Regional and climate-driven factors affecting the migrations of sockeye salmon (*Oncorhynchus nerka*) smolts in Alaska

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Abstract

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The downstream migration of salmon smolts is triggered by a combination of responses to multiple environmental indicators, imposed on internal circannual rhythms, that result in variation between populations in timing. Using long-term data on daily smolt counts and associated environmental variables from multiple sources across Alaska, I tested the hypothesis that variation in migration timing between different sockeye salmon populations could be explained by differences in local environmental conditions. I first analyzed the peak, width, and interannual variation of the smolt migration period for eight populations from southwestern and southcentral Alaska. I then modeled the median emigration date and width of the emigration period as a function of stream temperature, air temperature, and precipitation to assess how each population responds to combinations of seasonal

environmental cues that serve as indicators for the onset of downstream migration or conditions in the recipient environment (sea surface temperature). Lastly, I used the results of my analysis to identify spatial variation in the response of distinct salmon populations to environmental factors and identify trends in the migration timing of those populations. Through my analysis, I found that sea surface temperature and freshwater temperature are the primary environmental factors that control median smolt emigration date, while the width of the smolt emigration window is influenced primarily by freshwater temperatures and precipitation, with significant site-by-site variation.

Introduction

Many species exhibit migratory life histories, allowing them to utilize different habitats and food sources at different stages of their lives (Baker 1978; Dingle 1996). Many of these animals are iconic species, recognizable and valued as part of the global biodiversity, such as birds and butterflies. However, other species, notably fishes, are not only representatives of the natural world but also support valuable fisheries and paly extensive roles in their ecosystems. Among these, perhaps the best known are the Pacific salmon of the genus *Oncorhynchus.* These fishes share a common anadromous life history. Juveniles are born in freshwater, migrate to sea after a growth period that can range from days to years, spend between one or more years feeding in the ocean, then commence sexual maturation and return to their natal streams to spawn and die (Quinn, 2018). Like all migratory animals, their urge to move reflects responses to external environmental stimuli on a background of internal, circannual rhythms. Thus migration is triggered by complex combinations of internal and external processes, on a template of evolutionary ecology (Shaw 2016). That is, the tendency to migrate, the timing of migration, and the spatial patterns have evolved over many generations based on the conditions in the different habitats used by the species for feeding and breeding. However, each year the timing of the group's migration (and of each individual) involves responses to proximate stimuli such as temperature and the regular changes in photoperiod that synchronize internal rhythms (Ramenofsky and Wingfield 2007; Goossens et al. 2020). As the climate changes, environmental conditions on a given date change, yet the photoperiod that plays such an important role in triggering migration does not, Moreover, altered conditions in the immediate environment that the animals experience may not correspond to conditions in the environment to which they will migrate, leading to a mismatch in phenological adaptation.

Among Pacific salmon, sockeye salmon (*O. nerka*) are unique in their extensive use of lakes as their primary freshwater habitat for feeding prior to seaward migration, as opposed to the streams and rivers typical of other species (Quinn 2018). Adult sockeye salmon spawn in rivers and streams associated with lakes or in the lakes themselves, and juveniles quickly migrate to the and feed for typically one or two years prior to seaward migration via the lake's outlet. Juvenile growth depends on a number of factors relating to lake condition, including genetic origin, temperature, insect and plankton abundance, and intraspecific competition due to juvenile sockeye abundance and density (Edmundson and Mazumder, 2001; Rich et al., 2009; Reed et al., 2010). After one to two years of rearing, depending on lake conditions, growth rates, and genetic factors, juveniles undergo a series of physical and physiological transformations to prepare for downstream migration and entry into the marine environment (Carr-Harris et al., 2018; Achord et al. 2007). The survival of juvenile salmon at sea is often affected by the match between entry date and local conditions (Scheuerell et al. 2009; Morita and Nakashima 2015; Freshwater et al. 2019).

The transition of juvenile sockeye fry into smolts, and the initiation of seaward migration, is regulated by a complex set of physiological responses linked to multiple environmental cues (Byrne et al., 2003), as with other salmonids (Hoar 1976; Clarke and Hirano 1995), and the importance of this phase for successful entry into marine waters and subsequent survival has long been appreciated (e.g., Wedemeyer et al. 1980). In general, spatial variation in the timing of onset of migration for smolts across the range of Pacific salmon is primarily regulated by variations in photoperiod between different latitudes, with local environmental conditions playing a much larger role in determining fine-scale variations in river systems across similar latitudes (Hartman et al. 1967; Spence and Hall, 2010; Spence and Dick, 2014). In particular, freshwater conditions, such as flow, water temperature, and physical watershed characteristics are especially important. Differences in the migration timing of distinct populations, especially within a similar range of latitudes, is likely a response to a combination of environmental factors that maximize the likelihood of a favorable marine environment following ocean entry (Antonsson and Gudonjsson, 2012) and also differences in conditions in the freshwater habitats (e.g., Peven 1987).

