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

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Samantha M. Wilson[1] ✉, Jonathan W. Moore[1], Eric J. Ward[2], Clayton W. Kinsel[3], Joseph H. Anderson[3], Thomas W. Buehrens[3], Charmaine N. Carr-Harris[4], Patrick C. Cochran[3], Trevor D. Davies[5], Mark R. Downen[3], Lyse Godbout[6], Peter J. Lisi[3], Marisa N. C. Litz[3], David A. Patterson[7], Daniel T. Selbie[8], Matthew R. Sloat[9], Erik J. Suring[10], Ian A. Tattam[11] & Garth J. Wyatt[12]

Global climate change is shifting the timing of life-cycle events, sometimes resulting in phenological mismatches between predators and prey. Phenological shifts and subsequent mismatches may be consistent across populations, or they could 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.

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 (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 such as

A full list of affiliations appears at the end of the paper. ✉e-mail: swilson471@gmail.com

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 (for example, meta-population). 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, 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 kilometres 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 (for example, boreal copepods, euphausiids, larval fish)[7,24,25]. Differential rates of change between salmon ocean arrival and prey availability could lead to phenological mismatches that 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 and 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 analysed a unique dataset on smolt outmigration phenology containing data from 66 populations (where population is considered a unique site-species combination) spanning 18° latitude (~3,500 km) from Alaska to Oregon, for a time series ranging between 1951 and 2019 (a combined 1,858 years of data). We paired this dataset with the spring phenology of coastal Pacific Ocean primary productivity, as derived from satellite-inferred chlorophyll-a concentration (Sea-viewing Wide Field-of-view Sensor (SeaWiFS), Moderate Resolution Imaging Spectroradiometer-Aqua (MODIS-Aqua)).

Results

Changes in smolt outmigration phenology

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

Some species exhibited high rates of phenological change in peak timing, while others did not change substantially over the observed period (Fig. 1). Chum (*O. keta*) and pink (*O. gorbuscha*) salmon, which emigrate soon after emergence, had the fastest average rate of advancement in outmigration timing (mean = 7.8 days per decade and 5 days per decade earlier, respectively; Fig. 1). Coho salmon and steelhead trout, which generally spend one or more years in fresh water after emergence, had much lower average rates of peak change (mean = 0.1 days per decade and 0.5 days per 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 per 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 per 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. These results were not impacted by the length of the time series (Extended Data Table 2–4). Thus we discovered that across their North American range, different salmon species have different average rates of phenological change that were not strongly associated with measured environmental or geographic 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 per 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 per decade), 17 of 26 populations were trending towards advancing phenology, whereas nine 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-Aqua satellites; chlorophyll-a) to quantify the potential mismatch between salmon phenology and the phenology of ocean prey.

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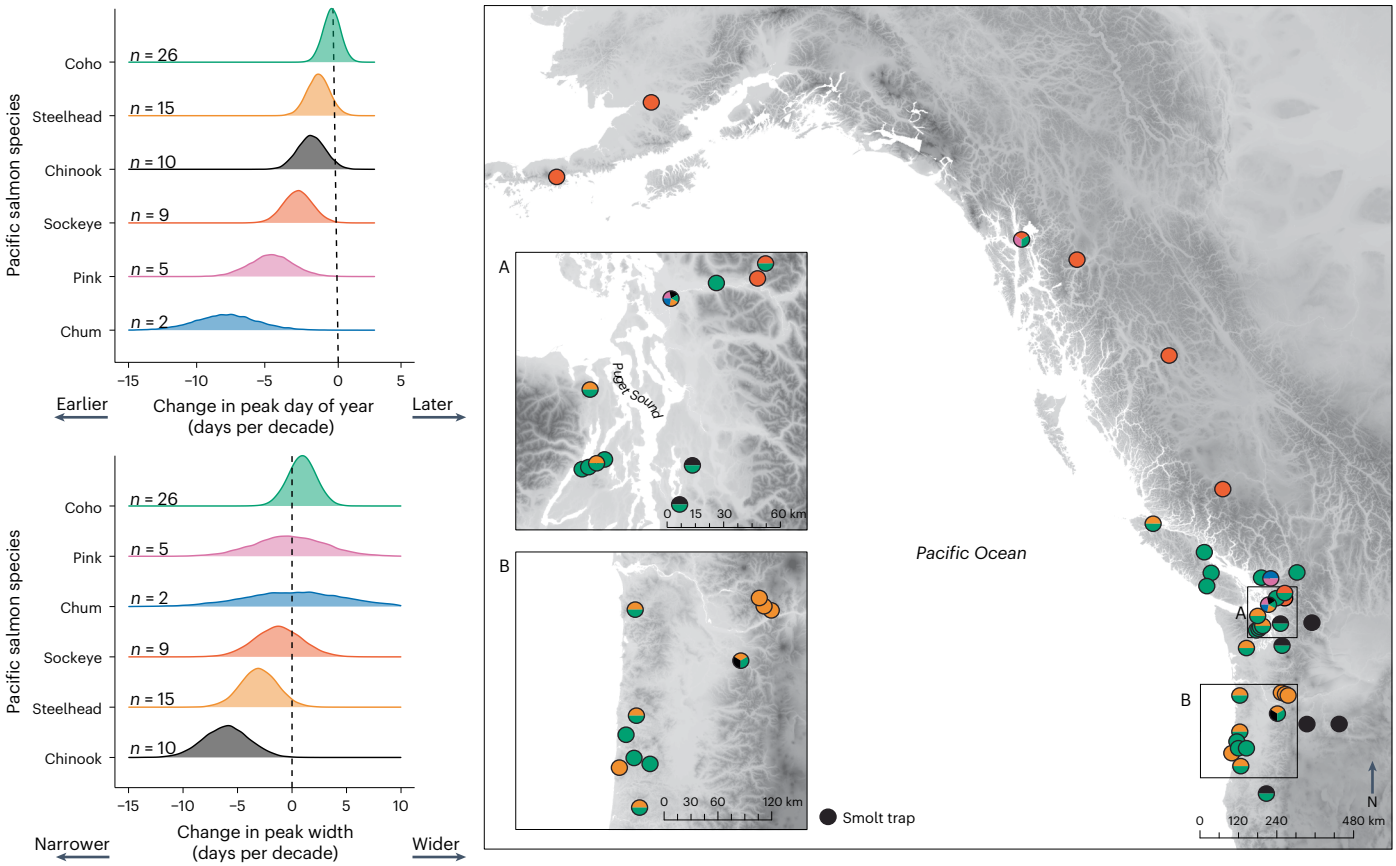

