Temporal patterns in adult salmon migration timing across southeast Alaska

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Abstract

Pacific salmon migration timing can drive population productivity, ecosystem dynamics, and human harvest. Nevertheless, little is known about long-term variation in salmon migration timing for multiple species across broad regions. We used long-term data for five Pacific salmon species throughout rapidly warming southeast Alaska to describe long-term changes in salmon migration timing, interannual phenological synchrony, relationships between climatic variation and migratory timing, and to test whether long-term changes in migration timing are related to glaciation in headwater streams. Temporal changes in the median date of salmon migration timing varied widely across species. Most sockeye populations are migrating later over time (11 of 14), but pink, chum, and especially coho populations are migrating earlier than they did historically (16 of 19 combined). Temporal trends in duration and interannual variation in migration timing were highly variable across species and populations. The greatest temporal shifts in the median date of migration timing were correlated with decreases in the duration of migration timing, suggestive of a loss of phenotypic variation due to natural selection. Pairwise interannual correlations in migration timing varied widely but were generally positive, providing evidence for weak region-wide phenological synchrony. This synchrony is likely a function of climatic variation, as interannual variation in migration timing was related to climatic phenomenon operating at large- (Pacific decadal oscillation), moderate- (sea surface temperature), and local-scales (precipitation). Surprisingly, the presence or the absence of glaciers within a watershed was unrelated to long-term shifts in phenology. Overall, there was extensive heterogeneity in long-term patterns of migration timing throughout this climatically and geographically complex region, highlighting that future climatic change will likely have widely divergent impacts on salmon migration timing. Although salmon phenological diversity will complicate future predictions of migration timing, this variation likely acts as a major contributor to population and ecosystem resiliency in southeast Alaska.

Keywords: climate change, heterogeneity, migration timing, phenology, phenotypic variation, salmon, synchrony, temperature

Received 19 November 2014; revised version received 19 November 2014 and accepted 26 November 2014

Introduction

Pacific salmon (*Oncorhynchus* sp.) are critical components of ecosystems throughout coastal areas of the northern Pacific Ocean (Willson & Halupka, 1995; Gende *et al.*, 2002; Hocking & Reynolds, 2011), and the timing of their migration into freshwater directly influences numerous consumers (e.g. Ben-David, 1997; Schindler *et al.*, 2013) and the phenology of other organisms (Moore & Schindler, 2010; Lisi & Schindler, 2011). While climate-induced phenological changes are well-described for many organisms (Parmesan, 2006), our understanding of phenological trends in fish, including salmon, is limited (Parmesan, 2007; Thackeray *et al.*, 2010). This is surprising given that changes in Pacific salmon migration timing could have ecosystem level consequences (e.g. impact consumer phenol-ogy, resource use, and even food web dynamics) (Gende *et al.*, 2002; Moore & Schindler, 2010; Lisi & Schindler, 2011; Schindler *et al.*, 2013), alter the availability of salmon for commercial harvest (Schindler *et al.*, 2010), and influence Pacific salmon population dynamics and evolutionary trajectories (e.g. Martins *et al.*, 2010; Crozier *et al.*, 2011; Hinch *et al.*, 2012; Kovach *et al.*, 2012).

The timing of adult salmon migration into freshwater for reproduction is a critically important life-history trait that often differs among populations because of strong local adaptation to heterogeneous environmental conditions, including climatic variation (Taylor, 1991; Quinn & Adams, 1996; Eliason *et al.*, 2011; Lisi *et al.*, 2013). Variation in freshwater and oceanic conditions (e.g. temperature and stream discharge) can affect salmon migration timing by altering environmental cues and selection for certain migratory phenotypes (e.g. Quinn & Adams, 1996; Hodgson *et al.*, 2006; Mundy &

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Evenson, 2011; Kovach *et al.*, 2013). Thus, directional climatic change can lead to temporal changes in salmon migration timing (Crozier *et al.*, 2008; Kovach *et al.*, 2013; Otero *et al.*, 2014). Recent evidence suggests that environmental changes have led to multiple adult salmon populations migrating earlier than they did historically (Quinn & Adams, 1996; Cooke *et al.*, 2004; Taylor, 2008; Kovach *et al.*, 2013), but there are no region-wide assessments of changes in migration timing across multiple Pacific salmon species. There is a clear need to measure temporal trends in median dates of migration timing (here forward = MDMT) at larger spatial scales including multiple species to determine whether salmon are demonstrating consistent phenological shifts (indicative of a response to region-wide environmental changes such as climatic warming) or highlight important interpopulation and interspecies variation suggestive of differential responses to climatic or environmental variation.

Additionally, research on long-term changes in phenological variation within salmon populations or other organisms is notably lacking (Diez *et al.*, 2012). Changes in phenological variation within populations can occur via shifts in phenotypic variation such as the duration of migratory events (here forward = DMT) (Kovach *et al.*, 2013), or due to changes in between-year variation in average migration timing (i.e. process variation; here forward = PVMT) (see Fig. 1). Rapid decreases in phenotypic variation can be indicative of natural selection (Brodie *et al.*, 1995; Olsen *et al.*, 2009; Carlson *et al.*, 2011), and such shifts were consistently observed in Pacific salmon at one location (Kovach *et al.*, 2013). Indeed, salmon migration timing has a strong genetic basis, (Carlson & Seamons, 2008) raising the possibility that it can rapidly respond to natural selection. If this were the case (i.e. direction selection was influencing salmon migration timing), we would expect decreases in phenotypic variation in populations demonstrating the strongest directional changes in migratory timing. Ultimately, migratory duration can also be thought of

as evolutionary potential, and therefore, reduced duration can be an indicator of reduced resiliency within populations (Sgrò *et al.*, 2011), with important implications for species that depend on the temporal availability of salmon resources (Schindler *et al.*, 2013).

On the other hand, interannual process variation – a component of phenology that has been largely overlooked – is indicative of environmentally induced variation in migratory behavior between years. Increases in PVMT can signal increased environmental stochasticity and, therefore, population or ecosystem vulnerability (Seekell *et al.*, 2011; Dakos *et al.*, 2012). Increases in PVMT can also be problematic for salmon consumers because increased interannual variance makes predicting the temporal distribution of salmon resources more difficult (Mundy & Evenson, 2011). Thus, changes in PVMT may have important implications for salmon populations and ecosystem dynamics.