Early marine survival in the period immediately following ocean entry is a critical because much of the total marine mortality seems to occur at this time (e.g., Fukuwaka et al. 2002; Wertheimer et al. 2007; reviewed in Quinn 2018 and Beamish 2018) life-history factor for salmonids (Freshwater et al., 2016). Mismatch between the timing of ocean entry for the bulk of the run and abundance of phytoplankton can have catastrophic consequences for salmonid stocks in the form of increased mortality due to physiological stress and lower growth rates as a result of low food availability Therefore, salmon have evolved to initiate seaward migration of smolts at a time such that the favorability of ocean conditions upon entry is maximized, both in terms of water temperatures and food availability (Cooney et al. 1995;

Satterthwaite et al., 2014). Because the abundance of adult salmon is highly sensitive to survival rates in the early marine stage, understanding how the interplay between these dynamics may be changing is a critical step towards managing salmon fisheries under shifting climate regimes in the North Pacific (Scheuerell et al., 2009).

Considerable effort has been devoted to understanding factors that influence variation of the migration timing for juvenile salmonids across both geographic and environmental gradients, with a particular focus on Atlantic salmon (Otero et al. 2014). However, much less effort has been devoted to exploring the variation of physical drivers as fine spatial scales and explaining these variations as a direct relationship between environmental cues and migration habits. Sockeye salmon in Alaska provide a highly suitable model organism for addressing these questions due to the abundance of large, stable populations at a consistent latitude, as well as the diversity of physical habitats that they occupy across their range in the region. However, unlike salmon that feed in rivers prior to seaward migration, and thus experience highly variable flow conditions that might affect timing, sockeye salmon in lakes experience a changing environment from which they must migrate volitionally and not be forced, as might occur if a flooding river.. This study aims to characterize the peak and width of the smolt migration window for sockeye populations across Alaska, and determine the relative importance of a range of environmental factors in explaining both the timing of smolt emigration (long-term average and interannual variation) and spatial variation in timing between populations that will enter the ocean in proximate and more distant areas. To the extent that timing is an adaptation to marine conditions that the fish will experience, we would predict similar timing of ocean entry by fish from lakes with differing conditions. Alternatively, if timing is primarily an adaptation to leave the lakes in which the salmon have been feeding, we would expect migration to differ among lakes in the same region if they experience different conditions in the lakes (e.g., date of ice out, temperature, etc.).

Methods

Data Collection

I selected study sites to cover a range of habitats and salmon-bearing ecosystems across southwestern and southcentral Alaska along a similar latitudinal band , from 56 to 62 degrees N, to control for the effect of photoperiod on smolt emigration timing (Figure 1). Based on a combination of this criterion and availability of long-term smolt sampling records, I selected the Kvichak, Egegik, Ugashik, and Wood rivers in Bristol Bay, Afognak and Spiridon lakes on Kodiak Island, Summit and Crosswind lakes in the Copper River system, and the Chignik River on the Alaska Peninsula. Smolt sampling methodologies varied between sites and between years, but included rotary screw traps, fyke nets, counting weirs, and in-river sonar arrays. I acquired data through personal communication with staff from the Alaska Department of Fish and Game, the Bristol Bay Science and Research Institute, and the University of Washington. These datasets span periods ranging from 1969 to 2015 in the Kvichak River to 2000 through 2016 in Spiridon Lake (Table 1).

Statistical Analysis

Statistical analyses were performed using a generalized additive model regression approach to allow for nonlinear relationships between environmental factors and the timing of sockeye salmon smolt downstream migration. Response variables included the median date of downstream emigration (DOY_{50}) and the width of the smolt emigration period (DOY_{25}-DOY_{75}), which allowed me to assess the impact of environmental predictor variables on both the seasonal timing of smolt emigration and the effect of environmental changes on the temporal distribution of downstream emigration. To standardize environmental observations across all study sites, I utilized May-June averaged temperatures in the outlet rivers, May-June sea surface temperature, March-June air temperature averages, and May-June precipitation as predictor variables for each study site.

I utilized a similar approach for both response variables, median date and width, to select the most robust regression model. Four candidate models, with various combinations of linear relationships and nonlinear smoothing functions as well as fixed and random effects were assessed for each response variable. Models included a basic generalized additive regression model with a smoothing function applied to each environmental predictor variable, precipitation (mm), freshwater, sea surface, and air temperatures, a regression with interaction terms to allow for region- and site-specific differences in the effect of each variable, and models that allowed for random effects based on each site and region-level grouping of systems. For each model, I specified a restricted maximum likelihood approach to estimate smoothing parameters in order to minimize overfitting of the model. To select the most robust regression for width and median emigration date, I compared each model using AIC as well as direct comparisons of model fit to identify the most appropriate model. I constructed and compared regression models in R Studio 3.3.6 using the mgcv and nlme statistical software packages.