Fig. 1 | Species-specific shifts in outmigration phenology. Location of smolt enumeration facilities (right) and posterior distribution of the mean shift in outmigration peak phenology (left, top) and breadth of outmigration window (left, bottom) of six species of North American anadromous Pacific salmon (coho = green, pink = pink, chum = blue, steelhead = orange, sockeye = vermillion, Chinook = black). Left top: 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: more negative values indicate outmigration distributions of species are becoming narrower, whereas those with more positive values are becoming broader.

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 prey phenology. We compared the rate of change in peak smolt outmigration phenology between 1999 and 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 and Extended Data Fig. 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 and Extended Data Figs. 3–5). Where phytoplankton phenologies were changing, more salmon were lagging behind spring phytoplankton phenological change rather than outpacing it. Specifically, 13 of 60 populations had substantially increasing temporal mismatches (greater than eight days per decade difference in the rate of phenological shifts between 1999 and 2019), with 12 of the 13 salmon populations lagging behind the advancement of the spring phytoplankton bloom, and only one of 13 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 species resilience, unpredictable changes could complicate broad assessments of climate vulnerability and prescriptive management of populations.

Peak outmigration phenology changed at different rates across species, a result consistent with smaller-scale studies of salmon outmigration phenology[3,27,28]. Chum and pink salmon shifted their peak phenology more quickly than other species. However, chum and pink salmon were represented by a small number of sample sites due to limited funds for expensive long-term monitoring programmes. Despite the small sample sizes, individual chum populations had higher rates of change than individual populations within other species, indicative of species-level increased rates of phenological shifts. The deficiency

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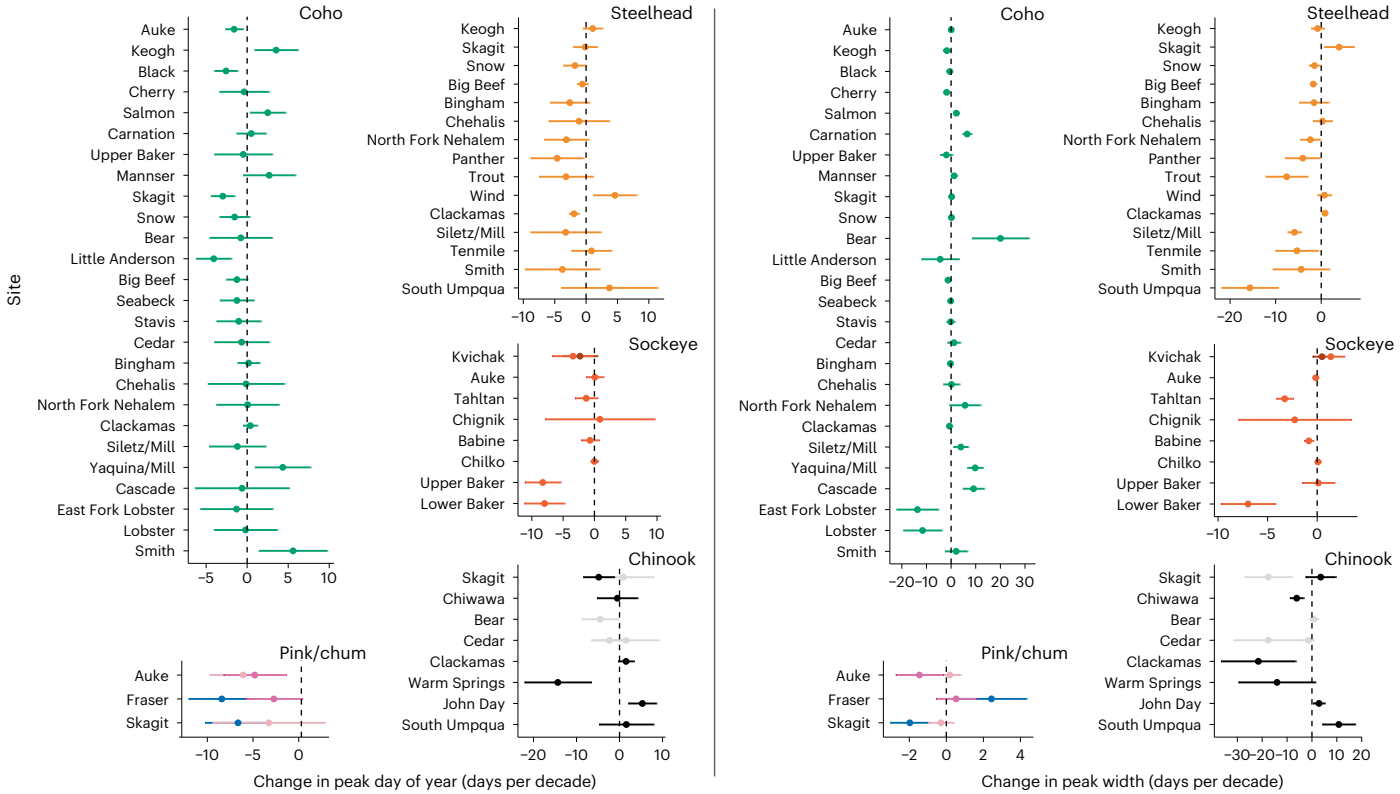

Fig. 2 | Population-specific outmigration phenology in six Pacific salmon species. Shift in peak outmigration phenology (left) and change in breadth of outmigration distribution (right) of populations of six species of North American anadromous Pacific salmon (coho = green, chum = blue, steelhead = orange, 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 Supplementary Table 1.

in data collection on pink and chum salmon limits understanding of climate change-driven impacts on these widely distributed and important species. While pink and chum salmon had shifting phenologies, on average, coho salmon phenologies were not shifting, consistent with previous studies. For example, peak outmigration timing of Auke Creek, Alaska, odd-year pink salmon advanced by 4.9 days per decade (ref. 3), whereas peak outmigration of Auke Creek coho salmon did not change over a 37-year period. Thus we discovered that across their North American range, different salmon species have different average rates of phenological change.

