ICES Journal of Marine Science, 2024, Vol. 82, Issue 1, fsae135
https://doi.org/10.1093/icesjms/fsae135
Received: 10 May 2024; **revised:** 2 September 2024; **accepted:** 3 September 2024
Advance access publication date: 10 October 2024
Food for Thought

Adapting management of Pacific salmon to a warming and more crowded ocean

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Abstract

The North Pacific Ocean is warming and overall Pacific salmon abundance is higher now than at any other time in the past century. This increase in abundance is in large part due to warming-related changes in marine ecosystems at northern latitudes that primarily benefit pink salmon, and industrial-scale hatchery production to support commercial fisheries. A large body of evidence indicates that increasing and more variable ocean temperatures, as well as competition among salmon at sea, are associated with shifts in salmon productivity, body size, and age at maturation. However, these relationships vary by species, location, and time, resulting in increased harvest opportunities in some regions and exacerbated conservation concerns in others. The weight-of-evidence suggests North Pacific salmon nations should, as a minimum, limit further increases in hatchery salmon production until there is a better scientific understanding of hatchery and wild salmon distribution at sea, how they interact, and how the consequences of these interactions are influenced by broader climate and ecosystem conditions. Coordinated research to overcome knowledge gaps and develop strategies to reduce unintended interactions between hatchery and wild salmon could be funded (in part) by a tax placed on industrial-scale hatchery salmon releases. A tax would formalize recognition that there are finite prey resources to support salmon in the ocean and that both prey and wild salmon represent a "common property" whose use should not be without cost to those that seek to benefit from them. We highlight additional approaches salmon nations can take to adapt to changing conditions and suggest that improved communication and collaboration among North Pacific salmon research and management agencies will be key to balancing the benefits and risks of a warming and more crowded ocean.

Keywords: competition at sea; climate change; hatcheries; international cooperation

A warming and more crowded North Pacific Ocean

The North Pacific is getting warmer and experiencing more frequent temperature extremes (Laufkötter et al. 2020), both on its surface (Fig. 1) and at depth (Reagan et al. 2024). Regionally, consistent with Arctic amplification of global warming, ocean warming is occurring faster at northern latitudes than equatorial ones, with the Arctic Ocean warming at four times the global average (Rantanen et al. 2022). Ocean warming can now be unequivocally linked to humans, as illustrated by climate attribution studies that indicate recent sea surface temperatures at the North Pacific scale have reached levels that would have been virtually impossible in the preindustrial (1800s) climate (Litzow et al. 2024).

Coincident with ocean warming, there are now, on average, more salmon in the North Pacific than at any time in the past century (Fig. 2), with 2018, 2019, 2021, and 2023 as four of the highest abundance years on record since 1925. In the North Pacific, abundances (i.e. number of salmon that survive to become adults) are dominated by three species: pink (*Oncorhynchus gorbuscha)*, chum (*O. keta*), and sockeye salmon (*O. nerka*). Other species [i.e. chinook (*O. tshawytscha*), coho (*O. kisutch*), and masu salmon (*O. masou*), and plus steelhead trout (*O. mykiss*)] constitute <5% of the total abundance (Ruggerone and Irvine 2018). While the majority of these salmon are of natural origin, ∼25% of recent numerical estimates of adult pink, chum, and sockeye abundance are of hatchery origin (Ruggerone and Irvine 2018). When converted to biomass and including immature fish, hatchery-produced fish (primarily chum salmon that are larger and rear for longer in marine waters than most other salmon) represent ∼40% of total salmon biomass in the North Pacific (Ruggerone and Irvine 2018).

Pacific salmon responses to warming and competition vary in space and over time

A large body of evidence indicates that salmon growth and survival are associated with ocean temperatures and oceanographic processes. For example, salmon survival has been repeatedly shown to correlate with (i) sea surface temperatures (SSTs) that can index the habitat conditions salmon experience during early marine life (Mueter et al. 2002, Malick et al. 2017, Malick 2020); (ii) broader scale indices of ocean temperature [e.g. Pacific Decadal Oscillation (PDO); Mantua et al. 1997]; and (iii) ocean currents and circulation patterns [North Pacific Gyre Oscillation (NPGO); Di Lorenzo et al. 2008]. These direct and indirect relationships with temperature are hypothesized to arise from changes in oceanographic conditions (as reflected indirectly by SST) and their