Results

Timing of Smolt Emigration

Sockeye salmon smolts varied in the central tendency and width of the smolt migration period between river systems across southwestern and south-central Alaska. The median emigration date (DOY_{50}) over the period of record ranged from as early as May 24 for the Chignik River system to July 5 for the Wood River system in Bristol Bay (Table 1). Interannual variation in median emigration date was similar across all systems, with a standard deviation ranging from roughly +/- 4 to 6 days in all systems except for the Chignik River (+/- 10.8 days).

The width of the period over which the 25th to 75th percentile of the annual smolt emigration passes also varied, from 4.58 days for the Egegik River to 27 days in the Wood River (Table 1). Data were insufficient to characterize the width of the smolt emigration period for the Copper River basin because daily counts were being available for one system, Crosswind Lake. As with the median migration date, year-to-year variation in width of the migration period was consistently between 2-5 days for all systems except the Chignik River (+/- 8.3 days) and the Wood River (+/- 8.4 days).

Regional Patterns

In general, sockeye populations exhibited spatially correlated patterns of smolt emigration timing and duration, with populations showing more similarity to others in the same region compared to those in distant regions (Figure 2). In particular, clear similarities in timing and duration emerged for the included sockeye populations from the Bristol Bay region, with the exception of the Wood River system, and populations in the Kodiak archipelago. The Kvichak, Egegik, and Ugashik populations exhibit both a similar median emigration date (May 28-June 1) and width of emigration period (4.58-5.79 days) while the Wood population both migrates much later (July 5) and over a much more protracted period (27 days). In contrast, sockeye populations from the Copper River basin, a region that differs significantly in major geological and hydrological watershed characteristics as well as draining into a very different ocean environment, the Gulf of Alaska as opposed to the Bering Sea, exhibited a much later median emigration date (June 14-17). In addition, while sockeye populations in the Kodiak and Alaska Peninsula region exhibited similar median emigration dates to Bristol Bay populations, the average width of the emigration period was consistently much wider (7.8-14 days).

Environmental Factors

Freshwater temperatures at smolt sampling sites and sea surface temperatures at ocean entry locations for smolts in Bristol Bay and the Gulf of Alaska varied significantly between study sites both on a system-by-system and a regional scale (Figure 3). Systems in Bristol Bay experienced generally similar freshwater temperatures in terms of both long-term average temperatures during the smolt emigration period as well as year-to-year variability in temperatures. In contrast, variability in freshwater temperature between systems in both Kodiak Island and the Copper River basin was much higher, with systems displaying high variance in both long-term average temperatures and inter-annual variation. Sea surface temperatures across all regions were more consistent across the time period covered by this study (Figure 3). Sea surface temperatures for Chignik, Kodiak Island, and Copper River systems displayed both similar long-term average sea surface temperatures and year-to-year variation. Bristol Bay sea surface temperatures exhibited similar variation, but a lower overall long-term average.

Regression Analysis

Regression analysis of the impact of environmental variables including freshwater temperature, sea surface temperature, air temperature, and precipitation identified significant impacts of several variables on both median emigration date and width of the emigration period that varied by region. Model selection using both AICc and comparisons of R^2 and model weights heavily favored a less complex structure for both width and median emigration date (Table 2). While both direct comparisons of adjusted R^2 values and delta AICc supported both the most complex model structure that incorporated interaction terms allowing for a comparison of the impact of environmental covariates by region and a simpler structure with a global smoother for each variable, comparisons of model weights provided very little support for the more complex structure. However, models for both response variables heavily favored a model structure that incorporated random effects accounting for unmeasured variation between study sites across all indicators of model fit. Overall, both final models suggest that, while environmental conditions drive the migratory behavior of sockeye salmon smolts across all sites the relative impact varies significantly from site to site.

The final model I selected for median emigration date modeled DOY_{50} as a nonlinear function of air temperature, sea surface temperature, precipitation, and water temperature, with a random error structure allowing for unmeasured environmental variance between study sites (Table 2). This final model identified significant relationships between sea surface temperature and freshwater temperature, but not precipitation or air temperature, on the median timing of smolt emigration in a given year (Figure 4). The final R^2 value for this regression was 0.795, indicating a strong fit based on the specified model structure and selected environmental variables. The significance of the random error term approximating unmeasured variance between study systems also suggests site-specific factors that influence median emigration date.

While the model-building and selection process for width (DOY_{25}-DOY_{75}) of the smolt migration period resulted in a similar final model structure, the results of the regression analysis were less conclusive in terms of goodness-of-fit of the final model. The final regression structure modeled the width of the smolt emigration period in days as a nonlinear function of sea surface temperature, precipitation, air temperature, and freshwater temperature, and a random error term allowing for unmeasured variation by study site (Table 2). Final model R^2 was 0.632. Including additional environmental variables or random error terms for region-level variance did not improve model fit, and in some cases resulted in worse overall fit. Using this regression structure, I found that both freshwater temperature and precipitation, but not sea surface temperature, were significant contributors to the width of the smolt emigration period at the $p<0.05$ level (Figure 5). Again, the significance of the random error term suggests important site-specific factors that influence smolt migration behavior. Thus while median emigration date was more heavily influenced by the environmental conditions included in this study, the width of the emigration period relied more on factors outside the scope of this analysis.

