

Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile sockeye salmon

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

Abstract: Survival during early marine life stages is hypothesized to contribute disproportionately to variation in salmonid recruitment, yet estimates of cumulative mortality are constrained by knowledge of how long juveniles reside in specific regions. We used otolith microstructure techniques to examine the relationship between migratory rate and ocean entry characteristics of juvenile sockeye salmon (*Oncorhynchus nerka*). We observed differences in migratory rate between catch locations that are consistent with divergent migratory behaviours. Individuals captured in northern regions were typically older, larger at ocean entry, and migrated more rapidly. Migratory rate was also correlated with entry size, phenology, population group, and year. Next, we compared “lingering” individuals captured nearshore during fall surveys to juveniles from the same populations captured during the peak summer migratory period. We determined that individuals that entered after 24 May and at smaller sizes (<85 mm) had a greater probability of being captured late in the year. Our findings demonstrate that the entry characteristics of sockeye salmon are strongly correlated with migratory variation within populations and suggest these traits may directly influence juvenile behaviour.

Résumé : S’il a été postulé que la survie durant les premières étapes de la vie en mer jouerait un rôle disproportionné dans la variation du recrutement des salmonidés, les estimations de la mortalité cumulative sont limitées par les connaissances sur le temps de résidence des juvéniles dans des régions précises. Nous avons utilisé des techniques d’analyse des microstructures d’otolites pour examiner le lien entre le taux de migration et des caractéristiques de l’entrée dans l’océan de saumons sockeyes (*Oncorhynchus nerka*) juvéniles. Nous avons observé des variations du taux de migration entre lieux de prise qui concordent avec des comportements migratoires divergents. Les individus capturés dans des régions nordiques étaient typiquement plus vieux et plus grands au moment de l’entrée dans l’océan et ils migraient plus rapidement. Le taux de migration était également corrélé à la taille au moment de l’entrée, à la phénologie, au groupement de population et à l’année. Nous avons ensuite comparé les individus « traînards » capturés près des côtes durant des enquêtes automnales aux juvéniles des mêmes populations pris durant la pointe de la migration à l’été. Nous avons déterminé que les individus qui entraient en mer après le 24 mai et à des tailles plus petites (<85 mm) étaient plus susceptibles d’être capturés tard durant l’année. Nos constatations démontrent que les caractéristiques de l’entrée en mer des saumons sockeyes sont fortement corrélées aux variations migratoires au sein des populations et donnent à penser que ces caractères pourraient exercer une influence directe sur le comportement des juvéniles. [Traduit par la Rédaction]

Introduction

Long distance migrations are associated with high fitness costs that can result in variation across a suite of characteristics (Dingle 1996) — one manifestation of this variability is differences in migratory rate. Migration rate directly determines the ecological environment an individual encounters, including predator and prey communities, pathogen sources, and dynamic abiotic conditions. Simultaneously, migration rate can influence individual condition through physiological processes such as heightened energy demands or transitions to novel physical environments (Hinch et al. 2006). As a result, estimates of migratory rate or the duration of residency in specific regions are valuable when studying migratory species, especially for those taxa that experience bottlenecks in survival during long distance movements.

Sockeye salmon (*Oncorhynchus nerka*) is an anadromous species exploited by commercial, recreational, and First Nations fisheries. Populations in the southern portion of the species’ range have experienced variable, but generally poor, recruitment in recent

years that appears linked to low marine survival rates (Peterman and Dorner 2012). Although sockeye salmon productivity is correlated within regions (Peterman and Dorner 2012), the environmental predictors of marine survival rates differ among populations across relatively small spatial scales (Ye et al. 2015). Because populations do not migrate homogeneously at sea (Tucker et al. 2009; Beacham et al. 2014a), temporal and spatial variability in the distribution of juveniles may influence population-specific mortality rates via differential interactions with predators (Christensen and Trites 2011), pathogen sources (Miller et al. 2014), or foraging conditions (Mackas et al. 2004; McKinnell et al. 2014). Therefore, quantifying differences in migratory rate among and within sockeye salmon populations will be particularly important to understanding their dynamics at sea.

Variation in migratory rate in salmonids may be linked to several ecological characteristics. First, evidence from terrestrial systems suggests age can have strong effects on migratory ability in repeat migrants (Marra et al. 1998; Sergio et al. 2014). Sockeye

Received 3 September 2015. Accepted 21 April 2016.

C. Freshwater and F. Juanes. Department of Biology, University of Victoria, Victoria, BC V8W 3N5, Canada.

M. Trudel. Department of Biology, University of Victoria, Victoria, BC V8W 3N5, Canada; Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada.

T.D. Beacham, L. Godbout, C.-E.M. Neville, and S. Tucker. Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada.

Corresponding author: Cameron Freshwater (email: camfresh@uvic.ca).

© Her Majesty the Queen in right of Canada 2016. Permission for reuse (free in most cases) can be obtained from RightsLink.

salmon, being semelparous, lack the opportunity to improve their individual migratory behaviours over time. However, juveniles that have spent multiple years rearing in freshwater may exhibit different behaviours (e.g., timing of out-migration; [Jonsson et al. 1990](#); [Kovach et al. 2013](#)), which could result in older individuals migrating more rapidly ([Fisher et al. 2014](#)). Second, migratory rate may be associated with body size so that larger juveniles move north more rapidly. Although maximum relative swimming speeds decline with body size due to bioenergetic and physical constraints, absolute swimming speeds are predicted to be consistently greater in larger individuals ([Brett 1965](#); [Ware 1978](#); [Trudel and Welch 2005](#)). Movement rates may further diverge as migration progresses due to size-dependent differences in foraging and risk-taking behaviours ([Mittelbach 1981](#); [Werner et al. 1983](#); [Walters and Juanes 1993](#)). Third, evidence suggests that Pacific salmon marine distributions are influenced by environmental conditions that change seasonally ([Burke et al. 2013](#)). Ocean entry phenology will determine the environment that juvenile sockeye salmon initially encounter and may, as a result, moderate migratory rate. Finally, the migration speeds of adult sockeye salmon typically vary between populations and reflect the distances they must travel to reach spawning sites ([Crossin et al. 2007](#)). If similar processes influence juveniles, the migratory rates of populations at sea may vary by ocean entry location or migratory route.

While sockeye salmon generally appear to migrate rapidly from ocean entry points ([Burgner 1991](#); [Welch et al. 2009, 2011](#)), estimates of nearshore residency and migratory rate are relatively rare and, in some cases, conflicting. Uncertainty in how long juveniles utilize specific areas may have contributed to the lack of consensus as to whether marine mortality rates are greatest within nearshore environments (e.g., the Strait of Georgia, [Beamish et al. 2012](#)), offshore regions ([Welch et al. 2011](#)), or both ([McKinnell et al. 2014](#)). The majority of previous work has focused on Fraser River populations, which enter the ocean in the Strait of Georgia and then typically migrate north through Johnstone Strait ([Tucker et al. 2009](#)). Residency estimates within the Strait of Georgia from tagging studies that utilize the Pacific Ocean Shelf Tracking (POST) array are 9–34 days, depending on population and year ([Welch et al. 2009, 2011](#); [Rechisky et al. 2015](#)). These acoustic tagging studies have also estimated migration rates to be 15–24 km·day⁻¹, or approximately 1 body length per second (bl·s⁻¹) ([Welch et al. 2009](#); [Melnichuk et al. 2010](#); [Rechisky et al. 2015](#)). Conversely, nearshore residency estimates calculated from the catch per unit effort (CPUE) of research surveys in the Strait of Georgia are longer (31–54 days; [Preikshot et al. 2012](#)). While [Preikshot et al. \(2012\)](#) did not explicitly calculate migratory rate, their residency estimates suggest considerably slower movements of approximately 4 km·day⁻¹, or less than 0.5 bl·s⁻¹.

While these studies provide valuable information, both approaches have limitations. First, due to tag burden concerns, acoustic telemetry studies can currently only target larger smolts ([Welch et al. 2009, 2011](#); [Rechisky et al. 2015](#)). Tagged individuals are typically 2-year-old smolts, which are generally 60–80 mm larger than the population average ([Welch et al. 2009](#)) and often make up less than 5% of the out-migrating group each year ([Irvine and Akenhead 2013](#)). Although [Melnichuk et al. \(2010\)](#) determined that sockeye salmon size was not correlated with migratory rate at sea, their analysis was restricted to tagged smolts that were at least 150 mm long and it is possible that smaller fish exhibit different migratory behaviours ([Welch et al. 2011](#); [Preikshot et al. 2012](#); [Beacham et al. 2014b](#)).

