Title: Phenological shifts and mismatch with marine productivity vary among Pacific salmon species and populations

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Abstract

Global climate change is shifting the timing of life-cycle events, sometimes resulting in phenological mismatches between predators and prey. While phenological shifts and subsequent mismatches may be consistent across populations, they could instead vary unpredictably across populations within the same species. For anadromous Pacific salmon (*Oncorhynchus* spp.), juveniles from thousands of locally-adapted populations migrate from diverse freshwater habitats to the Pacific Ocean every year. Both the timing of freshwater migration and ocean arrival, relative to nearshore prey (phenological match/mismatch), can control marine survival and population dynamics. Here, we examined phenological change of 66 populations across six anadromous Pacific salmon species throughout their range in western North America with the longest time series spanning 1951 - 2019. We show that different salmon species have different rates of phenological change, but that there was substantial within-species variation that was not correlated with changing environmental conditions or geographic patterns. Moreover, outmigration phenologies have not tracked shifts in the timing of marine primary productivity, potentially increasing the frequency of future phenological mismatches. Understanding population responses to mismatches with prey are an important part of characterizing overall population-specific climate vulnerability.

Main textIntroduction

Shifts in the timing of life-history events, or phenology, are some of the most pervasive ecological impacts of climate change[1,2]. The magnitude and direction of phenological responses to climate change differ among species[3], life histories[4,5], and trophic levels[6–8]. Such differing rates of phenological change decrease the magnitude of overlap in species interactions[9], which can reduce the fitness and survival of consumers, if the timing of important consumer life history events becomes decoupled from their prey (i.e., match/mismatch hypothesis)[10–13]. Thus, consumers that track prey phenology should be less vulnerable to this dimension of climate change. To date, the focus of the field of phenological change and mismatch has been on species-specific phenological shifts[1,8], whereas intra-specific diversity in phenological change and mismatch remains poorly described[14]. Yet intra-specific diversity is foundational for species resilience to anthropogenic stressors like climate change[15]. Specifically, inter-population variation in phenology and thus mismatch could provide response diversity[15] to climate change and thus resilience and stability to the aggregate (e.g., metapopulation). Within a given population, higher variability in phenology may lead to increased resilience to shifts in prey phenology as they have a broader window of phenological expression and increased likelihood of continued overlap with prey[16]. Thus, understanding inter- and intra-specific variation in phenological change and mismatch remains a key challenge for identifying species- and population- level vulnerability to global change.

Every year, hundreds of billions of juvenile Pacific salmon (*Oncorhynchus* spp.) migrate from freshwater environments to the ocean, and their survival can depend upon how well their timing of ocean arrival aligns with peak prey abundance[17–19]. Despite this common challenge, Pacific salmon occupy a vast diversity of freshwater habitats ranging from warm arid regions of

California to the Arctic Circle, requiring seaward migrations of tens to thousands of kilometers from inland spawning streams. Consequently, there exists remarkable intra-specific diversity in local adaptations, life histories, and phenology[20,21]. The timing of juvenile salmon emigration varies greatly across populations and can depend upon both heritable and plastic traits[22] that respond to species- and population-specific proximate and ultimate cues, including temperature, photoperiod, barometric pressure, and flow rates[23]. Both peak outmigration timing and within-population phenological diversity of Pacific salmon may be changing as a result of climate change[3]. Indeed, climate change may be impacting the freshwater conditions that cue salmon emigration timing, such as water temperatures, differently than the marine conditions that control phenologies of marine prey (e.g., boreal copepods, euphausiids, larval fish) [7,24,25]. Differential rates of change between salmon ocean arrival and prey availability could lead to phenological mismatches which could impact salmon marine survival and population productivity[17,19,26]. It is unclear if juvenile salmon outmigration timing is keeping pace with changes in marine prey phenology across their range[3,27,28].

Here we quantify change in smolt outmigration phenologies and potential temporal mismatches with marine prey for culturally, ecologically, and economically important Pacific salmon. Our goal was to quantify phenological change across populations from all five species of anadromous and semelparous Pacific salmon in western North America as well as steelhead trout (*O. mykiss*), determine whether phenological shifts could be predicted based on key biological, environmental, or geographic variables known to impact salmon outmigration phenology[29,30], and examine the possibility of increasing phenological mismatches through time. We compiled and analyzed a unique dataset on smolt outmigration phenology containing data from 66 populations (where population is considered a unique site-species combination) spanning 18

97 degrees latitude (~3500 km) from Alaska to Oregon, for a time series ranging between 1951 to
98 2019 (a combined 1858 years of data). We paired this dataset with the spring phenology of
99 coastal Pacific Ocean primary productivity, as derived from satellite-inferred chlorophyll-a
100 concentration (SeaWiFS, MODIS-A).