Discussion

This analysis revealed significant differences in both the timing and width of the smolt emigration period on a geographic scale, as well as significant effects of multiple environmental covariates on the timing of smolt emigration that varied from region to region, indicating support for the broader hypothesis that, while the general timing of smolt migration is driven by similar factors across all systems, these relationships vary from system to system based on each watershed's distinct characteristics. First, regardless of region, freshwater temperatures, sea surface temperatures, and air temperatures are clearly associated with the timing of sockeye salmon smolt emigration. While freshwater environmental conditions provide the impetus for juveniles to initiate their seaward migration, this analysis suggests that the response to those environmental cues is likely timed to maximize the chances of encountering a favorable ocean environment, as measured by sea surface temperature. Secondly, physical differences in watershed characteristics and geography play a major role in influencing the variability of the response of juvenile sockeye to environmental factors across different river systems. Differences in marine environments between the Gulf of Alaska (Chignik, Copper River, and Kodiak Island) and the eastern Bering Sea (Bristol Bay) ecosystems likely explain the observed differences between long-term averages in SST in these regions. Although water temperature, air temperature, and sea surface temperature were significant factors at varying levels for all systems, some degree of spatial variability was observed. Given the similar photoperiod experienced at the latitudes across all study sites during the window of migration, this variability likely arises due to site-specific variation in environmental conditions dictated by physical and biological characteristics outside the scope of this analysis (Spence and Hall, 2010; Spence and Dick 2014; Carr-Harris et al., 2018). Therefore, incorporating a more complete set of observations that includes both biological characteristics and a wider range of environmental and physical observations from a larger sample of sockeye salmon populations both within and outside of Alaska is necessary. Using a larger dataset would make it possible to more fully assess these relationships and generate a set of models with more predictive ability on a widely generalizable scale.

Freshwater environmental conditions are closely linked to both the timing of smolt migration and the size and age of migrating smolts (Harvey et al., 2020; Bøe et al., 2016). However, the influence of water temperature in regulating migration timing differs from population to population. For example, in both Bristol Bay and Kodiak Island, the median date of smolt emigration hovers around DOY 149-152. However, the range of temperatures experienced by smolts over the migration period in the Egegik, Kvichak, and Ugashik rivers ranged from roughly 3 to 8.5 degrees Celsius, while stream temperatures for streams in Kodiak ranged between from around 7 to 15 degrees Celsius. Although these fish typically migrate to sea over a similar timeframe, the sharp difference in stream temperatures during the migration period highlights the importance of other environmental factors in controlling the smolt migration process, and supports the conclusion that no single temperature threshold triggers seaward migration (Spence and Dick, 2014). Biological responses that vary by population and differing physical characteristics of rearing environments that impact watershed-scale influences of climate both play major roles in determining the relative impact of water temperature on migration timing (McCormick et al., 2002; Griffiths et al., 2014; Jonsson and Jonsson, 2016). While water temperature plays a role regardless of system or population, other factors, such as density-dependent effects on growth rate and length of the growing season, can influence migratory behavior through impacts on the relative proportion of juveniles ready to migrate in a given year and different behavioral responses of outmigrating cohorts of different sizes and ages (Kovach et al., 2013; Jonsson and Jonsson, 2016; Jonsson et al., 2017).

The timing of salmonid life history transitions, which can have implications for the availability of food resources for juvenile fish, size at the time of migration, and ultimately survival to maturity, is a key factor in determining the significance of climate-driven shifts in smolt emigration timing. In general, salmon smolt migration is timed such that ocean conditions, especially prey availability, is maximized, allowing for an abundant food supply with less competition for resources and thus an overall higher growth rate (Satterthwaite et al., 2014; Miller at al., 2014). Higher growth rates, and therefore higher probability of survival, are closely linked to the timing of ocean entrance (Freshwater et al., 2016; Weinheimer et al., 2017; Godbout et al., 2018). Consequently, mismatches between the timing of peak prey availability in the nearshore marine environment and the peak timing of sockeye smolt emigration can have negative consequences for survival to adulthood. Therefore, given that juvenile salmon initiate their seaward migration in response to cues in the freshwater environment historically linked to positive ocean conditions, shifts in climatic regimes that disrupt these linked patterns have the potential to significantly impact survival rates. In particular seasonal disruptions in phytoplankton blooms that cause early or late peaks in abundance in both the marine and freshwater environments are linked to significantly depressed growth and survival in salmon populations across North America (Hampton et al., 2006, Chittenden et al., 2010; Chittenden et al., 2018). Conversely, an extended window of migration, in which juveniles migrate to sea over a longer period of time, can mitigate the impacts of mismatched entry timing by maximizing the probability that at least some proportion of migrants will encounter a favorable marine environment (Morita and Nakashima, 2015; Jokikokko et al.; 2015).

