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Interactions between life history and the environment on changing growth rates of Chinook salmon

Jack H. Buckner[a], **William H. Satterthwaite**[b], **Benjamin W. Nelson**[c], **and Eric J. Ward**[d]

[a]Graduate Group in Ecology, University of California Davis, One Shields Road, Davis , CA 95616, USA; [b]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 110 McAllister Way, Santa Cruz, CA 95060, USA; [c]Long Live the Kings, 1326 5th Avenue, #450, Seattle, WA 98101, USA; [d]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd E, Seattle, WA 98112, USA

Corresponding author: **Jack H. Buckner** (email: jhbuckner@ucdavis.edu)

Abstract

Fish in all the world's oceans exhibit variable body size and growth over time, with some populations exhibiting long-term declines in size. These patterns can be caused by a range of biotic, abiotic, and anthropogenic factors and impact the productivity of harvested populations. Within a given species, individuals often exhibit a range of life history strategies that may cause some groups to be buffered against change. One of the most studied declines in size-at-age has been in populations of salmon; Chinook salmon in the Northeast Pacific Ocean are the largest-bodied salmon species and have experienced long-term declines in size. Using long-term monitoring data, we develop novel size and growth models to link observed changes in Chinook size to life history traits and environmental variability. Our results identify three distinct trends in size across the 48 stocks in our study. Differences among populations are correlated with ocean distribution, migration timing, and freshwater residence. We provide evidence that trends are driven by interannual variation in certain oceanographic processes and competition with pink salmon.

Key words: life histories, environmental change, pink salmon, competition, state-space models, *Oncorhynchus tshawytscha*

Introduction

Many fish species around the world targeted by commercial or recreational fisheries have exhibited declines in mean size; examples include Atlantic salmon (Quinn et al. 2006; Kuparinen et al. 2009), groundfish in the North Sea (Greenstreet and Hall 1996), Australian reef fishes (Audzijonyte et al. 2020), and species of Pacific salmon (Oke et al. 2020). Understanding the factors that drive these trends is critical for identifying and distinguishing among threats, such as impacts of climate change (Sheridan and Bickford 2011), fishery-induced evolution (Conover et al. 2009), shifting spatial distributions (Pinsky et al. 2020), competition among species (Ruggerone and Nielsen 2004), and changes in predation and natural mortality (Ohlberger et al. 2019). Accounting for temporal declines in size affects both conservation and fisheries management: smaller fish have been shown to have reduced reproductive capability, further exacerbating the decline of small populations (Barneche et al. 2018; Ohlberger et al. 2020), and populations of smaller fish provide fewer ecosystem services, such as providing prey for predators and transportation of nutrients from the ocean to freshwater environments (Oke et al. 2020).

Some of the longest-studied declines in body size have been in populations of Pacific salmon (*Oncorhynchus* spp.) (Ricker 1981). Declines have been found across multiple species; however much of the attention has focused on declines in Chinook salmon (*Oncorhynchus tshawytscha*; (Lewis et al. 2015; Ohlberger et al. 2018; Xu et al. 2020)). Chinook salmon are the largest and most economically valuable species of Pacific salmon and have experienced the sharpest decline in size over time (Oke et al. 2020). This species has experienced many of the same pressures that have caused changes in size in other fish populations, including harvest, changing abiotic conditions, interspecific competition, and predation (Ohlberger et al. 2018).

One of the challenges in understanding mechanisms responsible for declines in size is the life history diversity of Chinook salmon. Across the range of the species, there is significant diversity in life history traits and migratory behaviors (Quinn 2018). Examples of trait diversity include variable age at maturity and different ocean distributions. Furthermore, Chinook salmon are anadromous and migrate from freshwater habitats to the ocean in their first or second year of life. There are also differences in the phenology of their spawning migrations, with stocks in our study region returning to spawn in the spring, summer, fall, or late fall. Furthermore, there is an important distinction between spring and summer run stocks that typically mature in the freshwater environment and fall and late fall stocks that mature in the ocean before their spawning migrations (Quinn 2018).

This variation in life history is likely to interact with changing environmental conditions to shape trends in growth and body size in Chinook salmon. Variability in ocean distribution exposes stocks to different marine environments where the productivity regime is driven by independent or even opposing oceanographic processes (Mantua et al. 1997; Hare et al. 1999; Wells et al. 2008; Kilduff et al. 2014; Malick et al. 2017; Dorner et al. 2018). Even in cases where two stocks share the same environment, differences in migration timing and other traits can cause them to respond differently to the same patterns of environmental variation (Wells et al. 2008; Greene et al. 2010). The resultant potential for interactions between life history diversity and environmental change must be accounted for in any complete causal explanation of the observed changes of size in this species. Furthermore, different responses to the environment between stocks within a larger stock complex can reduce the variability of trends experienced by this larger stock complex, stabilizing ecosystem services and functions (Hilborn et al. 2003; Schindler et al. 2010). These so-called portfolio effects are most often invoked in relation to variation in abundance over time. However, changes in body size also contribute to the productivity of salmon populations and can, in principle, be stabilized through a similar averaging process. In these ways, life history diversity is likely to shape the causes and consequences of changing body sizes in fish populations.

To better understand these processes, we leverage long-term monitoring data to shed light on variation in trends in body size exhibited between stocks of Chinook salmon and the potential drivers of this variation. We focus on three questions: (1) How do changes in size-at-age differ across populations of Chinook salmon? (2) Are there life history characteristics or other traits that underlie the differences in trends?, and (3) What factors may be causing populations to respond differently to the same changes in environmental conditions? We focused on hatchery-origin Chinook salmon populations from the coastal regions of Washington and Oregon, including the Columbia River Basin. The Columbia River represents the single largest watershed-level source of Chinook salmon production (Shelton et al. 2019), with a large range of within-basin life history variation reflective of local adaptation and deep phylogenetic differences (Waples et al. 2004; Moran et al. 2013). Thus, these populations provide a unique opportunity to shed light on how changing environmental conditions may interact with life history variation to determine long-run decline in size.

Another advantage of focusing on these populations is that they are monitored closely with coastwide tagging programs (particularly fish of hatchery origin). Since the 1970s, juvenile fish have been marked with unique coded-wire tags (Johnson 2004). When these individuals are later encountered as adults (in spawning surveys or captured in fisheries), these tags provide information about survival, maturation and size-at-age, and spatial distribution in coastal waters of North America. These long-term monitoring data provide an opportunity to disentangle potential confounding effects between the environmental divers of changes in body size in this species and their interaction with the diverse range of life history strategies.

To analyze these data, we developed two novel statistical methods. First, we developed a new algorithm to categorize variation in trends of size-at-age between populations over time. This approach is similar in spirit to dynamic factor analysis (DFA) (Zuur et al. 2003), in that the model identifies groups or "clusters" of populations that experienced similar trends in length-at-age over time but aims to make an improvement in interpretability over DFA by uniquely assigning each population to a latent trend. Second, we developed a state-space modeling approach to identify factors that may influence the observed trends in size-at-age, leveraging information between cohorts overlapping in their ocean residency to identify the effects of interannual variation in ocean conditions on growth. These two methodological advances in combination with the long-term tagging data allow us to produce novel insights into the processes that govern the changes in size-at-age in Chinook salmon populations.

