Range-wide life-history diversity and climate exposure in Chinook salmon

by

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Abstract

Climate change risk for migratory species is intertwined with their life-history diversity. Here I quantify climate risk, exposure, and phenological adaptive capacity in Chinook salmon during their spawning migrations for populations from across their North American range. First, I assessed how migration timing varies with watershed characteristics. Populations with longer migration distances and from higher elevations entered freshwater earlier. Second, I quantified climate exposure and risk by linking migration timing data to recent (1990s) and future (2040s) water temperatures. Nearly a quarter of populations will be exposed to future temperatures above thermally stressful thresholds. Third, I assessed the rate and direction of phenological shifts that would enable Chinook to adapt to climate warming. Spring populations would need to shift earlier, while fall populations would need to shift later. Broadly, my thesis highlights that climate exposure, risk and adaptive capacity are structured by phenology and latitude in a diverse migratory species.

Keywords: climate change; life history; migration; Pacific salmon; phenology; water temperature

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Chapter 1.

Range-wide life-history diversity and climate exposure in Chinook salmon

1.1. Abstract

Climate change is threatening ecologically and culturally important species. For species with broad ranges and complex life cycles, such as migratory Pacific salmon, climate impacts may vary across space and diverse life-history strategies. Here I quantify climate risk – a function of exposure, sensitivity and phenological adaptive capacity - across the North American range and remarkable phenological diversity of Chinook salmon (*Oncorhynchus tshawytscha*). I compiled data on adult upstream migration timing and its environmental covariates for 295 populations of Chinook salmon spanning 29 degrees of latitude from California to Alaska. I linked this migration timing data to recent (1990s) and future (2040s) water temperatures to quantify thermal exposure during freshwater entrance timing. At northern latitudes, Chinook migration timing was compressed to three months during the summer, while at southern latitudes migration occurred across months before and after stressful peak summer temperatures. Earlier migration timing was associated with longer migration distances and greater elevations gained. Climate risk was highest for mid-latitude populations that have not yet adapted to migrate before and after peak summer temperatures, as climate change will increasingly expose them to temperatures above thermally stressful thresholds. If Chinook salmon phenology were to keep pace with projected climate warming by the 2040s, the majority (75%) of populations would need to migrate earlier in the year, pulling their migration farther apart from their fall spawning phenology. Collectively, these findings showcase how latitude and life-history diversity structure climate change risk and indicate the importance of preserving existing migration timing diversity and adaptive capacity across the broad range of a migratory species.

1.2. Introduction

Assessing climate change risk to species of societal and ecological importance is an urgent scientific priority in this warming world. Climate change risk to population viability is a function of exposure and sensitivity, potentially mediated by adaptation (Foden and Young 2016). Exposure, or the climate variability experienced by a species, depends on the magnitude of climate change across its range and seasonal habitat use (Williams et al. 2008; Pacifici et al. 2015). For migratory species, such as anadromous fishes, which use different habitats across their complex life cycles, assessing exposure entails linking current and future climate conditions with variation in life history traits like migration timing (Pacifici et al. 2015). However, climate risk is not only influenced by the timing and degree of exposure but also by a species' sensitivity, which is based on characteristics such as physiological thermal tolerances (Foden and Young 2016; Crozier et al. 2019). Furthermore, in response to climate change, species are adapting their geographic ranges, phenologies, and physiological tolerances through either phenotypic or genetic means (Parmesan and Yohe 2003; Bradshaw and Holzapfel 2006; Williams et al. 2008). These core dimensions of climate change risk – exposure, sensitivity, and adaptive capacity – could vary greatly across both space and life histories for broadly-distributed and biodiverse species. Given that management generally focuses on the population scale (Waples et al. 2004), understanding population-level climate risks is particularly relevant to guide forward-looking conservation and management action.

Pacific salmon (*Oncorhynchus* spp.) are a group of migratory species with complex life cycles that fuel fisheries and food webs across their vast native North American range (Schindler et al. 2003; Ford and Ellis 2006). Climate change impacts salmon across their life cycle via stressors such as warming sea surface temperatures, changing ocean productivity, and shifting and intensifying flow and thermal regimes in fresh water (Crozier et al. 2021). In particular, climate change during the energetically demanding freshwater migration of adult salmon may expose individuals to sublethal and lethal risks and decrease survival and reproduction. For these migrating adults, elevated stream temperatures can increase rates of disease transmission, delay migration, contribute to *en route* and pre-spawn mortality, and even reduce egg viability (Martins et al. 2012). For example, over 1300 chum salmon (*O. keta*) died in the Koyokuk River, Alaska during a historic heat wave in 2019 (Westley 2020) and up to 65% of individuals from some

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Columbia River Chinook (*O. tshawytscha*) stocks die on their upstream journey in hot years (Bowerman et al. 2021). Given that over a third of Pacific salmon populations are at risk in the lower latitudes of their range (Gustafson et al. 2007), there is an urgent need to understand the dimensions of climate risk across their range.

As cold-water specialists, Pacific salmon are sensitive to excessively warm water temperatures. Many physiological processes display threshold dynamics that lead to impaired performance at temperatures above critical thermal limits (Huey and Kingsolver 1989). While studies of sockeye salmon indicate that thermal performance and its associated physiological optima and limits can vary across populations (Eliason et al. 2011), these have yet to be quantified across all species of Pacific salmon and thus common thresholds can be useful to quantify climate risk. In adult Chinook salmon, water temperatures that surpass 21-22°C can delay migration as individuals stop swimming to conserve energy, and prolonged exposure to temperatures greater than 18°C can increase thermal stress, with consequences on fitness (USEPA 2003; von Biela et al. 2020; Zillig et al. 2021). Climate change is causing freshwater temperatures to increasingly surpass these physiological thresholds, and quantifying thermal exposure above these species-level thresholds in sensitivity can elucidate climate risk (Mantua et al. 2010; Isaak et al. 2018; Islam et al. 2019).

For migratory species, variation in the timing of life-history events among populations may drive differences in climate exposure across populations. Chinook salmon display one of the most diverse arrays of life histories among Pacific salmon (Waples et al. 2008), which makes them uniquely informative for studies of population-specific exposure to climate change. Adult Chinook salmon exit the ocean to begin their upstream freshwater migration throughout the year— and are most often classified a unique population, or run, based on this spring, summer, fall, or winter river entrance timing (Healey 1991). After a freshwater migration that may range up to three thousand kilometers, they spawn predominantly through the late summer and fall (Healey 1991). Thus, depending on their population-specific river entrance timing, Chinook salmon either spawn immediately or hold in colder spawning habitats for many months without feeding (Quinn et al 2016). Diversity in migration timing is also linked to variation in morphological and reproductive traits: early-migrating Chinook enter freshwater at lower reproductive maturity, but have higher fat reserves to carry them through their long and energetically costly migrations (Healey 2001; Kinnison et al. 2001; Hearsey and Kinziger

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2015). These diverse migratory patterns in salmon are thought to potentially reflect local adaptations to historic thermal and hydrological regimes experienced along in-river migratory corridors and spawning grounds (Brannon et al. 2004; Beechie et al. 2006; Quinn et al. 2016). For example, sockeye salmon (*O. nerka*) in warm watersheds have adapted to migrate either before or after peak summer temperatures (Hodgson and Quinn 2002). Given that population-specific migration timing may be driven by thermal regimes and other selective pressures (Quinn et al. 2016), it is possible that watershed characteristics structure exposure and thereby climate risk. Extensive research has investigated these links between environment and Chinook salmon life history in juveniles (Apgar et al. 2021), on watershed or regional scales (Beechie et al. 2006; Eiler et al. 2014), and with regards to genetic relatedness (Waples et al. 2004). However, an analysis of watershed correlates of Chinook salmon migration timing on a range-wide scale is lacking. More broadly, describing the diversity of Chinook salmon migration timings and their associated environmental correlates can shed light on thermal exposure across the range and diverse life histories of the species.

It is possible that Pacific salmon could avoid some of the impacts from warming rivers through shifts in the timing of their upstream migrations, a form of adaptive capacity. Species, including Chinook salmon (Mantua et al. 2015), are thought to be more readily able to cope with climate changes through behavioral and phenological (e.g., migration timing) adaptations, rather than physiological adaptations (Bradshaw and Holzapfel 2006). Indeed, shifts towards earlier migration have already been observed in some populations of sockeye and Chinook (Crozier et al. 2008a, 2011), and simulations show that these phenological shifts could help population persistence under climate change under some scenarios (Reed et al. 2011). Although there is strong evidence for a simple genetic control on migration timing (Thompson et al. 2019), it is likely that a combination of both plastic and genetic processes control phenological responses to environmental change (Crozier et al. 2008a; Williams et al. 2008).

However, understanding the adaptive capacity of a migratory species requires an understanding of both the predicted pace and direction of phenological change. For a species to successfully adapt to climate change, phenological shifts should keep up with the rate of climate warming (Reed et al. 2011). Further, in species with complex life histories, there could be trade-offs in climate change pressures across the life cycle (Crozier et al. 2008b; Crozier and Hutchings 2014). For example, a warming climate

should select for a shift towards later optimal spawn timing in the fall because warm temperatures would accelerate incubation rates of over-wintering eggs, while optimal migration timing might shift either earlier or later to avoid increasing peak summer temperatures (Crozier et al. 2008a). Thus, selection for earlier migration timing will oppose pressure for optimal spawn timing and pose a novel suite of climate risks such as longer freshwater residency prior to spawning and increased physiological stress for migrating adults. In other words, climate pressures could either be working synchronously, forcing the timing of different life stages in the same direction, or, of more concern, divergently driving life stages apart into a potential climate change "trap". Thus, it remains to be seen whether populations have the adaptive capacity to keep pace with climate change, and whether these potential shifts could conflict with other life-history constraints.

Here I examine components of climate risk – exposure, sensitivity and phenological adaptive capacity - in adult Chinook salmon migration across the entirety of their native North American range. My goal was to assess the complex interactions between life-history diversity and climate risk across the range of the species – therefore I asked the following questions: First, what is the diversity in adult migration timing and how is this diversity related to environmental characteristics? Second, how do different populations of Chinook salmon differ in their thermal exposure to temperatures above sensitivity thresholds? Third, how quickly and in which direction would Chinook salmon populations need to shift their phenologies in order to adapt to a changing climate? To answer these questions, I first compiled adult migration timing from nearly 300 populations ranging from California to Alaska and examined how this migration timing varies with environmental covariates. Second, I assessed thermal exposure by linking migration timing data to recent and future river temperatures, and quantified current and future risks that populations would encounter temperatures that exceed established thermal sensitivity thresholds. Third, I quantified the direction and magnitude of potential phenological shifts that would need to occur for Chinook salmon adult migration to keep up with the pace of climate change. Collectively, I discovered that climate exposure and risk was structured by latitude and migration timing, and that climate warming will drive phenological divergence within many populations.

1.3. Methods

1.3.1. Overview

In this study, I assessed climate risk across the native North American range of Chinook salmon for the adult migration portion of their life cycle. To this end, I compiled migration timing data, freshwater temperature data, and geospatial environmental data, and conducted three sets of analyses using different combinations of these data. First, I used the migration timing data, the water temperature data, and the environmental data to assess diversity in adult migration timing and how it covaries with a range of environmental characteristics at both the watershed region and population scales. Second, I combined the migration timing data with the water temperature data to quantify each population's thermal exposure during river entrance timing. As a metric of climate risk, I compared patterns in thermal exposure to temperatures above sensitivity thresholds for recent (1990s) and future (2040s) conditions. Third, I used the thermal exposure metrics to quantify the magnitude and direction of phenological shifts that would have to occur for each population if thermal exposure were to remain constant in the future.

1.3.2. Data Description

1.3.2.1. Migration timing data

To assess the diversity in adult migration timing across the range of Chinook salmon, I compiled a geographically expansive database on adult upstream migration timing for 295 populations spanning 29 degrees of latitude from California's Central Valley to Alaska and Canada's Yukon River. Data was sourced from a range of reports, publications, and publicly available databases. Examples of these include Alaska Department of Fish and Game's daily salmon escapement counts, available through the State of Alaska's Salmon and People synthesis data from NCEAS (Clark and Brenner 2017), the Columbia Basin PIT Tag Information System database (PTAGIS 2019), Fisheries and Oceans Canada Genetic Stock ID data for Fraser River Chinook (Parken et al. 2008), as well as other sources listed in Table A1. These sources included count data sampled daily or several times a week using a range of methods such as weir counts, sonar, gill net sampling and radiotelemetry. I derived each population's mean

migration timing by first calculating the weighted mean and variance of each year's count data at river entrance. I then calculated the mean and variance of river entrance date using data from all years in order to obtain a migration timing window for each population.

Given that data for some populations were observed at upstream tributary confluences, while others were observed at the mouths of mainstem river systems, I standardized all the migration timing datasets to the timing of river entrance into freshwater (i.e., the timing of entrance to the mouth of each mainstem river system). River entrance timing was chosen because it was assumed to be representative of the warmest conditions encountered along a population's migratory pathway. Although rivers exhibit diverse longitudinal thermal profiles, rivers are thought to warm asymptotically downstream (Caissie 2006), and a recent assessment has shown that approximately two thirds of Pacific Northwest rivers exhibit warming or uniform thermal profiles (Fullerton et al. 2015). Regardless, the mouth of the river represents the first conditions encountered during migration and may form a potential bottleneck if temperatures surpass thermal stress thresholds. To standardize the data, I back-calculated river entrance timing for populations observed in tributaries based on the distance travelled from the point where fish were counted to the mouth of their respective river system, and daily migration rates (more information about the distance calculations is available in the spatial data description below). River mouth locations were georeferenced to the upper extent of each system's estuary or ocean influence. Migration rates for each watershed were obtained from a literature scan for telemetry studies that directly measured migration rates across the full adult migratory pathway of a population and were matched as closely as possible to different populations and run timing groups (Table A2). Finally, to compare patterns across geographic scales, populations were organized into 9 broad watersheds or watershed aggregates, termed "watershed regions". These were meant to delineate the tributaries of large single watersheds (for example, the Fraser or the Columbia) or similarly sized regions containing smaller watersheds (for example, small coastal watersheds of Southeast Alaska).

