



FEATURED PAPER

Phenological Diversity of Salmon Smolt Migration Timing within a Large Watershed

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Abstract

Although there is growing concern that climate change might drive phenological mismatches between predators and prey, it is possible that within- and among-species phenological variation provides resilience against such a mismatch. One key life history event that may be vulnerable to climate-induced mismatch is the seaward migration of juvenile salmon relative to the spring bloom of their marine zooplankton prey. Here, we quantified phenological diversity of out-migration timing among salmon populations within a large watershed and its implications for climate mismatches with marine zooplankton. Specifically, we sampled juvenile Sockeye Salmon *Oncorhynchus nerka* throughout the spring and early summer in the estuary of the Skeena River, a vast watershed with numerous locally adapted salmon populations that support commercial, recreational, and First Nations fisheries, and we used genetic stock identification to link the fish to their population of origin. We found that Sockeye Salmon were migrating through the estuary for more than 50 d, with peak emigration for different populations varying by over 5 weeks. The out-migration timing of specific populations was related to geographic factors, including elevation of the rearing lake and the river distance between individual rearing lakes and the estuary, with different populations arriving 1.5 d later for

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every 100 m of elevation or 3 d later for every 100 km of river distance. Concurrent with sampling, we quantified the estuarine prey of juvenile Sockeye Salmon; zooplankton species composition and abundance varied throughout the smolt migration period, and the different salmon populations encountered different prey abundances upon ocean entry. Together, these results indicate underappreciated phenological diversity in this harvested metapopulation, which may contribute to response diversity and metapopulation-level resilience to climate change.

Worldwide increases in temperature observed during the present century have driven shifts in phenology—the timing of seasonal biological events—for many species (Parmesan and Yohe 2003; Parmesan 2006). Global temperature increases of 0.13°C per decade since 1950 (IPCC 2013) correspond with mean documented phenological advances of 5.1 d/decade during the past 50 years for terrestrial and marine species (Root et al. 2003). However, phenological responses to thermal change are not synchronous between species (CaraDonna et al. 2014) and vary by habitat (Thackeray et al. 2010), life history (Winder and Schindler 2004; Adrian et al. 2006), trophic level (Thackeray et al. 2010; Poloczanska et al. 2013), and functional group (Edwards and Richardson 2004). These phenological responses likely differ because different environmental cues, including photoperiod and temperature change, initiate biological events for different species (Robinson et al. 2009; Ovaskainen et al. 2013). There is emerging evidence that climate change can decouple the phenologies of species interactions, such as between predators and their prey species (e.g., Winder and Schindler 2004; Penuelas and Filella 2013), resulting in a temporal mismatch that causes reduced fitness, recruitment, and abundance (Cushing 1990).

Phenological variation within and among species may attenuate ecosystem responses to climate-induced mismatches. For instance, phenological variation among species may conserve ecosystem function in a changing climate by reducing the potential for phenological mismatch between interacting species at different trophic levels (Bartomeus et al. 2013; Burkle et al. 2013; Iler et al. 2013). Phenological diversity may also vary at the population level, and within-species phenological diversity could provide resilience to metapopulations facing environmental change. Although the importance of within-species population diversity for the maintenance of ecosystem processes is increasingly appreciated (Luck et al. 2003), there is limited understanding of population-level phenological diversity and its potential importance for climate change resilience. The downstream migration of juvenile anadromous salmonids to the marine ecosystem is one example of an important life history period that is potentially vulnerable to climate-induced mismatch, which may be mediated by population-level diversity. Diadromous salmonids, which support important coastal fisheries in

the Pacific Northwest, spawn and rear in freshwater before migrating downstream to marine feeding areas. During this early marine phase, young salmon of some species, including Sockeye Salmon *Oncorhynchus nerka*, feed principally on zooplankton. There is accumulating evidence that the degree to which the timing of the seaward migration for salmon aligns with abundant zooplankton prey can ultimately control salmon survival (Beaugrand and Reid 2003). Survival of salmon is higher when their out-migration coincides with peak prey abundance (Chittenden et al. 2010; Satterthwaite et al. 2014; Malick et al. 2015). Earlier smolt migration timing has been linked to higher survival to adulthood for Chinook Salmon *O. tshawytscha* and steelhead *O. mykiss* populations (Scheuerell et al. 2009). Survival during the first year at sea can control salmon productivity; for example, marine conditions in the first year at sea determine adult returns for steelhead (Moore et al. 2014), and synchronous year-class failures have been observed for different species of salmon and herring entering coastal waters of a given region in the same year (Beamish et al. 2012). Zooplankton phenology is shifting earlier, and the timing of peak abundances for different species of marine plankton has advanced by an average of 7.6 d/decade (Richardson 2008). There is also some evidence that smolt migration timing may also be advancing for some species, populations (Manhard et al. 2017), and life history types (Kovach et al. 2013) of salmon. For example, Atlantic Salmon *Salmo salar* smolt migration timing has advanced 2.5 d/decade across the North Atlantic basin (Otero et al. 2014). Thus, the phenology of out-migrating salmon and their zooplankton prey may be increasingly mismatched. Given the ongoing and predicted climatic changes to salmon ecosystems, an understanding of the phenology of out-migrating salmon and their marine prey is increasingly important.

The out-migration of smolts from different salmon populations that enter the ocean at the same location, such as populations from large watersheds, could either be synchronous or exhibit population-level phenological diversity. For example, many different locally adapted salmon populations may exist within large river systems, and it is possible that all populations within a large watershed might exhibit synchronous out-migration and thus be similarly vulnerable to mismatch with their zooplankton prey.

The timing of animal migrations has presumably evolved to coincide with the availability of specific resources, such as feeding opportunities, at the destination habitats (Both and Visser 2001). Alternatively, additional constraints or selective pressures during the freshwater phase could lead to phenological diversity of different salmon populations within large watersheds. Such phenological diversity could contribute to response diversity among these populations and potentially conveys climatic resilience to the metapopulation and to fisheries that integrate across this diversity. Although previous work has indicated that phenological traits are heritable (Carlson and Seamons 2008) but constrained by photoperiod, freshwater temperature (McCormick et al. 2002), and geographic factors (Achord et al. 2007), previous studies of salmon smolt out-migration timing from large rivers have been performed in systems with hatchery propagation that has potentially modified the local population diversity (e.g., Achord et al. 2007; Satterthwaite et al. 2014). There is a rich understanding of the remarkable diversity in many different traits across salmon populations (Quinn 2005) and its importance to the response diversity and the stability of salmon and their fisheries (Hilborn et al. 2003), yet the potential for population diversity in out-migration phenology among salmon populations remains relatively understudied.

Here, we quantify intraspecific diversity in downstream migration timing, a key phenological trait at the nexus of climate change and salmon resilience. Specifically, we examine whether Sockeye Salmon from the Skeena River, British Columbia, exhibit population-level phenological diversity in downstream migration. Our study objectives were to quantify the phenological diversity of smolt migration timing across populations, examine geographical factors that are associated with migration timing for the different populations, and assess how migration timing for the different populations relates to the timing of zooplankton abundance, which is related to food availability in the estuary. Collectively, our results indicate remarkable phenological diversity within this large watershed that can influence the response and resilience of these harvested salmon to climate change.

