

# Temporal patterns and ecosystem correlates of chum salmon (*Oncorhynchus keta*) migration phenology in the Pacific Northwest

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**Abstract:** Understanding and quantifying migration phenology of commercially harvested Pacific salmon (*Oncorhynchus* spp.) is a cornerstone for managing sustainable populations. Here, we use a multidecadal data time series together with a hypothesis-driven framework to evaluate migration phenology in adult fall and winter ecotype chum salmon (*O. keta*) in a poorly studied but highly managed system — the South Puget Sound (SPS) of Washington State, USA. Using generalized additive mixed models that accounted for temporal autoregressive dynamics, we examined the effect of commercial harvest, climate variation, intraspecific density dependence, and predator buffering on migration timing and run duration. SPS chum salmon are migrating earlier over time, especially the winter ecotype that showed the strongest temporal shift from historical timing. Migration timing shifts were closely associated with regional marine climate regimes, local scale freshwater availability, and increasing pinniped abundance. We conclude that there is potential for the winter ecotype migration converging with that of the fall ecotype and that directional change in migration phenology may be driven by a unique combination of ecosystem factors.

**Résumé :** La compréhension et la quantification de la phénologie des migrations des saumons du Pacifique (*Oncorhynchus* spp.) faisant l'objet d'une exploitation commerciale constituent un des éléments essentiels de la gestion de populations pérennes. Nous utilisons une série de données multidéennales jumelée à un cadre modulé par différentes hypothèses pour évaluer la phénologie de la migration de saumons kétas (*O. keta*) adultes des écotypes automnal et hivernal dans un système peu étudié, mais faisant l'objet d'une gestion intense, le sud du Puget Sound (SPS, État de Washington, États-Unis). En utilisant des modèles mixtes additifs généralisés qui tiennent compte de la dynamique autorégressive temporelle, nous examinons les effets de l'exploitation commerciale, des variations climatiques, de la dépendance intraspécifique sur la densité et de la modulation par les prédateurs sur le moment et la durée des migrations. Les saumons kétas du SPS migrent de plus en plus tôt, en particulier ceux de l'écotype hivernal, qui présentent le plus grand décalage temporel par rapport aux observations passées. Les changements du moment de la migration sont étroitement associés aux régimes climatiques marins régionaux, à la disponibilité locale d'eau douce et à l'augmentation de l'abondance de pinnipèdes. En conclusion, il est possible que la migration de l'écotype hivernal converge avec celle de l'écotype automnal et que les changements directionnels de la phénologie des migrations soient modulés par une combinaison unique de facteurs écosystémiques. [Traduit par la Rédaction]

## Introduction

Predicting migratory behavior of commercially harvested salmonids is important for managing and maintaining sustainable populations. However, evaluating the underlying biotic and abiotic mechanisms that drive migration phenology remains complex, as it requires long-term systematic monitoring and corresponding relevant ecological and environmental data. In response to these challenges, recent advances in tracking technology, ocean climate modeling, genetics, and ecosystem monitoring have paved the way for improving our knowledge base (Iverson et al. 2019). Nevertheless, a rapidly changing climate in concert with spatially variable adaptive management strategies over the past several decades have altered the ecology of some salmonid populations, thereby reducing predictability of regional migration behavior and limiting the ability of local fisheries managers to respond to variations in run timing of critical populations.

For commercially exploited anadromous salmonids, quantitatively evaluating the effects of human-induced selection (i.e., harvest and hatchery), predatory selection, and adaptation to climate variation on migratory behavior can be challenging and complex (Kuparinen and Merilä 2007). For instance, early spawning migration timing due to climate warming may be a maladaptive strategy because the risk of prespawn mortality or spawning failure may increase with elevated water temperatures earlier in the year (Morita 2019; Taylor 2008). Thus, it is suspected that harvesting of late migrants by fisheries along with hatchery-based practices that select for early arriving spawners to meet spawning goals may be advancing timing of spawning (Morita 2019; Quinn et al. 2007; Tillotson et al. 2018; Tillotson and Quinn 2018). Consequently, increased fishing pressure later in the year may drive or amplify selection against a late-migration phenotype and impact population sustainability of an individual ecotype within a region (Morita 2019).

Received 14 October 2020. Accepted 22 March 2021.

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**Table 1.** Hypothesized explanatory indicators relating to chum salmon migratory phenology in the South Puget Sound of Washington State.

Hypotheses	Geographic scale	Indicators–mechanisms
H1 — Run timing vs. year and ecotype	Regional and local	Year by ecotype (winter vs. fall)
H2 — Duration vs. midpoint and ecotype	Regional and local	Midpoint by ecotype (winter vs. fall)
H3 — Run timing vs. peak of harvest timing	Regional and local	Annual peak week of harvest
H4 — Run timing and duration vs. local environmental variation and ecotype	Local	Precipitation, freshwater availability by ecotype (winter vs. fall)
H4 — Run timing and duration vs. regional environmental variation and ecotype	Regional	Sea surface temperature, sea surface salinity by ecotype (winter vs. fall)
H5 — Run timing and duration vs. intraspecific density dependence and ecotype	Regional	Total returning run size by ecotype (winter vs. fall)
H6 — Run timing and duration vs. predator buffering and ecotype	Regional	Seal density by ecotype (winter vs. fall)

Along with direct anthropogenic effects, recent studies have documented that climate warming in the Anthropocene is correlated with phenological shifts in life-history events and a rapid evolution of migration timing across many marine vertebrates (Crozier and Hutchings 2014; Manhard et al. 2017; Anderson et al. 2013; Crozier et al. 2011), including Pacific salmon and steelhead (*Oncorhynchus* spp.) (Kovach et al. 2015; Cooke et al. 2004; Kennedy and Crozier 2010). For multiple species of Pacific salmonids, adult migration has shifted earlier or later in the year and shortened in duration, resulting in natural selection against season-based ecotypes and observable genetic changes to populations (Kovach et al. 2012, 2015; Manhard et al. 2017). The phenological synchrony occurring within and across Pacific salmonid species suggests that large-scale climate processes may play a role in migration timing. Indeed, observed shifts in adult salmon migration timing have been linked to various climatic phenomenon. For example, negative correlations exist between migration timing and sea surface temperature operating at regional scales in Alaska (Kovach et al. 2015; Carey et al. 2017). Thus, rapidly changing marine conditions such as recent marine heatwaves in the eastern Pacific may alter selection pressures on phenology (Gienapp et al. 2014; Nielsen et al. 2020).

