

Demographic changes in Chinook salmon across the Northeast Pacific Ocean

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Abstract

The demographic structure of populations is affected by life history strategies and how these interact with natural and anthropogenic factors such as exploitation, climate change, and biotic interactions. Previous work suggests that the mean size and age of some North American populations of Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are declining. These trends are of concern because Chinook salmon are highly valued commercially for their exceptional size and because the loss of the largest and oldest individuals may lead to reduced population productivity. Using long-term data from wild and hatchery populations, we quantified changes in the demographic structure of Chinook salmon populations over the past four decades across the Northeast Pacific Ocean, from California through western Alaska. Our results show that wild and hatchery fish are becoming smaller and younger throughout most of the Pacific coast. Proportions of older age classes have decreased over time in most regions. Simultaneously, the length-at-age of older fish has declined while the length-at-age of younger fish has typically increased. However, negative size trends of older ages were weak or non-existent at the southern end of the range. While it remains to be explored whether these trends are caused by changes in climate, fishing practices or species interactions such as predation, our qualitative review of the potential causes of demographic change suggests that selective removal of large fish has likely contributed to the apparent widespread declines in average body sizes.

KEYWORDS

age composition, climate, fishing, population demography, predation, size-structure

1 | INTRODUCTION

Populations respond to a variety of natural and anthropogenic factors that alter their dynamics and demography. The age-structure and size-structure of populations are responsive to environmental conditions, harvesting by humans, fluctuations in population density, diseases and species interactions such as predation, via changes in individual growth and size-dependent mortality. Intense harvesting can lead to age-truncated or juvenescent populations and thus reduced average sizes (Anderson et al., 2008; Hutchings & Baum, 2005; Sharpe & Hendry,

2009), climate warming has been suggested to cause widespread declines in organism body sizes (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Sheridan & Bickford, 2011), and it has long been recognized that changes in the age-structure or size-structure of a population can result from size-selective predation (Ebenman & Persson, 1988; Werner & Gilliam, 1984) as well as from shifts in competitive interactions within and between species (Jenkins, Diehl, Kratz, & Cooper, 1999; Walters & Post, 1993). Ultimately, the age and size demographics of a population are determined by the complex interactions among these factors, because they typically experience multiple stressors simultaneously.

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Chinook salmon is the largest and most highly valued species of Pacific salmon in North America. This anadromous species is native to the sub-arctic North Pacific Ocean and adjacent freshwater habitats. Chinook salmon are caught in recreational, commercial and subsistence fisheries and are preyed upon by a diverse group of predators, including iconic birds and mammals such as bald eagles (*Haliaeetus leucocephalus*), brown bears (*Ursus arctos*) and killer whales (*Orcinus orca*). Previous work and anecdotal knowledge suggest that the average size and age of Chinook salmon returning to their natal rivers have declined in recent decades. In particular, the oldest and largest fish seem to be disappearing from many populations. For instance, studies on Alaskan Chinook salmon have shown consistent decreases in the average size at return along with declining proportions of the oldest age classes, especially ocean age-4 fish (Kendall & Quinn, 2011; Lewis, Grant, Brenner, & Hamazaki, 2015). Similar trends towards declining mean weights of Chinook salmon caught in commercial fisheries along the west coast of North America were reported a few decades ago (Bigler, Welch, & Helle, 1996; Ricker, 1981), yet the causes of declining mean weight in the catch remained elusive. Furthermore, there has been no systematic assessment of the degree to which these changes in age-structure and size-structure are expressed across the native North American range of Chinook salmon, from California to western Alaska. Reductions in the average size of Chinook salmon are of concern because the loss of the oldest and largest individuals from a population can cause reduced population productivity, destabilize populations and negatively affect the long-term viability of Chinook salmon fisheries (Calduch-Verdiell, MacKenzie, Vaupel, & Andersen, 2014; Healey & Heard, 1984; Hixon, Johnson, & Sogard, 2014; Schindler et al., 2013).

A critical step towards understanding the causes of changes in Chinook salmon age-size structure is to identify whether changes in the overall mean length or weight result from changes in size-at-age, age composition or both. In addition, while each population may exhibit specific life history characteristics and face particular challenges with respect to environmental change and human impacts, understanding the spatial patterns of changes in age-structure and size-structure may provide key insights for understanding the most important causes of demographic change. Here, we examine changes in the size-at-age (length in mm) and age composition (ocean ages) of Chinook salmon along the west coast of North America over the past four decades. Specifically, we characterize common trends in size-at-age and age composition over time, identify important spatial patterns along the coast, and discuss previously suggested and novel hypotheses about the potential causes of demographic changes in Chinook salmon in the light of our findings.

2 | MATERIAL AND METHODS

2.1 | Chinook salmon ecology

The geographic distribution of Chinook salmon historically ranged from southern California to western Alaska and from northern Japan to north-east Siberia (Healey, 1991). Chinook salmon are anadromous and hatch and rear in freshwater, migrate to the ocean for most of their

life and return to their natal rivers to spawn (Quinn, 2005). Juvenile Chinook salmon typically spend 0, 1 or 2 years in freshwater before emigrating to the marine environment. Once in the ocean, many populations migrate thousands of kilometres northward along the west coast of North America, and populations from western Alaska migrate into the Bering Sea. However, the marine distribution patterns of Chinook salmon differ by region of origin, and some populations exhibit more local marine distributions, especially those from Puget Sound, southern Oregon and California (Weitkamp, 2010). The fish spend one to 5 years in the ocean to feed and gain most of their body mass before returning to their natal streams to spawn and then die. Northern populations tend to spend more time at sea (Quinn, 2005).

2.2 | Size and age time-series data

2.2.1 | Data sources

We gathered Chinook salmon size and age data from three different databases. First, coded-wire tag data were downloaded from the Regional Mark Information System (RMIS, www.rmis.org), a database of the Pacific States Marine Fisheries Commission (PSMFC), which contains release and recovery data for marked hatchery populations along the coast, from California to Alaska (note that RMIS contains some non-marked double index tags, i.e., tags used on fish without clipping the adipose fin). Our data set contained a total of 73 hatchery populations covering the time period 1977–2015. Second, data of wild (and hatchery) Chinook salmon returning to the Columbia River system were obtained from the Age and Scales database of the Washington Department of Fish and Wildlife (provided by D. Warren, WDFW). This data set contained six wild populations and catch records for the time period 1983–2011. Third, a data set with age and size information for wild Chinook salmon from Alaska was obtained from the Alaska Department of Fish and Game (ADFG; Lewis et al., 2015). The data set contained 10 wild populations and covered the time period 1977–2015. Fish age for all three data sets was estimated from scales. The grouping by river or watershed was determined by data availability, and while some of these groups are managed as “stocks,” we refer to all groups as “populations.”

The complete data set for our analyses contained a total of ~1.5 million individual measurements for 85 Chinook salmon populations with ocean-entry locations along the west coast of North America (Table S1; Figure 1). While this data set covers the North American range of the species, from western Alaska to northern California, many more populations exist that are either not monitored or for which data were not available, especially wild populations. Wild populations in our data set originate from western/south-central Alaska and from the Columbia River, whereas hatchery populations cover most of the range, from northern California to south-central Alaska.