METHODS

Study system.—The Skeena River (Figure 1) drains a catchment of nearly 55,000 km² and supports the second-largest average return of Sockeye Salmon in British Columbia after the Fraser River. There are at least 30 genetically distinct populations of Sockeye Salmon that spawn throughout the Skeena River watershed (Morrell 2000), totaling approximately 3 million fish from 1985 to 2012 (PSC 2016). Most of the known Skeena River Sockeye Salmon populations are lake type, generally spawning

in tributaries upstream of freshwater lakes, where they rear for one or more years prior to initiating the seaward migration (Gottesfeld and Rabnett 2008). The different Skeena River Sockeye Salmon rearing lakes are analogous to conservation units designated by Fisheries and Oceans Canada under the Wild Salmon Policy (Fisheries and Oceans Canada 2009). In the Skeena River watershed, there are two known river-type populations of Sockeye Salmon, which spawn and rear for at least one growing season in river main stems, but there are no populations of ocean-type Sockeye Salmon, which migrate to sea immediately after hatching. There has been some enhancement of Sockeye Salmon populations in the Skeena River, including two artificial spawning channels constructed in the 1970s on tributaries to Babine Lake, the largest natural freshwater lake in British Columbia. The spawning channel-enhanced component has increased the abundance and relative proportion of Sockeye Salmon returning to Babine Lake, which now produces more than 90% of the aggregate return in some years (Wood 2008). Multiple populations of wild and enhanced Sockeye Salmon spawn in Babine Lake, but genetic resolution between the different populations from Babine Lake is lower than that between populations originating from different lakes throughout the Skeena River watershed (Beacham et al. 2014b). The different populations of Skeena River Sockeye Salmon exhibit varying trends in productivity or stock status relative to historic abundances. Although some populations, including the major wild and enhanced populations from Babine Lake, have followed a general trend of declining production during the past two decades, stable or increasing returns have been observed for some smaller populations during the same time period (Skeena Salmon Program data sets: extended time series of catch and escapement estimates for Skeena River Sockeye Salmon, Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, and Coho Salmon *O. kisutch* stocks; available at <http://data.salmonwatersheds.ca/data-library/>).

Diversity of Sockeye Salmon rearing lakes.—We hypothesized that the geographic characteristics of the different rearing lakes could affect the timing of out-migration for the different populations of Sockeye Salmon from the Skeena River. The timing of fry emergence, length of the growing season, and freshwater zooplankton availability are influenced by water temperature and clarity as well as the timing of the onset of thermal stratification, ice formation, and ice breakup (Quinn 2005). These abiotic factors are influenced by each rearing lake's elevation, depth, latitude, and proximity to the coast. Sockeye Salmon rearing lakes in the Skeena River watershed range from low-elevation coastal lakes less than 100 km (network river distance) from the estuary, which rarely freeze during the winter, to systems in the high interior, which may be more than 1,500 m in

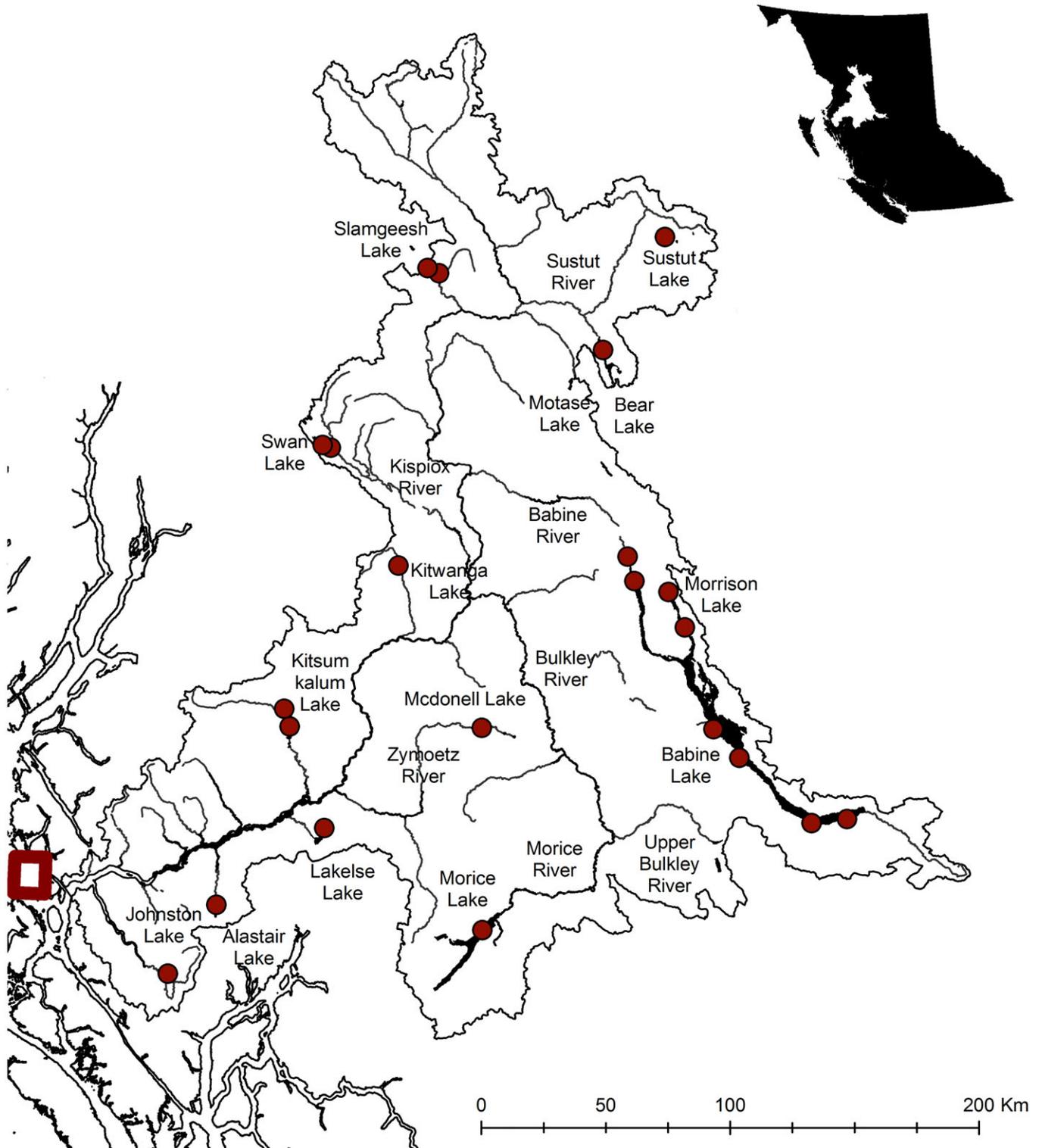


FIGURE 1. Map of the Skeena River and its watershed boundary, with major tributaries and Sockeye Salmon rearing lakes labeled. Points indicate spawning areas for genetically identified juvenile Sockeye Salmon captured in the estuary during 2013 and 2014; some rearing lakes contain multiple populations. Estuary sampling area is indicated by the rectangle near the bottom-left corner of the map.

elevation and over 500 km from the coast and may be covered by ice for more than 6 months of the year (Supplementary Table S1 available in the online version of this article; Figure 1). Water clarity, which influences primary production and therefore food availability, ranges from (1) turbid, glacial lakes supporting low densities of Sockeye Salmon fry and producing relatively small smolts or smaller fry that remain in freshwater for an additional year prior to initiating the seaward migration to (2) relatively warm, clear lakes with better growing conditions that support higher densities and produce larger smolts (Table S1). The fry rearing capacity of most of the rearing lakes in the Skeena River watershed has been estimated using the photosynthetic rate (PR) model, which predicts the optimal number and biomass of fry and the number of adult spawners required to produce that biomass based on total annual carbon production at each lake (Hume et al. 1996; Shortreed et al. 1998; Shortreed and Morton 2000). Most populations of lake-type Sockeye Salmon from the Skeena River migrate to sea after rearing in freshwater for 1 year, with a small proportion from some populations remaining in freshwater for an additional year. Exceptions include Morice Lake, a glacial system that primarily produces 2-year-old smolts, and Alastair Lake, which produces variable proportions of 1- and 2-year-old smolts in different years (Bilton and Smith 1969). Smolt enumeration programs located on the Babine, Kitwanga, and Slamgeesh rivers have reported that larger, older smolts are among the first to migrate to sea (Skeena Fisheries Commission, Gitanyow Fisheries Authority, and Gitksan Watershed Authorities, unpublished data). Although the different rearing lakes that support the population diversity of Sockeye Salmon have fundamentally different geographic and biological attributes that may be linked to smolt out-migration timing, young salmon from throughout this watershed all transit through the same estuary during the smolt migration (Anderson et al. 2015; Moore et al. 2015).