The consistency with which salmon and other organisms respond – via shifts in phenology – to climatic warming depends on whether populations respond synchronously to interannual climatic variation. Our current understanding of how climatic variation influences salmon ecology (e.g. phenology and demography), and therefore synchrony, is unclear and sometimes contradictory. For example, some researchers have argued that there is strong regional synchrony in population recruitment (Peterman *et al.*, 1998; Mueter *et al.*, 2002b), while other research has shown that adjacent populations and metapopulations demonstrate widely varying responses to climatic variation (Hilborn *et al.*, 2003; Rogers & Schindler, 2011). While oceanic and freshwater conditions are frequently invoked as important drivers of adult salmon phenology (Hodgson *et al.*, 2006; Mundy & Evenson, 2011; Crozier *et al.*, 2011; Kovach *et al.*, 2013), it is unknown whether sources of climatic variation have similar impacts on phenology for different populations and species. Given this uncertainty, there is an urgent need to describe phenological synchrony among salmon populations
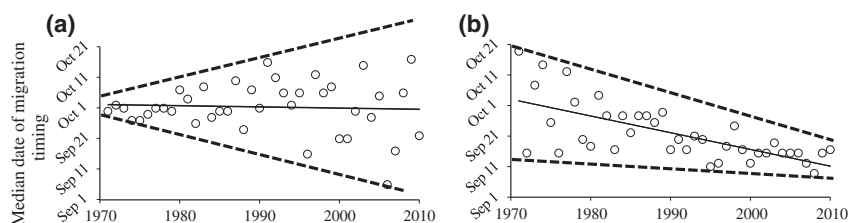
Fig. 1 Examples of possible temporal changes in the median date and interannual variation in migration timing. In panel (a) the median date of migration timing (MDMT) has been stable (black trend line) from 1970 to 2010, but interannual process variance (PVMT) has increased (as depicted by the distance between the two dashed lines); migratory events occur at the same time on average but are more variable from year to year. Panel (b) depicts a temporal shift toward earlier migration timing (MDMT) and a decrease in interannual process variation (PVMT); migratory events are occurring earlier and are less variable from year to year.

and directly test whether relationships between migration timing and important sources of oceanic and freshwater variability vary across populations and species.

Physical environmental heterogeneity may also influence relationships between phenology and climate by buffering certain populations from dynamic conditions. In southeast Alaska, glaciers act as a dramatic source of environmental variation that influences numerous aquatic and terrestrial dynamics (e.g. Milner *et al.*, 2000). Although increasing temperatures are predicted (Bryant, 2009; Wolken *et al.*, 2011) and have been observed (e.g. Kovach *et al.*, 2013) for streams throughout southeast Alaska, glacially influenced streams can show very different patterns because glacial runoff stabilizes stream temperatures (Hood & Berner, 2009; Fellman *et al.*, 2014). As a result, long-term changes in migration timing of salmon populations spawning in glacially influenced streams may differ from salmon populations in nonglaciated streams that are subject to directional temperature changes occurring throughout the region.

We used monitoring data throughout southeast Alaska, USA – a rapidly warming region (Stafford *et al.*, 2000) that is undergoing major biotic and abiotic changes as a result of climate change (Wolken *et al.*, 2011) – to characterize long-term patterns in migration timing for five Pacific salmon species (sockeye – *Oncorhynchus nerka*; coho – *O. kisutch*; Chinook – *O. tshawytscha*; chum – *O. keta*; and pink – *O. gorbuscha*). Specifically, we addressed four questions: (1) How consistent are temporal changes in MDMT, DMT, and PVMT across salmon populations and species? (2) Is interannual variability in migration timing synchronous within species? (3) How is climatic variation related to migration timing and do relationships vary across populations and species? (4) Are long-term changes in migration timing and interannual variation in migration timing different in glaciated vs. nonglaciated watersheds?

Materials and methods
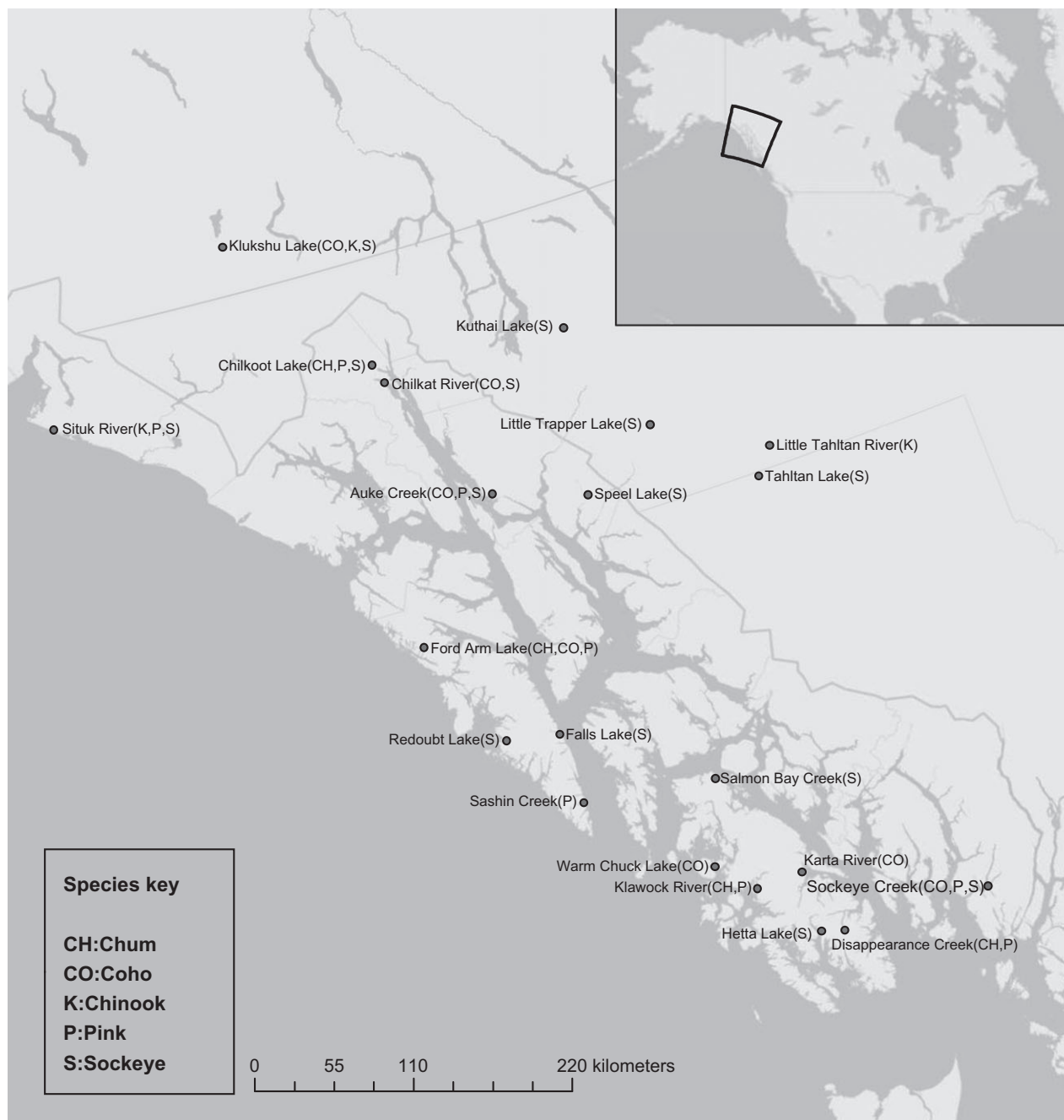
Migration timing data

