

Fecundity trends of Chinook salmon in the Pacific Northwest

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Abstract

Fecundity is an important demographic parameter that contributes to the productivity of anadromous fish stock dynamics. Yet, studies on fecundity patterns in Pacific salmon (*Oncorhynchus* spp.) often only include a few years of data, limiting our ability to understand spatio-temporal trends. Here, we used data on 43 hatchery Chinook salmon (*O. tshawytscha*, Salmonidae) populations in Washington State to evaluate whether average fecundity changed over the past three decades. We then used data from a subset of stocks (18) to evaluate the relationship between fecundity and body length. Our results revealed significant changes in fecundity across the 25-year study period with most stocks showing declines in fecundity over the past decade. Results further showed that Chinook salmon have decreased in length over this same period and that annual variation in mean length explains a majority (62%) of annual variation in mean fecundity. Specifically, we estimated that a 1-mm reduction in length results in 7.8 fewer eggs (95% CI = 6.6–8.9). Given that the majority of Pacific Northwest Chinook salmon in the environment and harvested in fisheries originate from hatchery releases and that nearby hatchery and wild populations generally have similar ocean distributions, these results likely reflect patterns for many populations not included. Combined, our results highlight the need to consider changes in body size and egg production when assessing the dynamics of anadromous fish populations and designing management or conservation plans, particularly for depressed populations.

KEYWORDS

egg production, hatchery, Pacific Salmon, population demographics, productivity, spatio-temporal

1 | INTRODUCTION

Fecundity of anadromous salmon populations is an important demographic parameter that partially determines population productivity. Changes in fecundity can therefore impact a population's ability to recover from depletion, impact the ability of a population to support sustainable fisheries, or limit the number of eggs available to hatcheries supporting depressed populations or harvest programs. If gone undetected, reduced fecundity at the population level can result in over

estimating productivity if spawning stock size is assumed proportional to fecundity, which is a common assumption in spawner-recruit models (Beverton & Holt, 1957; Quinn & Deriso, 1999; Ricker, 1954). Yet, current management frameworks lack information on spatio-temporal dynamics of salmon fecundity and how demographic changes or climate change impacts those dynamics. Understanding the factors driving changes in fecundity over decadal time scales and across a broad range of salmon ecosystems can help improve management of at-risk populations (Shelton et al., 2012; Staton et al., 2021).

[Correction added on 24 May 2023, after first online publication: The affiliation of author 'James P. Losee' has been updated in this version.]

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Fecundity of Pacific salmon (*Oncorhynchus* spp.) is strongly associated with body size such that larger females have increased reproductive potential compared to smaller conspecifics (Beacham & Murray, 1993; Healey & Heard, 1984; McGregor, 1923; Nicholas & Hankin, 1989; Ohlberger et al., 2020). Over the past several decades, body sizes of North American Chinook salmon (*O. tshawytscha*, Salmonidae) have declined, possibly driven by selective fishing practices, predation, changes in climate, and inter-specific competition (Losee et al., 2019; Ohlberger et al., 2018, 2019; Oke et al., 2020; Ricker, 1981). Widespread declines in body size suggest a reduction in the reproductive potential of Chinook salmon populations due to fewer eggs being spawned per female. Indeed, Oke et al. (2020) suggested that recent declines in Alaska Chinook salmon body size may have led to a 15% decline in egg production per female. Empirically, linking declines in body size to changes in reproductive potential, however, has been difficult due to limited long-term datasets of Chinook salmon fecundity.

Changes in body size and fecundity are particularly relevant in the Pacific Northwestern USA, where many Chinook salmon populations are listed under the U.S. Endangered Species Act and are expected to face increasing pressures due to climate change (Crozier et al., 2021; Kareiva et al., 2000). Productivity of Chinook salmon in the Pacific Northwest has remained low over the past three decades and numerous environmental and anthropogenic factors have been implicated including marine and freshwater conditions, hydroelectric dams, habitat degradation, predation, and climate change (Allendorf et al., 1997; Nehlsen et al., 1991; Nelson et al., 2019; Welch et al., 2021). These potential factors have largely been examined for their impacts on egg-to-adult survival, however, some of these factors could also be driving changes in body size and subsequent shifts in the number of eggs spawned.

In the North Pacific, approximately 40% of salmon biomass is from hatchery origin fish (Ruggerone & Irvine, 2018) and in the Pacific Northwest hatchery production of Chinook salmon greatly exceeds natural production in the major salmon producing regions, including Puget Sound and Columbia River Basin (CTC, 2022; Daly et al., 2012; Losee et al., 2019; Shelton et al., 2019). High hatchery abundances relative to natural origin fish have increased the economic, ecological, and cultural significance of hatchery Chinook salmon and harvest objectives, treaty obligations, and conservation actions increasingly rely on hatchery produced Chinook salmon throughout the region (Appleby et al., 2014; WDFW, 2017). For these reasons, managers have invested heavily in monitoring hatchery Chinook to produce accurate estimates of the number of fish released, adult returns, body size, fecundity, survival, and recruitment to fisheries, providing opportunities to examine population demographic changes over broad spatial and temporal scales.

In this study, we asked whether fecundity of hatchery Chinook salmon in Washington State changed over the past three decades, and if so what is the relationship between fecundity and body length. We compiled a large dataset of time series of Chinook salmon fecundity from 43 hatchery populations that included three run-timing groups (fall, spring, and summer) across Washington State. We then

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used univariate and multivariate time series methods to examine trends in fecundity. We further used Bayesian hierarchical models to estimate relationships between fecundity and body length simultaneously for a subset of stocks with body length data. This multi-step modeling approach, combined with an extensive dataset of fecundity time series, allowed us to quantify changes in fecundity and body length across multiple spatial and temporal scales.

