



Biennial patterns in Alaskan sockeye salmon ocean growth are associated with pink salmon abundance in the Gulf of Alaska and the Bering Sea

Peter S. Rand ^{1,*} and Gregory T. Ruggerone ²

¹Prince William Sound Science Center, P.O. Box 705, 700 New England Cannery Road, Cordova, AK 99574, United States

²Natural Resources Consultants, Inc., 4039 21st Avenue West, Suite 404, Seattle, WA 98199, United States

*Corresponding author. P.O. Box 705, 700 New England Cannery Road, Cordova, AK 99574, United States. E-mail: prand@pwssc.org

Abstract

In response to ocean heating and hatchery production, pink salmon (*Oncorhynchus gorbuscha*) returning from the North Pacific Ocean steadily increased after 1975, leading to concerns about their influence on food webs and competition with other species. Using measurements of distance between scale annuli of 24 584 individual sockeye salmon (*O. nerka*), we examined growth during their 2 or 3 years at sea from 1977 to 2015 for eight populations in Alaska. We found significant, negative autocorrelations at 1 lag year in annual growth of sockeye salmon, with a consistent pattern of lower growth in odd years, i.e. opposite to the biennial pattern of pink salmon abundance. Peak pink salmon abundances reduced growth of sockeye salmon from 7 to 14% during the second year in the ocean compared with growth when pink salmon abundance was low, while third-year growth was reduced up to 17%. The overall effect of pink salmon abundance on sockeye growth was over two times greater than the effect of sockeye salmon abundance. Production hatcheries and ocean heating contribute to the competitive dominance of pink salmon, underscoring the need to consider this unintended anthropogenic effect on the growth and productivity of sockeye salmon throughout the North Pacific.

Keywords: Sockeye salmon; pink salmon; competition; carrying capacity; ocean growth

Introduction

Growth and body size of Pacific salmon (*Oncorhynchus* spp.) affect their survival, reproductive fitness, and future production potential, define their economic value in global seafood markets, and are key factors in meeting the dietary needs of subsistence users. However, body size of Pacific salmon has been declining in many regions over the past four decades, raising concern about factors influencing the decline (Bigler et al. 1996, Oke et al. 2020, Ohlberger et al. 2023). While oceanographic factors may influence salmon growth (Ruggerone et al. 2007, Martinson et al. 2008, Wells et al. 2008, Jeffrey et al. 2017, Buckner et al. 2022), a key biological factor is competition among the growing abundance of total Pacific salmon in the ocean in response to record high abundances of pink salmon (*Oncorhynchus gorbuscha*) and to industrial-scale hatchery production of pink and chum salmon (*O. keta*, Ruggerone and Irvine 2018). The changing conditions in high latitude regions in the northern hemisphere and past introductions have led to a dramatic expansion of the range of pink salmon into the Arctic and Atlantic Oceans in recent years (Dunmall et al. 2013, Sandlund et al. 2019, Diaz Pauli et al. 2023, Lennox et al. 2023). There is an urgent need now to understand the food web and ecosystem impacts of pink salmon as they increase in abundance in their native range and expand their global distribution.

Abundance of pink salmon returning from the North Pacific Ocean increased steadily from ~170 million adults per year in the early 1970s to nearly 800 million fish in 2021, when they represented nearly 80% of all Pacific salmon (Ruggerone and

Irvine 2018, Ruggerone et al. 2023). This prodigious rise in abundance appears to be driven by ocean heating and substantial hatchery production, which contributed ~82 million adults per year during 2005–2015. Diet overlap between pink and sockeye salmon is high (Davis 2003, Graham et al. 2021), and studies indicate pink salmon affect the growth, adult size, maturation, survival, and abundance of sockeye salmon (Petterman 1982, Bugaev et al. 2001, Ruggerone et al. 2003, Ruggerone et al. 2005, Ruggerone and Connors 2015, Ruggerone et al. 2016, Connors et al. 2020). These and other species interaction studies benefit from the natural experiment offered by the strong biennial pattern of pink salmon abundance, which stems from their fixed 2-year life cycle: abundance of maturing pink salmon is high in odd years and low in even years (Krkosek et al. 2011, Irvine et al. 2014). Oceanographic and other variables are not known to cause the biennial patterns that have been observed in species that compete with pink salmon for prey (Ruggerone et al. 2023).

Here we examine patterns of sockeye salmon growth at sea over three decades for eight populations, including seven from the Gulf of Alaska region and one from the southeastern Bering Sea. Effects of pink salmon on sockeye salmon growth have yet to be fully evaluated for Gulf of Alaska populations (Martinson et al. 2008). Specifically, we test for biennial patterns in the annual growth of sockeye salmon across this broad region, and test for negative relationships between annual sockeye salmon growth and abundances of pink and sockeye salmon, as expected if inter- and intra-specific competition is occurring. Man-

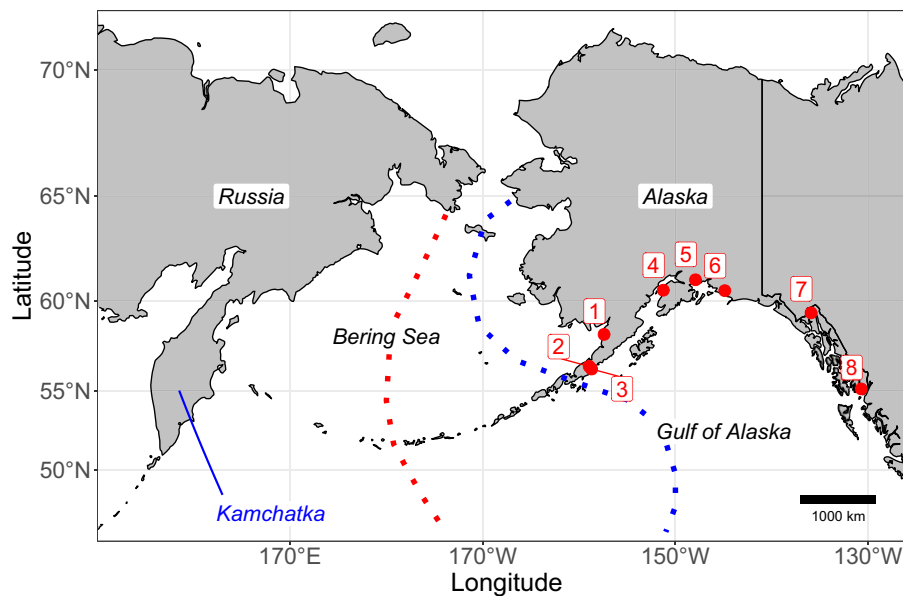


Figure 1. Location of the eight populations of sockeye salmon in Alaska: 1—Egegik (Bristol Bay), 2—Black (Alaska Peninsula), 3—Chignik (Alaska Peninsula), 4—Kenai (Cook Inlet), 5—Coghill (Prince William Sound), 6—Copper (southcentral Alaska), 7—Chilkat (northern Southeast Alaska), and 8—Hugh Smith Lake (southern southeast Alaska). The dotted blue line shows the approximate range of eastern Kamchatka pink salmon extending eastward into the Gulf of Alaska (150°W) and Bering Sea, and the dotted red line shows North American pink salmon extending westward to the central North Pacific Ocean (180°E) and Bering Sea (Radchenko et al. 2018).

agement implications of these species interactions are discussed.