Fish sampling.—Sockeye Salmon smolts were captured in the Skeena River estuary in 2013 and 2014 using trawl (2013 and 2014) and purse seine (2014 only) sampling gear. Several smolts were also collected opportunistically during beach seine sampling that targeted other salmon species during the 2014 season. Weekly trawl samples were collected at six sites in the estuary of the Skeena River from the beginning of May until the beginning of July in both years (Carr-Harris et al. 2015; Moore et al. 2016). The trawl, which was 18 m long with a 5- × 4.6-m opening, was fished from a chartered gill-net vessel, *HMV Pacific Coast*, and was towed for a targeted duration of approximately 15 min per set. In 2014, we used a purse seine as a secondary gear at six stations that were sampled weekly between May and July. The purse seine, which was 9 m deep and 73 m long with 50-mm-mesh

webbing at the tow end and 12-mm-mesh webbing at the bunt, was deployed using a 3-m skiff to tow the bunt end away from a larger vessel and hold the net open into the tidal current for a targeted duration of 5 min per set. At the end of each set, the purse seine was closed while hauling the net into the larger vessel. Fish were transferred from the seine net into buckets by using dip nets, and the number of individuals of each species was enumerated. A subsample of Sockeye Salmon (up to 50 individuals from each sampling event, up to 100 individuals per day, and up to 300 individuals per week) was lightly anesthetized with tricaine methanesulfonate (MS-222), lengths were recorded to the nearest millimeter, and a small piece of caudal fin was removed for genetic analysis and stored in ethanol (2013 and 2014) or Whatman filter paper (2014). These fish were released after a recovery period in aerated buckets. For more information about field methods, see Carr-Harris et al. (2015) and Moore et al. (2016).

Genetic analysis.—Microsatellite DNA analysis was used to determine the populations of origin for genetically determined juvenile Sockeye Salmon captured in 2013 and 2014 (subsampling procedure described above). The DNA was extracted from desiccated tissue samples and was amplified by PCR at 14 microsatellite loci for Sockeye Salmon (Beacham et al. 2005). The PCR products were size-fractionated, and allele sizes were determined with an ABI 3730 capillary DNA sequencer (Applied Biosystems). Genotypes were scored with GeneMapper version 3.0 (Applied Biosystems) using an internal lane sizing standard (Withler et al. 2007). Allele frequencies were compared with genetic baselines of 245 Sockeye Salmon populations from 20 regions throughout the northeast Pacific (Beacham et al. 2014a). Individual probabilities and population proportions were assigned using a modified, C-based version of the program BAYES (Pella and Masuda 2001; Neaves et al. 2005). Genetic analyses were performed at Fisheries and Oceans Canada's Molecular Genetics Laboratory (Pacific Biological Station, Nanaimo, British Columbia).

Statistical analyses.—We used trawl capture data to determine the peak timing of overall smolt abundance for Sockeye Salmon in the estuary, to compare the overall timing for the smolt migration in 2013 and 2014, and to compare smolt migration timing with the timing of peak abundances for the different zooplankton taxa in both years. We constructed a generalized additive model (GAM) to predict the mean CPUE for each year after estimating the normalized CPUE for a 20-min set. The GAMs applied a nonparametric smooth function to the date of capture and a parametric factor for the year of capture and utilized a negative binomial distribution with a log link. We used ANOVA to compare models that included terms for day and year of capture with models

that excluded year to determine whether the year of capture had an effect on CPUE.

We used linear models to test whether Sockeye Salmon smolt migration timing varied by year, population, or both. We used a nested model framework, with data from the two sample years nested within the different populations, to determine whether year of capture, population of origin, or both were significant predictors for the date of capture in the estuary. Finally, we built a series of linear mixed-effects models to test whether physical and biotic characteristics of rearing lakes affected the timing of migration for the different populations of Sockeye Salmon from the Skeena River. We included a random term for population and fixed terms for the river distance, elevation and latitude, and lake productivity. Elevation and latitude are related to several factors that may influence the timing of onset of the downstream migration, including temperature, timing of ice breakup, and photoperiod. River distance, which was calculated as the network distance from each natal lake to the estuary, will affect the duration of the downstream migration. The productivity of a given lake may affect the size and abundance of smolts. For the productivity term, we used S_{max} , the optimal spawner escapement derived from the PR model, divided by the surface area of each lake (Shortreed et al. 1998, 2007; Shortreed and Morton 2000). We constructed a series of models including every combination of random and fixed terms, which were fitted using maximum likelihood, and we used Akaike's information criterion (AIC) to identify models with the highest support. Only specimens that originated from the Skeena River watershed and whose genetic determination exceeded a 90% probability threshold for correct assignment were included in linear and linear mixed-effects models. To address the uncertainty of genetically separating the different Sockeye Salmon populations from Babine Lake, we conducted a sensitivity analysis by re-running the linear mixed-effects models after pooling samples by rearing lake (the only lakes with multiple populations in our study were Babine Lake and Kitsumkalum Lake in the lower Skeena River watershed) and using lake rather than population as a random effect. To address potential biases related to a higher proportion of non-Babine Lake Sockeye Salmon in our sample resulting from a 90% probability threshold, we repeated the above analyses on data sets that included individuals whose population or lake of origin exceeded probability thresholds of 50% and 70%. Finally, to test which random effect resulted in the best fit, we compared two sets of global models fitted with restricted maximum likelihood that included all fixed effects and a random effect for either population or lake using both data sets (i.e., all individuals for which the probability of correct assignment to a given population exceeded the 90%

threshold and all individuals for which the probability of correct assignment to a given lake exceeded 90%). All statistical analyses were conducted within the R programming environment (R Core Team 2017).

We estimated the expected duration of downstream migration from the rearing lakes to determine whether it explained the variation in downstream migration timing for the different populations. The duration of the downstream migration from Babine Lake to the estuary was estimated using tags from an existing smolt weir at the outlet of Nilkitkwa Lake, immediately downstream of Babine Lake, where a mark-recapture project was carried out to enumerate out-migrating Sockeye Salmon smolts in 2013 and 2014. Between 3,000 and 3,120 smolts per day from Babine Lake were marked by applying colored staples posterior to the dorsal fin, and these smolts were released into Nilkitkwa Lake (Macdonald and Smith 1980). Approximately 1 million tags were applied to out-migrating smolts between May 5 and June 7 in both years, representing approximately 1% of the total smolt migration in 2013 and 1.5% of the migration in 2014. We captured several tagged smolts during estuary sampling and estimated the number of days that marked smolts swam in transit between Babine Lake and our estuary capture sites. The average distance traveled per day was estimated as the quotient of the river distance between the smolt weir and a reference point in the estuary and the number of days that elapsed after release upstream of the smolt weir. An estimate of the duration of the downstream migration for non-Babine Lake populations was calculated as the quotient of the network distance from each natal lake to the estuary and the average distance traveled per day calculated for Babine Lake smolts.