2 | METHODS

2.1 | Fecundity, length, and age data

We used average fecundity data collected from 43 hatchery Chinook salmon populations throughout Washington State across the span of 25 years (1995–2019; Figure 1 and Table S1). Average annual fecundity (eggs per female) for a stock was calculated in two ways, depending on whether an automated egg sorter was available. For facilities using an automated egg sorter, total eggs were enumerated when live and dead eggs were separated. The total sorted egg count was then divided by the total number of females. For facilities lacking an automated sorter, a subsample of manually counted eggs were collected from the broodstock following spawning to obtain an average individual egg weight. The individual egg weight was then divided into the total egg mass to estimate the total number of eggs collected. The average fecundity was then derived by the total egg take divided by the total number of females spawned.

The proportion of females spawned varied across years and hatcheries. Typically, a random subset of the females were spawned to reach the egg-take goal and insure sampling was representative of the full return. The mean number of females spawned across all stocks and years was 709 and stock-specific means ranged from 30 to 3090 (Table S2). Only stocks that had at least 10 years of data for

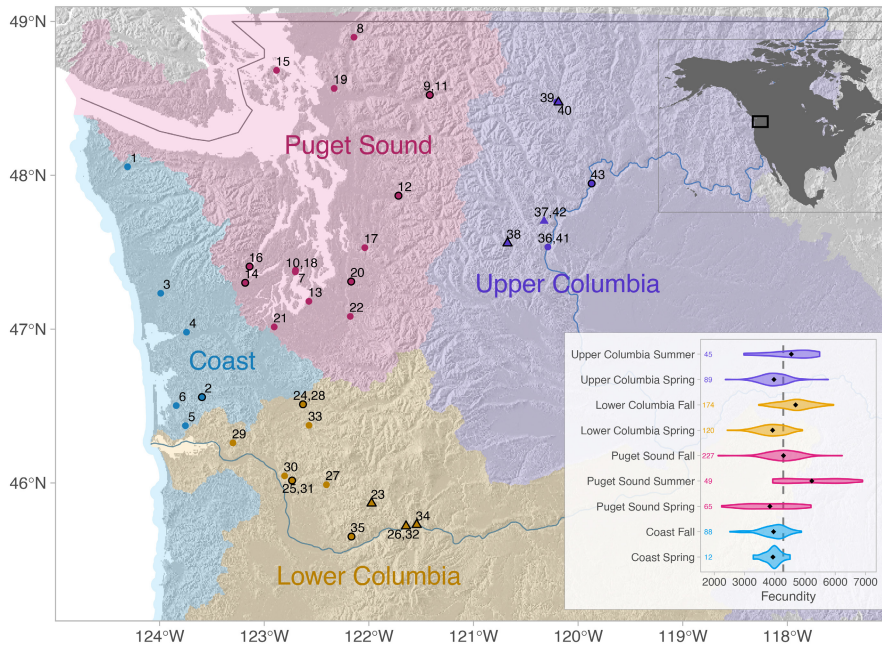


FIGURE 1 Map of study region and hatchery locations. Points indicate the Chinook hatchery locations and numbers correspond to the 'number' column in [Table S1](#). Solid circles indicate hatcheries operated by Washington Department of Fish and Wildlife and solid triangles indicate hatcheries operated by the U.S. Fish and Wildlife Service. Points with a black outline indicate hatcheries where length data were available. Inset violin plot shows full fecundity distributions grouped by region and run timing. Black dots inside violins show group-specific mean fecundity, vertical dashed line shows mean fecundity across all stocks, and numbers on left show sample sizes for each group.

the period 1995–2019 were retained for the analysis. Furthermore, we removed stocks where adult sampling methods were inconsistent during the time series in a way that may have influenced fecundity estimates. For example, we excluded the Elwha River stock because in most years females were collected on the spawning grounds, which could bias egg count estimates.

The 43 stocks were grouped into four geographic regions based on the location of each hatchery ([Figure 1](#); [Table S1](#)). Regions were defined based on watersheds; specifically, hatcheries located on rivers that drain into the Pacific Ocean along the outer coast of Washington were classified in the Coast region, hatcheries on rivers flowing into Puget Sound were classified in the Puget Sound region, and hatcheries located on tributaries to the Columbia River were classified as either the Lower Columbia (below Snake River confluence) or Upper Columbia regions. Stocks were also grouped into one of three run-timing groups: spring, summer, or fall based on adult return timing ([Table S1](#)). The fall run timing was most common with 23 stocks, followed by the spring run timing with 15 stocks, and the summer run timing was least common with five stocks.

For a subset of stocks (18 stocks; [Table S1](#) and [Table S3](#)), body length and age composition data were used to evaluate relationships between fecundity and body size. The subset of stocks with length and age data were geographically distributed across all three regions ([Figure 1](#)). For each of the 18 hatcheries, fork length data were collected at the time of spawning by measuring the distance in centimeters from the snout to the fork of the tail. Fish age was estimated either through the enumeration of freshwater and saltwater annuli read from the anterior region of scale samples collected from the preferred area (Gilbert, 1912) or by the extraction and identification of coded-wire tags that are commonly applied to a portion of most hatchery stocks (Solomon & Vander Haegen, 2017). For the 10 hatcheries operated by the Washington Department of Fish and Wildlife, the length and age data were obtained from the Regional Mark Information System database (RMIS; <http://www.rmpc.org>),

which contains detailed records of coded wire tag (CWT) releases of salmon from hatcheries throughout Washington State. Only CWT data from hatchery escapements were used to better capture size of spawning females. Because not all fish used in hatchery broodstock have a CWT, the RMIS data represent a subset of the females used in broodstock and also included some females that were in surplus to the hatchery broodstock needs.