In general, salmon-bearing watersheds across western and northern North America are projected to experience consistently higher temperatures and lower summer flows over the course of the 21st century (Islam et al., 2019). These shifting climate regimes and their impacts on the availability and quality of freshwater rearing habitat for juvenile salmon will affect salmon at every level (Whitney et al., 2016; Sundt-Hansen et al., 2018; Zhang et al., 2019). Changes in climate have been linked to deviations from long-term life history patterns in many species of salmon over the course of the 20th and 21st centuries (Kovach et al., 2013; Reed et al., 2011; Cline et al., 2019). Many of these life history impacts are most pronounced during juvenile stages of growth and development, as changes in rearing environment have long-term implications for size-at-age, freshwater residence time, and the timing of seaward migration (Otero et al., 2014; Honea et al., 2017). Rapid environmental changes can lead to shifting productivity of rearing lakes, earlier migration due to changing seasonality of environmental cues, and population-level shifts in life history strategies (Carter et al., 2017; Manhard et al., 2017; Sparks et al., 2014). The sensitivity of the timing of sockeye salmon smolt migration to environmental conditions holds significant implications in the face of shifting seasonal temperature and weather regimes across Alaska. In particular, integrating the effects of earlier migration timing due to changes in climate into future management actions is critical for mitigating the impacts of climate change on salmon fisheries.

In summary, this study outlines the general timing of the smolt emigration window across western and southcentral Alaska, and aims to develop an understanding of how climate-driven environmental conditions in the region shape the behavior of juvenile sockeye salmon. I found that, while environmental factors significantly affect the migration of smolts, the shape and significance of those impacts vary on a spatially explicit basis. Recognizing how these relationships differ on a regional scale from population to population allows for adaptive management and modeling strategies that take into account site-specific biotic and abiotic factors when considering future approaches to sustainable management of Alaskan salmon fisheries. As the most commercially valuable salmon species in the state, sockeye salmon are a critical element of Alaska's economy. Defining the relationship between climate and juvenile salmon emigration timing is a necessary step to better understand the impacts of climate change on the state's salmon fisheries and develop a framework for projecting future salmon survival and abundance. Future research efforts should be directed to incorporating a wider range of observations from salmon populations both within and outside of Alaska to develop a more robust predictive model that takes into account variation on a wider spatial scale.

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Table 1. Summary of long-term average median smolt migration date and width of smolt migration period, by system.

System	Median Migration Date	Width of Migration Period
Bristol Bay		
Kvichak River	149 +/- 4.93	5.79 +/- 2.90
Egegik River	148 +/- 4.41	4.58 +/- 2.22
Ugashik River	152 +/- 4.06	5.50 +/- 1.79
Wood River	187 +/- 5.02	26.64 +/- 8.41
Chignik		
Chignik River	144 +/- 10.8	14.0 +/- 8.30
Kodiak Island		
Afognak Lake	150 +/- 5.30	12.0 +/- 4.74
Spiridon Lake	149 +/- 6.48	7.81 +/- 3.43
Copper River		
Crosswind Lake	163 +/- 5.75	5.8 +/- 2.96
Summit Lake	168 +/- 5.68	NA

Table 2. Comparison of model fits.

Median migration date

Model	R^2	ΔAICc	Model weight
Global smooth with rand. eff.	**0.793**	**0**	**0.946**
Region-specific smooth with rand. eff.	0.908	-5.806	0.052
Global smooth	0.894	-11.866	0.003
Region-specific smooth	0.685	-30.491	0.00

Width of migration period

Model	R^2	ΔAICc	Model weight
Global smooth with rand. eff.	**0.632**	**0**	**0.631**
Region-specific smooth with rand. eff.	0.601	-1.827	0.253
Global smooth	0.572	-3.63	0.103
Region-specific smooth	0.514	-7.007	0.013