1.3.2.2. Water temperature data

In order to quantify thermal exposure across the range of Chinook salmon, I compiled a water temperature dataset for sites corresponding to the mouths of each mainstem river system for recent conditions (1990s) and future climate change conditions half a century

later (2040s). The 1990s and the 2040s were chosen for consistency with the North Pacific Rim water temperature database from the Riverscape Analysis Project (Whited et al. 2012), which I used to generate climate change predictions for the water temperature data. The 1990s were the most recently available historical decade in the RAP database, while the 2040s were the first available decade with climate change projections. For the 1990s, observed water temperatures were sourced from the NorWeST Stream Temperature Database (Isaak et al. 2017), the USGS National Water Information System (USGS 2016) and Fisheries and Oceans Canada's eWatch database (see Table A3 for a full list of sites and sources). Observed water temperatures were summarized by their daily mean. Overall, 188 of the 295 populations had water temperature data available for their mainstem river segments and thus were the focus of the analyses on population-specific thermal exposure and phenological shifts. The RAP database, although optimized and available across a large spatial range, was locally inaccurate when tested against observed water temperatures. Thus, to generate climate change predictions for the 2040s, I used the RAP database to calculate the mean difference between water temperatures during the 1990s (the last available historic decade) and projected water temperatures during the 2040s (for a moderate A1B climate change scenario). I then applied this climate change difference to the observed 1990s water temperatures to generate the projections for the 2040s that were used in this study.

1.3.2.3. Spatial and environmental data

I compiled a geospatial dataset of watershed characteristics to calculate migration distances for the back-calculated river entrance timing (section 1.3.2.1), as well as to extract environmental covariates of migration timing (section 1.3.3.1). In order to standardize the spatial reference point at which covariates were extracted, each population in the dataset was georeferenced to the location of the mouth of the tributary in which it spawns. Additionally, each population was spatially associated to the mouth of its mainstem river system (for coastal streams, these two points were defined as the same). To calculate migration distances, I combined river network data for each watershed region from the USGS National Hydrography Dataset (for the United States), the Freshwater Atlas Stream Network data from GeoBC (for British Columbia) and NRCAN's National Hydrographic Network (for the Yukon). Using the QNEAT3 Network Analysis Toolbox in QGIS 3.18, I generated an Origin-Destination-Matrix where origins

were defined as the mouth of each population's spawning tributary, and the destinations were the mouth of each mainstem river system. The resulting output was a least-cost distance calculation along the river network flowlines for each population's migration pathway from the river mouth to its spawning tributary. Next, I extracted elevation data from the USGS North America Elevation 1-kilometer resolution DEM for each tributary mouth and mainstem point. Elevation data were used to calculate the net elevation gained across the migratory pathway, as well as the slope, by dividing the elevation gained by the migration distance. In order to generate a metric of migration difficulty, or work, I multiplied elevation gained by the migration distance of each migratory pathway (as per Eliason et al. 2011a).

1.3.3. Analyses

1.3.3.1 Diversity of migration timing and environmental covariates

I investigated environmental covariates of migration timing with two sets of explanatory analyses. First, to evaluate how water temperature shapes windows of thermal suitability for migration within each watershed region, I examined the relationship between water temperature and migration probability at the watershed scale. Second, I used watershed and migratory corridor characteristics to investigate covariates of earlier and later migration timing at the population scale. All statistical analyses were conducted using the statistical software R version 3.5.2 (R Core Team 2018).

For the first analysis on thermal suitability for migration, I modelled weekly migration probability as a function of mean weekly temperature for each watershed region. Specifically, migration probability referred to the probability that migration is occurring at a given temperature in a given watershed, across all populations. I used the recent (1990s) observed temperature data, summarized by weekly mean, and a binary presence-absence variable for migration timing generated by aggregating all populations migrating through each mainstem site within a watershed region. I used a generalized linear model with a logit link function to model the probability of migration as a function of temperature. To allow for a unimodal (i.e., the characteristic shape of curves describing species responses to temperature (Huey and Kingsolver 1989)) relationship between water temperature and the probability of migration, I included a second-order polynomial term for the effect of temperature. To allow for differences in the mean probability of

migration across watersheds (i.e., the intercept of the linear model), I included a fixed effect of watershed region.

For the second analysis on covariates of earlier and later river entrance timing, I modeled migration timing at the population level using variables that fall broadly within two categories: watershed characteristics and characteristics of the migratory corridor (a full list of covariates and their data sources can be found in Table A4). First, the watershed characteristics category included landscape-level characteristics that are linked to thermal regime, such as latitude and the elevation of the spawning grounds (as hypothesized in Brannon et al. 2004; Quinn et al. 2016; Beechie et al. 2008). The thermal regimes of the spawning grounds set constraints on the timing of spawning, with earlier spawning happening at cooler temperatures so that developing eggs accumulate enough degree days during the over-wintering period. This sets an expectation for the necessary arrival timing at the spawning grounds, and thus a constraint on the timing of river entrance. Second, the migratory corridor characteristics category was comprised of characteristics that define the scope of the upstream migration, such as migration distance, slope, or migratory work (a metric of the difficulty of migration defined as the product of migration distance and elevation) (Quinn et al. 2016). These migratory characteristics may set additional constraints on river entrance timing. Populations undertaking steeper or more difficult migrations might enter fresh water earlier. Longer migrations set a requirement for how long the migration itself will take, therefore determining how early river entrance timing must happen relative to spawn timing.

With these hypotheses in mind, I ran sets of simple linear regressions within each watershed region, across all the covariates of interest. I compared standardized effect sizes for all covariates across each watershed region and assessed the significance (i.e., $p < 0.05$) of relationships between each covariate and each population's mean migration timing. Some geographically similar watershed regions were combined for sample size (Central Alaska was combined with Western Alaska; Coastal California and Oregon was combined with Central Valley; Southeast Alaska was combined with North and Central Coast BC). Regions were assessed with different models given the potential for different factors to be important in different regions. Broadly, this analysis allowed me to assess which environmental characteristics were associated with earlier or later migration timing within the window of thermally suitable migration conditions within each watershed region.

1.3.3.2. Recent and future thermal exposure and risk

In order to quantify population-specific thermal exposure during river entrance timing, I matched each population to the water temperature site at the mouth of the mainstem river system it migrates through. For each population within each river system, I quantified two thermal exposure metrics (in °C) for recent (1990s) and projected future conditions (2040s). The two metrics were mean thermal exposure, meant to represent average thermal conditions during a population's migration window, and extreme thermal exposure, a measure of potential acute thermal stress experienced by each population. Population-specific migration timing windows were defined by the lower and upper 95% confidence intervals of mean river entrance timing. For the mean thermal exposure metric, I calculated a weighted average of the temperatures experienced during each population's migration timing window, with daily temperatures weighted by the daily migration timing distribution in order to more accurately represent the temperatures experienced by the daily proportions of the total run size of migrating adults (as per Hague et al. 2011). For the extreme thermal exposure metric, I used the full timeseries of temperatures within a population's migration timing window and calculated the 90th percentile of the distribution of temperatures experienced throughout the window. Given that thermal stress may be amplified with exposure to temperatures that surpass sensitivity thresholds, I assessed population-specific exposure above established thresholds of 18°C and 21°C as a metric of climate risk. The threshold of 18°C was chosen as a conservative lower estimate for the onset of thermal stress, and 21°C was chosen as a threshold at which migration is delayed, based on behaviors observed in the field (USEPA 2003; Richter and Kolmes 2005; Zillig et al. 2021).

1.3.3.3. Pace and direction of potential phenological shifts

I used the metric of recent mean thermal exposure, combined with the future 2040s thermal regime to estimate how quickly each population would have to shift its timing in order to adapt to a changing climate (i.e., shift its timing in order to keep the same thermal exposure). I calculated a moving average of the 2040s thermal regime using each population's respective migration timing window, with daily temperatures weighted by the daily migration timing distribution (as per section 1.3.3.2). I then found the new migration window which corresponded to the equivalent thermal exposure, and that was on the same side of the peak summer temperature for each site. This assumption implies that a population would not shift its timing across warmer peak temperatures that

surpass its historic thermal exposure. If multiple windows of equivalent thermal exposure were found, the closest to the original migration timing was chosen. This analysis assumed that the migration window didn't vary in width (i.e., the standard deviation of migration timing remained constant). I calculated the difference between the baseline migration timing window and the new window of thermal exposure to determine the total number of days by which each population would need to shift its timing in order to adapt to climate change over 5 decades. This number was divided by 5 to generate an estimate of the pace (in days per decade) and direction (either earlier or later) of phenological change, as quantitative metrics of pressures on the adaptive capacity of Chinook salmon populations.

1.4. Results

1.4.1. Diversity of migration timing and environmental covariates

Adult migration timing exhibited remarkable diversity across the nine watershed regions spanning the broad range of Chinook salmon (Figure 1). Migration timing diversity was greater towards the south, and more constricted in northern latitudes. For example, in the Central Valley, Chinook salmon migration spanned 10 months of the year, while populations at northern latitudes were constrained to a migration period within three months of the year. The seasonal phenology of migration varied across latitudes, with peak migration in the north occurring during mid-summer, while migration at southernmost latitudes waned during mid-summer months, displaying a bimodal pattern of migration occurring predominantly in the winter, spring, and fall.
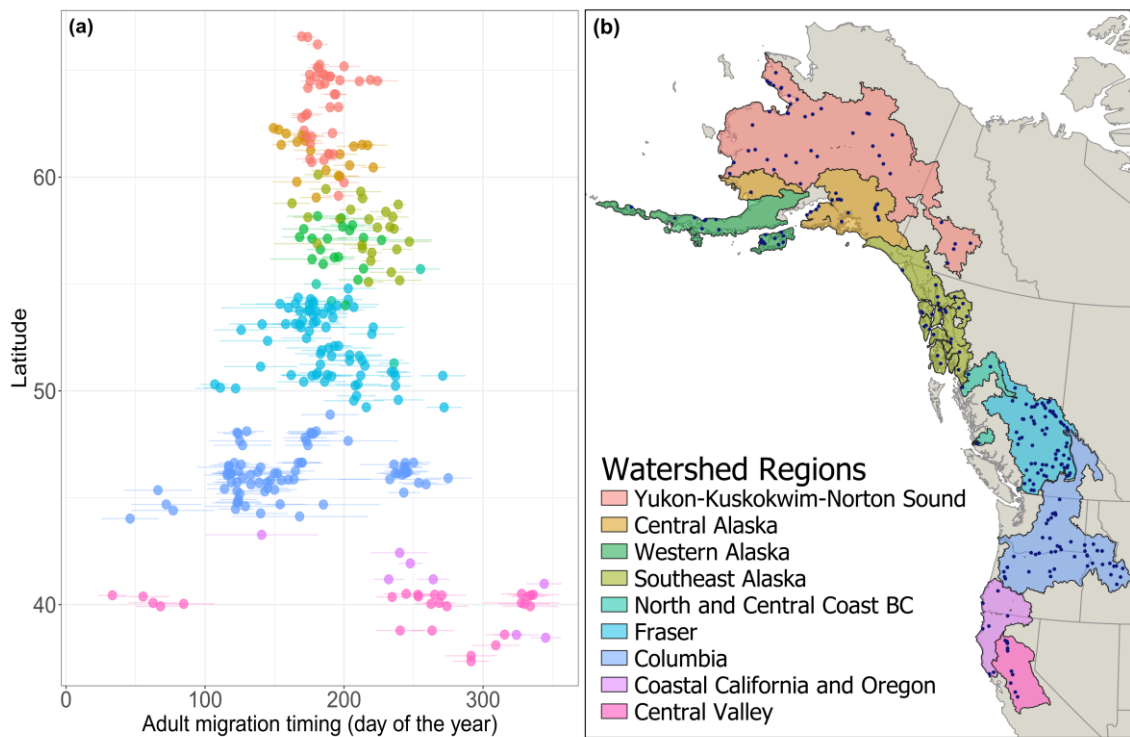
Figure 1   **Migration timing diversity of 295 Chinook salmon populations across the range of the species, with each population plotted in panel a) by its mean and standard deviation of river entrance timing, with points colored by watershed region. Panel b) shows the coordinants of corresponding spawning tributaries in dark blue points, within their respective watershed regions.**

Weekly water temperature had significant effects on the probability of migration across watershed regions, with significant support for a unimodal relationship ($p < 0.001$ for both the first-order and second-order parameters, Table A5). This unimodal relationship was apparent in low latitude watersheds that experience higher maximal water temperatures (i.e., Columbia, Coastal California and Oregon, Central Valley in Figure 2), where the probability of migration was low at both low and high temperatures, and peaked around 16-17°C. However, in high latitude watersheds that experienced lower maximal temperatures (i.e., Yukon-Kuskokwim-Norton Sound, Central Alaska, and Fraser River in Figure 2), the probability of migration was low at low temperatures and peaked at the upper ranges of temperatures experienced within each region. Broadly, the effect of temperature on the probability of migration was consistent across all watershed regions ($p < 0.001$, Table A5), although there were differences in the mean probability among watersheds ($p < 0.001$ for all fixed effects of watershed, Table A5). The fixed effect of watershed allows for the probability curve to shift either up, in watersheds where more populations are migrating across more weeks of the year, or down, in watershed regions where fewer populations are migrating across fewer weeks of the year, thus affecting mean migration probabilities. In short, it appears that across watershed regions, there is a consistent window of suitable temperatures during which Chinook salmon migrate, and that in watersheds where water temperatures reach higher temperatures, Chinook migration slows during these peak temperatures.
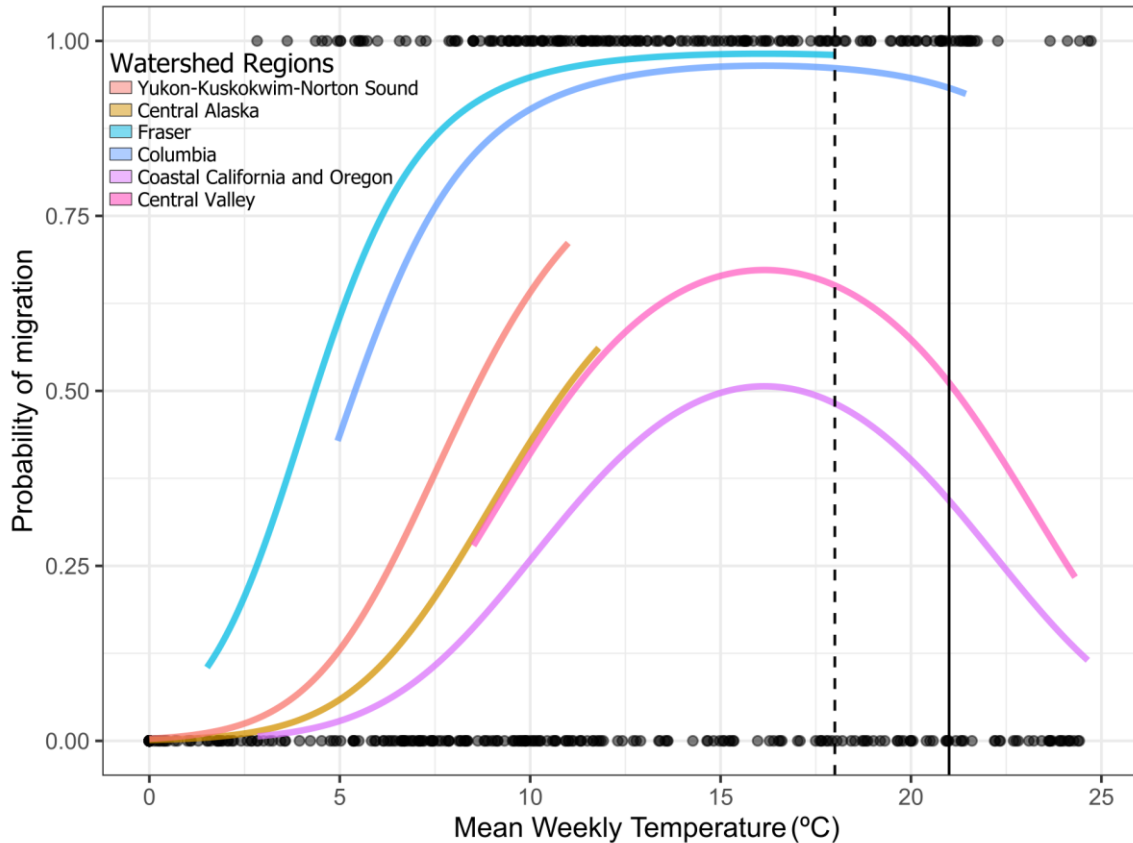
Figure 2   **Probability of migration as a function of mean weekly temperature for each watershed. Dashed lines represent a threshold of 18°C (onset of thermal stress) and solid lines are at a 21°C threshold (migration delay). Points are weekly observations of migration presence or absence across all watersheds and predicted probability of migration curves are plotted across the range of temperatures experienced within each watershed region.**