We used long-term monitoring data from the Alaska Department of Fish and Game (ADFG) and the National Oceanic and Atmospheric Administration (NOAA) to characterize patterns of migration timing for all five species of Pacific salmon occurring throughout southeast Alaska. ADFG and NOAA monitor salmon population abundances using fish weirs to capture and count all, or a substantial portion, of adult salmon as they migrate upstream to spawn. Fish weirs are generally operated continuously throughout the migration period for their primary target species, thereby providing daily counts that can be used to quantify various aspects of migratory behavior (e.g. MDMT, DMT, and PVMT).

Specifically, data were available from 64 populations (i.e. streams or rivers), but the temporal duration and consistency of sampling varied widely across locations and for different species at a location. We filtered our data by removing populations with multimodal migratory distributions, or whose mean annual abundance (or count) was <100 individuals. We also removed data from those specific years where population abundance was <100, or the number of days during which weirs were operated was <20, as both phenomena may be indicative of incomplete sampling. For purposes of describing interannual patterns in migration timing, we only retained data from those salmon populations having a minimum of 10 years of data spanning at least 20 years. We also removed two populations because they were monitored within 5 miles of a hatchery that produced the same species. Nevertheless, distance to hatchery was unrelated to any of our response variables (*data not shown*) suggesting that hatchery operations did not have an appreciable effect on the results presented here. At each location, we combined data from even- and odd-year pink salmon populations because this provided more locations that matched our temporal criteria, and we did not find any substantial differences between broodlines in terms of long-term phenological changes (*data not shown*).

In total, we used data from 7 coho, 14 sockeye, 3 Chinook, 4 chum, and 8 pink salmon populations spanning 21 different freshwater streams (Table S1; Fig. 2). The earliest migrating fish were sockeye in the lower Situk (average median date of migration timing = July 10), while the latest migrating population was coho in Chilkat Lake (average median date of migration timing = October 8). Across all species and populations, the average temporal duration of the time series was 36.1 years (SD = 7.1), while the average number of observations (i.e. years of data) was 27.8 (SD = 9.9).

Data analysis

Temporal trends in migration timing. Linear regressions of year vs. MDMT and DMT were used to measure within population changes in migratory behavior over time. The number of days over which the central 90% of fish migrated past each weir was used for our measurement of DMT. To test the hypothesis that large directional changes in MDMT may be associated with decreases in DMT due to natural selection, we performed a linear regression of the temporal changes in DMT vs. the absolute value of changes in MDMT. A negative trend would be suggestive of a reduction in DMT associated with large shifts in MDMT and thus possible selection. We also used linear regressions to test whether changes in MDMT or DMT were associated with average population abundance or the duration of the time series for each population. Along the same lines, we used a *t*-test to determine whether changes in migration timing were greater for those populations ($n = 15$) that had data before and after the major PDO shift that occurred in the northern Pacific Ocean between 1976 and 1977 (Mantua *et al.*, 1997). That event has been associated with major phenotypic trends in some populations (Crozier & Hutchings, 2014).

Fig. 2 Locations of long-term monitoring sites for Pacific salmon migration timing throughout southeast Alaska. The species monitored at each site are labeled immediately following the name of each location (see legend).

To measure whether PVMT changed over time, we took the residuals from the regressions of MDMT vs. year, and regressed the absolute values of those residuals vs. year. We used de-trended values so that long-term changes in MDMT did not bias results. Some caution should be used in interpreting standard errors around population-specific changes in interannual process variance, as heteroscedasticity was necessarily present in the greatest shifts, but the estimates themselves should be unbiased. We used *t*-tests to determine whether mean changes in migration timing (MDMT, DMT, and PVMT) within each species and across all species were different from zero.

Phenological synchrony. We used pairwise Pearson's correlations between median dates of migration timing to measure the degree of synchrony in phenology across adult salmon populations. We calculated correlations between all population pairs within a species that had at least 5 years of

overlapping data. We do not present data for Chinook and chum, as only 3 and 6 pairwise combinations (respectively) met these criteria. We used t-tests to test whether average correlations for each species were different than zero. Mantel tests, calculated in Program R (R Development Core Team, 2012) package 'vegan' (Oksanen et al., 2012), were used to test whether there was a spatial effect of synchrony between populations within a species. Correlations in the abundances of Pacific salmon populations throughout the northern Pacific, and within southeast Alaska, generally decline as distance increases between populations (e.g. Pyper et al., 2001; Mueter et al., 2002a), suggesting a similar pattern may be present for other ecological dynamics including migration timing. Linear pairwise distances between stream mouths were estimated using ARCMAP 10.0 (ESRI, Redlands, CA, USA).