101 *Results*

102 ***Changes in smolt outmigration phenology***

103 To determine the rate of phenological change for each population, we modelled yearly
104 smolt emigration peak timing and temporal range (the number of days between the 25th and 75th
105 percentile) and determined the rate of change for each metric across the timespan of the data (20
106 years minimum). A sensitivity analysis revealed that the 20-year minimum time series was
107 sufficient to capture trends (Extended Data Fig. 1, Supplementary Information 1.1). Using a
108 hierarchical state-space model framework, we estimated the peak outmigration date and its rate
109 of change across years separately for each population. Seventeen site-specific variables (e.g.,
110 distance to the ocean, rate of spring temperature change) were used to determine if any variables
111 correlated with the rate of change of smolt phenologies. We also examined how the temporal
112 range in outmigration changed across years, to test the possibility that the outmigration range
113 was narrowing (Fig. 1).

114 Some species exhibited high rates of phenological change in peak timing, while others did
115 not change substantially over the observed period (Fig. 1). Chum (*O. keta*) and pink (*O.*
116 *gorbuscha*) salmon, which emigrate soon after emergence, had the fastest average rate of
117 advancement in outmigration timing (mean = 7.8 days/decade and 5 days/decade earlier,
118 respectively; Fig. 1). Coho salmon and steelhead trout, which generally spend one or more years

in freshwater after emergence, had much lower average rates of peak change (mean = 0.1 days/decade and 0.5 days/decade earlier, respectively).

Other than species, no other environmental factors clearly and consistently correlated with shifts in peak change. Comparison of weighted linear regressions demonstrated that the most parsimonious model included species, trap elevation, and an interaction between species and trap elevation (Extended Data Table 1). In this model, there was a significant effect of trap elevation and interaction between trap elevation and species on the rate of change in peak outmigration. The relationship between trap elevation and peak change for Chinook was positive (0.997 days/decade later for every increase in 1 unit log(m)) whereas relationship between trap elevation and peak change for steelhead was negative (-0.377 days/decade earlier for every increase in 1 unit of log(m)) (Extended Data Fig. 2). Despite the significance of the interaction between trap elevation and species, these variables contributed little predictive power. Cross validation showed that the species-only model had the same root mean square error (RMSE = 0.30) as the model with species, trap elevation, and an interaction (RMSE = 0.30) indicating that the additional variable did not increase the predictive power. Thus, we discovered that, across their North American range, different salmon species have different average rates of phenological change which were not strongly associated with measured factors.

We discovered higher variation in phenological change within species than among species, with intra-specific variation accounting for 60% of the total variation among populations, whereas inter-specific variation accounted for 40% (Fig. 2). Overall, 46 of the 66 observed salmon populations were emigrating earlier with 16 of those being statistically significant (95% confidence intervals did not span 0). As a result, average spring migration phenology was becoming earlier by 1.4 days/decade across all populations but was highly variable in both the

magnitude and direction of shifts within species. For example, while on average coho salmon did not exhibit any substantial phenological changes in outmigration timing (mean = 0.1 days/decade), 17 of 26 populations were trending towards advancing phenology, whereas 9 populations had the opposite pattern in phenology. Thus, while there were species-level patterns, perhaps due to different intrinsic or extrinsic drivers of migration timing, there was even greater fine-scale population variation in migratory phenological change.

The two species with the greatest diversity of life histories – steelhead trout and Chinook salmon – showed the greatest reduction in breadth of timing of migration. Specifically, steelhead trout and Chinook salmon exhibited changes in smolt outmigration range (Fig. 1), of which 11 of 15 steelhead trout populations (8 significantly), and 5 of 9 Chinook salmon populations (4 significantly) were trending narrower.

Phenological mismatch in juvenile salmon with prey

We paired our smolt outmigration phenology dataset with satellite-derived estimates of spring phytoplankton phenology (SeaWiFS, MODIS-A; chlorophyll-a) to quantify the potential mismatch between salmon and the phenology of ocean prey. Trophic dynamics in the North Pacific are largely driven by bottom-up forcings[31]. As such, phytoplankton phenology was used as a proxy for salmon phenology. We compared the rate of change in peak smolt outmigration phenology between 1999 – 2019 to the rate of change in the spring phytoplankton bloom across the 20-year time span, in each corresponding coastal region, to determine if there were any phenological mismatches (Fig. 3). Phenological mismatches appear to be growing in the Northern California Current, driven by the spring phytoplankton bloom becoming earlier relative to smolt migration (Fig. 3, Extended Data Figure 3). But these regional patterns in phenological mismatch were not significant (95% confidence interval of the difference in the rate of change

