

Climate and competition influence sockeye salmon population dynamics across the Northeast Pacific Ocean

Brendan Connors, Michael J. Malick, Gregory T. Ruggerone, Pete Rand, Milo Adkison, James R. Irvine, Robert Campbell, and Kristen Gorman

Abstract: Pacific salmon productivity is influenced by ocean conditions and interspecific interactions, yet their combined effects are poorly understood. Using data from 47 North American sockeye salmon (*Oncorhynchus nerka*) populations, we present evidence that the magnitude and direction of climate and competition effects vary over large spatial scales. In the south, a warm ocean and abundant salmon competitors combined to strongly reduce sockeye productivity, whereas in the north, a warm ocean substantially increased productivity and offset the negative effects of competition at sea. From 2005 to 2015, the approximately 82 million adult pink salmon (*Oncorhynchus gorbuscha*) produced annually from hatcheries were estimated to have reduced the productivity of southern sockeye salmon by ~15%, on average. In contrast, for sockeye at the northwestern end of their range, the same level of hatchery production was predicted to have reduced the positive effects of a warming ocean by ~50% (from a ~10% to a ~5% increase in productivity, on average). These findings reveal spatially dependent effects of climate and competition on sockeye productivity and highlight the need for international discussions about large-scale hatchery production.

Résumé : Si la productivité des saumons du Pacifique est influencée par les conditions océaniques et les interactions entre espèces, les effets combinés de ces deux facteurs demeurent toutefois mal compris. En utilisant des données sur 47 populations nord-américaines de saumons rouges (*Oncorhynchus nerka*), nous présentons des preuves de variations à de grandes échelles spatiales de la magnitude et de la direction des effets du climat et de la concurrence. Dans le Sud, les effets combinés d'un océan chaud et d'une abondance de saumons concurrents ont entraîné une forte réduction de la productivité des saumons rouges, alors que dans le Nord, un océan chaud a accru substantiellement la productivité et contré les effets négatifs de la concurrence en mer. Il est estimé que, de 2005 à 2015, les quelque 82 millions de saumons roses (*O. gorbuscha*) adultes produits annuellement en éclosérie ont causé une réduction de 15 % en moyenne de la productivité des saumons rouges du Sud. En comparaison, il a été prédit que, pour les saumons rouges à l'extrémité nord-ouest de leur aire de répartition, le même niveau de production en éclosérie a réduit de 50 % les effets positifs du réchauffement de l'océan (l'augmentation de la productivité passant de 10 % à 5 % en moyenne). Ces constatations révèlent des effets variables dans l'espace du climat et de la concurrence sur la productivité des saumons rouges et soulignent la nécessité de discussions internationales sur la production en éclosérie à grande échelle. [Traduit par la Rédaction]

Introduction

Climate change is having a profound effect on the world's ocean ecosystems, where it poses challenges to species persistence and fisheries sustainability (Cheung et al. 2010; Gattuso et al. 2015; Pörtner et al. 2019). As the world's oceans warm and experience more frequent extremes (e.g., marine heat waves; Di Lorenzo and Mantua 2016; Cheng et al. 2019), species may be negatively or positively impacted depending on their distribution, and these effects can vary strongly across geographic gradients (Hoegh-Guldberg and Bruno 2010; Pinsky et al. 2013). In addition to direct effects on both the abundance and distribution of species, ocean climate may mediate the consequences of ecological

processes (e.g., interactions among species) and be filtered through the life history characteristics of individual populations (Blois et al. 2013). As a result, the consequences of changing climate on marine species, and the economies and ecosystems that depend on them, can be difficult to predict and manage.

In addition to impacts from climate change, large increases in abundance of some fish species in the North Pacific Ocean over the past several decades have altered the dynamics of a wide variety of species from phytoplankton and zooplankton to seabirds and salmon (Springer and van Vliet 2014; Batten et al. 2018). Indeed, more Pacific salmon (*Oncorhynchus* spp.) have returned to fresh water from the North Pacific Ocean in recent years than at any time in the previous 90 years (Ruggerone and Irvine 2018).

Received 2 December 2019. Accepted 14 April 2020.

B. Connors.* Fisheries and Oceans Canada, Institute of Ocean Sciences, 9860 W. Saanich Rd., Sidney, BC V8L 5T5, Canada.

M.J. Malick.* NRC Research Associateship Program, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.

G.T. Ruggerone.* Natural Resources Consultants, Inc., Seattle, WA 98199, USA.

P. Rand and R. Campbell. Prince William Sound Science Center, PO Box 705, 300 Breakwater Avenue, Cordova, AK 99574, USA.

M. Adkison. University of Alaska Fairbanks, College of Fisheries and Ocean Sciences, Juneau, AK 99801, USA.

J.R. Irvine. Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.

K. Gorman. Prince William Sound Science Center, PO Box 705, 300 Breakwater Avenue, Cordova, AK 99574, USA; University of Alaska Fairbanks, College of Fisheries and Ocean Sciences, Juneau, AK 99801, USA.

Corresponding author: Brendan Connors (email: brendan.connors@dfo-mpo.gc.ca).