Methods

Data

Length-at-age data

We analyzed observations of length-at-age of coded wire tagged (CWT) hatchery-origin Chinook salmon from the Columbia River basin and coastal Washington and Oregon recorded in the Regional Mark Information System (RMIS) (www.rmpc.org). The data set includes information on groups of fish at the point of release (release date, size, and location) and when individuals from this group are recovered as adults at hatcheries and in escapement surveys. Summary statistics describing the stocks included in that analysis are provided in Supplementary Materials 1. To analyze changes in length-at-age, we matched the observations of releases and recoveries by tag code to link the observed length of the adult fish (fork length) to its release location and date as well as life history characteristics. Age is defined as the year of recapture minus the brood year. We restricted our analysis to individuals that were released from the Columbia River Basin or coastal Washington and Oregon that had non-missing values for sex and fork length. Furthermore, we restricted our analysis to observations of fish recovered in hatcheries or on spawning grounds to avoid issues with gear selectivity from marine and freshwater fisheries. A full list of sampling methods used to recover the individuals included in our study is given in Table S1.2. Including multiple sampling methods in our data could bias the observed trends if the frequency of each method changes over time. However, we found limited evidence for size selectivity between the sampling methods included in our analysis of length-at-age (Fig. S2.2). Furthermore, the frequency of each sampling method was largely consistent over the study period (Fig. S2.1).

We assigned all individual observations ($n = 1\,406\,913$) to groups that we refer to as stocks based on their adult run timing (spring, summer, fall, and late fall), sex, the age of release from the hatchery (1 or 2), and the RMIS basin from which they were released. We restricted our analysis to stocks and years for which there were at least ($n = 10$) observations so

that we could compute both the sample mean and standard error for the group. In addition, we omitted stocks with fewer than 15 years of length-at-age data.

Ocean distribution index

We expect variation in the trends in length-at-age of each stock to depend in part on ocean distribution. Because many stocks in our analysis have a different ocean distribution (Weitkamp 2010; Shelton et al. 2019), ocean distribution indices (ODI) were constructed by compiling the CWT recoveries for each stock in marine fisheries. We then restricted the samples to fish recovered at least 2 years after release and computed the mean latitude of the observations. Some observations were missing precise geographical coordinates and were instead reported by fishery areas; we assigned coordinates to these cases based on the mean latitude of catches in the fishery area. This assumption has little effect on the final index (Fig. S3.1).

The ODI aggregates observations across age classes and between years to generate a single value for each stock. This procedure is well-motivated because the distributions of Chinook salmon are known to be relatively stable across years (Weitkamp 2010; Shelton et al. 2021). However, several potential sources of bias need to be considered. The ocean distribution of Chinook salmon changes across age classes, with younger fish remaining closer to their river of origin (Weitkamp 2010). Because ODI aggregates across age classes, differences in the age composition of samples for each stock will affect its value. In general, the age compositions of the samples were similar, but some stocks had larger numbers of fish younger ocean ages (Fig. S3.1). To test the effects of these differences on the ODI, we calculated a new index using only samples with ocean age three (the most common age class). This alternative index was highly correlated with the ODI (0.933), indicating that the effects of age composition are likely to be small.

Furthermore, because the ODI is based on fishery-dependent data, it is sensitive to the distribution of fishing effort across space during the study period. Despite this, we do not attempt to correct of sampling effort. Our goal is to understand the differences in ocean distribution between stocks. If each stock is sampled with the same distribution of fishing effort, differences in the ODI between stock will reflect differences in their ocean distribution. However, biases may still arise when two conditions hold (1) the distribution of sampling (fishing) effort changes over time and (2) the frequency of observations between years varies for each stock (Fig. S3.3). To test the effects of variable fishing effort, we constructed an index that only used samples from 1979 to 1994, because fishing effort is thought to have been stable over this period (Weitkamp 2010). There was a strong correlation between this index and ODI (0.916), suggesting any bias caused by changes in fishing effort over time is small.

Environmental covariates

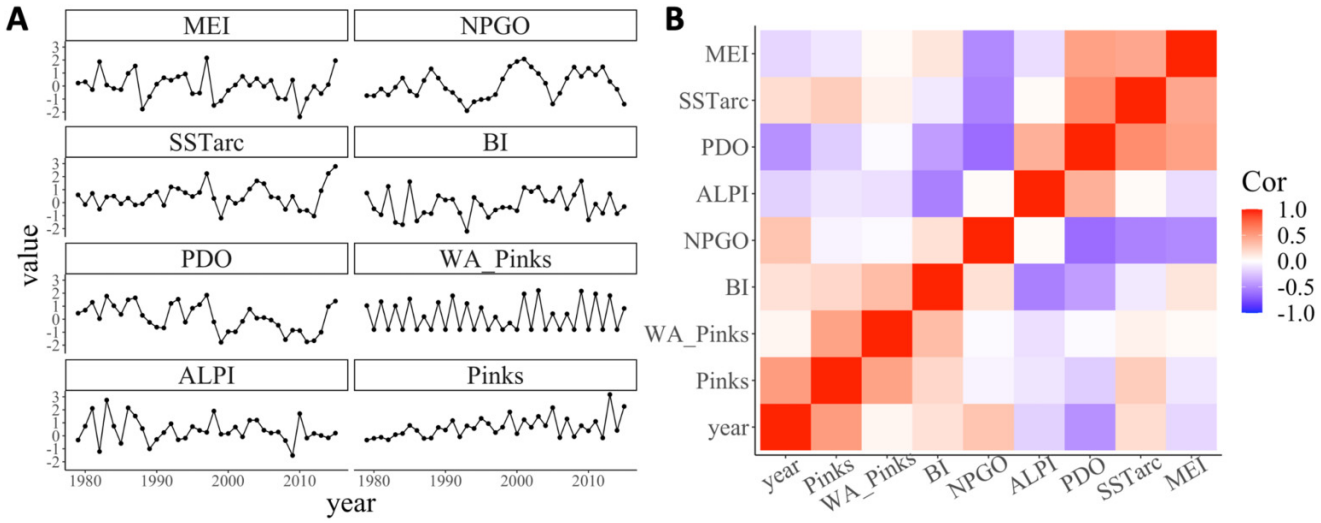
To identify factors that may be driving the observed trends in length-at-age over time, we analyzed the relationship between length-at-age and eight indices of biotic and abiotic ocean conditions that have previously been considered as drivers of changing salmon sizes. These indices include both large-scale oceanographic and atmospheric conditions in the Northeast Pacific Ocean and the abundance of potential competitors. We considered five climate indices: (1) the Pacific Decadal Oscillation (PDO; Zhang et al. 1997), which is the first principal component of North Pacific sea surface temperature anomalies, (2) the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), which is the second principal component of sea surface height anomalies in the North Pacific, (3) the Aleutian Low-Pressure Index (ALPI; Surry and King 2015) which describes the state of the Aleutian Low, a semi-permanent atmospheric low-pressure system in the central North Pacific, (4) the multivariate El-Nino Index (Kobayashi et al. 2015), (5) the North Pacific Current bifurcation index (BI; Malick et al. 2017) which describes latitudinal shifts in the North Pacific Current, and (6) SST-arc (Johnstone and Mantua 2014) which describes sea surface temperature (SST) anomalies in the Northern California Current and Gulf of Alaska. In addition to these indices of abiotic conditions, we included two indices of pink salmon (*Oncorhynchus gorbuscha*) abundance, because pink salmon have been identified as potential competitors with Chinook (Ruggerone and Nielsen 2004; Connors et al. 2020). We used estimates of total pink salmon run size (i.e., catch plus escapement) from all large populations in Washington State and the Fraser River as a proxy for abundance in the Northern California Current (Litz et al. 2021) and estimates of Pink salmon abundance in North America from (Ruggerone and Irvine 2018) extended through 2020 using data from (Ruggerone et al. 2021) as a proxy for abundance in the Gulf of Alaska. All environmental indices available on sub-annual increments were averaged to the calendar year. We standardized each of the indices to have a mean of zero and variance one. The time series and covariance matrix of these indices are shown in Fig. 1.