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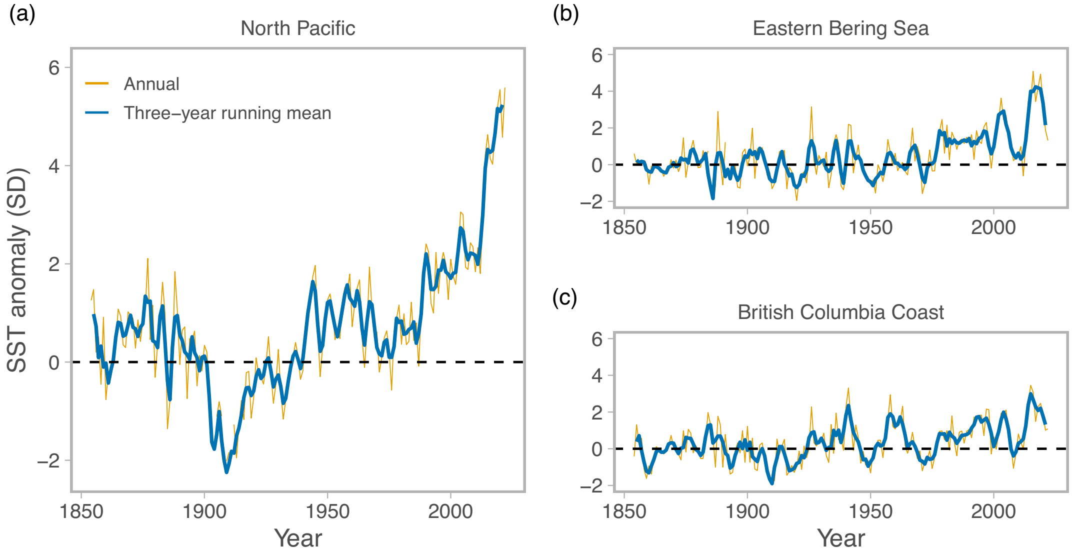

Figure 1. Sea surface temperature (SST in °C) anomalies for (a) North Pacific, (b) Eastern Bering Sea, and (c) British Columbia coastal waters through 2023 relative to 1854–1949 averages. Both annual and 3-year running average anomalies are shown. Data from data NOAA ERSSTv5 (Huang et al. 2017).

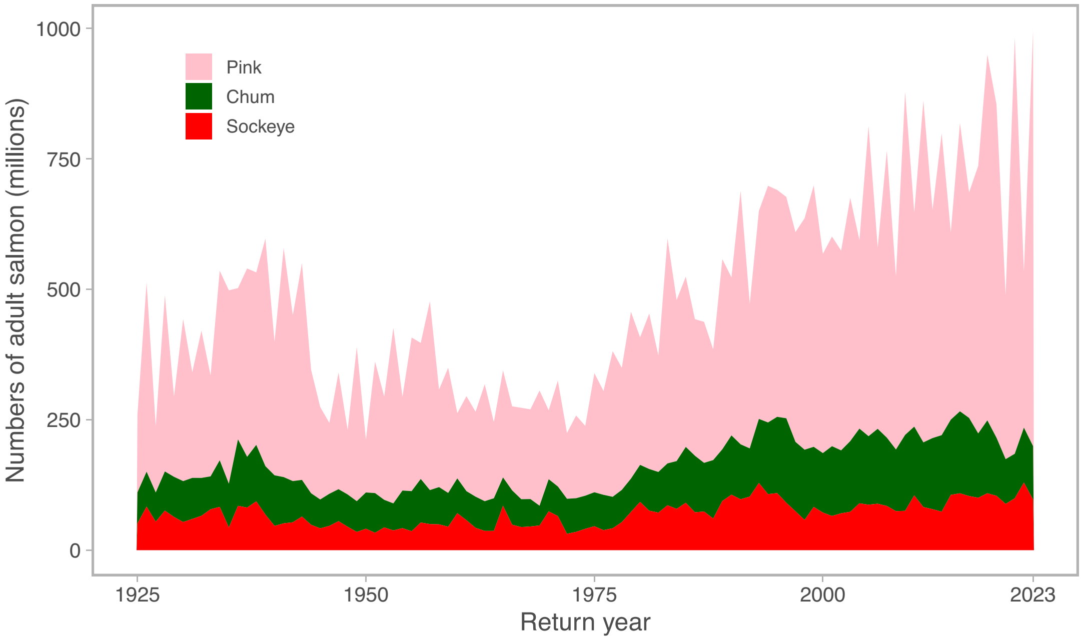

Figure 2. Annual abundances of pink, chum, and sockeye salmon (catch and spawners) returning to Asian and North American watersheds from 1925 to 2023. Time series through 2015 is from Ruggerone and Irvine (2018); estimates from 2016 to 2023 were derived using "approach 3" in Ruggerone and Irvine (2018), which uses the relationship between harvest rate and $\log_e$ total catch for a given species and region from 1996 to 2015 to estimate the harvest rate and total abundance based on catch alone from 2016 to 2023. Catch data from 2016 to 2023 taken from NPAFC (2024a).

