may vary inter-annually so that its effects are only apparent in years of poor survival (Woodson et al. 2013). As a result, selective mortality may intermittently drive body size variation in these populations, but be absent during our sampling years because marine survival rates were average or high (DFO 2012, 2014).

Long distance migrations occur in many taxonomic groups and have been identified as periods with especially high fitness costs (Alerstam et al. 2003). Although migrations are influenced by many biological traits, body size may be particularly important due to its effect on maximum movement rates (Ware 1978), foraging breadth (Mittelbach 1981), energy storage (Huss et al. 2008), predator avoidance (Sogard 1997), and future reproductive fitness (Peters 1983). Our findings indicate that the distribution of juvenile Sockeye Salmon during marine migration varies predictably with body size, at least during the initial migratory period. Furthermore, variation in body size during migration among the studied populations and years was predominantly driven by individual traits present prior to freshwater emigration, specifically initial size and phenology, rather than processes that took place en route, such as differential growth and size-selective mortality. While the importance of individual variation to migration has been widely recognized in terrestrial systems, it has been relatively rarely studied in aquatic species (with the notable exception of partial migration; e.g. Brodersen et al. 2008). Our results strongly suggest that aquatic migrations cannot be viewed as simple, homogenizing events that influence populations and individuals uniformly. To successfully manage and conserve migratory species a detailed understanding of their ecology during these long-distance movements is essential.

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Table 1. Parameter estimates of linear models examining fork length at capture (log transformed) from Vancouver Island and Fraser River datasets. Population identity and year were coded as dummy variables. Model parameters were estimated relative to Sproat Lake individuals in 2007 (VI dataset) and Lower Adams individuals in 2008 (FR dataset). All parameters are statistically significant (CI does not overlap 0).

Dataset	Explanatory Variable	Estimate (± 95% CI)
Vancouver Island	Latitude	0.07 ± 0.004
n = 684	Great Central	-0.05 ± 0.015
	Year	0.15 ± 0.013
Fraser River	Latitude	0.05 ± 0.006
n = 327	Chilko	0.02 ± 0.019

Table 2. Means ± SD of individual juvenile sockeye salmon traits estimated from otolith microstructure across datasets and years. Data ranges are shown in parentheses. Capture region- and population-specific data are presented in Figures S2-S5.

Estimated Variable	Fraser River	Vancouver Island	
	2008	2007	2008
	(*n* = 103)	(*n* = 113)	(*n* = 149)
Size at Capture (mm)	123 ± 13 (94 – 175)	125 ± 22 (86 – 205)	145 ± 25 (91 – 200)
Marine Entry Check Radius (µm)	569.7 ± 46.9 (500.0 – 766.5)	562.8 ± 56 (451.51 – 774.87)	602.0 ± 65.5 (449.3 – 813.4)
Marine Residency (days)	47 ± 6 (31 – 59)	58 ± 8 (38 – 59)	56 ± 9 (32 – 84)
First Weekly Increment (µm)	16.4 ± 3.1 (8.1 – 25.5)	13.6 ± 3.1 (6.9 – 22.2)	14.3 ± 2.8 (7.4 – 21.0)
Last Weekly Increment (µm)	19.6 ± 2.9 (13.7 – 27.3)	21.7 ± 3.3 (12.6 – 33.6)	20.9 ± 3.1 (12.7 – 28.8)

Table 3. AICc rankings and the estimated fit of the top models (ΔAICc < 2). If multiple models had equivalent rankings, the top ranked model (bolded) was the model with the fewest number of parameters (Burnham and Anderson 2002). Models with no explanatory variables include only an intercept term.