Within regions, adult migration phenology was associated with migration distance, migratory work, latitude, elevation, and latitude*elevation. The negative coefficients for latitude in Central-West Alaska and the Fraser River suggests that earlier river entrance timing was associated with higher latitude rivers in these watersheds, although the positive coefficient for the Columbia River suggests the opposite relationship (Figure 3A). Earlier river entrance timing was also significantly associated with higher elevation rivers in the Yukon-Kuskokwim-Norton Sound, Central-West Alaska, Alaska-British Columbia Coast, and Fraser River watershed regions (Figure 3B). Finally, earlier river entrance timing was significantly associated with higher latitude*elevation gradients, as well as longer and more difficult migrations in the Yukon-Kuskokwim-Norton Sound,

Central-West Alaska, and Fraser River watershed regions (Figure 3C-E). Slope was not significantly associated with river entrance timing in any of the watershed regions (Figure 3F). Thus, in most watershed regions, watershed and migratory corridor characteristics are significantly associated with differences between early- and late-migrating populations. Given that migration timing can influence climate exposure (see section 1.4.3), these watershed and migratory corridor characteristics may structure patterns in climate risk across regions.
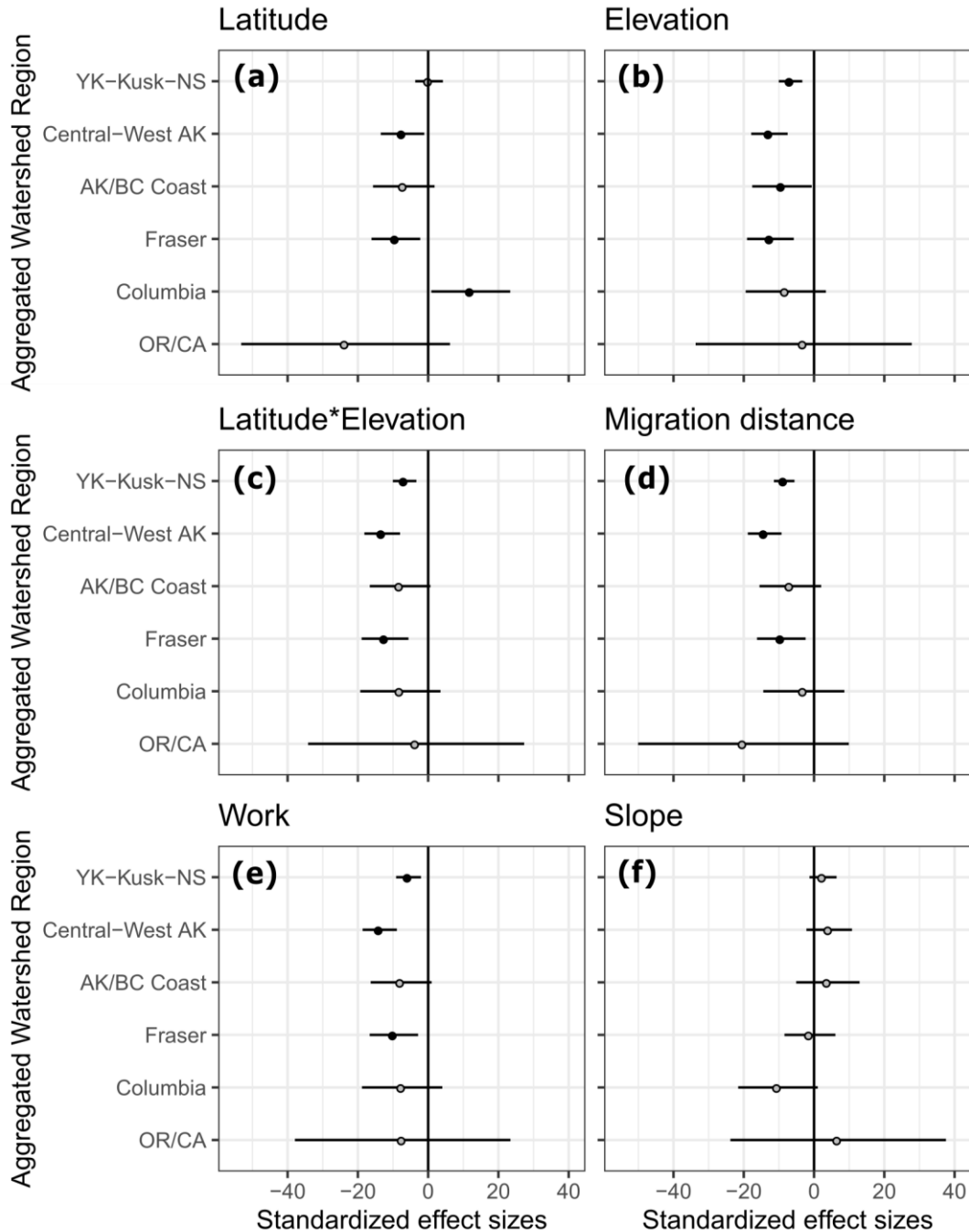
Figure 3   **Standardized effect sizes and 95% confidence intervals for six environmental covariates of river entrance timing across six watershed regions. Watershed characteristics include the latitude of the spawning grounds (a), the elevation of the spawning grounds (b), and a latitude*elevation gradient variable (c). Migratory corridor characteristics include migration distance (d), migratory work (distance*elevation) (e), and the average slope across the migratory corridor (f). Significant effects (p < 0.05) are represented by solid black circle, non-significant effects are open circles. Negative standardized effect sizes indicate earlier river entrance timing.**

1.4.2. Recent and future thermal exposure and risk

Thermal exposure among populations of Chinook salmon varied greatly with migration timing and latitude (Figure 4A). Across all populations, the mean thermal exposure metric was 14.5°C and the 90th percentile extreme thermal exposure metric was 17.5°C. Lower latitude populations generally had higher exposure to warmer water temperatures than higher latitude populations, with the southernmost Central Valley watershed region of California experiencing the greatest recent mean thermal exposure (mean 1990s exposure of 15.4°C, Table A7), and the adjacent Coastal California and Oregon region experiencing the greatest extreme thermal exposure (extreme 1990s exposure of 19.1°C, Table A7). In contrast, higher latitude watershed regions, such as the Yukon-Kuskokwim-Norton Sound and Central Alaska watersheds which span Alaska and Canada's Yukon region, had lower recent thermal exposure (mean 1990s exposure of 10.6°C and 11.3°C respectively, Table A7). Migration timing also strongly structured thermal exposure. Populations that migrate in the summer and throughout the fall, such as the fall runs in California's Central Valley and Washington's Columbia River, as well as the summer run in the Fraser River region, had the highest mean thermal exposures (mean 1990s exposure of 19.9°C, 18.4°C and 16.1°C respectively, Table A8). In contrast, spring and late fall run populations had the lowest thermal exposure throughout the year (mean 1990s exposure of 12.9°C and 11.5°C, respectively, Table A6). Thus, patterns in recent thermal exposure are linked to both migration timing and latitude across the broad range of Chinook salmon.
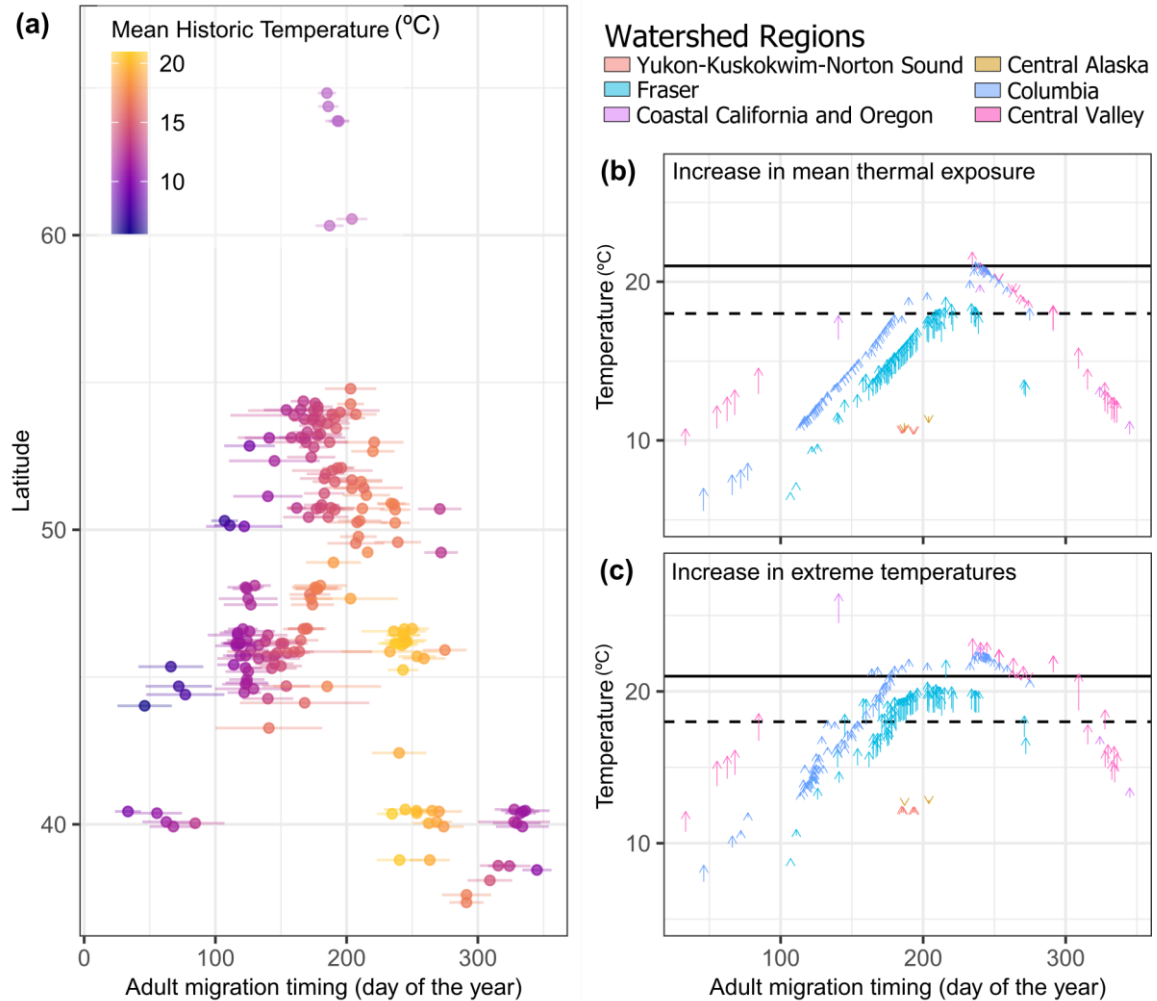
Figure 4 **Thermal exposure as a function of migration timing and latitude. Panel a) shows run timing for the subset of populations for which temperature data is available, with points colored by each population's mean recent thermal exposure during their migratory window. Right panels compare increases in two different thermal exposure metrics: b) mean thermal exposure during the migratory window and c) 90th percentile of the temperatures experienced during the migratory window. Arrows depict change from recent (1990s) to future conditions (2040s). Dashed and solid lines represent thresholds of 18°C (onset of thermal stress) and 21°C (migration delay), respectively. Note the outlier in panel c), the North Umpqua River, which already experiences temperatures near 24°C during its migration window, and will experience extreme temperatures beyond 25°C under climate change conditions.**