Zooplankton sampling.—We collected zooplankton samples in 2013 and 2014 to compare food availability for juvenile Sockeye Salmon smolts during their out-migration period. Zooplankton samples were collected biweekly from mid-April until mid-July in 2013 and 2014 from a fish sampling station located in the Skeena River estuary near the Kinahan Islands, approximately 10 km from the northern exit of the Skeena River (54°13.4'N, 130°22.3'W), where Sockeye Salmon smolts were captured in 2013 and 2014 and have been observed feeding during these and previous years (C. N. Carr-Harris, unpublished data). In both years, vertical plankton tows were conducted during daylight hours using a simple conical plankton net with a mouth diameter of 57 cm and 250- μ m mesh. Samples were collected to a maximum depth of 20 m, which includes the depth stratum where juvenile salmon are known to feed (Straty and Jaenicke 1980). Zooplankton samples were preserved in 5% formalin buffered with seawater and were later rinsed through a 150- μ m sieve. Subsamples were drawn from each

sample by using a Folsom plankton splitter, and zooplankton were sorted by taxonomic category and enumerated using a Leica M70 dissecting microscope. The relative abundances of zooplankton taxa were determined by dividing the number of individuals in each category for each sample by the maximum number of individuals encountered during the sampling period.

RESULTS

Fish Sampling and Genetic Analysis

Juvenile Sockeye Salmon were captured from May 13 to July 1, 2013, and from May 7 to July 4, 2014. The overall timing of the Sockeye Salmon smolt out-migration was similar in 2013 and 2014, with smolts present in the estuary for at least 6 weeks in each year. The GAMs predicted peak abundances of juvenile Sockeye Salmon on May 31 for both years (Figure 2A), with mean predicted CPUEs of 18.0 smolts per 20-min set on May 31, 2013, and 27.3 smolts per 20-min set on May 31, 2014. We

captured 562 juvenile Sockeye Salmon by trawl in 2013; 776 juveniles were captured by trawl and 3,165 were captured by purse seine in 2014, with an additional eight captured opportunistically by beach seine in 2014. Of these, a subsample of 407 specimens was submitted for genotyping in 2013, and a subsample of 952 specimens was submitted in 2014. Genetic determinations to population of origin were obtained for 361 (89%) of the specimens submitted in 2013 and 768 (81%) of those submitted in 2014. The lower success rate for 2014 samples was mostly attributable to tissue samples that were too small to permit extraction of sufficient genetic material for amplification. Genotyping was not successful for a small number of samples (5 in 2013; 6 in 2014) that exceeded a threshold of five missing microsatellite loci, most likely because of errors in speciation (these fish were removed from subsequent analysis). Of the genetically identified specimens, 96% originated from the Skeena River watershed, and the remainder were assigned with varying probability to populations in the Nass and Stikine rivers, southeast Alaska, and the north and central coasts of British Columbia. We

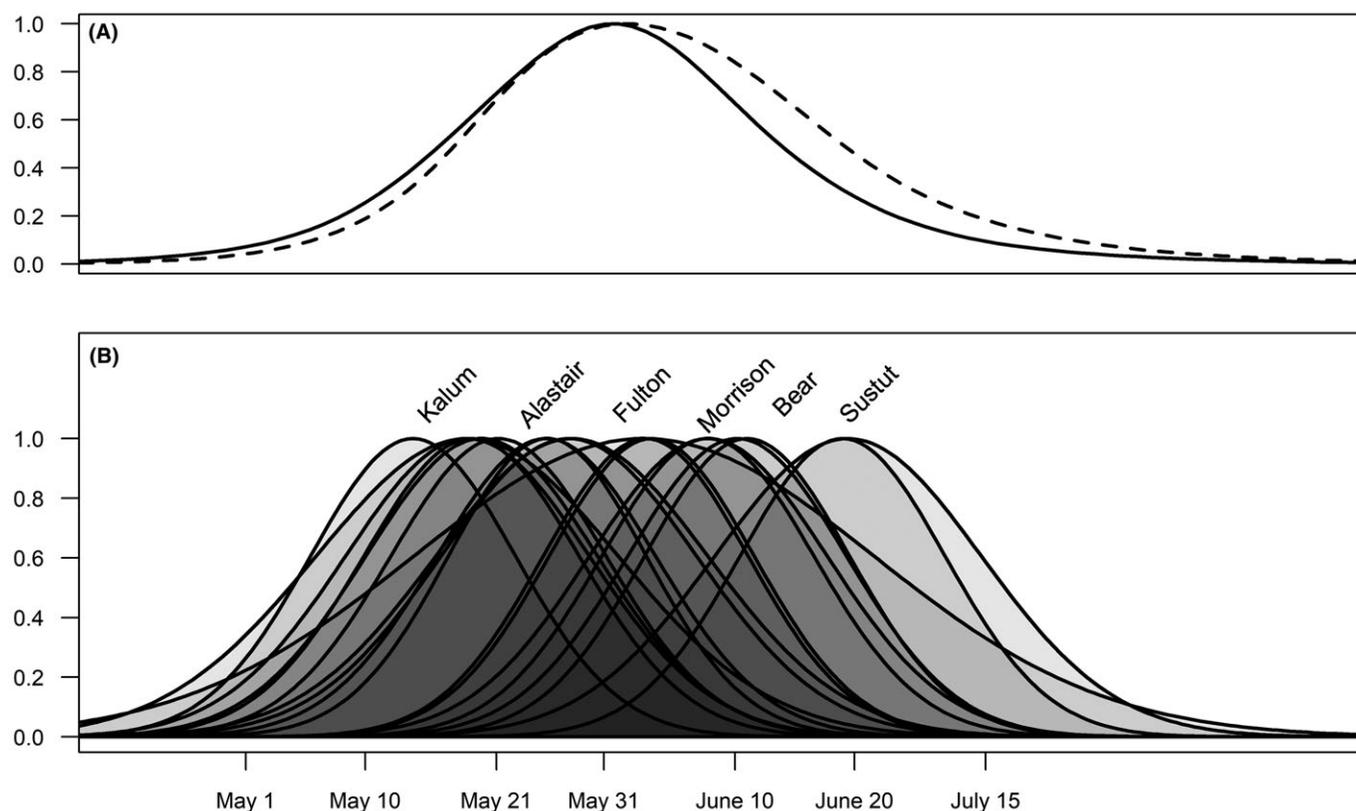


FIGURE 2. (A) Fitted generalized additive model predictions for trawl catch per unit effort (Sockeye Salmon smolts per 20-min set) from May to July in 2013 (dashed line) and 2014 (solid line), normalized by dividing predicted values by the maximum predicted value for each year so that the highest value is 1 for both years; and (B) probability distribution of estuarine residence timing for different Skeena River Sockeye Salmon populations. Individual probability curves depict a normal distribution using the mean and SD from linear model coefficients (see Table 1) of estimated peak dates of estuarine capture for Skeena River populations sampled in 2013 and 2014. Probability curves are normalized such that the maximum mean value for all populations is 1.

captured Sockeye Salmon from at least 22 genetic populations throughout the Skeena River watershed (Table 1). Among the total number of successful genetic determinations, 23% from 2013 ($n = 87$) and 38% from 2014 ($n = 288$) exceeded the 90% probability threshold of correct assignment to an individual population. Furthermore, 82% of the successful genetic determinations from 2013 ($n = 287$) and 90% of those from 2014 ($n = 686$) exceeded the 90% probability threshold of correct assignment to a given lake. Reducing the threshold probability of assignment to a given population to 70% resulted in sample sizes of 183 for 2013 and 504 for 2014, while a probability threshold of 50% for a given population produced sample sizes of 287 for 2013 and 687 for 2014 (Table S2). Applying a 70% threshold probability of correct assignment to a given lake resulted in sample sizes of 315 for 2013 and 721 for 2014; a probability threshold of 50% for a given lake resulted in sample sizes of 332 for 2013 and 741 for 2014. Most individuals whose first probability of assignment was less than 90% were from Babine Lake. In both

years, non-Babine Lake populations accounted for 36% of individual assignments for Skeena River Sockeye Salmon at a 90% probability threshold, 22% at a 70% probability threshold, 17% at a 50% probability threshold, and 16% ($n = 171$) for all samples with no probability threshold applied.