SSM Metric	Explanatory Variables in Model	ΔAICc	Log-likelihood	r^2
Variance	**None**	0.00	-88.01	NA
	Year	1.03	-87.03	0.05
Skewness	**None**	0.00	-4.64	NA
Kurtosis	**None**	0.00	-22.06	NA
	Latitude	0.54	-20.83	0.07
	Year	1.19	-21.16	0.04

Figure Captions:

Figure 1. Map of study area showing approximate trawl locations (open circles 2007; open triangles 2008) and sampling regions (dashed line polygons) of juvenile Sockeye Salmon used in otolith microstructure analyses of this study. Symbols for 2007 and 2008 are offset by 0.075° west and east, respectively. Locations of spawning populations are: Great Central Lake (inverted triangle), Sproat Lake (diamond), Chilko Lake (circle), and Lower Adams River (square).

Figure 2. Stylized representation of juvenile Sockeye Salmon otolith. Dark grey zone near core represents larval growth, the white band represents a winter annulus that divides periods of normal growth occurring during the first year in freshwater (inner light grey zone) and marine (outer light grey zone) periods, respectively. Dashed line represents radius measurement to the marine entry check. The inset photograph is a 400x image of a polished otolith showing the marine entry check (indicated by white arrow) and daily micro-increments.

Figure 3. Path diagram representing the hypothesized relationships between population, year, early marine characteristics, and size at capture for (a) Vancouver Island and (b) Fraser River juvenile Sockeye Salmon. Direct paths from population and year to size at capture (shown in grey) were added post hoc to achieve adequate model fit.

Figure 4. Latitudinal gradient in the body size of Sockeye Salmon post-smolts originating from four southern BC populations: (a) Sproat Lake, (b) Great Central Lake, (c) Chilko Lake, and (d) Lower Adams River. Black lines represent linear models regressing log-transformed fork length against latitude. Open squares and dashed lines represent individuals captured in 2007, closed squares and solid lines individuals captured in 2008. Note log scale used on y-axis.

Figure 5. Structural equation models examining the direct and indirect effects of population identity, year of capture, and early marine characteristics on size during migration of juvenile Sockeye Salmon originating from (a) Vancouver Island and (b) Fraser River. Non-significant predictor variables and paths are not shown to improve readability (see Fig. 3 for full tested models). Population identity, year, and freshwater age were coded as dummy binary variables; however, no Fraser River juveniles were collected in 2007 and too few Fraser River age-2 juveniles were included to estimate the effect of age in this dataset. Therefore estimates in (a) are relative to age-1, Sproat Lake individuals captured in 2007 and in (b) are relative to Chilko Lake individuals. Path coefficients reflect standardized variables. Grey and black lines represent significant relationships with standardized effect sizes ≤0.3 and >0.3, respectively; line width reflects the relative strength of the correlation.

Figure 6. Relationship between latitude and size-selective mortality metrics: (a) variance, (b) Pearson's kurtosis coefficient, and (c) Pearson's skewness coefficient. Each sampling point represents the catch of a specific population in a given capture region for one year.

Figure 1.