Projected increases in thermal exposure due to future climate change also varied greatly across the range and migration timing diversity of Chinook salmon (Figure 4B and C). For lower latitude watershed regions spanning California, Oregon, and Washington, increases in mean thermal exposure from the 1990s to the 2040s were higher in very early and very late-migrating populations (i.e., the spring and late-fall runs, mean increases of 0.8°C and 1.4°C respectively, Table A6), indicating that population migration timing will strongly drive future climate change risk. However, increases in the 90th percentile extreme thermal exposure metric appeared uniform throughout the year (Figure 4C). In some populations, the magnitude of increase from recent to future exposure was greater in the extreme temperatures versus the mean temperatures (e.g., Coastal California and Oregon spring run extreme thermal exposure in the 2040s is 0.4°C higher than mean thermal exposure, Table A8). Thus, climate change will drive increases in mean and extreme thermal exposure across the range and migration timing diversity of Chinook salmon.
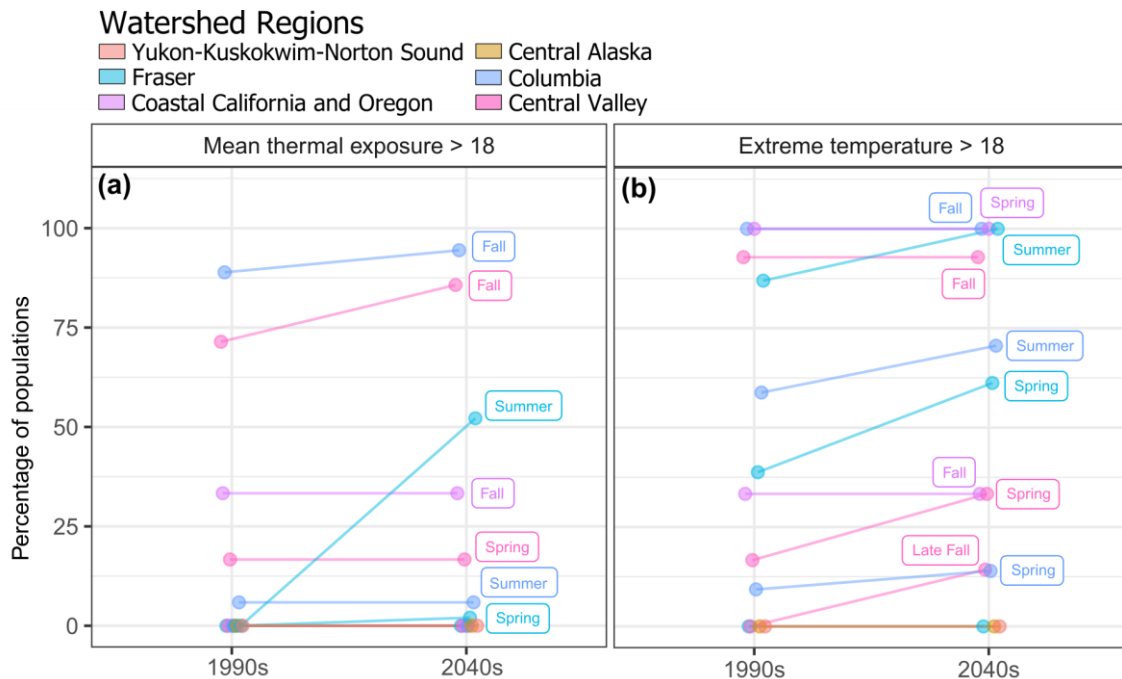
Figure 5   **Percentage of populations experiencing thermal stress above a threshold of 18°C, aggregated by run timing group and watershed. Colors represent different watershed regions and for visual simplicity, labels are only appended to run timing groups that increase in percentage. Panel a) shows populations with mean thermal exposure above 18°C; panel b) shows populations with extreme thermal exposure above 18°C**

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Climate change across the range of Chinook salmon will increasingly expose migrating adults to temperatures above thermal sensitivity thresholds, an index of climate risk (Figure 5). Overall, from the 1990s to the 2040s, the percentage of populations with mean thermal exposure above 18°C, a threshold above which thermal stress generally begin to accrue, increased from 15% to nearly a quarter (23%) of all populations. More specifically, in the 1990s climate risk above 18°C was highest in the fall-run groups of the Columbia River (88%), Central Valley (71%) and Coastal California and Oregon (33%) watershed regions, followed by the Central Valley spring run (16%) and the Columbia River summer run (6%) (Figure 5A). Meanwhile, in the 2040s, the Fraser River summer- and spring-run population were also exposed to temperatures above 18°C (52% and 2% of populations). From the 1990s to the 2040s, the Fraser River summer-run populations experienced the greatest increase in exposure to temperatures above 18°C with a jump from 0% to 52% of populations having a mean thermal exposure above 18°C. This mid-latitude region is where climate risk is predicted to increase the most, presumably because migration timing has not yet historically adapted to warm summer water temperatures. Furthermore, the percentage of populations exposed to extreme temperatures above 18°C increased from 46% to 56% from the 1990s to the 2040s (Figure 5B). Results for thermal exposure above a threshold of 21°C can be found in the appendix (Figure A5).

1.4.3. Pace and direction of potential phenological shifts

Predicted shifts in migration timing that would need to occur for Chinook salmon populations to adapt to a warming climate varied greatly across watershed regions and run timing groups (Figure 6A). Overall, shifts in timing of up to 5.2 days/decade earlier and 3.2 days/decade later over 50 years would have to occur for populations to maintain constant levels of thermal exposure (Figure 6B). These shifts were generally greater in magnitude within the Fraser River and Central Alaska (mean shifts of 2.3 days/decade in both), than in the Columbia (0.9 days/decade), Coastal California and Oregon (1.4 days/decade), and Central Valley (1.3 days/decade) regions (Table A10). In general, early-migrating populations such as the Central Valley spring and the Fraser River summer runs will have to shift much more than other run timing groups (mean shifts of 2.9 days/decade in both, Table A9). Meanwhile, late-migrating populations, such as fall-

run populations across all regions, will generally need to shift their timing less (range: 0.8-1.1 days/decade, Table A11).

Populations also differed dramatically in the direction of predicted migration timing (Figure 6A). Many more populations (120, ~75% of populations) would have to shift their migration timing earlier in the year (a divergence from their spawn timing), while 40 populations (~25%) would have to shift their timing later in the year. Within watersheds, these ratios ranged from overwhelming shifts towards earlier timing in the Fraser River (85% of populations) to a majority of populations shifting towards later timing in the Coastal California and Oregon watershed region (66%) (Figure A8). A majority of the spring- and summer-run populations (92% and 82% respectively) would have to shift their timing earlier in the year, while a majority of the fall-run populations (79%) would have to shift their timing later in the year (Figure A9). Given that pressure for earlier migration timing is associated with a novel suite of climate risks such as divergent pressures on migration and spawn timing, as well as extended freshwater holding periods, these analyses suggest that spring-and summer-run populations are disproportionately challenged to adapt to a warming climate.
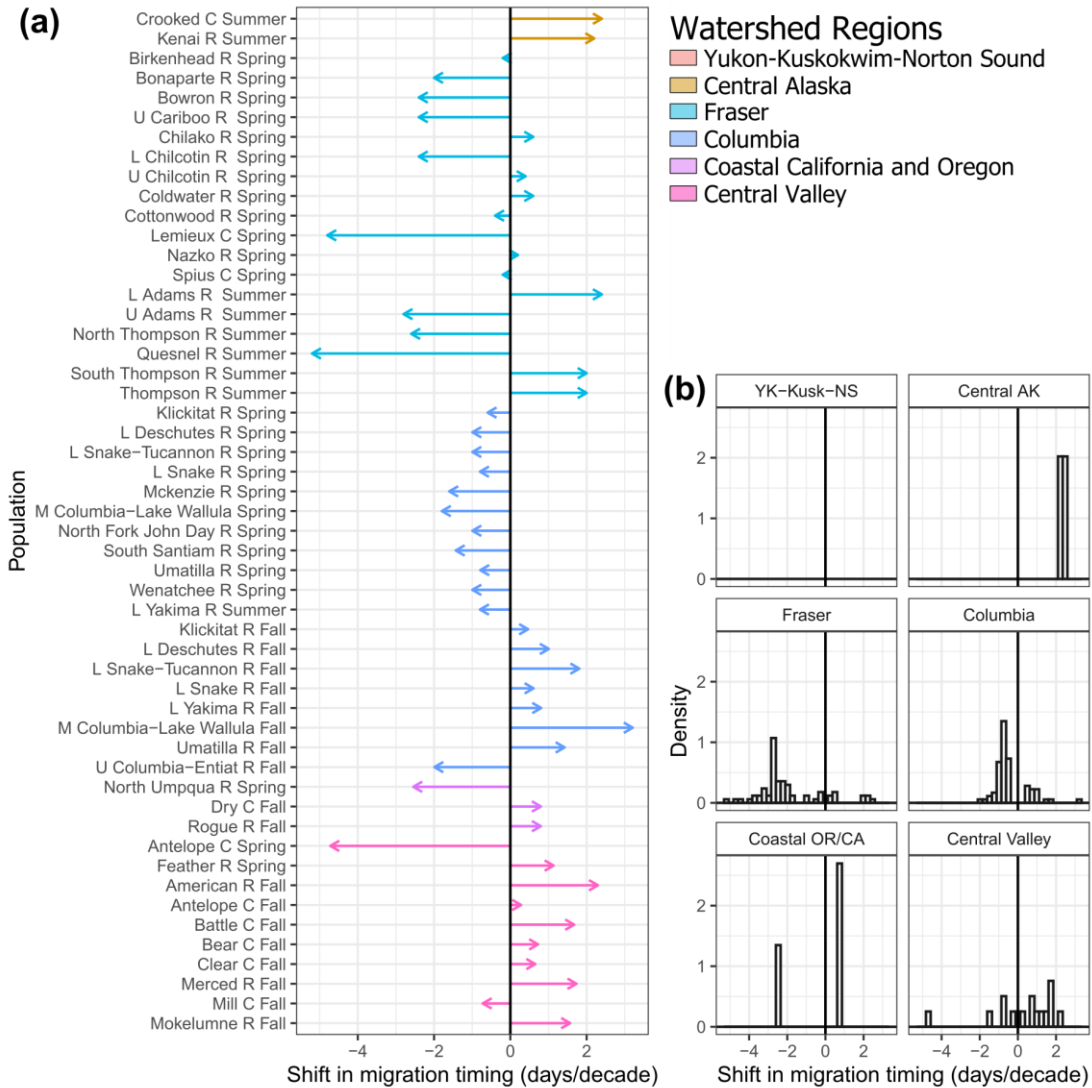
Figure 6 **Potential for shifts in migration timing from 1990s to 2040s conditions if populations were to maintain constant levels of mean thermal exposure: Panel a) presents a representative subset of populations with arrows depicting number of days by which mean migrating timing day could change, ordered by latitude and colored by watershed region and panel b) aggregates the distributions of shifts by watershed region and direction (earlier or later timing)**

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1.5. Discussion

1.5.1. Synthesis of climate change risk and adaptation

Here I quantified recent and future climate exposure, risk, and adaptation across the North American range of Chinook salmon, a species of enormous cultural and ecological importance. I offer three key takeaways with regards to climate change risk during upstream migration of adult salmon. First, climate risks are structured by both latitude and migration timing. On average, lower latitude regions are higher in thermal exposure, but within each of these regions, the timing of river entrance influences population-specific thermal experience, with higher exposure for populations migrating during peak summer temperatures. Second, although they are exposed to stressful temperatures, populations at lower latitudes have broadly evolved to avoid migrating during peak summer temperatures, with most low latitude populations now migrating before or after water temperatures peak. However, mid-latitude regions, namely the Fraser River, saw the greatest forecasted increases in climate risk above a sensitivity threshold of 18°C, as they have presumably not yet adapted to avoid migrating during peak summer temperatures. Third, if populations were to adapt to a changing climate by shifting their phenology, the majority (75%) would need to migrate earlier in the year, putting conflicting pressures on different life stages, which could represent a climate change "trap". Thus, these different components of climate risk highlight the complex interplay between climate change and life-history diversity across the broad range of this species.

1.5.2. Diversity of migration timing and environmental covariates

Chinook salmon populations vary greatly in the phenology of their adult migrations. The data displayed a clear latitudinal gradient in migration timing (Figure 1), consistent with previously described patterns in spawn timing (Healey 1991; Beechie et al. 2008; O'Malley et al. 2010), which have been shown to be largely driven by variation in thermal regimes across habitats in other salmonids (Brannon 1987; Hendry et al. 1998; Austin et al. 2019). Similarly, the broad divergent pattern in migration timing described here may be linked to the thermal regimes that populations experience along their migratory corridors. In lower latitude watershed regions, adult migration was less frequent during the hot summer months, splitting the general pattern of migration into a bimodal distribution of early- and late-migrating populations. This is presumably the evolutionary

product of selection against migrating during thermally stressful summer temperatures, which is also thought to drive earlier migration timing in some sockeye salmon populations (Hodgson and Quinn 2002). Overall, these broad geographic patterns in migration timing reflect seasonal windows of thermal suitability for migration along mainstem migratory corridors, which vary in their timing across the range of Chinook salmon (Brannon et al. 2004). As climate change drives increases in peak water temperatures across watersheds, these windows of thermal suitability may shift accordingly and exert further selective pressures on migration timing. While each system is different, high latitude watersheds may start to display migration timing patterns that resemble those of lower latitude regions as migration timing adapts to the shifting windows of thermally suitable conditions for migration. In short, major river systems across the range of Chinook salmon may offer glimpses into potential future patterns in the migration timing diversity of the species.

Beyond simple latitudinal gradients, environmental covariates indicate that higher elevations and higher latitudes, which are proxies for cooler thermal regimes at the spawning grounds, as well as longer migrations, are associated with earlier entrance timing in most watershed regions (Figure 3). These results broadly align with the hypothesis that watershed and migratory corridor characteristics drive long-term population-specific selection on timing at the regional scale (Brannon et al. 2004; Beechie et al. 2008; Quinn et al. 2016), although other factors may also influence migration. For example, trade-offs between growth opportunities and risks of mortality in the ocean (Quinn et al. 2016) or in freshwater (Katinic et al. 2015), as well as other migratory corridor characteristics such as the presence of hydrological barriers that must be passed early in the season in order to access suitable spawning habitat (Brannon et al. 2004). These patterns and the power to detect them have also presumably been altered in some regions such as the Columbia due to the non-random loss of interior (and often spring-run) populations due to impassable dams (Gustafson et al. 2007; McClure et al. 2008). Regardless, watershed features have shaped the timing of adult Chinook salmon migration, which in turn will influence their thermal exposure and thus climate risk.

1.5.3. Recent and future thermal exposure

Patterns of thermal exposure indicate that exposure to stressful temperatures varies with migration timing and latitude. Seasonal patterns in recent and future thermal exposure reveal that populations migrating in mid-summer and fall experience the highest temperatures during their upstream migration (Figure 4). In particular, the highest percentages of thermally stressed populations were in low-latitude fall- and summer-run groups of California, Oregon, Washington, and British Columbia (Figure 5). These findings mirror previous analyses of the southern half of the range of Chinook which found that phenology predicts thermal stress, and that fall-run populations exhibited higher thermal stress during adult migration (FitzGerald et al. 2021). However, as climate warms from the 1990s to the 2040s, populations migrating early in the year will experience higher increases in thermal exposure. This particularly high risk in spring-run life histories, which generally undergo longer freshwater migrations towards higher-elevation spawning grounds in interior regions, has also been noted by previous climate vulnerability assessments (Crozier et al. 2019). Furthermore, here I also show that populations that migrate at mid-latitudes during mid-summer (e.g., the summer run of the Fraser River) will also be challenged by climate change, as they have not yet evolved to avoid stressful peak summer temperatures and will increasingly be exposed to temperatures above thermal stress thresholds by the 2040s. Thus, while there is a broad body of work that assesses species-level (Parmesan and Yohe 2003; Pinsky et al. 2013; Pacifici et al. 2015; Sunday et al. 2015) and geographic patterns (Loarie et al. 2009; Burrows et al. 2011) in climate risk, here I reveal remarkable within-species variability in climate risk driven by diversity in migration timing.