2.2.2 | Data manipulation

Release and recovery data of hatchery populations from the RMIS database (California, Oregon, Washington, British Columbia and

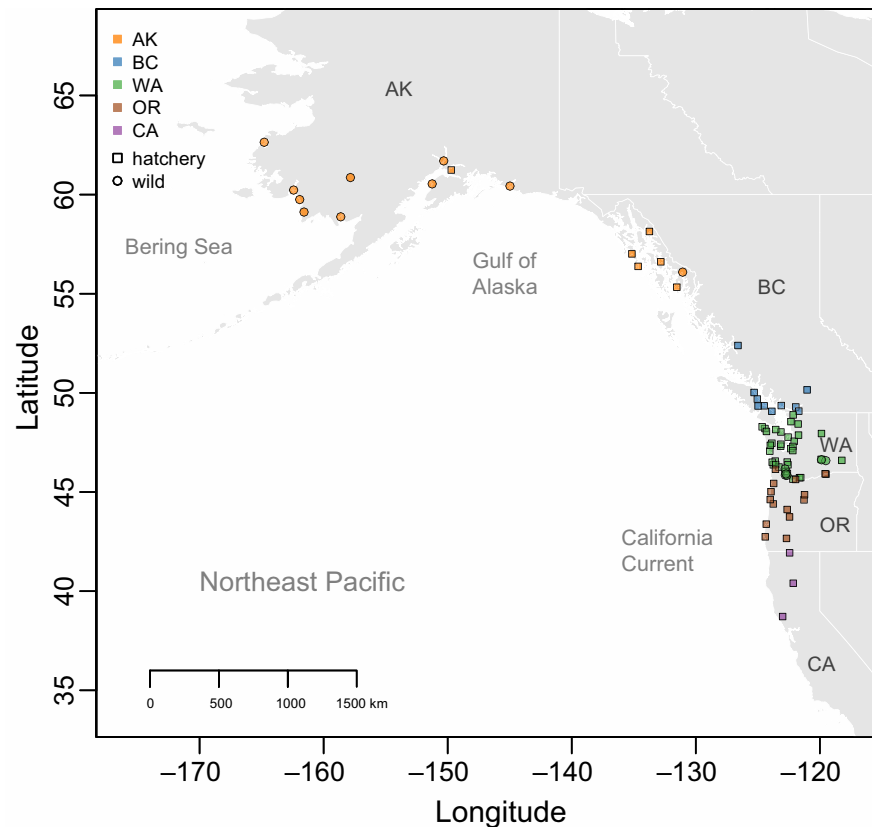


FIGURE 1 Map of study area. Shown are all wild (circles) and hatchery (squares) populations included in the analyses coloured by state/province: Alaska (orange), British Columbia (blue), Washington (green), Oregon (brown) and California (purple). Large marine ecosystems along the west coast of North America are indicated (East Bering Sea, Gulf of Alaska and California Current)

Alaska) were combined using individual tag codes or release IDs. Release groups with specific comments as well as all individuals caught in “Juvenile Sampling” or “High Seas” fisheries were not used in the analyses. Troll fisheries included in the data set catch a small proportion of Chinook salmon that would not have matured in the year of capture. This proportion was assumed to be constant through time. Columbia River populations from the WDFW database were categorized into *wild*, *mixed* and *hatchery* populations, and only those marked as wild were used in the analyses (six populations). Individual measurements smaller than 100 mm and larger than 1,500 mm were assumed to be misreported and excluded from the analysis. Populations with five or fewer years of data were also excluded. For wild populations, fishery information was converted to the RMIS fishery codes to allow fitting common models including hatchery and wild fish. Data with body length measured as snout to fork (SNF) and mid-eye to fork (MEF) were used. MEF lengths (~7.5% of data) were converted to SNF using an empirical formula: $SNF = 1.101MEF - 15.878$ (Pahlke, 1989), while other length codes were dropped from the analysis (<0.7% of data).

2.2.3 | Size and age metrics

Analyses of changes in size-at-age and age composition were based on the ocean age of the fish (i.e., the number of years a fish spent in marine waters). For example, a fish spending 4 years at sea and having four winter annuli in the ocean zone of the scale was designated as “ocean-4.” We included ocean ages 1–5 in the analyses,

with ocean ages 2–4 being the most frequently observed in our data set. Ocean-5 fish are rare in many populations, especially south of Alaska. Ocean-1 fish might be selected against by some of the fisheries and sampling methods used for capture. Age determination of Chinook salmon from scales is known to have observation error, but the accuracy of scale age data is typically about 90% (McNicol & MacLellan, 2010).

2.3 | Statistical approaches for quantifying changes

We used three different complementary approaches for assessing the temporal and spatial patterns in size-at-age and age composition of Chinook salmon populations along the coast: (i) multinomial logistic regression (MLR) was used to investigate temporal trends and spatial patterns in age composition, (ii) linear mixed effects (LME) modelling was used to identify coast-wide time trends in the size-at-age, and (iii) dynamic factor analysis (DFA) was used to model the spatial patterns of changes in the size-at-age as well as in the mean age of the populations. These approaches are explained in detail below.

2.3.1 | Multinomial logistic regression

To evaluate support for coast-wide trends in the age composition of Chinook salmon, we analysed fish recovery data using a hierarchical Bayesian MLR model (Hosmer, Lemeshow, & Sturdivant, 2013). In this framework, covariates (time) can be linked to latent proportions,

that is age composition, where the observed data are multinomial counts. Only populations with at least 10 years of data were included in the analysis. Univariate logistic regression estimates effects of covariates on an observed binary response, using a logit link function. Multinomial logistic regression extends this model to a multivariate setting, where individual fish may be assigned to one of five age classes.

The probability of a sampled fish being of age a from population p in time t was modelled using a logit link with corresponding probabilities $\text{logit}(\hat{p}_{a,t,p}) = \frac{\exp(B_{0,a,p} + B_{1,a,p} \cdot t)}{1 + \sum_{a=1}^4 \exp(B_{0,a,p} + B_{1,a,p} \cdot t)}$. For identifiability, we used ocean-5 fish as a reference group for all populations, setting $\exp(B_{0,5,p} + B_{1,5,p} \cdot t) = 1$. Because interpretation of model output is relative to the reference group, changing the reference group does not change the model results. The intercept terms, representing age compositions unique to each population in the first year of the data set, were assigned a Dirichlet prior with equal densities (uniform on the simplex), $B_{0,a=1:5,p} \sim \text{Dir}(\mathbf{1})$. Tests showed that results were insensitive to the choice of densities of the Dirichlet prior. Priors were assigned independently to each population such that no grouping was implied a priori by this choice. Because we are interested in population-specific, as well as global trends in age composition, the temporal slope terms were modelled hierarchically. The slopes were assumed to be drawn from a common distribution for each age, such that $B_{1,a,s} \sim N(\mu_a, \sigma_a)$, where μ_a and σ_a represent the mean and standard deviation of slopes for age a , in logit space. Finally, we used a multinomial observation model to link observed counts to predictions. For each individual, fish i recovered in time t from population p , this can be expressed as $Y_{i,t,p} \sim \text{Multinomial}(\hat{p}_{a=1:5,t,p}, N = 1)$.

We implemented the Bayesian multinomial regression model in STAN (Stan Development Team, 2016a) run via the R package *rstan* (Stan Development Team, 2016b). For each ocean age model, three MCMC chains were run for 4,000 iterations following a warm-up period of 1,000 iterations (no thinning). We examined model convergence using the effective sample size, Rhat, and by monitoring chains for divergent transitions using trace plots.