Methods

We applied models to detect biennial patterns (odd and even year) in annual scale growth of sockeye salmon from eight populations in Alaska as a means to link their growth to biennial abundances of pink salmon (Ruggerone et al. 2023). We also evaluated the effect of sockeye salmon abundance in the North Pacific to determine if they explained variation in annual growth of sockeye salmon at sea.

Scale growth data

We examined annual marine scale growth from eight sockeye salmon populations in the Gulf of Alaska and Bering Sea regions during 1977–2015. Linear distances (mm) between scale annuli of sockeye salmon were measured as an index of annual growth at sea (Fukuwaka and Kaeriyama 1997) by the Mark, Tag, and Age Lab of the Alaska Department of Fish and Game (ADF&G), who followed procedures described in Hagen et al. (2001) and Ruggerone et al. (2007). Scales were selected for measurement only when: (i) measurers agreed with the age determination previously made by ADF&G; (ii) the scale shape indicated that the scale was removed from the ‘preferred area’; and (iii) circuli and annuli were clearly defined and not affected by scale regeneration or resorption along the measurement axis. The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first saltwater annulus. Scale measurements included both circuli and annuli measurements within each growth zone in fresh water and the ocean but only annual growth during each year at sea are reported here, e.g. SW1, SW2, and SW3. The goal was to measure 25 males and 25 females per year from each age and each population. A total of

24 584 sockeye salmon scales were included in this analysis. All eight populations included measurements of ocean age-3 sockeye salmon (i.e. salmon maturing after three winters at sea), and two populations (Egegik and Copper) included measurements of ocean age-2 sockeye salmon (salmon maturing after two winters at sea). Growth during the homeward migration was not analysed because many scales were partially resorbed in this zone.

The following eight populations were sampled: Egegik River (Bristol Bay), Black Lake (Chignik drainage on the Alaska Peninsula), Chignik Lake (Chignik drainage), Kenai River (upper Cook Inlet), Coghill Lake (Prince William Sound), Copper River (southcentral Alaska), Chilkat River (northern Southeast Alaska), and Hugh Smith Lake (southern southeast Alaska, Fig. 1). All populations were sampled in the lower river by weir, beach seine, or fish wheel, except Chignik and Black Lakes (commercial purse seine in Chignik Lagoon) and Copper River (commercial drift gillnet). For the autocorrelation analysis, we excluded population-specific annual values when sample size (number of individual scales) for a given sex in an age group was <10, and when <20 scales were available for each freshwater age class (1 and 2 year olds). Two exceptions were made for Coghill and Hugh Smith populations, which consisted of only scales with a single freshwater age class (1 year old), so the mean scale growth for those populations consisted of just a single freshwater age class. The autocorrelation analysis (description below) was conducted separately for each year at sea (SW) and ocean age at return (ocean age-2 or ocean age-3).

North Pacific salmon abundance

To test for intra- and inter-specific competition effects on the eight populations of sockeye salmon, we obtained annual sockeye and pink salmon abundance values from Ruggerone and Irvine (2018). Sockeye salmon abundances were summed

for the North Pacific Ocean, owing to their relatively broad range at sea (Myers et al. 1996, Myers et al. 2007). For example, genetic data indicate the presence of Bristol Bay and Gulf of Alaska populations of sockeye salmon off the coast of eastern Kamchatka, and many Gulf of Alaska sockeye salmon in the central Bering Sea (Habicht et al. 2010).

To represent competitive pressure from pink salmon at an aggregate level, we summed the adult abundances of this species originating from two regions: eastern Kamchatka (an oblast of the Russian Federation) and North America (Fig. 1). Eastern Kamchatka pink salmon are the most easterly distributed of Asian pink salmon and reportedly migrate east to $\sim 150^\circ\text{W}$ in the Gulf of Alaska and are also highly abundant in the Bering Sea (Fig. 1; Radchenko et al. 2018). North American pink salmon are produced in Alaska, British Columbia, and the US Pacific Northwest region, and they migrate west to $\sim 170^\circ\text{E}$, but relatively few occur in the Bering Sea (Ruggerone and Irvine 2018). During our study period (1977–2015), mean annual abundance of sockeye salmon was 85 million fish (range: 54–129 million) and the mean annual abundance of pink salmon from eastern Kamchatka and North America was 230 million fish (range: 122–466 million). Abundances of pink salmon were greater in odd compared with even years with a stronger biennial pattern among eastern Kamchatka (5.2 times more in odd years) than North American pink salmon (1.4 times more in odd years). Sockeye salmon abundance did not exhibit a biennial pattern, owing to their more complex life history.

To illustrate the even-odd-year pattern in pink salmon abundance, we detrended the time series (there was a significant positive trend in abundance during 1977–2015) prior to fitting the autocorrelation time series model (see description below). We removed the linear trend from the time series using the ‘detrend’ function in the ‘pacmra’ package (v. 2.0) in R.

Scale growth analysis

We tested for autocorrelation in a time series of scale growth during discrete periods of ocean residence (SW1, SW2, and SW3) for each ocean age at return (ocean age-2 and ocean age-3) and each sockeye salmon population. The time series consisted of mean growth during 1977–2015. There were some year gaps in the dataset, indicated with arrows in the plots in Supplementary Figs S1, S2, and S3. We computed autocorrelation at lag year 1 and partial autocorrelation at lag year 2 (acf and pacf functions in package ‘stats’, version v. 4.2.2, passing the argument ‘na.action = na.pass’ in the ‘acf’ function call to accommodate gaps in the time series). A significant negative autocorrelation at lag year 1 indicates the presence of a biennial pattern in growth and provides evidence that the level of competition with pink salmon differs between even and odd years (Ruggerone et al. 2016). A significant positive partial autocorrelation at lag year 2 indicates a positive correlation with growth two years earlier after removing correlation in the time series at a lag of 1 year.