Cluster analysis: identifying stock groupings and trends

Overview

To understand how changes in size-at-age differ across populations of Chinook salmon, we developed a novel clustering algorithm to identify groups of stocks with similar trends in body size through time. We used the mean length of 4-year-olds from each brood year to characterize trends in size-at-age for each stock. Age four was chosen because it is the most common age at maturation for the stocks included in our study and comprised the largest number of observations in our data set. Our clustering approach is similar to conventional unsupervised clustering approaches (e.g., *k*-means clustering; MacQueen 1967) and allowed us to identify groups or "clusters" of stocks with similar trends in length-at-age without making any explicit assumptions about the biological processes that cause the trend. We then compared the characteristics of the stocks in each cluster to identify biological characteristics that may cause the observed differences in the trends. This approach allows our analysis to uncover all

Fig. 1. (A) time series of each index of environmental conditions included in the analysis. (B) Covariance matrix of the indices over time.



the common patterns of length-at-age observed in our data set, regardless of whether they are caused by observed or unobserved characteristics of each stock.

Time series

We defined a time series describing changes in size for each stock by computing the average length-at-age four from each brood year. To control for differences in average length between stocks, we subtracted the mean length for each stock. Each time series was then divided by the standard deviation of length-at-age across all stocks, a step which only changed the scaling of the time series, not the differences between them. We calculated trends for stocks that had sufficient data (10 or more observations) to estimate the mean length-at-age in 20 years spanning a 25-year period; stocks meeting these criteria are listed in Table 1. All years were given equal weight in the analysis regardless of the number of observations available. Four data points appeared to be outliers (exceeded 4 standard deviations from mean length-at-age); these points were removed, and a sensitivity analysis demonstrated that omitting these points did not change our findings (Fig. S7.1).

Algorithm

We identified groups of stocks with similar time series using a modified version of the *k*-means clustering algorithm. The *k*-means algorithm identifies groups of observations within a data set, such that the Euclidean distance between observations within a group is minimized. In the standard *k*-means algorithm, each observation is defined as a set of real-valued measurements arranged into a *d*-dimensional vector. In our application, each observation corresponds to a stock and each of the *d*-dimensions describes a year in the time series. Observations are assigned to one of *k* clusters through an iterative process. To initiate the algorithm, observations are randomly assigned to one of the *k* clusters. Then, a two-step process begins; (1) for each of the clusters, the mean value of observations in each of the *d*-dimensions is calculated and (2) each observation is then reassigned to the cluster with the most similar mean values as measured by the mean squared error (MSE). These two steps are repeated iteratively until no observations change their assignment in step 2.

We modified this basic approach to accommodate missing data and to increase its sensitivity to a long-run trend in size by estimating the mean length-at-age for each cluster with a smoothing function. The smoothing function for each cluster was estimated by fitting a generalized additive model describing the relationship between the size-at-age time series and brood year for each cluster using the mgcv R package (Wood 2011). Observations were then reassigned to clusters based on the MSE between the observed value of the time series for each stock and the smoothing trend for each cluster. This modified algorithm was implemented in the R programming language (R Core Team 2022), and pseudo-code for the algorithm can be found in Supplementary Materials 4.

Relationships between life history and cluster assignments

To answer our second question (are there life history characteristics or other traits that underlie the differences in trends between population groups?), we analyzed relationships between the groupings identified by the clustering analysis and the life history characteristics of each population. We identified the relative importance of life history characteristics and the geographic region of the stock for predicting cluster assignment using a random forest classification algorithm implemented in the R "randomForest" package (Liaw and Wiener 2002). Random forest was used over parametric regression techniques because of the flexibility in including complicated interactions and allowing for nonlinear relationships. Specifically, we fit a model that predicted clus-

Table 1. Characteristics of each stock included in the analysis.

Name	Regression model group	Cluster	Run	Release age	ODI	Sex	Release region	Release basin	Brood year range
WILL Spring.1(F)	1	1	Spring	1	53.2	F	Lower Columbia River	WILL	1978–2013
WILL Spring.1(M)	1	1	Spring	1	53.2	M	Lower Columbia River	WILL	1978–2013
TILN Spring.1 (F)	1	3	Spring	1	50.0	F	Northern Oregon	TILN	1982–2013
UPSK Spring.1 (F)	1	1	Spring	1	50.1	F	Skagit River	UPSK	1985–2013
TILN Spring.1 (M)	1	3	Spring	1	50.0	M	Northern Oregon	TILN	1982–2013
UPSK Spring.1 (M)	1	1	Spring	1	50.1	M	Skagit River	UPSK	1985–2013
STIL Summer.1 (F)	1	1	Summer	1	50.6	F	Northern Puget Sound	STIL	1987–2013
STIL Summer.1 (M)	1	3	Summer	1	50.6	M	Northern Puget Sound	STIL	1987–2013
SIYA Fall.1 (F)	1	3	Fall	1	53.1	F	Northern Oregon	SIYA	1978–2013
SIYA Fall.1 (M)	1	3	Fall	1	53.1	M	Northern Oregon	SIYA	1978–2013
LEWI Fall.1 (F)	1	3	Fall	1	51.0	F	Lower Columbia River	LEWI	1976–2013
MNPR Fall.1 (F)	1	3	Fall	1	52.6	F	Upper Columbia River	MNPR	1976–2013
QUHO Fall.1 (F)	1	3	Fall	1	53.6	F	Washington Coast	QUHO	1984–2013
SAWA Fall.1 (F)	1	3	Fall	1	52.7	F	Lower Columbia River	SAWA	1976–2013
TILN Fall.1 (F)	1	3	Fall	1	53.8	F	Northern Oregon	TILN	1982–2013
WILR Fall.1 (F)	1	3	Fall	1	53.3	F	Willapa Bay	WILR	1982–2013
LEWI Fall.1 (M)	1	1	Fall	1	51.0	M	Lower Columbia River	LEWI	1976–2013
MNPR Fall.1 (M)	1	3	Fall	1	52.6	M	Upper Columbia River	MNPR	1976–2013
QUHO Fall.1 (F)	1	3	Fall	1	53.6	M	Washington Coast	QUHO	1984–2013
SAWA Fall.1 (M)	1	3	Fall	1	52.7	M	Lower Columbia River	SAWA	1976–2013
TILN Fall.1 (M)	1	3	Fall	1	53.8	M	Northern Oregon	TILN	1982–2013
WILR Fall.1 (F)	1	3	Fall	1	53.3	M	Willapa Bay	WILR	1982–2013
SAND Late Fall.1	1	3	Late Fall	1	53.4	F	Lower Columbia River	SAND	1979–2012
UMAT Late Fall.1 (F)	1	3	Late Fall	1	52.7	F	Central Columbia River	UMAT	1982–2012
SAND Late Fall.1 (M)	1	3	Late Fall	1	53.4	M	Lower Columbia River	SAND	1979–2012
COWL Fall.1 (F)	2	1	Fall	1	49.2	F	Lower Columbia River	COWL	1976–2013
GREL Fall.1 (F)	2	2	Fall	1	48.9	F	Lower Columbia River	GREL	1976–2012
WIND Fall.1 (F)	2	1	Fall	1	47.7	F	Lower Columbia River	WIND	1976–2012
YOCL Fall.1 (F)	2	2	Fall	1	46.3	F	Lower Columbia River	YOCL	1976–2012
COWL Fall.1 (F)	2	3	Fall	1	49.2	M	Lower Columbia River	COWL	1976–2013
GREL Fall.1 (F)	2	2	Fall	1	48.9	M	Lower Columbia River	GREL	1976–2011
WIND Fall.1 (F)	2	2	Fall	1	47.7	M	Lower Columbia River	WIND	1976–2012
YOCL Fall.1 (F)	2	2	Fall	1	46.3	M	Lower Columbia River	YOCL	1976–2012
WILL Spring.2 (F)	3	1	Spring	2	52.9	F	Lower Columbia River	WILL	1978–2013
WILL Spring.2 (M)	3	1	Spring	2	52.9	M	Lower Columbia River	WILL	1977–2013
PRGC Summer.2 (F)	3	1	Summer	2	52.1	F	Upper Columbia River	PRGC	1976–2013
MEOK Summer.2 (M)	3	1	Summer	2	52.6	M	Upper Columbia River	MEOK	1976–2013
PRGC Summer.2 (M)	3	1	Summer	2	52.1	M	Upper Columbia River	PRGC	1976–2013
UMAT Late Fall.2 (F)	3	3	Late Fall	2	51.3	F	Central Columbia River	UMAT	1983–2011
UMAT Late Fall.2 (M)	3	1	Late Fall	2	51.3	M	Central Columbia River	UMAT	1983–2011
COWL Spring.2 (F)	4	1	Spring	2	48.9	F	Lower Columbia River	COWL	1976–2013
DESC Spring.2 (F)	4	1	Spring	2	48.5	F	Central Columbia River	DESC	1977–2013
GRIA Spring.2 (F)	4	1	Spring	2	48.6	F	Snake River	GRIA	1983–2013
UPSK Spring.2 (F)	4	1	Spring	2	49.3	F	Skagit River	UPSK	1981–2010
COWL Spring.2 (M)	4	1	Spring	2	48.9	M	Lower Columbia River	COWL	1976–2013
DESC Spring.2 (M)	4	1	Spring	2	48.5	M	Central Columbia River	DESC	1977–2013
GRIA Spring.2 (M)	4	1	Spring	2	48.6	M	Snake River	GRIA	1982–2013
UPSK Spring.2 (M)	4	1	Spring	2	49.3	M	Skagit River	UPSK	1981–2010