These patterns in climate risk imply that warming water temperatures may have drastically different effects on Chinook salmon populations across their range. Broadly, exposure to high temperatures can have sublethal impacts such as bioenergetic depletion, increased disease transmission and reduced egg viability (Martins et al. 2012) and has already been linked to increased pre-spawn mortality and reduced fitness in Chinook (Bowerman et al. 2021) and other salmon species (Minke-Martin et al. 2018; Westley 2020). Furthermore, evidence for population-specific adaptation to different critical thresholds (Eliason et al. 2011; Zillig et al. 2021) suggests that even extreme temperatures in excess of what populations are historically adapted to can be considered thermally stressful, regardless of whether they surpass established critical

thermal limits of 18 or 21°C (e.g., Hague et al. 2011). However, populations at northern latitudes may be migrating below their physiological optima and increases in temperature due to climate warming may broaden the thermally optimal windows when they can migrate. Thus, climate change is broadly expected to increase exposure to temperatures above thermally stressful limits (Mantua et al. 2010; Isaak et al. 2018) but may widen the window of suitable temperatures for migration in northern watersheds.

1.5.4. Pace and direction of potential phenological shifts

Phenological shifts have the potential to mitigate some of the impacts of climate warming. Here I calculated how quickly each population would have to shift its timing to adapt to a changing climate. Overall, migration timing shifts of up to 5.2 days earlier or 3.2 days later per decade would have to occur if populations were to maintain constant levels of thermal exposure over 5 decades (Figure 6). This rate may be within the immediate adaptive capacity of the species to keep pace with climate change, given that phenological shifts of 3.2 days/decade earlier (Crozier et al. 2008a) and up to 2.5 days/decade later (Kovach et al. 2015) have been observed in Chinook populations of the Columbia River and Southeast Alaska. However, other selective pressures on timing may also confound population-level responses to climate change. These include both natural and anthropogenic processes, such as fluctuating demographics and oceanic conditions, artificial temporal selection from fisheries and hatchery influences (Tillotson et al. 2021), or the ongoing selective pressures of the watershed characteristics described in section 1.5.2 and Quinn et al. 2016. Thus, responses to climate change may be more complex than a straightforward phenological shift in the peak timing of migration.

The adaptive capacity of a species will not only be challenged by high rates of phenological change, but also their directionality of phenological forcing across the life cycle (Crozier and Hutchings 2014). Climate change may exert conflicting selective pressures on different salmonid life stages, which may limit adaptation (Crozier et al. 2008a; Wainwright and Weitkamp 2013). For example, warming freshwater temperatures may shift optimal spawn timing later in the year to compensate for accelerated egg development at high temperatures, while optimal migration timing may shift either earlier or later (Crozier et al. 2008a). Our results suggest that 75% of populations would have to shift towards earlier adult migration timing with warming

temperatures, subjecting them to divergent pressures across their life cycles. In particular, spring- and summer-run populations that migrate before peak summer temperatures will be pushed earlier, further away from their current optimal spawn timing, lengthening the amount of time individual fish will have to hold before spawning. This could expose them to higher temperatures, energetic costs, and risks of predation (Crozier et al 2008). Thus, earlier migrants may be vulnerable to "climate traps". The opposing selective pressures of climate change on migration timing and spawn timing may compromise the ability of salmon to adapt to a warming climate.

1.5.5. Caveats

This study assessed the components of climate risk – exposure, sensitivity, and adaptive capacity - across the broad range of a diverse migratory species, and thus made several simplifying assumptions that are important to consider. First, to quantify thermal exposure, I used river entrance temperatures, assuming that the downstream reaches of major watershed systems would be the most thermally stressful areas encountered along a population's pathway. However, longitudinal patterns in river temperatures can be complex and, in some watersheds, interior regions could get hotter than downstream river entrances (Stafford et al. 2000; Fullerton et al. 2018; Pitman and Moore 2021). Thermal exposure estimates could be improved with water temperature observations and predictions that span regions and international boundaries. Additionally, I did not consider the potential for behavioral thermoregulation in cold water refuges along the migratory pathway to affect thermal exposure. While cold water refuges are undoubtedly important in some situations, simulations have suggested that cold-water refuge use, while providing short-term relief from high temperatures, may not result in substantial energetic savings over the course of an individual's migration (Snyder et al. 2020), and river temperatures could warm to the point where holding pools become thermally intolerable. Furthermore, the temperature forecasts used in this dataset could be conservative estimates of the impacts of climate change, particularly at high latitudes which are warming at much higher rates than the rest of the planet (IPCC 2021). Another key assumption in this study was with regards to the selection of the thermal limits of 18°C and 21°C as metrics of sensitivity. These specific values may be conservative estimates of physiologically stressful temperatures; while frequently used in the literature, they do come from studies of populations inhabiting the lower half of the

latitudinal range of the species, which may be adapted to warmer water temperatures (USEPA 2003; Richter and Kolmes 2005; Zillig et al. 2021). Populations at high latitudes, on the other hand, may be adapted to cooler thermal regimes and may experience thermal stress or migration delays at lower temperature thresholds than lower latitude populations (Zillig et al. 2021), in line with previous findings on population-specific thermal limits in sockeye salmon (Eliason et al. 2011a). A key research priority for future studies is understanding and integrating intraspecific variation in thermal limits into climate risk assessments. With regards to adaptive capacity, the predictions of phenological shifts were based off the assumption that each population would maintain constant thermal exposure as they shift. However, exposure to temperatures above thermal stress thresholds, are more likely to drive shifts in timing. Moreover, these predictions focused on one life-stage and one pathway of impact (warming water temperatures), whereas climate change has many symptoms (e.g., shifting flow regimes (Beechie et al. 2006; Thompson et al. 2019)). Adaptation to climate change will be influenced by multiple physical and biological processes operating across the salmon life cycle (Crozier et al. 2021; Tillotson et al. 2021). Also, water temperatures are not only controlled by air temperatures, but also watershed activities such as forestry, reservoir management, water withdrawals and channel engineering (Poole and Berman 2001), which can exacerbate warming temperatures. Thus, effective management of watershed activities and habitat restoration could mitigate some climate change risks and promote salmon population resilience (Poole and Berman 2001; Beechie et al. 2012). While these caveats all contribute uncertainties, the large scope of the analyses mandates some assumptions and I believe that they are unlikely to change the key findings that migration timing and latitude structure the different elements of climate risk.

1.5.6. Conservation implications

Chinook salmon are a species of enormous ecological, cultural, and economic importance. Yet over half of populations are considered extinct or endangered in their southern range (Gustafson et al. 2007) and there are alarming trends in abundance, size, and age across their range (Ohlberger et al. 2018; Oke et al. 2020). While these trends are undoubtedly driven by multiple pressures, warming rivers are increasingly causing harm to some Chinook salmon populations (Bowerman et al. 2021). Here I document climate change risks to different regions and migration timing groups. While

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there is general appreciation that lower latitude populations may have higher climate exposure (Crozier et al. 2019), here I also reveal that mid-latitude regions will be increasingly challenged by climate change as they have yet to adapt to thermally stressful summer temperatures. Furthermore, although thermal exposure during river entrance timing is higher in fall-run populations, spring-run fish may be compromised in their ability to shift their phenology in response to climate change because of conflicting climate pressures across their life cycle. These populations, which are already in severe decline across their range (Myers et al. 1998; Gustafson et al. 2007), may be disproportionately impacted by climate warming. Given that the alleles that control spring-run phenology are thought to be unlikely to re-evolve after they are lost from a watershed (Thompson et al. 2019), management and conservation action should aim to conserve the genetic variation underlying migration timing to help support the adaptive capacity of Chinook salmon in the face of climate change. Protecting suitable thermal regimes via conservation and restoration of habitat and floodplain connectivity, dam removal, and holistic management of watershed activities may help maintain phenotypic and genetic diversity and bolster resilience to environmental change (McClure et al. 2008; Beechie et al. 2012; FitzGerald et al. 2021). More broadly, mitigating greenhouse gas emissions to slow the pace of climate change will increase the chances that management and conservation efforts will successfully help protect biodiversity within key species such as Chinook salmon.

Chapter 2.

2.1. General Discussion

Global climate change is threatening biodiversity and driving species responses through shifts in distribution, phenology, and physiology (Parmesan and Yohe 2003; Bradshaw and Holzapfel 2006; Williams et al. 2008). In this thesis, I show that climate risk – a function of exposure, sensitivity, and phenological adaptive capacity – is shaped by migration timing as well as latitude in adult Chinook salmon across their native North American range. First, I found that Chinook salmon display great diversity in the timing of their spawning migrations, with narrow seasonal migration patterns at high latitudes and wider patterns at low latitudes. Across watershed regions, migration was constrained to consistent thermal windows, suggesting that migration timing in adult Chinook salmon has largely evolved to avoid thermally stressful temperatures in some watershed regions. Populations from higher-elevation and more distant watersheds initiated their freshwater migrations earlier in the year than those travelling to lower-elevation and less distant watersheds. Second, I found that although thermal exposure is higher in lower latitude regions, populations in mid-latitude regions (i.e., Fraser River) are projected to experience the greatest increases in climate risk. Third, I found that if populations were to adapt to a changing climate by shifting their phenologies, the majority (75%) would need shift their migration earlier in the year. This directional shift would put conflicting pressures on different life stages across the complex life cycle of Chinook salmon, potentially reducing their capacity to adapt to a changing climate.

More broadly, this work reflects the complex interplay between climate history, life-history diversity, and climate risk across geographic and ecological scales. From the individual to the ecosystem scale, temperature is one of the dominant drivers of life history evolution through its influence on growth, phenology, and survival (Martins et al. 2012; Bellard et al. 2014). Across the range of a species, this past selective pressure translates into differential expression of life-history phenotypes across geographic and climatic gradients (Brannon et al. 2004; Beechie et al. 2008). For Chinook salmon, historically warm summer water temperatures have "unzipped" migratory phenologies in lower latitudes (Figure 1). Within broad watershed regions, windows of thermal suitability in mainstem river migratory corridors determine the seasons that are appropriate for

migration. Migration timing has presumably evolved to avoid thermally stressful temperatures at lower latitudes, while maximizing thermal performance by migrating as close as possible to optimal temperatures at higher latitudes. Across populations within a watershed, fine-scale variation in population-specific river entrance timing has evolved to balance and optimize the demands and selective pressures of each population's migratory and spawning conditions (as shown in this thesis), as well as other factors such as trade-offs between growth opportunities and predation risk in the ocean and freshwater (Katinic et al. 2015; Quinn et al. 2016). However, within a population this fine-scale migration timing determines the thermal experience, or exposure, of a population. As warming temperatures exert directional selective pressures on migration timing, the divergent pattern will widen in lower latitudes, further unzipping migration timing. For species with complex life cycles, the thermal signals of climate change, in conjunction with other drivers, integrate across multiple life stages to shape patterns of biodiversity. Of critical importance, however, is that this biodiversity reciprocally defines climate exposure and current and future risks. Thus, this thesis highlights the interplay between evolutionary history, life-history biodiversity, and climate risk across continental to regional scales.

2.2. Future research directions

I believe that my work provides a key step forward in understanding life history-diversity and climate risk in Chinook salmon. Future research along the following lines of questioning would further advance understanding of thermal exposure, sensitivity, and adaptive capacity:

2.2.1. Other impacts of climate change

Human-induced climate change has increased global surface temperatures by ~1.06°C since the preindustrial baseline (IPCC 2021). But warming water temperatures, which were the focus of my thesis, are only one symptom of climate change. In freshwater, climate change will also contribute to shifting flow regimes due to changing precipitation and snowmelt patterns, with an intensification in the severity of low- and high-flow events (Kang et al. 2016; Ul Islam et al. 2019). Given that Pacific salmon are adapted to the hydrological regimes of their natal rivers (Beechie et al. 2006), an analysis of shifting

flow patterns, as well as thermal regimes, may provide more accurate estimates of the phenological shifts that may occur in response to climate change. In the ocean, warming temperatures and acidification may shift the marine distributions of different populations, which may impact the timing of their arrival to coastal waters (Martins et al. 2012) and thus their river entrance timing. Therefore, the impacts of climate change on environmental factors other than temperature may exert conflicting pressures on migration timing and the ability of Pacific salmon to adapt to warming freshwater temperatures.

On the other hand, climate change may open new local opportunities for Pacific salmon. For example, warming water temperatures at the northern limits of the range of salmon have led to range expansion into the Arctic, and glacial melt may allow certain populations to colonize novel habitats (Nielsen et al. 2013; Pitman et al. 2021). In the context of my thesis, warming water temperatures in northern watersheds may allow some populations to migrate at temperatures that are closer to their physiological optima, precluding the need for phenological adaptation, and broadening the thermally suitable windows for migration. However, as climate change continues beyond the 2040s, even Pacific salmon from northern latitudes will be increasingly exposed to and challenged by warming water temperatures (Westley 2020). Furthermore, climate impacts in other life stages may offset benefits to migrating adults. For example, rising ocean surface temperatures may cause range-wide declines in marine survival, thus overshadowing any potential gains in freshwater survival (Crozier et al. 2021). In short, multiple climate processes acting across the life cycle will determine how the realized impacts of climate change on Pacific salmon differ from predictions made for any one given life stage.

2.2.2. Managing for population-specific thermal limits

Evidence for differences in physiological tolerance among populations is well documented across species of Pacific salmon and other taxa (Richter and Kolmes 2005; Eliason et al. 2011; Bennett et al. 2021; Zillig et al. 2021). Given that thermal tolerance limits are a trait that influences a population's sensitivity and response to climate change, future climate risk assessments would benefit from including population-specific limits (Williams et al. 2008, e.g., Farrell et al. 2008). In adult sockeye salmon, optimal and critical thermal limits have been found to be associated with recent historic (1995-2008)

peaks and ranges of water temperatures encountered along the migratory pathways of several Fraser River populations (Eliason et al. 2011). However, data on these physiological limits, which are typically derived from time-consuming individual-based thermal performance experiments, are currently lacking in Chinook salmon, and represent a priority research area. The historic water temperature ranges experienced by each population, on the other hand, depend on river entrance timing, spawning ground destinations and annual variation in temperatures (Eliason et al. 2011), which can be derived from spatial environmental data to provide insight on population-specific ranges of optimal temperatures. It may be possible to develop predictive models of physiological tolerance through combining these data, some of which I have assembled in this thesis, to help shed light on the variation in thermal tolerances inherent in Chinook salmon.