We fit two forms of a generalized linear mixed model (GLMM; Bolker 2015) to determine effects of abundance of pink salmon on sockeye growth. The first model evaluated effects of even and odd years on ocean growth of sockeye salmon:

$$G_{ij} \sim \beta_0 + \beta_1 \text{EvenOdd} + \mu_{0j} + \mu_{1j} + \mu_{2j} + \varepsilon_{ij} \quad (1)$$

where G is distance (mm) between scale annuli that reflects average somatic growth of sockeye salmon for the i -th observation of the j -th group, β_0 is the overall intercept, β_1 is the fixed effect coefficient for EvenOdd (categorical variable indicating whether it was an even or odd year), μ_{0j} , μ_{1j} , and μ_{2j} are the random effects of freshwater age at smolting (1 or 2 years), sex, and year nested within population, and ε_{ij} is the residual error (assumed to be Gaussian). Our model analyzes data at the scale of individual observations and accounts for multiple levels in the data (from the sex to freshwater age of individuals to individuals nested within populations and years); thus, the model is structured to account for the non-independence of observations at multiple scales.

The second model tested for the effects of competitor abundance on sockeye scale growth:

$$G_{ij} \sim \beta_0 + \beta_1 \text{PINK} + \beta_2 \text{SOCK} + \mu_{0j} + \mu_{1j} + \mu_{2j} + \varepsilon_{ij} \quad (2)$$

where G is distance (mm) between scale annuli that reflects average annual somatic growth of sockeye salmon for the i -th observation of the j -th group, β_0 is the overall intercept, β_1 and β_2 are the fixed effect coefficients for PINK, the abundance of pink salmon that Alaska sockeye salmon are likely to encounter in a given year at sea (sum of pink salmon abundance originating in North America and eastern Kamchatka, Russia), and SOCK (abundance of sockeye salmon in the North Pacific), respectively, μ_{0j} , μ_{1j} , and μ_{2j} are the random effects of freshwater age at smolting (1 or 2 years), sex, and year nested within population, respectively, and ε_{ij} is the residual error (assumed to be Gaussian). Potential salmon competitor metrics (abundance of mature and returning adults) were aligned with the year of sockeye growth at sea. The same hierarchical model structure described for equation (1) above was applied to this model as well. Models were fit using the ‘lme4’ package v. 1.1–31 in R. We estimated VIF (variance inflation factor, a measure of collinearity among the variables in the model) and determined all variables had $\text{VIF} < 4.0$ prior to model fitting. For the model described in equation (2), for the maximal model, we chose the best submodel fit by AICc (using the step function in ‘lmerTest’ package v. 3.1–3 in R). We computed marginal and conditional R^2 for GLMM (the amount of variation explained by the fixed effects in the model and the variance explained by the entire model, respectively) using the rsquaredGLMM function in ‘MuMin’ package v. 1.47.1 in R). We tested for autocorrelation in the residuals of the model fits (Durbin-Watson test) using the ‘DHARMA’ package v. 0.4.6 in R.

We estimated the range of sockeye salmon scale growth predicted in the best fit model in equation (2) (expressed as a percentage) from the range of salmon abundances during the period of record (i.e. North American/eastern Kamchatka pink salmon and North Pacific sockeye salmon). This measure (delta growth or dGrowth) allowed us to estimate the relative influence of inter- vs. intra-specific density dependence on ocean growth in sockeye salmon.

Results

Biennial patterns and autocorrelation results

The time series of pink salmon abundances (in eastern Kamchatka, North America, and the two regions combined) during 1977–2015 exhibited significant negative lag 1-year auto-

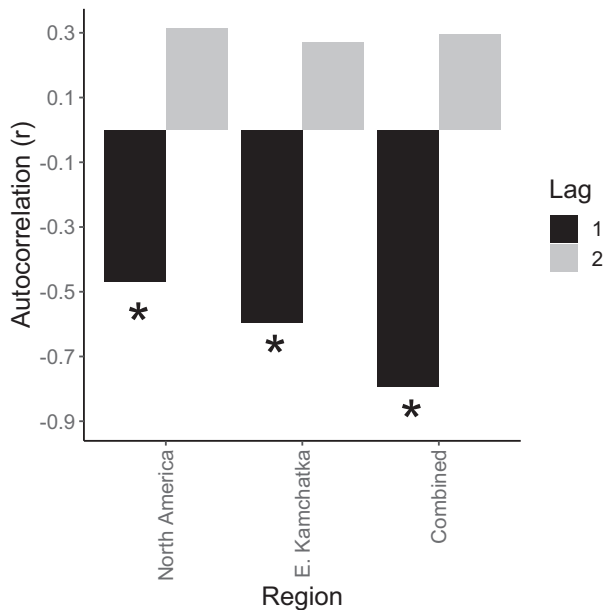


Figure 2. Autocorrelation of North American and eastern Kamchatka pink salmon abundances during 1977–2015. The right set of bars represents the combined abundance of the two regions. Lag 1 (black bars) is the 1-year autocorrelation, and lag 2 (grey bars) is the 2-year partial autocorrelation. Asterisks indicate significant correlation at $P < .05$.

correlations (Fig. 2). The negative lag 1 autocorrelation stems from the alternating-year pattern of abundance in which maturing pink salmon abundance is higher in odd years than in even years. We did not find a significant partial autocorrelation at a 2-year time lag but it tended to be positive (Fig. 2).

We did not find evidence of negative autocorrelation in sockeye salmon scale growth during SW1 for any population or age group, indicating that sockeye salmon scale growth during the first year at sea did not exhibit biennial growth. In addition, there was no significant autocorrelation at lag 1 year for ocean age-2 populations of Egegik and Copper (Supplementary Fig. S1).

All eight ocean age-3 sockeye salmon populations exhibited negative lag 1 autocorrelation in SW2 and SW3 with six and seven out of the eight populations showing a statistically significant effect during SW2 and SW3, respectively (Fig. 3a and b). Black (SW2), Hugh Smith (SW2), and Copper (SW3) were the only combinations of populations and life stages that did not show significant autocorrelation. Only Chilkat exhibited positive partial autocorrelation at lag 2 year for SW2, while Egegik, Black, Copper, and Hugh Smith exhibited positive partial autocorrelation at lag 2 year for SW3 (Fig. 3a and b).