Note: The far-left column "Regression model groups" defines the life history group the stock was included in for the regression analysis. For this analysis stocks were divided based on the release age and ocean distribution index. The column "Brood year range" indicates the first and last brood year for which length at age data was available.

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assignment based on the ODI, migration timing, release type, and release region. Each variable included in the categorization model is listed in Table 2. The "importance" of each variable in the fitted model was measured by mean decreasing Gini (Liaw and Wiener 2002). To visualize these relationships in the data, we plotted the correlations between life history traits and cluster assignments in Fig. 2.

Growth increment model

Model overview

To identify factors that may cause the observed trends in size over time, we developed a model to estimate the correlation between indices of environmental conditions and growth. One difficulty of modeling the effect of abiotic conditions on growth is that observed length-at-age represents the integrated effects of the environment over the life of an individual, so a simple correlation between a lagged environmental variable and length-at-age may be misleading. Instead, we developed a model that takes advantage of the fact that overlapping cohorts experience the same ocean conditions for part of their life span to identify the effect of ocean conditions on growth each year. That said, because individuals are only measured once, our results may also reflect changes in size-dependent maturation or mortality. However, we assume such confounding effects are similar across years, allowing us to identify years with faster or slower growth.

Our growth model estimates a latent process that describes the mean length of each cohort as they grow between years. The growth rate of each cohort in any given year is taken to be the product of a year-specific factor that describes the quality of ocean conditions g_t and an age-specific factor f_a that accounts for slower growth rates as the fish age. The observation model accounts for sampling errors and size-selective effects of different sampling methods. The correlation between environmental indices and growth is estimated by modeling the year-specific effects g_t as a linear function of the environmental indices.

Model details

Process model

The process model describes the average length $\widehat{l}_{s,a,y}$ of a fish of age a born in year y from stock s released at age a_r. We assume that $l_{s,\,a,\,y}$ is defined as the sum of the initial length $l_{s,\,0,\,y\,-\,a,}$ and annual growth increments, which are taken to be the product to an age (f) and year-specific factor (g)

$$(1) \qquad l_{s,a,y} = \widehat{l}_{s,0,y-a} + \sum_{i=a_r}^{a} f_{s,i} g_{s,y-a+i}$$

We assume that the age-specific factors are a linearly decreasing function of age

$$(2) \qquad f_a = (1 - \alpha_s a)$$

where $\alpha \in (0, 1/a_{\max})$. The year-specific factors are a linear function of the environmental indices $\boldsymbol{X}_t$, and autocorrelated process errors $\epsilon_{s,t}$

$$(3) \qquad g_{s,t} = b_{0,s} + \boldsymbol{b}_{1,s}\boldsymbol{X}_t + \epsilon_{s,t}$$

We assume that all process errors $\epsilon_{s,t}$ follow an auto regressive process (AR1) independent between stocks with stock-specific coefficient ρ_s.

Observation model

The observation or data model links predictions of mean length-at-age of a cohort to the individual measurements of length that we observe. We assume that the length of individuals is normally distributed, with a constant variance for each stock and age combination across years but we allow for different variances across stocks and ages. We assume that the sampling process may be size-selective and represent the selectivity with fixed effects (F_{gear}) for the sampling methods used to collect the individual. We also include fixed effects for each age class to account for size-dependent maturation. Given these assumptions, the length of individual i from stock s of age a in cohort y is $l_{i,s,a,y}$ is given by

$$(4) \qquad l_{i,s,a,y} \sim N\left(l_{s,a,y} + FE_{age} + FE_{gear}, \sigma_{s,a}\right).$$

To increase the efficiency of the estimation algorithm, we fit the model to the mean length of individuals from each combination year, age, stock, and sampling method. In addition to calculating the estimated mean lengths $\widehat{l}_{s,a,y,g}$, we also calculated the standard error $\widehat{\sigma}_{s,a,y,g} = \frac{\sigma_{s,a}}{\sqrt{N_{s,a,y,g}}}$, where $N_{s,a,y,g}$ is the number of individuals in the sample to account for sampling variance. Finally, we include an overdispersion term σ_{disp} to account for observation errors not associated with the statistical sampling process

$$(5) \qquad \widehat{l}_{s,a,y,g} \sim N\left(l_{s,a,y} + FE_{age} + FE_{gear}, \widehat{\sigma}_{s,a,y,g} + \sigma_{disp}\right).$$