Impacts of climatic and habitat variation on migration timing. We used linear-mixed effect models to test for relationships between interannual variation in migration timing and climatic variables that have been shown to be correlated with MDMT in several Pacific salmon populations (Hodgson et al., 2006; Keefer et al., 2008; Crozier et al., 2011; Mundy & Evenson, 2011; Kovach et al., 2013). Specifically, we tested whether interannual variation in MDMT across populations was related to climatic conditions operating at large- (Pacific decadal oscillation – PDO), moderate- (sea surface temperatures near stream of origin – SST), and local-scales (precipitation and air temperature within stream drainages). Furthermore, we tested whether relationships were consistent or variable across populations.

For each species, we averaged monthly PDO values (Mantua et al., 1997; http://jisao.washington.edu/pdo/PDO.latest) from the 6 months preceding migration into freshwater (sockeye/Chinook: February–July; pink/chum: March–August; coho: April–September). Similarly, we used 3-month average SST values from areas used by each population in their final migration toward freshwater. SST values were obtained from the International Comprehensive Ocean-Atmosphere Data Set. Average monthly values for locations in the northern portion of our study were obtained from a grid located at 60°N–57°N and 142°W–133°W, while values for populations in the south came from a grid located at 58°N–55°N and 138°W–131°W.

Unfortunately, empirical stream temperature and flow data were not available for many of the streams included in this study. As such, we used downscaled (2 km spatial resolution) monthly air temperature (Temp) and precipitation (Precip) predictions (http://www.snap.uaf.edu) based on observed historical data and the PRISM climate model (Daly et al., 2002). We averaged monthly predictions for each 2 km grid cell within the watershed where salmon were counted. For each population, we used the Temp and Precip values from the same month as the average (across all years) median date of migration timing, but for those populations whose average median date was within the first 5 days of a month, we used the values from the preceding month (i.e. the month during which approximately half of the fish migrated). Temp and Precip data at finer temporal scales (e.g. daily) were unavailable for our study area. Additionally, the Temp and Precip

data were only available up until 2009. As such, we did not use any data post-2009 for linear-mixed modeling.

Precip and Temp are moderately to highly correlated with stream temperature and flow throughout southeast Alaska, especially for streams with little glacial influence (e.g. Kovach et al., 2013; Fellman et al., 2014; Shanley & Albert, 2014). However, because the air temperature data are derived from predictions, and the air-stream temperature relationship varies across space (Arismendi et al., 2014), there is uncertainty in the local climatic data used in our analyses. For all climatic variables, we extracted a complete time series spanning 1960–2009. We then standardized the time series by subtracting the mean and dividing by the standard deviation and subsequently extracted yearly values that corresponded with each population time series.

A step-down model selection approach (Zuur et al., 2009) and AIC (Burnham & Anderson, 2002) were used to identify an optimal model(s) that predicted interannual variation in migration timing as a function of climatic variation. We first fit a linear model that contained the additive effects of all predictor variables (we did not test for any interactions) and then fit models with increasingly complex random effect structures. After identifying the optimal random effect structure, we removed poorly supported predictor variables (i.e. fixed factors – PDO, SST, Temp, and Precip). We used various random effect structures to directly test whether different populations had consistent or heterogeneous responses to interannual climatic variation. We first fit a model with a random intercept for population of origin nested within species. Within this hierarchical structure, we then tested for a random slope effect for each predictor variable. Support for a random slope effect provides evidence for heterogeneous relationships between interannual climatic variation and migration timing across populations and species. Alternatively, support for a random intercept (i.e. population nested within species) in combination with only fixed effects (no random slopes) suggests that populations consistently respond to sources of climatic variation. After identifying the optimal random structure, we iteratively removed the least-supported fixed effects until all remaining fixed effects were supported by the data. Specifically, we eliminated predictor variables that did not reduce AIC by at least 2.0 relative to a less parameterized model (Arnold, 2010). Restricted maximum likelihood was used for all model selection comparisons, while maximum likelihood estimation was used for final parameter estimates (Zuur et al., 2009). We used package 'nlme' (Pinheiro et al., 2014) in Program R for all linear-mixed modeling.

Finally, we used t-tests to determine whether temporal trends in MDMT for salmon populations in glacially influenced streams ($n = 14$) differed from nonglacial streams. F-tests for equality of variance were used to test whether the variation surrounding long-term changes in phenology differed between glacial and nonglacial streams. Because glacially influenced streams are partially buffered from climatic variation, we predicted that salmon populations in glacially influenced streams would have smaller mean changes in the MDMT and less variation surrounding shifts in MDMT than salmon populations occupying nonglacial streams. The

presence or the absence of glaciers within a watershed was determined from the 2010 Global Land Ice Measurements Space data set (http://nsidc.org/) in GIS.

Results

Temporal trends in migration timing

Temporal changes in the MDMT were variable across species and across populations within species (Fig. 3a).
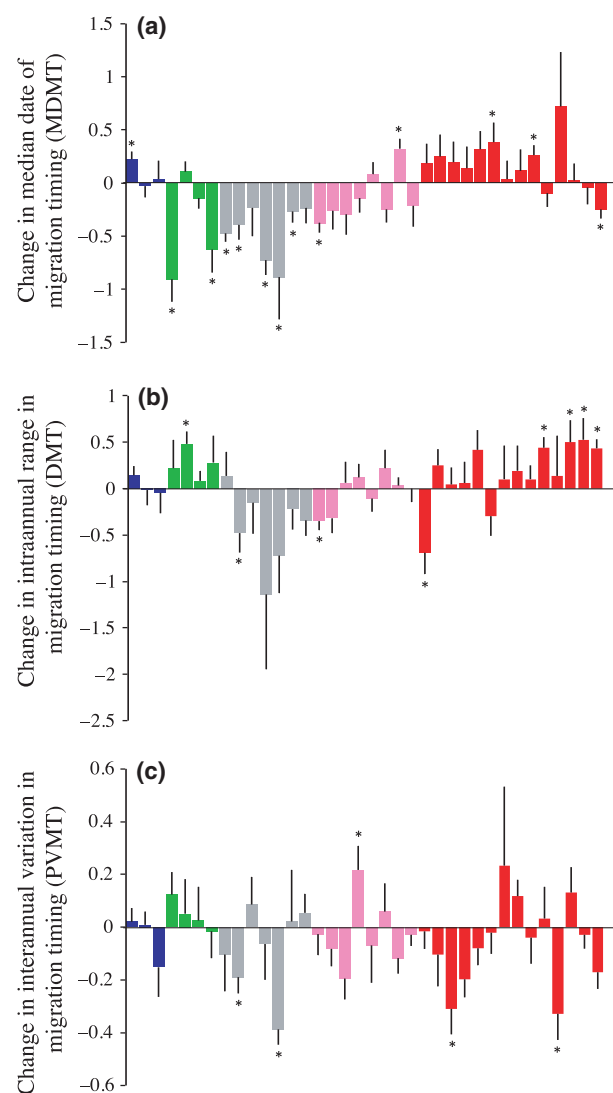
Fig. 3 Changes in salmon phenology across southeast Alaska. Each bar represents a different population, error bars are standard errors, blue = Chinook, green = chum, gray = coho, pink = pink, red = sockeye. Panel (a) is the change in the median dates of migration timing (MDMT), (b) is the change in the intra-annual range (i.e. variation) in migration timing over time (DMT), and (c) is the change in interannual process variation in the median date of migration timing (PVMT). Significant estimates ($\alpha = 0.05$) are noted with an * symbol.