Based on model-predicted population-specific age proportions in each year, we calculated the relative change in the median proportions between the beginning and the end of the assessed time series for each population. The relative change was calculated as the difference between the average proportions in the two 5-year periods from 1979 to 1983 and 2001 to 2005 (brood years), thus covering a time period with complete age observations for most populations.

2.3.2 | LME models

We used a LME approach to model the size-at-age of Chinook salmon based on individual-level observations ($n = \sim 1.5 \times 10^6$) covering the brood years 1975–2009. Hence, data were not aggregated for this analysis. We fit linear mixed models to data for each age class of interest (ocean ages 1–5), where the response variables (length in mm) were normally distributed. The models were fit using the package *nlme* (v.3.1-128, Pinheiro & Bates, 2010) in R (v.3.3.2, R Core Team, 2016).

The initial model contained all explanatory variables, including year (up to 35 levels), rearing type (two levels: hatchery and wild), fishery (up to 38 levels), freshwater age (three levels: ages 0, 1 and 2), run type (five levels: spring, summer, fall, late fall and upriver bright) and sex (three levels: male/female/unknown) as factors, and day of year of sampling as continuous variable. The term “fishery” here refers to the fishery codes used by RMIS (see Table S1). The number of categories for some of the factors varied slightly between age-groups due to differences in data availability, that is few samples in that category for a given age-group. Categories with at least 25 observations were included in the analysis. It should be noted that sex may be estimated with unreliable external characteristics in ocean-phase fish (Lewis et al., 2015). We therefore fit the same mixed effects model without sex as a factor to confirm that our conclusions would not change. We also fit the same models based on escapement data only (as defined by the RMIS fishery group) to ensure that the conclusions would not depend on the inclusion of potentially selective fishery data.

An interaction between year and rearing type was included to test for different time trends in size-at-age between hatchery and wild fish. An interaction between year and state was not included due to missing observations for several year–state combinations. Random intercepts for each year nested within population were used to account for the lack of independence of the data within years and populations. We tested for the inclusion of nested random effects by comparing models with and without random effects using a likelihood ratio test and AIC model selection. Based on preliminary model runs without variance structure and subsequent visual analysis of the residuals for homogeneity of variances, we also tested for the inclusion of weights by year or population. We fit models of the following form: $L_i = \beta_0 + \beta_1 \text{FE}_1 + \dots + \beta_n \text{FE}_n + b_{p|y} + \epsilon_i$, where β_0 is the intercept, β_1, \dots, β_n are regression coefficients of the various fixed effects (FE), $b_{p|y}$ is a normally distributed random effect for year (y) nested in population (p) $\sim N(0, \sigma_b^2)$ and ϵ_i is a normally distributed error term $\sim N(0, \sigma^2)$.

The most parsimonious combination of fixed effects was determined using AIC based multimodel inference using the *MuMIn* package (v.1.15.6, Burnham & Anderson, 2002) by evaluating the complete set of models with all possible combinations of fixed effects. Models that differed in their random effects were compared using restricted maximum likelihood (REML), while models with different fixed effects structures were compared using maximum likelihood parameter estimation (ML). The final models were fit using REML.

2.3.3 | Dynamic factor analysis

To identify the spatial coherence in the temporal trends in size-at-age and age composition between regions, for example between states, we applied DFA, a multivariate time-series analysis approach (Zuur, Tuck, & Bailey, 2003). For this analysis, we constructed population-specific time series of mean age and mean size-at-age, that is using aggregated population-level time series that do not account for

differences in sample size (as opposed to the LME approach). Mean age was computed in brood years for which each age-group could have been observed. Only populations with at least 5 years of data were included in the analyses.

In DFA, the time series are modelled as a linear combination of hidden trends, which reflect the temporal variation shared among the time series, and population-specific error terms: $y_t = Z x_t + v_t$, where the hidden trends (x_t) are modelled as random walk processes with a noise component (w): $x_t = x_{t-1} + w_t$. Matrix Z contains factor loadings on the shared/hidden trends (x_t), and $v_t \sim \text{MVN}(0, R)$ is the residual error, which is assumed to be multivariate normally distributed (MVN) with mean zero and variance-covariance matrix R . The process noise $w_t \sim \text{MVN}(0, I)$ is assumed to be multivariate normally distributed with mean zero and variance-covariance matrix I , which is the identity matrix such that the hidden trends are independent. The initial state vector is set to a mean of zero and a diagonal variance-covariance matrix with large variances. Because we were interested in the most common trend shared among the time series, we only fit one-trend models. We used a variance-covariance matrix (R) with shared variances and no covariance among populations because preliminary tests using AIC model selection indicated *diagonal and equal* as the most parsimonious error structure for the mean size-at-age and mean age time series. Time series were z-scored (de-meaned and standardized) to account for differences in means and variances.

We implemented DFA in a Bayesian framework using an implementation of the model in STAN. Code to run the Bayesian DFA is available on GitHub: <https://github.com/nwfs-timeseries/stats> (Ward, Scheuerell, & Holmes, 2018). For each ocean age model, we ran 10,000 iterations following a warm-up period of 10,000 iterations. We examined convergence across parameters using the effective sample size, Rhat, and monitoring chains for divergent transitions using trace plots. The Bayesian estimates corresponded to those generated by a DFA in a maximum likelihood framework using the package MARSS (Holmes, Ward, & Wills, 2012).

2.4 | Additional time-series data

To perform a qualitative review of the commonly hypothesized causes of changes in Chinook salmon age-size structure, we gathered time-series data on key indices such as overall fishing pressure,

the number of hatchery fish, climate variables and the number of marine mammal predators in the ocean. Specifically, we compiled data on total commercial catches and the number of hatchery releases of Chinook salmon in the North Pacific Ocean (www.npafc.org), coastal sea surface temperatures in summer (July–September) and winter (January–March) for a rectangle defined by latitudes 41.0°–54.3° north and longitudes 125.6°–135° west (data source: www.esrl.noaa.gov, Kalnay et al., 1996), ocean climate indices such as the PDO (Pacific Decadal Oscillation, <http://research.jisao.washington.edu>) and NPGO (North Pacific Gyre Oscillation, www.o3d.org/npgo), and the abundances of resident killer whales and other marine mammal predators (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). Killer whale numbers were based on abundances of Southern Residents (Center for Whale Research, 2017), Northern Residents (Ellis, Ford, & Towers, 2007), Southeast Alaska Residents and index pods of Gulf of Alaska Residents (Allen & Angliss, 2013). Missing years of data for Southeast Alaska and Gulf of Alaska Residents were interpolated using an annual growth rate of 2.9% (estimated average rate of increase in all non-Southern Residents).