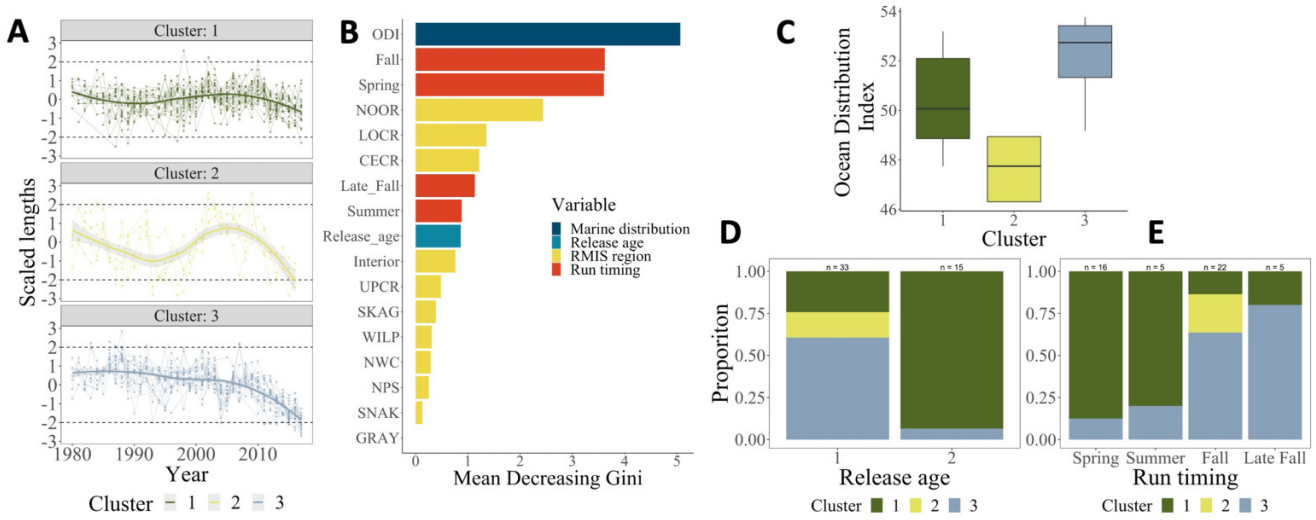
Model fitting

To analyze the effect of the environmental indices on growth, we separated the data into four groups based on life history characteristics. These life history groups were formed by separating the stock into two groups based on the age at release from the hatchery (age 1, 2) and then dividing each of these groups again based on the ODI, yielding four groups. We used an ODI of 50.0 as a cutoff between stocks with northern and southern distributions. These groupings were chosen because our cluster analysis indicated that stocks with different ocean distributions and release ages exhibited different trends in size-at-age. Run timing also predicted the difference in trends between stocks. We chose to group to the stocks by release age rather than run timing because these two traits are highly correlated; summer and spring run stocks generally released at age two and fall and late fall released at age one. Release age provided a simple binary representation of the effect of these life history characteristics on the trends in length-at-age.

Table 2. Variables included in the random forest model.

Variable name	Interpretation	Values
ODI	The ocean distribution index, defined by the mean latitude of CWT recoveries in the marine environment	Min: 45°Max: 55°
Run timing	Timing of spawning migration	Spring, summer, fall, late fall
Release age	The age of release from the hatchery	1, 2
Interior	Indicator variable for stocks from the Columbia River basin	True, False
RMIS region	Geographic region of origin for the stock	CECR, LOOR, NOOR, NWC, SKAG, SNAK, UPCR, NPS, WILP

Fig. 2. Results from cluster analysis. Time series of length-at-age four for each cluster of stocks (A), variable importance from random forest classification algorithm (B), and association of ocean distribution (C), run timing (D), and freshwater residence (E) with cluster assignment.



The life history group for the stocks included in the cluster analysis is listed in Table 1. For each group, we calculated the sample mean and variance for each stock, age, year, and sampling method combination. We fit the model to each group of stocks independently using Bayesian inference implemented with Hamiltonian Monte Carlo (HMC) using the Stan modeling language via the R package "rstan" (Stan Development Team 2020). Priors for this analysis are given in Table S5.1. The HMC runs were checked for convergence using the "shinystan" package (Stan Development Team 2017). We used visual diagnostics to ensure mixing between the HMC chains and $\widehat{R}$ statistics to ensure samples would provide accurate quantile estimates (Stan Development Team 2020).

We initially fit a model with all covariates and a second model that excluded SSTarc because of high correlations between it and PDO (Fig. 1). Initial model results showed significant relationships between growth and BI for several of the run groupings. To better understand this relationship, we fit a model that included NPGO, BI, and an interaction term between these two variables. The mechanism that links the BI to productivity is hypothesized to interact with the NPGO (Malick et al. 2017).

Results

How do changes in size-at-age differ across populations of Chinook salmon?

We found at least three distinct trends in size-at-age across the 48 stocks included in our analysis. These included a cluster of stocks that showed a consistent declining trend across all years included in the study (Fig. 2A cluster 3), one cluster with an oscillating pattern that has a minimum in the late 1990s and again in the 2010s (Fig. 2A cluster 2), and a third group of stocks that exhibited less variation in length-at-age over time (Fig. 2A cluster 1). These three patterns are consistent with long-run declines in the average size across the study region documented previously (Ohlberger et al. 2018), but they provide a more nuanced picture. There is substantial heterogeneity in the trends of size-at-age between stocks, and the consistencies within these heterogeneous responses indicate that multiple causal mechanisms may be at work. However, it is notable that all three patterns we identify show a decline in length-at-age starting between 2000 and 2010 and continuing until the end of the time series.

To test if the three trends we identified were sufficient to describe the observations in our data set, we used the same

modeling procedure with $k = 2$, 4, and 5 clusters. Cluster assignments (Fig. 3) change substantially between $k = 2$, $k = 3$, and $k = 4$, but less so when a fifth cluster was added. Increasing the number of clusters from two to three resulted in a greater improvement in model fit than the increase from three to four clusters, providing support for the choice of $k = 3$ (Fig. S6.1). To ensure our conclusions are robust to this modeling choice, Supplementary Materials S.6 recreates the results presented in Fig. 2 for $k = 2$ and $k = 4$. We find similar trends are identified when additional clusters are added to the analysis and that the correlations between life history characteristics and the cluster assignment of each stock are robust to this choice as well.

Are there life history characteristics or other traits that underlie the differences in trends?

We found that the cluster assignments corresponded with the ocean distribution and life history characteristics of each stock. We used a random forest classification algorithm to identify whether life history characteristics, ocean migrations, or the freshwater region best predicted the population's trend in length-at-age. The classification algorithm had an out-of-bag error rate (the estimated probability that the model will incorrectly assign an observation) of 29%, indicating that the life history characteristics and ocean distribution contained a substantial amount of information about the trends in length-at-age. The ODI and run timing had the highest variable importance scores (Fig. 2B). The importance of ocean distribution along with run timing indicated that both hypotheses might be true: populations with different marine distributions presumably experience different changes in conditions and different trends in size, and populations with different life histories (i.e., hatchery run timing, which is strongly correlated with hatchery release age) respond differently to the same changes in conditions.

To further support these inferences, we plotted the relationships between group assignment and ocean distribution, run timing, and hatchery release age (Figs. 2C–2E) This more detailed analysis indicated that the ODI predicted whether a population experienced a long-run decline (cluster 3) or the oscillating trend (cluster 2), with populations with more northerly distribution experiencing long-run declines. In addition to run timing, release age predicted the strength of the trends in length-at-age. Spring run stocks and stocks with release age two were primarily assigned to cluster one, which exhibited the more stable trend in size-at-age. However, it should be noted that run timing and release age are correlated with spring and summer run stocks more likely to be released at age two; therefore, it is difficult to determine which of these two factors causes the differences in trends.

What factors underlie the observed trends in length-at-age?