Timing

The different populations of Sockeye Salmon within the Skeena River exhibited different smolt migration timing (Table 1; Figure 2B). The estimated mean peak dates of capture for the different populations for individuals exceeding a 90% threshold probability of correct assignment ranged from May 14 for smolts from Kitwanga Lake to June 19 for smolts from Sustut Lake (Table 1; Figures 2B, 3), a difference of 5 weeks. Linear modeling indicated that date of capture was affected by population (ANOVA: $P < 0.0001$) but not by year ($P = 0.2395$) for the 2 years of data available. Linear correlation coefficients indicated that population explained 51% of the variability in date of estuary capture for juvenile Sockeye Salmon with a greater than 90% probability of assignment to a given population, and lake explained 40% of the variability for those with a greater than 90% probability of assignment to a given lake.

There was evidence that geographic factors were linked to smolt migration timing for the various populations. The mean date of estuary residence for Skeena River Sockeye Salmon populations was correlated with river distance and elevation but not with latitude or productivity (Figure 4). Given strong support for including population but not year as an effect in the linear models (ANOVA, chi-square test: $P = 0.1178$), we used AIC to compare linear mixed-effects models with random terms that allowed the intercept to vary by population or rearing lake using pooled data from both years of sampling. Although the geographic variables accounted for less variation than population, AIC values indicated higher support for models that included any combination of river distance, elevation, latitude, and productivity as fixed effects than for models that included only a random term for population with no fixed effects for 2013, 2014, and both years combined (Table S3). Because there was considerable correlation between pairs of geographic variables (river distance and elevation: $R^2 = 0.94$; river distance and latitude: $R^2 = 0.70$; elevation and latitude: $R^2 = 0.68$), we could not determine which combination of these factors contributed most to smolt migration timing for the different populations of Sockeye Salmon. Values of AIC indicated the highest support with very little difference (AIC difference = 0.40) for models that included a single term for river distance or elevation for each year of data and for both years combined. River distance and elevation were significant covariates ($P < 0.05$) in models that included a

TABLE 1. Lakes of origin, sample sizes, and mean dates of estuary capture for Skeena River Sockeye Salmon populations represented in 2013 and 2014 estuary sampling. Sample size indicates the number of individuals for which the probability of genetic determination was greater than 90%.

Population	Lake	Sample size	Mean date	SD (d)
Kitwanga	Kitwanga	2	May 14	0.0
Kalum	Kitsumkalum	10	May 19	4.5
Stephens	Stephens	16	May 19	4.7
Upper Babine	Babine	39	May 19	4.0
Williams	Lakelse	12	May 20	5.8
Damshilqwit	Slamgeesh	1	May 21	–
McDonnell	McDonnell	6	May 21	3.8
Alastair	Gitnadoix	31	May 25	9.9
Kalum	Kitsumkalum	6	May 25	2.5
Lower Babine	Babine	26	May 27	8.6
Nanika	Morice	18	May 27	4.1
Grizzly	Babine	1	May 30	–
Fulton	Babine	138	Jun 2	8.6
Swan	Swan	2	Jun 3	0.0
Tahlo	Tahlo	4	Jun 3	1.0
Johnston	Johnston	7	Jun 8	18.3
Pierre	Babine	20	Jun 8	11.0
Four Mile	Babine	6	Jun 10	17.4
Morrison	Morrison	3	Jun 11	1.7
Pinkut	Babine	1	Jun 12	–
Salix	Bear	2	Jun 19	0.0
Sustut	Sustut	24	Jun 19	13.0

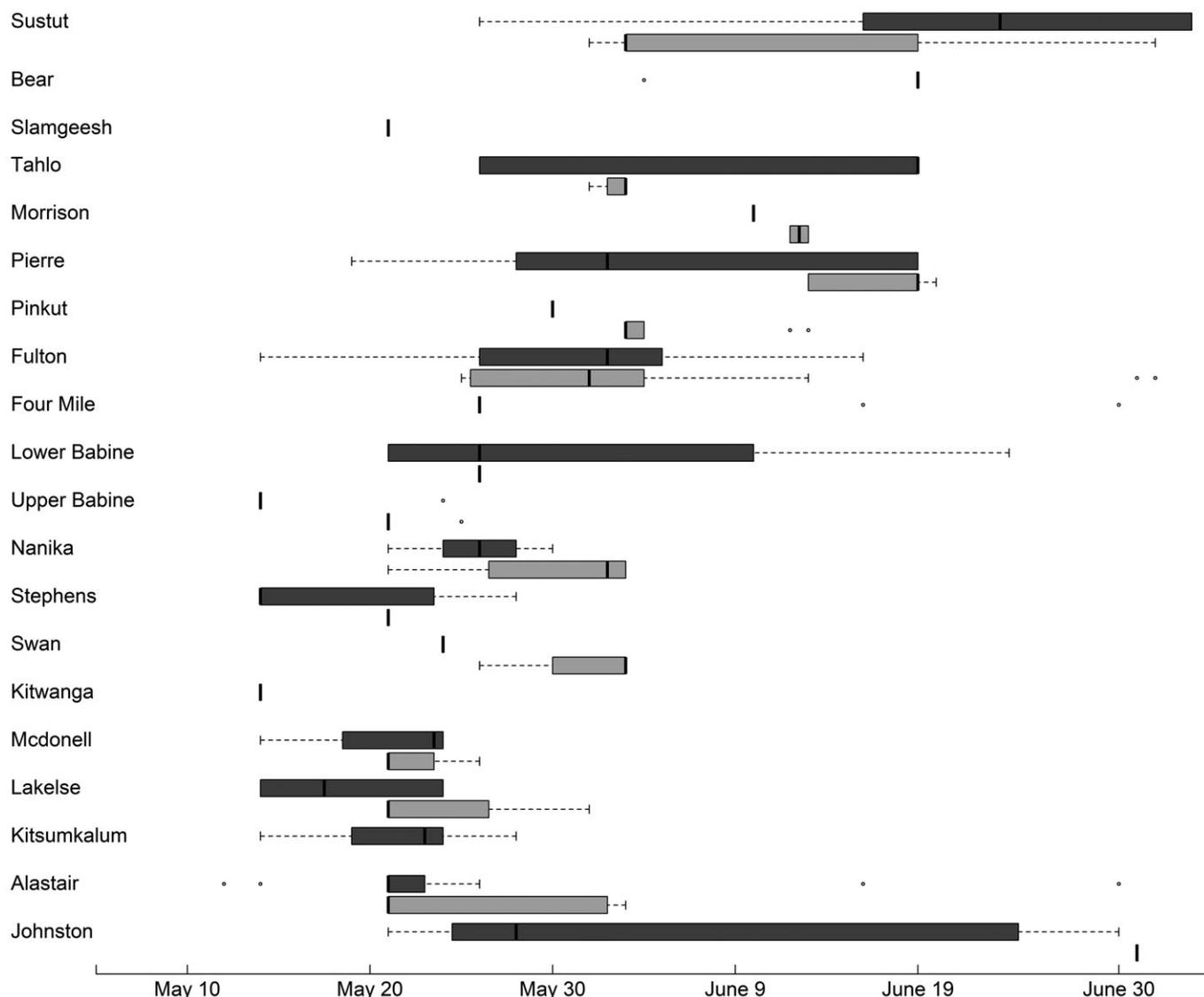


FIGURE 3. Box plots of estuary capture dates for Skeena River Sockeye Salmon smolts by population and year of capture for individuals with a greater than 90% probability of assignment to a given population. Smolts captured in 2013 are shown in light gray, and smolts captured in 2014 are shown in dark gray. The boxes represent the first and third quartiles, and the bold vertical line indicates the mean capture date for each population/year.