spans 0, where 0 indicates that salmon and phytoplankton phenology are shifting at the same rate; Fig. 3). In fact, while both the spring phytoplankton bloom and salmon populations have exhibited phenological shifts over the 20-year period (Extended Data Fig. 3), there was little correlation between them (correlation = 0.17), indicating that salmon outmigration timing is not tracking shifts in spring primary productivity. For example, salmon often had phenologies that were shifting while the corresponding spring phytoplankton bloom in their region was not shifting (Fig. 3, Extended Data Figure 3). Where phytoplankton phenologies were changing, more salmon are lagging behind spring phytoplankton phenological change rather than outpacing it. Specifically, 13 of 60 populations had substantially increasing temporal mismatches (greater than 8 days per decade difference in the rate of phenological shifts between 1999 – 2019) throughout our truncated time series, with salmon outmigration phenology of 12 populations lagging behind the advancement of the spring phytoplankton bloom, and the remaining population outpacing the spring phytoplankton bloom. Our study indicates that salmon outmigrations are not tracking changes in phytoplankton phenology, a potential harbinger of future phenological mismatches and decreased marine survival under climate change.

Discussion

Here we reveal that the impacts of climate change are manifesting differently among populations within economically- and culturally-important migratory fish. In fact, while there were differences across species, idiosyncratic intra-specific diversity comprised the majority of variation in phenological change. The outmigration phenology of juvenile salmon relative to ocean prey can determine growth and survival in the early marine period[17–19], and declines in marine survival have been implicated in collapses of many populations and their associated fisheries[32]. While population-level response diversity in the face of global change could increase

188 species resilience, unpredictable changes could complicate broad assessments of climate
189 vulnerability and prescriptive management of populations.

190 Peak outmigration phenology changed at different rates across species, a result consistent
191 with smaller-scale studies of salmon outmigration phenology[3,27,28]. Chum and pink salmon
192 shifted their peak phenology more quickly than other species. However, chum and pink salmon
193 were represented by a small number of sample sites due to limited funds for expensive long term
194 monitoring programs. Despite the small sample sizes, individual chum populations had higher
195 rates of change than individual populations within other species, indicative of species-level
196 increased rates of phenological shifts. The deficiency in data collection on pink and chum
197 salmon limits understanding of climate change-driven impacts on these widely distributed and
198 important species. While pink and chum salmon had shifting phenologies, on average coho
199 salmon phenologies were not shifting, consistent with previous studies. For example, peak
200 outmigration timing of Auke Creek, Alaska odd-year pink salmon advanced by 4.9 days/decade[3],
201 whereas peak outmigration of Auke Creek coho salmon did not change over a 37-year period.
202 Thus, we discovered that, across their North American range, different salmon species have
203 different average rates of phenological change.

204 A combination of changes in environmental cues, shifts in life history, and genetic
205 selection could be driving these species-specific shifts in smolt migration timing [22,33]. For
206 example, because pink and chum salmon migrate to the ocean soon after hatching, their
207 outmigration phenologies are tightly related to both freshwater incubation temperatures and
208 shifts in adult migration/spawn timing[27]. Warmer overwinter incubation temperatures could lead
209 to earlier outmigration timing in the spring. In addition to shifts in life history, other plastic
210 responses to environmental change, or genetic selection due to freshwater or marine survival

could also result in changes in migration timing. For instance, because pink and chum salmon have smaller juveniles that feed on lower trophic level prey than other salmon, they are likely to be more strongly impacted by shifts in marine zooplankton phenology and so may be subject to stronger selection on outmigration timing in the early marine life stage[26].

Despite species-specific shifting in outmigration timing, much of the variation in shifts in outmigration timing remained unexplained. Of the 17 watershed-level characteristics we tested, only species was a strong predictor of population-level phenological change. Ice-off date, water temperature, photoperiod, among other factors have all been correlated to smolt outmigration timing within individual populations[20]. However, proxies such as air temperature and latitude were not correlated across populations. It is likely that watershed complexity, local adaptations, and different local manifestations of climate change create response diversity that cannot be predicted by these data[15]. For example, in response to warming temperatures, most, but not all, populations had earlier outmigration timing. For 84% of populations, the slope of relationship between annual peak and mean air temperature three months before migration was negative while for the other 16% of populations the slope was positive, demonstrating that most populations have earlier migrations in warm years, but a few had later migrations in warm years (Fig. 4). Thus, a similar change in temperature could cause phenological shifts of different magnitudes and directions across populations, a form of response diversity to climate warming. This suggests that while phenology and phenological change of well-studied populations could be predicted [3,27], those results are unlikely to generalize across populations or species. Phenological change is generally studied at the population level, but too commonly reported as a species-level change, neglecting potential local drivers of population variability[14]. Furthermore, management often relies on indicator populations which are thought to be representative of other

populations of the same species, however, our results suggest that indicator populations may not represent phenological changes in other populations. Our results reveal that broad-scale climate change will manifest unpredictably in species with a high degree of local adaptation that use diverse habitats, such as Pacific salmon.