Age-specific fecundity data were not available for the 18 stocks with age-specific length data. Therefore, to align the annual stock average fecundity values with the age-specific body length data, we used a weighted mean of body length across ages for each year where the weights were equal to the proportion of fish returning in each age class. More specifically, for each hatchery and year, we first calculated age proportions of hatchery female spawners using the available age data either from CWT (WDFW hatcheries) or hatchery records (USFWS hatcheries). These age proportions represented total age and therefore do not distinguish between yearling and sub-yearling releases. We then calculated mean length across all ages, weighting each age-specific length by the proportion of female returns for that age group. We also evaluated an alternative method for calculating average annual body length where we used the mean body length of the modal age for each stock, but tests indicated this alternative method did not qualitatively change parameter estimates.

2.2 | Statistical models

We used univariate state-space models to estimate individual stock fecundity trends (Auger-Méthé et al., 2021). The model was composed of a state equation and an observation equation. The state equation was a random walk, $x_t = x_{t-1} + w_t$ where $w_t \sim N(0, \sigma_w)$, that represented a latent fecundity trend. The observation equation linked the latent trend and fecundity observations (y) and took

the form $y_t = x_t + v_t$ where $v_t \sim N(0, \sigma_v)$. We chose a random walk to model the latent fecundity trend because it allows for a wide variety of potential trends. Models were fit separately for each stock and each fecundity time series was scaled to mean zero and unit variance prior to model estimation. There is no previous value to condition for the first state (x_1) on, therefore, we estimated the first state as a parameter and used a normal prior distribution with a mean of zero and standard deviation of 5. Weakly informative priors were used on the process and observation standard deviation parameters (i.e., Gamma(1, 1)). We used Markov Chain Monte Carlo implemented in Jags (v4.3.0) to estimate parameters and R (v4.1.2) to evaluate results. For each univariate model, we ran four chains for 150,000 iterations following a 10,000 iteration warm-up and only retained every 25th iteration.

To estimate common trends in fecundity and length-at-age across all stocks, we used dynamic factor analysis (DFA) (Zuur et al., 2003). Given a set of time series, DFA allows estimating a specific number of latent trends and a set of loadings that represent linear effects of a trend on the observed data. The DFA models took the form $y_t = Zx_t + v_t$. Similar to the univariate models, we allowed the latent trends (x_t) to evolve through time according to a random walk: $x_t = x_{t-1} + w_t$. The matrix Z specifies the factor loadings that link the latent trends and observed data. The residual error (v_t) and process error (w_t) were assumed to be multivariate normally distributed with mean 0 and variance-covariance matrices R and I , respectively. The process error matrix was set to the identity matrix resulting in each latent trend being independent. For the observation variance-covariance matrices, we used a shared variance term and no covariances (i.e., diagonal and equal), which assumes the errors are independent and identically distributed (i.i.d.). To check the sensitivity of this i.i.d. assumption, we also fit a model with separate variances for each time series (i.e., diagonal and unequal).

For fecundity, we fit models with 1–4 trends. For length-at-age, we only fit single-trend models because we were interested in the most common shared trend. Separate models were fit for each of the three most common age classes (age-3, age-4, and age-5) and only body length of females was included in the analysis. We also fit fecundity DFA models that only included the subset of stocks that had size data to verify that the fecundity trends of this subset were similar to the full data set. DFA models were estimated using Stan (v2.21.0) and the bayesdfa package in R (<https://github.com/fate-ewi/bayesdfa>). DFA models were fit using 4 chains run for at least 2000 iterations each following a 2000 iteration warm-up period (minimum of 8000 total posterior samples).

We used a Bayesian hierarchical regression model to estimate the relationship between fecundity and adult female body length (McElreath, 2020). The model was a varying slope and intercept model that assumed slopes and intercepts were exchangeable among stocks: $y_{i,t} = \alpha_i + \beta_i L_{i,t} + \epsilon_{i,t}$ where $y_{i,t}$ is fecundity for stock i in year t , α_i is the stock specific intercept that was assumed to be normally distributed with mean μ_α and standard deviation σ_α , β_i is the stock-specific slope that was assumed to be normally distributed with mean μ_β and standard deviation σ_β , L is fork length in millimeters, and

ϵ is the residual error assumed to be normally distributed with mean 0 and standard deviation σ_ϵ . The parameters μ_α and μ_β represent the common intercept and slopes shared among all stocks. The intercept was given a normally distributed prior with mean 0 and standard deviation 700 and the slope was given a normally distributed prior with mean 0 and standard deviation 50. Standard deviation parameters were assigned zero-truncated Student-t priors with mean 0, standard deviation 50, and 3 degrees of freedom (Figure S1). Models were estimated using the brms R package and Stan using four chains run for 2000 iterations each following a 2000 iteration warm-up (8000 total posterior samples). Both the fecundity and body length data were mean centered prior to model estimation.

Convergence and fit of all models were assessed using effective sample size, \hat{R} , and visual methods (e.g., trace-plots and posterior predictive checks). All estimated parameters had an effective sample size of at least 500, \hat{R} values less than 1.05, and no divergent transitions were observed for the models run in Stan.

3 | RESULTS

3.1 | Trends in fecundity

The univariate analysis revealed significant changes in average fecundity for the majority of stocks during the period 1995–2019 (30 of 43; Figure 2 and Figure S2). The trends varied across regions and run-timing groups, but most stocks showed a decline in fecundity in recent years (Figure 2). In particular, most fall run stocks in Puget Sound, Lower Columbia, and Coast regions showed a decline in fecundity for the period 2010–2018 (Figure 2). In contrast, Puget Sound spring run stocks showed moderate increases in fecundity and Upper Columbia spring run stocks had mostly stable fecundity since 2005. Across all stocks, the average decline in fecundity between 2009 and 2017 was 19% and ranged between 0% and 35%. For example, average fecundity for the Spring Creek Fall hatchery stock declined from 5399 in 2009 to 3685 in 2017, a 32% decline.