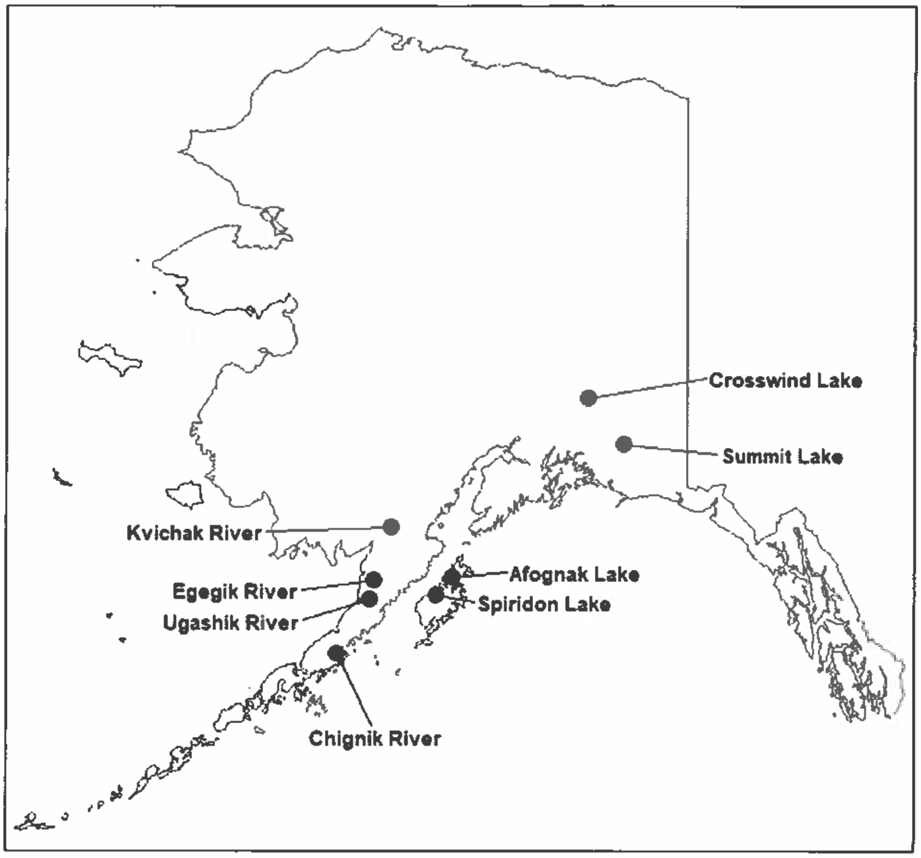

Figure 1. Location of study sites used for analysis within Alaska.

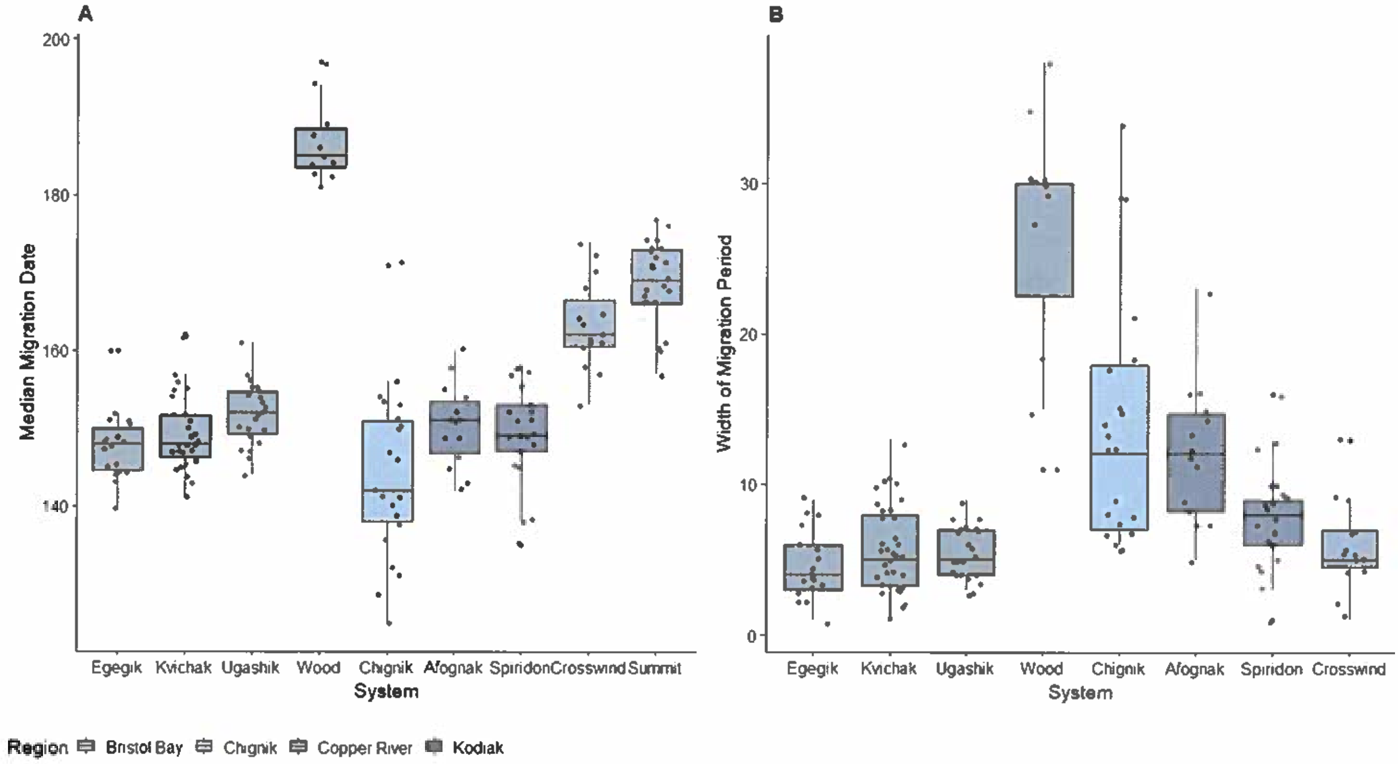

Figure 2. A) Median migration timing for sockeye salmon smolts, by system. B) Width of smolt emigration period, by system.