*These authors contributed equally to this work.

Copyright remains with the author(s) or their institution(s). This work is licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/) (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Pink salmon (*Oncorhynchus gorbuscha*) numerically dominate the abundance of salmon in the North Pacific (average 500 million adults per year), and ~22% of salmon in recent decades (40% of biomass) are from salmon released by hatcheries in Asia and Alaska (primarily pink and chum (*Oncorhynchus keta*), which account for the majority of biomass; Ruggerone and Irvine 2018). These salmon are broadly distributed and overlap in the North Pacific Ocean (Myers et al. 1996; Beacham et al. 2014), where they can compete for common prey with other pelagic consumers (Kaeriyama et al. 2000; Bugaev et al. 2001; Davis et al. 2005; Johnson and Schindler 2009). Increased hatchery production in recent years has fueled debate about the potential for adverse effects on North Pacific ecosystems and has led to calls for international cooperation among North Pacific nations to reduce total releases of hatchery-reared juvenile salmon into the North Pacific Ocean (Holt et al. 2008; Debertin et al. 2017).

While the effects of climate change and increased competition among salmon for limited food resources have each been documented, the joint effects of these stressors on salmon productivity are poorly understood (but see Debertin et al. 2017; Cunningham et al. 2018). In particular, there has been little analysis of the potential mediating effect of ocean climate on density-dependent interactions across geographic gradients. Such mediating effects may occur, for example, as a result of climate-induced reductions (or increases) in growth during early life phases leading to increased (or decreased) sensitivity to density-dependent effects during later life phases. Alternatively, ocean climate may mediate the effects of density dependence within the same life phase. Here, we capitalize on a large dataset of sockeye salmon (*Oncorhynchus nerka*) populations from across the eastern North Pacific (Fig. 1a), along with information on ocean climate conditions and indices of potential salmon competitors at sea (Fig. 1b) to quantify the combined effects of ocean warming and increasing competition on sockeye salmon across their range.

Methods

Sockeye salmon data

We used spawner (escapement) and recruitment (adult offspring, including those caught in fisheries) data for 47 sockeye populations across their North American range (Fig. 1; also refer to online Supplementary Information, Table S1¹). This dataset is updated from that described in Peterman and Dorner (2012); however, we only retained populations with detailed age composition information by brood year (i.e., years spent in fresh water and the ocean). The resulting dataset spanned the 1950 to 2009 brood years, 26 different ocean entry points, and 21 different life history types (i.e., unique combinations of freshwater and marine residence), although most populations were dominated by one to three life histories and had shorter brood year time series. We organized the dataset into three large marine ecosystems because they exhibited shared trends in productivity at this scale (Peterman and Dorner 2012) and because oceanographic processes, and salmon responses to them, tend to differ across these regions. Specifically, all populations that enter the ocean in British Columbia and Southeast Alaska were assigned to the West Coast ecosystem, populations that enter the ocean in south central Alaska were assigned to the Gulf of Alaska ecosystem, and western Alaska populations were assigned to the Bering Sea ecosystem (Fig. 1a).

Because of variability in the beginning of productivity time series among populations and ocean regions (Table S1¹), and the large-scale ocean regime shift that occurred in 1976–1977, we truncated our time series to begin after the 1975 brood year. This ensured that there was balanced representation of stocks through

time and among ocean regions in our analyses and that our inference was not confounded by the well-documented 1976–1977 ocean regime shift (Mantua et al. 1997). In sensitivity analyses, we also fit the models to the complete time series (Supplemental Information¹).

Ocean climate index

We used sea surface temperature (SST) near ocean-entry points for juvenile sockeye salmon populations during the period of outmigration to index early marine ocean conditions experienced by juvenile salmon. Specifically, we used monthly extended reconstructed SST data (NOAA ERSSTv5) to calculate stock-specific SST indices (Liu et al. 2015; Huang et al. 2017). We first calculated monthly SST anomalies for each $2^\circ \times 2^\circ$ grid cell using 1950–2010 as the base period. We then calculated the annual stock-specific SST indices by averaging the SST anomalies across (i) grid cells whose centers were within 400 km of the ocean entry point of a given salmon stock and (ii) the months roughly corresponding to juvenile salmon outmigration and early marine residency (April–July for West Coast stocks, May–August for Gulf of Alaska stocks, June–September for Bering Sea stocks; Mueter et al. 2002).

Competitor index

We used the abundance of pink salmon across the North Pacific (Ruggerone and Irvine 2018) in the second and third years of sockeye marine life as an index of competition for food. This approach is consistent with research that has suggested sockeye from Southeast Alaska through British Columbia primarily exhibit responses to pink salmon during their second and third growing seasons (Connors et al. 2012; Ruggerone and Connors 2015). Some sockeye smolts from the Gulf of Alaska region and south may also interact with pink salmon during early marine life, but evidence for adverse interactions during the first year at sea is typically weaker (McKinnell and Reichardt 2012; Ruggerone and Connors 2015). In sensitivity analyses (Supplemental Information¹), we also considered the total numerical abundance and biomass of North Pacific pink, chum, and sockeye, as well as just numerical abundance of North American pink salmon, as alternative competitor indices in addition to a detrended North Pacific pink salmon competitor index.