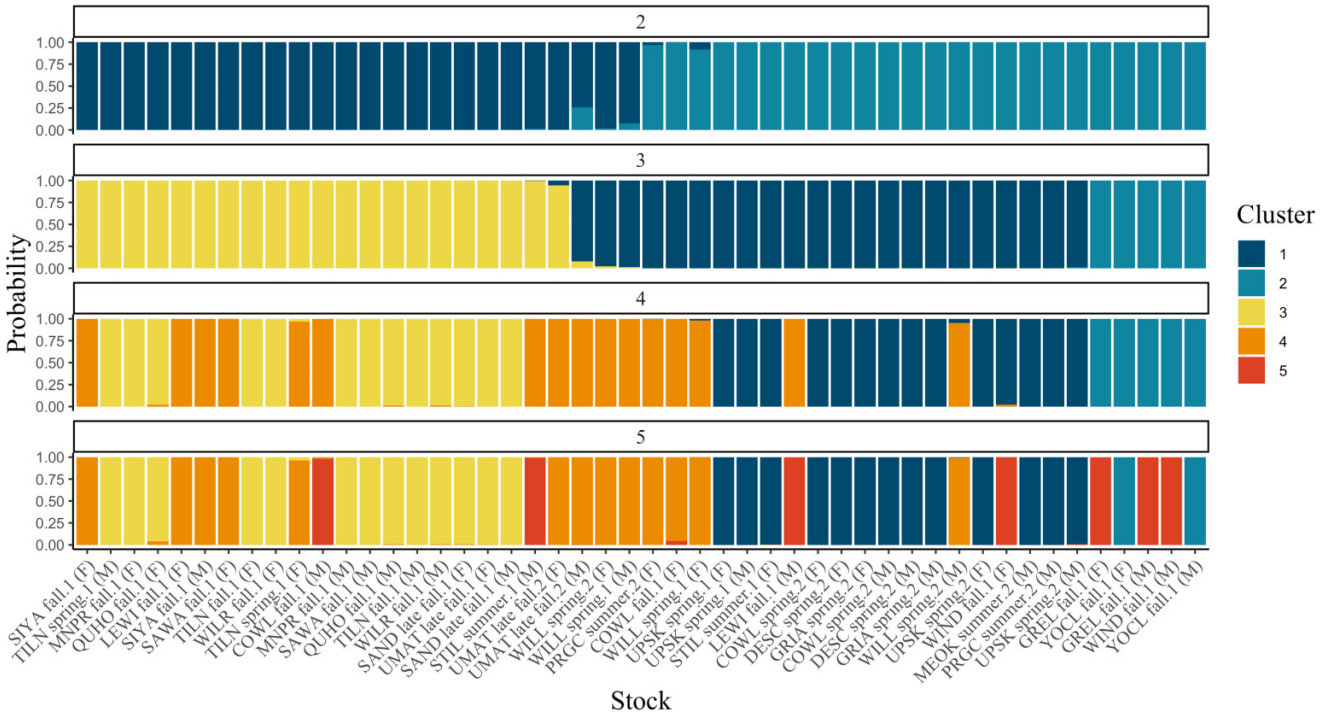
Our regression analysis showed that each of the stock groups had distinct responses to variation in the environmental indices (Fig. 4). However, three groups exhibited positive responses to the BI and negative responses to the Alaska pink salmon index. The two northern groups had particularly strong relationships with the Alaska pink salmon index, while the southern ocean distribution group (release age one) had a particularly strong positive correlation with the BI. In addition to these two main patterns, there was a consistently negative relationship between the El-Nino index and growth for all groups. We also found a negative association between Washington pink salmon abundance and the northern release age two stocks and a positive relationship between NPGO and growth for the release age two southern groups. However, the widths of the credible intervals likely overstate the amount of evidence for each of these relationships given the large number of hypotheses tested in this analysis ($7 \times 4 = 28$), and the strong assumptions about the functional form of the effects of ocean conditions on growth made in our state-space model. However, the results are consistent with the hypothesis that interspecific competition with pink salmon affects growth, and that growth is affected by inter-annual variation in productivity driven by the bifurcation of the North Pacific Current.

The correlation between the BI and growth is consistent with patterns of recruitment in sockeye, pink, and chum salmon populations (Malick et al. 2017). The putative mechanism linking the productivity of salmon populations to this environmental index is variation in the horizontal transport of nutrients in the northern portion of the California current. This process is also affected by NPGO-like variation in the North Pacific Current. To further analyze this mechanism, we fit models including NPGO, BI, and their interaction to length-at-age data for the two life history groups with southern-ocean distributions. We focused on these two groups because prior work has shown that the effect of these processes is stronger for stocks in this region (Malick et al. 2017). We found positive associations between growth and the BI and NPGO for both groups. However, the effect of NPGO was weak for the release age one stocks. The effect of the interaction between these variables was weak in both cases (Fig. 5).

Robustness tests

The growth increment model assumes that variations in ocean conditions have the same effect on growth across all ages within a stock grouping. Although it is very likely that some factors affect all age groups similarly, there may also be age-specific responses to changes in ocean conditions caused by ontogenetic niche shifts. In Supplementary Materials S.8, we include two alternative models which relax this assumption by (1) including random effects for each age cohort and (2) including process errors into the growth equations for each cohort. Results from these analyses are shown in Fig. S8.1 and do not change the qualitative nature of the findings presented in the main text. The model also assumes that the age-specific component of the growth increments f_a declines linearly with age (eq. 2). We constructed an alternative model with a more flexible relationship between growth rate and age and again found qualitatively similar results (Fig. S8.2).

Fig. 3. The cluster assignments of each stock for $k \in \{2,3,4,5\}$. The "probability" on the *y*-axis is calculated by taking the log-sum-exponential of the mean squared distance of each stock's time series to the trend from each cluster.