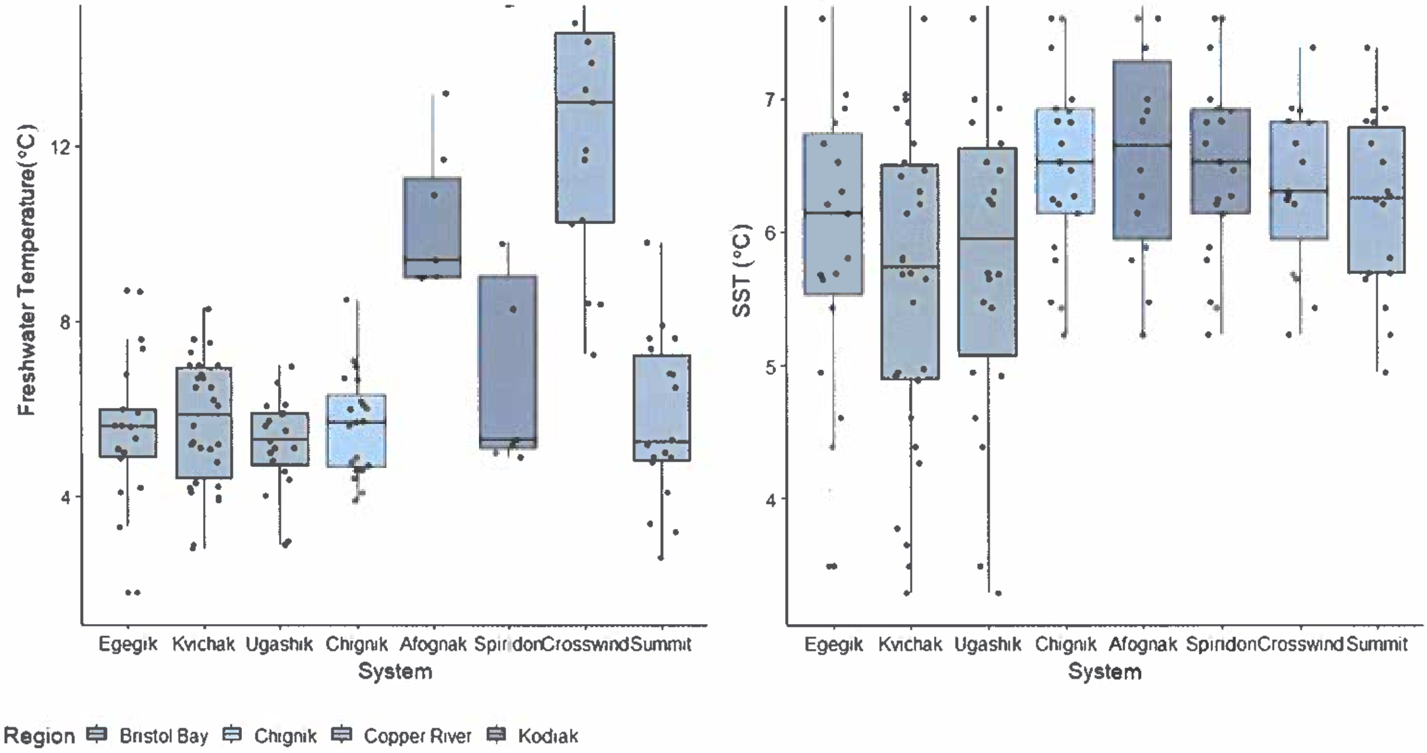

Figure 3. Summary of freshwater temperature (A) and sea surface temperature (B), by study system.