3 | RESULTS

3.1 | Spatial and temporal patterns in age composition

The age composition of many of the Chinook salmon populations along the coast has changed considerably over the past few decades. Pronounced changes in age composition were found in Alaskan populations, where the proportions of younger ocean ages have increased and the proportions of older ocean age classes have decreased over time (Figure 2). In particular, ocean-5 fish that used to make up 3%–5% of the runs have become essentially non-existent (<0.5%) in recent years, and proportions of ocean-4 fish have also declined sharply. The declining trend in the proportions of older ocean ages is also apparent but slightly weaker in Washington, Oregon, and basically absent in California and British Columbia. Consequently, the overall mean age of all populations combined by state declined most significantly in Alaska, declined slightly in Washington, Oregon and California, and increased over time in British Columbia. These

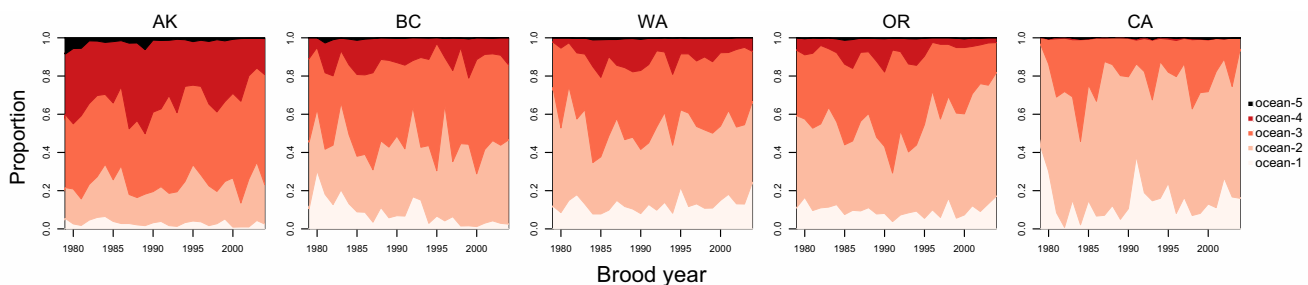


FIGURE 2 Age proportions of Chinook salmon by state/province. Shown are mean proportions of ocean-1 fish (bottom polygons, light red) to ocean-5 fish (top polygons, black) by brood year

same trends were highlighted by the DFA analysis. The most common trend in mean age shared among populations showed a relatively continuous decline over time (Figure 3). Most populations from Alaska, Oregon and Washington (except some of the wild populations) followed this trend of declining mean age, while most populations from British Columbia showed the opposite trend (i.e., mostly negative loadings on the DFA trend). Wild populations from Alaska followed the declining trend in mean age, similar to hatchery populations from Alaska, whereas the wild populations from Washington showed weaker associations with the declining trend (Figure 3).

The multinomial regression model further illustrated that the proportions of older age-groups are consistently lower in recent brood years (2001–2005) compared to the early period (1979–1983). In populations with ocean-5 fish, the proportion of this age-group

has consistently declined (Figure 4), and proportions of ocean-4 have also declined in over 75% of the populations examined coast-wide. While these findings suggest some shared temporal trends in the age proportions along the coast, our analysis also highlighted significant differences in age trends between regions, indicating region-specific factors affecting the age composition of Chinook salmon populations. The most substantial changes were found for Alaska, where proportions of ocean-2 and ocean-3 fish increased and those of ocean-4 and ocean-5 fish decreased in almost all populations (Figure 4). At the southern end of the distribution range, where the age-structure is generally shifted towards younger ocean ages, the loss of older individuals implies declining proportions of ocean-4 and often ocean-3 fish, especially in California. A clear latitudinal cline is therefore evident for ocean-3 fish, such that proportions of most

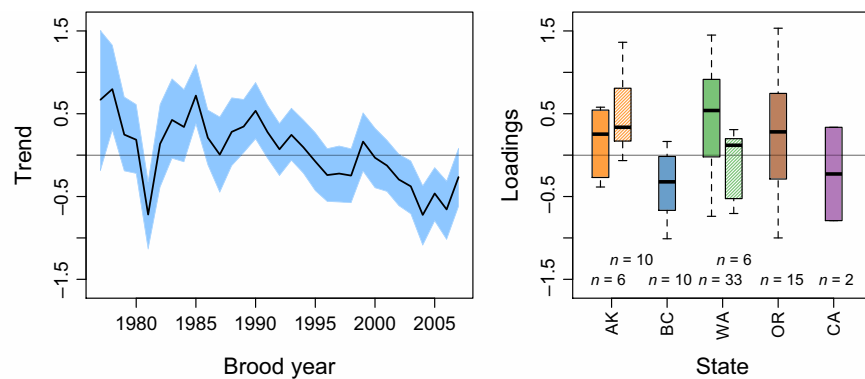


FIGURE 3 Dynamic factor analysis (DFA) of mean age of Chinook salmon along the west coast of North America. Common trend in mean ocean age of all populations by brood year (left) shown as medians (black line) with 95% credible intervals (blue bands). The right panel shows the loadings by each state/province on this common trend. Plots show median values (thick lines), 25th and 75th quartiles (boxes), and 1.5 times the interquartile range (whiskers, outliers omitted). Filled boxes indicate hatchery populations and shaded boxes indicate wild populations. The number of populations in each region is indicated at the bottom

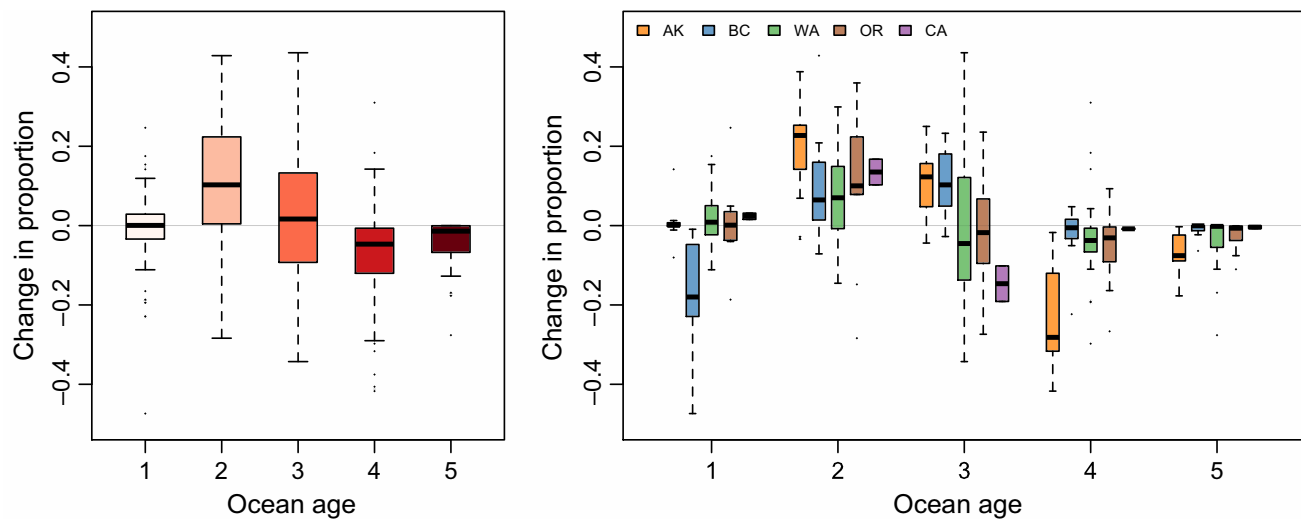


FIGURE 4 Coast-wide changes in age proportions of Chinook salmon along the North American west coast. Relative changes in the proportion of each ocean age between the early and late periods of the time series. Box plots are based on population-specific age proportions predicted by the multinomial logistic regression model and show median values (thick lines), 25th and 75th quartiles (boxes), 1.5 times the interquartile range (whiskers) and outliers (circles). Colours on the left indicate ocean ages 1–5 (light to dark red), and colours on the right refer to Alaska (orange), British Columbia (blue), Washington (green), Oregon (brown) and California (purple)

populations examined increased in Alaska and British Columbia, increased or decreased in Washington and Oregon, and decreased in California.