Effects of even and odd year on ocean growth of sockeye salmon

Annual scale growth of the eight sockeye salmon populations was significantly less in odd years when pink salmon were abundant compared with even years when pink salmon were typically much less abundant. Among the two ocean age-2 populations, scale growth was less in odd years during the second (−8.8%, SW2, $P < .0001$, Supplementary Fig. S1) but not in the first year (SW1) at sea. Among ocean age-3 sockeye salmon, the difference in scale growth during odd vs. even years at sea increased with age. Odd-year growth at life stage

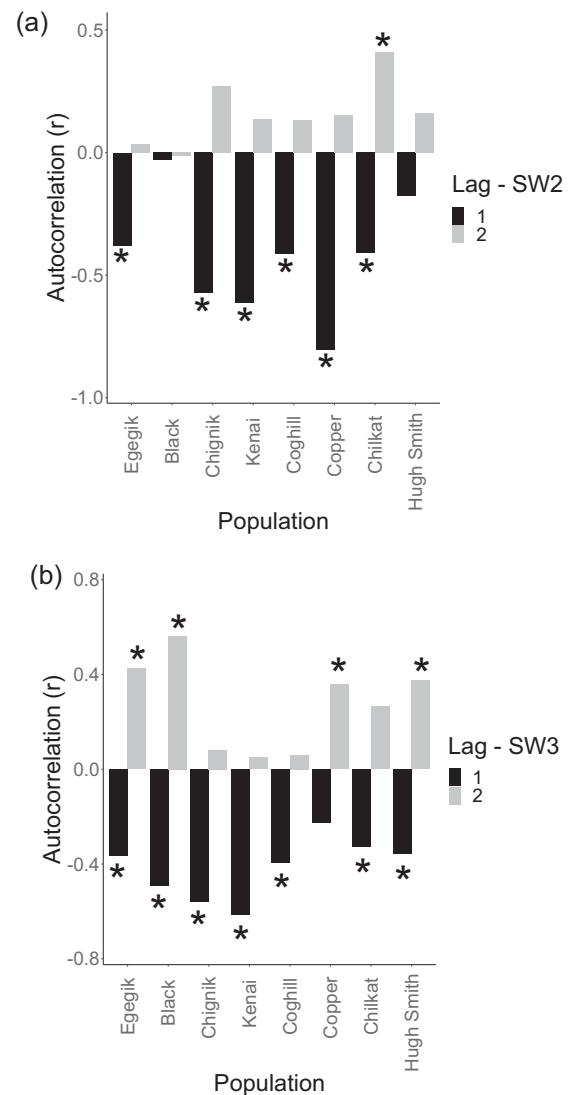


Figure 3. (a) Autocorrelation of (a) ocean age-3 sockeye salmon scale growth during the second (SW2) and (b) third (SW3) years at sea. Lag 1 (black bars) is the 1-year autocorrelation, and lag 2 (grey bars) is the 2-year partial autocorrelation. Asterisks indicate significant correlation at $P < .05$.

SW1 in ocean age-3 sockeye salmon was 2.2% less than that in even years ($P = .0002$), whereas odd-year growth at life stages SW2 and SW3 averaged 6.3% ($P < .0001$, Supplementary Fig. S2) and 12.3% ($P < .0001$, Supplementary Fig. S3) less, respectively, compared to even years.

Effects of salmon abundance

We found strong evidence indicating that high abundance of pink and sockeye salmon contributed to the reduced growth of sockeye salmon, especially during the second and third years at sea. During SW2, scale growth of both ocean age-2 and age-3 sockeye salmon was negatively correlated with abundance of pink salmon; growth during SW2 of ocean age-2 sockeye salmon was also negatively correlated with abundance of North Pacific sockeye salmon (Table 1). During life stage SW3, scale growth of ocean age-3 sockeye salmon was negatively correlated with abundance of pink and sockeye salmon (Table 1, Fig. 4). Scale growth during SW1 was negatively correlated with pink salmon abundance for ocean age-3 (Table 1),

Table 1. Results of the generalized linear mixed model [GLMM, equation (2)] relating individual scale growth at three different ocean life stages (SW1, SW2, and SW3) for two age groups (ocean ages 2 and 3) from eight sockeye salmon populations to the abundance of pink and sockeye salmon in the North Pacific Ocean.

Best fit model	R ²	Factor	Coeff.	Standard error	P value	dGrowth
<i>Ocean age-2 sockeye salmon</i>						
SW2~PINK	0.04/0.42	PINK	−0.036	0.0079	<0.0001	−14%
<i>Ocean age-3 sockeye salmon</i>						
SW1~PINK	0.01/0.31	PINK	−0.009	0.0033	0.01	−3%
SW2~PINK + SOCK	0.02/0.29	PINK	−0.019	0.0027	<0.0001	−7%
		SOCK	−0.039	0.0148	0.03	−3%
SW3~PINK + SOCK	0.08/0.32	PINK	−0.031	0.0028	<0.0001	−17%
		SOCK	−0.056	0.0170	0.002	−6%

Best model fit was determined based on AICc. Factor PINK is the annual sum of eastern Kamchatka and North American pink salmon abundance, and SOCK is annual North Pacific sockeye abundance. Units of coefficients involving annual salmon abundance are in scale growth (mm)/100 million salmon. R² for model fits are the marginal and conditional coefficients of determination for generalized mixed-effect models. dGrowth calculations were based on low and high abundances of pink salmon and sockeye salmon, as described in methods.