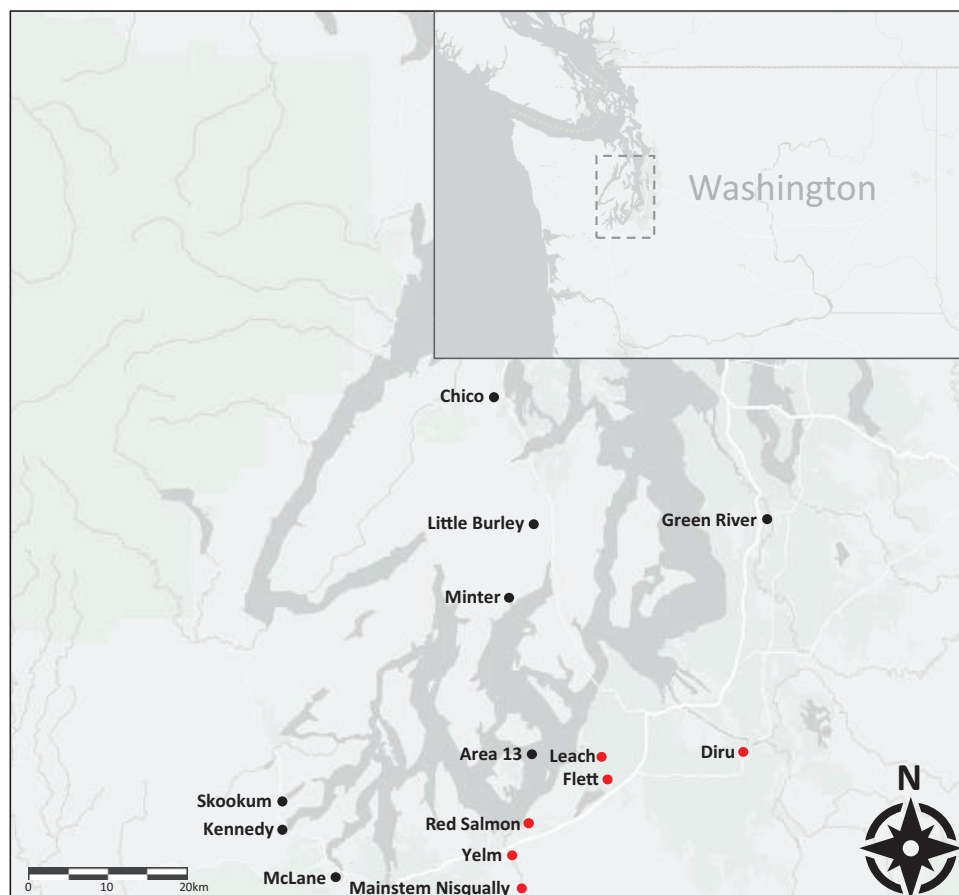
Aside from recent stochastic marine climate variability, studies examining higher rates of Pacific salmon predation by large marine mammals have recently increased in the literature (Velikanov and Radchenko 2013; Shuntov and Ivanov 2015; Chasco et al. 2017; Thomas et al. 2017; Wargo Rub et al. 2019). Results from recent studies have suggested that salmon productivity shows a stronger relationship with pinniped density (i.e., predatory–prey interactions) than that of anthropogenic factors such as hatchery releases (Nelson et al. 2019; Kendall et al. 2020; Berejikian et al. 2016). Thus, higher predator abundances over the last decade are hypothesized to have a similar selection effect on salmon mortality as coastal fishing, by efficiently selecting or targeting larger-bodied individuals, particular stocks, ecotypes, or species (Morita 2019). Therefore, it is suspected that predators synchronize presence with adult salmon migrations (Nelson et al. 2019; Morita 2019).

Intra- and interspecific density-dependent effects on salmon survival, growth, and life history are well known for outmigrating juvenile salmon (Skoglund et al. 2011; Rich et al. 2009); however, heritability of phenotypic variation in migration timing and its relationship with density-mediated phenological effects in adult salmon have been poorly documented in the literature. Nevertheless, some have suspected that interannual abundances are correlated with directional shifts in spawning migration timing and run duration (Carey et al. 2017). Directional selection in migratory phenology can be associated with abundance; thus, overall declines in salmon abundance may result in density-dependent effects or loss of phenotypic variation that is reflected in their migratory phenology.

Chum salmon (*Oncorhynchus keta*) are an ecologically and economically important species throughout their range in North America due to their large size, characteristically high densities, and extensive commercial harvest. Chum salmon also have the widest natural geographic distribution of any of the Pacific salmonids and are historically one of the most abundant (Groot and Margolis 1991). Chum salmon spend the vast majority of their life in marine waters but spawn and hatch in fresh water. Specifically, juveniles emerge from the gravel in spring, maturing from ages 2 to 6 in the Pacific Ocean, and return to spawn in their natal stream as late summer, fall, or early winter ecotypes (i.e., migratory phenotypes; Groot and Margolis 1991). During these critical adult migratory periods of the year, the timing of seasonal changes of river flow and water availability are critical factors for determining arrival timing of chum salmon on the spawning grounds (Connor and Pflug 2004). For instance, chum salmon are adapted morphometrically to river flow in their natal streams (Beacham 1984) and thus require a minimum threshold of water availability to initiate spawning migration. Furthermore, some studies have suggested that sea surface salinity and temperature changes, which are often correlated with freshwater inflow and precipitation (Li et al. 2019), may be related to olfactory imprinting and spawning migration timing (Kim et al. 2015).

Here we used generalized additive regression models that account for temporal autoregressive dynamics to evaluate migratory timing and duration of adult fall and winter ecotype chum salmon in the South Puget Sound (SPS) of Washington State, USA. Specifically, we used a multidecadal dataset including escapement data from 12 stocks and sport and commercial harvest from two regional marine fishing areas to describe long-term changes in salmon migration phenology and to examine relationships between regional and local abiotic and biotic ecosystem indicators. We tested six different hypotheses to explain patterns of timing and duration of run migration in adult SPS chum salmon by seasonal ecotype (Table 1): (i) migratory phenology has changed over time such that peak and midpoint of the run has shifted earlier in the year compared with historical timing (Quinn and Adams 1996; Juanes et al. 2004; Taylor 2008; Kovach et al. 2012; Crozier et al. 2011); (ii) directional changes in migratory timing are due to natural selection against later-timed salmon as measured by duration, such that earlier run timing is correlated with shorter run durations through time (Kovach et al. 2015); (iii) directional changes in migratory timing are due to harvest selection, such that peak of commercial harvest is occurring later in the year over time and is inversely correlated with migratory timing (Morita 2019; Tillotson and Quinn 2018; Quinn et al. 2007); (iv) migratory phenology is affected by climate variation operating at regional and local scales, especially precipitation, which is correlated with sea surface salinity and stream flow, such that higher fall and winter precipitation, lower salinity, and higher temperatures are correlated with earlier timed migration and shorter duration in Pacific salmon (Kovach et al.

**Fig. 1.** Chum salmon (*Oncorhynchus keta*) long-term monitoring locations (i.e., unique populations) in South Puget Sound, Washington, USA. Localities with winter populations are denoted with red dots and fall populations with black dots. Map produced with ArcMap 10.8.1 using location data from WDFW (personal communication) and light gray canvas base map from ArcGIS Online. [Colour online.]