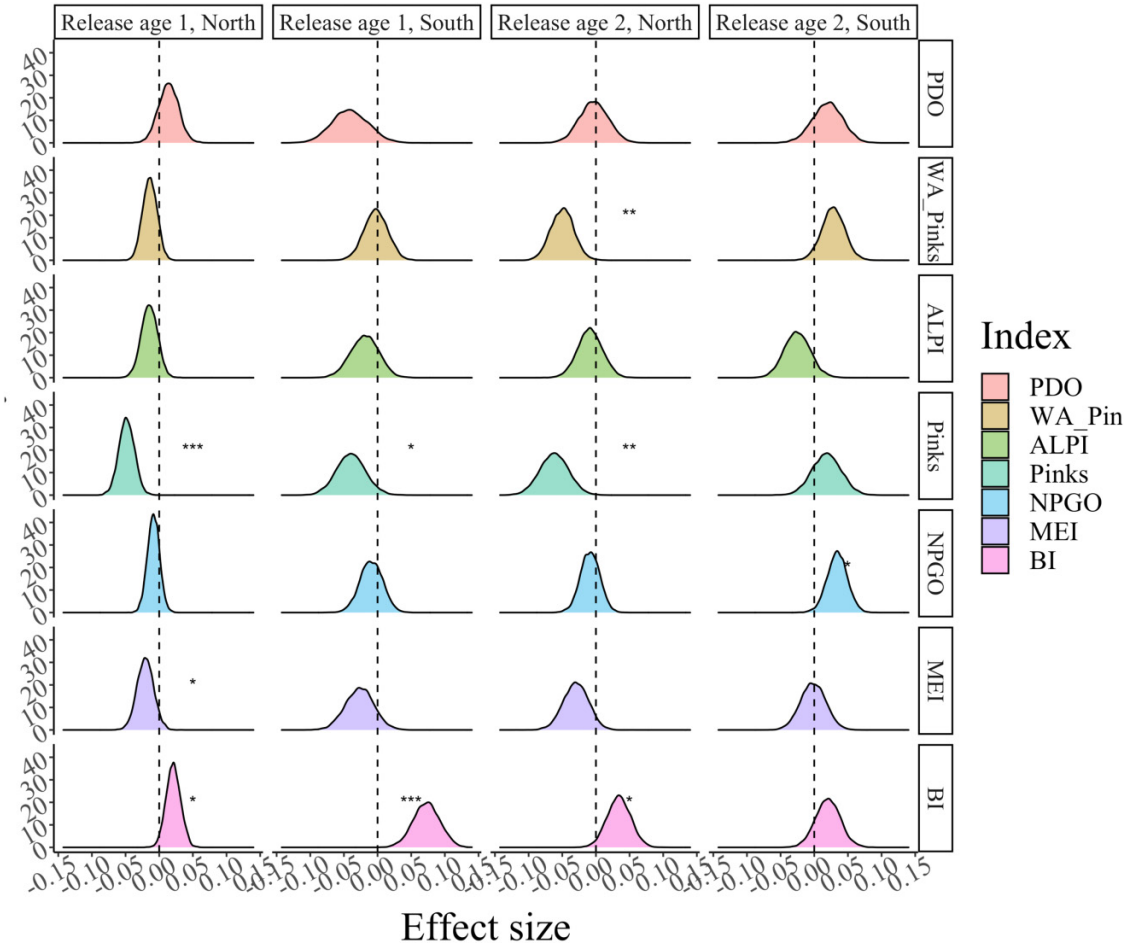
Discussion

Our study asks three primary questions: (1) How do changes in size-at-age differ across populations of Chinook salmon in the Pacific Northwest? (2) Are there life history characteristics or other traits that underlie the differences in trends? And (3) What factors may be causing populations to respond differently to the same changes in environmental conditions? Results from our analysis provide evidence of at least three distinct trends of size-at-age across the populations included in our study, suggesting that there are discrete sets of mechanisms that drive the observed patterns. The differences in trends between stocks were associated with differences in ocean distribution; stocks with more northerly ocean distributions had qualitatively distinct trends from other stocks. Our analysis also identified additional variation between stocks with similar ocean distributions that was correlated with life history characteristics. These findings suggest that differences in trends of size-at-age between stocks are primarily driven by exposure to different environmental conditions due to differences in ocean distribution, and the relative use of freshwater and the marine environment through their life cycle.

Although these findings appear to be robust, it is unknown how well they generalize from the hatchery stocks included in our study to wild conspecifics. Hatchery and wild origin fish from the same populations exhibit similar ocean distributions (Weitkamp 2010) and therefore may experience similar ocean conditions. However, the impacts of other life history characteristics identified in our study seem less likely to generalize to wild origin populations. Like their hatchery counterparts, wild Chinook salmon migrate to the ocean in either their first (ocean types) or second year of life (stream type). However, during the period of freshwater residence, they experience very different conditions living in the natural environment. This may not matter if growth is dominated by the marine phase of the life cycle; however, there might be legacy effects from this early life phase that set wild origin fish on a distinct growth trajectory.

We were unable to fully resolve question 3: identifying the processes that are driving the trends in length-at-age. Our state-space regression model indicated several possible mechanisms, including the effects of competitors and ocean conditions, but there are several limitations to this type of analysis. First, time-series correlation analyses tend to have limited statistical power because the size of the data sets is inherently limited to the length of the study period (Pyper and Peterman 1998). In our case, we had 35 years of data on salmon growth to compare with inter-annual variation in ocean conditions. Also, our environmental indices are only proxies for the hypothesized causal mechanisms and do not measure them perfectly. This limits the amount of variation that can be explained by the model because the estimated effect of the indices is expected to be smaller than the true effect of the underlying biological process due to the errors in variables bias (Walters and Martell 2004). Finally, our state-space modeling approach assumed a specific structural relationship between interannual environmental variability and size-at-age, although the qualitative nature of our results does seem to be robust to relaxing core assumptions (Supplementary Materials section 5). All of these factors limit the strength of evidence that can be produced by our analysis

Fig. 4. Posterior distribution of the coefficients between growth of each stock grouping (columns) and the environmental indices (rows). The vertical dashed marks the origin on each plot and the stars indicate the overlap between the posterior distribution and the origin (∗ < 0.05, ∗∗ < 0.01, ∗∗∗ < 0.001).



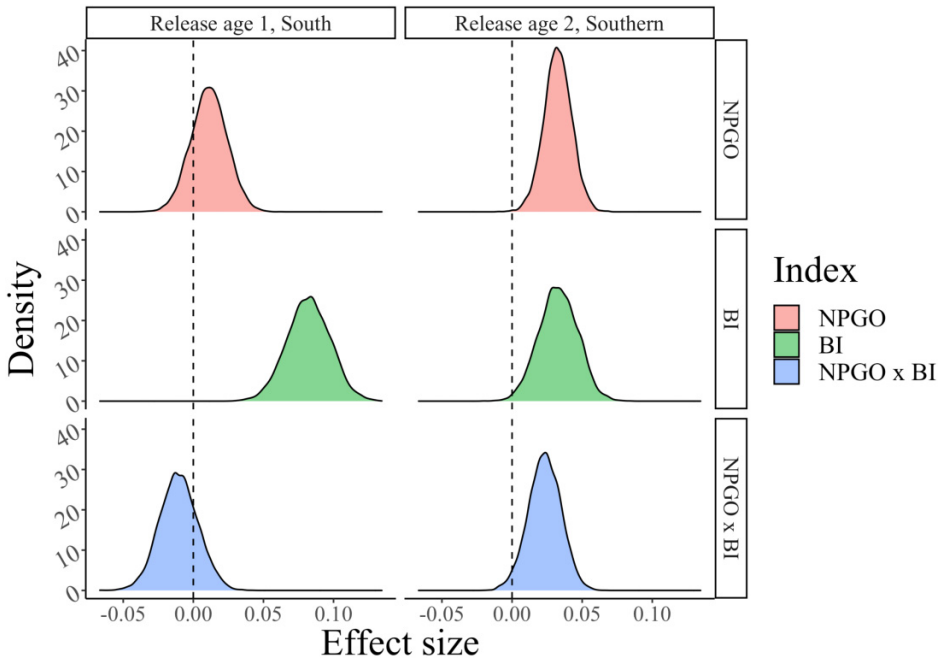
for any given hypothesis. Furthermore, our analysis focused on potential bottom-up effects on the size-at-age of Chinook salmon and did not account for possible top-down mechanisms (e.g., Ohlberger et al. 2019; Manishin et al. 2021). Because of these limitations, it is important to consider our findings in the context of prior work on the topic and other forms of evidence.

Evidence for oceanographic processes

Different responses to interannual variation in abiotic ocean conditions are a possible explanation of the differences in trends in size-at-age between populations we identified in our analysis. The productivity of salmon populations varies along the west coast due to distinct oceanographic regimes in the California Current, Gulf of Alaska, and the transition zone in between. Primary productivity in these regions is partly controlled by variability in the North Pacific Current, which affects upwelling and downwelling in the California Current and Gulf of Alaska and through horizontal transport of nutrients (Mantua et al. 1997; Malick et al. 2017). Prior studies have found that interannual variation in the growth of Chinook salmon in the Gulf of Alaska, Puget Sound, and Central California was driven by different oceanographic processes (Wells et al. 2008). This variation in productivity regimes could contribute to the difference in trends in size-at-age between populations with northern versus more southerly ocean distributions.

Consistent with this idea, we found positive relationships between growth and the BI. This index is associated with horizontal transport of nutrients caused by interannual variation in the North Pacific Current, which affects productivity in the transition region between the California Current and the Gulf of Alaska. This relationship is consistent with the productivity of pink, chum, and sockeye salmon in the same region (Malick et al. 2017). Other physical oceanographic processes may play a role; we found consistently negative (though not statistically significant) relationships between growth and El Nino conditions and consistent with Wells et al. (2006) a positive relationship between NPGO and size-at-age for one population groupings. However, the relationships between growth and abiotic conditions were relatively similar across the life history groups, including those with different ocean distributions (Fig. 4). This may suggest that variation in abiotic conditions has a limited ability to explain the observed differences in trends in size between stocks.

Fig. 5. Posterior distribution for the effect of NPGO, BI, and their interaction on the growth of the two southern stock groupings.