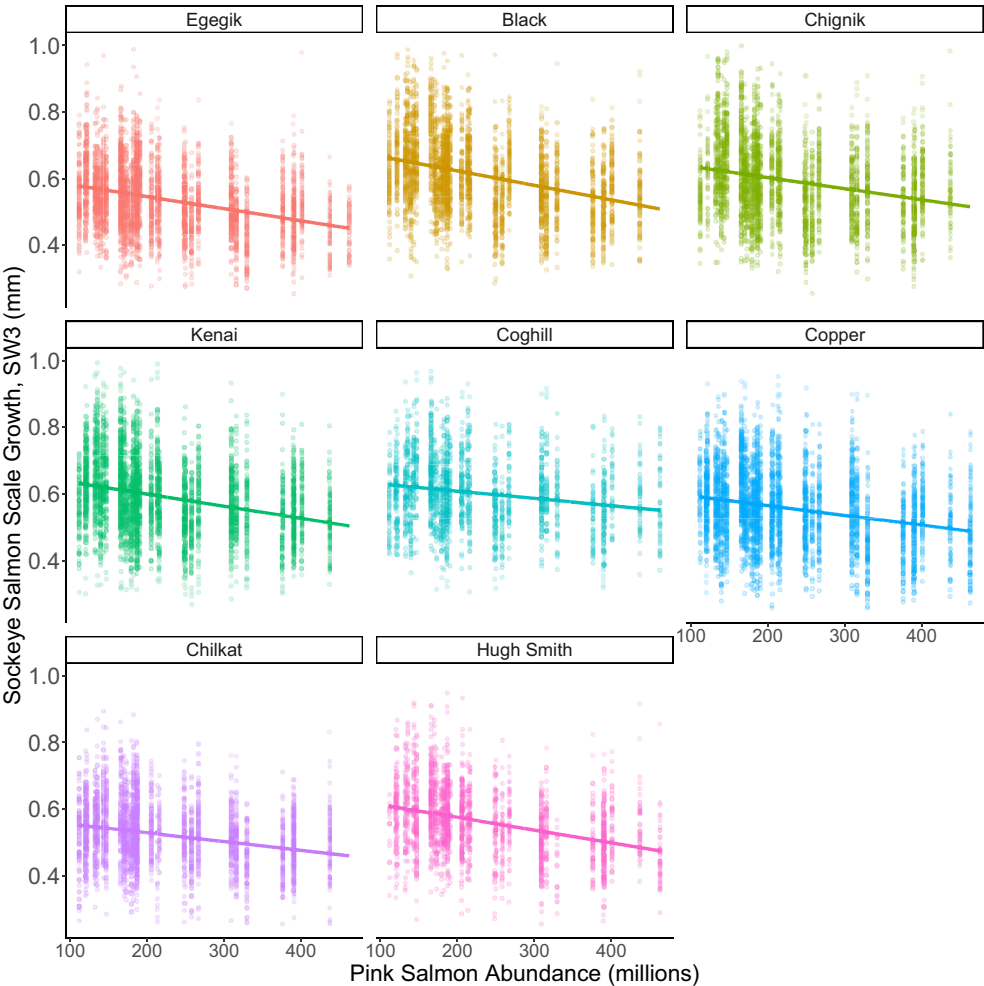


Figure 4. Regression-corrected plots of annual sockeye salmon scale growth during the third year at sea for populations originating from the Gulf of Alaska and Bering Sea regions in relation to pink salmon abundance (sum of abundance from eastern Kamchatka and North America). Individual fish scale growth values are shown.

but not for ocean age-2 sockeye salmon. Growth during SW1 was not correlated with sockeye salmon abundance for either age group (Table 1). We determined that the residuals of the best fit models were not significantly autocorrelated ($P > .05$) and the models explained 29–42% of the annual scale growth variability ($R^2 = 0.29$ – 0.42 , fixed and random effects com-

bined, Table 1). The amount of variation in growth of individual salmon scales explained by the fixed effects of pink and sockeye salmon abundance was 1–8% of the total ($R^2 = 0.01$ – 0.08 , Table 1).

In years of high abundances of pink salmon, scale growth during SW2 of ocean age-2 and ocean age-3 sockeye salmon

declined by 14% and 7%, respectively, compared with growth when pink salmon abundance was low (dGrowth, Table 1). During the life stage of SW3, scale growth declined 17% when pink salmon abundance increased from low to high levels (Table 1, Fig. 4). Although the per capita effect of sockeye salmon abundance on growth was higher on SW2 and SW3 growth (model coefficients -0.039 and -0.056 , respectively) than the per capita effect of pink salmon abundance on SW2 and SW3 growth (model coefficients -0.019 and -0.031 , respectively), the total effect of sockeye salmon abundance on scale growth of ocean age-3 salmon (-3% for SW2 and -6% for SW3) was less than that of pink salmon given the greater interannual fluctuations and the overall magnitude in pink salmon abundance (Table 1). Accounting for the higher overall levels of abundance of pink salmon in the North Pacific (the product of the model coefficients in Table 1 and the mean abundance of each of the species in the North Pacific during 1977–2015), we estimated that pink salmon abundance had over twice the level of effect on growth relative to the abundance of sockeye salmon.

Discussion

Our analyses of scale growth from seven populations of sockeye salmon returning to watersheds in the Gulf of Alaska region and one population returning to the southeastern Bering Sea provide multiple lines of evidence for inter- and intra-specific competition for prey at sea. Scale growth of ocean age-2 and ocean age-3 sockeye salmon during the second (SW2) and third (SW3) years at sea was consistently less in odd years, corresponding with high odd-year abundances of pink salmon originating from eastern Kamchatka and North America. Over the 39-year period, sockeye salmon growth declined with increasing abundances of pink salmon (SW1, SW2, and SW3) and sockeye salmon (SW2 and SW3). The total effect of pink salmon on sockeye growth was over 2 times greater than that of sockeye salmon, owing in part to the greater fluctuations and overall magnitude of pink salmon abundance. Annual growth rates of sockeye salmon that we report here, as measured by spacing in scale annuli, were reduced by as much as 17% in years of high pink salmon abundances in the North Pacific.

Given the relationship between scale growth and final length, we would expect ocean age-2 sockeye salmon to show a biennial pattern in final lengths given that these fish cannot compensate for poor growth experienced in an odd year with higher growth in the following even year. Indeed, the only biennial pattern noted in final lengths in our data set was for ocean age-2 fish. Fish entering the ocean in an even year and competing with odd-year pink salmon during their second and final full growing season returned 2% shorter in body length, on average, than conspecifics that entered the ocean in an odd year (t -test, $P < .0001$). Oke et al. (2020) reported a 2.1% decline in length at return of sockeye salmon during a multidecadal period and noted a negative relationship with North Pacific pink salmon abundance. Based on an established allometric relationship between length and mass in sockeye salmon (Froese and Pauly 2023), body length reductions of this magnitude correspond to a greater percentage change in mass ($\sim 6\%$ of body mass), which could have important ecological and economic consequences.