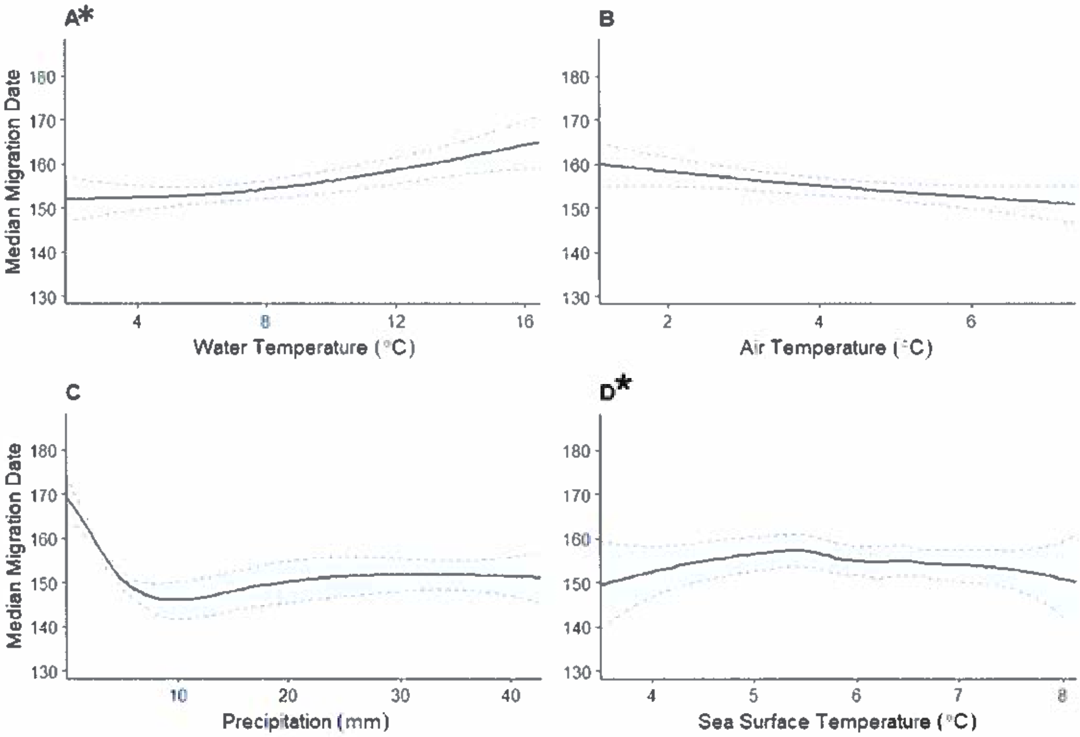

Figure 4. Modeled relationships between median smolt migration date and water temperature (A), air temperature (B), precipitation (C), and SST (D).

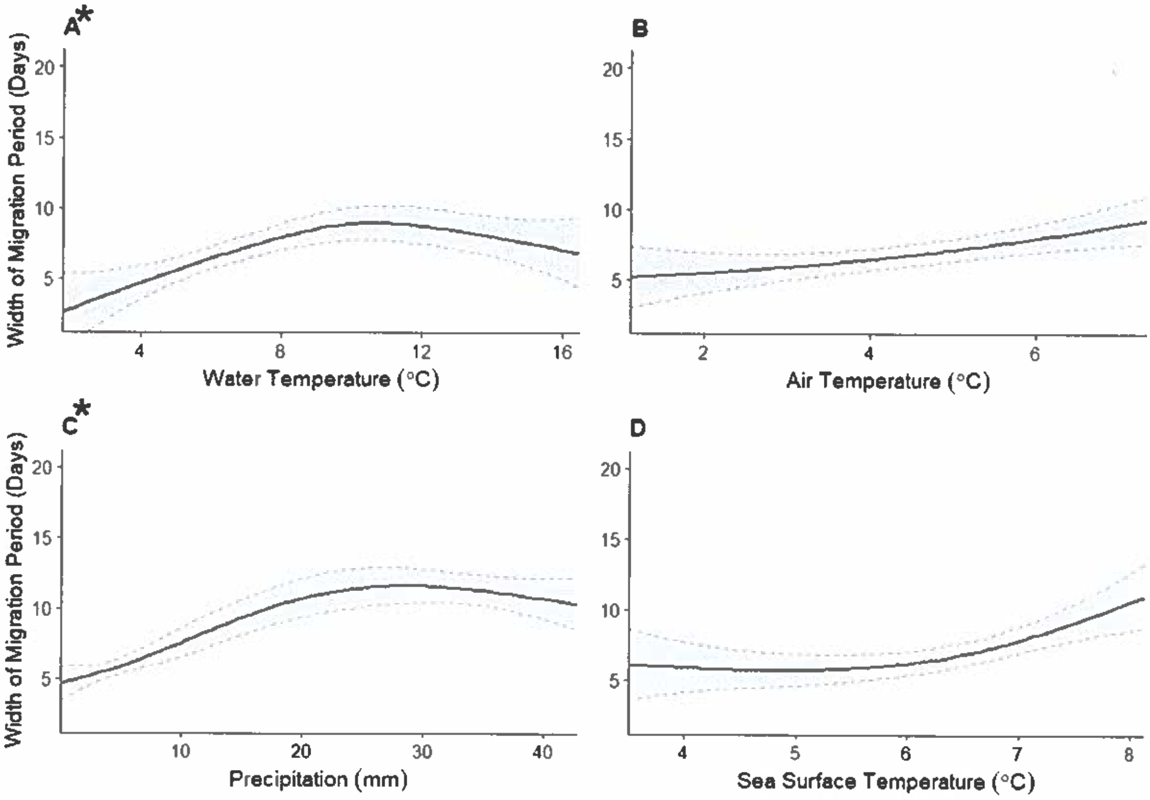

Figure 5. Modeled relationships between width of smolt migration period and water temperature (A), air temperature (B), precipitation (C), and SST (D).