Hierarchical stock-recruitment modelling

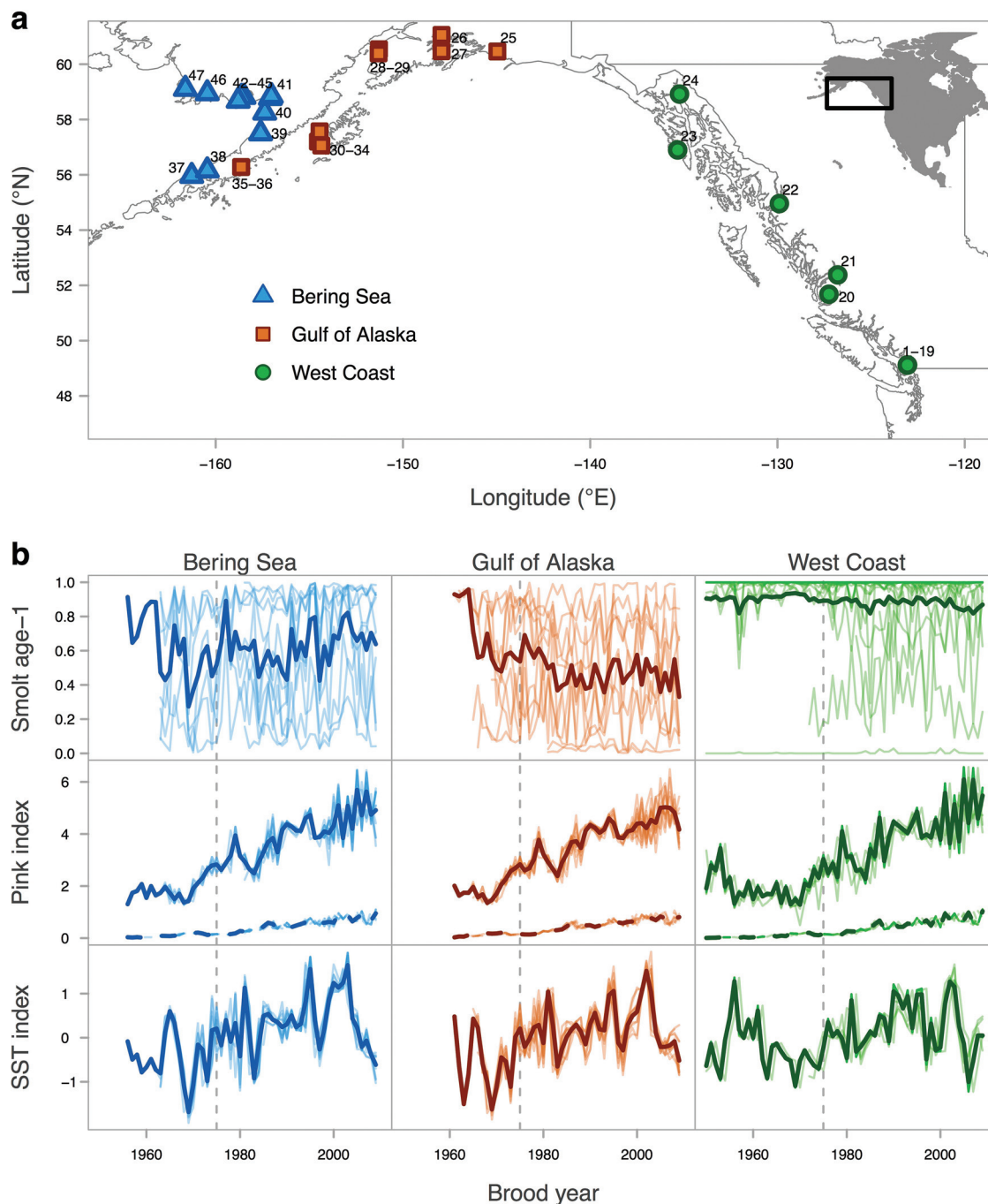
We modeled sockeye productivity as a function of spawner abundance, early marine ocean conditions, and competitor abundance:

$$\begin{aligned} \log_e(R_{i,t}/S_{i,t}) &= \alpha_i + \beta_i S_{i,t} + \gamma_i \text{SST}_{i,t+k} + \kappa_i \text{Comp}_{i,t+j} \\ &\quad + \chi_i (\text{SST}_{i,t+k} \text{Comp}_{i,t+j}) + \epsilon_{i,t} \\ (1) \quad \epsilon_{i,t} &= \phi \epsilon_{i,t-1} + \sqrt{1 - \phi^2} \delta_{i,t} \\ \delta_{i,t} &\sim \text{Normal}(0, \sigma_i^2) \end{aligned}$$

where R and S are recruitment and spawner abundance, respectively, for population i in brood year t , α is intrinsic productivity, β is the strength of within population density dependence, γ is the stock-specific coefficient for early marine ocean conditions, SST is an index of early marine ocean conditions (i.e., sea surface temperature) in year $t+k$, where k is the number of years after spawning the population entered the ocean, κ is the stock-specific coefficient for the competition index, Comp is an index of competitor abundance in year $t+j$, where j is the number of years after spawning the population interacted with the competitors, χ is the stock-specific interaction coefficient, and ϵ is the residual error

¹Supplementary Information are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0422>.