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

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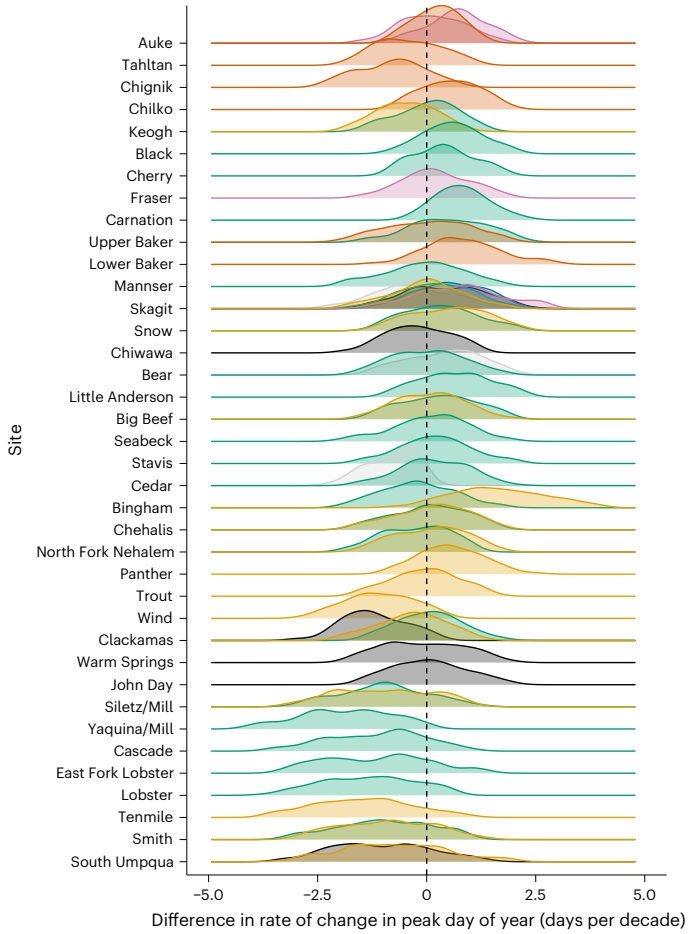

Fig. 3 | Mismatch between the rate of change in peak smolt outmigration phenology and the rate of change in the spring phytoplankton bloom. Differences in the rate of phenological mismatch between the spring phytoplankton bloom and salmon outmigration timing. Where modelled distribution of differences 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 Supplementary Table 1.

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 chlorophyll-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 chlorophyll-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 adaptations, life histories or unassessed natal watershed characteristics. With sufficient investment in monitoring and management, a more place-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 the conservation of 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 occasionally the fall, after spending between several weeks to several years in fresh water. Federal, state, provincial and Indigenous governments in the United States and Canada and community groups have been monitoring smolt emigration since the mid-1950s. These monitoring programmes 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

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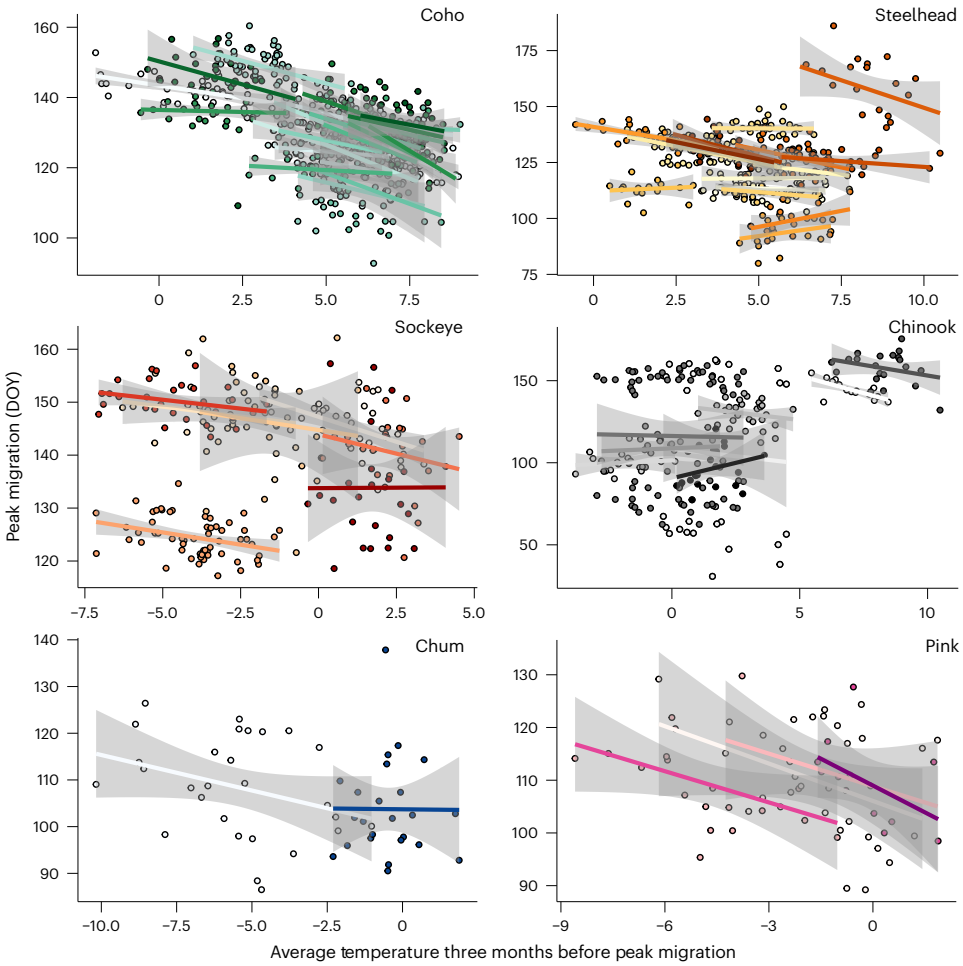

Fig. 4 | Response of salmon outmigration phenology to air temperature changes. Response diversity of salmon populations to change in air temperature (in °C). Colours represent species and shade of line represents different populations. Grey shaded region represents 95% confidence region for slope of the relationship between average air temperature three months before migration and annual peak outmigration day of year (DOY). 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.

using mark-recapture methods where a subset of fish were captured in traps (for example, 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 modelled annual emigration for each population to identify peak and breadth of outmigration (that is, 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 (for example, 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 modelled throughout the migration window using one of four hierarchical models. We used hierarchical 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.