3.2 | Spatial and temporal patterns in size-at-age

Inclusion of a nested year-in-population random effect was supported in all five size-at-age models (one for each ocean age). Four of the five selected models included fixed effects for brood year, rearing type, fishery, freshwater age, run type and sex as factors, and day of year of capture as a continuous variable. The selected ocean-5 model, which contained the fewest data, did not include freshwater age and day of year, but otherwise had the same structure. In addition, the interaction between the fixed effects of year and rearing type (hatchery or wild) was not supported in the models with the exception of the ocean-1 model. Hatchery-origin and wild populations thus did not show significantly different temporal trends except for the youngest age class. The conditional R^2 values of the selected models for ocean ages 1–5 were 0.70, 0.51, 0.37, 0.45 and 0.56. Hence, the variance explained by the fixed and random effects was between 37% and 70%.

The year effects of the size-at-age models showed that the size of Chinook salmon across their entire North American range has varied greatly over the past four decades. All ocean ages from ocean-1 to ocean-5 show some year-to-year variation and clear temporal trends in size-at-age (Figure 5). The overall trend is that the size-at-age of ocean-1 and ocean-2 fish has increased, while the size-at-age of ocean-4 and ocean-5 (and to some extent ocean-3) fish has decreased over time. The increasing size trend of young fish was found in most hatchery populations, but was generally weaker or absent in wild populations, especially those from Alaska (see below). The size decline in ocean-4 and ocean-5 fish was found for almost all hatchery and wild populations and was most rapid during the recent 10–15 years (i.e., since about 2000). Our findings suggest that since the late 1970s, average sizes (lengths) have *increased* by about 7% and 3% for ocean ages 1 and 2, respectively, whereas sizes have *decreased* by about 5%, 7% and 9% for ocean ages 3, 4 and 5, respectively. The coast-wide decline in the size-at-age of older fish has occurred almost continuously over time, although some shorter periods of stable or increasing sizes have occurred (Figure 5). It is worth noting, however, that the nested year-in-population random effects suggest considerable among-population variation in the predicted sizes and the temporal trends in size-at-age (Figure S1).

Hatchery fish were generally larger at ocean entry and remained larger compared to wild fish up to ocean age-3 ($p < .0001$), but this size difference diminished throughout ocean residence, and average sizes were similar for ocean ages 4 and 5 ($p > .05$, Figure 6). On average, hatchery fish were more than 20% larger than wild fish at ocean ages 1 and 2. Similarly, freshwater age influences the size of ocean ages during the first three years at sea, but this difference weakened for ocean-4 and disappeared for ocean-5 fish (Figure S2). Day of capture had a positive effect in all ages, that is larger fish were caught later in the year, but this effect also continuously weakened from ocean age 1–5. The various run types showed only slight differences

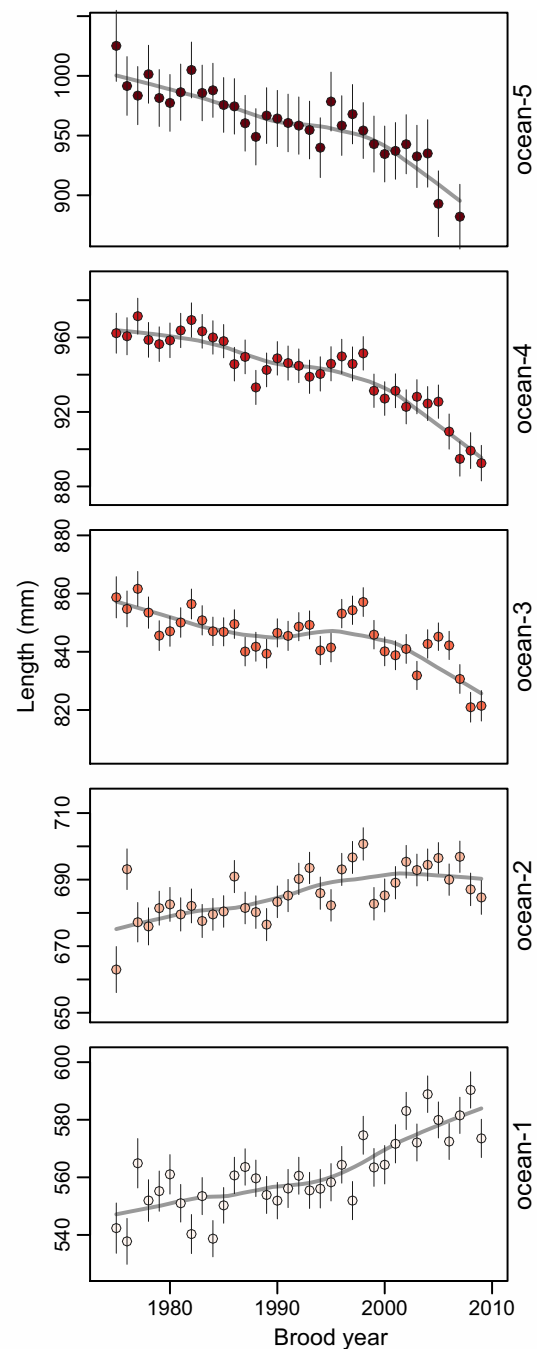


FIGURE 5 Linear mixed effects predictions of size-at-age for Chinook salmon across the North American west coast. Annual predictions for the size-at-age of each age-group (circles, with standard errors), from ocean-1 (bottom) to ocean-5 (top). The grey line illustrates the time trend in size-at-age (loess smoother with span=0.5). Year predictions were made by setting all other predictors to median values (continuous variables) or the most common category (factors) [Colour figure can be viewed at wileyonlinelibrary.com]

in size-at-age, with fall and summer runs being generally larger than spring runs. Finally, there was a significant effect of fishery on size-at-age, where the smallest Chinook salmon were caught in ocean

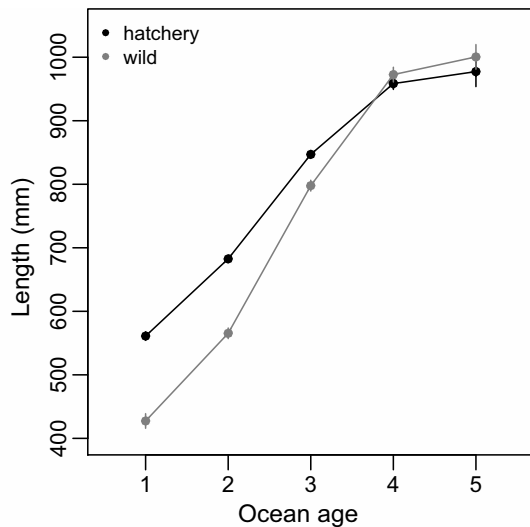


FIGURE 6 Hatchery vs wild Chinook salmon. LME predictions for the size-at-age of hatchery and wild Chinook salmon for each ocean age

troll fisheries and the largest fish were caught in escapement fisheries (in-river or terminal fisheries). The normalized residuals of the LME model showed some heterogeneity in residual variance, specifically a decrease in the residual variance over time for ocean ages 4 and 5 (Figure S3). Including this variance structure in the model, by allowing for different variances per year, did not change the model selection or predictions (but was computationally costly due to the large amount of length data).

The DFAs with one common trend for each ocean age across all populations extracted shared trends that closely matched the temporal trends described by the LME year effects (Figure 7). The dominant size-at-age trends were shared among many of the populations (by definition), yet some differences between regions and rearing types became apparent. For instance, most hatchery populations loaded strongly on the positive size trend of ocean age 1 and 2 fish, whereas most wild populations from western Alaska and several of the wild populations from the Columbia River did not follow this trend. Populations along the coast from western Alaska to northern Oregon loaded strongly on the declining size trend of ocean-4 fish, including wild and hatchery fish. In contrast, populations from southern Oregon and California as well as those from Puget Sound, a region with a higher proportion of populations that do not migrate far in the ocean, showed weak or even negative loadings on the dominant trends of ocean-4 fish and thus did not follow the declining size trend (Figure S4).