Fig. 1. Sockeye salmon stock ocean entry locations and time series of ocean entry age diversity and climate and competitor time series. (a) Ocean entry locations for stocks in the West Coast (green circles), Gulf of Alaska (orange squares), and Bering Sea (blue triangles) ecosystems. (b) Time series of the proportion of smolts entering the ocean at age-1 (top row); pink salmon abundance indices (middle row; in hundreds of millions), where solid lines show total abundance and dashed lines show hatchery contributions; and SST indices (bottom row; anomaly in °C). Thin light lines show stock-specific time series for each ecosystem, and thick dark lines show the mean across all stocks in the ecosystem. Brood years range from 1950 to 2009, and the 1976–1977 ocean regime shift (1975 brood year) is denoted by the dashed vertical grey line in panel (b). Map in panel (a) created using the *rnatualearth* R package (South 2017). [Colour online.]



term assumed to be first-order autocorrelated, with correlation parameter ϕ and variance σ^2 .

Juvenile sockeye salmon produced from a single brood year of spawners can enter the ocean over multiple years. Therefore, for each stock, we calculated brood-year-specific climate and competition indices as a weighted average equal to the brood year and stock-specific proportion of smolts entering the ocean each year

(Mueter et al. 2002; Ruggerone and Connors 2015; Malick et al. 2017).

We used Bayesian hierarchical models to estimate the effects of ocean conditions and competitor abundance on sockeye salmon productivity. We modeled the stock-specific parameters α_i , γ_i , κ_i , and χ_i hierarchically by assuming they arise from common prior distributions (i.e., these parameters were assumed exchangeable

Table 1. Summary of estimated model coefficient posterior distributions for each variable.

Ecosystem	Coefficient	Lower 95% CI	Mean	Upper 95% CI	% change in R/S
Bering Sea	SST	0.12	0.21	0.29	22.88
Gulf of Alaska	SST	0.01	0.08	0.17	8.87
West Coast	SST	-0.21	-0.13	-0.05	-12.08
Bering Sea	Comp	-0.19	-0.09	-0.01	-9.03
Gulf of Alaska	Comp	-0.18	-0.09	0.00	-8.50
West Coast	Comp	-0.32	-0.24	-0.15	-21.01
Bering Sea	SST × Comp	-0.02	0.05	0.12	5.37
Gulf of Alaska	SST × Comp	-0.08	-0.01	0.05	-1.04
West Coast	SST × Comp	-0.06	0.02	0.10	2.32

Note: The Lower 95% CI and Upper 95% CI columns give the lower and upper bounds of the 95% credibility interval, respectively. The Mean column gives the mean of the posterior distribution. The percent change in return per spawner (R/S) column gives the mean percent change in productivity (R/S) given a one standard deviation unit increase in a given covariate.

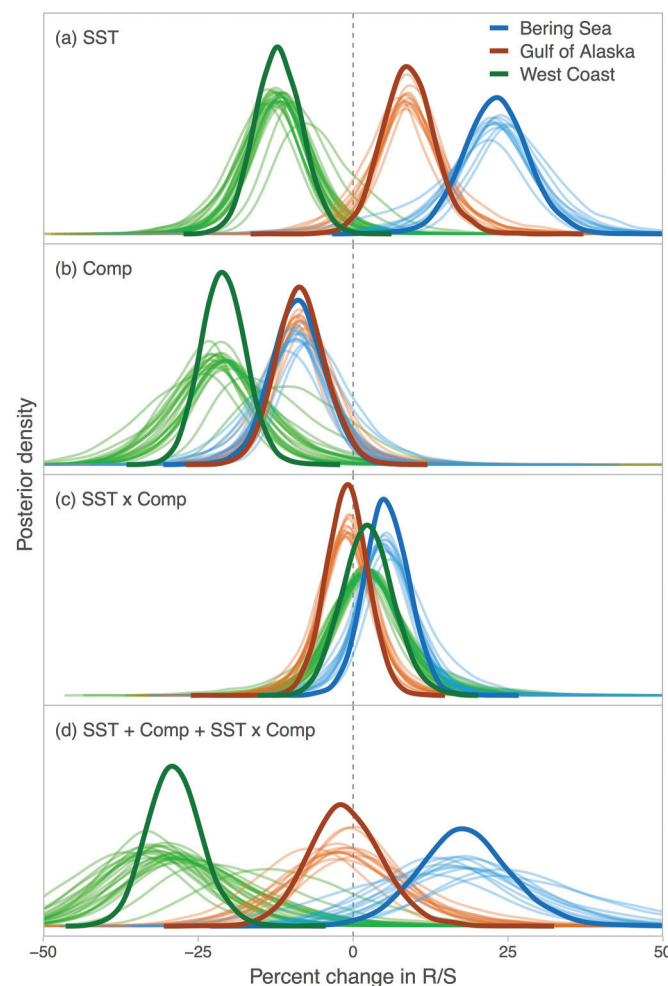
among a subset of stocks). For Fraser River stocks (No. 1–19 in Fig. 1a), spawner abundances were in units of effective female spawners (i.e., female spawner abundance adjusted for unspawned eggs), whereas for all other stocks spawner abundances were total male and female spawners. Thus, α_i parameters were split into two groups (one group that included Fraser River stocks and another group that included all non-Fraser River stocks) that were exchangeable within each group but not between the two groups. We assumed that the climate and competition parameters γ_i , κ_i , and χ_i were exchangeable among stocks within the same ocean ecosystem. Previous research has indicated large variations in the magnitude of the stock-specific density dependence and residual variance parameters for sockeye salmon populations (Mueter et al. 2002; Su et al. 2004; Malick et al. 2017), and so we assumed β_i and σ_i^2 were independent among stocks (i.e., nonexchangeable among stocks). We also assumed the autocorrelation parameter ϕ was common to all stocks (Malick et al. 2017). Further details on priors, model fitting, assessment of convergence, and sensitivity analyses are provided in the online Supplemental Information¹. Code and data to reproduce our analyses are archived in Connors and Malick (2020).