The range in outmigration timing decreased in Chinook salmon and steelhead trout, indicating lost phenological diversity. This lost diversity could be driven by changing freshwater cues, selection against early or late migrants, or loss of life-history diversity[3] due to habitat contraction, decreased population abundance, and hatchery practices[34]. Indeed, abundance of many populations of steelhead trout and Chinook salmon has decreased dramatically over the observed period[32] and populations have suffered widespread non-random habitat losses[34]. For example, headwater streams are more likely to become disconnected or lost from the watershed, leading to a loss of diverse populations that depend on that habitat[34]. Furthermore, hatchery propagation could erode diversity; we excluded hatchery-origin fish and focused on datasets enumerating natural-origin (unmarked) fish, given clearer linkages to environmental change. However, adult hatchery-origin fish that spawned naturally in the wild produce natural-origin juveniles encountered in some of the study populations. Widespread hatchery propagation can alter genetic variation and outmigration timing[35]. Human activities that decrease phenological diversity and narrow the outmigration window are likely to erode population-level resilience to phenological shifts in marine prey by increasing the likelihood of mismatches [36].

Using satellite-derived chlorophyl-a as a proxy for ocean productivity, we showed that salmon are shifting their phenologies independently from the spring marine phytoplankton bloom, which could lead to future phenological mismatches. While satellite derived chlorophyl-a can be used to estimate the timing of phytoplankton productivity, it cannot differentiate

between phytoplankton species and is up to several trophic levels removed from salmon prey. Preferred prey of juvenile salmon differs across ocean ecosystems, estuaries, and species. For example, pink and chum salmon, which enter estuaries at smaller sizes tend to eat large zooplankton, while steelhead trout, which enter estuaries at larger sizes tend to eat larval fish, decapod larvae, and euphausiids[37]. Regardless, the timing of the spring phytoplankton bloom indicates the onset of primary productivity that cascades upward through trophic levels, to the zooplankton, ichthyoplankton, and larval fish that collectively compose juvenile salmon diets [37,38]. Indeed, the timing of the coastal ocean phytoplankton bloom can impact population productivity in pink salmon[26] and timing of zooplankton biomass peak can impact survival of coho salmon[17] and steelhead trout[19]. Thus, timing of the phytoplankton bloom can be indicative of phenological mismatch between juvenile Pacific salmon and their prey which can influence marine survival, recruitment, and population productivity[17,19,26].

Here we show that populations are changing their phenology at different and unpredictable rates. This lack of predictability in population-level responses is likely driven by complex local manifestations of broad-scale climate patterns such as differences in local adaptions, life histories, or unassessed natal watershed characteristics. With sufficient investment in monitoring and management, a more placed-based management strategy, with a strong focus on life-history traits and demographic trends in individual populations, could increase the likelihood of detecting and managing for climate driven changes for specific populations[39]. Yet, these findings also suggest that the specific predictions that come from well-monitored indicator populations may not be transferable to other populations. Therefore, management systems of salmon will need to be robust to unpredictable population responses to climate change. Conservation approaches that promote response diversity, such as conservation of the diverse genetics, life-

histories, and habitats, will foster resilience in this era of ongoing climate change[36,40]. While globally coherent patterns of climate-driven phenological shifts reshuffle species interactions, local manifestations of climate change may be quite unpredictable as complex systems evolve and adapt.

Methods

Smolt migration datasets

Pacific salmon smolts are monitored annually throughout their range in North America, from Alaska to California, with smolts counted as they emigrate from natal freshwater rearing watersheds before entering the ocean. Smolts generally emigrate from rearing lakes, rivers, and streams during the spring or fall, after spending between several weeks to several years in freshwater. Federal, State, Provincial, and Indigenous governments in the United States and Canada, as well as community groups, have been monitoring smolt emigration since the mid-1950s. These monitoring programs intercept and enumerate smolts during the migration season, using a variety of techniques such as full fence weirs, in which all fish were counted, or using mark-recapture methods where a subset of fish were captured in traps (e.g., inclined plane trap, floating trap, rotary screw trap) or seines, and marked, released, and captured again to determine abundance. Here, we collated data from 41 sites representing six species (66 site-species combinations or populations) of natural-origin (predominantly wild/unmarked), spring emigrating Pacific salmon populations that had been monitored for >20 years, primarily seeking those that had limited hatchery influence, and counted natural-origin smolts separately from hatchery produced smolts (1858 cumulative years across all sites and species). We refer to each

unique site-species combination as a population throughout the manuscript, but recognize that some site-species combinations, particularly those at river mouths represent metapopulations, while those in the headwaters may represent partial populations.