For sockeye and Chinook, the majority of populations (11 of 14 and 2 of 3, respectively) are migrating into freshwater later than they did historically. Alternatively, most populations of coho (7 of 7), pink (6 of 8), and chum (3 of 4) are migrating into freshwater earlier. Thus, average changes in the MDMT across populations within species were positive for Chinook and sockeye, and negative for chum, coho, and pink salmon (Table 1). The average changes in migration timing for sockeye (0.16 days later per year) and coho (0.46 days earlier per year) were statistically significant ($P = 0.024$ and $P = 0.003$). Of the 12 statistically significant ($P < 0.05$) temporal trends in the MDMT, 8 were toward earlier migration timing, and the greatest temporal changes ($b_1 = -0.73 \sim -0.91$) were all toward earlier migration timing.

Similarly, temporal shifts in the DMT varied widely across populations and species (Fig. 3b). Migration events occurred over increasingly longer periods of time in most populations of chum (4 of 4), and sockeye salmon (12 of 14), but the majority of coho and Chinook salmon populations (6 of 7 and 2 of 3, respectively) are migrating over a shorter period of time than they did historically. Average changes in the DMT within species mirrored these patterns (Table 1), and the average temporal changes in DMT for chum (0.27 days longer per year) and coho (0.42 days earlier per year) were significant ($P > 0.05$). At a population level, the majority of significant temporal changes in the DMT were toward longer migratory events (5 of 8). There was a significant ($P = 0.02$) negative correlation ($r = -0.39$) between the absolute value of the change in the MDMT and the change in the DMT. Thus, greater temporal changes in migration timing were associated with decreases in the duration of migration timing.

Interannual variance in phenology appears to be diminishing for many populations throughout southeast Alaska as PVMT decreased over time for the

Table 1 Average temporal changes in the median date (MDMT), duration (DMT), and interannual process variation in migration timing (PVMT) for Pacific salmon populations across southeast Alaska

Species	n	Change in MDMT	Change in DMT	Change in PVMT
Chinook	3	0.08	0.03	−0.04
Chum	4	−0.39	**0.27***	0.05
Coho	7	**−0.46***	**−0.42***	−0.08
Pink	8	−0.14	−0.04	−0.03
Sockeye	14	**0.16***	0.16	−0.06
Overall	36	−0.10	0.00	−0.04

Bold values with an * are significantly different than zero ($\alpha = 0.05$). n is the number of populations.

majority of populations (Fig. 3c; Table 1), but only five trends were significantly different from zero (4 of the 5 significant changes were negative trends). Changes in the MDMT, DMT, or PVMT (either the raw values or the absolute values) were not significantly related to whether time series included values before and after the PDO shift between 1976 and 1977 ($P > 0.10$), the average abundance of each population ($P > 0.21$), or the duration of each time series ($P > 0.19$).

Phenological synchrony

Pairwise interannual correlations in migration timing between populations of salmon throughout southeast Alaska were highly variable, ranging from -0.78 to 0.94. Mean correlations across population pairs within each species were positive for coho ($r = 0.062$, $P = 0.40$; $n = 19$), pink ($r = 0.20$, $P < 0.001$; $n = 26$), and sockeye ($r = 0.082$, $SE = 0.03$; $n = 87$) salmon (too few data were available for Chinook and chum), suggesting that there is some, albeit weak, within-species phenological synchrony in this region. Interestingly, correlations in migration timing were unrelated to pairwise geographic distance between populations (Fig. 4). Mantel tests for nonrandom relationships between pairwise distance and pairwise correlations in migration timing were nonsignificant for all species ($P > 0.625$).

Impact of climatic and habitat variation on migration timing

There was strong evidence that climatic variation operating at large-, moderate-, and local-scales was related to interannual variation in the median date of migration timing for Pacific salmon populations across southeast Alaska. The optimal model predicting interannual variation in migration timing included the additive effects of PDO, SST, and Precip, as well as a random effect for population nested within species (Table 2). Not surprisingly, the random intercept accounts for the vast majority of variation in the data (Table 2), but including PDO, SST, and Precip as fixed predictors also results in substantive reductions in AIC (3.59–18.75 lower) compared to less parameterized models. There was no evidence for a random slope effect for any of the climatic predictor variables. AIC values for models with a random effects structure containing only the random intercept were always less than AIC values for models with a random slope and random intercept, suggesting that the salmon populations included in this analysis respond similarly to those climatic variables.