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

Second, we used a Student's t distribution, which differs from the normal distribution in that when the degrees-of-freedom parameter is small, the Student's t distribution can have more extreme tails.

$$f(x) = \text{Student's}\,t\,(\mu, \upsilon, \sigma_x) \quad (2)$$

Application of either the normal or Student's 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 such as selectivity[41]. This distribution involves fitting two truncated

normal distributions, joined by a common mean, but allowed to have different variances.

$$f(x) = \left\{ \begin{array}{l} \text{normal}\left(\mu, \sigma_{x_1}\right), x < \mu \\ \text{normal}\left(\mu, \sigma_{x_2}\right), x > \mu \end{array} \right\} \quad (3)$$

For the purposes of our application, this translates to the shape of outmigration before and after the peak being different. Finally, as a fourth model, we extended the double-normal concept to a double Student's *t* distribution. This double Student's *t* differed from the double normal in allowing both the variance and degrees of freedom to differ between pre- and post-peak curves.

$$f(x) = \left\{ \begin{array}{l} \text{Student's } t\left(\mu, \upsilon_1, \sigma_{x_1}\right), x < \mu \\ \text{Student's } t\left(\mu, \upsilon_2, \sigma_{x_2}\right), x > \mu \end{array} \right\} \quad (4)$$

Equations (1)–(4) describe process models fit to daily smolt abundance in a single year, modelled 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 υ 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's *t* or double Student's *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:

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

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

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 modelled random effects in log space so that σ_y is the standard deviation in year *y* (for example, for models (1) and (2) above), $\ln(\sigma_0)$ is the mean shape parameter and γ_σ is the standard deviation among shape parameters. Because both trends are modelled 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:

$$\mu_y \sim \text{normal}\left(\mu_0 + \beta_\mu \times \upsilon, \sigma_\mu\right) \quad (7)$$

$$\ln\left(\sigma_y\right) \sim \text{normal}\left(\ln\left(\sigma_0\right) + \beta_\sigma \times \upsilon, \gamma_\sigma\right) \quad (8)$$

All other parameters are as before, but the inclusion of β_μ and β_σ allow for linear trends in the location and shape of these distributions through time. Equations (7) and (8) describe changes for symmetric models with a single variance parameter (equations (1) and (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[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); we refer to the number of days between the 25th and 75th quartiles as the range of the data for each year. The annual trend in peak width was modelled 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 the 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 change in minimum, mean and maximum air temperature and precipitation between the first year of monitoring and 2013 (Supplementary Table 1). 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 programme ClimateNA (v.5.21)[46]. Briefly, latitude, longitude and elevation were estimated for random points that were placed in each watershed (one for every 2 km^2 of watershed area, with points placed at least 500 m apart) using ArcGIS. Watersheds were delineated using ArcGIS 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 (1) hatchery production in a nearby watershed < 100 km away allowing for a low level of hatchery-origin strays, (2) some within-basin hatchery production of the target species in the distant past (for example, > 25 years ago), or both (1) and (2); 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 < 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 programmes employing a high proportion of natural-origin broodstock would probably 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 (that is, proportion of Hatchery Origin Spawners > 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 with natural population demographics.

We compared weighted linear models containing key geographic (for example, latitude of the capture location, distance between the capture location and the ocean, watershed area), environmental (for example, rate of change of mean, minimum and maximum seasonal air temperatures and precipitation) and biological (for example, 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. Because 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 and Extended Data Fig. 2). Post hoc comparison of rates of change of species showed 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 1,000 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 1,000 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 and 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 and Extended Data Fig. 5) 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 that 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 lato[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 than 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, SeaWiFS (1999–2010) and the MODIS-Aqua (2003–2019) from the Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov). Global daily composites were subset to 29 2° × 2° grid cells along the coast between 42–60° N, 161.5–124.5° W (Extended Data Fig. 4). We concatenated daily composites into eight-day composites to limit missing data due to clouds. Finally, the eight-day composite-surface chlorophyll-a concentration estimates for each 9 km × 9 km pixel were averaged to create an eight-day average for each grid cell. For overlapping years between 2003 and 2010, we compared eight-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. 4). Additionally, coastal regions are prone to high spectral reflectance for SeaWiFS and MODIS-Aqua satellites[49]. Using this method, we created sequential eight-day chlorophyll-a concentration estimates from 1 January to 1 August 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 eight-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 and 2019 (corresponding to availability of spring phytoplankton bloom data) (Extended Data Fig. 5). Only populations with more than ten years of data were used, as populations with less than this generally did not produce valid estimates of rates of change (Extended Data Fig. 1). Of the original populations included, only 60 populations had greater than ten years of data collected between 1999 and 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 (Extended Data Fig. 5). Each salmon population was paired with the coastal region in which they would enter the ocean (that is, marine entrance; Supplementary Table 1).

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: (1) provided data and/or ideas or assisted with analyses, (2) provided feedback on proposal through attendance of the webinar and/or written feedback, (3) 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 that 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 programmes has begun in the last 10–20 years[39], but in most cases, these programmes were too recent (too few years of data) to be included in our analyses.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are available on Dryad (https://doi.org/10.5061/dryad.dfn2z356g). Data provided are calculated peak-change and peak-range data. Source data are provided with this paper.