Second, estimates of migratory rate based on CPUE are driven by the relative abundance of an entire population and cannot identify individual variation in migratory patterns. However, juvenile sockeye salmon belonging to a given population are widely distributed at sea ([Tucker et al. 2009](#)), which suggests considerable individual variation in migratory rate or ocean entry timing. Of particular interest are a “lingering” group of individuals that are

captured in southern regions in October and November — well after the majority of their cohort has migrated north ([Tucker et al. 2009](#)). Because juvenile sockeye salmon survival is predicted to improve with early arrival at maturation grounds in the Gulf of Alaska ([McKinnell et al. 2011](#)), it is unclear why a fraction of the population is consistently found inshore, late in the year, where mortality rates are likely higher. We predict that these individuals may be constrained by body size or ocean entry phenology to migrate after the bulk of their cohort.

We used otolith microstructure techniques to estimate individual variation in the migratory rate of four populations of British Columbia (BC) sockeye salmon originating from Vancouver Island or the Fraser River. Next, we tested a series of hypotheses to identify potential drivers of this variation: (i) that 2-year-old individuals exhibit different spatial distributions and migration rates as 1-year-old juveniles, (ii) migratory rate is correlated with ocean entry size and phenology, and (iii) the early marine characteristics of juveniles captured in the fall differ from those captured in the summer. Finally, because Pacific salmon can exhibit stock- and year-specific early marine characteristics, we also tested for inter-population and inter-annual differences in migratory rate.

Methods

Juvenile fish collection and populations

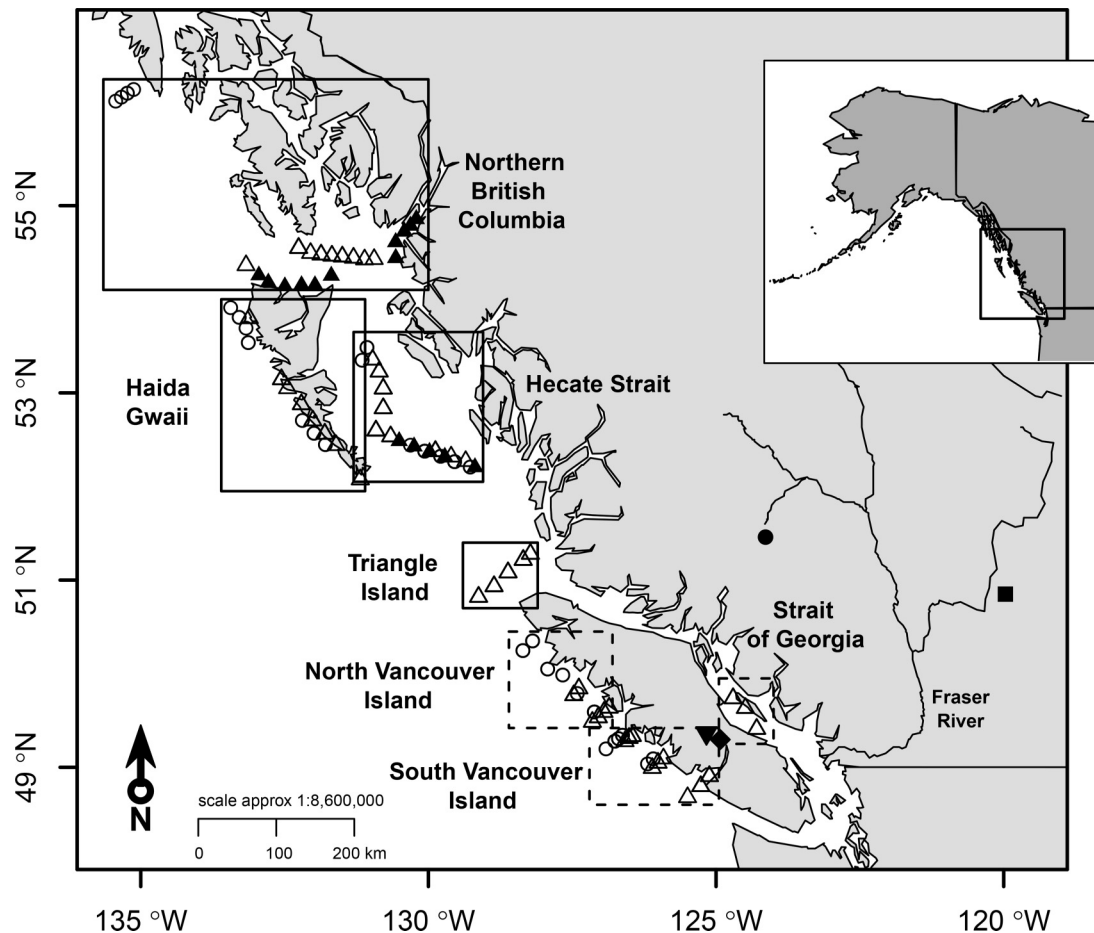
We collected juvenile sockeye salmon in 2007 (22 June – 5 July) and 2008 (21 June – 3 July; 9–19 October) along a south–north gradient from southern BC to the Alaskan border ([Fig. 1](#)). Fish were captured with a mid-water rope trawl hauled at the surface for 15–30 min at 5 knots (~9.8 km·h⁻¹) by CCGS W.E. Ricker and F/V Viking Storm. We randomly selected up to 30 juvenile sockeye salmon from each net tow for sampling. We recorded fish fork length and mass and removed both sagittal otoliths at time of capture. We also preserved tissue samples from the operculum 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](#)).

Our analysis focused on individuals belonging to four of the most abundant populations captured in research trawls. Lower Adams River and Chilko Lake populations 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](#)). Vancouver Island populations include Great Central Lake and Sproat Lake, which rear 26 km and 8 km from the coast, respectively, enter the open ocean via Barkley Sound, and migrate north. North of Vancouver Island, all four populations are commonly captured together and appear to share similar migratory pathways to their maturation grounds in the Gulf of Alaska ([Tucker et al. 2009](#); [Beacham et al. 2014a, 2014b](#); [Fig. 1](#)).

Otolith microstructure

We used otolith microstructure to estimate the size at ocean entry, migratory rate, and freshwater age of captured juveniles. A previous experimental study confirmed that 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](#)). Because otolith micro-increments are formed daily after marine entry for at least 100 days ([Freshwater et al. 2015](#)), we estimated the length of ocean residency by enumerating the increments observed between the marine entry check mark and otolith periphery. Finally, we determined the number of years an individual spent rearing in freshwater by counting annuli, large opaque bands visible with a

Fig. 1. Map of study area showing approximate trawl locations (open circles, summer 2007; open triangles, summer 2008; filled triangles, autumn 2008) and sampling regions (solid polygons, northern regions; dashed polygons, southern regions). Symbols for 2007 and 2008 are offset by 0.075°W and 0.075°E, respectively. Locations of spawning populations are: Great Central Lake (inverted triangle), Sproat Lake (diamond), Chilko Lake (filled circle), and Lower Adams River (square). Figure created using R statistical software and the “maps” package (<http://CRAN.R-project.org/package=maps>).



microscope under transmitted light, which represent periods of winter growth (Zhang and Beamish 2000).

We used cellSens Imaging Software (Olympus Scientific Solutions America) to measure four otolith microstructure characteristics: marine entry check radius, total radius, number of daily increment after marine entry check mark, and freshwater age. After mounting otoliths (details in Freshwater et al. 2015), measurements were made dorsal and perpendicular to the anterior-posterior centerline of the otolith. Measurements were repeated three times per otolith and the average was used in subsequent analysis. If any measurements could not be completed, the otolith was discarded (40 out of 443). The number of individuals retained for otolith analyses across different populations, years, and sampling periods is summarized in Supplementary Table S1¹.