4 | DISCUSSION

4.1 | Changes in age-size structure

We found that the size-structure and age-structure of Chinook salmon have changed considerably across the Northeast Pacific

Ocean since the late 1970s. While changes in age proportions showed some region-specific trends, many of the populations coast-wide have experienced declines in the proportion of ocean-4 and ocean-5 fish, and proportions of ocean-2 fish have generally increased. Furthermore, the size-at-age of ocean-1 and ocean-2 has increased over time, at least in most hatchery populations, whereas the size-at-age of ocean-4 and ocean-5 fish has declined considerably, especially since about 2000. In addition to the temporal trends in age composition and size-at-age, our results also showed significant effects of other explanatory variables, including rearing type, fishery, freshwater age and run type. Hatchery-origin fish were found to be considerably larger than wild fish during the first 2 years of ocean residence, but this size difference disappears for older ocean ages, suggesting faster growth rates that lead to larger size-at-age early in life but similar maximum sizes.

Declining sizes of older ocean fish were found for both wild and hatchery Chinook salmon along the coast. Our spatial analysis of changes in size-at-age revealed that the dominant trends are remarkably consistent across the entire Northeast Pacific Ocean. Most populations along the northern and central part of the coast, from western Alaska through northern Oregon, follow the declining size trend of ocean-4 fish. Furthermore, populations from Southeast Alaska, British Columbia, coastal Washington and the Columbia River tend to follow the increasing size trend of ocean-1 and -2 fish. The difference between hatchery and wild Chinook salmon in Alaska for younger ocean ages could either result from different growth trajectories of hatchery vs. wild fish, consistently increasing release sizes of hatchery fish, or from differences between regions, because most of the hatchery populations were from Southeast Alaska, whereas the majority of wild populations were from central and western Alaska.

Previous work documented changes in Chinook salmon age-size structure in some of the regions analysed here. For instance, it was shown that the mean size (length) of some Chinook salmon populations in Alaska has declined by up to 10% since the early 1980s, concurrent with declines in mean age (Lewis et al., 2015). These authors also found that the size and age trends were consistent for data derived from commercial gill net fisheries and in-river weir counts. Similarly, the mean age of Chinook salmon returning to Nushagak River, western Alaska, as well as the size of the older fish, has declined in the same time period (Kendall & Quinn, 2011). Earlier studies had reported declines in mean weight of Chinook salmon caught in commercial fisheries in many regions of North America (Bigler et al., 1996; Ricker, 1981). Interestingly, the weight trends for British Columbia were not as continuous as for other regions (Bigler et al., 1996; Ricker, 1981), which is in line with a recent study showing that the weight of Chinook salmon caught in British Columbia fisheries has declined in the 20 years prior to the early 1970s, increased up to about 2000, and thereafter decreased again (Jeffrey, Côté, Irvine, & Reynolds, 2017). This pattern in the mean weight of the fish might be caused by changes in the age composition. Our results suggest that age trends of populations from British Columbia differ from those observed elsewhere. However, the trends in size-at-age of most

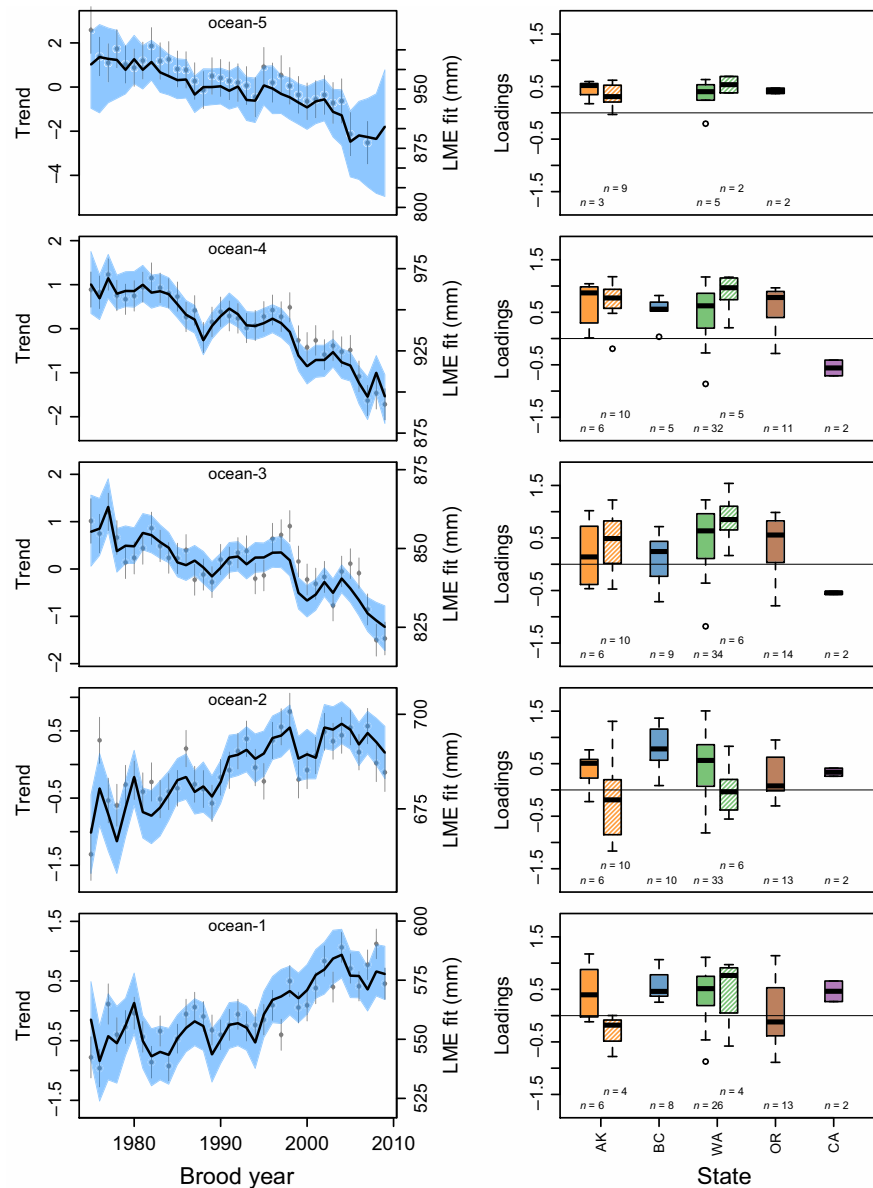


FIGURE 7 Dynamic factor analysis of size-at-age for Chinook salmon. Common trend in size-at-age among all populations (left) showing the median estimate (black line) with 95% credible intervals (blue bands), along with predictions from the LME (grey circles and error bars), as well as the loadings on the common trend clustered by region (right, ordered north to south) for ocean ages 1 (bottom) to 5 (top). Filled boxes indicate hatchery populations and shaded boxes indicate wild populations. The number of populations in each region is indicated at the bottom

populations from British Columbia are coherent with the size trends observed coast-wide.