single fixed effect for each; however, neither was significant in models that included a combination of these variables. Models that included a single fixed effect suggested that the timing of downstream migration was negatively correlated with river distance, latitude, and elevation. The predicted downstream migration timing was 3.1 d (SE = 1.3) later for every 100 km of increasing river distance ($P = 0.0259$), 1.5 d (SE = 0.58) later for every 100 m of elevation ($P = 0.0184$), or 5.4 d (SE = 3.0) later for every 1° increase in latitude ($P = 0.0875$).

Linear mixed-effects model results were similar after grouping Babine Lake Sockeye Salmon samples and rerunning all models for data sets that included samples

whose probability of genetic determination to (1) individual population and (2) rearing lake exceeded 90%. For example, the predicted timing of downstream migration was 3.1 d (SE = 1.4) later for every 100 km of increasing river distance ($P = 0.0465$), 1.4 d (SE = 0.56) later for every 100 m of elevation ($P = 0.0185$), and 6.5 d (SE = 2.7) later per 1° of latitude ($P = 0.0269$) for the larger data set (probability of genetic assignment to a given lake >90%). Likewise, mixed-effects model results were similar when the models were run using data sets produced with different probability thresholds of correct assignment. For example, based on a data set for which the probability of genetic assignment to a given

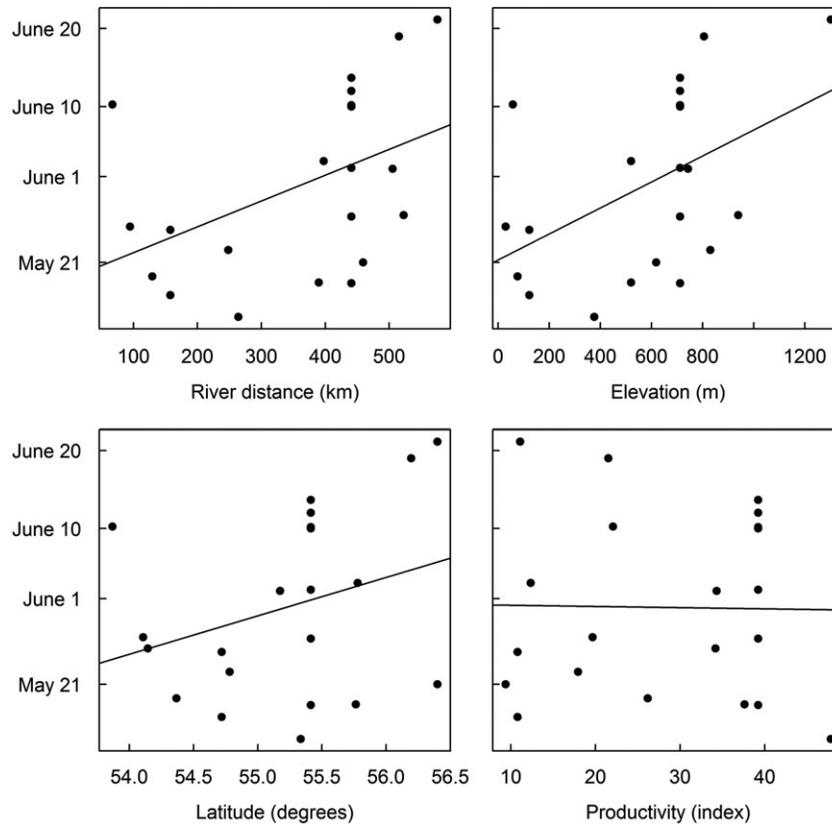


FIGURE 4. Bivariate plots of mean estuarine capture date for all Skeena River Sockeye Salmon populations that were encountered in the estuary, with lines indicating fitted linear model predictions for river distance ($r^2 = 0.21$, $P = 0.0301$), elevation ($r^2 = 0.23$, $P = 0.0281$), latitude ($r^2 = 0.10$, $P = 0.144$), and productivity ($r^2 = 0.00$, $P = 0.907$).

population exceeded a threshold of 50%, the predicted timing of downstream migration was 3.3 d (SE = 1.1) later for every 100 km of increasing river distance, 1.5 d (SE = 0.52) later for every 100 m of elevation, and 6.4 d (SE = 2.6) later for every degree of latitude. For a data set in which the probability of genetic assignment to a given lake exceeded 50%, the predicted timing of downstream migration was 3.2 d (SE = 1.2) later for every 100 km of increasing river distance, 1.5 d (SE = 0.54) later for every 100 m of elevation, and 6.6 d (SE = 2.6) later for every 1° of latitude. Based on comparisons of global models using both data sets where the probabilities of assignment to a given population and to a given lake exceeded 90%, population was a better random effect than lake.

Opportunistic recapture of tagged smolts from the Babine Lake enumeration project allowed us to estimate the duration of travel from the lake to the estuary. Genetic analysis of a single tagged smolt captured in 2013 indicated that it originated from Babine Lake (Fulton River population) with a 77% probability of correct assignment. In 2014, we captured nine smolts bearing tags from the Babine Lake smolt enumeration project between

May 5 and May 19; these individuals had been marked at the weir between 9 and 16 d prior to capture in the estuary. Under the assumption of an extra day of travel to swim from the release site back to the lake outlet, the mean duration of the downstream migration was 10.8 d for these smolts, translating to an average velocity of about 40 km/d. Assuming similar downstream velocity for other populations, the expected duration of the downstream migration ranged from 2 d for smolts migrating from Alastair Lake (a distance of 67 km to the estuary) to 14 d for Sustut Lake smolts, which migrate from 575 km upstream. This estimated 12-d variation in duration of the downstream migration for the Skeena River Sockeye Salmon populations is one-third of the range of estuary residence time (36 d) observed in our sample data.