Body size is commonly back-calculated from hard structures by regressing otolith or scale size at capture against body size at capture. However, these techniques fail to account for how individual body-structure relationships may deviate from the population average and can introduce additional error (Francis 1990). Therefore, we estimated size at ocean entry from marine entry check radii by using scale proportional (SPH) and body proportional hypotheses (BPH) as described in Francis (1990), then used the mean of these two methods as our entry size estimate. Al-

though these techniques are distinct from direct correlations between body size and otolith size, they do use this relationship to provide initial model parameters and, therefore, require a strong correlation between these two metrics. In this data set, the correlation between otolith radius and size at capture was significant ($r^2 = 0.79$, $df = 419$, $P < 0.001$; Supplementary Fig. S1¹).

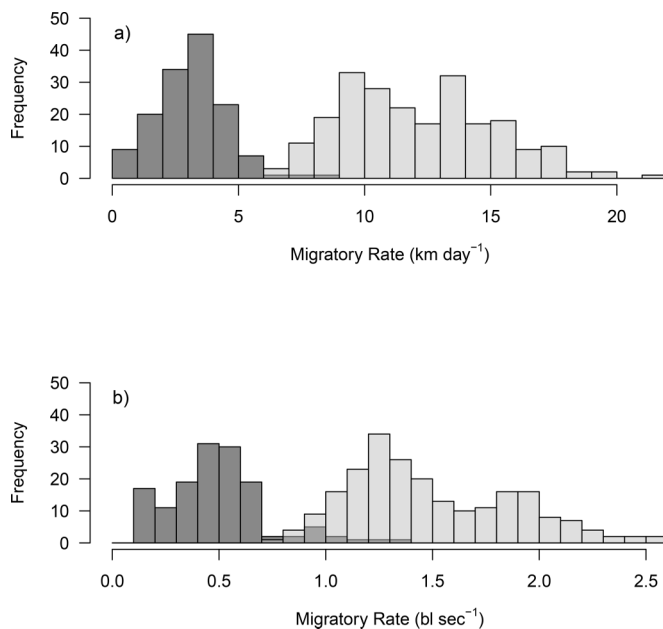
Data analyses

We conservatively estimated migration distance as the linear distance in kilometres between an individual's ocean entry point (based on population identity) and capture location, after accounting for the Earth's curvature. In the case of Vancouver Island juveniles, this distance was measured from the mouth of Barkley Sound to the capture location and the length of the sound added afterwards. We then divided linear migration distance by the number of days since ocean entry to use as an estimate of migratory rate. We also converted migratory rate in kilometres per day ($\text{km}\cdot\text{day}^{-1}$) to body lengths per second ($\text{bl}\cdot\text{s}^{-1}$) using estimates of fork length at ocean entry; however, we did not account for changes in size during migration.

We used chi-squared analysis to test the hypothesis that the observed number of age-2 smolts at each capture location during the summer surveys was not significantly different from a random

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0425>.

Fig. 2. Migratory rate in (a) kilometres per day and (b) body lengths per second (bl·sec⁻¹) of Vancouver Island (*n* = 261) and Fraser River (*n* = 104) juvenile sockeye salmon captured during summer surveys. Dark grey and light grey bars represent individuals caught in southern and northern sampling region, respectively.



distribution. Next, we used Mann-Whitney tests to determine whether mean migratory rate, size at entry, and phenology differed between age-1 and age-2 juveniles. Because only two age-2 Fraser River juveniles were captured, all analyses examining differences between age groups focused only on Vancouver Island populations (i.e., Great Central Lake and Sproat Lake individuals).

To examine the effects of ocean entry characteristics on migratory rate, we fit linear regressions with migratory rate kilometres per day as the response and fork length at ocean entry, entry date, population aggregate (Fraser River or Vancouver Island), and year as explanatory variables. We chose to aggregate populations because we had data for only two populations per watershed and because initial analyses showed migratory rates within an aggregate were similar; however, we speculate differences between populations may be important when examining diverse population assemblages within regions. Preliminary analyses also indicated that migratory rate was strongly bimodal, with each distribution well defined by capture location (Fig. 2). Therefore, we included capture region (whether an individual was caught north or south of Vancouver Island's northwestern point, Fig. 1) as an explanatory variable to account for this underlying variation and ensure adequate model fit. To determine whether the ocean entry characteristics of northern- and southern-caught fish differed, we also tested for interactions between capture region and all other explanatory variables. Because freshwater age was strongly correlated with entry fork length, it was not included as an explanatory variable. We only included summer-caught fish in this analysis to minimize temporal variability and pseudoreplication within regions.

We used Box-Cox power law transformations to identify the optimal exponent to meet normality assumptions for the response variable and raised migratory rate data to the 0.7 power before we fit linear models. To avoid misinterpreting interactions when comparing models, we centered all categorical explanatory variables, and centered and scaled to a standard deviation of one all continuous explanatory variables (Schielzeth 2010). We confirmed explanatory variables were not collinear using variance inflation factors (VIF < 3 indicates minimal collinearity) and

Table 1. Number of age-1 and age-2 Vancouver Island juveniles captured in each sampling region.

	S-VI	N-VI	TI	HS	HG	N-BC
Age-1	64	55	11	52	29	21
Age-2	2	4	0	10	3	10

Note: Regions are shown in Fig. 1 and abbreviations are as follows: S-VI, southern Vancouver Island; N-VI, northern Vancouver Island; TI, Triangle Island; HS, Hecate Strait; HG, Haida Gwaii; N-BC, northern British Columbia.

tested for adequate model fit by examining quantile-quantile plots and the distribution of residuals.

Next, we used Mann-Whitney tests to compare migratory rates of individuals captured in fall surveys to those captured in northern and southern regions during the summer. We used generalized linear models (GLMs) with a binomial response variable to determine whether early marine entry characteristics could be used to distinguish individuals captured in the summer from juveniles of the same population captured in the same region during fall surveys. The only sampling regions where at least 8 individuals were captured in both seasons were Hecate Strait and northern BC in 2008 — therefore, all samples collected in other regions and in 2007 were excluded from this analysis. Because no Sproat Lake individuals were captured in fall surveys, we also excluded this population from the analysis. To account for quasi-separation in the initial GLMs, we used a bias-reduction estimator developed by Firth (1993) and implemented with the logistf package (Heinze et al. 2013) in R version 3.1.3 (R Core Team 2014). We included size at ocean entry, entry date, and population identity as explanatory variables and season of capture (summer or autumn) as the binomial response variable in the saturated model.

For both linear models and binomial GLMs, we used an information theoretic approach to identify top ranked models with Akaike's information criterion adjusted for small sample sizes (AIC_c). If several models had equivalent AIC_c scores (i.e., $\Delta AIC_c < 2$), the most parsimonious model was retained (Burnham and Anderson 2002; Grueber et al. 2011). We conducted all statistical analyses in R version 3.1.3 (R Core Team 2014).

Results

Summer-caught juveniles

Among Vancouver Island juveniles, age-2 individuals were not distributed uniformly across sampling regions ($\chi^2 = 22.6$, *df* = 5, $P < 0.001$) and older juveniles were nearly four times more abundant in northern sampling regions (Table 1). Age-2 fish had a significantly faster mean migratory rate ($W = 1569$, $P < 0.001$; Fig. 3a). Older individuals were also significantly larger at ocean entry than age-1 juveniles ($W = 1004$, $P < 0.0001$; Fig. 3b) and tended to enter later in the year, with this difference approaching statistical significance ($W = 2629$, $P = 0.056$; Fig. 3c).

Estimates of migratory rate ranged from 0.8 to 21.3 km·day⁻¹ (0.1 to 2.5 bl·s⁻¹). The distributions were bimodal and were strongly correlated with capture region (Fig. 2). The mean (\pm SD) migratory rate of individuals captured south of Vancouver Island was significantly slower than those captured in northern sampling regions (3.1 ± 1.4 versus 12.1 ± 3.0 km·day⁻¹; $W = 31191$, $P < 0.0001$; Figs. 2, 4, 5) and individuals were significantly smaller at ocean entry (75 ± 13 versus 95 ± 18 mm; $W = 26255$, $P < 0.0001$; Fig. 4a). Although differences between regions were less extreme, southern-caught fish typically also had been at sea for significantly shorter periods (mean \pm SD: 55.6 ± 10.0 days in northern regions versus 51.9 ± 7.3 days in southern regions; $W = 19322$, $P < 0.001$; Fig. 4b, Supplementary Fig. S2¹).