influence on primary and secondary production and hence abundances of prey and predators. There is strong evidence for spatial variation in these responses, ranging from generally negative relationships at more southern latitudes (e.g. northern California Current north to southern British Columbia) to strongly positive ones further north (e.g. Bering Sea in Alaska) (Fig. 3; Mueter et al. 2002, Malick et al. 2017, Connors et al. 2020, Malick 2020). These differences in effects are hypothesized to arise from differences in oceanographic processes between regions with the generally beneficial effect of warming in the north (e.g. Gulf of Alaska and Bering Sea) arising from increased prey production, especially during early marine life (Brodeur et al. 1996, Moss et al. 2005, Ruggerone et al. 2005, 2007, Cross et al. 2009). At more southern latitudes (e.g. northern California Current), warming ocean temperatures are associated with reduced primary and secondary production. Warming temperatures are also associated with reduced prey availability and nutritional content (Mackas et al. 2007, Ashlock et al. 2021, Garzke et al. 2023), as well as increased metabolic requirements, especially for larger salmon

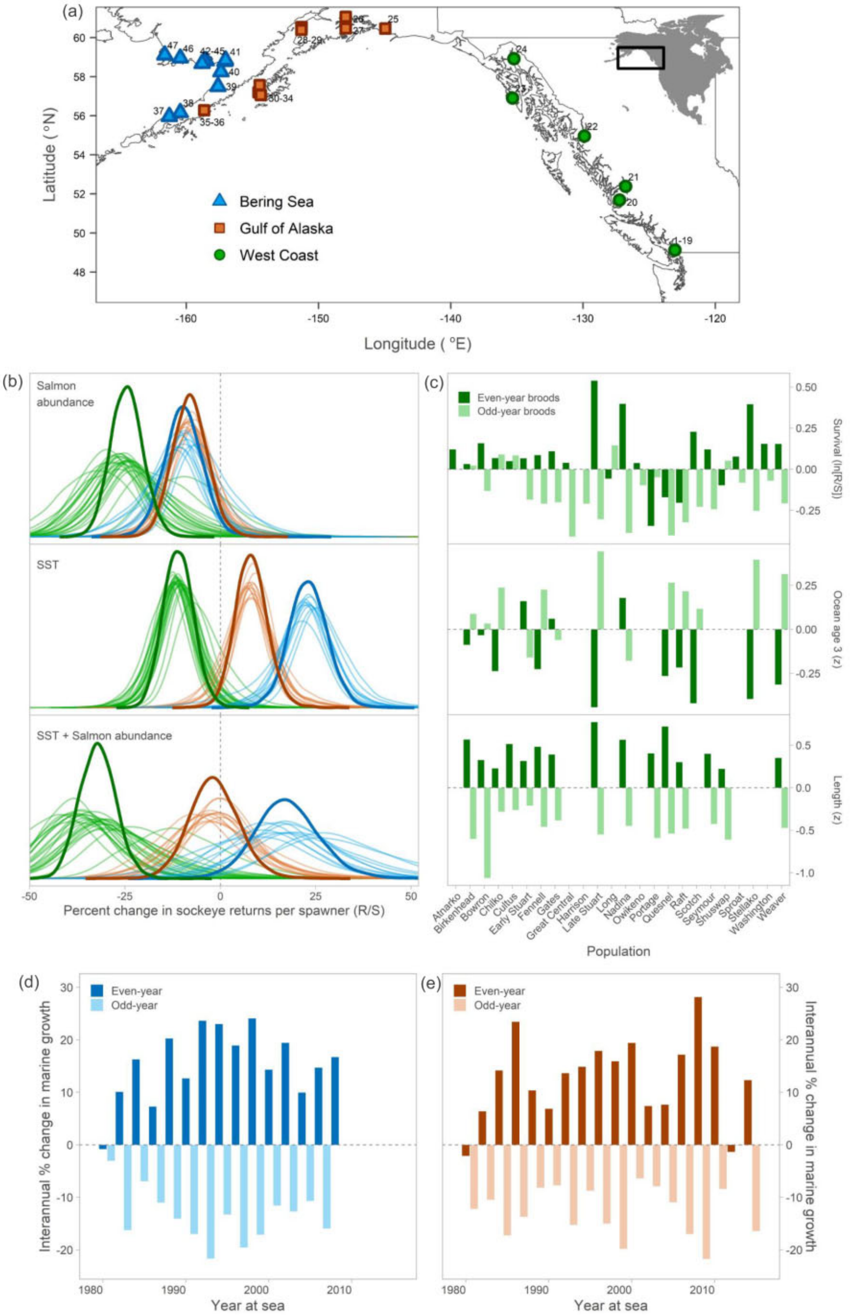

Figure 3. Influence of warming oceans and increasing salmon abundance on sockeye across the eastern North Pacific. (a) Ocean entry locations for sockeye populations in the West Coast (circles), Gulf of Alaska (squares), and Bering Sea (triangles) ecosystems. (b) Posterior probability distributions of the predicted effect of total pink, chum, and sockeye salmon competitors (top), sea surface temperature (SST; middle), and the combined effect from all covariate terms (bottom), on sockeye returns per spawner of 47 sockeye salmon populations originating from the Bering Sea, Gulf of Alaska, and west coast of North America (southeast Alaska and British Columbia). Posterior hyperdistributions of the covariate effects are in bold lines, with individual population-specific posterior distributions illustrated by the thin lines. Covariate effects are standardized (i.e. per standard deviation unit increase in each covariate), which equates to 1.5°C SST and 181 million salmon above the mean. Derived from Connors et al. (2020). (c) Mean survival (top), proportion of ocean age-3 sockeye salmon in the adult return (middle), and length-at-age of 24 sockeye salmon populations (1978—2005) from British Columbia to Washington state [bottom; West Coast region in panel (a)] during odd- versus even-numbered brood years, which interact with above and below average pink salmon abundance at sea. Values are normalized (z) relative to the entire data time series, except survival, which is the mean residual ($\log_e$ recruits per spawner) from the spawner recruitment relationship. Reproduced from Ruggerone and Connors (2015). (d) Mean interannual change (%) in scale growth [difference between a given year and adjacent years for five Bristol Bay (Bering Sea region in panel (a)] sockeye populations (Kvichak, Egegik, Naknek, Ugashik, and Wood River) during the third year at sea in odd versus even years, i.e. relatively high and low pink salmon abundance, respectively. Reproduced from Ruggerone et al. (2016). (e) Mean interannual change (%) in scale growth for seven Gulf of Alaska sockeye populations (Chignik, Black, Kenai, Coghill, Copper, Chilkat, and Hugh Smith) during the third year at sea in odd versus even years. Derived from Rand and Ruggerone (2024).