By examining growth during discrete years of ocean residence in this study, we could more accurately quantify the strong competitive effects associated with biennial abundances of pink salmon than if we had relied upon adult sockeye salmon lengths that reflect cumulative effects after 2 or 3 years at sea (see above). Complex salmon life histories often mask the adverse effects of pink salmon. For example, our findings indicate a potential scale growth decline of 23% during the third year at sea if total abundances of eastern Kamchatka and North American pink salmon (equating to a reduction of 17%) and North Pacific sockeye salmon (equating to a reduction of 6%) are high (see Table 1). These values underestimate density-dependent growth to the extent that growth-related mortality led to fewer returns of slower-growing sockeye salmon (Connors et al. 2020). Further, there is growing concern over the long-term increase in pink salmon abundance and the potential scenario of consecutive years of high pink salmon abundance, as was noted in 2018/2019 (Ruggerone et al. 2021). These consecutive years of high pink salmon abundance were followed by exceptional declines of all five species of Pacific salmon throughout the North Pacific Ocean in 2020.

Our findings are consistent with other studies of competition for prey between pink salmon and sockeye salmon in their second and third seasons at sea, while also providing new information on the effects of pink salmon on growth of sockeye salmon populations returning to watersheds bordering the Gulf of Alaska. Based on population data for 47 sockeye populations across North America (1977–2015), Connors et al. (2020) estimated that a 119 million increase in North Pacific abundance of pink salmon (1 standard deviation of the mean) was associated with a 9% decline in sockeye salmon productivity in the Gulf of Alaska and Bering Sea, and a 21% decline in British Columbia and southeast Alaska, after accounting for sea surface temperature. In Bristol Bay, Alaska, pink salmon have been linked to reduced and biennial scale growth during the second and third years at sea, smaller size-at-age, reduced and biennial smolt-to-adult survival, reduced and biennial adult returns from smolt migrations, and biennial forecast error (Ruggerone et al. 2003, Ruggerone et al. 2005, Ruggerone et al. 2016, Ohlberger et al. 2023). Sockeye salmon in the Fraser River, British Columbia, exhibit reduced and biennial size at age and productivity, and delayed maturation (Ruggerone and Connors 2015). We also detected a weak biennial pattern and a weak effect of pink salmon abundance during the first year of ocean age-3 sockeye salmon, which is generally consistent with growth and/or survival studies at Kodiak Island, Prince William Sound, and northern British Columbia (Peterman 1982, Martinson et al. 2008, Ward et al. 2017). Adverse effects of pink salmon on body size of sockeye salmon have also been reported in Russia (Bugaev et al. 2001) and all regions of Alaska (Oke et al. 2020).

A synthesis of studies involving interactions of pink salmon with other marine species indicates pink salmon can have a significant influence on the species and ecosystems of the North Pacific Ocean (Ruggerone et al. 2023). High abundances of pink salmon can initiate a trophic cascade in the Bering Sea and central North Pacific Ocean, whereby predation by numerous pink salmon in odd years leads to fewer zooplankton and more phytoplankton, with opposite patterns in even years (Batten et al. 2018). Biennial patterns and negative correlations with pink salmon are reflected in the growth and/or abundance of other species, including for-

age fish (four species), squid, all Pacific salmon and steelhead trout (*O. mykiss*), seabirds (11 species), humpback whales (*Megaptera novaeangliae*), and southern resident killer whales (*Orcinus orca*; Ruggerone et al. 2023). Although pink salmon are commonly considered to be planktivores, they also consume squid and small fish during their second year at sea (Davis 2003, Kaeriyama et al. 2004). These nekton prey are key to the growth of higher-trophic-level salmon such as Chinook (*O. tshawytscha*) and coho salmon (*O. kisutch*) and steelhead trout, as well as older sockeye salmon. Availability of these high-energy prey is critical given the higher energetic demands of larger salmon in a warming ocean (Davis et al. 1998, Welch et al. 1998, Rand 2002, Beauchamp 2009). The synthesis of studies provides evidence that pink salmon affect the growth, age at maturation, and/or survival of the higher trophic level salmon, including Chinook salmon, whose size and abundance have declined for decades throughout their range (Bigler et al. 1996, Lewis et al. 2015, Cunningham et al. 2018, Oke et al. 2020).

The reduction in annual growth of the eight sockeye salmon populations in relation to increasing pink and sockeye salmon abundances adds to the growing body of evidence indicating a limited capacity of the ocean to support both wild and hatchery salmon (Peterman 1978, 1984a, 1984b, Cooney and Brodeur 1998, Percy et al. 1999, Holt et al. 2008, McMillan et al. 2023, Ruggerone et al. 2023). During 2005–2015, ~82 million hatchery pink salmon returned per year from the North Pacific Ocean (Ruggerone and Irvine 2018), a value that is more than all wild chum salmon and about equal to wild sockeye salmon during this period. Hatcheries, primarily in Alaska and Russia, continue to release ~1.4 billion pink salmon per year, 2000–2022 (NPAFC 2023), even though total pink salmon abundance has reached record-high levels in recent years (e.g. ~800 million fish in 2021; Ruggerone et al. 2023). The growing abundance of wild and hatchery pink salmon in the North Pacific since 1955 is highly correlated with the North Pacific ocean heat content ($r = 0.71$, a measure of the total energy absorbed and stored by oceans; Levitus et al. 2012, NOAA 2022), suggesting that humans have contributed to the rapid increase in pink salmon abundance through both hatchery production and their contributions to ocean heating (Ruggerone et al. 2023). The mean annual return of ~82 million hatchery pink salmon during 2005–2015 was estimated to reduce sockeye salmon productivity by ~5% in the Bering Sea, 6% in the Gulf of Alaska, and 15% in British Columbia and southeast Alaska after accounting for sea surface temperature (Connors et al. 2020). Hatchery pink salmon contribute to the release of 5.1 billion hatchery salmon per year (NPAFC 2023), and total hatchery salmon production is estimated to represent 40% of the total immature and adult salmon biomass in the North Pacific Ocean, largely from pink and chum salmon (Ruggerone and Irvine 2018). Thus, hatchery production, coupled with human-derived climate change (Litzow et al. 2023) likely has had unintended effects on wild salmon.

In conclusion, we present new evidence indicating the effect of pink and sockeye salmon abundance on annual growth of sockeye salmon originating from seven watersheds in the Gulf of Alaska region, and one in the southeastern Bering Sea. Our findings build upon robust and consistent findings showing the competitive dominance of pink salmon over sockeye salmon. It is important to recognize that in the present era, hatchery releases represent a classic ‘zero-sum’ game, where

an incremental increase in hatchery releases results in some loss of growth and productivity of wild salmon through increased competition at sea. Understanding this dynamic is critical for making responsible decisions related to the management of salmon hatcheries and conservation of wild Pacific salmon.