2015; Manhard et al. 2017; Carey et al. 2017; Oke et al. 2019); (v) migratory phenology is affected by density-dependent interactions with other chum salmon, such that the duration of the run is longer with increasing run size and occurs earlier in the year with decreasing total run size (Carey et al. 2017); and (vi) migratory phenology is affected by predator buffering such that increased predator presence is driving selection for later timed chum salmon leading to earlier run timing and shorter duration (Morita 2019; Nelson et al. 2019). Finally, given a potential relationship between migratory phenology and the environmental effects tested in our time-series regression models, we attempt to identify the optimal environmental conditions that are correlated with the highest probability of occurrence of migratory peak count and midpoint over time. Specifically, we used mixture modeling to identify environmental thresholds that may be useful for regional and local in-season chum salmon management in the SPS.

## Methods

### Data collection

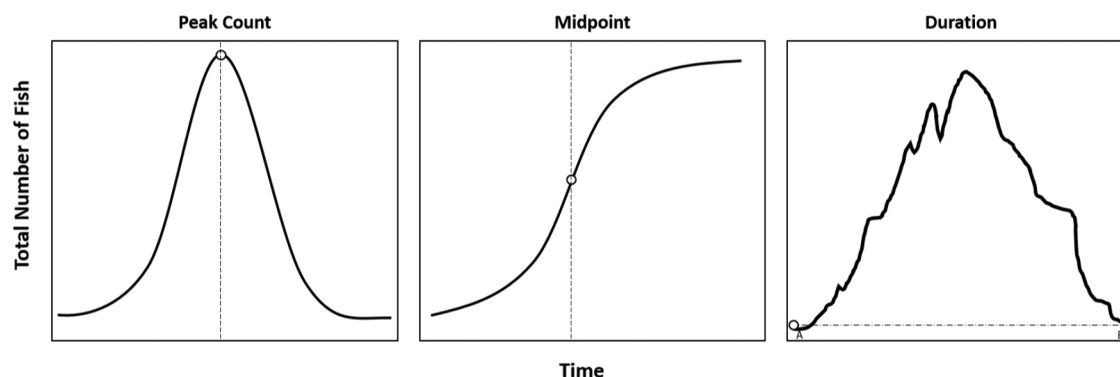
#### Migration timing and duration data

Our study focused on natural populations of chum salmon originating from the SPS of Washington State (Fig. 1). The SPS represents the southern extent of the larger Puget Sound fjord estuary complex, encompassing a basin topography and hydrology with unique physical and chemical process (Preikshot and Beattie 2001). In the SPS, much of the large-scale oceanic physical and

chemical processes are muted due to the inlet geography; thus, organismal interactions with the environment are often different in the SPS as compared with the North Puget Sound and Hood Canal regions. While hatchery production of chum salmon occurs in the SPS, natural and hatchery-origin chum returns are differentiated based on the counts of adults returning to hatcheries versus natural spawning grounds along various river extents. Salmon fisheries in the SPS are monitored and co-managed by Puget Sound Treaty Indian Tribes (Tribes) and the Washington Department of Fish and Wildlife (WDFW) (Clark 1985). Tribes and WDFW monitor salmon populations from marine commercial, sport, and subsistence fisheries, as well as by escapement counts of live and dead fish in-river during spawning periods of the year. Thus, we used a long-term monitoring dataset collected by both Tribal and WDFW biologists to characterize patterns of migration timing and duration for SPS chum salmon. Weekly counts were generated from walking surveys of spawning reaches or indexes for each population, where observers would count the number of live and dead salmon. Those weekly counts were then adjusted based on the percent visibility determined by the observer. To ensure all available chum salmon were accounted for during a season, we conducted spawning surveys every week from late September to January for fall run chum and late October through February for winter run chum (see WDFW Spawning Ground Survey Database: <https://wdfw.wa.gov/fishing/management/sgs-data>; WDFW 2003; Hatchery Escapement Reports: <https://wdfw.wa.gov/fishing/management/hatcheries/escapement#weekly-reports>). Subsequently, using weekly



**Fig. 2.** Metrics for assessing chum salmon (*Oncorhynchus keta*) migratory return in South Puget Sound, Washington, USA. From left to right: **peak live count**: week of fishing season when the number of chum salmon observed reached its peak — denoted with vertical dotted line; **run midpoint**: week of fishing season when 50% of total live chum salmon count was reached — denoted with vertical dotted line; and **duration**: number of weeks that chum salmon were observed during migration — denoted with horizontal dotted line, points A to B.



counts of returning salmon, we quantified annual migratory metrics: peak count week of migration (peak), midpoint week of migration (midpoint), and duration of migration as measured by number of weeks (duration) (Fig. 2). Using the same dataset, we also collected the annual peak week of harvest by commercial fisheries operating in marine areas 10 and 11 of SPS. Peak week of harvest represented the timing of highest catch per unit effort (CPUE) by the most influential chum salmon fishery, but also reflected the general timing of the highest fishing pressure exerted during the overall chum salmon migration.

Migratory metric peak was collected from six fall (Kennedy, McLane, Minter, Little Burley, Chico) and five winter run (Flett, Leach, Yelm, Mainstem Nisqually, Red Salmon) chum salmon populations from 1974 to 2017, as there was sampling consistency across these populations for the long-term temporal duration (~43 years). Migratory metrics midpoint and duration were collected from one winter (Diru) and four fall (Kennedy, Green River, Area 13, Minter) run chum salmon populations from 1992 to 2017 (~25 years). All sites were selected given the following criteria for retention in the dataset for further evaluation: (i) having no more than 14 days between peak and subsequent surveys and (ii) having a full season surveyed and peak live count.

#### Climate data

We collected marine and atmospheric climate data that has previously been shown to correlate with run timing and duration in multiple anadromous salmonid populations (Kovach et al. 2012, 2015; Quinn and Adams 1996; Cooke et al. 2004; Taylor 2008). Because salmonids interact with the environment at multiple spatial scales, we included regional and local scale indicators. At the regional scale, we collected 3-month average (October–December) sea surface salinity and sea surface temperature for each year of available run timing data in our long-term dataset (peak: 1974–2017, midpoint and duration: 1992–2017). Sea surface temperature and sea surface salinity data were collected from Race Rocks Lighthouse in the Strait of Juan de Fuca, a long-term climate dataset managed by Fisheries and Oceans Canada (<http://www.pac.dfo-mpo.gc.ca/index-eng.html>). At the local scale, we aggregated monthly mean river flow discharge data (flow) from three SPS US Geological Survey river monitoring stations (Huge Creek, Nisqually Mainstem, Green River) with data collected during the study period 1974–2017 (<https://waterdata.usgs.gov/nwis>). Because empirical stream flow data were not available across the complete period for many streams included in this study, we also collected monthly mean precipitation averaged across multiple weather stations nearest to study locations (i.e., salmon

monitoring locations) in the SPS region via NOAA's National Climatic Data Center (<https://www.ncdc.noaa.gov/cdo-web/>). We averaged each climate indicator by month and matched a moving 3-month average (October–December or November–January based on fall and winter ecotypes, respectively) record to each year of available data on migration run timing and duration.