However, there was clear heterogeneity in the variance across species and populations. In other words, the amount of interannual variation in the median date of migration timing varied substantially across species and populations. Including a variance structure for 'species' decreased AIC by 81.4 relative to the optimal model without a variance structure. Moreover, a variance structure for 'population' decreased AIC by 213.6 relative to the optimal model without a variance structure. Diagnostic tests for the latter model (MDMT ~ PDO + SST + Precip, random effect = population nested within species, variance structure = population) did not violate major model assumptions (e.g. heteroscedasticity and normality; Figs S1 and S2), and we used this model for final parameter estimation (Table 3). Parameter estimates for the fixed effects indicate that the median date of migration timing was later during years with positive anomalies from the Pacific decadal oscillation (PDO = 0.569, SE = 0.26), earlier when sea surface temperatures were warmer (SST = -0.969, SE = 0.25), and earlier when precipitation during the peak migratory period was higher (Precip = -0.557, SE = 0.23). There was no evidence that
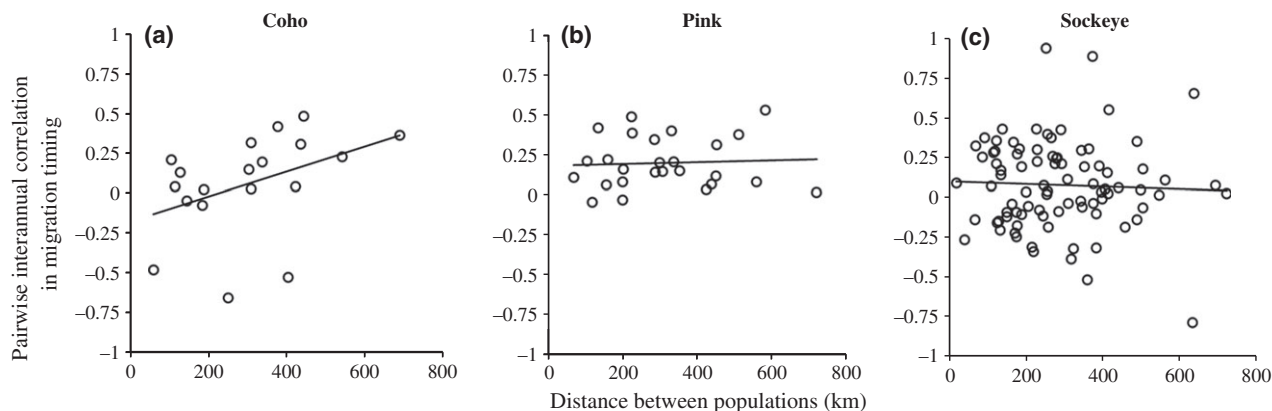
Fig. 4 Pairwise interannual correlations in migration timing as a function of distance between population pairs for coho (a), pink (b), and sockeye (c) salmon. The fitted lines are linear regressions of the correlations vs. distance.

Table 2 Step-down model selection results for linear-mixed models predicting interannual variation in the median date of migration timing for Chinook, chum, coho, pink, and sockeye salmon populations throughout southeast Alaska

Fixed effects	Random intercept	Random slope	Variance structure	AIC
PDO + SST + Temp + Precip				8657.8
PDO + SST + Temp + Precip	Species/Pop			6895.6
PDO + SST + Temp + Precip	Species/Pop	PDO		6898.4
PDO + SST + Temp + Precip	Species/Pop	SST		6902.4
PDO + SST + Temp + Precip	Species/Pop	Temp		6902.2
PDO + SST + Temp + Precip	Species/Pop	Precip		6899.5
PDO + SST + Precip	Species/Pop			6894.5
PDO + SST	Species/Pop			6898.1
PDO + Precip	Species/Pop			6913.3
PDO + SST + Precip	Species/Pop			6906.1
PDO + SST + Precip	Species/Pop		Species	6813.1
PDO + SST + Precip	**Species/Pop**		**Pop**	**6681.0**

Climatic variables include the Pacific decadal oscillation (PDO), sea surface temperatures in southeast Alaska (SST), and watershed-scale monthly precipitation (Precip) and air temperatures (Temp) that occurred during freshwater migration. The random intercept was population (Pop) nested within species (Species). Pop and Species were also used to model heterogeneity in model variance. The best-supported model (i.e. lowest AIC) is highlighted in bold.

Table 3 Parameter estimates for the best-supported model predicting interannual variation in the median date of migration timing for Chinook, chum, coho, pink, and sockeye salmon populations throughout southeast Alaska

Parameter	Estimate	SE	t-value	P-value
Fixed effects				
Intercept	233.75	10.62	22.06	0
PDO	0.57	0.26	2.14	0.0271
SST	−0.97	0.25	−3.95	0.0001
Precip	−0.56	0.23	−2.39	0.0171
Random effects (SD)				
$\sigma^{Species}$	22.82			
σ^{Pop}	14.90			
$\sigma^{Residual}$	4.73			

SE, standard error; PDO, Pacific decadal oscillation; SST, sea surface temperature; Precip, watershed-scale (stream of migration) monthly precipitation during migration; $\sigma^{Species}$, variance of the random intercept for 'species'; σ^{Pop}, variance of the random intercept for 'population' nested within 'species'; and $\sigma^{Residual}$, residual variance.

Temp was related to interannual variation in the median date of migration timing.

There was little evidence that salmon in glacially influenced streams exhibited different long-term trends in migration timing from salmon populations spawning in nonglacial streams. Specifically, temporal changes (either the raw values or the absolute values) in the MDMT, DMT, and PVMT did not differ between populations from glacially and nonglacially influenced streams ($P > 0.31$). Similarly, there was no significant difference ($P > 0.12$) between populations from glacial and nonglacial streams in the variability surrounding long-term changes in salmon migration timing.

Discussion

Temporal changes in adult salmon migration timing varied widely across species and even populations within species in spite of consistent region-wide climatic warming of 1.4–2.4 °C throughout southeast Alaska (Stafford et al., 2000; Wing et al., 2006). While strong shifts in migration timing have occurred, changes were often contrasting between species and to a lesser degree populations within species. There was some evidence for weak phenological synchrony within species, but correlations in interannual variation in migration timing between populations were not related to geographic distance and were highly variable, suggesting that local processes have a major impact on long-term phenology for these fish. The synchrony – albeit weak – occurring within species likely reflects the impact of climatic variation on migratory behavior. Indeed, climatic drivers operating on a continuum of scales were related to interannual variation in migration timing. Nevertheless, heterogeneous changes in migration timing and weak phenological synchrony observed across the region imply that we will have a limited ability to accurately predict future salmon migration timing at a population scale. The impressive phenological diversity found across southeast Alaska may, however, help stabilize population dynamics and buffer ecosystem processes against rapid environmental change.