Covariation among fecundity time series was moderate with an average pairwise correlation of 0.23 (Figure 3 and Figure S3). Within stock-groups (region and run timing) correlations tended to be higher on average (mean $r=0.34$) compared to between stock-group correlations (mean $r=0.21$), suggesting stocks located closer together have more similar fecundity trends. Among the nine stock groups, the Upper Columbia spring run stocks had the lowest within group correlations (Table 1), whereas the Lower Columbia and Puget Sound fall run stocks had the highest within group correlations on average (Table 1). Across stock groups, Upper Columbia and Puget Sound spring run stocks had the lowest average correlations with stocks in other groups, whereas the Upper Columbia summer run stocks had the highest average correlations.

DFA models with more than a single trend did not include latent trends that were different from zero at the 95% probability level, indicating little support for multiple shared trends. The single trend DFA model further supported the result of significant

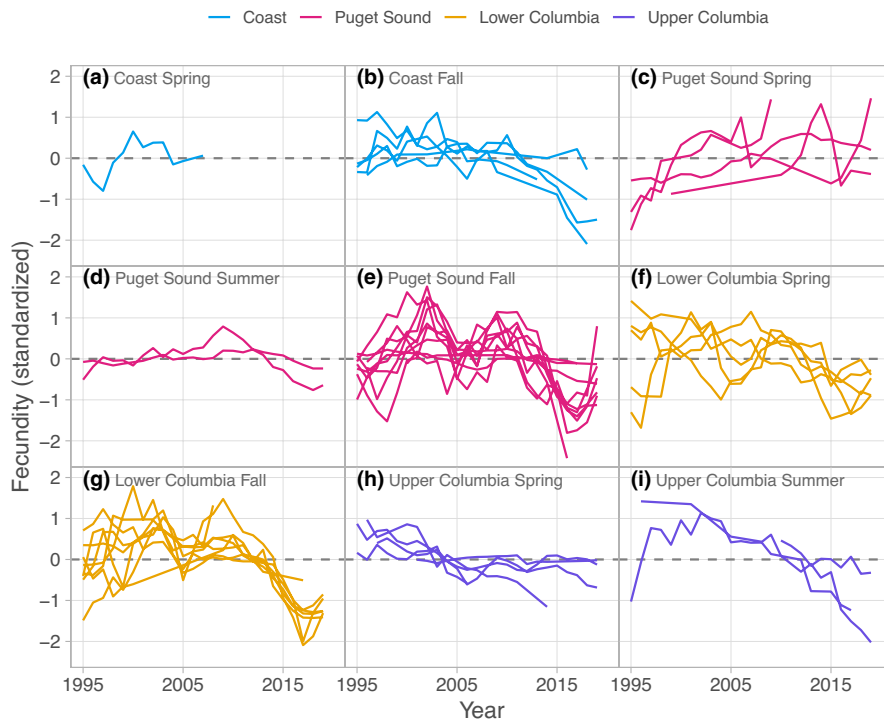


FIGURE 2 Fecundity trends from the univariate state-space random walk models. Lines show the latent fecundity trend (x_t) for each stock and trends are grouped by region and run timing.

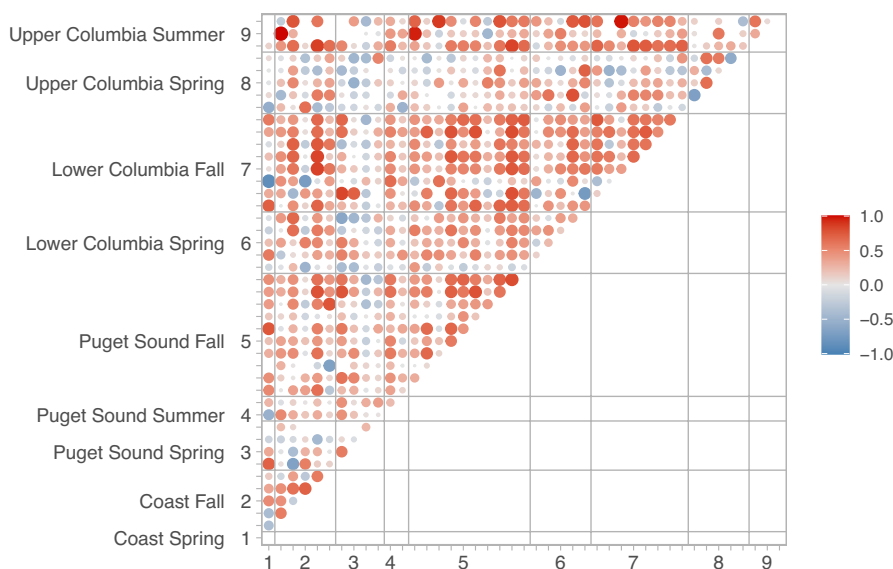


FIGURE 3 Pairwise correlations of fecundity time series. Positive correlations are shown in red and negative correlations in blue. Area of each bubble is proportional to the magnitude of the pairwise correlation between two stocks. Correlations were computed using the raw fecundity data.

changes in fecundity across the 25-year study period (Figure 4a). The common trend was characterized by peaks in fecundity in 2002 and 2009 followed by below average fecundity since 2014. Fall run stocks in the Puget Sound, Lower Columbia, and Coast regions had the strongest positive loadings on the common trend (Figure 4b; Figure S4). In contrast, most spring run stocks in the Puget Sound and Upper Columbia regions did not load significantly on the common trend, suggesting alternative fecundity trends for these stocks.

The DFA model fit using only the subset of stocks with length data showed a nearly identical trend and loadings as the model that included all stocks, suggesting that the fecundity trend for this subset of stocks is representative of the larger dataset (Figure S5). Similarly, the DFA model fit using a diagonal and unequal observation

error variance-covariance matrix did not appreciably change the estimated common trend or loadings (Figure S6).