Results and discussion

Numerous marine species exhibit latitudinal gradients in responses to a warming ocean and, consistent with previous work (e.g., Mueter et al. 2002; Litzow et al. 2019), we found similar evidence for this in sockeye salmon productivity (Table 1). At the southern end of the sockeye salmon range (West Coast here), a warmer ocean during early marine life was related to reduced productivity, but in the middle and northwestern end of their range a warming ocean was associated with increased productivity (Figs. 2a and S1¹). The effect of a warming ocean was estimated to be 2.5 times stronger at the northwestern end of their range (23% increase in recruits per spawner per standard deviation unit (SDU) increase in SST; $\approx 1.5^\circ\text{C}$) than in the middle (9% increase), whereas sockeye in the southern portion of their range were predicted to experience a 12% reduction in productivity (Table 1). The range of ocean temperatures encountered by sockeye salmon during early marine life are well within their physiological limits, suggesting that processes correlated with SST (e.g., stratification, phenology of spring bloom, advection affecting delivery of nutrients or zooplankton to coastal areas, or fish growth energetics) as opposed to direct temperature effects, drive these SST–sockeye productivity relationships.

Increasing competitor abundance was negatively associated with sockeye productivity at the southern end of their range, where a 1 SDU increase in competitor abundance (≈ 119 million salmon) was predicted to result in a $\sim 21\%$ reduction in recruits-per-spawner (Table 1; Figs. 2b and S1¹). In contrast, we found evidence of a weaker negative association between competitor abundance and sockeye productivity in the Gulf of Alaska and

Fig. 2. Posterior probability distributions of the predicted effect of (a) SST, (b) competitors, (c) an interaction between the two, and (d) the combined effect from all covariate terms, on sockeye salmon survival. Overall hyperdistribution of the covariate effects are in bold lines, with individual stock-specific distributions illustrated by the light lines. Covariate effects are standardized (i.e., per standard deviation unit increase in each covariate), which equates to 1.5°C SST and 119 million pink salmon. [Colour online.]



northwestern end of the sockeye range ($\sim 9\%$ reduction in both regions; Table 1; Figs. 2b and S1¹).

The combined effects of a warming ocean and increasing salmon competitor abundance (and their interaction) across the

North Pacific shifted from negative to positive across the sockeye range from south to north. At the southern end of their range our analysis predicts a 30% reduction in recruits produced per spawner for every increase of 1.5 °C in SST and 119 million salmon competitors (Figs. 2d and S1¹). The combined SST and competitor effects were highly variable in the middle of the sockeye range (Fig. 2d), but positive at the northwestern end of their range where the negative influence of competition was offset by a stronger positive influence of ocean temperature such that the same magnitude of increases in ocean temperature and competitors as above were predicted to result in a 19% increase in the number of recruits produced per spawner.

We found weak evidence that the effect of increasing ocean temperature during early marine life mediates the consequences of competition later in marine life at the northwestern end of the sockeye range (i.e., a positive interaction term whose credible intervals still overlap zero; Table 1; Fig. 2c). In contrast, the interaction terms for the other two ocean regions were smaller and more centered around zero. The weakly positive interaction term for the Bering Sea stocks suggests that as the ocean warms, the predicted effect of competition becomes weaker (i.e., it is antagonistic). We hypothesize that this may occur because a warming ocean during early marine life that increases sockeye productivity and perhaps growth at the northwestern end of their range may also make sockeye less sensitive to density-dependent interactions later in marine life.