Chinook salmon populations that spawn in north-east Asia, at least those in Kamchatka (Russia), seem to exhibit similar age and size trends as observed for North American populations (Bugaev et al., 2015; Popova, 2015). Specifically, long-term data series from the Bolshaya Vorovskaya River in south-western Kamchatka suggest that mean sizes and proportions of ocean-4 and ocean-5 fish have been declining since the late 1970s (Popova, 2015). These shifts in mean size and age closely resemble the trends reported here for North American populations, although it is not clear whether size-at-age has declined, or whether the negative trend in mean size resulted from shifts in age composition alone. Marine distributions of Russian Chinook salmon populations overlap with those of western and central Alaskan populations in the western parts of the Bering Sea and Gulf of Alaska (Larson et al., 2013).

4.2 | Consequences of demographic change

The loss of old and large individuals from a population can have important ecological and economic implications. Declines in the average size and age can cause a reduction in population productivity, because smaller salmon have lower fecundity and lower offspring survival, and may not be able to dig deep enough redds to reduce susceptibility to scouring (Healey & Heard, 1984; Hixon et al., 2014). Smaller fish could also reduce the transport of marine-derived nutrients into freshwater and terrestrial ecosystems (Moore et al., 2011; Schindler et al., 2003), unless abundances increase. Furthermore, a less diverse age-structure may decrease population stability through increased variability in abundance (Anderson et al., 2008; Hsieh et al., 2006) or weaker portfolio effects through reduced life history complexity (Schindler et al., 2010). Finally, due to their ecological importance and high social and market values, large fish are

of particular value to Chinook salmon fisheries, and an erosion of the age-size structure may negatively affect their long-term viability (Calduch-Verdiell et al., 2014; Healey & Heard, 1984).

4.3 | Potential causes of observed changes

The reported changes in the size and age distribution of Chinook salmon populations across the Northeast Pacific could be responses to a variety of factors. Commonly hypothesized causes of change in salmon age-size structure include (i) size-selective harvest, (ii) environmental change such as changes in temperature regimes or ocean productivity that affect growth and mortality rates, and (iii) impacts of hatchery practices and increased competition for food (including non-Chinook hatchery populations). A previously overlooked hypothesis attributes the observed changes to (iv) predation by marine mammals, especially a growing number of resident killer whales and their size-selective predation on Chinook salmon (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). In the following, we present these hypotheses in detail and discuss their qualitative consistency with the findings reported in this paper. A summary of data relevant for evaluating these hypotheses at a broad geographic scale is provided in Figure 8.

4.3.1 | Harvest

The loss of the oldest and largest fish, as described for several Chinook salmon populations, is commonly attributed to size-selective fishing. Previous work has suggested that size declines in Chinook salmon may be caused by sufficiently strong and selective fishing and the resulting evolutionary trait changes by showing that size-selective fishing could produce an evolutionary response towards smaller average sizes and ages of Chinook salmon within a few decades if exploitation rates and size selectivity are sufficiently strong (Bromaghin, Nielson, & Hard, 2011; Eldridge, Hard, & Naish, 2010; Hard, Eldridge, & Naish, 2009). In practice, it is difficult to evaluate whether the observed phenotypic change is caused by an underlying genetic response. The expected impacts of size-selective fishing are generally consistent with the observed pattern that fish return at smaller sizes and younger ages in many rivers and regions. However, size limits vary by state, selection curves vary among fisheries (e.g., troll, gillnet, subsistence and recreational fisheries) and fishery selectivity tends to be weak (e.g., Kendall & Quinn, 2011). While one may expect a lag in the demographic response of fish populations to fisheries selection, at least on the order of a few generations, most of the coastal fisheries were well developed by the 1970s, and exploitation rates have been declining since the 1990s (Hilborn et al., 2012; Figure 8). However, the decline in the size of ocean-4+ fish has accelerated since about 2000. Exploitation rates vary greatly among populations even within the same region (Lewis et al., 2015), yet most populations along the west coast, that is north of central Oregon, exhibit a common decline in size-at-age (Figure 7). Some of the populations have experienced relatively low harvest

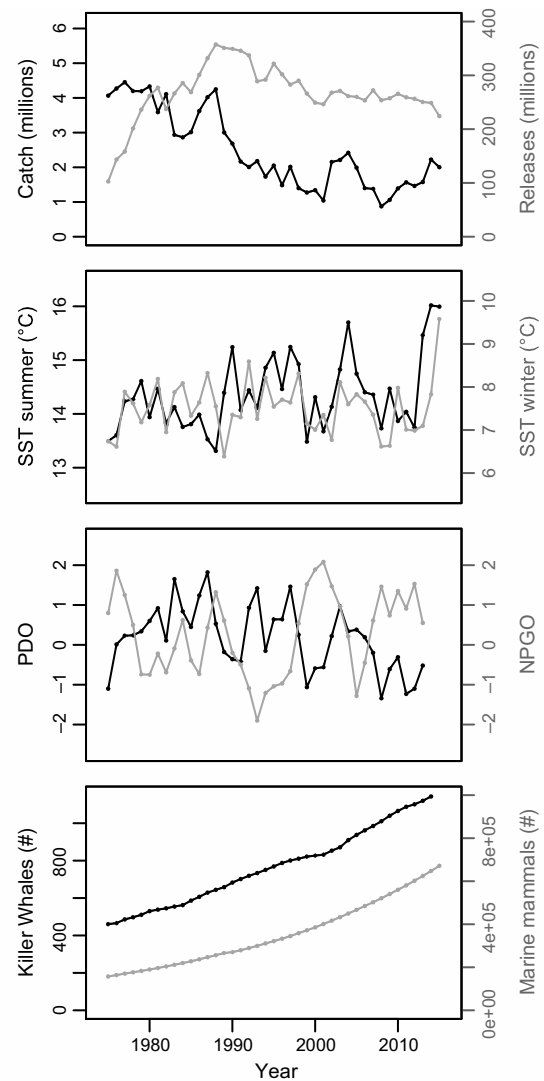


FIGURE 8 Annual indices of fishing pressure, hatchery releases, climate variation and predation. Shown are (a) total commercial catches and hatchery releases of Chinook salmon in the North Pacific Ocean, (b) coastal sea surface temperatures in summer and winter, (c) ocean climate indices PDO and NPGO, and (d) abundances of resident killer whales and other marine mammal predators. Black (left) and grey (right) y-axes apply to black and grey time series

rates (CTC, 2016; JTC, 2006). For example, exploitation rates of the Nushagak and Goodnews rivers populations are rather low (<40%) compared to those of other western and central Alaskan populations (>50%), for example the Yukon and Copper rivers, while the declining trends in size-at-age are similarly pronounced (Lewis et al., 2015).

4.3.2 | Hatcheries

Total hatchery releases of Chinook salmon into the Pacific Ocean increased substantially during the 1970s and somewhat during the 1980s and have since been declining (Figure 8). Hatchery-reared fish could alter the age-size structures of populations coast-wide via two

mechanisms: direct effects on competition for resources in the ocean (Ruggerone & Goetz, 2004), or as a consequence of selective breeding and introgression of selected genotypes into wild populations, especially small populations in close geographic proximity to hatcheries (Van Doornik et al., 2013). The selective breeding of Chinook salmon in hatcheries might have produced faster-growing fish that attain larger sizes during the first two or 3 years in the ocean but do not reach larger maximum sizes compared to wild fish. Alternatively, larger sizes of hatchery fish during the early ocean phase could be a result of the larger size at release from the hatcheries. Introgression of hatchery-reared fish might have contributed to increased size-at-age of ocean-1 and ocean-2 fish in wild populations. A larger size-at-age of young ocean fish may further contribute to a decrease in the proportion of older ocean ages at return if maturation is primarily determined by size. Nevertheless, these trends cannot explain the decline in size-at-age of ocean-4 and ocean-5 fish that is apparent in all wild populations, including many that are not exposed to hatchery strays. For instance, the trend of declining size-at-age of ocean-4 and ocean-5 fish is prevalent among wild populations in western Alaska that experience no introgression of hatchery genotypes because no Chinook salmon hatcheries currently operate in western Alaska (Stopha, 2017). The observed changes in size-at-age suggest that growth conditions for younger fish have improved (larger size of ocean-1 and ocean-2 fish), and the continuous decline in the size of older fish is not consistent with the hypothesized effect of increased intraspecific competition.