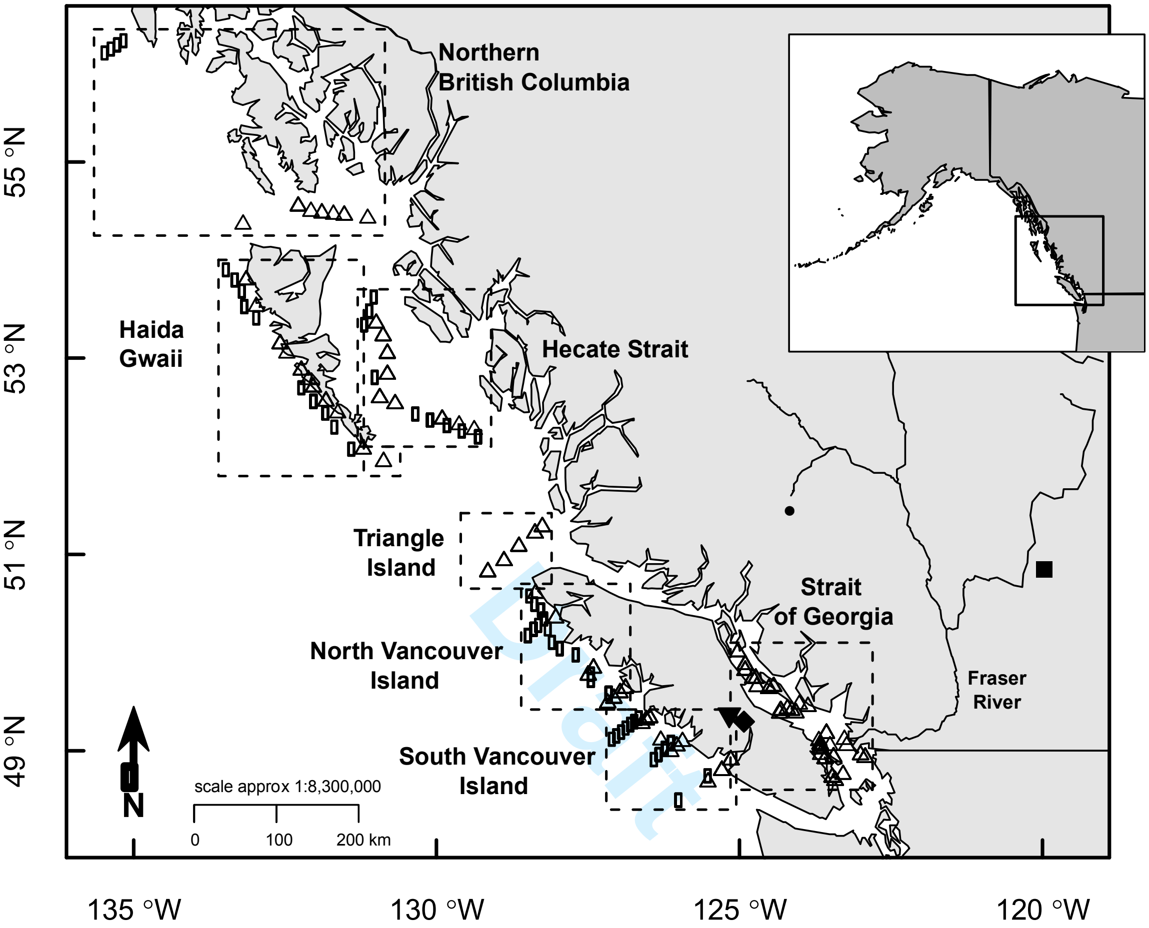

Northern British Columbia
Haida Gwaii
Hecate Strait
Triangle Island
North Vancouver Island
South Vancouver Island
Strait of Georgia
Fraser River
N
scale approx 1:8,300,000
0
100
200 km
55 °N
53 °N
51 °N
49 °N
135 °W
130 °W
125 °W
120 °W

Figure 2.