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

S.M.W. collated data and completed analysis. S.M.W. and J.W.M. designed the study and wrote the paper. E.J.W. developed models. S.M.W., J.W.M., E.J.W., C.W.K., J.H.A., T.W.B., C.N.C.-H., P.C.C., T.D.D., M.R.D., L.G., P.J.L., M.N.C.L., D.A.P., D.T.S., M.R.S., E.J.S., I.A.T. and G.J.W. contributed to data collection and writing.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Samantha M. Wilson.

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[1]Earth to Ocean Research Group, Simon Fraser University, Burnaby, British Columbia, Canada. [2]Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, USA. [3]Washington Department of Fish and Wildlife, Olympia, WA, USA. [4]Fisheries and Oceans Canada, North Coast Stock Assessment Division, Prince Rupert, British Columbia, Canada. [5]British Columbia Ministry of Forests, Fish and Wildlife Branch, Victoria, British Columbia, Canada. [6]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada. [7]Fisheries and Oceans Canada, Cooperative Resource Management Institute, School of Resource and Environmental Management Simon Fraser University, Burnaby, British Columbia, Canada. [8]Fisheries and Oceans Canada, Pacific Region, Science Branch, Cultus Lake Salmon Research Laboratory, Cultus Lake, British Columbia, Canada. [9]Wild Salmon Center, Portland, OR, USA. [10]Corvallis Research Laboratory, Oregon Department of Fish and Wildlife, Corvallis, OR, USA. [11]East Region Fish Research, Oregon Department of Fish and Wildlife, Eastern Oregon University, La Grande, OR, USA. [12]Portland General Electric, Estacada, OR, USA. ✉e-mail: swilson471@gmail.com

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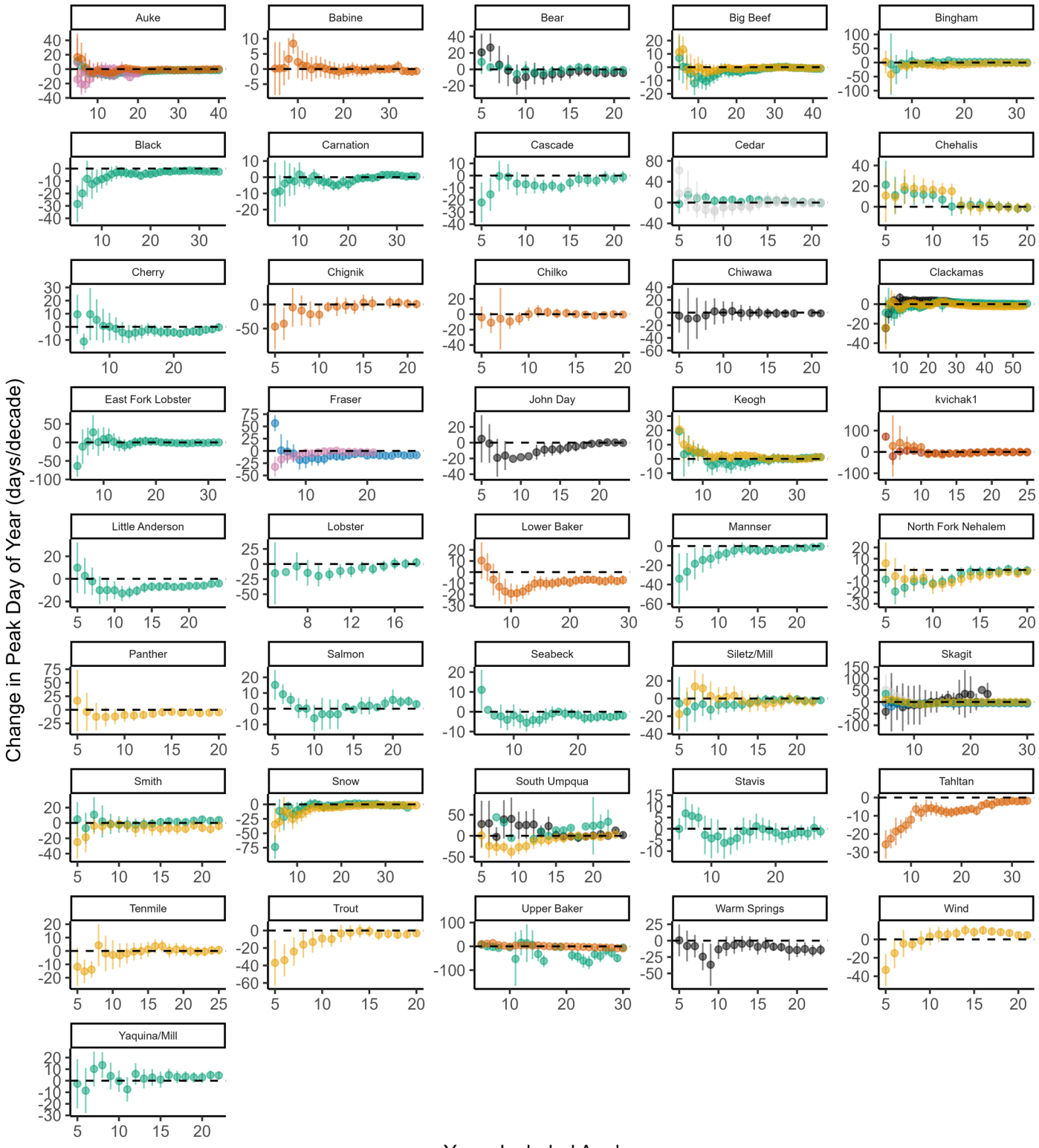

Extended Data Fig. 1 | Rate of change in peak outmigration timing modelled with increasing numbers of sequential years of data. Rate of change was calculated beginning with using only the five most recent years of outmigration data and re-running the analysis again for each successive year added. Thus, each point above represents a model run, beginning with five which included the most recent five years of data, and ending with the complete dataset. Species are represented by colours with coho (green), pink (pink), sockeye (vermillion), Chinook (black), chum (blue) and steelhead (orange). Vertical lines (error bars) represent 95% confidence interval, point represents mean. When models did not converge, confidence intervals were not produced. More information on sites is located in Supplementary Table 1.