(Davis et al. 1998, Beauchamp 2009). Responses to warming vary within regions over time for several salmon species (Litzow et al. 2018), likely due to, at least in part, the emergence of climate conditions that have no analogue in the historical record. For example, climate conditions including sea-level pressure, regional temperature, wind mixing, and alongshore water transport during 2014–2019 appear to be unique in the historical record for the Gulf of Alaska, and these novel conditions are associated with a switch to unique, negative correlations between the PDO and salmon abundance in the Gulf of Alaska, contrasting with positive or neutral correlations during previous decades (Litzow et al. 2020).

There is also a large and growing decades-long body of evidence indicating that high abundances of salmon and density-dependent interactions among salmon at sea reduce salmon growth (Peterman 1984, Ruggerone et al. 2003, McKinnell and Reichardt 2012, Oke et al. 2020, Ohlberger et al. 2023, Rand and Ruggerone 2024), delay maturation (Ruggerone and Connors 2015, Cline et al. 2019), and reduce salmon survival (Cunningham et al. 2018, Kendall et al. 2020, Litz et al. 2021, Ohlberger et al. 2022, Ruggerone et al. 2023). Context matters, and for some populations, especially of sockeye salmon, these effects are in general more apparent for salmon that originate at southern latitudes than northern latitudes (Fig. 3). These effects have been hypothesized to be due to the negative effects of a warming ocean on primary and secondary productivity at more southern latitudes, at least partially compounding the negative effects of competition, while the opposite is hypothesized to occur at more northern latitudes (Connors et al. 2020). For Chinook, coho, and chum salmon, however, competition for prey in the north also appears to be affecting growth, survival, and abundance (Ruggerone et al. 2012, 2023, Shaul and Geiger 2016, Kaeriyama 2022). In addition, there is evidence that competitive interactions may be influenced by life history and associated ocean distributions; e.g. Chinook salmon migrating northward from the Pacific Northwest show stronger evidence of competition with pink salmon than do Chinook populations remaining further south, where pink salmon are less abundant (Buckner et al. 2023).

Changing thermal habitat and shifting salmon abundance

Ocean temperature influences the distribution of physiologically suitable habitat for Pacific salmon and, in turn, their distribution at sea. Distribution in relation to historical temperatures has been inferred from high seas salmon surveys (Welch et al. 1995, 1998, Lindley et al. 2021, Langan et al. 2024). As the ocean warms, there is an expectation that a redistribution of salmon northward will occur (Shelton et al. 2021). The absolute amount of suitable habitat in the North Pacific is expected to shrink; those species with the narrowest thermal tolerance (like Chinook and sockeye) are expected to experience the largest reductions in thermal habitat (e.g. 88% reduction in summer habitat for Chinook) under climate change (Abdul-Aziz et al. 2011). This reduction in thermal habitat due to warming may further exacerbate competition among salmon at sea by reducing the areas in which they forage for a limited prey base, as well as increasing the distance southern populations need to migrate to reach foraging areas in the north (Larson et al. 2013). While warming is expected to open up new marine habitats for salmon in the Arctic (e.g. Dunmall et al. 2018, 2024), it is likely of a much smaller magnitude than the projected reduction in habitat in the North Pacific and Bering Sea (Lindley et al. 2021). Warming ocean temperatures may also increase bioenergetic demands, particularly for larger-bodied species like Chinook and chum, which may further compound direct and indirect competition among salmon for prey (Beauchamp 2009), though these effects may be partially offset by shifts to cooler and less bioenergetically costly habitats.