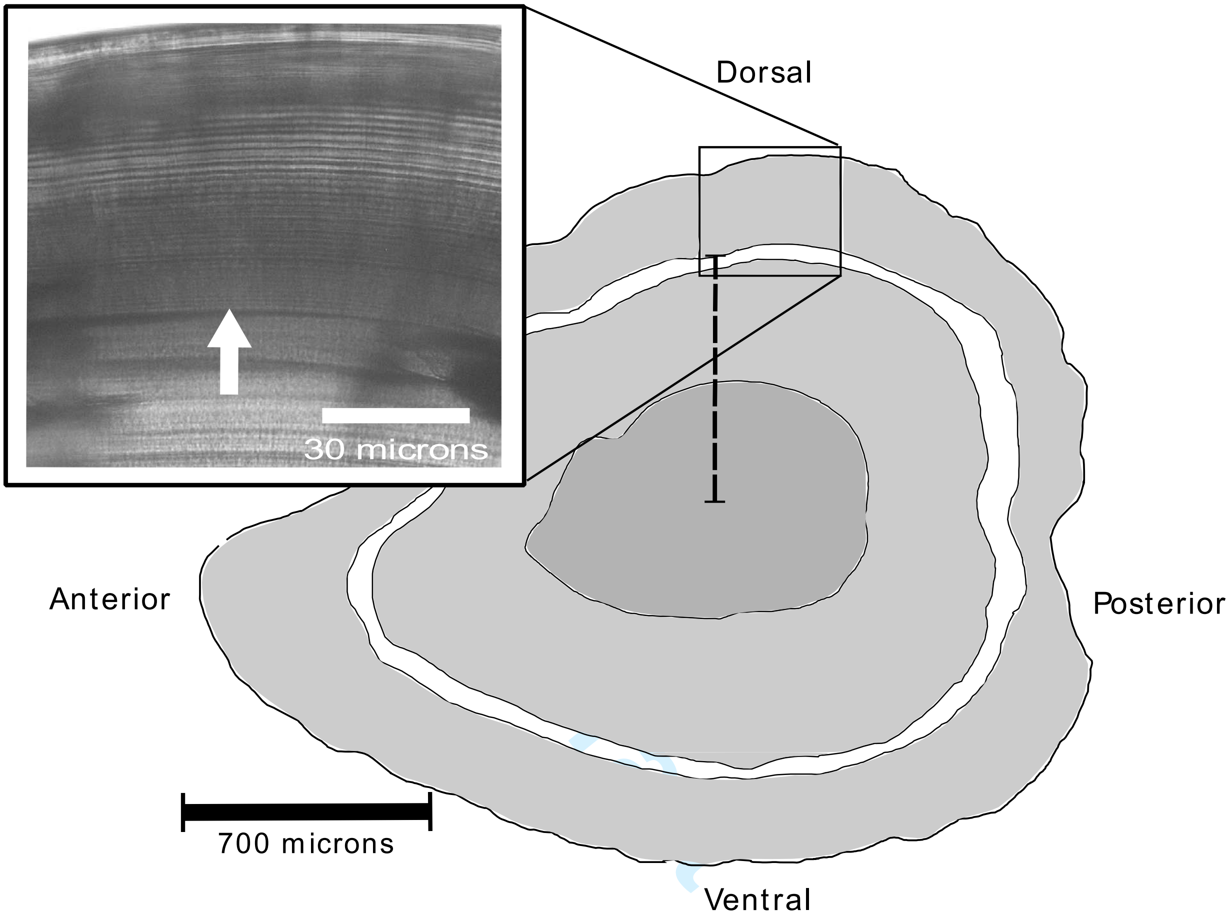


Figure 3.