In the top ranked model, entry size, phenology, population aggregate, and capture year were significantly correlated with migratory rate after accounting for the underlying variation in

Fig. 3. Mean (a) migratory rate, (b) size (fork length; FL) at ocean entry, and (c) entry date of age-1 and age-2 Vancouver Island juvenile sockeye salmon captured in summer surveys; error bars represent 95% confidence intervals.

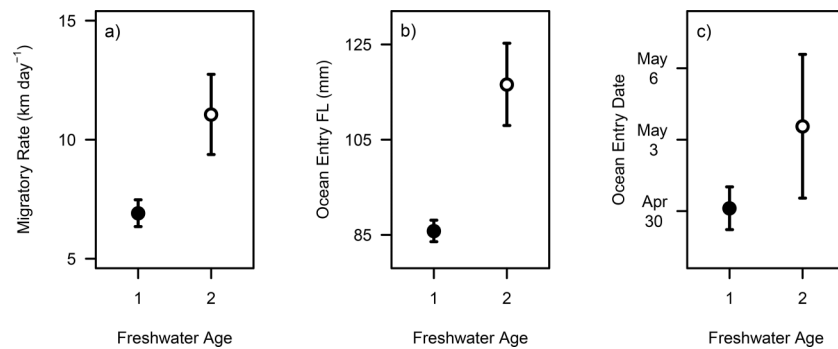
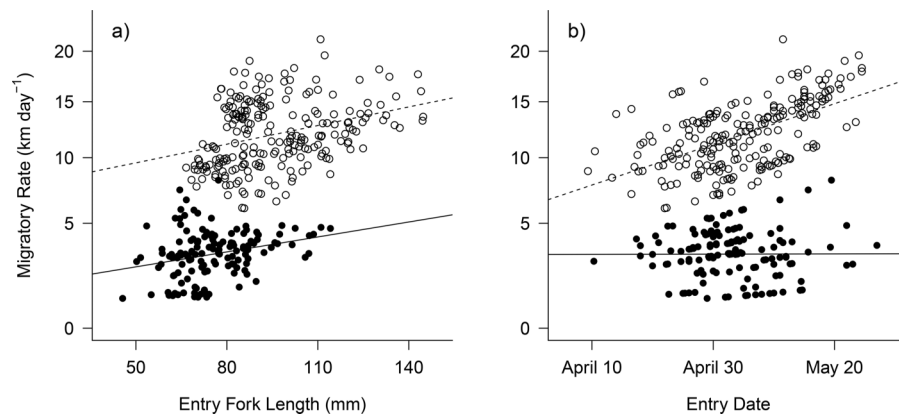


Fig. 4. Relationship between migratory rate and (a) back-calculated size at ocean entry or (b) entry date for juveniles captured during summer surveys. Dashed and solid lines represent regressions for northern (open symbols) and southern (closed symbols), respectively. Note that the y axes are power law transformed with an exponent of 0.7 and that explanatory variables are represented by raw data, rather than scaled and centered as in models.



migratory rate associated with capture location ($r^2 = 0.91$; Figs. 4, 5; Supplementary Table S2¹). The fastest migrants were juveniles that entered at large sizes, relatively late in the year, and originated from Fraser River populations. Although the correlation between body size and migratory rate was consistent between capture regions, there were significant interaction effects between capture region and the other explanatory variables (Fig. 5; Supplementary Table S2¹). As a result, the effects of entry date and population aggregate on migratory rate were greater among fish captured in the north, while the effect of sampling year was stronger in southern regions.

Fall-caught juveniles

Individuals captured in Hecate Strait and northern BC during fall surveys and retained in this analysis were identified as belonging to Great Central Lake, Lower Adams River, and Chilko Lake population groups. Fall-caught juveniles migrated at a significantly slower rate than individuals from the same populations caught in similar locations during the summer (mean \pm SD: 14.7 ± 2.6 versus 5.7 ± 0.9 km·day⁻¹; $W = 0$, $P < 0.0001$), but more rapidly than those captured in southern regions during the summer (mean \pm SD: 3.1 ± 1.4 km·day⁻¹; $W = 6849$, $P < 0.0001$). Furthermore, marine entry characteristics could be used to identify summer- and fall-caught juveniles captured in the same region. The top ranked GLM for predicting season of capture (Δ AIC of next best model > 7) included back-calculated estimates of entry date and entry size as explanatory variables ($\beta_{\text{Entry Date}} = 0.39$, 95% CI = 0.18 – 2.01 ; $\beta_{\text{Entry FL}} = -0.36$, 95% CI = -2.96 – -0.07 ; Fig. 6, Supplementary Table S3¹). Population was not retained as an explanatory variable in the top model (Supplementary Table S3¹).

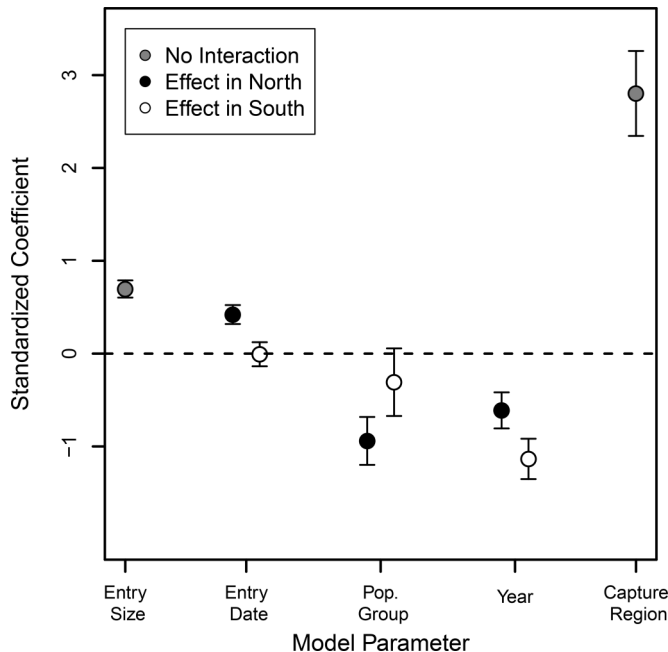
Juvenile sockeye salmon entering after approximately 24 May and at less than 82 mm fork length had a greater probability of being captured in fall than in summer surveys. Although the size distributions of summer- and fall-caught fish overlapped considerably, fall captures exhibited significantly lower variance in size at ocean entry (70.6 versus 379.6 mm; Levene's test: $F = 40.0$, $P < 0.0001$; Fig. 6b).

Characteristics estimated from otolith microstructure are summarized by population aggregate, year, and sampling period in Supplementary Table S4¹.

Discussion

We observed extensive individual variation in the marine distribution and migratory rate of sockeye salmon juveniles originating from both the Fraser River and Vancouver Island. Individuals exhibited at least two distinct migratory patterns — either migrating rapidly from ocean entry points or residing for several weeks in southern regions while moving north more slowly. Older age-2 juveniles tended to be more common further north and larger juveniles migrated more rapidly. Lingering juveniles captured in Hecate Strait and northern BC during fall surveys migrated more slowly than individuals captured in the same regions during summer and, like southern-caught juveniles, may have reared for several weeks relatively close to ocean entry points. Additionally, fish caught during fall surveys differed from individuals captured in the same regions during the peak summer migration period by entering the marine environment later in the year and at a smaller size. The heterogeneity we observed suggests that individual variation in ocean entry characteristics within populations

Fig. 5. Standardized coefficient estimates with 95% CI from the top model describing variation in migratory rate among summer caught juvenile sockeye salmon. Grey circles represent parameters with no significant interaction with capture region. Black and white circles show parameters estimates for northern and southern caught juveniles, respectively (i.e., account for significant interaction effects). Because categorical variables were estimated relative to individuals from the Fraser River, fish that migrated in 2007, or fish that were captured in southern regions, negative values are associated with those juveniles migrating more quickly.



may influence the migratory behaviour of juvenile sockeye salmon and, as a result, how they interact with their marine environment.