4.3.3 | Interspecific competition

Increased interspecific competition for food with other Pacific salmon is expected to be of minor importance, because older Chinook salmon feed at a higher trophic level than other species (Johnson & Schindler, 2008). While changes in growth can result from changes in food abundance or competition, our findings suggest that growth conditions for younger fish have actually improved and support increased growth rates, which is difficult to reconcile with general shifts in ocean productivity or carrying capacity. In addition, competition among Pacific salmon is believed to be most intense during the first two or 3 years of ocean life (Ruggerone & Connors, 2015). Negative effects of direct competition with other salmonids are therefore unlikely to be the driving mechanisms of declining size-at-age among older Chinook salmon. However, indirect effect of increasing abundances of other salmonids on the prey base of older Chinook salmon in the ocean, for instance through impacts on other life-stages of the prey that are not targeted by Chinook salmon or through more complex food web linkages, cannot be ruled out as a potential driver of changes in age-size structure.

4.3.4 | Environmental variation

Previous work on Chinook salmon suggests that changes in ocean temperature are not strongly linked to changes in growth and average size of adult fish (Ricker, 1981; Ruggerone, Nielsen, & Agler, 2009). While the faster life history with higher growth rate

and smaller maximum size could be a response to climate warming (Cheung et al., 2013; Gardner et al., 2011; Ohlberger, 2013; Sheridan & Bickford, 2011), temperatures in the coastal waters of the Northeast Pacific (Figure 8) have been highly variable with only weak increasing trends over the past few decades (Johnstone & Mantua, 2014). Ocean conditions in the Northeast Pacific are strongly linked to large-scale climate phenomena such as El Niño Southern Oscillation (ENSO), the North Pacific Gyre Oscillation (NPGO) and Pacific Decadal Oscillation (PDO). These climate indices are known to affect the survival and productivity of Pacific salmon in the ocean (Hare, Mantua, & Francis, 1999; Kilduff, Di Lorenzo, Botsford, & Teo, 2015; Mantua, Hare, Zhang, Wallace, & Francis, 1997; Ohlberger, Scheuerell, & Schindler, 2016), but their patterns of variability are most strongly expressed at the interannual and interdecadal time scales (Figure 8).

4.3.5 | Natural mortality

Changes in natural mortality, for instance due to predation by marine mammals, have so far been largely overlooked as a potential cause of changes in Chinook salmon age-structure and size-structure. Like fishing, predation may cause shifts in the size and age composition of populations via the removal of individuals and/or selection for different phenotypes such as faster growth and earlier maturation (evolutionary change). Marine mammals that prey on Chinook salmon include pinnipeds and cetaceans such as harbour seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*) and resident killer whales. Many of these predators have increased in abundance in coastal waters of the Northeast Pacific during the past decades, primarily due to harvest bans established since the 1970s by the US Marine Mammal Protection Act and the US Endangered Species Act (Magera, Flemming, Kaschner, Christensen, & Lotze, 2013). A recent study estimated that consumption of Chinook salmon biomass by marine mammals, including pinnipeds and killer whales, has nearly tripled since the mid-1970s (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). Predation by pinnipeds, however, is unlikely to cause declines in the average age and size of adult fish, because these predators mostly select large juvenile and small adults, do not show a preference for Chinook salmon compared to other salmonids and are mostly concentrated near river mouths (Adams et al., 2016; Thomas, Nelson, Lance, Deagle, & Trites, 2017).

Resident killer whales, on the other hand, selectively prey upon Chinook salmon, particularly the oldest and largest individuals (Ford et al., 1998; Hanson et al., 2010; Herman et al., 2005). About 90% of Chinook salmon eaten by residents are 4–6 years old (Ford & Ellis, 2006), and the abundance of resident killer whales has continuously increased since the 1970s (Matkin, Ward Testa, Ellis, & Saulitis, 2014; Ward et al., 2016). Currently, the total number of resident killer whales in the Northeast Pacific Ocean is estimated to be at least 2300 individuals (Muto et al., 2017), with many populations increasing 2–3× over the last 40 years. However, abundance estimates

are uncertain for resident killer whales inhabiting the Bering Sea and coastal waters along the Aleutian Islands.

Bioenergetics calculations suggest that the residents currently inhabiting the coastal waters between northern California and southern Alaska (not including those along the Aleutian Islands and in the Bering Sea) consumed roughly 10^4 metric tons of Chinook salmon in 2015, which is ~70% of the total marine mammal consumption by weight (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). This is equivalent to an annual consumption of about 2.3 million adult-sized Chinook salmon, and similar to the recent annual commercial catch in the North Pacific Ocean (~2 million Chinook salmon, Irvine et al., 2009). While the relative contributions of harvest and natural predation vary by population and region, total coast-wide mortality of Chinook salmon has increased over time despite reductions in fishery harvest. Chinook salmon are exposed to predation by resident killer whales along the coast, and exposure to predation during ocean residence depends on population-specific ocean distributions and migration patterns (Larson et al., 2013; Weitkamp, 2010). Predation intensity is likely highest for coastal populations from Washington, British Columbia and south-eastern Alaska, somewhat uncertain for populations in western Alaska, and lowest for populations that do not exhibit the long coastal migrations such as those from California and southern Oregon, as well as some Puget Sound populations. This spatial pattern of exposure to predation is generally coherent with the observed patterns in the declining size of older Chinook salmon across the Pacific coast (Figures 7 and S4) and warrants more examination of the potential of increased predation for contributing to the changing demographic characteristics we have documented in this study.

5 | CONCLUSIONS

Chinook salmon are highly valued for their large size and nutritional value by humans and apex predators alike. Here, we report on the loss of the largest and oldest fish from many populations across the west coast of North America. Declines in size-at-age were found to be common coast-wide and were most pronounced in northern populations. The southernmost populations, in contrast, showed no or weak trends in size-at-age. Furthermore, while the loss of the oldest fish and corresponding decline in mean age was found for the majority of populations, trends in age compositions differed between regions. Most notably, populations from British Columbia for which we had data did not follow the decline in mean age.

Our qualitative assessment of the potential causes of changes in age-size structure suggests that common hypotheses such as harvest, environmental change and hatchery effects are not consistent with nor sufficient to explain observed patterns of demographic change in Chinook salmon observed across space and time. The causes of the declining size and age trends are likely complex and involve multiple factors that may interact. Changes in predation rates on the oldest and largest fish by expanding populations of resident killer whales is a

hypothesis that appears largely consistent with the observed changes, but it remains untested. In the light of the presented findings, this and other hypotheses should be evaluated in more detail in future studies before firm conclusions about the underlying causes can be drawn.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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