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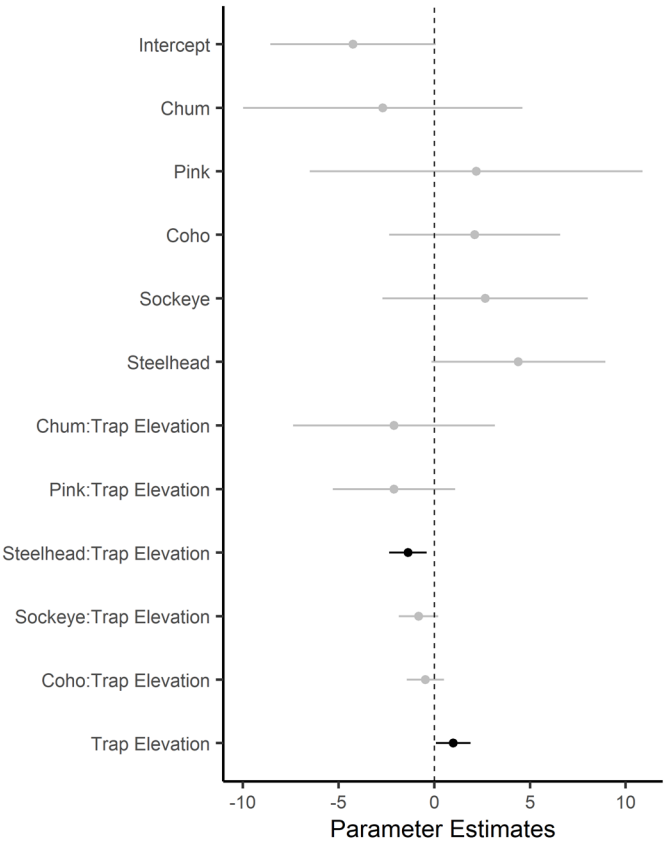

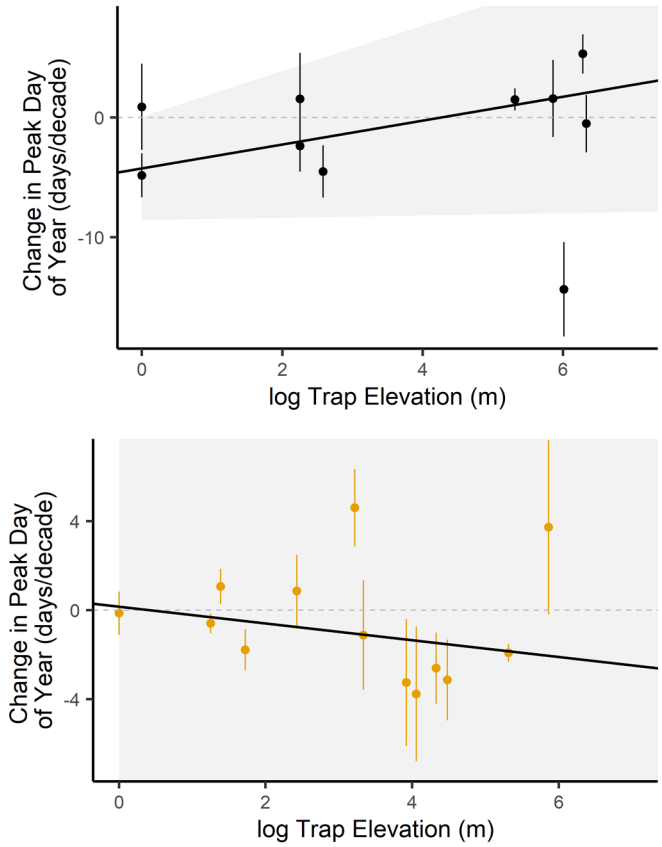

Extended Data Fig. 2 | Top model parameter estimates for shifts in peak outmigration phenology. Top model parameter estimates (left) and the relationship between log trap elevation and change in peak phenology for Chinook salmon (right, top) and steelhead trout only (right, bottom). Left panel: black bars are parameters for which confidence intervals do not overlap with zero, indicating a significant effect; grey bars overlap zero and are not significant. Point is the mean, horizontal error bars represent the 95% confidence interval. Right panel: colours indicate the salmon species (coho = green, pink = pink, chum = blue, steelhead = orange, sockeye = vermillion, Chinook = black), grey background indicates 95% confidence region for relationship between log trap elevation and rate of change in peak outmigration timing. More information on sites is located in Supplementary Table 1.

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Extended Data Fig. 3 | Comparison of the rate of change in peak outmigration timing for salmon and spring phytoplankton phenology. Rate of change in peak outmigration timing for salmon (coho (green), pink (pink), sockeye (vermillion), Chinook (black), chum (blue) salmon and steelhead (orange) trout) and spring phytoplankton phenology (dark green) between 1999 and 2019 (truncated salmon time series). Where curve (95% confidence interval) overlaps 0 (horizontal dashed line) species phenologies are not shifting. Overlap between spring phytoplankton phenology and salmon phenology curves indicates that they are shifting at the same rate.