We conducted sensitivity analyses to further examine the evidence for competition stemming from the combined abundances or biomass of pink, sockeye, and chum salmon in addition to climate effects, at both a North Pacific and North American scale. Inferences from these analyses were broadly similar to those presented here for pink salmon, though the estimated effect of the interaction between climate and competition for West Coast stocks and of competition for Gulf of Alaska and Bering Sea stocks varied to some degree depending on which competitor index was used (Supplemental Information, Table S5¹ and Figs. S2–S6¹). In addition, when our analysis was repeated with all available brood years of data, including those before the 1976–1977 ocean regime shift that strongly influenced both sockeye and pink salmon abundances, we found that the evidence for competition effects on productivity in the Bering Sea and the Gulf of Alaska, but not West Coast, declined while the effect of SST remained similar (Table S5¹ and Fig. S9¹). Other studies have found some evidence for nonstationarity in salmon – ocean climate relationships (Mallick 2020), including a weaker negative effect of SST on sockeye productivity in West Coast region stocks after a pronounced decline in Aleutian Low variance in 1988–1989 (e.g., Litzow et al. 2019). We found no evidence to support nonstationarity in climate effects when we repeated our analysis on a dataset that was truncated to only consider the time period after 1988–1989 (Supplemental Information, Table S5¹ and Fig. S8¹).

Our findings are supported by previous research on Bristol Bay (Bering Sea) sockeye salmon that indicated the survival benefits from greater early marine growth offset the adverse effects of pink salmon on sockeye salmon during late marine life. Abundances of both pink and sockeye salmon in the North Pacific doubled after the 1977 ocean regime shift, and greater productivity of Bristol Bay sockeye salmon is associated with greater early marine growth (Ruggerone et al. 2007). Sockeye salmon originating from the Bering Sea interact with relatively few pink salmon during early marine life and numerous pink salmon during subsequent years when they are distributed farther west, leading to reduced growth, survival, and abundance of sockeye salmon (Ruggerone et al. 2003). Pink salmon effects on sockeye salmon are expressed by strong biennial patterns that cannot be explained by ocean climate. However, when examining adult returns per par-

ent spawner, the complex life history of Bering Sea sockeye salmon (multiple years of residence in freshwater and ocean habitats) may make the detection of these biennial patterns more difficult. In other words, progeny from each brood year interact with both odd-year (abundant) and even-year (less abundant) pink salmon, potentially dampening the pink salmon effect on returns from the brood year. In contrast, sockeye salmon from the southern region, such as Fraser River, have relatively simple life histories dominated by a single age class (age-1.2) that maintains the biennial pattern in population characteristics (Ruggerone and Connors 2015).

Though a growing body of evidence suggests that competition among salmon at sea can influence salmon growth, maturity, and productivity, the potential for food resources to limit salmon production across the North Pacific continues to be vigorously debated (Amoroso et al. 2017; Shuntov et al. 2017). While the majority of salmon production is from wild populations, hatchery production increasingly contributes to the number of salmon at sea. For example, the abundance of hatchery pink salmon during 2005–2015 (82 million adults per year, or 17% of all pink salmon) exceeded the abundance of wild chum salmon and was equal to the abundance of wild sockeye salmon over the same time period (Ruggerone and Irvine 2018). In addition, there are strong geographic differences in hatchery production. For example, Alaskan hatchery production of pink salmon represented 18–49% of total annual pink salmon produced in Alaska from 2005 to 2015.

Our analyses allow us to quantify what the potential consequences of hatchery production may be for sockeye productivity across their range. Using the parameter estimates from eq. 1 (Table 1), we estimate that total hatchery production of pink salmon has reduced sockeye productivity at the southern end of their range by ~15%, on average, over the past decade (2005–2015; Supplemental Information¹). This suggests that hatchery production has contributed to the depressed productivity of sockeye salmon in British Columbia, some of which have recently been assessed as at risk of extinction (COSEWIC 2017). In contrast, above-average SST conditions in the Gulf of Alaska and Bering Sea regions over the past decade are estimated to have largely offset the negative effects of hatchery production on sockeye productivity. In the Gulf of Alaska, hatchery pink salmon production is estimated to have reduced sockeye productivity by ~5%, on average, over the past decade, while in the Bering Sea the positive influence of above-average SST has led to an increase in productivity of ~5%, on average, compared with an increase of 10%, on average, if no hatchery production had occurred (Supplemental Information¹).

Sockeye exhibit a remarkable degree of variation in life histories (Quinn 2018). This life history diversity (e.g., variable age at ocean entry or maturity), which can dampen the effects of a variable environment on salmon survival and abundance (Moore et al. 2014), may also moderate the effects of ocean climate and competition on sockeye by spreading the consequences of adverse climate and competition across multiple life histories within a cohort. This buffering effect may be particularly important for moderating the effects of competition because of the high-frequency variation in competitor abundance from year to year due to the fixed 2-year life cycle of pink salmon. The loss of life history diversity, for example due to climate warming (Cline et al. 2019), has the potential to increase the vulnerability of sockeye populations to the adverse effects of variable environmental conditions and reduce the stability of these populations and the fisheries that depend on them. As such, future research should seek to better understand how life history diversity mediates the consequences of a warming ocean and density-dependent interactions among salmon at sea on salmon dynamics.