Acknowledgements

We thank Brendan Connors and two anonymous reviewers for providing constructive comments on the manuscript.

Author contributions

P.R. and G.R. initiated the study. G.R. contributed data. P.R. carried out analysis. Both authors wrote, reviewed, and edited the manuscript.

Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: The authors do not have an competing interests to declare.

Funding

This is a contribution to the National Center for Ecological Analysis and Synthesis project State of Alaska Salmon and People (Award # 5124 from the Gordon and Betty Moore Foundation). Bev Agler and colleagues at the Mark, Tag, and Age Lab of Alaska Department of Fish and Game measured the salmon scales as part of Alaska Sustainable Salmon Fund grants to the second author. Support to the lead author was provided by the Wrangell-St. Elias National Park and Preserve, the Alaska Sustainable Salmon Fund, North Pacific Research Board, and the Exxon Valdez Oil Spill Trustee Council.

Data availability

Data available on request.

References

- Batten SD, Ruggerone GT, Ortiz I. Pink Salmon induce a trophic cascade in plankton populations around the Aleutian Islands. *Fish Oceanogr* 2018;27:548–59. <https://doi.org/10.1111/fog.12276>
- Beauchamp DA. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *Am Fish Soc Symp* 2009;70:1–19.
- Bigler BS, Welch DW, Helle JH. A review of size trends among North Pacific salmon (*Oncorhynchus* spp). *Can J Fish Aquat Sci* 1996;53:445–65. <https://doi.org/10.1139/f95-181>
- Bolker BM. Linear and generalized linear mixed models. In: GA Fox, S Negrete-Yankelevich, VJ Sosa (eds.), *Ecological Statistics: Contemporary Theory and Application*. Oxford: Oxford University Press, 2015.
- Buckner J, Satterwaite WH, Nelson BW et al. Interaction between life history and the environment on changing growth rates of Chinook salmon. *Can J Fish Aquat Sci* 2022;80:648–62. <https://doi.org/10.1139/cjfas-2022-0116>
- Bugaev VF, Welch DW, Selifonov MM et al. Influence of the marine abundance of pink (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. *Fish*

- Oceanogr 2001;10:26–32. <https://doi.org/10.1046/j.1365-2419.2001.00150.x>
- Connors B, Malick MJ, Ruggerone GT *et al.* Climate and competition influence sockeye salmon population dynamics across the northeast Pacific Ocean. *Can J Fish Aquat Sci* 2020;77:943–9. <https://doi.org/10.1139/cjfas-2019-0422>
- Cooney RT, Brodeur RD. Carrying capacity and North Pacific salmon production: stock enhancement implications. *Bull Mar Sci* 1998;62:443–64.
- Cunningham CJ, Westley PAH, Adkison MD. Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. *Global Change Biol* 2018;24:4399–416. <https://doi.org/10.1111/gcb.14315>
- Davis ND, Myers KW, Ishida Y. Caloric values of high seas salmon prey organisms and simulated salmon ocean growth and prey consumption. *North Pac Anadr Fish Comm Bull* 1998;1: 146–62.
- Davis ND. *Feeding Ecology of Pacific Salmon (Oncorhynchus spp) in the Central North Pacific Ocean and central Bering Sea, 1991–2000*. Hakodate: Hokkaido University, 2003.
- Diaz Pauli B, Berntsen HH, Thorstad EB *et al.* Geographic distribution, abundance, diet, and body size of invasive pink salmon (*Oncorhynchus gorbuscha*) in the Norwegian and Barents Seas, and in Norwegian rivers. *ICES J Mar Sci* 2023;80:76–90. <https://doi.org/10.1093/icesjms/fsac224>
- Dunmall K, Reist JD, Carmack EC *et al.* *Pacific Salmon in the Arctic: Harbingers of Change*. Fairbanks, AK: Alaska Sea Grant, University of Alaska Fairbanks, 2013.
- Froese F, Pauly D. FishBase. World Wide Web electronic publication. 2023. <https://www.fishbase.org/au/v4> (22 February 2024, date last accessed).
- Fukuwaka M, Kaeriyama M. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Can J Fish Aquat Sci* 1997;54:631–6. <https://doi.org/10.1139/f96-307>
- Graham C, Pakhomov EA, Hunt BP. Meta-analysis of salmon trophic ecology reveals spatial and interspecies dynamics across the North Pacific Ocean. *Front Mar Sci* 2021;8:1–17. <https://doi.org/10.3389/fmars.2021.618884>
- Habicht C, Seeb LW, Myers KW *et al.* Summer–fall distribution of stocks of immature sockeye salmon in the Bering Sea as revealed by single-nucleotide polymorphisms. *Trans Am Fish Soc* 2010;139:1171–91. <https://doi.org/10.1577/T09-149.1>
- Hagen PT, Oxman DS, Agler BA. *Developing and Deploying a High-Resolution Imaging Approach for Scale Analysis*. Juneau, AK: North Pacific Anadromous Fish Commission, 2001, 11.
- Holt C, Rutherford MB, Peterman RM. International cooperation among nation-states of the North Pacific on the problem of competition among salmon for a common pool of prey resources. *Mar Policy* 2008;32:607–17. <https://doi.org/10.1016/j.marpol.2007.11.001>
- Irvine JR, Michielsens CJ, O'Brien M *et al.* Increasing dominance of odd-year returning pink salmon. *Trans Am Fish Soc* 2014;143:939–56. <https://doi.org/10.1080/00028487.2014.889747>
- Jeffrey KM, Cote IM, Irvine JR *et al.* Changes in body size of Canadian Pacific salmon over six decades. *Can J Fish Aquat Sci* 2017;74:191–201. <https://doi.org/10.1139/cjfas-2015-0600>
- Kaeriyama M, Nakamura N, Edpalina R *et al.* Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish Oceanogr* 2004;13:197–207. <https://doi.org/10.1111/j.1365-2419.2004.00286.x>
- Krkosek M, Hilborn R, Peterman RM *et al.* Cycles, stochasticity and density dependence in pink salmon population dynamics. *Proc Biol Sci* 2011;278:2060–8.
- Lennox RJ, Berntsen HH, Garseth ÅH *et al.* Prospects for the future of pink salmon in three oceans: from the native Pacific to the novel Arctic and Atlantic. *Fish Fisheries* 2023;24:759–76. <https://doi.org/10.1111/faf.12760>
- Levitus S, Antonov JJ, Boyer TP *et al.* World ocean heat content and thermocline sea level change (0–2000 m), 1955–2010. *Geophys Res Lett* 2012;39:L10603. <https://doi.org/10.1029/2012GL051106>
- Lewis B, Grant WS, Brenner RE *et al.* Changes in size and age of Chinook salmon *oncorhynchus tshawytscha* returning to Alaska. *PLoS One* 2015;10:e0130184. <https://doi.org/10.1371/journal.pone.0130184>
- Litzow MA, Malick MJ, Kristiansen T *et al.* Climate attribution time series track the evolution of human influence on North Pacific sea surface temperature. *Environ Res Lett* 2023;19:014014. <https://doi.org/10.1088/1748-9326/ad0c88>
- Martinson EC, Helle JH, Scarnecchia DL *et al.* Density-dependent growth of Alaska sockeye salmon in relation to climate-oceanic regimes, population abundance, and body size, 1925 to 1998. *Mar Ecol Progr Ser* 2008;370:1–18. <https://doi.org/10.3354/meps07665>
- McMillan JR, Morrison B, Chambers N *et al.* A global synthesis of peer-reviewed research on the effects of hatchery salmonids on wild salmonids. *Fish Manag Ecol* 2023;30:446–63. <https://doi.org/10.1111/fme.12643>
- Myers KW, Aydin KY, Walker RV *et al.* *Known Ocean Ranges of Stocks of Pacific Salmon and Steelhead as Shown by Tagging Experiments, 1956–1995*. Seattle: North Pacific Anadromous Fish Commission, University of Washington, 1996.
- Myers KW, Klovach NV, Gritsenko OF *et al.* Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *North Pac Anadr Fish Comm Bull* 2007;4:159–77.
- NOAA. *Heat Content Basin Times Series*. Washington, DC: National Centers for Environmental Information, 2022.
- NPAC. *Pacific Salmonid Hatchery Release Statistics 24 July 2023 Edn*. Vancouver: North Pacific Anadromous Fish Commission, 2023.
- Ohlberger J, Cline TJ, Schindler DE *et al.* Declines in body size of sockeye salmon associated with increased competition in the ocean. *Proc Royal Soc B* 2023;290:20222248. <https://doi.org/10.1098/rspb.2022.2248>
- Oke KB, Cunningham CJ, Westley PAH *et al.* Recent declines in salmon body size impact ecosystems and fisheries. *Nat Commun* 2020;11:4155. <https://doi.org/10.1038/s41467-020-17726-z>
- Pearcy WG, Aydin KY, Brodeur RD. What is the carrying capacity of the North Pacific Ocean for salmonids? *PICES Press* 1999;7:17–23.
- Peterman RM. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). *Can J Fish Aquat Sci* 1984a;41:1825–9. <https://doi.org/10.1139/f84-223>
- Peterman RM. Effects of Gulf of Alaska sockeye salmon (*Oncorhynchus nerka*) abundance on survival, body size, growth rate, and age at maturity of British Columbia and Bristol Bay, Alaska sockeye populations. *Can Tech Rep Fish Aquat Sci* 1984b;No. 1302.
- Peterman RM. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. *Can J Fish Aquat Sci* 1982;39:904–13. <https://doi.org/10.1139/f82-121>
- Peterman RM. Testing for density dependent marine survival in Pacific salmonids. *J Fish Res Board Can* 1978;35:1434–50. <https://doi.org/10.1139/f78-226>
- Radchenko VI, Beamish RJ, Heard WR *et al.* Ocean ecology of pink salmon. In: RJ Beamish (ed.), *The Ocean Ecology of Pacific Salmon and Trout*. Bethesda, MD: American Fisheries Society, 2018.
- Rand PS. Modeling feeding and growth in Gulf of Alaska sockeye salmon: implications for high-seas distribution and migration. *Mar Ecol Progr Ser* 2002;234:265–80. <https://doi.org/10.3354/meps234265>
- Ruggerone GT, Agler BA, Connors BM *et al.* Pink and sockeye salmon interactions at sea and their influence on forecast error of Bristol Bay sockeye salmon. *North Pac Anadr Fish Comm Bull* 2016;6:349–61. <https://doi.org/10.23849/npafcb/349.361>
- Ruggerone GT, Connors BM. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon