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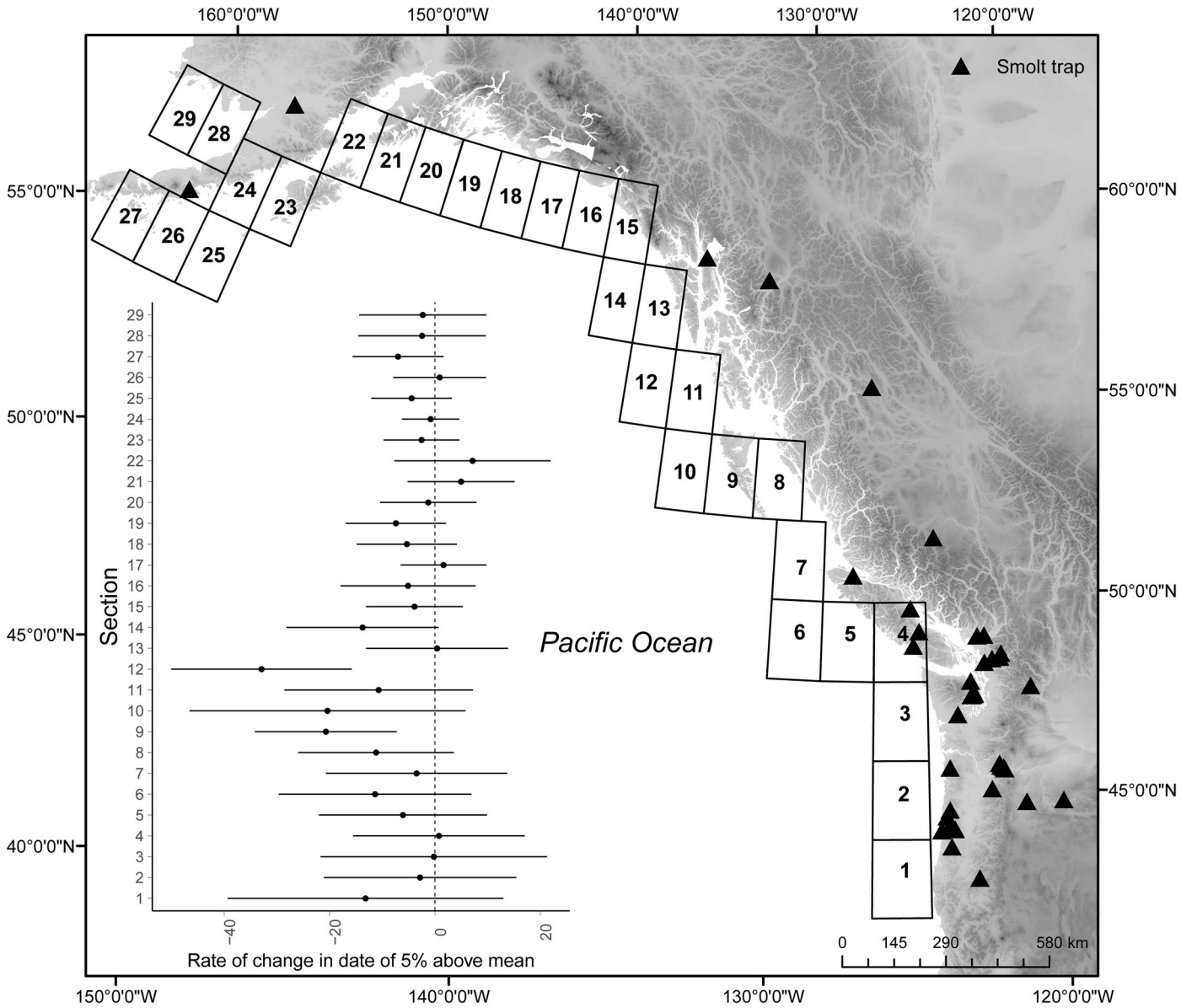

Extended Data Fig. 4 | Map of satellite derived chlorophyll-a 2 × 2 degree sections 1–29, with trap locations (black triangles). Inset is the rate of change in initial peak of chlorophyll-a (first day above the 5% of the annual mean chlorophyll-a) time period spans from 1999–2019 (n = 20 for all sections). Points represent mean rate of change, horizontal error bars represent 95% confidence intervals.

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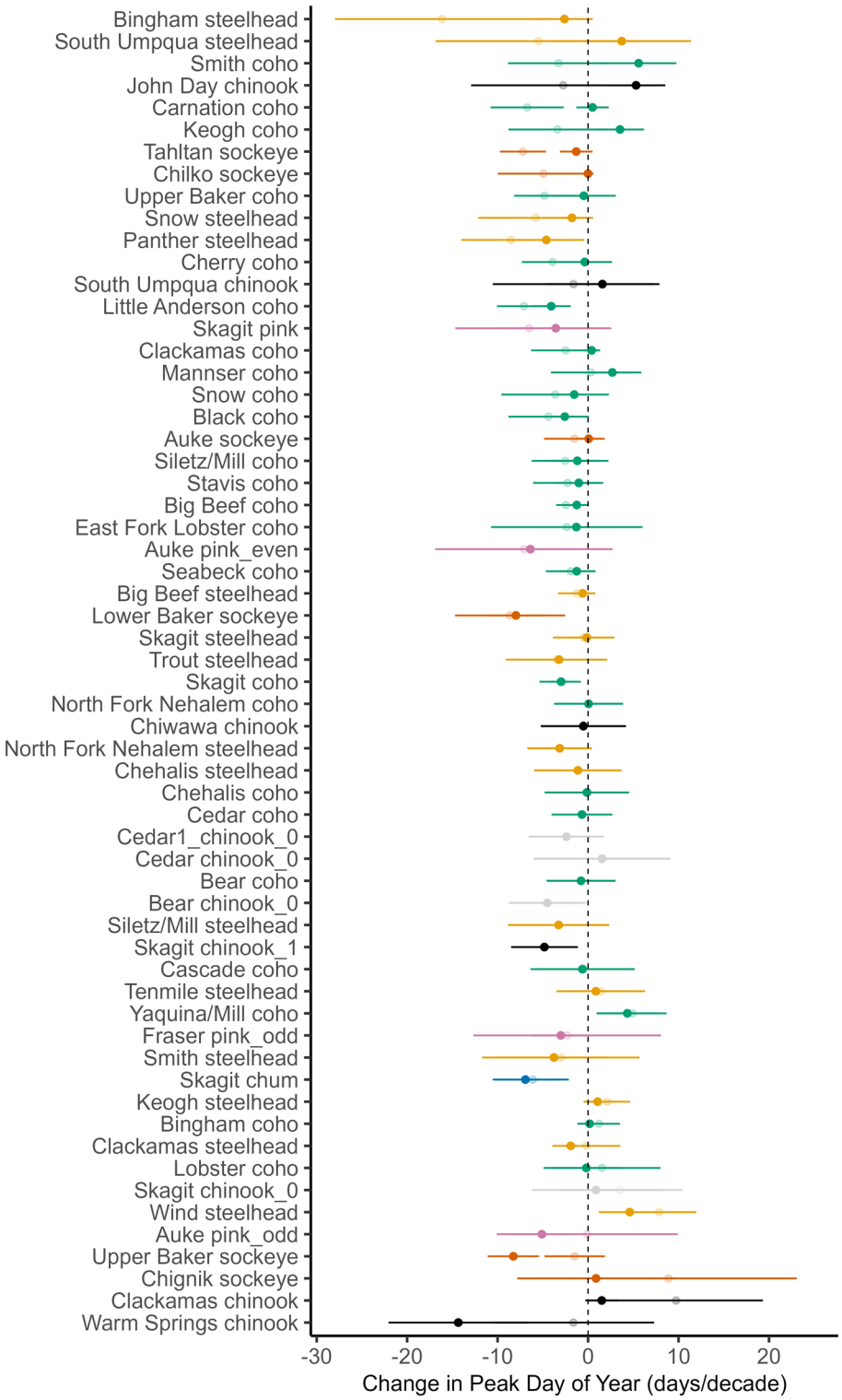