Zooplankton Analyses

There was considerable within-year variability in the composition of estuary zooplankton communities throughout the smolt migration period in 2013 and 2014 (Figure 5). The zooplankton samples collected in both years were dominated by small calanoid copepods, mostly *Acartia longiremis* and *Pseudocalanus minutus*. The timing of peak abundance

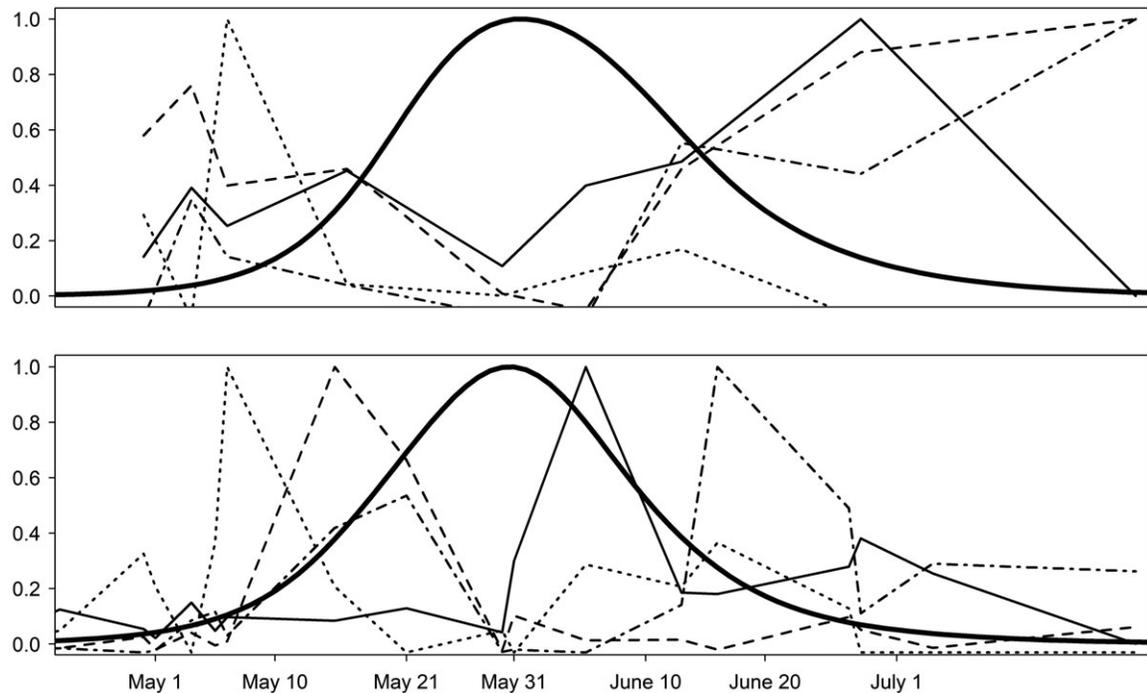


FIGURE 5. Temporal trends in relative abundance of Sockeye Salmon smolts (thick solid lines) and known zooplankton prey taxa, including calanoid copepods (thin solid lines), euphausiids (dashed lines), larvaceans (dotted lines), and decapods (dashed and dotted lines), indicating relative abundance of each zooplankton taxon during each sampling event throughout the smolt migration season in 2013 (top panel) and 2014 (bottom panel). The smoothed Sockeye Salmon abundance values were generated from predicted generalized additive model output values for each day during the time series (see Figure 2A). All values for zooplankton and Sockeye Salmon are normalized so that the maximum value for each taxon is 1.

for small calanoid copepods varied in the 2 years sampled, with the highest abundances observed at the beginning of July in 2013 and at the beginning of June in 2014. The highest relative abundance of decapod larvae was observed at the beginning of May during both years, and a second peak of decapod abundance occurred in mid-June of 2014. Euphausiid abundance was bimodal in both years, with peak abundances of nauplii observed during the first week of May in 2013 and during the second week of May in 2014, followed by peaks in abundance of the larger calyptopis and furcilia stages at the beginning of July in 2013 and toward the end of August in 2014. Timing for larvaceans was bimodal in both years, with peaks observed at the beginning of May and end of July in 2013 and during mid-May and mid-June in 2014 (Figure 5). In both years, the timing of peak abundance for juvenile Sockeye Salmon coincided with minimum abundances for many known zooplankton prey items (Figure 5).

DISCUSSION

We discovered considerable among-population variation in Sockeye Salmon smolt migration timing that was geographically structured in the Skeena River watershed. We observed a 36-d difference in peak migration timing for the first and last populations to appear in the estuary.

In contrast, there was little variation in the overall smolt migration timing for Sockeye Salmon between the 2 years sampled, and the timing for the different populations appeared to be coherent between years. The migration phenology for the different populations had a strong geographic signature, with higher support for models that included any combination of geographic variables than for models that included only terms for population or lake. Specifically, we observed later timing for populations that originated from further upstream and from higher latitudes and elevations within this large watershed. These findings were robust to uncertainties in genetic determination among the populations of Sockeye Salmon from Babine Lake.

Our observation of later migration timing with increasing elevation is consistent with a previous study of Columbia River Chinook Salmon, which found that juvenile migration timing was 1 d later for every 122 m of elevation gain (Achord et al. 2007). There are plausible explanations as to why the different geographic variables might influence smolt migration timing. For example, the timing of departure may be constrained by conditions in the rearing lakes. River distance, which is closely correlated with elevation, is also correlated with latitude because the Skeena River watershed is elongated along a north-south axis. The timing of spring ice breakup for inland lakes is

delayed with increasing latitude and altitude. During the spring, solar radiation (and thus insolation) increases with increasing day length. Spring melt is further delayed by the high albedo (reflection coefficient) of frozen lakes. Data collected from smolt enumeration programs in the Skeena River watershed demonstrate that peak juvenile Sockeye Salmon out-migration from smaller rearing lakes usually occurs shortly after the timing of ice breakup (smolt weir data; Gitksan Watershed Authorities, unpublished data; Gitanyow Fisheries Authority, available at <http://www.gitanyowfisheries.com/kitwanga-smolt-fence-enumeration>). Given the high heritability of phenological traits ($h^2 = 0.51$; Carlson and Seamons 2008), freshwater geographic constraints may have imposed selective pressures that interact with historical marine conditions to produce structured migration timing between different populations of Sockeye Salmon such as those we observed in the Skeena River watershed. Our study thus provides a key example of geographic organization of phenology (also see Bradshaw and Holzapfel 2008).

The geographic pattern of smolt out-migration timing was more pronounced than predicted based on the observed speed of observed downstream migration. Our estimates of the duration of the downstream migration, which were derived from smolt tag data from Babine Lake, suggested that Sockeye Salmon smolts migrate at approximately the velocity of the river current. If this is true for smolts from all populations of Skeena River Sockeye Salmon, the expected range of estuary arrival time would be 2–14 d between populations originating from the furthest upriver and furthest downstream systems. However, sampling in 2013 and 2014 indicated that the peak smolt migration timing for the different populations of juvenile Sockeye Salmon varied by more than 5 weeks during the spring migration. Furthermore, the timing of estuarine residence varied between different populations of Sockeye Salmon smolts that originated from the same lake. In our study, the only lakes with multiple populations were Kitsumkalum Lake, which includes two populations representing 16 fish in our sample, and Babine Lake, which accounted for nine populations and approximately 85% of all smolts that we captured in the estuary. We observed phenological diversity among smolts representing the various populations from Babine Lake, with mean timing of estuary capture ranging from May 19 to June 15, 2014. In addition, there was more support for models that included population rather than lake. These data provide evidence for phenological variation among the populations of a single lake in addition to a geographic component to smolt migration timing. Genetic and geographic factors may affect smolt migration timing for the Babine Lake populations of Sockeye Salmon. Previous studies have suggested that Sockeye Salmon fry rear close to their natal streams in Babine Lake (Groot 1972),

which is over 150 km long. Our findings suggest that variation in smolt migration timing for Sockeye Salmon is more finely organized than at the lake level, but we note the challenge of separating the different Babine Lake populations genetically. A more robust genetic baseline combined with more information about the geographic distribution of smolts prior to the onset of migration could improve our understanding of factors that contribute to smolt migration timing for the different populations.