3.2 | Trends in body length and length-at-age

The common body length trends for all age groups evaluated showed declining and below average adult body length since 2013 (Figure 5; Figure S7). The average percent change in body length across stocks between 2009 and 2017 was -4.1% for age-3 (range = -14.5% – 13.6%), -5.4% for age-4 (range = -12.9% – 2.0%), and -3.6% for age-5 (range = -9.2% – 2.9%). For instance, body length for Spring Creek Fall age-4 Chinook declined from 925 mm in 2009 to 806 mm in 2017, a 12.9% decline.

TABLE 1 Mean pairwise correlations of fecundity for Chinook salmon stocks.

Stock group	N stocks	\bar{r} within group	\bar{r} across groups
Coast Spring	1	–	0.15
Coast Fall	5	0.31	0.21
Puget Sound Spring	4	0.21	0.06
Puget Sound Summer	2	0.23	0.21
Puget Sound Fall	10	0.36	0.27
Lower Columbia Spring	5	0.19	0.20
Lower Columbia Fall	8	0.42	0.28
Upper Columbia Spring	5	0.06	0.08
Upper Columbia Summer	3	0.34	0.34

Note: 'N stocks' gives the number of Chinook salmon hatchery stocks in the stock group; ' \bar{r} within group' gives the mean within group correlation; and ' \bar{r} across groups' gives the mean across group correlation.

The length trends across age groups were highly correlated ($r=0.87$ for age-3 and age-4, $r=0.79$ for age-3 and age-5, and $r=0.96$ for age-4 and age-5; Figure 5). However, differences did occur in the trends prior to 2010. Age-5 Chinook body lengths were largest (relative to age-5 fish) during the early part of the time series (prior to 2002), whereas age-3 Chinook were largest (relative to age-3 fish) during the middle part of the time series (2005–2011). Age-4 Chinook showed an intermediate pattern with two peaks in body length (2002 and 2009) prior to the more recent decline.

3.3 | Body length and fecundity relationship

The Bayesian hierarchical model revealed that body length was significantly and positively related to fecundity across the 18 stocks with an estimated 1-mm decline in length resulting in a reduction in egg production of 7.8 (95% CI = 6.6–8.9; Figure 6; Figure S8). On average, this translates into a 10-mm decline in body length resulting in a 1.8% reduction in fecundity. There was little stock-specific variation from the common length effect, both in the hierarchical model (Figure 6a) and individual stock-specific regression models fit separately for each stock (Figure S9), suggesting all stocks followed similar relationships between length and fecundity. The hierarchical model had an R^2 value of 0.62 (95% CI 0.58–0.65), indicating body length accounts for the majority of variability in fecundity, but other factors also likely impact fecundity (Figure S10).

The common DFA age-specific length trends were also strongly and positively correlated with the common DFA fecundity trend (Figure S11). Correlations between length and the fecundity trend were strongest for age-4 Chinook ($r = 0.91$), followed by age-5 ($r = 0.87$) and age-3 ($r = 0.75$) (Figure S11).

4 | DISCUSSION

In this study, we found evidence for significant changes in Chinook salmon fecundity across Washington State over the past 25 years; average fecundity for most stocks has been declining over the past decade and has been below the long-term average since 2014. We further show for a subset of those stocks with body length data that Chinook salmon have decreased in body length over this same period and that annual variation in mean length explains a majority (62%) of annual variation in mean fecundity, suggesting that declines in fecundity are driven, in large part, by declines in body length. Together, our results provide strong evidence that (1) Chinook salmon populations have directional changes in fecundity across decadal time scales, and (2) temporal shifts in female body size are associated with changes in fecundity at the population level across a broad geographic range.

Our results indicate fecundity declines are likely driven by temporal shifts in Chinook salmon body length, adding to many decades of research showing that fecundity is higher in larger females compared to smaller females (Beacham & Murray, 1993; Galbreath & Ridenhour, 1964; Healey & Heard, 1984; McGregor, 1923; Ohlberger et al., 2020). For instance, our model indicated that about 62% of the variation in fecundity is explained by body length, which matches previous studies that estimated body size explains about 50% to 70% of the variation in fecundity (Beacham & Murray, 1993; Healey & Heard, 1984; Kaufman et al., 2009). The scaling of reproductive potential with body size is a common feature of marine and anadromous fish populations (Barneche et al., 2018; Marshall et al., 2021) and highlights a central consequence of widely observed declines in Pacific salmon body size: the potential for reduced population level egg production and subsequent impacts on population productivity. The consequences of body size declines could be further exacerbated if larger females disproportionately contribute to a population's reproductive potential compared to smaller conspecifics (i.e., hyperallometry), as recent research has suggested (Barneche et al., 2018; Marshall et al., 2021; Ohlberger et al., 2020). We, however, found little evidence for hyperallometry, possibly because we used population level annual means for body size and fecundity rather than data on individual females, which could mask a non-linear relationship by decreasing the effect of body size on fecundity for the smallest and largest females. Even in the absence of hyperallometry, however, declines in fecundity could still have strong impacts on estimates of salmon productivity since salmon production dynamics are generally modeled using numbers of fish, rather than biomass.