Measuring population- specific phenological shifts

We modeled annual emigration for each population to identify peak and breadth of outmigration (i.e. peak width), and simultaneously fit a trend in peak day through time. In some populations, multiple juvenile life history forms with unique outmigration timing had been previously described (e.g. ocean type fry that migrate soon after hatching vs. river type smolts that migrate to the ocean more than a year after emerging), and so we provide separate estimates for them based on a date cut-off. Thus, several sites have two peaks described, one for each life history type. For each species and site, log daily abundance (either as raw counts, or as mark-recapture expanded estimates, depending on capture methodology and which count was believed to be the best estimate of abundance) for each year was modeled throughout the migration window using one of four state-space hierarchical models. We used state-space models to distinguish a data or observation model from the latent phenological trend. We considered four alternative process models for each dataset. Our simplest model used a normal approximation to describe the shape of the outmigration distribution.

$$f(x) = normal(\mu, \sigma_x) \qquad \text{eq (1)}$$

Second, we used a Student-t distribution, which differs from the normal distribution in that when the degrees of freedom parameter is small, the Student-t distribution can have more extreme tails.

$$f(x) = Student\text{-}t(\mu, v, \sigma_x) \qquad \text{eq (2)}$$

Application of either the normal or Student-t models assumes symmetry in the distribution of outmigration before and after the peak. As a third model, we relaxed the assumption of symmetry and used a double normal distribution as a process model. The double normal distribution is widely used in fisheries to model quantities like selectivity[41]. This distribution involves fitting two truncated normal distributions, joined by a common mean, but allowed to have different variances.

$$f(x) = \begin{Bmatrix} normal(\mu, \sigma_{x_1}), & x < \mu \\ normal(\mu, \sigma_{x_2}), & x > \mu) \end{Bmatrix} \quad \text{eq (3)}$$

For the purposes of our application, this translates to the shape of outmigration before and after peak to be different. Finally, as a fourth model, we extended the double normal concept to a double Student-t distribution. This double Student-t differed from the double normal in allowing both the variance and degrees of freedom to differ between pre- and post- peak curves.

$$f(x) = \begin{Bmatrix} Student - t(\mu, v_1, \sigma_{x_1}), & x < \mu \\ Student - t(\mu, v_2, \sigma_{x_2}), & x > \mu) \end{Bmatrix} \quad \text{eq (4)}$$

Equations (1-4) describe process models fit to daily smolt abundance in a single year, modeled by a distribution with a peak μ, and variance σ_x. Because each dataset in our analysis includes multiple years, the means, variances, and degrees of freedom v in these equations can be further subscripted by year, allowing the parameters to change through time. For simplicity, we did not consider time-varying degrees of freedom for the Student-t or double Student-t model in equations (2) and (4). For the mean and variance parameters, we considered two hierarchical models. First, we developed models that allowed the means and standard deviations to be estimated as random effects,

$$\ln(\mu_y) \sim normal(\ln(\mu_0), \sigma_\mu) \quad \text{eq (5)}$$

$$\ln(\sigma_y) \sim normal(\ln(\sigma_0), \gamma_\sigma) \quad \text{eq (6)}$$

where $\ln(\mu_y)$ is the log of the peak location parameter in year *y*, μ_0 is the estimated global mean across years, and σ_μ is the variation in peak dates. For the variance model, we also modeled random effects in log space so that $\sigma_y$is the standard deviation in year *y* (for example for models 1 – 2 above), $\ln(\sigma_0)$ is the mean shape parameter, and γ_σ is the standard deviation among shape parameters. Because both trends are modeled in log space, these can be interpreted as exponential change in normal space. Treating either the means μ_y or variance parameters σ_y hierarchically assumes that these parameters are drawn from a common distribution.

While these random effects models are flexible, the focus of our inference is estimating phenological shifts, so we evaluated a separate series of random effect models that include trends in the mean and variance of these distributions,

$$\mu_y \sim normal(\mu_0 + \beta_\mu \cdot v, \sigma_\mu) \quad \text{eq (7)}$$

$$\ln(\sigma_y) \sim normal(\ln(\sigma_0) + \beta_\sigma \cdot v, \gamma_\sigma) \quad \text{eq (8)}$$

All other parameters are as before, but the inclusion of β_μ and β_σ allows for linear trends in the location and shape of these distributions through time. Equations 7 – 8 describe changes for symmetric models with a single variance parameter (equations 1 – 2 above) – our models for asymmetric distributions allowed the pre- and post-peak shape parameters to have different estimated trends.