An alternative explanation for the apparent lack of differences reflects our data and modeling choices. Because we modeled length, our analysis implicitly gives more weight to the effect of conditions early in the life cycle when individuals experience the greatest increases in length. The differences in ocean distribution between the stocks are the smallest during this phase of the life cycle (Weitkamp 2010), potentially explaining the observed similarities in regression coefficients. Our choice to model lengths may also affect our estimates of the effect of competition with pink salmon, which has been shown to be stronger later in the life cycle of other salmon species (Ruggerone et al. 2007, 2016).

Importantly, the climate indices included in our analysis cannot explain the long-run declining pattern observed in the stocks with northerly ocean distributions. This does not rule out bottom-up oceanographic processes as a causal factor because the oceanographic indices are only proxies for factors like prey availability and temperature that directly affect growth. Furthermore, the indices included in our analysis do not exhaustively describe variation in abiotic conditions in this region, and some additional or unknown processes may also influence growth. However, other explanations may still be more appropriate. For example, consistent with Lewis et al. (2015) and Ohlberger et al. (2019), we found the declining trend in length-at-age was steeper for older age classes in these population groupings. These trends could imply that there are age-specific factors not accounted for in our analysis causing poor growth conditions for older individuals in these populations, but it is also consistent with the top-down mechanisms discussed below.

Pink salmon

Our regression model provided evidence for an effect of pink salmon abundance on the growth of Chinook salmon in each of the population groupings. All estimated effects were negative, which is consistent with the expected result of competition. However, the index of Alaska pink salmon abundance showed consistent increasing trends over time; thus, any correlations may be the result of the match of these long-run trends rather than an underlying causal relationship. Despite these limitations on our ability to measure the effect of pink salmon, there is substantial evidence for interspecific competition between salmonids in the marine environment affecting growth, survival, and maturation (Ruggerone and Nielsen 2004; Shaul and Geiger 2016; Cunningham et al. 2018; Litz et al. 2021). Pink salmon are likely to have the largest competitive effects due to their high abundance and possible competitive dominance (Ruggerone and Nielsen 2004), but their effects may also simply be easier to measure because of their 2-year cycles in abundance. Furthermore, much of the evidence for competition with pink salmon comes from chum, sockeye, and coho salmon (Ruggerone and Goetz 2004; Oke et al. 2020; Claiborne et al. 2021), only providing indirect support of competitive effects on Chinook. However, there is direct evidence for competition between pink salmon and Chinook salmon during early life stages (Kendall et al. 2020), and Chinook salmon have dietary overlap with pink salmon that are in the second year of their life cycle (Davis 2003; Davis et al. 2009). Dietary overlap with pink salmon has been shown to affect the growth of coho salmon in the Gulf of Alaska, and similar processes could affect the growth of Chinook (Shaul and Geiger 2016).

Top-down mechanisms

The processes discussed in the previous sections implicitly attribute the observed changes in average length-at-age to changes in growth. However, size-dependent mortality can also explain changes in the average size of a population.

There are several potential sources of size-dependent natural mortality in salmon populations. First, because salmon die after spawning, changes in size-dependent maturation patterns could result in changes in size at the population level. For example, if faster growing individuals within the population begin maturing at earlier ages the individuals left in the population reaching older age classes will on average be smaller. For this process to produce a trend in size-at-age, there would need to be a mechanism driving changes in maturation rates. This could be caused by changes in hatchery practices, which have resulted in larger individuals being released from the hatchery over time (Nelson et al. 2019), which could, in turn, cause earlier maturation. Similarly, interspecific competition has also been shown to change maturation schedules in salmonids (Cline et al. 2019).

Other sources of size-dependent mortality for salmon include predation (Woodson et al. 2013) and fisheries (Kendall et al. 2009). Increases in size-selective harvest or predation would cause a decline in average size within age classes and a truncation of the age distribution by removing larger and older individuals from the population. These effects can be augmented by adaptation of slower growth rates and faster maturation rates to avoid predation. Changes in harvest rates over the time period considered in our study are not consistent with this hypothesis (Ohlberger et al. 2018), but the observed changes in size and age structure of the population can be accounted for by increased predation by marine mammals, particularly Northern Resident killer whales (Ohlberger et al. 2020). This explanation would match three distinct features of our observations. First, the populations with the sharpest declines in size-at-age exhibit sharper declines among older age groups. These populations also exhibit a change in age structure consistent with increases in size-dependent natural mortality (Ohlberger et al. 2019), and, as we show, populations with greater spatial overlap with coastal populations of fish-eating whales (i.e., more northerly distributions) show the largest declines in size-at-age. Finally, we observe that spring and summer run populations, which are smaller on average for a given total age, do not experience as sharp of declines in size-at-age as the fall-run populations independent of their ODI. It is unclear whether this pattern should be expected, given the hypothesis that changes in size and age structure are caused by predation. However, this pattern could provide a test of the predation hypothesis that is independent of the evidence that has previously been considered.

Conclusions

Regardless of which factors are causing the observed trends in size, the variation in patterns of growth between stocks has implications for the population dynamics of this species and our understanding of their marine ecology. Spatial distribution has previously been shown to cause variation in productivity between salmon populations, with a range of oceanographic processes creating variable conditions at spatial scales ranging from a few hundred miles (Kilduff et al. 2014) to the entire west coast (Mantua et al. 1997; Mueter et al. 2002; Malick et al. 2017). Prior work has emphasized the location of river mouths as the key driver of this spatial variability in production because of the importance of the early marine period for survival and recruitment (Beamish and Mahnken 2001). Our results show that space also plays an important role in driving patterns of growth. However, because growth occurs through the marine life stage, variation in ocean distribution between stocks is the critical factor. In addition to the spatial dimension, our results indicate that life history traits determine how Chinook salmon respond to changing ocean conditions. Our regression analysis allowed us to identify whether stocks with different characteristics had different responses to specific sources of environmental variation. However, the full set of biological processes that cause the observed interaction between life history traits and environmental conditions remains an open question.

A final question our results highlight is whether variation in patterns of growth between stocks can stabilize ecosystem functions and services provided by Chinook salmon through portfolio effects. The productivity of populations is determined by two factors, recruitment and growth. Prior studies on portfolio effects have primarily focused on recruitment as the driver of variation in productivity in salmon populations (Carlson and Satterthwaite 2011; Kilduff et al. 2014). However, the recent declines in size among all species of Pacific salmon have demonstrated that the second factor, growth, cannot be taken for granted. Among the stocks included in our study, the distinct trends in size over time could underly a portfolio effect. However, all four distinct trends exhibit a declining pattern in the last decade of the data set. We are unable to identify if this pattern is a coincidence caused by the temporary alignment of independent factors driving changes in size among these populations or if it is a sign of a novel mechanism that affects all stocks similarly. Time may help differentiate between these hypotheses, but the clear differences among stocks leading up to this point provide useful context for understanding the mechanisms and implications of this developing pattern.

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Data availability statement

All data used in our analysis are publicly available on the Regional Mark Information System (Johnson 2004). The code used for data analysis can be found on GitHub: https://github.com/Jack-H-Buckner/Chinook_growth_and_life_histories.git.

Author information

Author ORCIDs

Jack H. Buckner https://orcid.org/0000-0001-8767-8583
William H. Satterthwaite https://orcid.org/0000-0002-0436-7390

Author contribution

Conceptualization: JHB, WHS, BWN, EJW
Data curation: BWN
Formal analysis: JHB
Investigation: JHB
Methodology: JHB, EJW
Supervision: WHS, EJW
Validation: JHB
Writing – original draft: JHB
Writing – review & editing: JHB, WHS, BWN, EJW

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2022-0116.

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