#### Predator data

We used estimates of seal density as an index of predator density. Chum salmon represent a major portion of seal diet in Washington State (Lance and Jeffries 2007; Lance et al. 2012), and increased harbor seal (*Phoca vitulina*) abundance covaries with other pinnipeds as well as apex predators including killer whales (*Orcinus orca*) (Chasco et al. 2017). We retrieved harbor seal data that included coastal density estimates that covered the span of our data time series via personal communication with the authors of Nelson et al. (2019). The seal density dataset included average density of seals relative to kilometres of shoreline across the Washington Coast, Strait of Georgia, Puget Sound, and Strait of Juan de Fuca combined. Seal densities were derived using a combination of aerial survey data and a univariate state-space model (Nelson et al. 2019).

#### Analysis

##### Temporal trends and ecosystem drivers

We used generalized additive mixed models (GAMMs) to evaluate the importance of ecosystem indices on chum salmon migration phenology. Generalized additive models are an extension of generalized linear models and account for nonlinear relationships between the response and explanatory variables with the addition of a smoothed function (Guisan et al. 2002; Hastie and Tibshirani 1987; Wood 2006, 2018). GAMMs are also an extension of generalized additive models in that they allow for the inclusion of random effects and correlation structures (Lin and Zhang 1999).

All indicators tested in GAMMs — sea surface salinity, sea surface temperature, precipitation, flow, seal density, peak harvest, and total run size — were standardized following Cade (2015) to allow for equal scale comparison. Total run size was collected using yearly run reconstructed counts for SPS fall and winter chum salmon populations and matched to each year of available run timing data (1974–2017). Run reconstructed chum totals include both recreational catch, commercial catch, and river-based escapement data for the region, maintained by WDFW. Flow and precipitation were highly correlated ( $r = 0.86$ ), despite differences in area of collection. Consequently, we selected

precipitation as a proxy for local water availability (Kovach et al. 2015) and excluded flow from the analysis due to collinearity and their similar representation of freshwater availability in the ecosystem. In all models, we included a fixed interaction with ecotype (fall versus winter) to accommodate for differential migratory phenologies and independent environmental interactions by season.

For each hypothesis (H1 through H6), we built independent GAMMs of the general form:

$$Y = \beta_0 + \sum_{k=1}^n S_k(x_k)$$

where  $Y$  was the migratory metric peak, midpoint, or duration based on the particular hypothesis (Table 1; i.e., each GAMM included a single migratory metric and single explanatory variable by season),  $\beta_0$  was the intercept term, and  $\sum_{k=1}^n S_k(x_k)$  was the sum of each smoothed explanatory variable, where  $S_k$  represented a one-dimensional smoothing function of the  $x_k$  explanatory variable. All GAMMs used a Gaussian distribution with an identity link function, and we restricted the dimension of the basis used to represent the smooth function (a thin-plate regression spline) for each parameter to 3 (i.e., degrees of freedom of 2, which is equivalent in complexity to a quadratic curve). These parameters were set to prevent overfitting and create conservative, ecologically interpretable models (Wood 2006; Fisher et al. 2018; Guntenspergen 2014). Using the upper limit of 3 degrees of freedom specified above, the estimated degrees of freedom was determined by fitting with GCV (generalized cross validation; Wood 2018).

GAMMs were fitted with an autoregressive corAR1 error structure, representing an autocorrelation structure of order one, in which the variance is assumed to be heterogeneous and residuals from measurements at adjacent time points have some estimated correlation. Temporal autocorrelation structures are often applied to time-series analysis to control for the lack of independence associated with temporal data (e.g., Box et al. 1994; Jeffrey et al. 2017). Autocorrelation function plots of model residuals without an autoregressive structure revealed correlation outside the default confidence bounds for each of our migratory metrics, thus supporting a need to include a temporal correlation structure (Wood 2018). We compared a lag one autocorrelation structure (corAR1) and moving-average correlation structure (corARMA,  $p = 1$ ,  $q = 1$ ) for each individual GAMM and determined the best-fitting structure using the lowest AIC<sub>c</sub> (Burnham and Anderson 2002;  $\Delta AIC_c$  min. > 2 from competing models). Our data supported use of the AR1 correlation structure with Year nested within Population. The nested format estimated a single parameter  $\phi$  or AR(1) coefficient but avoids assuming that residuals across populations are correlated. GAMMs were also fitted with a random effect (Population) to allow each population to have their own random intercept.

The outputs of all models were assessed and validated using the function gam.check (Wood 2018), which generates residual plots and diagnostic measures for the estimated degrees of freedom applied to smoothed parameters. Specifically, it checks the residuals and determines whether the estimated degrees of freedom for each parameter is too low such that it forces over-smoothing. For all models presented in this study, gam.check did not indicate any relationships that would require an additional degree of freedom for estimation, and quantile-quantile plots of residuals determined that all models followed a 1:1 line checking the assumption of residual normality. Finally, to derive estimated migratory shifts (i.e., number of weeks) from historical timing, we used the predict.gam function (Wood 2018) to estimate mean

predicted peak, midpoint, and duration at the start and end of each time series for winter and fall ecotypes.

All statistical analyses and plots were generated using the statistical software R (R Core Team 2020), and statistical significance was established at  $\alpha < 0.05$ . Using the statistical software R, we used packages “mgcv” (Wood and Wood 2015), “visreg” (Breheny and Burchett 2013), “lme4” (Bates et al. 2007), and “gam4” (Wood and Scheipl 2014).

### Optimal environmental conditions

To investigate optimal environmental conditions associated with chum salmon migration phenology, we used normal mixture models. These models represented multimodal frequency distributions of environmental variables most associated with peak and duration that were not feasibly modeled in a regression context. Furthermore, these models provide a more detailed interpretation of multimodal distributions that are often lost when evaluating data distributions with a single mode (i.e., unimodal). In our study, we plotted the distribution of environmental variables associated with peak and duration in the fall and winter ecotypes and determined the presence of bimodal peaks suggesting that multiple optimums may exist. Normal mixture models were constructed using the “Mixtools” package and normalmixEM function via the statistical software R (Benaglia et al. 2009). To set up data for analysis, we matched sea surface salinity and precipitation values to midpoint and peak records by calendar day of year and parsed data by winter and fall ecotype groups. Subsequently, we used the resulting sea surface salinity and precipitation values only, and fit normal mixture models with one to two mixture components (i.e., one to two possible environmental local maxima or modes) for migratory metrics peak and midpoint for each ecotype. These models allowed us to parse out environmental parameter space and identify multiple local maxima (i.e., environmental modes most often associated with peak and midpoint across time). We then compared models with one versus two modes and used AIC<sub>c</sub> to determine the optimum number of modes (Burnham and Anderson 2002). Mixture models produced a percent incidence (i.e., percentage of data that fell under each mode or local maxima) across the complete time series, a mean estimate, and standard error for each mode.