Summer-caught juveniles

Our estimates of migratory rate were strongly bimodal for both Vancouver Island and Fraser River juveniles captured in summer, indicating differences in spatial distribution are associated with variation in travel speed, rather than differences in ocean entry timing alone. Because variation in migratory rate was strongly associated with capture location, even after accounting for individual differences in ocean entry characteristics, we suggest each mode may represent a distinct migratory phenotype. In the first, relatively large juvenile sockeye salmon appear to undertake a directed and rapid migration from their ocean entry points that is similar to results from studies tagging large age-2 juveniles (Welch et al. 2009; Melnychuk et al. 2010; Welch et al. 2011; Rechisky et al. 2015). Conversely, smaller individuals that enter the marine environment at approximately the same time appear to move away from their entry points more slowly — a pattern consistent with highly dispersed catches of juvenile sockeye salmon in the Strait of Georgia (Preikshot et al. 2012; Neville et al. 2013).

Size-dependent variation in migratory behaviour has been reported in several Pacific salmonids. For example, the smaller individuals in populations of pink salmon (*Oncorhynchus gorbuscha*) and steelhead trout (*Oncorhynchus mykiss*) rear in estuarine environments for relatively longer periods (Mortensen et al. 2000; Bond et al. 2008). Similarly, coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) juveniles either migrate rapidly offshore or overwinter on the continental shelf, with larger fish consistently observed further from ocean entry points (Morris et al. 2007; Fisher et al. 2014). Finally, juvenile salmon originating from hatcheries appear to move out of nearshore environments

more rapidly than wild individuals (Rice et al. 2011; Sturdevant et al. 2012), a pattern that may be linked to the larger mean size of hatchery fish.

Pacific salmon survival is thought to improve with early arrival on maturation grounds (McKinnell et al. 2012); however, delaying migration may be adaptive for smaller individuals if it allows them to substantially increase size and energy stores prior to moving offshore. This behaviour may be particularly important for Fraser River populations because foraging conditions immediately outside the Strait of Georgia appear poor (Ferriss et al. 2014; McKinnell et al. 2014). Furthermore, Morris et al. (2007) hypothesized that variation in migratory rate could create a portfolio effect by ensuring a fraction of individuals encounter adequate rearing conditions during their migrations and by reducing intraspecific competition en route. While there is no evidence that the populations of sockeye salmon we studied overwinter in large numbers in nearshore environments, subtle variation in migratory patterns within populations may act to stabilize marine mortality rates.

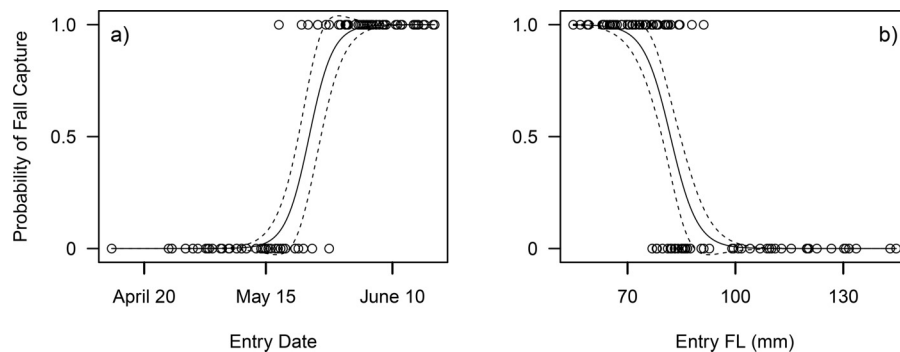
Even though we observed differences between age classes in spatial distribution and migratory rate, we suggest migratory behaviour is more strongly associated with size than age. Age-2 sockeye salmon were more common in northern sampling regions and migrated more rapidly than age-1 juveniles; however, both age groups were captured in concurrent sampling events, exhibited overlapping variation in migratory rate, and entered the marine environment at approximately the same time. Instead, the most consistent difference between age classes was body size, with age-2 juveniles being, on average, significantly larger.

The relatively strong correlation between migratory rate and back-calculated estimates of fork length at ocean entry across all populations provides additional evidence that migratory behaviour at sea is associated with body size. This pattern is also consistent with observations that larger juvenile Pacific salmon are typically observed further from shore, earlier in the year (Morris et al. 2007; Tucker et al. 2009; Beacham et al. 2014a, 2014b; Freshwater et al. 2016). Migratory rate may be intrinsically associated with fork length because both optimal cruising and foraging swimming speeds are positively correlated with body size in salmonids (Ware 1978; Trudel and Welch 2005). Alternatively, larger individuals may exhibit size-specific behaviours, such as greater risk taking (Werner et al. 1983) or more efficient foraging (Mittelbach 1981), that secondarily result in faster rates of migration.

Previous evidence of a strong relationship between fork length and swimming speeds (e.g., Ware 1978) does not make our findings novel in the broader context of fish behaviour; however, these results contrast with evidence from acoustic tagging studies on juvenile salmon in which coastal migration rates were not correlated with size (Melnychuk et al. 2010). We suggest that these divergent results are driven by differences in the initial size ranges that each study sampled (155–250 mm in Melnychuk et al. 2010; 45–150 mm in this study). Because migratory rate appears to be correlated with size only in smaller individuals, we suggest the relationship between fork length and migration speed may decouple past a threshold size. Beyond this limit, behaviour may be principally driven by other characteristics (e.g., growth, local foraging conditions). More broadly, our findings indicate that the movements of large age-2 juveniles may not be representative of all southern BC sockeye salmon juveniles, many of which are age-1 (Irvine and Akenhead 2013) and less than 120 mm when caught in nearshore waters (Neville et al. 2013).

This size-dependent variation in migratory behaviour becomes particularly important when using movement rates to estimate stage-specific survival. Because smaller individuals move north more slowly, they may be more sensitive to poor foraging conditions or high predator densities in nearshore environments. Ultimately, these individuals may experience relatively greater rates

Fig. 6. Predicted probability of juvenile sockeye salmon being captured in fall surveys (with 95% CI) as a function of back-calculated (a) ocean entry date or (b) entry fork length (FL). The fitted model in each panel contains the explanatory variable shown on the x axis when the second is held at its mean value. Sampled individuals were collected in 2008 and belonged to Chilko Lake, Great Central Lake, and Lower Adams River populations.



of mortality in regions such as the Strait of Georgia or Barkley Sound. Such differences may explain why evidence of high rates of nearshore mortality in juvenile sockeye salmon is currently mixed (Welch et al. 2011; Beamish et al. 2012; McKinnell et al. 2014).

Juveniles captured in northern regions that entered the marine environment later in the year also migrated more rapidly (e.g., individuals that entered in mid-May migrated $\sim 5 \text{ km} \cdot \text{day}^{-1}$ faster than those entering in late April). Seasonal increases in migratory rate may indicate that the relative benefits of arrival on maturation grounds increase as summer progresses, perhaps due to reduced zooplankton abundance in southern regions, which tends to peak in May–June on the west coast of Vancouver Island and Strait of Georgia (Harrison et al. 1983; Mackas et al. 2004). However, because there are also substantial energetic costs associated with faster swimming speeds (Ware 1978), these late-entry fish may arrive on maturation grounds in poor condition and experience reduced survival as a result. The relationship between entry phenology and migratory rate was only significant among juveniles caught in northern regions, which may suggest that smaller southern individuals are constrained to slower migratory rates or longer nearshore residency, perhaps due to greater costs from offshore movements (e.g., mortality, Healey 1980).

Because salmon migratory behaviour appears to be influenced by physical and biological conditions at multiple spatial scales (Burke et al. 2013), it was unsurprising that migratory rate varied with ocean entry location. For example, Vancouver Island populations captured north of Vancouver Island migrated at a significantly slower rate ($\sim 2 \text{ km} \cdot \text{day}^{-1}$) than Fraser River juveniles. Johnstone Strait may be particularly important in driving differences between Fraser River and Vancouver Island juveniles, as well as between Fraser River fish caught in northern or southern regions. Johnstone Strait is a narrow passage separating Vancouver Island and the BC mainland that is located immediately north of the Strait of Georgia. It is characterized by extreme tidal flows that create low levels of primary productivity and is hypothesized to be a region of poor growth and low survival (McKinnell et al. 2014). Fraser River juveniles may accelerate to pass through these poor foraging conditions or utilize prevailing surface currents, which tend to flow out of the Strait of Georgia through Discovery Passage via Johnstone Strait (Waldichuk 1957). If this is the case, the migratory rate of Fraser River fish may increase relative to Vancouver Island juveniles, which migrate through the weaker and predominantly southerly currents that are present off the west coast of Vancouver Island in early summer (Freeland et al. 1984).