- in the North Pacific Ocean. *Can J Fish Aquat Sci* 2015;72:818–33. <https://doi.org/10.1139/cjfas-2014-0134>
- Ruggerone GT, Farley E, Nielsen JL *et al.* Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fish Bull* 2005;103:355–70.
- Ruggerone GT, Irvine JR, Connors BM. Did recent marine heatwaves and record high pink salmon abundance lead to a tipping point that caused record declines in North Pacific salmon abundance and harvest in 2020? *North Pac Anadr Fish Comm Tech Rep* 2021;17:78–82.
- Ruggerone GT, Irvine JR. Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Mar Coastal Fish Dynam Manag Ecosyst Sci* 2018;10:152–68. <https://doi.org/10.1002/mcf2.10023>
- Ruggerone GT, Nielsen JL, Bumgarner J. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. *Deep Sea Res Part II* 2007;54:2776–93. <https://doi.org/10.1016/j.dsr2.2007.08.016>
- Ruggerone GT, Springer AM, van Vliet GB *et al.* From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems. *Mar Ecol Progr Ser* 2023;719:1–40. <https://doi.org/10.3354/meps14402>
- Ruggerone GT, Zimmerman M, Myers KW *et al.* Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish Oceanogr* 2003;12:209–19. <https://doi.org/10.1046/j.1365-2419.2003.00239.x>
- Sandlund OT, Berntsen HH, Fiske P *et al.* Pink salmon in Norway: the reluctant invader. *Biol Invasions* 2019;21:1033–54. <https://doi.org/10.1007/s10530-018-1904-z>
- Ward EJ, Adkison M, Couture J *et al.* Evaluating signals of oil spill impacts, climate, and species interactions in Pacific herring and Pacific salmon populations in Prince William Sound and Copper River, Alaska. *PLoS One* 2017;12:e0172898. <https://doi.org/10.1371/journal.pone.0172898>
- Welch DW, Ishida Y, Nagasawa K. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can J Fish Aquat Sci* 1998;55:937–48. <https://doi.org/10.1139/f98-023>
- Wells BK, Grimes CB, Sneva JG *et al.* Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska. *Fish Oceanogr* 2008;17:101–25. <https://doi.org/10.1111/j.1365-2419.2008.00467.x>

Handling Editor: Mikko Heino