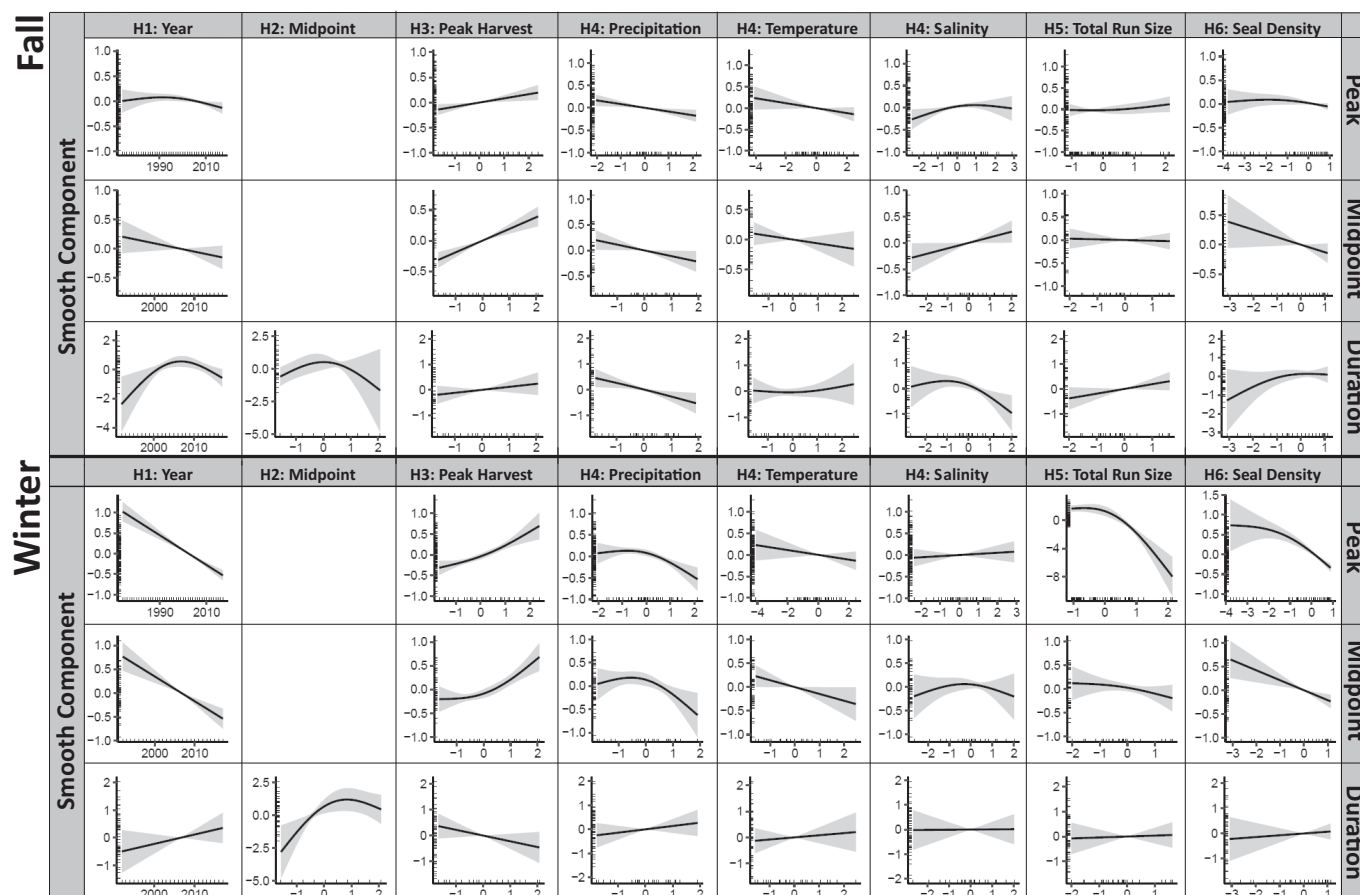
## Results

### H1

Our multimodel evaluation revealed that migratory timing — measured by peak count and midpoint of migratory run — shifted significantly towards earlier in the year for both the winter and fall ecotype chum salmon over the multidecadal time series (Figs. 3, 4). For the winter ecotype, GAMM prediction estimates supported an approximate 3-week shift in midpoint of migration and an approximate 4½-week shift in peak of migration towards earlier in the year (Fig. 4; also refer to online Supplementary material, S2<sup>1</sup>). For the fall ecotype, GAMM prediction estimates supported an approximate 1-week shift towards earlier in year for midpoint of migration (Fig. 4; Supplement S2<sup>1</sup>). Migratory run duration had a nonlinear relationship with midpoint of migration for the fall ecotype, such that run duration increased from 1975 to 2010, after which the relationship turned negative towards a decrease in run duration (Fig. 4; Supplement S2<sup>1</sup>). GAMM prediction estimates supported an approximate 2-week decrease in run duration for the fall ecotype over the most recent decade of the long-term dataset.

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-0392>.

**Fig. 3.** Generalized additive mixed model results for each hypothesis and ecosystem indicator described in Table 1, parsed by ecotype (fall and winter) and migratory metric (peak, midpoint, and duration). Hypothesis-based ecosystem indicators included Year, Midpoint, Peak Harvest, Precipitation, sea surface temperature (Temperature), sea surface salinity (Salinity), Total Run Size, and Seal Density. Nontested relationships are denoted with blank panels under H2: Midpoint column. Relationships between migratory metrics and hypothesis-based indicators are denoted with mean fit of the component smoother (i.e., black line), the grey bands represent 95% confidence intervals, and the tick marks on inside bottom of each plot indicate the data points. Please reference the online Supplementary materials<sup>1</sup> for further detail on model fit of relationship for each hypothesis.



## H2

Over the multidecadal data time series, duration had a nonlinear relationship with midpoint of both the fall and winter ecotypes, such that duration increased with midpoint to a turning point at which the relationship became negative and duration decreased with a later midpoint (Fig. 3; Supplement S2<sup>1</sup>). The temporal shift towards earlier migration in the winter and fall ecotypes were associated with a decrease in interannual variance of migratory phenology, as measured by an apparent decrease in duration of migration timing over the most recent decade for the fall ecotype and decrease in duration of migration timing over last few years for the winter ecotype (Figs. 3 and 4; Supplement S2<sup>1</sup>).

## H3

Peak timing of harvest was positively correlated with both winter and fall ecotype migration timing as measured by peak and midpoint of the migration (Fig. 3; Supplement S2<sup>1</sup>). Specifically, fishing pressure shifted earlier in time in concert with the temporal shift towards earlier timing of migration observed in the winter and all ecotypes.