Differences in migratory route may also ultimately influence survival. For example, variation in migratory route within salmonid populations is correlated with nearshore mortality rates

(Furey et al. 2015) and more extreme differences in migration pathways between populations are thought to influence population specific survival patterns (Ye et al. 2015). Unfortunately accurate estimates of juvenile marine survival are lacking for most sockeye salmon populations; however, it is possible that differences in migratory route or the energetic requirements of migration have contributed to high returns to Vancouver Island populations relative to Fraser River stocks in recent years (DFO 2012, 2014).

Although mean migratory rate was significantly greater in 2007 than 2008, the many variables that may influence migratory behaviour that were not accounted for in this study make it impossible to isolate specific drivers of interannual differences. This is particularly true with regards to juvenile salmonids, which can alter their movements due to a range of physical (e.g., flow, temperature) or biological conditions (e.g., density dependence, primary productivity) in freshwater (Sykes et al. 2009) and marine rearing habitats (Burke et al. 2013). Biophysical models specific to conditions on the BC shelf could be used to examine the relative importance of these processes to sockeye salmon.

Our estimates of juvenile sockeye salmon entry size, timing, and migratory rate from otolith microstructure are broadly consistent with field observations, as well as experimental and theoretical studies. On-going rotary screw trap surveys in the lower Fraser River capture out-migrating smolts of similar size ranges, from late April to mid-June with peak catches occurring in early to mid-May (C. Neville, unpublished data). The migratory rates we report are also within the ranges calculated from other studies (Welch et al. 2009; Melnychuk et al. 2010; Welch et al. 2011; Preikshot et al. 2012; Rechisky et al. 2015). Finally, our estimates of migratory rate do not appear to be physiologically unrealistic because they are below maximum sustainable speeds obtained in laboratory experiments ($3.3\text{--}8.2 \text{ bl} \cdot \text{s}^{-1}$; Brett and Glass 1973) or theoretical optimal cruising speeds obtained from models of oxygen consumption ($3\text{--}5 \text{ bl} \cdot \text{s}^{-1}$ at $10\text{--}20^\circ \text{C}$; Trudel and Welch 2005), and within the range obtained from coded wire tag (CWT) recoveries (mean $2.6 \text{ bl} \cdot \text{s}^{-1}$; Tucker et al. 2015).

Fall-caught juveniles

Fall-caught individuals migrated at slower rates than individuals captured in the same regions during summer surveys and this delayed migratory behaviour was strongly associated with marine entry characteristics. Specifically, individuals entering the ocean after 24 May had a high probability of being captured in fall surveys, while those that entered during peak out-migration periods in early to mid-May were likely to be caught in summer surveys. Although there was considerable overlap between seasons, entry size was also a significant predictor of season of capture. Fall-caught individuals tended to be smaller than 85 mm at ocean

entry and exhibited substantially less overall variation in body size than fish caught in northern regions during the summer. Conversely, population identity was a poor predictor of capture season and the probability of individuals migrating in the fall did not differ among the three populations we examined. The absence of Sproat Lake individuals in fall surveys is one exception and may be related to their relatively large juvenile size (Beacham et al. 2014b).

The nearshore distribution of juvenile fish captured during our fall survey suggests a migratory behaviour that is fundamentally different from that of the majority of juvenile sockeye salmon, which move offshore well before their first marine winter (Burgner 1991; Tucker et al. 2009). We suggest that there are two likely explanations for this pattern. First, though fall-caught individuals enter relatively late in the year, they may still co-migrate with juveniles that are normally captured during summer surveys. After reaching the coast of southeastern Alaska, these individuals may then delay or halt their migration. Alternatively, fall-caught juveniles may represent a migratory behaviour that is distinct from either group of summer-caught fish. While the ocean entry dates of fall-caught fish preceded our summer surveys and indicate they must have been at sea when we were sampling, fall-caught juveniles entered the marine environment nearly a month after summer-caught juveniles and may not strongly overlap spatially with the bulk of their cohort. If a late ocean entry date results in fall-caught fish remaining further inshore, these individuals may not be vulnerable to our summer surveys and ultimately migrate north independently.

Interestingly, a delayed northern migration by small juvenile sockeye salmon that enter late in the year would represent an intermediate strategy within the species. The majority of sockeye salmon populations enter the marine environment after rearing for several years in natal lakes, but several populations (e.g., the Harrison River stock) are dominated by “sea-type” individuals (Burgner 1991). No sea-type populations were included in our study; however, among Fraser River populations, sea-type juveniles enter the ocean without extensive freshwater rearing, late in the year (~July), and reside for several months in the Strait of Georgia (Tucker et al. 2009; Beacham et al. 2014a; Beamish et al. 2016). The lingering, fall-caught juveniles we describe here may move north after the peak migration in early summer, but before sea-type individuals. Such an expanded temporal and spatial distribution is consistent with widespread catches of juvenile sockeye salmon across the north Pacific (Tucker et al. 2009; Beacham et al. 2014a), as well as Morris et al.’s (2007) hypothesis that variation in migratory rate may buffer salmonid populations from mortality en route.

While some sea-type populations have returned at high rates in recent years (Beamish et al. 2016), it appears unlikely that the fall-caught individuals examined here would experience improved survival by delaying their migration. First, because fall-caught fish make up a small fraction of the overall catch (Tucker et al. 2009), rapid offshore migration appears to be under relatively strong selective pressure. Second, fall-caught juvenile sockeye salmon from Vancouver Island and the Fraser River fish co-occur with relatively high densities of juveniles from Rivers Inlet (Tucker et al. 2009). This pattern is noteworthy because the Rivers Inlet stock crashed in the early 1990s, with poor marine survival identified as a principal driver (McKinnell et al. 2001). If lingering individuals from Vancouver Island and Fraser River populations rear in the same environment as Rivers Inlet juveniles, they may experience similarly high rates of mortality.

We observed considerable variation in the distribution and migratory rate of juvenile sockeye salmon that was correlated with age, as well as ocean entry size, phenology, and population aggregate. It is possible that the entry characteristics we estimated directly contribute to differences in migratory behaviour. Alternatively, size, phenology, and migratory behaviour may simply

covary with one another; perhaps as genetically related subgroups within a population diverge. Regardless of the mechanisms that create variation in migratory behaviour, our results support growing evidence that the marine migrations of salmonids are far from homogeneous (Byron and Burke 2014). Unfortunately, because little is known about what drives differential survival during marine rearing, we can only speculate as to how variation in migratory behaviour will influence mortality. Yet, it appears clear that older, larger sockeye salmon juveniles that are caught in northern regions have the potential to experience very different environmental conditions than those captured further south. These differences will influence how long individuals are exposed to specific predator communities (Christensen and Trites 2011), the prey community that they encounter (Mackas et al. 2004; McKinnell et al. 2014), the pathogens they are exposed to (Miller et al. 2014), and the energy they accumulate to complete migrations and successfully overwinter (Trudel et al. 2007). Future work should seek to identify mechanisms of mortality throughout the migratory corridor and examine how they may differentially affect juvenile Pacific salmon that differ in entry size and timing.

Acknowledgements

We thank Tyler Zubkowski, John Morris, Mary Thiess, Yeongha Jung, Janelle Curtis, Larissa Rohrbach, Deborah Harstad, and the crew of the CCGS *W.E. Ricker* and *F/V Viking Storm* for assisting with the collection of *O. nerka* juveniles. We are grateful for the input of two anonymous reviewers, as well as several editors, whose comments greatly improved the quality of this manuscript. Funding was provided by a University of Victoria Graduate Fellowship, a Natural Sciences and Engineering Research Council of Canada (NSERC) PGS-D3 Scholarship, a Montalbano Scholar’s Fellowship, an Arne H. Lane Graduate Fellowship, the Liber Ero Foundation, Canada Foundation for Innovation (CFI) and BC Knowledge Development Fund (BCKDF) infrastructure grants (30766), NSERC Discovery Grant (418670-2013), Fisheries and Oceans Canada, and the Bonneville Power Administration (2003-009-00-29753). All applicable national guidelines for the care and use of animals were followed.