As a result of changes in suitable thermal habitat and positive effects on early marine growth and survival for salmon at northern latitudes (particularly for some sockeye and pink populations), a warming ocean is expected to continue shifting abundance of salmon northwards, creating new/more opportunities for harvest in the north and fewer opportunities in the south. Evidence for these shifts is already clear in historical trends in commercial landings, where catch has steadily increased at northern latitudes since the mid-1970s and declined at southern ones (Fig. 4). Record returns (and harvests) of salmon such as sockeye in Bristol Bay, Alaska, have been hypothesized to be in response, at least in part, to temperature-driven changes in ocean productivity, plankton abundance, and growth during early marine life (Ruggerone et al. 2005, 2007). In contrast, recent warming in the eastern Bering Sea appears to have reduced the energy density of juvenile chum salmon due to abundance of relatively poor-quality prey, potentially leading to declining adult returns (Farley et al. 2024). Of course other factors not associated with temperature change influence broad patterns in harvest (including myriad other stressors, particularly at southern end of range), but this general pattern of increasing abundance for some species at northern latitudes likely reflects, at least partially, previously hypothesized climate-mediated shifts in abundance (Hare and Francis 1995, Mantua et al. 1997). We note, however, that these climate-mediated shifts in abundance may have reached their limits for some species and populations as the conditions they experience are pushed outside their envelopes of historical variation that salmon are adapted to. For example, at the northern extent of their range, Chinook salmon population productivity appears to have become limited by warming freshwater habitats that reduce adult migration success (Howard and von Biela 2023), chum salmon abundance in this region has declined, and warming in the Gulf of Alaska appears to have exceeded suitable levels for some sockeye, causing recent commercial fishery collapses (Litzow et al. 2024).

Recent decades have also seen increases in the incidental harvest of Pacific salmon in the Arctic, including the Mackenzie River; many are considered to be strays from outside the area (Dunmall et al. 2018, Northern Hemisphere Pink Salmon Expert Group 2023). This expansion is likely to be due, at least in part, to a climate change-induced range-expansion corridor emerging in recent years (Dunmall et al. 2024). In other parts of the far north, like the Barents Sea in northern Scandinavia, which is warming at seven times the rate of the rest of the world's oceans (Rantanen et al. 2022), there has been a recent "explosion" of non-native pink salmon (Diaz Pauli et al. 2023), including vagrants captured as far west as the North American Arctic, all from what are now self-sustaining populations that resulted from introductions in north-western Russia (Northern Hemisphere Pink Salmon Expert Group 2023).