Strong temporal shifts toward earlier adult migration timing have been observed in several populations of sockeye (Quinn & Adams, 1996; Cooke *et al.*, 2004), pink (Taylor, 2008; Kovach *et al.*, 2013), and coho salmon (Kovach *et al.*, 2013). Across southeast Alaska, we found that populations of chum, pink, and especially coho salmon have been migrating into freshwater earlier than they did historically. All seven populations of coho salmon for which we had data have advanced their migration timing. On average, coho are migrating to spawn nearly a half a day earlier every year, or approximately 2 weeks earlier per time series (~30 years). Additionally, the strongest directional changes in the MDMT regardless of species were toward earlier migration timing (up to a month earlier in some populations).

The general pattern of earlier migration timing did not hold for Chinook or sockeye. Instead, a fairly consistent shift toward later migration timing was observed, especially in sockeye salmon. Sockeye salmon in southeast Alaska migrate during the summer months (on average all populations migrated between July 10 and September 2) when temperatures are at their highest and stream flows are at their lowest. These conditions can directly influence the selective pressures acting on sockeye salmon during their migration and spawning (Carlson *et al.*, 2011), and thus the observed changes reported possibly suggest that fish are delaying migration to avoid high temperatures or low flows (also see Crozier *et al.*, 2011). Our best-fit model predicting interannual variation in migration timing strongly suggests that salmon populations across the region migrate earlier when precipitation is higher (a surrogate for stream flow).

The mechanisms driving rapid shifts in salmon migration remain unclear (Cooke *et al.*, 2004; Taylor, 2008; Kovach *et al.*, 2013). Sources of anthropogenic selection, especially harvest or hatchery augmentation, can influence phenotypic and genetic diversity within salmon populations and drive evolution toward earlier migration timing and spawning (Quinn *et al.*, 2002, 2007). We avoided populations that are impacted by hatchery activities in these analyses, and salmon harvest in southeast Alaska – which largely occurs in distant seine, troll, and drift gillnet fisheries – is managed such that strong directional selection on certain migratory phenotypes is less likely than in highly targeted fisheries occurring at the mouths of major rivers (e.g. Bristol Bay, Alaska). Shifts in climatic or environmental conditions have been implicated in changes in adult migration timing for some salmon populations, but the abiotic drivers (e.g. stream temperature or flow and oceanic conditions) and consequences (i.e. maladaptive vs. adaptive migratory behavior) appear to

vary widely (Hinch *et al.*, 2012; Kovach *et al.*, 2012, 2013).

Sea surface temperatures and precipitation values, both of which were negatively related to migration timing, have increased slightly, but not significantly (i.e. *P*-values for trends were >0.05), over the course of many of our time series. PDO anomalies, which were positively related to migration timing, have decreased in the last several decades (see also Crozier & Hutchings, 2014). Nevertheless, the estimated climatic impacts on migration timing obtained from the best-supported linear-mixed model cannot account for the strong directional changes observed in many coho, chum, and pink salmon populations, or the consistent negative trends in sockeye salmon. In other words, the estimates for the climatic effects are not sufficiently large to produce the observed temporal shifts in MDMT (Table 3), as even the most extreme interannual fluctuations in PDO, SST, or Precip predict changes in migration timing on the order of several days, not several weeks. The degree to which climatic variation or change may be implicated in these rapid shifts merits further study, especially given the fact that timing of adult migration and spawning is closely linked to fitness and thus population dynamics in Pacific salmon (Dickerson *et al.*, 2005; Crozier *et al.*, 2008; Anderson *et al.*, 2010; Hinch *et al.*, 2012). The consistent, although contrasting, changes in migratory behavior for the different species strongly suggest that a region-wide driver is responsible. Climatic variation at some level or operating on some life stage is a likely mechanism that could produce this general pattern.

Despite the fact that glaciers are one of the most important physical features influencing freshwater habitats and stream temperatures throughout southeast Alaska (Hood & Berner, 2009; Fellman *et al.*, 2014), long-term changes in migration timing for populations inhabiting glacially influenced streams did not differ from populations in nonglacial habitats. Watersheds with <30% glacial coverage are still subject to warming as ambient temperatures increase (Fellman *et al.*, 2014), and all of the salmon-bearing streams used in this study had glacial coverage <30% (one watershed had 28.9% glacial coverage). Thus, changes in migration timing in glacially influenced streams (where they occurred) could potentially be due to changes in local environmental conditions, environmental conditions elsewhere, or other selective pressures. Regardless, shifts in migration timing occurred in both habitat types, with strong temporal changes in migration timing toward earlier and later dates in both glacial and nonglacial streams.

Within population variation in migration timing (DMT) is a major component of phenological diversity

that stabilizes salmon population dynamics (Gharrett *et al.*, 2013). Previous work found decreases in DMT across species and life histories at one location in southeast Alaska (Kovach *et al.*, 2013). The results presented here suggest that this pattern is not generally widespread throughout the region. While some populations are migrating over a shorter period of time than they did historically, temporal change in the DMT for many populations was minimal, and temporal increases in the DMT occurred in several populations. However, there were very strong decreases in DMT for coho salmon; in addition to migrating earlier over time, the duration of coho salmon migration events is, on average, 2 weeks shorter than they were historically. Decreases in phenotypic variation can occur via shifts in allele frequencies due to intergenerational or intragenerational selection (Brodie *et al.*, 1995; Carlson *et al.*, 2011). In support of this possibility, we found that the strongest directional changes in MDMT were associated with decreases in DMT (across all species and populations), suggesting that selection could be playing a role in influencing directional changes in MDMT in some populations. Median heritability of phenological traits in salmon is high ($h = 0.51$; Carlson & Seamons, 2008), and rapid evolutionary changes in migration timing have been observed for multiple salmon populations (Crozier *et al.*, 2011; Kovach *et al.*, 2012).