Complementary to body size effects, environmental conditions and density-dependent interactions experienced by Chinook populations throughout their range may also explain some of the variability in population-level reproductive potential. For instance, salmon life history traits such as fecundity are shaped by investment trade-offs with body size and egg size (Tuor et al., 2020); however, these relationships are often mediated by environmental conditions experienced in

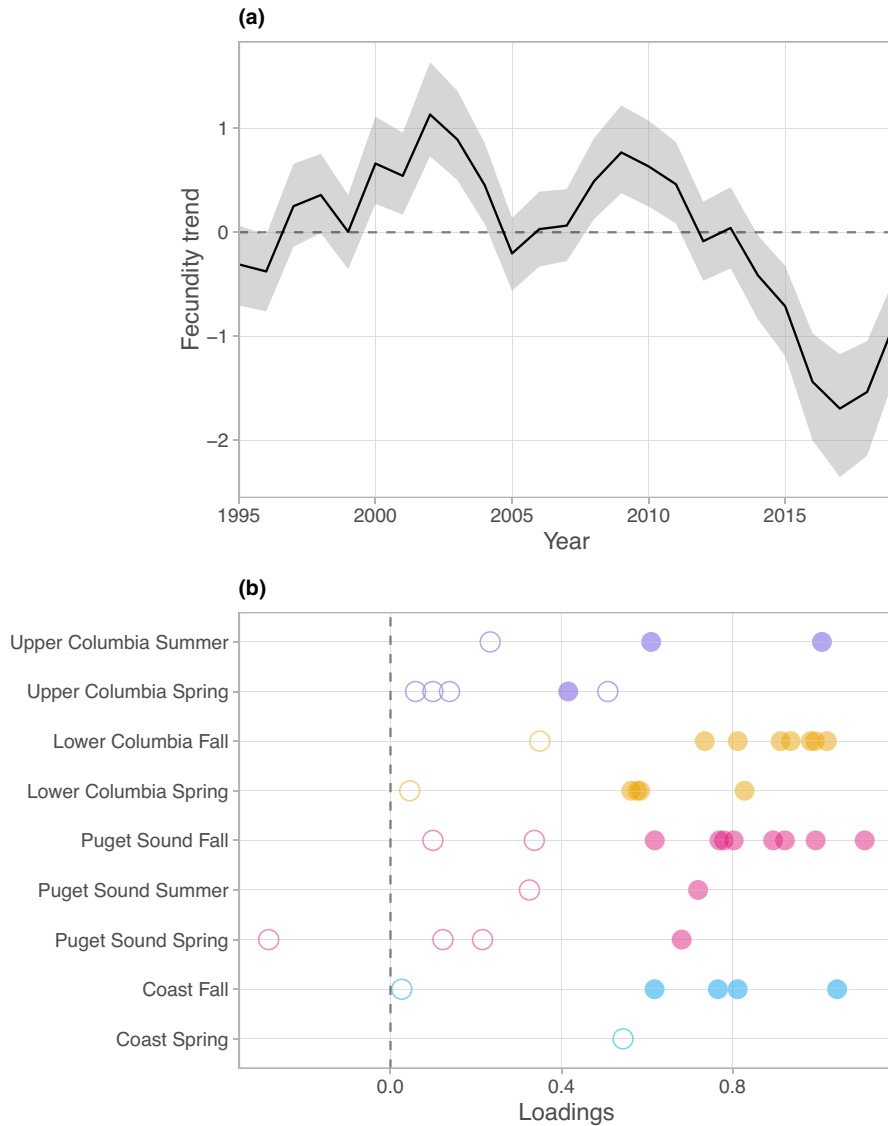


FIGURE 4 Common fecundity trend and stock-specific loadings from the DFA model. Top panel (a) shows the common fecundity trend across all stocks with 95% credibility interval. Bottom panel (b) shows the median stock-specific loadings on the single trend. Solid dots indicate loadings where the 90% credibility interval excludes zero.

the ocean where most growth occurs (Lewis et al., 2015). Large-scale climate phenomena such as North Pacific Gyre Oscillation (NPGO) and Pacific Decadal Oscillation (PDO)—indices known to affect survival and productivity in Pacific salmon—can regulate diet and have been linked to changes in Chinook growth, size, and fecundity (Lewis et al., 2015; Ohlberger et al., 2018). Additionally, density-dependent interactions related to competition for limited food resources are also known to affect growth, adult body size, and correspondingly fecundity in Pacific salmon (Claiborne et al., 2021; Jeffrey et al., 2017). Given the climate regime shift experienced by Pacific salmon populations over the recent few decades (Peterson & Schwing, 2003), understanding the relationship between reproductive investment, density-dependent interactions, and shifting environmental conditions may be critical for projecting future population sustainability of Washington State origin Chinook. Specifically, further exploring environmental factors such as NPGO and PDO, indices that capture climate shifts, prey-availability, and competitor abundances, is warranted for future studies exploring long-term fecundity changes in Chinook salmon in the Pacific Northwest.

The observed significant declines in Chinook salmon body length correspond with the results of numerous previous studies (Bigler et al., 1996; Jeffrey et al., 2017; Lewis et al., 2015; Oke et al., 2020). For instance, Ohlberger et al. (2018) showed widespread declines in body size and age proportions of adult Chinook salmon throughout the West Coast of North America. Similarly, Losee et al. (2019) showed recent declines in Chinook salmon body mass in Puget Sound. Several drivers of declines in Chinook body size have been implicated including size selective fishing practices (Ricker, 1981), environmental conditions (Lewis et al., 2015; Oke et al., 2020), inter-specific density-dependent effects (Ruggerone & Irvine, 2018), hatchery practices (Hankin et al., 2009; Johnson & Friesen, 2013), and increased natural mortality from predators, particularly killer whales (Ohlberger et al., 2019). Recent body size declines, however, are not unique to Chinook salmon and are also evident in pink, chum, and sockeye salmon, which are not primary prey items of killer whales (Hanson et al., 2021; Losee et al., 2019; Oke et al., 2020). These size declines across multiple species suggest that ocean conditions and density-dependent effects may be more important