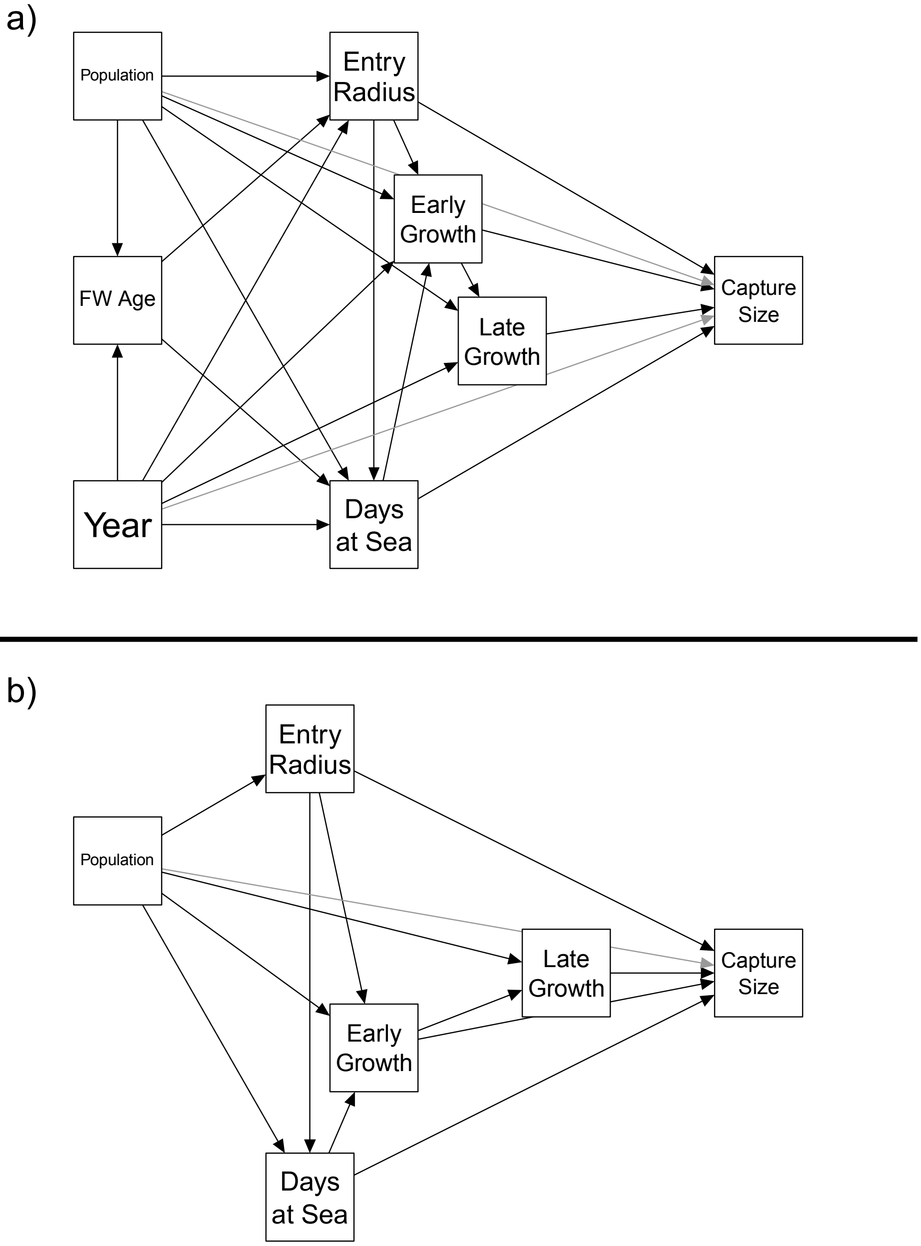

a)
Population
Entry Radius
Early Growth
FW Age
Late Growth
Capture Size
Year
Days at Sea
b)
Entry Radius
Population
Late Growth
Capture Size
Early Growth
Days at Sea

Figure 4.