Improved estimates of population-specific thermal limits across species of Pacific salmon and other fish would allow for more effective management of thermal regimes to protect cold-water salmonid habitats. For example, current USEPA recommendations for maximal temperature criteria are life-stage specific but lack consideration of population- or even species-specific differences in thermal tolerance across species of salmon and trout (USEPA 2003). Water quality guidelines for British Columbia are life-stage and species-specific, but also lack recognition of population-specific adaptations (BC MOECCS 2021). Given that Chinook salmon are thought to have somewhat higher thermal tolerances than other species of salmon (e.g., BC MOECCS 2021), and that populations of each species vary in their thermal physiology, managing thermal regimes with population-level thresholds may lead to more successful conservation action, particularly for populations at that are already threatened and challenged by climate change (Richter and Kolmes 2005; Zillig et al. 2021). In watersheds where thermal regimes are influenced by dams (e.g., the Columbia River and many others across the southern half of the range of Chinook) these thresholds should be considered in the management of dam operations. However, many watersheds across the range of Chinook are largely unregulated, and thus their flow and thermal regimes integrate multiple landscape-level processes. Conservation action that focuses on regulating upstream activities (e.g., forestry, agriculture, and water withdrawals) and reducing stressors to migrating fish (e.g., fishing) is critical (Poole and Berman 2001; Farrell et al. 2008). Furthermore, rather than using hard thresholds to trigger management actions, an alternative could be implementing watershed-specific criteria to maintain the spatio-

temporal complexity of natural thermal regimes (Poole et al. 2004; Richter and Kolmes 2005). This approach could help ensure that the historic water temperatures that Pacific salmon have adapted to are maintained for the future of the species.

2.2.3. Potential consequences of phenological adaptations on food webs and fisheries

Although Pacific salmon are resilient and may adapt their phenologies in response to climate change, shifts in migration timing may have downstream consequences on food webs and fisheries. Many organisms rely on adult salmon and may be adapted to the seasonal phenologies of their spawning migrations: in the ocean, resident killer whales follow and forage the coastal distributions of Chinook salmon, and in freshwater, predators and scavengers such as bears and invertebrates consume salmon and thrive off the nutrient pulses their carcasses provide to terrestrial ecosystems (Schindler et al. 2003; Ford and Ellis 2006). However, phenological shifts may alter the temporal availability of salmon as a resource and ecosystem service (Schindler et al. 2010; Kovach et al. 2013). Furthermore, from a fisheries perspective, shifts in the migration timing of abundant populations may lead to overlap with the timing of populations that are of conservation concern, exacerbating the risks inherent to mixed-stock fisheries (Moore et al. 2021). Genetic monitoring of population composition and timing can improve the management and conservation of complex stock aggregates in large watersheds (Parken et al. 2008), and provide insight into how shifts in the temporal availability of salmon might affect the ecosystems and communities they support.

2.2.4. Portfolio effects

As human activities continue to exert pressures on natural systems via climate change, habitat alteration and resource extraction, maintaining population resilience through diversity is paramount. Diversity, either as phenotypic variation in physiological and behavioral traits, or genetic variation, can bolster adaptive capacity and help populations withstand environmental change (Meyers and Bull 2002). However, the persistent directional selection exerted by climate change may reduce diversity and thus compromise a population's future adaptive capacity and resilience (Reed et al. 2011; Bellard et al. 2014). Furthermore, response diversity, or the diversity of different responses to environmental change among populations, can increase stability and

resilience across population aggregates or species (Braun et al. 2016). Maintaining this complexity of responses to environmental disturbance can help ensure the long-term sustainability and productivity of salmon watersheds that support fisheries (Hilborn et al. 2003; Cline et al. 2017). The remarkable life-history diversity of Chinook salmon described in this thesis, combined with evidence for population-specific adaptation in thermal performance, suggests the potential for high response diversity in the face of climate change. Future research on the extent to which different populations have already shifted their migration timings in response to ongoing climate change can help shed light on the diversity in potential responses across the species.

2.3. General conclusions

Throughout their long evolutionary histories, Pacific salmon species have survived and adapted to environmental disturbance regimes that have shaped patterns in life-history diversity across their ranges (Waples et al. 2008). Thus, there is no doubt that Pacific salmon are resilient and to a certain extent, have the capacity to persist in the face of anthropogenic pressures. However, climate change has caused warming water temperatures to reach peaks beyond what salmon have experienced in recent history (Farrell et al. 2008; Islam et al. 2019). Although my thesis shows that climate risk varies greatly across regions and life histories, there is an urgent need to address the anthropogenic drivers of warming freshwater temperatures. Conservation action that focuses on habitat restoration and effective management of watershed activities can help alleviate the pressures of climate warming. However, local watershed actions can only go so far in the face of persistent global change. Mitigating the rise in air temperatures by reducing greenhouse gas emissions is crucial to support the health of salmon populations across their range. Ultimately, a holistic approach that considers the myriad stressors acting on Pacific salmon across their life cycle and the environments they rely on, as well as their resilience and ability to adapt, is the key to ensuring the future of this uniquely valuable group of species.

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Appendix A. Supplemental Figures and Tables for Chapter 1

Table A1: List of migration timing data sources used for each watershed

Watershed Region	Source	Number of populations	Range
Central AK	(Savereide 2005)	6	2000-2004
Central AK	(Clark and Brenner 2017)	13	1994-2016
Central Valley	CDFW Hatchery Trap Count Database	5	2000-2017
Central Valley	CDFW reports	21	2006-2015
Central Valley	Tuolumne River TAC/FISHBIO	1	2009-2019
Coastal OR/CA	CDFW Hatchery Trap Count Database	6	2000-2003
Coastal OR/CA	(Flitcroft et al. 2016)	1	1991-2014
Coastal OR/CA	ODFW	1	2012-2018
Columbia	ODFW	4	2001-2018
Columbia	(PTAGIS 2019)	73	1998-2002
Columbia	YKFP	1	2007-2018
Fraser	(Parken et al. 2008)	73	1987-2019
North/Central Coast BC	DFO	3	1990-2016
North/Central Coast BC	(Nisga'a Fisheries and Wildlife 2019)	1	2000-2018
Southeast AK	(Clark and Brenner 2017)	24	1990-1991
Southeast AK	(Huebschwerlen and Boyce 2017; Huebschwerlen and Foos 2018; Foos and Bachynski 2019; Foos and Stark 2020)	1	2016-2019
Westward AK	(Clark and Brenner 2017)	19	1990-2016
YK-Kusk-NS	(Clark and Brenner 2017)	42	1990-2018

Table A2: Migration rates for each watershed and run timing group with sources

River System	Run timing group	Migration rate (km/day)	Source
Columbia River	fall	26.2	(Connor et al. 2019)
Columbia River	fall	26.2	(Goniea et al. 2006)
Columbia River	spring	26.3	(Keefer et al. 2004)
Columbia River	summer	26.3	(Keefer et al. 2004)
Copper River	summer	10.4	(Savereide 2005)
Klamath River	spring	7.4	(Strange 2012)
Klamath River	summer	11.6	(Strange 2012)
Klamath River	fall	6.8	(Strange 2012)
Klamath River	fall	5.0	(Strange 2012)
Kuskokwim River	summer	32.5	(Moses et al. 2019)
Sacramento-San Joaquin River	spring and fall	9.2	Michel 2012 (unpublished report)
Yukon River	summer	58.7	(Eiler et al. 2014)

Table A3: Water temperature data sources and site names

Site name	Latitude	Longitude	Mainstem Site	Watershed Region	Source
Kenai River at Soldotna AK	60.47693	-151.082	Crooked Creek, Kenai River	Central AK	USGS via Leslie Jones (*personal communication*)
32023	38.45597	-121.502	Sacramento River	Central Valley	USGS
31998	37.67639	-121.265	San Joaquin River	Central Valley	USGS
14321000	43.58595	-123.555	North Umpqua River	Coastal California and Oregon	USGS via NorWest
14372300	42.57844	-124.058	Rogue River	Coastal California and Oregon	USGS via NorWest
11464000	38.61324	-122.836	Russian River	Coastal California and Oregon	USGS via NorWest
14246900	46.18122	-123.183	Columbia River	Columbia	USGS via NorWest
Fraser_63	49.53852	-121.429	Fraser River	Fraser	DFO eWatch
Unalakleet River above Chiroskey River near Unalakleet AK	63.9343	-160.307	Inglutalik River	YK-Kusk-NS	USGS via Leslie Jones (*personal communication*)

Table A4: Watershed and migratory corridor characteristics used as covariates for migration timing

Characteristic	Metric	Data Source	Hypothesis	Source for hypothesis
Landscape-level characteristics linked to thermal regime				
Elevation of spawning grounds	Elevation (m) of spawning tributary at the mouth	DEM	Higher elevation spawning grounds → cooler temperatures at spawning grounds → earlier entrance	(Quinn et al. 2016)
Latitude	Latitude of spawning tributary	Georeferenced coordinates of tributary mouth	Higher latitude of spawning grounds → cooler temperatures at spawning grounds → earlier entrance	(Quinn et al. 2016)
Snowmelt/Rain-dominated system	Latitude x Elevation metric	DEM; Georeferenced coordinates of tributary mouth	Proxy for climatic/hydrological regime: eg. snowmelt dominated → cooler temperatures at spawning grounds → earlier entrance	(Beechie et al. 2006)
Characteristics of the migratory corridor				
Migration distance	Distance from the mouth of spawning tributary to the mouth of the mainstem	Distance calculated from river network data	Longer migration distance → earlier entrance	(Quinn et al. 2016)
Slope	Elevation change from mainstem mouth to tributary mouth	DEM	Higher slope → more challenging migration → earlier entrance	(Eliason et al. 2011)
Difficulty of migration	Work = distance x elevation	DEM; distance calculated from river network data	More challenging migration → earlier entrance	(Eliason et al. 2011; Quinn et al. 2016)

Table A5: **Parameter estimates for the second-order polynomial logistic regression model for the probability of migration as a function of mean weekly temperature and a watershed-level fixed effect**

Parameter	Estimate	Standard Error	p-value
temperature	0.92	± 0.13	<0.001
temperature^2	-0.03	± 0.004	<0.001
watershed: Central AK	-6.68	±0.94	<0.001
watershed: Central Valley	-6.74	± 0.94	<0.001
watershed: Coastal OR/CA	-7.44	±0.93	<0.001
watershed: Columbia	-4.16	±0.83	<0.001
watershed: Fraser	-3.48	±0.65	<0.001
watershed: YK-Kusk-NS	-5.80	±0.89	<0.001

**Table A6: Thermal exposure metrics (in ºC) broken down by run timing group**

Run	1990s mean	2040s mean	Climate change difference in mean	1990s extreme	2040s extreme	Climate change difference in extreme
Spring	12.9	13.7	0.8	16.1	16.9	0.9
Summer	15.3	16.1	0.7	17.8	18.8	1.0
Fall	18.7	19.2	0.5	20.8	21.5	0.7
Late-Fall	11.5	12.9	1.4	15.1	16.3	1.2

Table A7: Thermal exposure metrics (in ºC) broken down by watershed region

Watershed Region	1990s mean	2040s mean	Climate change difference in mean	1990s extreme	2040s extreme	Climate change difference in extreme
YK-Kusk-NS	10.6	10.4	-0.1	12.0	12.4	0.4
Central AK	11.3	10.8	-0.5	12.7	12.5	-0.1
Fraser	14.4	15.5	1.1	17.4	18.7	1.3
Columbia	14.7	15.0	0.4	17.4	17.8	0.4
Coastal OR/CA	14.7	15.6	0.8	19.1	20.0	1.0
Central Valley	15.4	16.3	0.9	18.1	19.2	1.1

Table A8: Thermal exposure metrics (in ºC) broken down by watershed region and run timing group