All models were fit separately to each dataset using maximum likelihood approaches, implemented in Template Model Builder[42] and R[43]. We used Akaike's Information Criterion (AIC[44]) to identify models most supported by the data. In a few cases, the models did not

converge (generally because of too many missing years) and were excluded from consideration. We summarized output from these best fit models by computing the quartiles of the distribution in each year (the dates when 25% and 75% of fish had been counted), from now on we refer to the number of days between the 25^{th} and 75^{th} quartiles as the range of the data for each year. The annual trend in peak width was modeled in a separate weighted linear model, where weight was assigned based on the inverse square of the variance.

Patterns in phenological shifts

We examined geographic, environmental, and biological variables for correlation with rate of change in peak outmigration phenology. Geographic variables were selected based upon prior research linking variables to phenology[29,30,35], and were determined from ArcGIS using 30 m rasters and delineated watersheds. These variables included latitude of the trap, distance to the ocean (distance between trap and the ocean in km following river polylines), trap elevation and mean and maximum elevation of watershed above the smolt trap (in m), gradient (elevation of trap divided by distance to the ocean), and watershed area above the smolt trap (in km^2).

Environmental variables included the rates of minimum, mean, and maximum air temperature and precipitation change between the first year of monitoring and 2013 (see Table S1 in supplementary information). Water temperatures were not available throughout the range of our sites, but water temperature and air temperature over open water are highly correlated and thus air temperatures can roughly approximate water temperature conditions[45]. Air temperature and precipitation were calculated using the program ClimateNA (v.5.21)[46]. Briefly, latitude, longitude and elevation were estimated for random points that were placed in each watershed (1 for every 2 km^2 of watershed area, with points placed at least 500 m apart) using GIS. Watersheds were delineated using GIS with the trap as the outlet point. Latitude, longitude, and

elevation for each point were used by ClimateNA to extrapolate monthly minimum, mean, and maximum air temperature and precipitation. We then averaged each variable for the summer (July to September; growing season), fall (October to December; spawning), winter (December to February; incubation), and premigration period (3 months before peak outmigration for each population) for each year. Using a linear model approach, we determined rate of change as the slope of the relationship between seasonal variable (temperature or precipitation) across years.

Biological variables included species and a categorical variable describing scale of local hatchery production. Species grouped all populations, no matter their age group, into one species. Hatchery influence was determined using a scale where 0 indicated no hatchery in the watershed, no history of hatchery influence, and the nearest hatchery was in a distant basin > 100 km away; Category 1 had no current hatchery production of the target species in the watershed, but either (a) hatchery production in a nearby watershed < 100 km away allowing for a low level of hatchery-origin strays, (b) some within basin hatchery production of the target species in the distant past (e.g., > 25 years ago), or both (a) and (b); Category 2 had ongoing, within basin hatchery production of the target species in which natural-origin fish typically outnumbered hatchery-origin fish on the spawning grounds (proportion of Hatchery Origin Spawners [pHOS] < 50%), and/or the number of natural-origin juveniles were comparable to, or greater than, the number of juveniles released from the hatchery. All or nearly all hatchery-origin fish were marked. Conservation hatchery programs employing a high proportion of natural-origin broodstock would likely be in this category; Category 3: Long history (multiple decades) of large-scale hatchery production in which hatchery-origin fish routinely outnumbered hatchery origin fish on the spawning grounds (i.e., pHOS > 50%), and/or the number of fish released from hatcheries was considerably greater than the number of natural-origin juveniles. Marking of

hatchery-origin fish allows for assessment of hatchery demographics compared to natural population demographics.

We compared weighted linear models containing key geographic (e.g., latitude of the capture location, distance between the capture location and the ocean, watershed area), environmental (e.g., rate of change of mean, minimum, and maximum seasonal air temperatures, and precipitation) and biological (e.g., species, scale of hatchery influence) variables. Linear models were weighted by the inverse of the variance in estimated rate of peak change, such that populations with higher variance in peak change estimate were weighted less than those with lower variance. Since species could be responding differently, we included interactions between species and other predictor variables. For the rare cases when traps were upstream of other traps, and therefore fish could be counted twice, we excluded the upstream trap from the analysis. This impacted only a few locations, and results did not differ if all populations or only mainstem populations were used. All populations were considered independent because most populations were the only monitored population in the watershed, so random effects models could not be fit. Apart from an interaction between species identity and trap elevation, no other variables or interactions explained variability in the rate of change in peak smolt outmigration timing (Extended Data Table 1, Extended Data Fig. 2). Post hoc comparison of rates of change of species showed on coho and chum salmon were changing at significantly different rates (Extended Data Table 2). We evaluated predictive performance of the top models using Monte Carlo cross-validation where the models were trained on 90% of the dataset and tested on the remaining 10%. This was completed 1000 times (each iteration assigning at random 90% of observations to the training set and 10% of observations to the test set). The overall RMSE was calculated by averaging the RMSE values from the 1000 test sets.