Increases in phenotypic variation at some locations could be due to a relaxation of selective forces, or as a result of stress-induced release of cryptic genetic variation for phenotypic plasticity (Ghalambor *et al.*, 2007). If that were true, interannual variation in migration timing (PVMT) should have increased if populations were exposed to novel and increasingly stochastic environments. Instead, there was a consistent, although weak, decrease in PVMT in salmon populations throughout southeast Alaska. This trend could be due to improved sampling over time (at each weir) rather than biological change – however, we have no reason to suspect that this occurred. Although the mechanism driving this pattern is unclear, decreasing interannual variability in salmon migration timing may be beneficial for the many consumer species that depend on salmon as an important resource (Ben-David, 1997; Schindler *et al.*, 2013).

The variability surrounding long-term changes in salmon migration timing may be explained by the fact that salmon experience a variety of selective pressures during their migration through the ocean and freshwater (Groot & Margolis, 1991; Quinn, 2005). Furthermore, divergent selective pressures between freshwater streams influence patterns of local adaptation, especially to temperature heterogeneity, across the landscape (Taylor, 1991; Fraser *et al.*, 2011). Temperature differences between streams drive selective pressures such that phenological events between geographically proximate salmon populations can differ by nearly a month (Lisi *et al.*, 2013). Similarly, local adaptation influences how salmon populations respond to interannual variation in temperature (or other environmental conditions), with some populations migrating earlier when temperatures are warm, while others delay migration for substantial periods of time (Hodgson & Quinn, 2002). Finally, because phenological traits have high heritability and respond rapidly to climate-induced natural selection, patterns of local adaptation are dynamic and can vary on contemporary timescales.

The pairwise interannual correlations in migration timing between populations of salmon throughout southeast Alaska emphasize that salmon display a wide variety of responses to interannual variation in climatic, environmental, or biotic sources of variation. While correlations in migration timing were weakly positive on average, many pairs of populations demonstrated independent ($r \sim 0.0$) and even contrasting (r up to -0.78) patterns of migration timing. Average correlations in migration timing for pink salmon ($r = 0.20$) were over twice that of sockeye or coho ($r \sim 0.06$–0.08), a consistency that may be explained by their comparatively simple life history (Quinn, 2005). Similarly, pair-wise correlations in marine survival of pink salmon populations are considerably higher than those of either sockeye or chum salmon (Mueter *et al.*, 2002b).

Correlations in migration timing were independent of geographic distance in each species, suggesting that interannual variation in migration timing is driven by population-specific responses to region-wide environmental change (e.g. climate warming) and/or fine-scale environmental variability within freshwater streams and rivers (Hodgson *et al.*, 2006). These findings generally corroborate other research showing that Pacific salmon population abundances can be asynchronous and differentially respond to climatic variation (Hilborn *et al.*, 2003; Schindler *et al.*, 2010; Rogers & Schindler, 2011; Rogers *et al.*, 2013). However, the relationships between interannual climatic variation and salmon migration timing examined here did not appear to vary across populations or species (i.e. there was no support for random slope effects in linear-mixed models). Thus, the observed heterogeneity must be driven by other sources of climatic, biotic, or environmental variation, many of which may be population specific. Fine-scale local adaptation in salmon migration timing can be strongly influenced by intrinsic and extrinsic mechanisms operating directly on adult migration itself (e.g. earlier migrating fish may be exposed to higher temperatures but can select optimal spawning locations), but also indirectly through selection on juvenile offspring

phenology, which is strongly influenced by the timing of adult spawning (Gharrett *et al.*, 2013). As such, intra-generational selection at the juvenile life stage can also influence subsequent adult migration timing. Surprisingly, we did not detect an effect of interannual temperature on the median date of salmon migration timing, a variable often associated with interannual variation in salmon phenology (described in Quinn, 2005). Unfortunately, we were forced to use modeled ambient air temperatures given a lack of empirical data, the resolution of which may be inadequate for predicting migratory behavior at the interannual and population scale (Arismendi *et al.*, 2014). Empirical stream temperatures were strongly related to adult migration timing for sockeye, pink, and coho salmon at one location used in this study (Kovach *et al.*, 2013), supporting this notion. Alternatively, our results may indicate that migratory behavior at a regional scale is better predicted by variation in temperature at moderate to large, rather than local, scales.

More generally, our results suggest that consistent climate-induced changes in migratory behavior are unlikely for species such as salmon that occupy highly diverse environments to which populations exhibit adaptive genetic variation. While climate-driven shifts in phenology are common in many taxa, intrapopulation and intraspecies variation in phenology is often poorly documented (Forrest & Miller-Rushing, 2010; Diez *et al.*, 2012), despite the importance of these sources of phenotypic diversity for population and ecosystem stability (Bolnick *et al.*, 2011; Naeem *et al.*, 2012). There is growing awareness, however, that phenological changes can vary across species, locations, communities, and even life-history strategies (Primack *et al.*, 2009; Ibanez *et al.*, 2010; Diez *et al.*, 2012; Kovach *et al.*, 2013), a pattern that is clearly evident here. The widespread phenological variability observed across southeast Alaska may have important implications for community dynamics and ecosystem services. For example, variation in salmon migration timing benefits organisms that consume salmon by allowing them to exploit multiple populations over longer periods of time (Schindler *et al.*, 2013). Phenological diversity within and between populations also contributes to portfolio effects that buffer salmon abundances from environmental variability (Schindler *et al.*, 2010; Gharrett *et al.*, 2013). Indeed, relative to other regions, Pacific salmon populations are quite stable in southeast Alaska (Baker *et al.*, 1996), a pattern that has been attributed to the environmental, genetic, and phenotypic diversity within this region (Bryant, 2009). Avoiding practices such as artificial selection via harvest (Allendorf *et al.*, 2008) or biotic homogenization through hatchery

supplementation (Olden *et al.*, 2004), will help conserve salmon phenological diversity and promote region-wide resiliency to future climatic change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Time-series used to describe temporal patterns in migration timing for Pacific salmon in Southeast Alaska. *n* is the number of years of data for each population and Time-span is the period over which those observations were made.

Figure S1. Standardized residuals vs. the fitted values from the best-supported model predicting inter-annual variation in salmon migration timing.

Figure S2. Residuals from linear mixed models predicting inter-annual variation in salmon migration timing as a function of the best-supported predictor variables Pacific decadal oscillation (PDO), Sea surface temperature (SST), and Precipitation (Precip).