## H4

GAMMs provided strong evidence that climatic variation operating at local to regional scales was related to interannual variation in the midpoint, peak, and duration of SPS chum salmon

migration (Fig. 3; Supplement S2<sup>1</sup>). GAMMs also suggested that fall and winter ecotypes responded differently across climate effects evaluated in our study. Local precipitation was negatively associated with all three migratory metrics for the fall ecotype and peak and midpoint of the winter ecotype (Supplement S2<sup>1</sup>). GAMMs suggested that precipitation had a negative correlation with the fall ecotype for peak, midpoint, and duration, while precipitation had a nonlinear relationship with peak and midpoint of the winter ecotype (Supplement S2<sup>1</sup>). Sea surface temperature had a negative relationship with midpoint of the winter ecotype, such that higher sea surface temperatures were associated with earlier run timing. Conversely, sea surface salinity had a positive relationship with midpoint of the fall ecotype, such that lower sea surface salinities were associated with earlier run timing (Supplement S2<sup>1</sup>). Sea surface salinity also had a nonlinear relationship with the duration of the fall ecotype (Supplement S2<sup>1</sup>).

## H5

Total returning run size effects were only relevant for the winter ecotype, as GAMMs supported a nonlinear relationship between peak timing of migration and total winter run size (Fig. 3; Supplement S2<sup>1</sup>). Thus, higher returning run sizes peak later in time as compared with smaller abundance run sizes.



**Fig. 4.** Temporal trends in migratory phenology metrics: duration, midpoint, and peak for chum salmon (*Oncorhynchus keta*) in the South Puget Sound of Washington State. Trends are parsed by winter (black circles) and fall (white circles) ecotype chum salmon and monitoring week.

## H6

GAMMs predicted that seal density had a negative correlation with midpoint and nonlinear correlation with peak of run for the winter ecotype. This suggests that increasing seal density may be correlated with earlier migration timing.

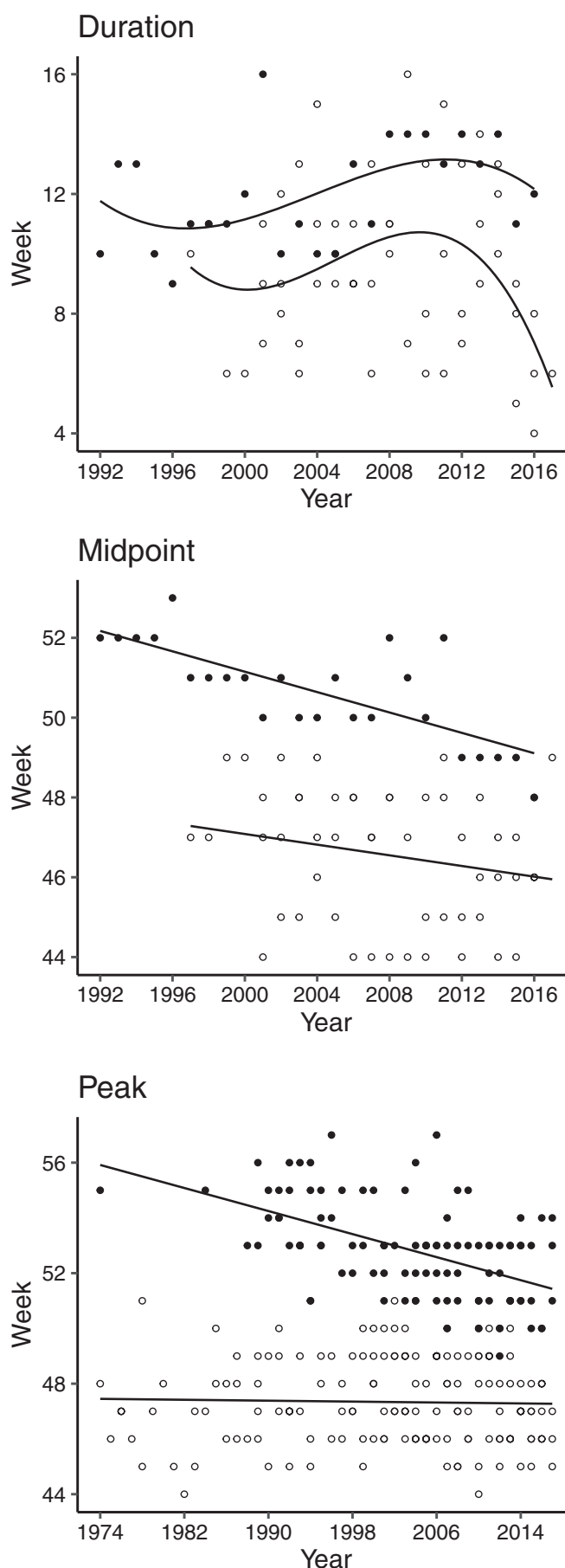
## Mixture models

We evaluated local precipitation optimums for peak of migration and regional sea surface salinity optimums for midpoint of migration based on their strong relationships with migratory phenology in both the fall and winter ecotypes (Fig. 3; Supplement S2<sup>1</sup>). Our AIC<sub>c</sub> evaluation supported mixture models with two precipitation optimums for the migratory peak of the fall ecotype both with 50% occurrence across the data series: a moving average of 6.9 and 14.2 cm (Table 2; Fig. 5). For migratory peak of the winter ecotype, mixture models determined 80% occurrence at a moving average of 15.3 cm and 20% occurrence at 27 cm (Table 2; Fig. 5). With regards to midpoint of migration salinity, AIC<sub>c</sub> evaluation supported mixture models with two salinity optimums for the peak and midpoint. Sea surface salinity-based models determined that the fall ecotype had 70% occurrence at 31.3 PSU and 30% occurrence at 30.8 PSU. For the winter ecotype, midpoint of migration had 86% occurrence at 31.2 PSU and 14% occurrence at 30.8 PSU.

## Discussion

In this study, we observed a strong temporal shift towards earlier adult migration timing in SPS chum salmon over the most recent decades. Migratory shifts of such nature are not uncommon across Pacific salmon and have been observed in nearly every anadromous species (Morita 2019). On average, SPS chum salmon migrate — based on peak count and midpoint over their respective time series — nearly 5 days earlier every decade. Some of the strongest directional shifts were documented in chum salmon that migrate during winter months. For example, winter ecotype chum salmon originating from the Nisqually River exhibited a peak count timing that moved  $\sim 3\frac{1}{2}$  weeks earlier across the 43-year time series. Our results closely mimic migratory shifts documented in pink (*Oncorhynchus gorbuscha*), chum, and coho (*Oncorhynchus kisutch*) salmon over  $\sim 30$  years in south-east Alaska (Kovach et al. 2015) and sockeye salmon (*Oncorhynchus nerka*) over  $\sim 60$  years in southern Washington (Crozier et al. 2011). These migratory changes along with the shifts observed in our study over the most recent few years for the fall ecotype and recent decade for the winter ecotype were also accompanied by a decrease in duration of migration timing, suggesting a potential for loss or phenotypic change in the behavior of later-spawning individuals (Kovach et al. 2015; Morita 2019).