We examined time series length to determine how time series length may influence rate of peak change. A sensitivity analysis revealed that the 20-year minimum time series was sufficient to capture trends (Extended Data Fig. 1, Supplementary Information 1.1). We found no evidence to support an effect of time series length on rate of change in peak (Extended Data Table 3, Extended Data Figure 4) or evidence that different biological or environmental correlates impacted rate of peak change determined using the truncated time series (Extended Data Table 4).

We quantified within and across population variation, using an intercept-only random effects model which included species as a random effect to compare variance that was explained by all species vs. total residual variance (variance of the species intercept divided by the sum of the species intercept and individual population residual variance estimate, multiplied by 100) (*sensu*[47]). A value close to 100 suggests that among-species variation explains almost all of the total variation, such that two populations from the same species are likely to be more similar that two individuals from different species. A value near zero suggests that the among-species variation is relatively low, such that two populations from different species are equally likely to be similar than two populations from the same species.

Satellite-derived Chlorophyll a

Remote-sensing satellite-derived chlorophyll-a concentration (mg/m^3) estimates were used as a proxy for salmon prey phenology. We used level-3 processed daily global composites (9 km × 9 km) of surface chlorophyll-a concentration from two satellites, Sea-viewing Wide Field-of-view Sensor (SeaWiFS; 1999 - 2010) and the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua; 2003 - 2019) from the Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). Global daily composites were subset to 29 2^o × 2^o grid cells

along the coast between 42 – 60°N, 161.5 – 124.5°W (Extended Data Fig. 5). We concatenated daily composites into 8-day composites to limit missing data due to clouds. Finally, the 8-day composite surface chlorophyll-a concentration estimates for each 9 km × 9 km pixel were averaged to create an 8-day average for each grid cell. For overlapping years between 2003 – 2010, we compared 8-day average chlorophyll-a for each grid cell between SeaWiFS and MODIS-Aqua. Coefficients for grid cells were consistent with other studies[26,48]. Therefore, for the overlapping years we used the average of composites from both satellites. Satellite chlorophyll-a estimates generally correspond with field observations of phytoplankton except during extremely high phytoplankton concentrations, which would not effect our estimate of spring phenology[49]. However, satellite-derived bloom estimates are unable to distinguish between dominant phytoplankton species and may mask divergent or species- specific phytoplankton phenology changes, which have been previously documented[22]. We used 2° × 2° grid cells, as these regions would encompass a large proportion of the early marine period for salmon (Extended Data Fig. 5). Additionally, coastal regions are prone to high spectral reflectance for SeaWiFS and MODIS-Aqua satellites[49]. Using this method, we created sequential 8-day chlorophyll-a concentration estimates from Jan 1 to Aug 1 for 20 years spanning 1999 – 2019 for each grid cell.

We determined the annual spring phytoplankton bloom for each grid cell, and then calculated the rate of change in the bloom date across years. Spring phytoplankton bloom was defined as the first 8-day composite that was 5% above the annual mean for that grid cell[50]. We used spring phytoplankton phenology as an indicator of the beginning of spring productivity in the ocean, and the initialization of a surge of spring productivity that spans trophic levels. However, trophic levels may have different rates of phenological change, which our approach would not capture[6,7].

Rate of change in spring phytoplankton bloom date was then determined with a linear model of spring bloom date by year.

Changes in smolt outmigration phenology were then determined using only years between 1999 – 2019 (corresponding to availability of spring phytoplankton bloom data) (Extended Data Fig 5). Only populations with more than 10 years of data were used, as populations with less than this generally did not produce valid estimates of rates of change (see Extended Data Fig. 1). Of the original populations included only 60 populations had greater than 10 years of data collected between 1999 – 2019, as we included present and historic smolt datasets in our data collection. Comparison of shifts in outmigration timing using full vs. truncated datasets can be found in the supplementary information. Each salmon population was paired with the coastal region in which they would enter the ocean (i.e., marine entrance; Table S1).