Watershed Region	Run	1990s mean	2040s mean	1990s extreme	2040s extreme	Climate change difference in mean	Climate change difference in extreme
Central AK	Summer	11.3	10.8	12.7	12.5	-0.5	-0.1
Central Valley	Late Fall	11.5	12.9	15.1	16.3	1.4	1.2
Central Valley	Spring	12.8	14.1	15.3	16.9	1.3	1.5
Central Valley	Fall	18.4	19	20.9	21.7	0.5	0.8
Coastal OR/CA	Fall	14.2	14.8	17.2	17.9	0.6	0.6
Coastal OR/CA	Spring	16.4	17.9	24.5	26.4	1.5	1.9
Columbia	Spring	12	12.4	15.1	15.4	0.4	0.3
Columbia	Summer	15.9	16.2	18.8	19.4	0.3	0.6
Columbia	Fall	19.9	20.3	21.6	22.2	0.4	0.6
Fraser	Fall	12.8	13.7	15.9	16.9	0.9	1.1
Fraser	Spring	13.6	14.7	16.8	18.1	1.1	1.2
Fraser	Summer	16.1	17.4	18.6	20	1.3	1.4
YK-Kusk-NS	Summer	10.6	10.4	12	12.4	-0.1	0.4
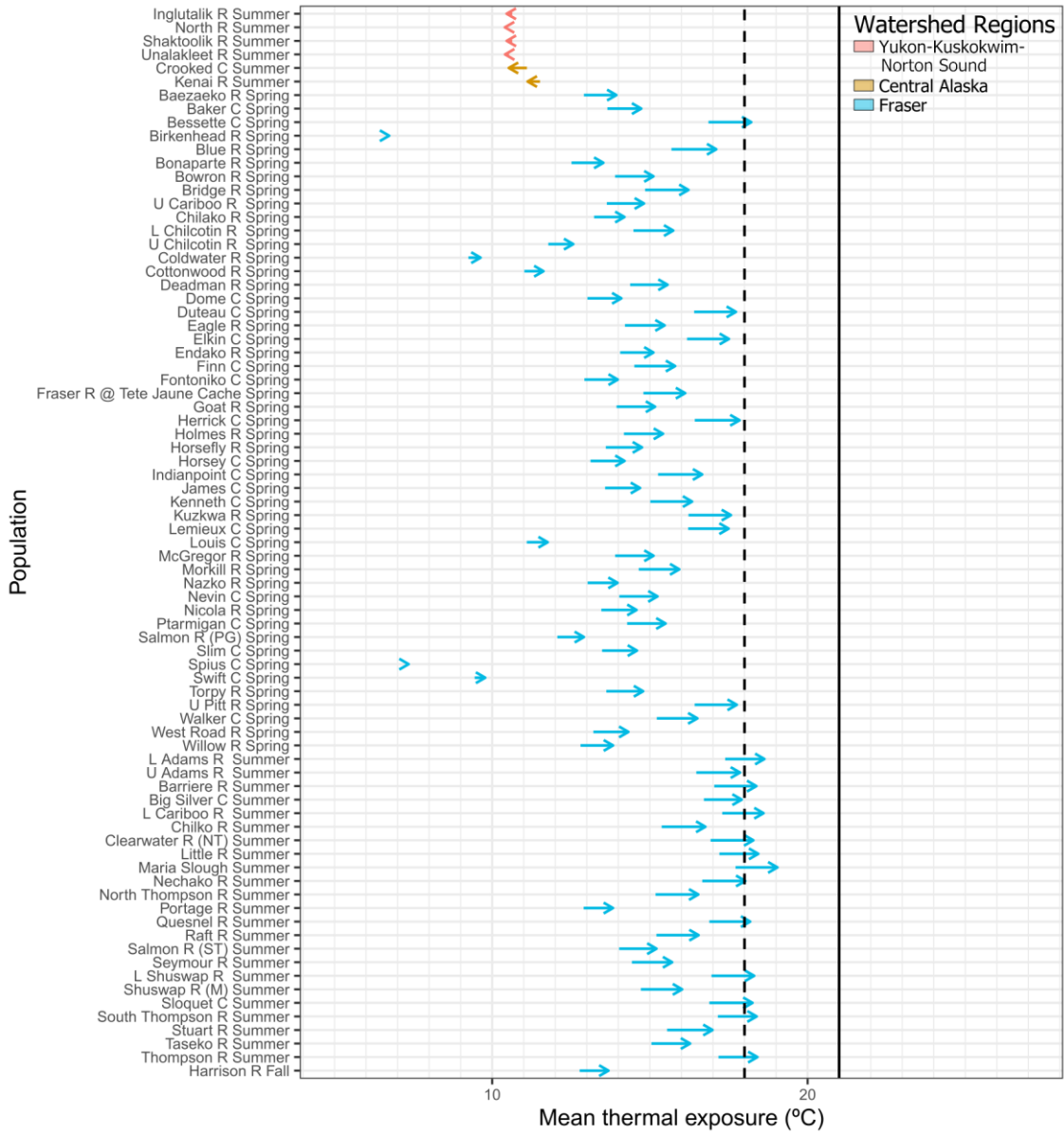
Figure A1: **Vectors of shift in mean thermal exposure from 1990s to 2040s for populations spanning the Yukon-Kuskokwim-Norton Sound, Central Alaska, and Fraser River watershed regions**
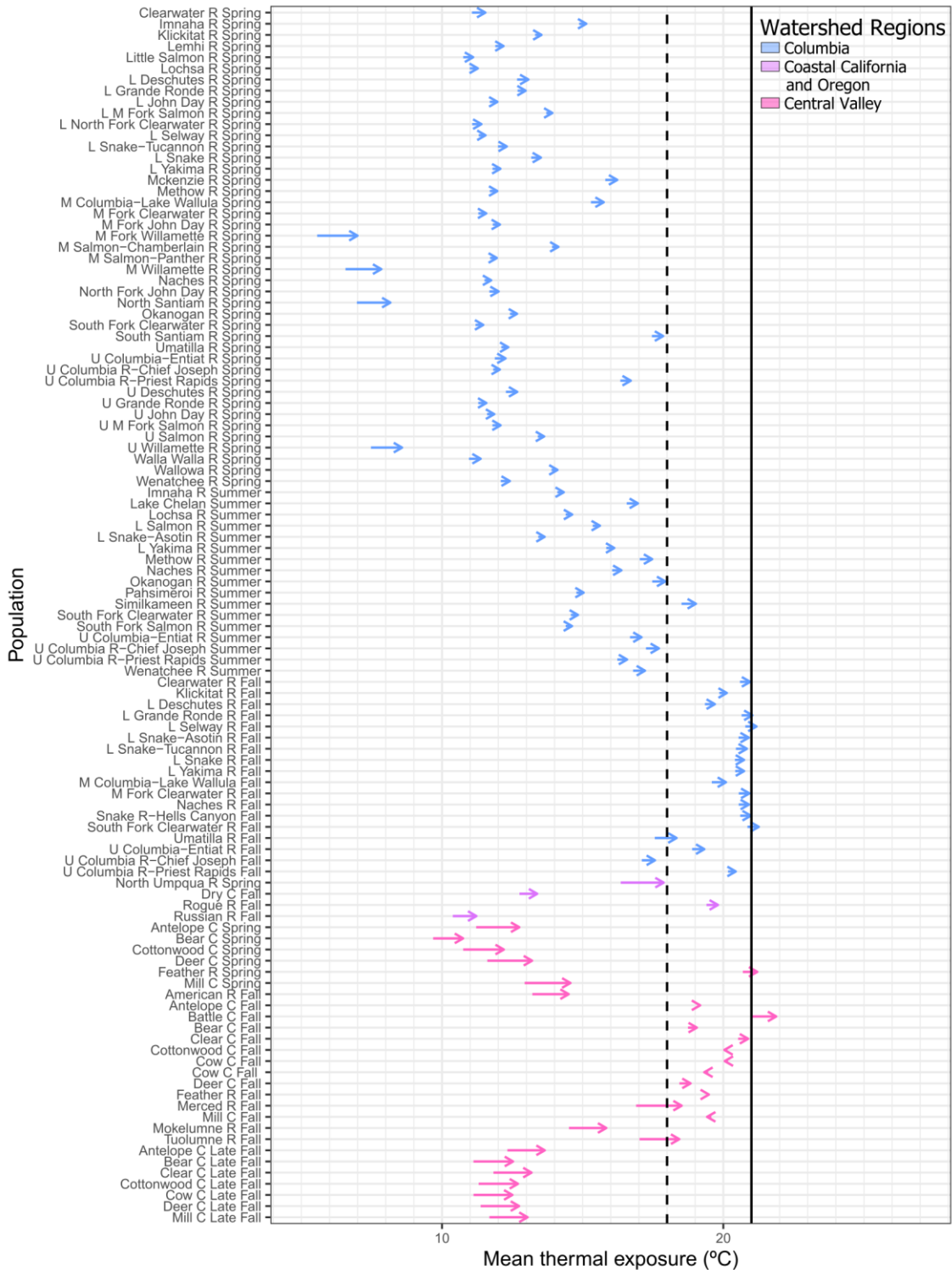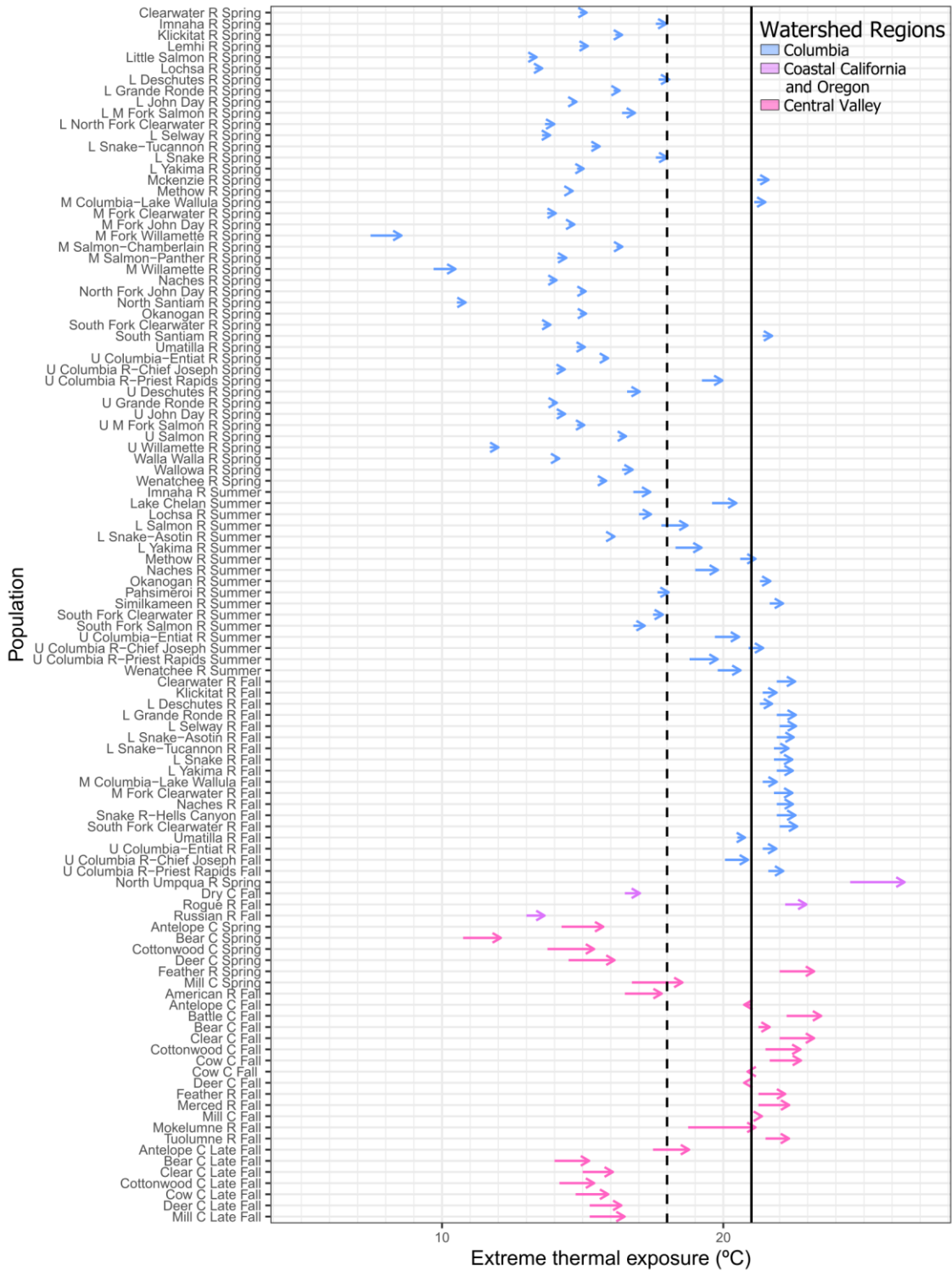
Figure A2: **Vectors of shift in mean thermal exposure from 1990s to 2040s for populations spanning the Columbia, Coastal Oregon and California, and Central Valley watershed regions**
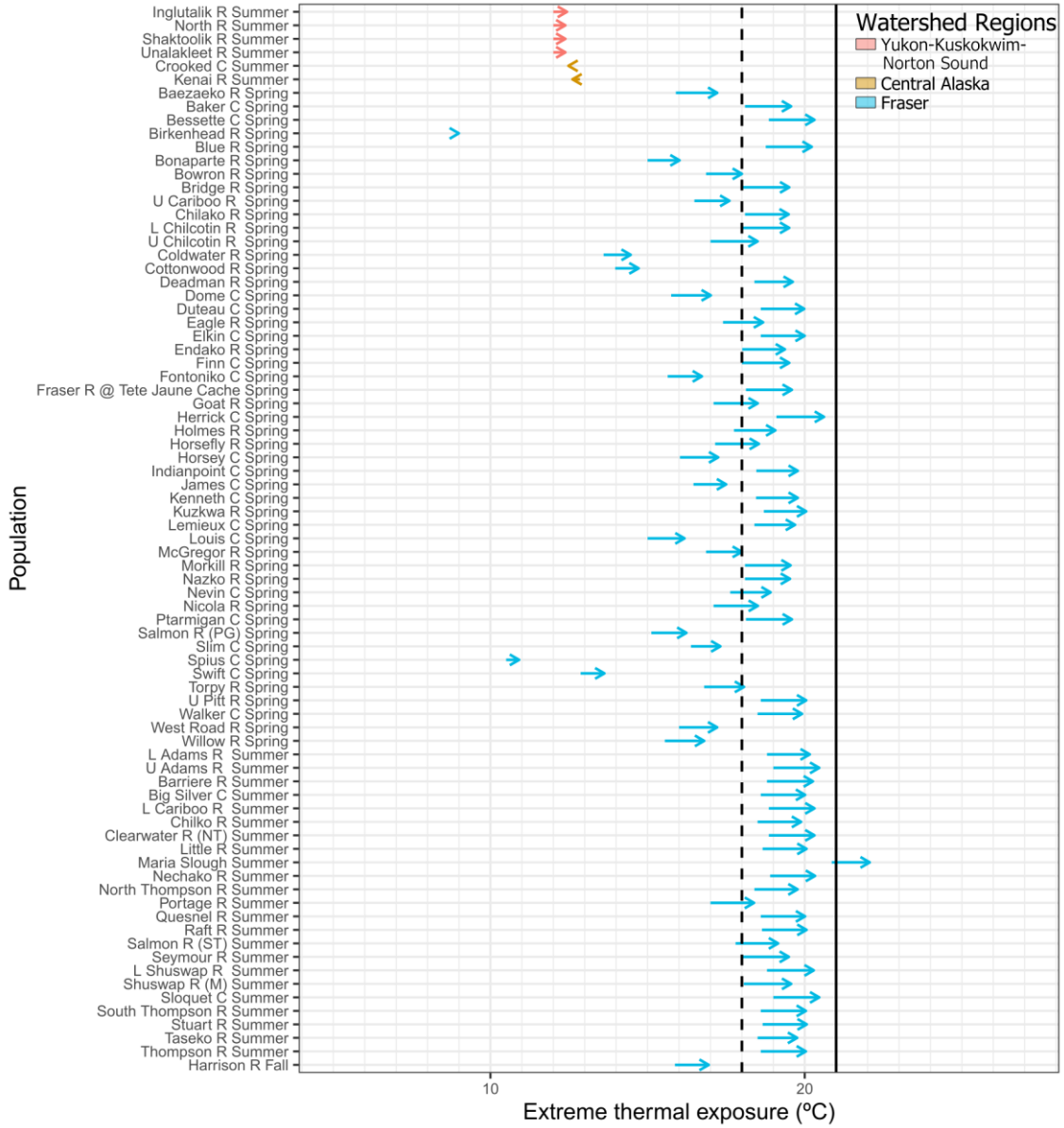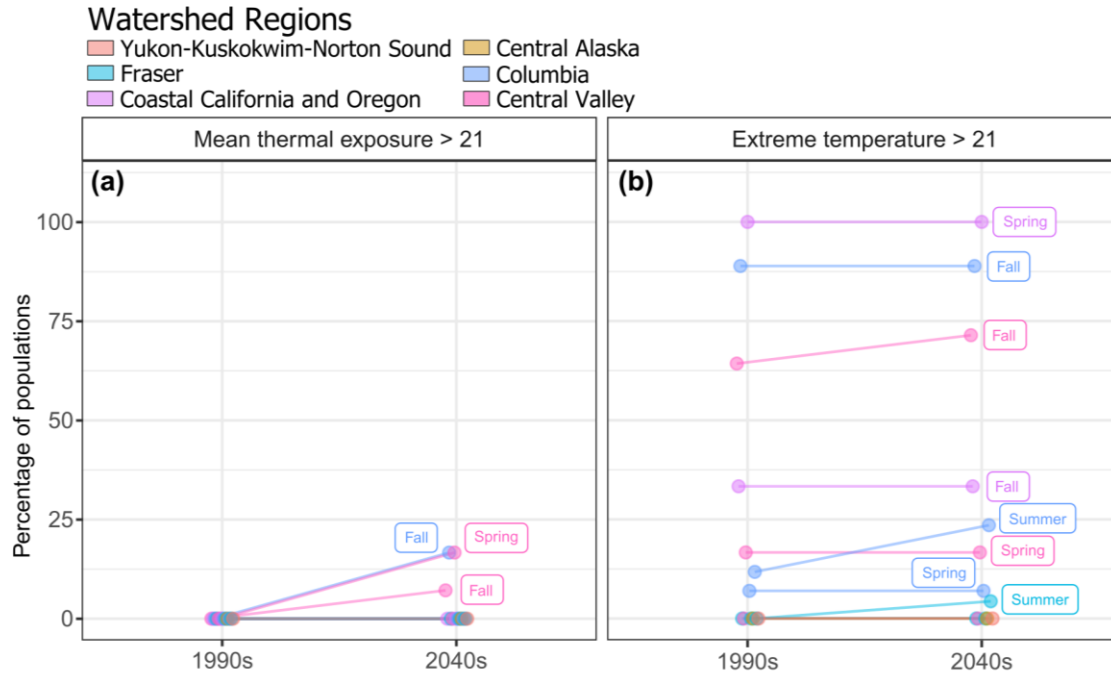
Figure A3: Vectors of shift in extreme thermal exposure from 1990s to 2040s for populations spanning the Yukon-Kuskokwim-Norton Sound, Central AK, and Fraser River watershed regions
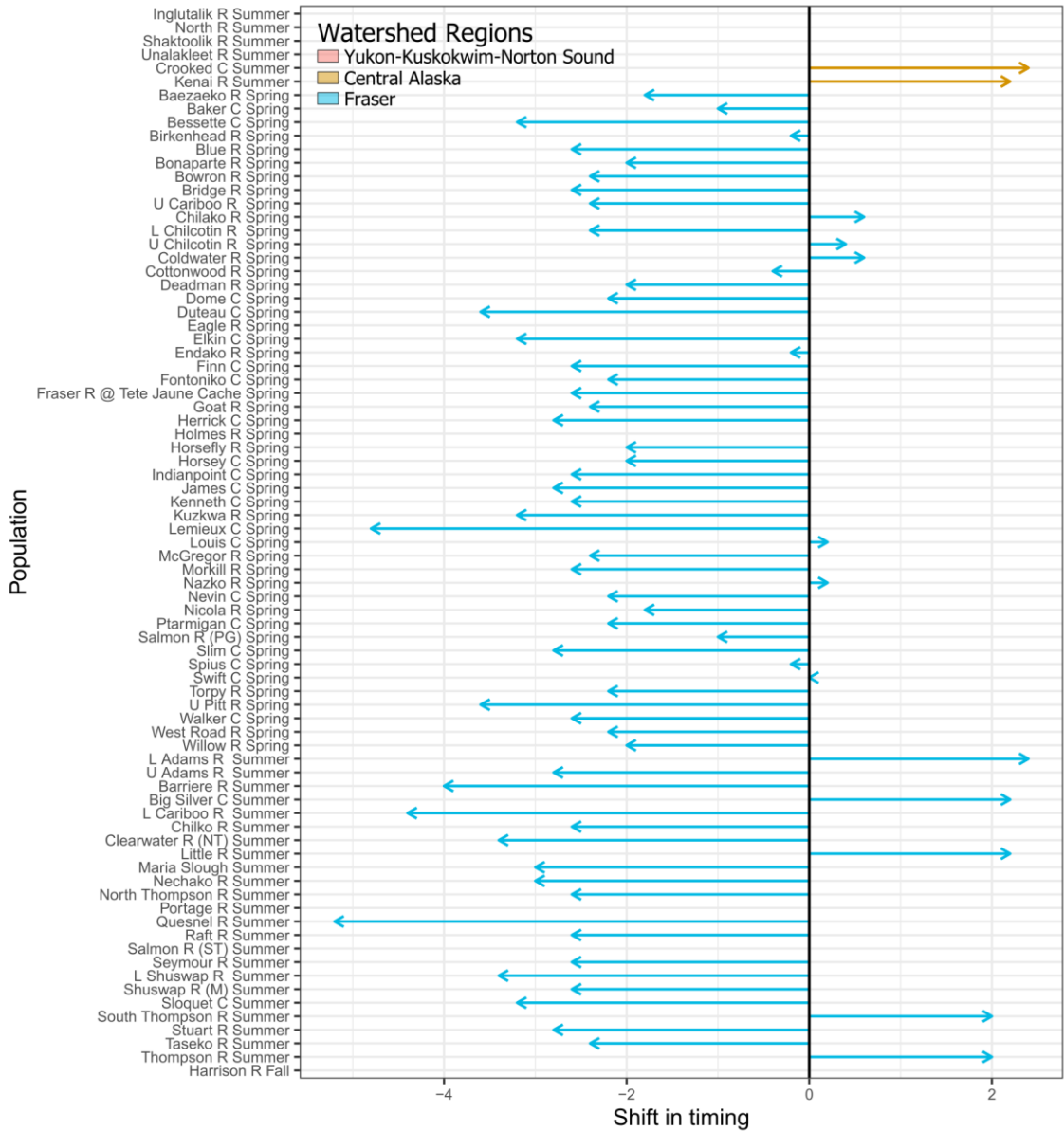
Figure A4: Vectors of shift in extreme thermal exposure from 1990s to 2040s for populations spanning the Columbia, Coastal Oregon and California, and Central Valley watershed regions