We report results from 2 years of sampling, which are not likely to capture the full range of interannual variability for Skeena River Sockeye Salmon. The timing of the Skeena River smolt migration is highly pulsed, and our subsampling strategy likely resulted in a higher proportion of non-Babine Lake and wild Babine Lake smolts captured before and after the migration peak in our samples. We addressed this potential bias by comparing timing for genetically identified Skeena River Sockeye Salmon with the timing of the aggregate run (which was calculated using the CPUE of all captured Sockeye Salmon, not just those that were selected for genetic analysis). We acknowledge that limited sample sizes for some of the smaller populations produced considerable uncertainty in the estimated peak times of estuary arrival and also that this study did not fully characterize the within-population variation in migration timing. Although applying a higher threshold for the probability of correct assignment increased our level of certainty in assigning individual fish to specific populations, this further restricted the sample sizes and may have introduced a potential bias by decreasing the relative proportion of Sockeye Salmon originating from Babine Lake in our sample. Our model results were generally unchanged for data sets produced from lower probability thresholds, but the estimated migration timing for some small populations with lower genetic resolution shifted when different probability thresholds were applied (Table S2). Genetic analyses were conducted for all available tissue samples collected in 2013 and 2014. Although it is not possible to obtain larger samples for the 2 years reported here, combining data from these years with samples collected in subsequent years may contribute to a better understanding of within- and among-population variability in smolt migration timing.

Estuary residence may contribute to the timing of observations in the estuary for the different populations. We used the date of smolt capture in the estuary as a proxy for migration timing. If smolts remain in the estuary for varying periods of time after the downstream migration, then the timing of ocean entry may be overestimated. Previous research suggests that Sockeye Salmon spend little time in estuaries relative to other salmon species, such as Chinook Salmon and Chum Salmon (Thorpe 1994; Weitkamp et al. 2014), but different populations may utilize estuaries for varying periods of time (Moore

et al. 2016). Other studies have found that smaller and ocean-type Sockeye Salmon may inhabit estuaries for a longer period of time. For example, smolts from the ultra-oligotrophic Owikeeno Lake, which are among the smallest lake-type Sockeye Salmon smolts in British Columbia (McKinnell et al. 2011), remain in estuarine waters within Rivers Inlet for over 1 month as they traverse the inlet (Ajmani 2012; Egorova 2016). Similarly, ocean-type smolts from the Harrison River (Fraser River basin) rear for months in the Strait of Georgia (Beamish et al. 2016). In our study, Sockeye Salmon smolts originating from Johnston Lake, which is the most coastal of the major Skeena River rearing lakes, did not fit the expected pattern of earlier migration timing from a lower-elevation lake. The mean date of peak migration for Johnston Lake smolts (June 7) was among the latest for the different populations of Skeena River Sockeye Salmon (Table 1); these smolts were captured in the estuary throughout the sampling period, unlike smolts from other populations, which exhibited shorter windows of estuary capture. Limnetic fry surveys conducted during 2010, 2014, and 2016 in Johnston Lake, an oligotrophic lake that drains into the lower Skeena River, recorded the highest densities and the smallest Sockeye Salmon fry observed anywhere in the Skeena River watershed (Doire and Carr-Harris 2015). The few Johnston Lake Sockeye Salmon juveniles that we captured in the estuary ($n = 10$) were considerably smaller (67.2 mm; SD = 7.3) than the average length of Sockeye Salmon smolts captured in 2014 from other systems in the Skeena River watershed (87.5 mm; SD = 11.0). The possibility of smaller smolts from Johnston Lake remaining in the estuary to rear for longer than their larger counterparts from other Skeena River rearing lakes provides one feasible explanation for our observations that is supported by the more compact temporal distributions of smolts from the other Skeena River populations captured in the estuary (Table 1; Figure 3).

The different populations of Skeena River Sockeye Salmon arriving at different times encountered different zooplankton prey communities in the estuary (Figure 5). Previous surveys of Sockeye Salmon smolt diets have reported high variability in stomach contents (Healey 1991; Brodeur et al. 2007) and high selectivity of food items with respect to the available zooplankton (Price et al. 2013), which may relate to the quality of available prey (Trudel et al. 2007; Tanasichuk and Routledge 2011). For example, growth and survival for juvenile Coho Salmon were correlated with the lipid content of consumed prey (Orsi et al. 2004; Trudel et al. 2007). Sockeye Salmon returns to Alberni Inlet, British Columbia, were positively correlated with the abundance of one euphausiid species, *Thysanoessa spinifera*, during their first summer at sea (Tanasichuk and Routledge 2011). Opportunities for feeding on higher-quality prey may benefit smolts in the

period immediately after the energetically expensive downstream migration. Thus, the quantity and quality of prey available to smolts when they arrive in estuarine habitats may be important for their long-term survival.

Zooplankton phenology, which is already quite variable, is likely to become more variable and to advance with climate change (Rubao et al. 2010). There was local evidence for long-term warming ocean temperatures, which are likely to drive phenological changes in zooplankton, including the known prey of juvenile salmon. Local monthly sea surface temperatures in April and May have increased by more than 0.70°C overall since 1964 (data available at <https://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884>). Although the 2 years of zooplankton data that we collected for the current study are obviously insufficient to examine for long-term trends, we found that the timing of peak abundance for most zooplankton taxa varied between 2013 and 2014, while the overall timing of peak abundance for juvenile Sockeye Salmon smolts and the order of appearance of the different populations remained relatively consistent across years. For our 2 years of study, the timing of peak abundances of juvenile Sockeye Salmon, driven by the smolt migration from the large, enhanced populations at Babine Lake, coincided with minimum abundances of zooplankton (Figure 5). Previous research suggests that zooplankton phenology advances with increasing ocean temperatures (Edwards and Richardson 2004; Hays et al. 2005; Richardson 2008; Poloczanska et al. 2013), and zooplankton biomass variability is correlated with sea surface temperature (Beaugrand and Reid 2003; Rubao et al. 2010). There is evidence that recent marine climate change is already affecting salmon populations. For example, sea surface temperatures have been correlated with Pink Salmon growth and survival (Mortensen et al. 1999), Atlantic Salmon stock size (Friedland et al. 2003), and historic abundances of Sockeye Salmon (Finney 2000). Thus, salmon productivity may already be responding to increasing ocean temperatures, and the potential for mismatches between phytoplankton, zooplankton, and salmon is likely to increase as ocean temperatures continue to rise.

The diversity of out-migration timing that we observed among Sockeye Salmon smolts within the Skeena River watershed has at least three major implications. First, phenological diversity broadens the timing distribution of salmon smolts in the estuary, potentially lessening competition for resources in the estuary as well as extending the availability of smolts as food for estuarine predators like birds. Second, given that different populations experience different early marine conditions, their phenological diversity is likely to contribute to different responses to earlier or later marine prey dynamics. For instance, earlier migrating populations may have better survival in years with earlier zooplankton blooms than populations that

migrate later. Phenological diversity of smolt migration timing, which is geographically structured, may protect some populations from warming marine conditions during ocean entry and may render other populations more vulnerable. Third, migration diversity may contribute response diversity and thus stability to processes that integrate across population diversity, such as metapopulation dynamics or fisheries harvests. The diversity of smolt migration timing could therefore contribute to the stability of salmon metapopulations and fisheries confronted with the challenges of marine climate change. There is considerable population-level diversity within large, salmon-bearing watersheds like the Skeena River, and this diversity can influence the sustainable management of the fish and fisheries. Although previous research has recognized that age structure diversity buffers populations from poor marine conditions by staggering the year of ocean entry (Schindler et al. 2010; Moore et al. 2014), we have shown here that population diversity also staggers the timing of ocean entry across populations within a year. Protection of habitat integrity and local adaptations can conserve diversity and evolutionary potential (Reed et al. 2011) and enable metapopulation sustainability (Anderson et al. 2015).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.