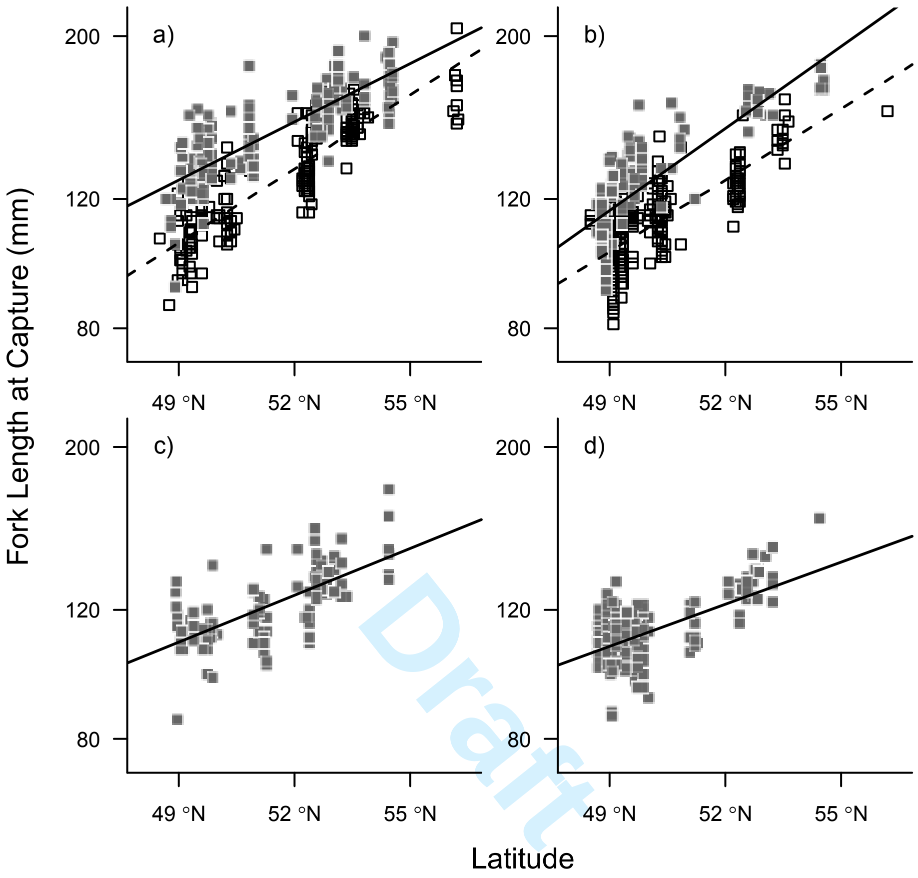

a)
b)
c)
d)
200
120
80
49 °N
52 °N
55 °N
Fork Length at Capture (mm)
Latitude

Figure 5.