Our evaluation of temporal chum salmon migration and duration patterns revealed both a positive and negative relationship between duration and midpoint of migration for winter and fall ecotype chum salmon over the complete time series. Previous studies have indicated that directional changes in migration timing are due to selection against later-timed salmon as measured by duration (Kovach et al. 2015). Our study may show support for that hypothesis such that in the recent decade shorter duration runs were associated with both extremely early and later-timed midpoints in both the fall and winter ecotypes (Fig. 4; Supplement S2<sup>1</sup>).



**Table 2.** Normal mixture model results of environmental local maxima or modes for migratory phenology in fall and winter ecotype chum salmon in the South Puget Sound of Washington State.

		Mode 1	Mode 2
<b>Precipitation (cm)</b>			
Fall peak	Incidence (%)	50	50
	Mean $\pm$ SE	6.85 $\pm$ 0.35	14.18 $\pm$ 0.72
Winter peak	Incidence (%)	80	20
	Mean $\pm$ SE	15.27 $\pm$ 0.77	27.04 $\pm$ 1.36
<b>Salinity (PSU)</b>			
Fall midpoint	Incidence (%)	30	70
	Mean $\pm$ SE	30.75 $\pm$ 3.50	31.31 $\pm$ 3.56
Winter midpoint	Incidence (%)	14	86
	Mean $\pm$ SE	30.75 $\pm$ 3.57	31.23 $\pm$ 3.63

Peak harvest was positively correlated with migration timing such that commercial fisheries are moving earlier over time and tracking the temporal migratory shift rather than acting as a selection factor. The SPS fall chum salmon fishery is actively monitored and actively managed based on return abundance. Specifically, when the in-season abundance as measured by a test fishery is estimated below regional escapement goals, the fishery is shut down, which has generally restricted or limited late-timed fishing over the past several decades. Given that little information is known about residence time of fall and winter ecotype chum in SPS fishing grounds, it is possible that early-timed fishing pressure could impact both fall and winter ecotypes; however, real-time genetic data from harvest would be needed to address such a factor. Nevertheless, harvest of both the fall and winter ecotypes may result in disruptive selection, driving higher variability rather than a temporal directional tendency in migration timing (see Tillotson and Quinn 2018; Morita 2019).

The timing of adult migration or freshwater re-entry by anadromous salmonids varies within and among species and is largely mediated by environmental conditions that maximize individual fitness. Some studies have suggested that earlier migration may be an adaptation to climate warming, as selection against late-migrating phenotypes have correlated with increasing sea surface temperature (Manhard et al. 2017). However, our study provided evidence for a relationship among local freshwater availability, regional sea surface salinity and temperature, and interannual variation in migration. Freshwater availability plays a critical role in life-history phenology for salmonids by providing environmental and chemical cues that shape life histories (Groot and Margolis 1991). Our results indicated that peak count moved earlier in time when freshwater availability increased for both winter and fall ecotypes. Thus, we suspect that SPS chum salmon may be responding to olfactory imprinting and physical water availability requirements that maximize potential to reach spawning grounds efficiently and successfully (i.e., reproductive fitness). While most of Washington's precipitation falls during the winter months, climate models show that extreme precipitation events are becoming more common during warm periods and decreasing during cool periods (Allan and Soden 2008). Our small regional sample of climate data also supports this theory, as mean precipitation from October to December significantly increased over the 43-year time series ( $P < 0.01$ ). Furthermore, freshwater flux (i.e., precipitation and evaporation) in marine environments is often correlated with mean patterns of salinity (Du et al. 2019). Thus, it is not surprising that our results indicated that lower sea surface salinities were correlated with earlier migration timing in fall chum salmon. Indeed, our climate data show that mean sea surface salinity from October to December is significantly decreasing over the 43-year time series ( $P = 0.048$ ), thereby acting as a potential underlying mechanism

for earlier timing of migration. Both regional and local climate data suggest that early adult migrants may continue to see increasingly suitable freshwater and marine water conditions earlier in the year that allow them to successfully reach spawning grounds. Additionally, higher sea surface temperatures were correlated with earlier run timing of winter chum, similar to the findings of Kovach et al. (2015) and Carey et al. (2017). These results potentially suggest that warming of sea surface temperatures over the past few decades are associated with earlier migration timing of late-migrant chum. Consequently, a combination of temporal changes in seasonal precipitation from winter to fall, lowered marine salinities, and higher sea surface temperatures may be driving adaptive phenology and serving as a driving force for directional selection in favor of early migrants for the fall and winter ecotypes.

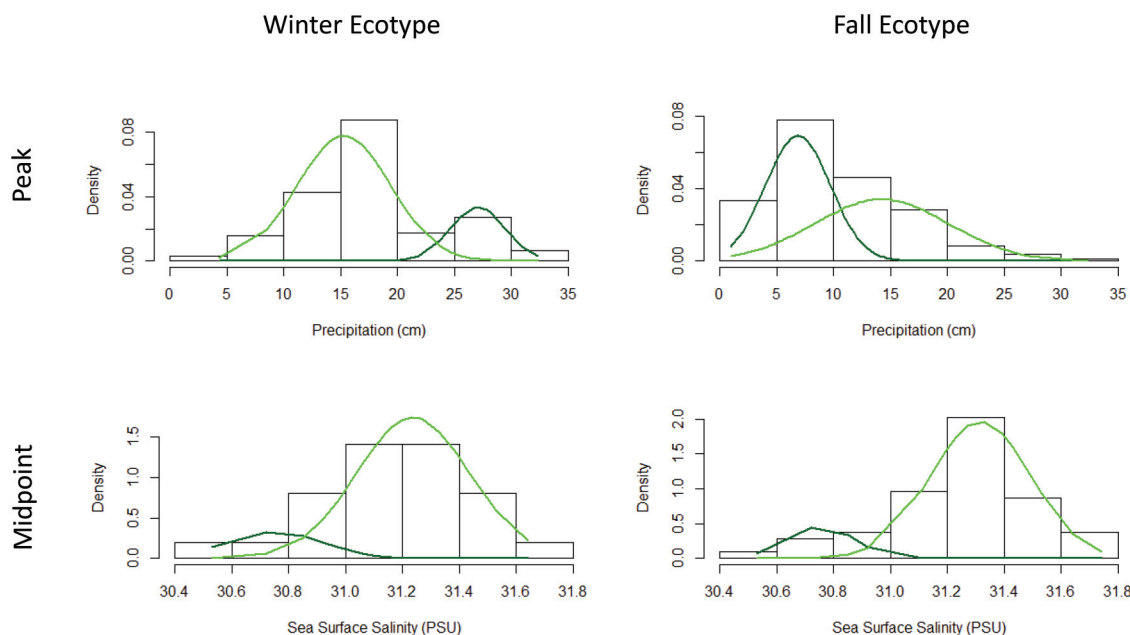
Recent research has indicated that Washington chum salmon may be experiencing a multidecadal decline in productivity (Litz et al. 2021). Our results support such conclusions, as our SPS total run size reconstructions show that some of the strongest negative deviations from a running mean over 44 years have occurred in the past 15 years. A positive relationship between total run size and peak of migration in winter ecotype chum salmon suggests that when total run size decreases, the migration timing shifts earlier in the year. Given the lack of hybridization with fall chum and low heritability associated with a declining population (M. Small, WDFW, personal communication), these results support the conclusion that the winter ecotype is being selected against and is potentially related to low phenotypic variation (Waples and Lindley 2018). This trend is likely to continue given the record low numbers of winter chum returning in recent years and suspected associated low numbers of outmigrating juveniles (M. Klungle, WDFW, personal communication).