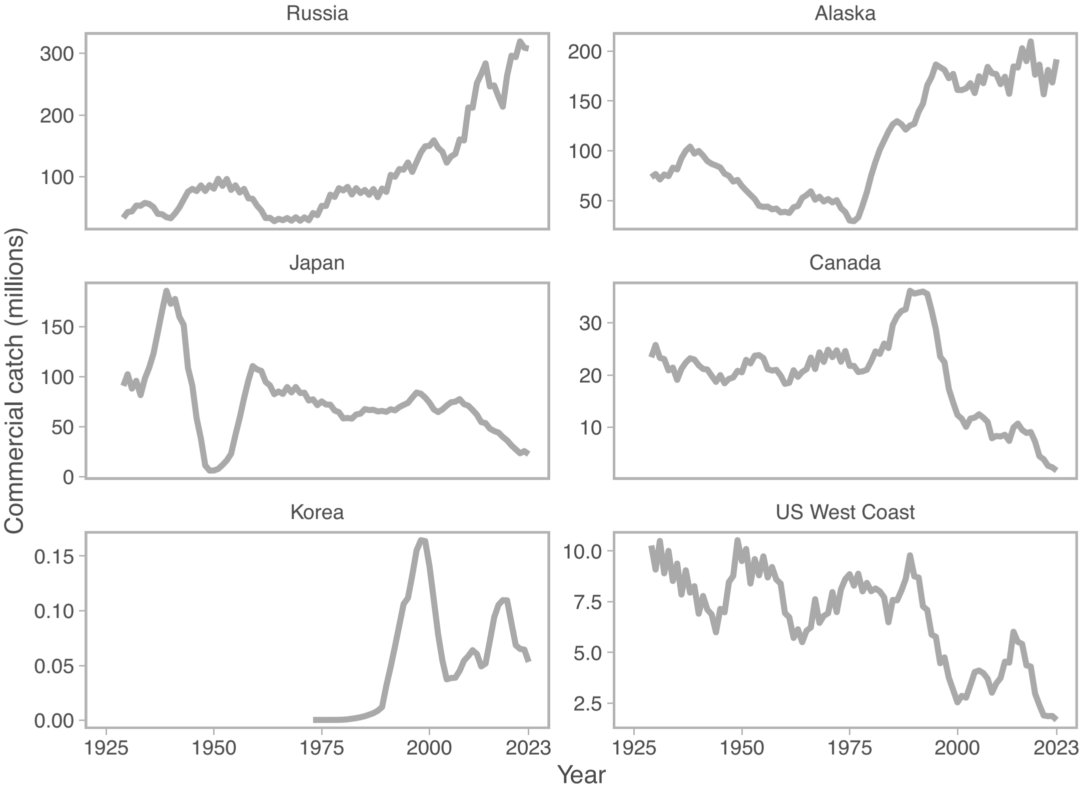

Figure 4. Commercial harvest of all five Pacific salmon species by country from 1925 to 2023. Values are 5-year running averages in millions of fish. Countries are approximately ordered north to south (top to bottom) and west to east (left to right). US West Coast includes salmon originating from Washington State, Oregon, Idaho, and California. Note variable *y*-axis ranges. Data from NPAFC (2024a).

Should salmon nations cooperatively manage, and consider limiting, hatchery production as ocean warms?

Industrial-scale artificial propagation of salmon to support commercial fisheries throughout Asia and North America has been undertaken for almost half a century. Artificial propagation also occurs at a much smaller scale to support recovery of at-risk populations. Total releases of hatchery fish, especially chum and pink salmon, have increased over time and in recent decades have been greater at more northern than southern latitudes, particularly in Alaska and Russia (Fig. 5). While these hatchery salmon benefited from relatively favorable northern ocean conditions during early marine life, unintended consequences may include exacerbated conservation risks for southern populations that often experience relatively poor early marine conditions and then to migrate north and have to compete with abundant salmon later in their marine lives (e.g. Larson et al. 2013, Connors et al. 2020, Buckner et al. 2022). Large-scale hatchery releases may also further intensify direct and indirect competition among salmon for prey as thermally suitable habitat shrinks with ocean warming. Thus, abundant hatchery salmon may inhibit the natural density-dependent compensatory response that provides resilience to wild salmon at low population abundances (Ricker 1954).

Questions about the extent to which ocean habitat can be limiting for salmon have been raised for decades (Peterman 1978, 1984, Kaeriyama et al. 2012, Kaeriyama 2022). This has led some to ask: *Should salmon nations cooperatively manage, and consider limiting, hatchery production as the ocean warms* (Heard 1998, Holt et al. 2008, Peterman et al. 2012)? This question has been raised in light of broad-scale evidence of declining size of salmon across the North Pacific (Bigler et al. 1996, Cooney and Brodeur 1998, Pyper and Peterman 1999, Oke et al. 2020) coincident with increasing hatchery production. Although the evidence for density-dependent interactions among salmon at sea has only grown, it largely comes from research involving the central and eastern North Pacific and Bering Sea. Some scientists have argued, based primarily on research in the western North Pacific, that salmon are not abundant enough to significantly alter prey availability for other salmon and cause reduced growth and survival (Shuntov and Temnykh 2005, Shuntov et al. 2017, Radchenko et al. 2018, Naydenko and Somov 2019, Somov et al. 2024). This alternative view may stem from differences between western and eastern North Pacific ecosystems in primary and secondary production and overall prey availability, and deserves further discussion to identify if there are areas within the North Pacific where density-dependent competition is not significant. We note, however, that most salmon populations migrate long distances at sea, and scientists have identified effects of high salmon density on salmon returning to most regions of North America and Asia.

A lack of broad recognition by hatchery managers and management agencies for the weight of evidence for the consequences of inter- and intraspecific competition among many salmon populations across the North Pacific has made cooperative management of hatchery production at the North Pacific scale difficult. This has been compounded by asymmetry in the incentives and disincentives to cooperation among the salmon-producing regions and nations (see Holt et al.