References

- Beacham, T.D., Candy, J.R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Deng, L., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2005. Estimation of stock composition and individual identification of Sockeye Salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. *Trans. Am. Fish. Soc.* **134**(5): 1124–1146. doi:10.1577/T05-005.1.
- Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014a. Stock-specific migration pathways of juvenile Sockeye Salmon in British Columbia waters and in the Gulf of Alaska. *Trans. Am. Fish. Soc.* **143**(6): 1386–1403. doi:10.1080/00028487.2014.935476.
- Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014b. Stock-specific size of juvenile Sockeye Salmon in British Columbia waters and the Gulf of Alaska. *Trans. Am. Fish. Soc.* **143**(4): 876–888.
- Beamish, R.J., Neville, C., Sweeting, R., and Lange, K. 2012. The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser River in 2009. *Mar. Coast. Fish.* **4**(1): 403–414. doi:10.1080/19425120.2012.676607.
- Beamish, R.J., Neville, C.M., Sweeting, R.M., Beacham, T.D., Wade, J., and Li, L. 2016. Early ocean life history of Harrison River sockeye salmon and their contribution to the biodiversity of sockeye salmon in the Fraser River, British Columbia, Canada. *Trans. Am. Fish. Soc.* **145**(2): 348–362. doi:10.1080/00028487.2015.1123182.
- Bond, M.H., Hayes, S.A., Hanson, C.V., and MacFarlane, R.B. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Can. J. Fish. Aquat. Sci.* **65**(10): 2242–2252. doi:10.1139/F08-131.
- Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* **22**(6): 1491–1501. doi:10.1139/f65-128.
- Brett, J.R., and Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd. Can.* **30**(3): 379–387. doi:10.1139/f73-068.

- Burgner, R.L. 1991. Life history of Sockeye Salmon (*Oncorhynchus nerka*). In Pacific salmon life histories. Edited by C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C.
- Burke, B.J., Liermann, M.C., Teel, D.J., and Anderson, J.J. 2013. Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. *Can. J. Fish. Aquat. Sci.* **70**(8): 1167–1177. doi:10.1139/cjfas-2012-0505.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Byron, C.J., and Burke, B.J. 2014. Salmon ocean migration models suggest a variety of population-specific strategies. *Rev. Fish Biol. Fish.* **24**(3): 737–756. doi:10.1007/s11160-014-9343-0.
- Christensen, V., and Trites, A.W. 2011. Predation of Fraser River Sockeye Salmon. Cohen Commission Tech. Rep. 8.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004. Energetics and morphology of Sockeye Salmon: effects of upriver migratory distance and elevation. *J. Fish Biol.* **65**: 788–810. doi:10.1111/j.0022-1112.2004.00486.x.
- Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Batten, S.D., Patterson, D.A., Van Der Kraak, G., Shrimpton, J.M., and Farrell, A.P. 2007. Behaviour and physiology of Sockeye Salmon homing through coastal waters to a natal river. *Mar. Biol.* **152**(4): 905–918. doi:10.1007/s00227-007-0741-x.
- DFO. 2012. Assessment of Area 23 sockeye and 2010 forecast (Barkley Sound, Alberni Inlet). DFO Canadian Science Advisory Secretariat Science Response.
- DFO. 2014. Pre-season run size forecasts for Fraser River Sockeye (*Oncorhynchus nerka*) Salmon in 2014. DFO Canadian Science Advisory Secretariat Science Response.
- Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Oxford, U.K.
- Ferriss, B.E., Trudel, M., and Beckman, B.R. 2014. Regional and inter-annual trends in marine growth of juvenile salmon in coastal pelagic ecosystems of British Columbia, Canada. *Mar. Ecol. Prog. Ser.* **503**: 247–261. doi:10.3354/meps10726.
- Firth, D. 1993. Bias reduction of maximum likelihood estimates. *Biometrika*, **80**: 27–38. doi:10.1093/biomet/80.1.27.
- Fisher, J.P., Weitkamp, L.A., Teel, D.J., Hinton, S.A., Orsi, J.A., Farley, E.V., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., and Trudel, M. 2014. Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. *Trans. Am. Fish. Soc.* **143**(1): 252–272. doi:10.1080/00028487.2013.847862.
- Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* **36**: 883–902. doi:10.1111/j.1095-8649.1990.tb05636.x.
- Freeland, H.J., Crawford, W.R., and Thomson, R.E. 1984. Currents along the Pacific Coast of Canada. *Atmos.-Ocean*, **22**(2): 151–172. doi:10.1080/07055900.1984.9649191.
- Freshwater, C., Trudel, M., Beacham, T.D., Neville, C.E., Tucker, S., and Juanes, F. 2015. Validation of daily increments and a marine-entry check in the otoliths of Sockeye Salmon *Oncorhynchus nerka* post-smolts. *J. Fish Biol.* **87**(1): 169–178. doi:10.1111/jfb.12688. PMID:25959504.
- Freshwater, C., Trudel, M., Beacham, T.D., Godbout, L., Neville, C.-E.M., Tucker, S., and Juanes, F. 2016. Disentangling individual- and population-scale processes within a latitudinal size-gradient in Sockeye Salmon. *Can. J. Fish. Aquat. Sci.* **73**(8). [Online ahead of print.] doi:10.1139/cjfas-2015-0344.
- Furey, N.B., Vincent, S.P., Hinch, S.G., and Welch, D.W. 2015. Variability in migration routes influences early marine survival of juvenile salmon smolts. *PLoS ONE*, **10**(10): e0139269. doi:10.1371/journal.pone.0139269.
- Grueber, C.E., Nakagawa, S., Laws, R.J., and Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**(4): 699–711. doi:10.1111/j.1420-9101.2010.02210.x. PMID:21272107.
- Harrison, P.J., Fulton, J.D., Taylor, F.J.R., and Parsons, T.R. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. *Can. J. Fish. Aquat. Sci.* **40**(7): 1064–1094. doi:10.1139/f83-129.
- Healey, M.C. 1980. The distribution and residency of Pacific salmon in the Strait of Georgia, British Columbia, in relation to foraging success. *Proceedings of the North Pacific Aquaculture Symposium*, **82**: 61–69.
- Heinze, G., Ploner, M., Dunkler, D., and Southworth, H. 2013. logistf: Firth's bias reduced logistic regression.
- Hinch, S.G., Cooke, S.J., Healey, M.C., and Farrell, A.P. 2006. Behavioural physiology of fish migration: salmon as a model approach. In *Fish physiology: behaviour and physiology of fish*. Edited by K. Sloman, S. Balshine, and R. Wilson. Academic Press, Oxford, London.
- Irvine, J.R., and Akenhead, S.A. 2013. Understanding smolt survival trends in Sockeye salmon. *Mar. Coast. Fish.* **5**: 303–328. doi:10.1080/19425120.2013.831002.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. *Anim. Behav.* **40**: 313–321. doi:10.1016/S0003-3472(05)80926-1.
- Kovach, R.P., Joyce, J.E., Echave, J.D., Lindberg, M.S., and Tallmon, D.A. 2013. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS ONE*, **8**(1): e53807. doi:10.1371/journal.pone.0053807.
- Mackas, D.L., Peterson, W.T., and Zamon, J.E. 2004. Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. *Deep Sea Res. Pt. II Top. Stud. Oceanogr.* **51**(6–9): 875–896. doi:10.1016/j.dsr.2.2004.05.011.
- Marra, P.P., Hobson, K.A., and Holmes, R.T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**(5395): 1884–1886. doi:10.1126/science.282.5395.1884.
- McKinnell, S.M., Wood, C.C., Rutherford, D.T., Hyatt, K.D., and Welch, D.W. 2001. The demise of Owikeno Lake sockeye salmon. *N. Am. J. Fish. Manage.* **21**(4): 774–791. doi:10.1577/1548-8675(2001)021<0774:TDOOLS>2.0.CO;2.
- McKinnell, S.M., Curchister, E., Groot, C., Kaeriyama, M., and Myers, K.W. 2011. The decline of Fraser River Sockeye Salmon in relation to marine ecology. *Cohen Commission Tech. Rep.* **4**: 195.
- McKinnell, S.M., Curchister, E., Groot, C., Kaeriyama, M., and Myers, K.W. 2012. PICES advisory report on the decline of Fraser River Sockeye Salmon in relation to marine ecology. *PICES Sci. Rep.* **41**: 149.
- McKinnell, S., Curchister, E., Groot, K., Kaeriyama, M., and Trudel, M. 2014. Oceanic and atmospheric extremes motivate a new hypothesis for variable marine survival of Fraser River Sockeye Salmon. *Fish. Oceanogr.* **23**(4): 322–341. doi:10.1111/fog.12063.
- Melnchuk, M.C., Welch, D.W., and Walters, C.J. 2010. Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. *PLoS ONE*, **5**(9): e12916. doi:10.1371/journal.pone.0012916.
- Miller, K.M., Teffer, A., Tucker, S., Li, S., Schulze, A.D., Trudel, M., Juanes, F., Tabata, A., Kaukinen, K.H., Ginther, N.G., Ming, T.J., Cooke, S.J., Hipfner, J.M., Patterson, D.A., and Hinch, S.G. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. *Evol. Appl.* **7**(7): 812–855. doi:10.1111/eva.12164.
- Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, **62**(5): 1370–1386. doi:10.2307/1937300.
- Morris, J.F.T., Trudel, M., Thiess, M.E., Sweeting, R.M., Fisher, J., Hinton, S.A., Orsi, J.A., Farley, E.V., and Welch, D.W. 2007. Stock-specific migrations of juvenile Coho Salmon derived from coded-wire tag recoveries on the continental shelf of western North America. *Am. Fish. Soc. Symp.* **57**: 1–18.
- Mortensen, D., Wetheimer, A., Taylor, S., and Landingham, J. 2000. The relation between early marine growth of Pink Salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. *Fish. Bull.* **98**: 319–335.
- Neville, C.-E.M., Trudel, M., Beamish, R.J., and Johnson, S.C. 2013. The early marine distribution of juvenile Sockeye Salmon produced from the extreme low return in 2009 and the extreme high return in 2010. *NPAFC Tech. Rep.* **9**: 65–68.
- Peterman, R.M., and Dorner, B. 2012. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. *Can. J. Fish. Aquat. Sci.* **69**(8): 1255–1260. doi:10.1139/f2012-063.
- Preikshot, D., Beamish, R.J., Sweeting, R.M., Neville, C.M., and Beacham, T.D. 2012. The residence time of juvenile Fraser River Sockeye Salmon in the Strait of Georgia. *Mar. Coast. Fish.* **4**(1): 438–449. doi:10.1080/19425120.2012.683235.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rechisky, E.L., Welch, D.W., Porter, A.D., Clark, T.D., Gale, M.K., Furey, N.B., and Hinch, S.G. 2015. Telemetry-based estimates of early marine survival and residence time of juvenile sockeye salmon in the Strait of Georgia and Queen Charlotte Strait, 2014. In *State of physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2014*. Edited by P.C. Chandler, S.A. King, and R.I. Perry. Can. Tech. Rep. Fish. Aquat. Sci. 3131.
- Rice, C.A., Greene, C.M., Moran, P., Teel, D.J., Kuligowski, D.R., Reisenbichler, R.R., Beamer, E.M., Karr, J.R., and Fresh, K.L. 2011. Abundance, stock origin, and length of marked and unmarked juvenile Chinook Salmon in the surface waters of greater Puget Sound. *Trans. Am. Fish. Soc.* **140**: 170–189.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**(2): 103–113. doi:10.1111/j.2041-210X.2010.00012.x.
- Sergio, F., Tanferna, A., De Stephanis, R., Jiménez, L.L., Blas, J., Tavecchia, G., Preatoni, D., and Hiraldo, F. 2014. Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, **515**: 410–413. doi:10.1038/nature13696. PMID:25252973.
- Sturdevant, M.V., Fergusson, E., Hillgruber, N., Reese, C., Orsi, J., Focht, R., Wertheimer, A., and Smoker, B. 2012. Lack of trophic competition among wild and hatchery juvenile chum salmon during early marine residence in Taku Inlet, Southeast Alaska. *Environ. Biol. Fishes*, **94**(1): 101–116. doi:10.1007/s10641-011-9899-7.
- Sykes, G.E., Johnson, C.J., and Shrimpton, J.M. 2009. Temperature and flow effects on migration timing of Chinook Salmon smolts. *Trans. Am. Fish. Soc.* **138**(6): 1252–1265. doi:10.1577/T08-180.1.
- Trudel, M., and Welch, D.W. 2005. Modeling the oxygen consumption rates in Pacific salmon and Steelhead: model development. *Trans. Am. Fish. Soc.* **134**(6): 1542–1561. doi:10.1577/T04-156.1.
- Trudel, M., Thiess, M.E., Bucher, C., Farley, E.V., MacFarlane, R.B., Casillas, E., Fisher, J., Morris, J.F.T., and Murphy, J.M. 2007. Regional variation in the marine growth and energy accumulation of juvenile Chinook Salmon and Coho Salmon along the west coast of North America. *Am. Fish. Soc. Symp.* **57**: 205–232.
- Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E., Wallace, C., Teel, D.J., Crawford, W., Farley, E.V., and Beacham, T.D. 2009.