Seal densities are increasing in coastal areas in the Northeast Pacific, especially after a climate regime shift in the late 1980s and early 1990s (Litzow et al. 2020; Nelson et al. 2019) (Fig. 6). While predator-prey interactions are complex and difficult to measure with regards to selection on migratory phenology, our study reveals a strong negative relationship between coastal seal densities and migratory run timing, especially in winter ecotype chum salmon. A critical piece to understanding the relationship between chum salmon and seal densities is that pinnipeds in general alter their diets in space and time based on local concentrations of prey (Chasco et al. 2017). While earlier run-timed chum salmon overlap with Chinook (*Oncorhynchus tshawytscha*) and coho salmon, late-timed chum salmon in December to January are the largest fish available during the winter time period and have been shown to be important prey for southern resident killer whales during this period (Ford and Ellis 2006). Thus, high predation pressure of adult chum salmon during winter could be associated with selection against late run timing. However, a caveat to this interpretation is that the seal density data used here are estimated model outputs from Nelson et al. (2019), which are relatively smooth and positive over time as an artifact of the autoregressive nature of the model. Consequently, the relationship between pinniped abundance and earlier migration timing could be expected given their natural inverse relationship.

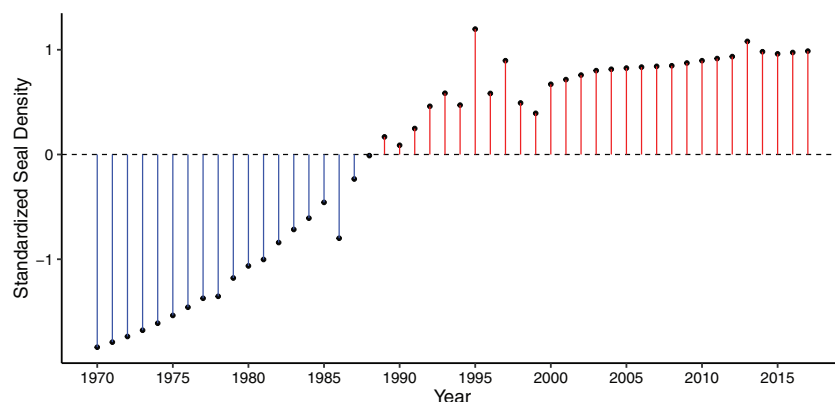
Using mixture models, we determined optimum precipitation thresholds for peak of the migration and optimum salinity thresholds midpoint of migration (Table 2). With peak run counts, our models suggested that precipitation thresholds were bimodal for both fall and winter ecotype chum salmon, which is indicative of how these returns temporally occur within a year across the SPS. With the fall ecotype, the run timing can occur as early as October and last until January, while with the winter ecotype the run timing can start in November and extend into early February. These extensive and overlapping seasonal ecotypes often occur with multiple peaks, despite the majority of each ecotype occurring at two distinct times of the year. Thus,



**Fig. 5.** Normal mixture model results of environmental optimums for migratory phenology in fall and winter ecotype chum salmon (*Oncorhynchus keta*) in the South Puget Sound of Washington State. The light green line indicates the primary component or optimum with the highest percentage of occurrence across the data series. The dark green line indicates a second component or optimum with the remaining proportion of occurrence across the data series. [Colour online.]



**Fig. 6.** Temporal trends in harbor seal (*Phoca vitulina*) density provided via Nelson et al. (2019). Seal density estimates are an average density of seals relative to kilometre of shoreline across the Washington Coast, Strait of Georgia, Puget Sound, and Strait of Juan de Fuca combined. Seal density is standardized by subtracting the mean and dividing by the standard deviation and colour-coded on positive or negative estimate deviations from zero. [Colour online.]



our results reflected the in-season temporal run size variability and indicated two optimal precipitation thresholds for peak count of the migration for fall and winter ecotype chum. Our normal mixture models suggested that midpoint timing across the data series often occurred at a salinity optimum of  $\sim 31$  PSU. These local and regional environmental optimums were stable throughout the multidecadal datasets, which implies that they could potentially be integrated into in-season run size models to improve estimation and reduce uncertainty around the extent of the return for each ecotype.

### Management implications

In Washington State, chum salmon are managed jointly by the WDFW and the Puget Sound Treaty Indian Tribes. As Puget Sound chum salmon are caught both commercially and for sport, they are managed using preseason forecasts that predict return

abundances for each year's summer, fall, and winter ecotype runs. Using these preseason forecasts and through a series of decision-making meetings known as the North of Falcon process, co-managers determine the total allowable catch and escapement goals by ecotype and region. Owing to the temporal and spatial resolution at which chum salmon are managed in Washington State, managing fall and winter chum salmon ecotypes into the future may require continued evaluation of commercial and recreational fishing pressure and close monitoring of hatchery practices on genetically independent ecotypes to reduce any potential artificial selection against late migrants. Additionally, preservation of genetic and phenotypic diversity in harvested salmonid populations is an important strategy for conservation management (Pellens and Grandcolas 2016; Koch and Narum 2020; Waples et al. 2008). Thus, in the face of rapid environmental change, genetically quantifying phenotypic expression and

local adaptation with regards to migration timing and changing local and regional climate regimes may improve real-time conservation management decisions. Finally, because of the potential of predator correlation with the phenology of the late-timed ecotype, monitoring and evaluating marine mammal predator presence and their effect on chum salmon is warranted throughout all of Puget Sound.

## Acknowledgements

We thank the numerous treaty tribal and WDFW biologists who monitored, enumerated, and recorded salmon returns across the South Puget Sound. We also thank technical staff from WDFW and the treaty tribes who assisted with carefully evaluating migratory patterns and improving management strategies for commercial and recreationally harvested salmon in the South Puget Sound of Washington State, specifically, Riley Freeman (WDFW), John Rohr (WDFW), Walker Duvall (Nisqually Indian Tribe, NIT), Tim Wilson (NIT), Rene Bracero (NIT), and Emiliano Perez (NIT).

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