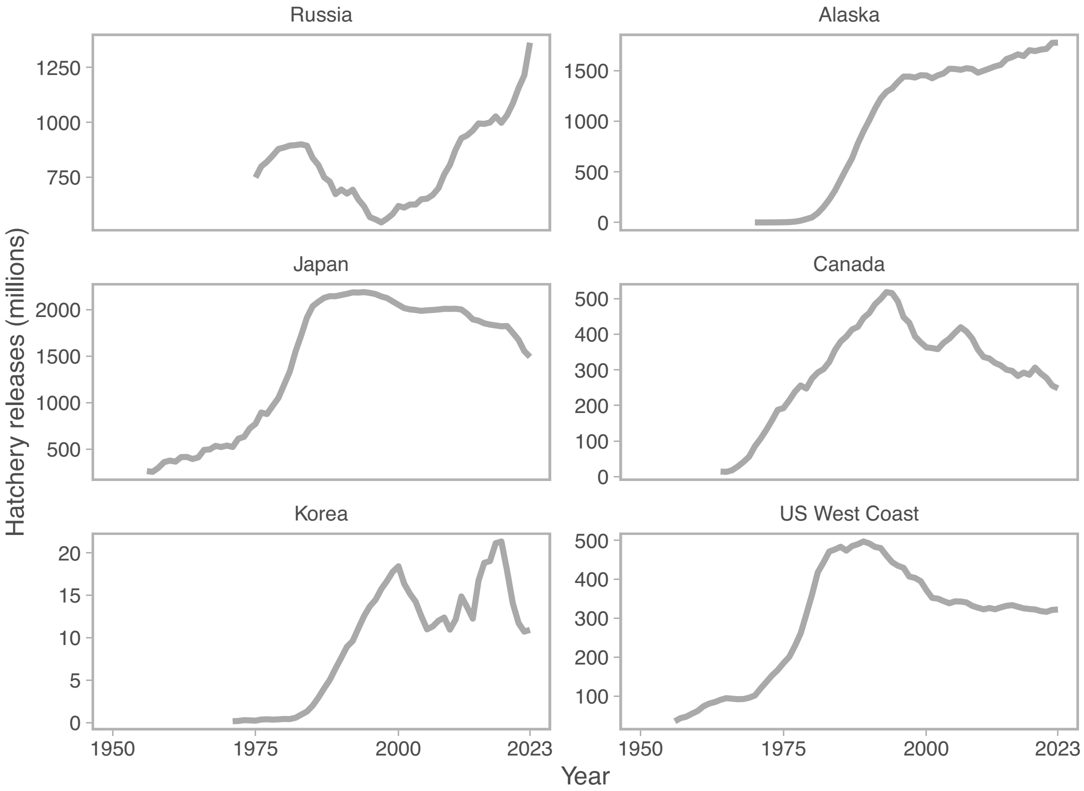

Figure 5. Hatchery releases of all Pacific salmon species by country from 1952 to 2023. Values are 5-year running averages. Countries are approximately ordered north to south (top to bottom) and west to east (left to right). US West Coast includes salmon originating from Washington State, Oregon, Idaho, and California. Note variable *y*-axis ranges. Data from NPAFC (2024b).

2008 for an excellent examination of this). For example, while large-scale hatchery production may have unintended effects on both local and distant wild salmon populations, hatchery production underpins harvests in the local fishery and provides socioeconomic benefits to it (Amoroso et al. 2017, Harrison and Gould 2022, Ohlberger et al. 2022).

Correlations underpin our understanding of salmon responses to ocean conditions and density-dependent interactions. While these correlations are usually assumed to be causative (e.g. based on consistent relationships relating salmon density to diet, growth, survival, and abundance), we are often reminded of the adage “correlation does not equal causation.” Manipulative experiments, which are the gold standard approach to establishing causation (Hilborn 2016), are logistically, socially, and economically impossible at the scale of the North Pacific. However, the natural experiment resulting from the strongly biennial patterns of pink salmon abundance (∼25 fold difference in abundance between odd and even years in some major North Pacific ecosystems) provides strong and consistent evidence in support of the hypothesis that pink salmon can directly and indirectly influence marine ecosystems. For example, 90 publications provide quantitative evidence in support of hypothesis that pink salmon can influence all five species of Pacific salmon, steelhead trout, four forage fish species, squid, 11 species of seabirds, and two cetaceans (Fig. 3; Table 1 and Supplement 2 in Ruggerone et al. 2023).

Adapting salmon management to a warming and more crowded ocean

There are, of course, inherent challenges to understanding the drivers of population dynamics for highly migratory and broadly distributed species like salmon that spend much of their lives at sea. Opportunities to fill key gaps in knowledge are identified in the North Pacific Anadromous Fish Commission 2023–2027 science plan (SSC 2023), and associated working group recommendations (NPAFC 2023). These planning documents were produced by a collaboration of the major salmon-producing nations, indicating broad support for additional science in these areas. Recommendations include coordinated research on the distribution and ecology of salmon at sea, including, e.g. increased investment in coordinated and cooperative ocean basin scale surveys (e.g. Beamish et al. 2023) and use of new technologies [genetics, eDNA (Deeg et al. 2023), autonomous sampling, next generation tagging and tracking, and otolith microchemistry]. They also include a need for more studies that compare populations, regions, and species to help statistically tease apart population (e.g. life history) and ecosystem factors (currents, food web, etc.) that influence (are associated with) responses to warming and competition (Malick et al. 2017, Connors et al. 2020, Buckner et al. 2022). Process-based studies could identify and inform proximate mechanisms for apparent ocean warming and competition effects, trophic dynamics (Graham et al. 2021), and seasonal and geographic patterns of prey abundance. They could also help better understand when, where, and why trophic cascades might occur (e.g. Batten et al. 2018, Naydenko and Somov 2019), tradeoffs between predation risk, prey patch density, and competition for prey while foraging in aggregations (Polyakov et al. 2022), and implications of increasing bioenergetic foraging requirements of salmon in a warming ocean on competition among salmon. Lastly, there is a well-recognized need for more comprehensive assessment and reporting of hatchery and wild contributions to spawning abundance and harvests across management jurisdictions, including mass marking 100% of hatchery fish so that hatchery salmon can be reliably identified and wild salmon status can be accurately evaluated.