Ethics and Inclusion Statement

Where necessary, data agreements were formed with data owners to maintain data sovereignty. The formal and informal agreements outlined the data and results sharing aspects of the project. Regardless of data agreements all data contributors (individuals, groups, organizations) were included in the study design phase, development of questions, and interpretation of the results. This was done through written proposals, webinars, and informal and formal written project updates.

All data contributors were provided an initial written project proposal and invited to a webinar where the project proposal was presented, and feedback was invited. The project proposal included questions, study design, aim and scope, and outlined expectations for authorship. All data contributors were welcome to authorship, given they met the following criteria: i) provided

data and/or ideas or assisted with analyses, ii) provided feedback on proposal through attendance of the webinar and/or written feedback, iii) provided feedback on the manuscript in a timely manner. Regardless of authorship status all data contributors were invited to a final webinar where results were presented, and there was an opportunity for feedback. A final report was distributed to all data contributors which shared analyses, main findings, and plan for publication.

When data was collected by Indigenous groups, data sharing agreements were made that respected data ownership/data sovereignty. These also included the mode of knowledge sharing preferred by data owners. Most data for this project were collected under the purview of Federal, Provincial, and State governments. However, we recognize that all of the data used in this project was collected on the traditional ancestral territories of Indigenous Peoples that have used and stewarded salmon for millennia. Increased revitalization of Indigenous-led fisheries programs has begun in the last 10 – 20 years[39], but in most cases these programs were too recent (too few years of data) to be included in our analyses.

Data Availability

Data will be available on Github or some other platform (Dryad). Data provided will be summarized yearly peak data and calculated peak change and peak range data.

Code Availability

Model code is available as an R package "phenomix" by Eric Ward on github at "ericward-noaa/phenomix".

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Author Contributions Statement

S.M.W collated data and completed analysis. S.M.W and J.W.M. designed the study and wrote the manuscript. E.J.W. developed models. All authors contributed to data collection and writing.

Competing Interests Statement

The authors declare no competing interests.

Figure Legends

Figure 1: Location of smolt enumeration facilities (right) and posterior distribution of the mean shift in outmigration peak phenology (left, top) and breadth of outmigration window (left, bottom) of six species of North American anadromous Pacific salmon (coho = green, pink = pink, chum = blue, steelhead = orange, sockeye = vermillion, Chinook = black). Left top panel: more negative values indicate species phenologies are shifting to be earlier in the year, whereas more positive values are shifting to be later in the year. Left bottom panel: more negative values indicate outmigration distributions of species are becoming narrower, whereas those with more positive values are becoming broader. (1/2 pg; 180 x 115mm)

Figure 2: Shift in peak outmigration phenology (left) and change in breadth of outmigration distribution (right) of populations of six species of North American anadromous Pacific salmon (coho = green, chum = blue, steelhead = orange, sockeye age 1+ = vermillion, sockeye age 2+ = dark vermillion, Chinook age 1+ = black, Chinook age 0+ = grey, odd year pink = dark pink, even year pink = light pink). Horizontal lines (error bars) represent 95% confidence interval, points represent mean. Where 95% confidence interval overlaps 0 (vertical dashed line), populations are not significantly changing outmigration date. Populations with more negative values are shifting to be earlier in the year or have narrower range in timing, whereas those with more positive values are shifting to be later in the year/wider outmigration window. Sites ordered by latitude (north to south, top to bottom), more information on sites, including sample size, is located in Table S1. (1/2 pg horizontal; 180 x 115 mm)

Figure 3: Differences in the rate of phenological mismatch between the spring phytoplankton bloom and salmon outmigration timing. Where modelled distribution of differences in rates (95% confidence interval) overlaps 0 (vertical dashed line) species phenologies are matching (shifting at the same rate), and departure from 0 indicates differing rates of phenological change and widening mismatch. Negative change ($y<0$) indicates that either 1) the spring phytoplankton bloom is becoming earlier relative to smolt migration or 2) the smolt outmigration is becoming later relative to the spring phytoplankton bloom, while positive change ($y>0$) indicates salmon outmigration is getting earlier relative to spring plankton phenology. Colours indicate the salmon species against which the rate of spring phytoplankton bloom phenology change was measured (coho = green, pink = pink, chum = blue, steelhead = orange, sockeye = vermillion, Chinook = black). Sites ordered by latitude (north to south, top to bottom), more information on sites is located in Table S1. (1/4 page vertical, 89 x 125 mm)

Figure 4: Response diversity of salmon populations to change in air temperature (in °C). Colours represent species and shade of line represents different populations. Grey shaded region represents 95% confidence region for slope of the relationship between average air temperature three months before migration and annual peak outmigration. A negative slope indicates that

peak outmigration timing was earlier in warmer years, where a positive slope indicates peak outmigration was later in warmer years.

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