Extended Data Fig. 5 | Comparison of rate of change in peak migration timing for full vs. truncated time series. Full time series includes all years when data were collected (closed circles), whereas truncated time series includes only smolt data collected from 1999–2019 (open circles). Colours indicate species where orange = steelhead trout, green = coho, black = Chinook, vermillion = sockeye, blue = chum, light pink = odd-year pink, dark pink = even year pink salmon. Ordered by difference in change of peak from negative to positive. More information on sites is located in Supplementary Table 1.

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Extended Data Table 1 | Top 10 models based on AICc ranking predicting change in peak outmigration day for full length dataset

Model Structure	K	ΔAIC	ω
Species * Trap Elevation	13	0.0000	0.1691
Species	7	2.1409	0.0580
Species + Trap Elevation	8	2.2325	0.0554
Species + Latitude	8	3.0083	0.0376
Species + Area	8	3.0602	0.0366
Trap Elevation	3	3.5032	0.0293
Species + Hatchery Scale	10	3.5748	0.0283
Species + Distance to Ocean	8	3.5948	0.0280
Species + Fall Max Air Temperature	8	3.8182	0.0251
Species + Mean Air Temp 3 months before migration	8	3.9564	0.0234

Bold models are top models as determined by ΔAICc <2.

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Extended Data Table 2 | P values of Bonferroni post hoc pairwise comparisons of the rate of change in peak phenology across species for full dataset

	Chinook salmon	Chum salmon	Coho salmon	Pink salmon	Sockeye salmon
Chum salmon	0.176				
Coho salmon	1.000	**0.018**			
Pink salmon	1.000	1.000	0.149		
Sockeye salmon	1.000	0.268	1.000	1.000	
Steelhead trout	1.000	0.051	1.000	0.478	1.000

Bold items indicate a significant effect with a $\alpha = 0.05$.

https://doi.org/10.1038/s41559-023-02057-1

Extended Data Table 3 | Model results of weighted linear model of time series length on the rate of shift in migration timing

Model Term	Coefficients (95% CI)
Intercept	-0.2277 (-0.8297, 0.3742)
Number of years	0.0063 (-0.0078, 0.0204)
Chum	0.4226 (-4.9931, 5.8384)
Coho	0.0545 (-0.5956, 0.7046)
Pink	0.2817 (-1.2706, 1.8339)
Sockeye	-0.0800 (-0.8199, 0.6598)
Steelhead	0.3926 (-0.2945, 1.0797)
No. years * chum	-0.0418 (-0.2374, 0.1537)
No. years * coho	-0.0033 (-0.0188, 0.0122)
No. years * pink	-0.0232 (-0.0713, 0.0249)
No. years * sockeye	-0.0012 (-0.0173, 0.0150)
No. years * steelhead	-0.0125 (-0.0285, 0.0035)

Coefficients are in days/year. No. years is the number of years of data included in the time series

https://doi.org/10.1038/s41559-023-02057-1

Extended Data Table 4 | Top model (<2 ΔAIC) and geographic, environmental, and biological predictor coefficients for change in peak outmigration day for truncated time series (1999–2019)

Model Terms	Coefficients (95% CI)
Intercept	**1.3126 (0.1310, 2.4940)**
Latitude	**-0.0314 (-0.0559, -0.0070)**

Coefficients are in days/year. Bold items indicate a significant effect, where the 95% confidence interval (95% CI) does not span 0.

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Corresponding author(s): Samantha Wilson

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☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Data processing was completed using R (v.3.6.3, 2020)
Data analysis	All models were fit separately to each dataset using maximum likelihood approaches, implemented in Template Model Builder and R (v3.6.3, 2020). Model code is available as an R package "phenomix" by Eric Ward on github at "ericward-noaa/phenomix".

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Data are available on Dryad. Data include summarized calculated peak change, peak range data and associated uncertainty as well as co-variates. DOI 10.5061/dryad.dfn2z356g

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Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Study was completed in two steps. Step 1: Model rate of change in peak outmigration timing, and rate of change in range of outmigration timing. Step 2: Using weighted linear regression determine variables (from a set of available environmental and biological variables) that can predict shifts in outmigration timing.
Research sample	Collated 42 datasets of 66 site-species combinations for six species of Pacific salmon. We considered unique site-species combination to be a population. Each dataset was at least 20 years long. Data was collected by federal, state, provincial and indigenous governments and organizations (see Table S1 for description).
Sampling strategy	Sample sizes were limited by the number of datasets of the required length (20 years)
Data collection	Datasets were collected between 2017 - 2019. All datasets that were 20 years long and counted hatchery fish separately from wild fish were included in the study. We used a combination of word-of-mouth and targeted emails to gather datasets
Timing and spatial scale	As many datasets as possible between Alaska to Oregon, with hatchery fish marked separately, that were at least 20 years in length.
Data exclusions	No data were excluded
Reproducibility	We created an R package 'phenomix' which can be used to reproduce data analysis. Data are available on Dryad
Randomization	Not relevant. Datasets were collected on salmon streams throughout coastal PNW. There was not need to randomize sampling.
Blinding	Not relevant.

Did the study involve field work? ☐ Yes ☒ No

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☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
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