There is now compelling weight-of-evidence across species, life stages, regions, and time that competition among salmon at sea is often substantial and can have population-level impacts (e.g. Fig. 3). While there are, and likely always will be, outstanding knowledge gaps, we argue that adapting salmon management to a warming and more crowded ocean requires actions that explicitly take this weight of evidence into account. These actions include limiting further increases in hatchery production at the North Pacific scale, and comprehensively evaluating the benefits and costs (ecological, social, and economic) of reducing the large numbers of hatchery salmon (primarily pink and chum salmon) released. Scientists and salmon managers need a better understanding of hatchery salmon effects on wild salmon, including their marine distributions, how they interact, and how this is influenced by the broader climate and ecosystem conditions in which these interactions occur. Other strategies to minimize adverse interactions between hatchery and wild salmon in the changing ocean environment should be identified.

Developing strategies and sharing scientific understanding will of course take greater coordination and collaboration among salmon nations, as well as financial resources to support it. We suggest that, at least in theory, such coordinated effort could be funded (in part) by a tax placed on hatchery releases. For example, a tax of one cent ($0.01) per fish released would generate ∼$50 million a year (assuming current magnitude of total hatchery releases). The funds raised by this tax could support monitoring and research efforts required to improve the knowledge about the role hatchery production plays in exacerbating competition among salmon at sea, and to develop management strategies to minimize those effects. The specifics of the tax would need to be negotiated among salmon nations, but this improved understanding should incentivize hatchery-producing regions and nations to support such a tax because our current understanding of interactions at sea is often inferred from survivors returning from the at-sea feeding grounds (as opposed to manipulative experiments), and essentially assumes that hatchery and wild fish are sympatric. A more nuanced understanding will likely identify where and when hatchery production is and is not likely to exacerbate conservation concerns and undermine recovery and which species and populations are most and least vulnerable to it. Importantly, the imposition of such a tax would formalize recognition among salmon nations that there are finite resources to support salmon in the ocean and that salmon represent a “common property” whose exploitation should not be without cost. Hatchery releases that are designed to support conservation and mitigation (largely Chinook, coho, and steelhead at more southern latitudes, which make up a small amount of total hatchery releases) could be exempt from the tax. Taxes or fees are often imposed on those that benefit from the use of common natural resource property; e.g. cattle grazing on public lands in the United States is permitted for those that pay a fee per head of cattle.

Adapting management, however, will require more than just reducing uncertainty in the role of hatchery production in exacerbating competition among salmon at sea and incentivizing coordination and collaboration. It will also likely require fundamental shifts in how fisheries are managed. For example, there will be an increasing need for a shift away from large mixed-stock (hatchery-wild) marine fisheries, which can intercept salmon originating from distant areas. Management of such fisheries is complex because at-risk populations often migrate through fishing areas along with more abundant and productive populations, including hatchery salmon. In such cases, a change in management regulations to use more terminal and selective fisheries (e.g. fishwheels and traps) can help to sustainably harvest abundant stocks while minimizing risk to weak ones (Gayeski et al. 2018, Atlas et al. 2021, Fairbanks Fishery Advisory Committee 2023). In addition, management may need to shift from a historical focus on maximizing harvests while avoiding overfishing, to increasing resilience to climate-induced shocks to fisheries and broader North Pacific ecosystems change (Litzow et al. 2024) by explicitly managing for a diverse portfolio of wild salmon populations that can help on aggregate to buffer against adverse responses to climate and ecosystem change (Schindler et al. 2010).

Acknowledgments

This manuscript is based on a presentation given at the International Year of the Salmon/North Pacific Anadromous Fisheries Commission synthesis symposium in the fall of 2022 in Vancouver, B.C. Randall Peterman, Nate Mantua, Dylan Glaser, Hannah Hunter, Dan Greenberg, and an anonymous reviewer provided helpful feedback on a previous version of this manuscript.

Author contributions

B.C., G.T.R., and J.R.I conceived of the manuscript; B.C. wrote the first draft; B.C., G.T.R., and J.R.I. edited, revised, and refined it.

Conflict of interest: None declared.

Funding

Partial financial support was provided by Fisheries and Oceans Canada.

Data availability

There are no new data associated with this article.

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Handling Editor: Howard Browman