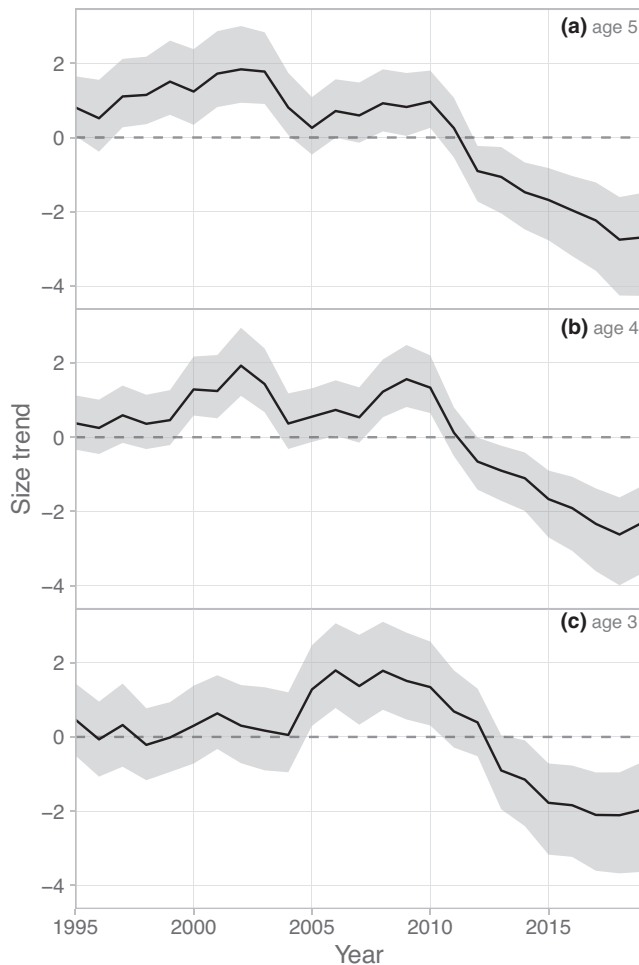


FIGURE 5 Common age-specific body-length trends. Solid lines show the common trend from the age-specific DFA models and grey regions give the 95% credibility interval. Top panel (a) shows age-5 trend, middle panel (b) shows age-4 trend, and bottom panel (c) shows age-3 trend.

drivers of the observed body size declines and consequent reductions in fecundity.

In addition to changes in size-at-age, changes in age structure could have important implications for understanding how changes in individual mean fecundity impact population level productivity. Several previous studies have indicated that Chinook salmon, on average, are returning at younger ages (Ohlberger et al., 2018; Oke et al., 2020). Although declines in age-at-return would likely reduce mean individual fecundity due to smaller mean size, how this impacts population-level egg production depends on the number of adult returns. For instance, if declines in mean age result from earlier maturation (e.g., via increased growth), there could be a neutral or positive impact on population level egg production due to less cumulative mortality risk between the time of release and the time of return. However, analyses of smolt-to-adult survival rates of Chinook salmon across Washington State show that smolt-to-adult survival rates have remained low (<2%) over the past two decades (Welch et al., 2021), indicating that the observed declines in mean

individual fecundity are likely to correspond with reductions in population level egg production.

We observed moderately strong coherence of fecundity trends across the 43 stocks, suggesting similar processes are driving the changes across a broad geographic region. While synchronous changes in body length across stocks is likely a primary driver of the coherence in fecundity trends, other factors may also contribute. In particular, similarities in fecundity trends could be partially driven by historical hatchery transfers of Chinook salmon within and across regions. For example, in the Puget Sound region, Green River origin Chinook salmon were frequently transferred to other Puget Sound rivers since the early 1900s (Ruckelshaus et al., 2006). Similar historical egg transfers were also common from Lower Columbia hatcheries to Upper Columbia hatcheries until the 1980s. These inter-basin transfers likely reduced genetic and life-history heterogeneity in these regions which may contribute to the similarity in fecundity trends across hatchery stocks (NOAA, 2007; WDFW, 2017).

Spring-run stocks in the Puget Sound and Upper Columbia River regions did not fit the common fecundity trend, and fall-run stocks comprised the majority of those included in the common trend. Spring-run Chinook typically enter freshwater from March–June compared to August–November for fall run stocks (Healey, 1991). Fall Chinook, therefore, have the potential to respond with changes in fecundity to variation in summer marine productivity and corresponding feeding and growth during the final summer before spawning (Brannon et al., 2004). In contrast, spring Chinook energy reserves for reproduction are set in the spring as these fish enter freshwater and cease feeding. However, the Lower Columbia spring-run stocks tended to have fecundity trends more similar to fall-run stocks, suggesting run timing is not the only factor contributing to the observed differences in fecundity trends. Alternatively, the observed differences in fecundity trends for the Puget Sound and Upper Columbia spring run stocks may be an artifact of the available data. For instance, there are fewer spring-run Chinook stocks in these regions compared to fall-run stocks and some of these spring Chinook populations have incomplete time series. Thus, there might simply be less data and consequently less power to discern patterns within the spring Chinook stocks in these regions as compared to the fall Chinook stocks.

The fecundity trends and relationships to body length in the hatchery stocks we studied likely extend to natural-origin Chinook salmon for at least three reasons. First, both hatchery and natural-origin fish from the same regions likely experience, generally, similar ocean conditions (Fisher et al., 2014). Indeed, Weitkamp (2010) showed broad similarities in spatial distribution of hatchery and wild Chinook salmon stocks in the Pacific Ocean. Environmental factors in the marine environment, such as temperature and food availability, should therefore similarly affect geographically proximate stocks, including the allocation of resources to ovarian development, which in salmon appears most strongly determined during the latter portion of marine residence (Campbell et al., 2006; Luckenbach et al., 2008). Second, the great majority of Chinook salmon are produced from hatcheries