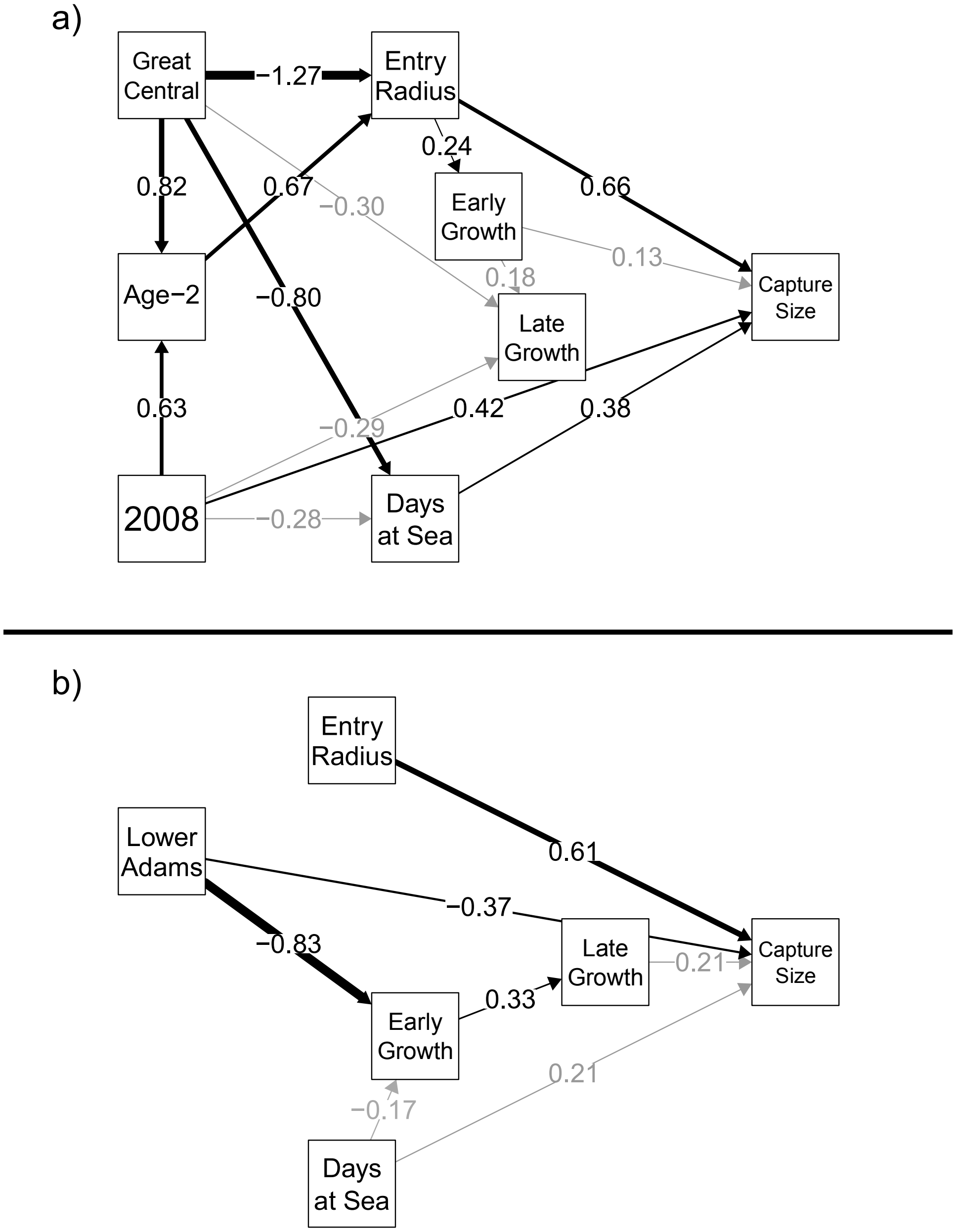
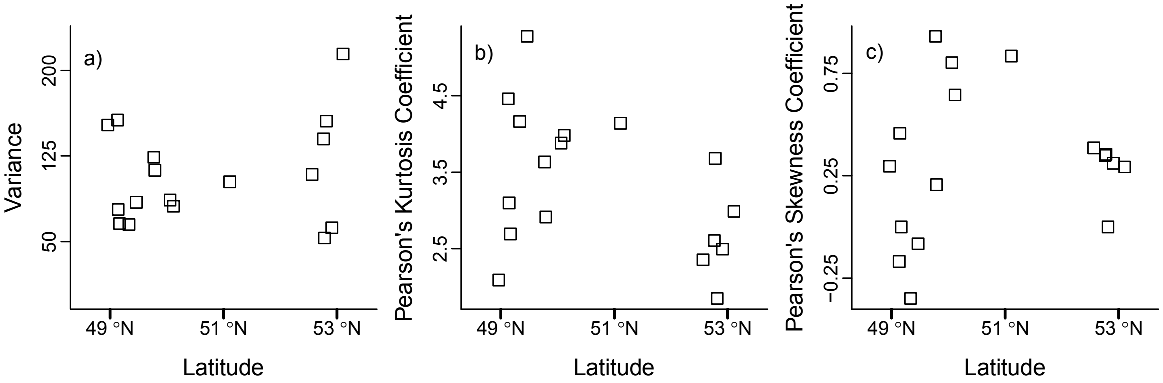

a)
Great Central
−1.27
Entry Radius
0.24
0.82
0.67
−0.30
Early Growth
0.66
0.13
Age−2
−0.80
0.18
Capture Size
Late Growth
0.63
−0.29
0.42
0.38
2008
−0.28
Days at Sea
b)
Entry Radius
Lower Adams
0.61
−0.37
Late Growth
−0.83
0.21
Capture Size
0.33
Early Growth
0.21
−0.17
Days at Sea

Figure 6.


a)
Variance
200
125
50
49 °N
51 °N
53 °N
Latitude
b)
Pearson's Kurtosis Coefficient
4.5
3.5
2.5
49 °N
51 °N
53 °N
Latitude
c)
Pearson's Skewness Coefficient
0.75
0.25
−0.25
49 °N
51 °N
53 °N
Latitude