- Seasonal stock-specific migrations of juvenile Sockeye Salmon along the west coast of North America: implications for growth. *Trans. Am. Fish. Soc.* **138**(6): 1458–1480. doi:[10.1577/T08-211.1](https://doi.org/10.1577/T08-211.1).
- Tucker, S., Thiess, M.E., Morris, J.F.T., Mackas, D., Peterson, W.T., Candy, J.R., Beacham, T.D., Iwamoto, E.M., Teel, D.J., Peterson, M., and Trudel, M. 2015. Coastal distribution and consequent factors influencing production of endangered Snake River Sockeye Salmon. *Trans. Am. Fish. Soc.* **144**(1): 107–123. doi:[10.1080/00028487.2014.968292](https://doi.org/10.1080/00028487.2014.968292).
- Waldichuk, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. *J. Fish. Res. Bd. Can.* **14**(3): 321–486. doi:[10.1139/f57-013](https://doi.org/10.1139/f57-013).
- Walters, C.J., and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.* **50**(10): 2058–2070. doi:[10.1139/f93-229](https://doi.org/10.1139/f93-229).
- Ware, D.M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Bd. Can.* **35**(2): 220–228. doi:[10.1139/f78-036](https://doi.org/10.1139/f78-036).
- Welch, D.W., Melnychuk, M.C., Rechisky, E.R., Porter, A.D., Jacobs, M.C., Ladouceur, A., McKinley, R.S., and Jackson, G.D. 2009. Freshwater and marine migration and survival of endangered Cultus Lake Sockeye Salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. *Can. J. Fish. Aquat. Sci.* **66**(5): 736–750. doi:[10.1139/F09-032](https://doi.org/10.1139/F09-032).
- Welch, D.W., Melnychuk, M.C., Payne, J.C., Rechisky, E.L., Porter, A.D., Jackson, G.D., Ward, B.R., Vincent, S.P., Wood, C.C., and Semmens, J. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc. Natl. Acad. Sci. U.S.A.* **108**: 8708–8713. doi:[10.1073/pnas.1014044108](https://doi.org/10.1073/pnas.1014044108).
- Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**(6): 1540–1548. doi:[10.2307/1937508](https://doi.org/10.2307/1937508).
- Ye, H., Beamish, R.J., Glaser, S.M., Grant, S.C., Hsieh, C.H., Richards, L.J., Schnute, J.T., and Sugihara, G. 2015. Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. *Proc. Natl. Acad. Sci. U.S.A.* **112**(13): E1569–E1576. doi:[10.1073/pnas.1417063112](https://doi.org/10.1073/pnas.1417063112). PMID:[25733874](https://pubmed.ncbi.nlm.nih.gov/25733874/).
- Zhang, Z., and Beamish, R.J. 2000. Use of otolith microstructure to study life history of juvenile Chinook Salmon in the Strait of Georgia in 1995 and 1996. *Fish. Res.* **46**: 239–250. doi:[10.1016/S0165-7836\(00\)00149-1](https://doi.org/10.1016/S0165-7836(00)00149-1).