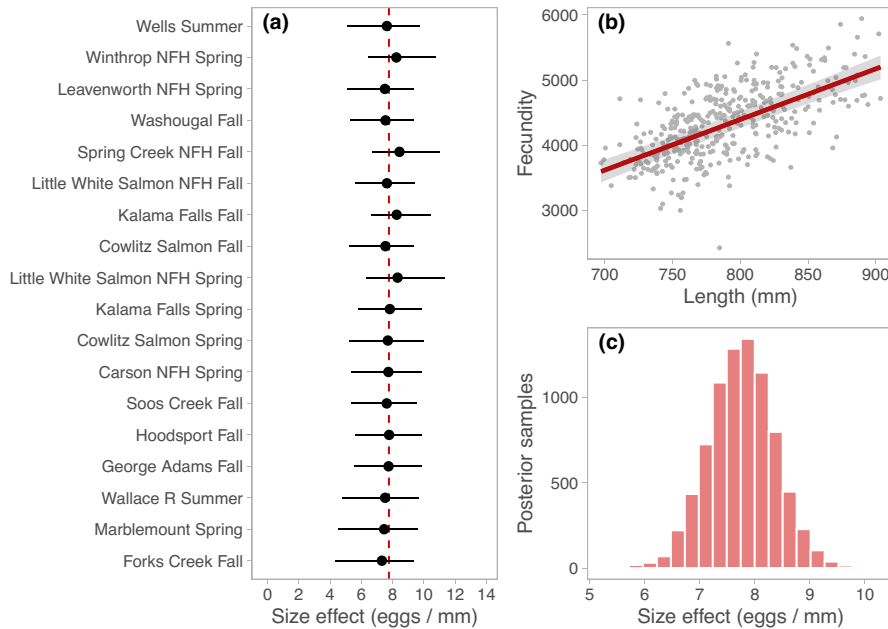


FIGURE 6 Estimated effect of female body length on fecundity. Left panel (a) shows the stock-specific effect of body length on fecundity (dots) with 95% credibility intervals and the red vertical dashed lines gives the common length effect across all stocks (μ_p). Upper right panel (b) shows the common length–fecundity regression line with 95% credibility interval. Light grey dots show the observed data. Lower right panel (c) shows a histogram of posterior samples for the common length effect (μ_p ; slope of red line in panel b).

in the main salmon producing regions of Washington State evaluated in this study, including Puget Sound and the Columbia River Basin (CTC, 2022; Daly et al., 2012; Losee et al., 2019; Shelton et al., 2019). Natural fish may be incorporated into hatchery broodstocks and hatchery-produced fish spawn naturally in nearly all river systems (Anderson et al., 2020). Thus, while there is evidence of some phenotypic differentiation between natural and hatchery components of some Chinook salmon populations (e.g., spawn timing; Austin et al. (2021)), the majority of populations share genetic influences from both hatchery and natural components (Anderson et al., 2020). Finally, although hatchery selection could impact fecundity or egg size over time (Heath et al., 2003), considerable evidence suggests that this has not been readily observed and more often no evidence is found that egg size or fecundity differ between hatchery and natural-origin fish (Beacham, 2010; Beacham & Murray, 1993; Quinn et al., 2004).

4.1 | Management implications

Widespread declines in fecundity have important implications for management and conservation of Chinook salmon populations. Importantly for threatened Chinook populations, fewer eggs spawned would be expected to reduce population productivity, impacting recovery rates and harvest opportunities (Peterman et al., 2000; Shelton et al., 2012). Further, changes in fecundity are not traditionally accounted for in stock assessment activities (Staton et al., 2021). Fecundity is often assumed proportional to spawning stock size and changes in fecundity independent of stock size pose a risk of over-estimating future population sizes and subsequent harvest rates (Quinn & Deriso, 1999; Shelton et al., 2012). Reduction in population productivity has additional consequences for prey availability for the endangered southern

resident killer whale population, which feeds predominately on Chinook salmon during the period of adult homeward migration (Hanson et al., 2021), and in regions heavily dominated by hatchery production (e.g., Puget Sound). Killer whale feeding success, however, is not only impacted by the number of Chinook salmon but also the size of returning adults and resident times of Chinook in nearshore areas.

Changes in fecundity also have important implications for hatchery programs in Washington State and the West Coast more broadly. Reduced fecundity has the potential to constrain egg take for hatchery operations that support a variety of conservation, harvest, and mitigation programs linked directly to threatened Chinook populations (Anderson et al., 2020; WDFW, 2017). Failure to meet egg-take goals for hatcheries poses both direct and indirect long-term risks for hatchery and wild Chinook salmon through a reduction of smolts released and consequently reduced adult returns, and reliance on transfers of eggs and fish between hatcheries to mitigate for lost production. Chinook salmon adapt to local conditions and eggs transfers, which are the only way to overcome egg-take shortfalls, can erode local adaptations such as smolt emigration timing, egg size, and adult return timing (Brannon et al., 2004; Healey, 1991). Further, transfers are not an option for many recovery or conservation hatchery programs, making declines in fecundity a threat to recovery efforts. Our data suggests that stocks located closer together have more similar fecundity trends, which may be the result of prior egg transfer between spatially adjacent stocks. However, non-adjacent stocks have dissimilar fecundity trends, which may suggest adaptation to local environmental conditions. Thus, transfer of eggs may incur higher risk with distance from origin or out of basin. Based on these consequences and the evidence for directional changes in fecundity across years and decades, we suggest future research focus on evaluating the consequences of fecundity changes within a management context.

5 | CONCLUSION

In conclusion, our results reveal that fecundity of Chinook salmon has changed over the past three decades and is associated with population-specific changes in body length. The coherence of the fecundity trends across a large number of stocks suggests that body length and fecundity of populations across a broad geographic region are affected by similar processes that are leading to recent declines. Because fecundity is an important demographic parameter that contributes to the productivity of anadromous fish stock dynamics, the significant changes in fecundity observed here for Chinook salmon can have important consequences for management and conservation of threatened populations. In particular, the results of this study highlight the need to consider changes in egg production and body size when assessing the current dynamics of anadromous fish populations and designing management plans for a sustainable future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest in relation to this paper.

DATA AVAILABILITY STATEMENT

Code and data used for this analysis is available at <https://github.com/michaelmalick/chinook-fecundity-trends>.

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