Increasing abundances of salmon across the North Pacific, and in particular pink salmon, have been linked to a trophic cascade in epipelagic waters, leading to fewer zooplankton, reduced

growth, survival and delayed maturation of salmon, reduced reproductive success of seabirds, and perhaps reduced foraging efficiency of southern resident killer whales (*Orcinus orca*) (Springer and van Vliet 2014; Ruggerone and Connors 2015; Batten et al. 2018; Ruggerone et al. 2019). Nonetheless, some jurisdictions (e.g., Alaska and Russia) continue to allow increasing hatchery production of pink and chum salmon with minimal consideration of adverse effects on distant salmon populations. Our findings highlight the importance of international cooperation to consider and potentially constrain the number of hatchery salmon released into the ocean to help Pacific salmon adapt to a warming and increasingly uncertain future.

Acknowledgements

We are grateful for the efforts of the many technicians and biologists who gathered and processed the salmon data used in this manuscript and to Jeanette Clark, Rich Brenner, and Stephanie Freund for compiling it. Ann-Marie Huang and three anonymous reviewers provided detailed and constructive feedback on an earlier version of the manuscript. This project was supported in part by the National Center for Ecological Analysis and Synthesis and the State of Alaskan Salmon and People project.

References

- Amoroso, R.O., Tillotson, M.D., and Hilborn, R. 2017. Measuring the net biological impact of fisheries enhancement: Pink salmon hatcheries can increase yield, but with apparent costs to wild populations. *Can. J. Fish. Aquat. Sci.* **74**(8): 1233–1242. doi:10.1139/cjfas-2016-0334.
- Batten, S.D., Ruggerone, G.T., and Ortiz, I. 2018. Pink Salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. *Fish. Oceanogr.* **27**(6): 548–559. doi:10.1111/fog.12276.
- Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014. Stock-specific size of juvenile Sockeye Salmon in British Columbia waters and the Gulf of Alaska. *Trans. Am. Fish. Soc.* **143**(4): 876–889. doi:10.1080/00028487.2014.889751.
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., and Finnegan, S. 2013. Climate change and the past, present, and future of biotic interactions. *Science*, **341**(6145): 499–504. doi:10.1126/science.1237184.
- Bugaev, V.F., Welch, D.W., Selifonov, M.M., Grachev, L.E., and Eveson, J.P. 2001. Influence of the marine abundance of pink (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. *Fish. Oceanogr.* **10**(1): 26–32. doi:10.1046/j.1365-2419.2001.00150.x.
- Cheng, L., Abraham, J., Hausfather, Z., and Trenberth, K.E. 2019. How fast are the oceans warming? *Science*, **363**(6423): 128–129. doi:10.1126/science.aav7619.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R.E.G., et al. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Change Biol.* **16**(1): 24–35. doi:10.1111/j.1365-2486.2009.01995.x.
- Cline, T.J., Ohlberger, J., and Schindler, D.E. 2019. Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nat. Ecol. Evol.* **3**: 935–942. doi:10.1038/s41559-019-0901-7. PMID:3113724.
- Connors, B.M., and Malick, M. 2020. Supplementary materials for Connors et al. doi:10.5281/zenodo.3813107.
- Connors, B.M., Braun, D.C., Peterman, R.M., Cooper, A.B., Reynolds, J.D., et al. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. *Conserv. Lett.* **5**(4): 304–312. doi:10.1111/j.1755-263X.2012.00244.x.
- COSEWIC. 2017. COSEWIC assessment and status report on the Sockeye Salmon *Oncorhynchus nerka*, 24 Designatable Units in the Fraser River Drainage Basin, in Canada [online]. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ont. Available from <http://www.registrelep.sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1>.
- Cunningham, C.J., Westley, P.A.H., and Adkison, M.D. 2018. Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. *Glob. Change Biol.* **24**(9): 4399–4416. doi:10.1111/gcb.14315. PMID:29774975.
- Davis, N.D., Fukuwaka, M., Armstrong, J.L., and Myers, K.W. 2005. Salmon food habits studies in the Bering Sea, 1960 to present. *N. Pac. Anadr. Fish Comm. Tech. Rep.* **6**: pp. 24–28.
- Debertin, A.J., Irvine, J.R., Holt, C.A., Oka, G., and Trudel, M. 2017. Marine growth patterns of southern British Columbia chum salmon explained by interactions between density-dependent competition and changing climate. *Can. J. Fish. Aquat. Sci.* **74**(7): 1077–1087. doi:10.1139/cjfas-2016-0265.
- Di Lorenzo, E., and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat. Clim. Change*, **6**(11): 1042–1047. doi:10.1038/nclimate3082.
- Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F., et al. 2015. Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science*, **349**(6243): aac4722. doi:10.1126/science.aac4722.
- Hoegh-Guldberg, O., and Bruno, J.F. 2010. The impact of climate change on the world's marine ecosystems. *Science*, **328**(5985): 1523–1528. doi:10.1126/science.1189930.