Figure A5: Percentage of populations experiencing thermal stress above a threshold of 21°C, aggregated by run timing group and watershed. Colors represent different watershed regions and for visual simplicity, labels are only appended to run timing groups that increase in percentage. Panel a) shows populations with mean thermal exposure above 21°C; panel b) shows populations with extreme thermal exposure above 21°C
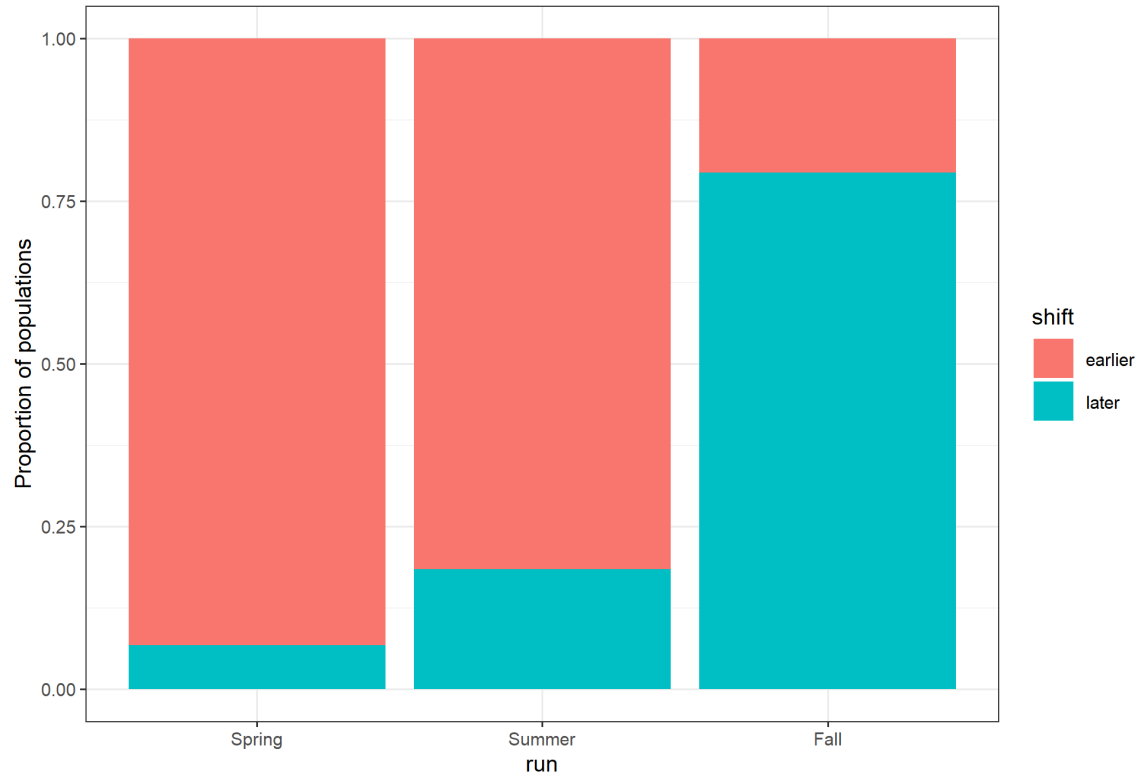
Figure A6: Magnitude (in days/decade) and direction of potential shifts in migration timing for each population spanning the Yukon-Kuskokwim-Norton Sound, Central AK, and Fraser River watershed regions

Figure A7: Magnitude (in days/decade) and direction of potential shifts in migration timing for each population spanning the Columbia, Coastal Oregon and California, and Central Valley watershed regions
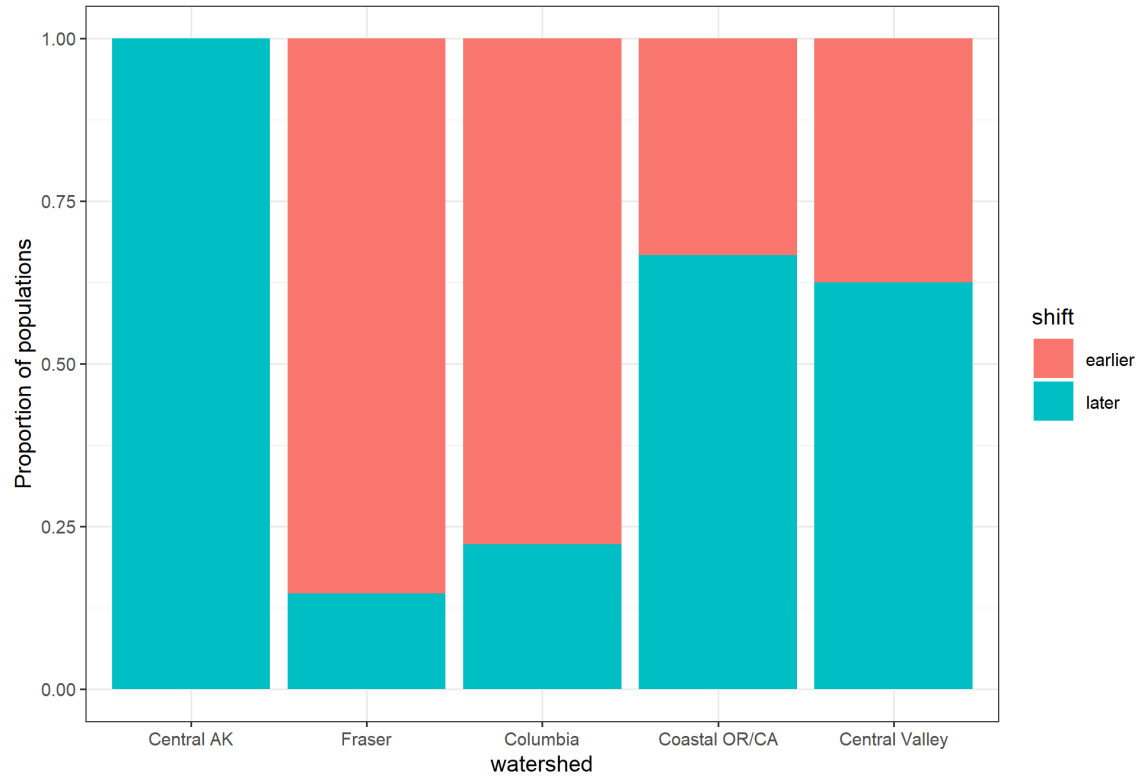
Figure A8: **Proportion of populations in each watershed that would need to shift their timing either earlier or later to adapt to a changing climate**

Figure A9: **Proportion of populations within in each run timing group that would need to shift their timing either earlier or later to adapt to a changing climate.**

Table A9: **Magnitude (in days/decade), standard deviation, and direction of shifts in migration timing broken down by watershed region and run timing group. NA values for the mean indicate that no populations were in a given group and NA values for the standard deviation indicate that only one population was in a given group.**

Watershed Region	Run	Mean difference in timing (days/decade) ± standard deviation of the mean difference	
		Earlier	Later
Central AK	Summer	NA	2.3 ± 0.1
Fraser	Spring	-2.2 ± 1.0	0.4 ± 0.2
Fraser	Summer	-3.2 ± 0.8	2.2 ± 0.2
Columbia	Spring	-0.9 ± 0.3	NA
Columbia	Summer	-0.8 ± 0.2	NA
Columbia	Fall	-1.5 ± 0.7	1.0 ± 0.7
Coastal OR/CA	Spring	-2.5 ± NA	NA
Coastal OR/CA	Fall	NA	0.8 ± 0.0
Central Valley	Spring	-4.7 ± NA	1.1 ± NA
Central Valley	Fall	-0.6 ± 0.5	1.3 ± 0.7

Table A10: **Magnitude (in days/decade), standard deviation and direction of shifts in migration timing broken down by watershed region. NA values for the mean indicate that no populations were in a given group and NA values for the standard deviation indicate that only one population was in a given group.**

Watershed Region	Mean difference in timing (days/decade) ± standard deviation of the mean difference	
	Earlier	Later
Central AK	NA	2.3 ± 0.1
Fraser	-2.5 ± 1.0	1.3 ± 0.9
Columbia	-0.9 ± 0.3	1.0 ± 0.7
Coastal OR/CA	-2.5 ± NA	0.8 ± 0.0
Central Valley	-1.3 ± 1.7	1.3 ± 0.6

Table A11:   **Magnitude (in days/decade), standard deviation and direction of shifts in migration timing broken down by run timing group.**

Run	Mean difference in timing (days/decade) ± standard deviation of the mean difference	
	Earlier	Later
Fall	-0.9 ± 0.7	1.1 ± 0.7
Spring	-1.6 ± 1.0	0.5 ± 0.3
Summer	-2.0 ± 1.3	2.2 ± 0.2