- Holt, C.A., Rutherford, M.B., and Peterman, R.M. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. *Mar. Pol.* **32**(4): 607–617. doi:10.1016/j.marpol.2007.11.001.
- Huang, B., Thorne, P.W., Banzon, V.F., Boyer, T., Chepurin, G., Lawrimore, J.H., et al. 2017. Extended reconstructed sea surface temperature, version 5 (ERSSTv5): upgrades, validations, and intercomparisons. *J. Clim.* **30**(20): 8179–8205. doi:10.1175/JCLI-D-16-0836.1.
- Johnson, S.P., and Schindler, D.E. 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecol. Res.* **24**(4): 855–863. doi:10.1007/s11284-008-0559-0.
- Kaeriyama, M., Nakamura, M., Yamaguchi, M., Ueda, H., Anma, G., Takagi, S., et al. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. *N. Pac. Anadr. Fish Comm. Bull.* **2**: 55–63.
- Litzow, M.A., Ciannelli, L., Cunningham, C.J., Johnson, B., and Puerta, P. 2019. Nonstationary effects of ocean temperature on Pacific salmon productivity. *Can. J. Fish. Aquat. Sci.* **76**(11): 1923–1928. doi:10.1139/cjfas-2019-0120.
- Liu, W., Huang, B., Thorne, P.W., Banzon, V.F., Zhang, H.-M., Freeman, E., et al. 2015. Extended reconstructed sea surface temperature version 4 (ERSST.v4): Part II. Parametric and structural uncertainty estimations. *J. Clim.* **28**(3): 931–951. doi:10.1175/JCLI-D-14-00007.1.
- Malick, M.J. 2020. Time varying relationships between ocean conditions and sockeye salmon productivity. *Fish. Oceanogr.* **29**(3): 265–275. doi:10.1111/fog.12469.
- Malick, M.J., Cox, S.P., Mueter, F.J., Dörner, B., and Peterman, R.M. 2017. Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fish. Oceanogr.* **26**(3): 268–281. doi:10.1111/fog.12190.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific Interdecadal Climate Oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**(6): 1069–1079. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.
- McKinnell, S., and Reichardt, M. 2012. Early marine growth of juvenile Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to juvenile pink (*Oncorhynchus gorbuscha*) and sockeye salmon abundance. *Can. J. Fish. Aquat. Sci.* **69**(9): 1499–1512. doi:10.1139/f2012-078.
- Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.* **83**(5): 1035–1046. doi:10.1111/1365-2656.12212. PMID:24673479.
- Mueter, F.J., Peterman, R.M., and Pyper, B.J. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* **59**(3): 456–463. doi:10.1139/f02-020.
- Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S., and Dahlberg, M.L. 1996. Known Ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. *N. Pac. Anadr. Fish Comm. Doc.* **192**(4).
- Peterman, R.M., and Dörner, B. 2012. A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. *Can. J. Fish. Aquat. Sci.* **69**(8): 1255–1260. doi:10.1139/f2012-063.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., and Levin, S.A. 2013. Marine taxa track local climate velocities. *Science*, **341**(6151): 1239–1242. doi:10.1126/science.1239352. PMID:24031017.
- Pörtner, H.O., Roberts, D., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., et al. (Editors) 2019. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. IPCC Intergovernmental Panel on Climate Change (IPCC).
- Quinn, T.P. 2018. The behavior and ecology of Pacific salmon and trout. University of Washington Press.
- Ruggerone, G.T., and Connors, B.M. 2015. 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.* **72**(6): 818–833. doi:10.1139/cjfas-2014-0134.
- Ruggerone, G.T., and Irvine, J.R. 2018. Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Mar. Coast. Fish.* **10**(2): 152–168. doi:10.1002/mcf2.10023.
- Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L., and Rogers, D.E. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish. Oceanogr.* **12**(3): 209–219. doi:10.1046/j.1365-2419.2003.00239.x.
- Ruggerone, G.T., Nielsen, J.L., and Bumgarner, J. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **54**(23–26): 2776–2793. doi:10.1016/j.dsr2.2007.08.016.
- Ruggerone, G.T., Springer, A.M., Shaul, L.D., and van Vliet, G.B. 2019. Unprecedented biennial pattern of birth and mortality in an endangered apex predator, the southern resident killer whale, in the eastern North Pacific Ocean. *Mar. Ecol. Prog. Ser.* **608**: 291–296. doi:10.3354/meps12835.
- Shuntov, V.P., Temnykh, O.S., and Ivanov, O.A. 2017. On the persistence of

- stereotypes concerning the marine ecology of Pacific salmon (*Oncorhynchus* spp.). *Russ. J. Mar. Biol.* **43**(7): 507–534. doi:[10.1134/S1063074017070045](https://doi.org/10.1134/S1063074017070045).
- South, A. 2017. *rnatuarearth*: World Map Data from Natural Earth. R package version 0.1.0 [online]. Available from <https://CRAN.R-project.org/package=rnatuarearth>.
- Springer, A.M., and van Vliet, G.B. 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proc. Natl. Acad. Sci.* **111**(18): E1880–E1888. doi:[10.1073/pnas.1319089111](https://doi.org/10.1073/pnas.1319089111). PMID:[24706809](https://pubmed.ncbi.nlm.nih.gov/24706809/).
- Su, Z., Peterman, R.M., and Haeseker, S.L. 2004. Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **61**(12): 2471–2486. doi:[10.1139/f04-168](https://doi.org/10.1139/f04-168).