

Density-dependent marine survival of hatchery-origin Chinook salmon may be associated with pink salmon

NEALA W. KENDALL,^{1,†} BENJAMIN W. NELSON ,² AND JAMES P. LOSEE¹

¹Washington Department of Fish and Wildlife, 1111 Washington St. SE, Olympia, Washington 98501 USA

²Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada

Citation: Kendall, N. W., B. W. Nelson, and J. P. Losee. 2020. Density-dependent marine survival of hatchery-origin Chinook salmon may be associated with pink salmon. *Ecosphere* 11(4):e03061. 10.1002/ecs2.3061

Abstract. Understanding how protected species influence the population dynamics of each other is an essential part of ecosystem-based management. Chinook salmon (*Oncorhynchus tshawytscha*) are critical prey for endangered southern resident killer whales (SRKWs; *Orcinus orca*), and increasing releases of hatchery Chinook salmon has been proposed to aid SRKW recovery. We analyzed 30 yr of data and found that density-dependent survival of hatchery Chinook salmon released into the central and southern parts of the Salish Sea (Washington, USA; and British Columbia, Canada) may be associated with the presence of naturally produced pink salmon (*O. gorbuscha*), which are highly abundant as juveniles only in even-numbered years. We first modeled hatchery Chinook salmon marine survival as a function of the numbers of juvenile Chinook released and the presence of emigrating juvenile pink salmon between 1983 and 2012. Then, we related reconstructed numbers of hatchery Chinook salmon returning to Puget Sound to the abundance of juvenile Chinook released in even (pink emigration) and odd (non-pink emigration) years from 1980 to 2010. We found that in some regions of the Salish Sea, both hatchery Chinook salmon marine survival and adult Chinook returns varied depending on the number of hatchery Chinook released and the presence of juvenile pink salmon. Specifically, in some regions survival of hatchery Chinook salmon decreased when greater numbers of juveniles were released into the Salish Sea in even years, when large numbers of pink salmon were present, but increased or remained stable when pink salmon were not present in large numbers (in odd years). This suggests lower, density-dependent survival of juvenile Salish Sea Chinook salmon during even outmigration years. Our analyses suggest that scientists and managers should further investigate potential mechanisms for density-dependent survival of hatchery Chinook salmon from Salish Sea hatcheries when designing strategies to maximize adult returns.

Key words: aquaculture; Chinook salmon; density dependence; hatcheries; marine survival; *Oncorhynchus*; pink salmon.

Received 4 September 2019; revised 31 December 2019; accepted 7 January 2020. Corresponding Editor: Hunter S. Lenihan.

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† E-mail: Neala.Kendall@dfw.wa.gov

INTRODUCTION

Ecosystem-based management has shown promise in improving the management of protected marine species affected by anthropogenic influences and natural factors (Levin et al. 2009, Tallis et al. 2010). At the same time, it is important to understand the population dynamics of individual components of an ecosystem. Management

actions related to multiple species can be difficult to implement when they affect individual species in different ways, there are demands on resources from multiple entities, and/or environmental conditions are compromised by decades of impacts (Leslie and McLoed 2007, Casazza et al. 2016, Marshall et al. 2016, Samhoury et al. 2017, Springer et al. 2018). Species recovery can be informed by understanding the linkages

between the components in an ecosystem (Samhoury et al. 2017), such as density-dependent interactions (Deriso et al. 2008), apparent competition (Holt and Bonsall 2017), and evaluating the success of previously implemented restoration and recovery actions (Jones et al. 2018).

Despite challenges, conservation and management of Pacific salmon (*Oncorhynchus* sp.) has increasingly sought to include ecosystem considerations (Malick et al. 2017) given that salmon are influenced by climate change (Crozier et al. 2008), the abundance of other (non-salmonid) species in the system (Wells et al. 2017), and the abundance of other salmonids (Ruggerone and Connors 2015). Of particular recent interest have been pink salmon (*O. gorbuscha*), the dominant adult salmonid species in the North Pacific Ocean (48% of total biomass since 1990; Ruggerone and Irvine 2018).

Density-dependent effects between pink salmon and other species, including salmon, have been documented by a number of studies. Density dependence can affect survival when resources are limited or predators are responsive to increased prey (Wells et al. 2017), and it can be associated with reduced growth and increased age at maturation (Ruggerone and Nielsen 2004, Cline et al. 2019, Grossman and Simon 2019). In the North Pacific Ocean, high pink salmon abundance has been thought to decrease zooplankton biomass, inducing trophic cascades down to the phytoplankton level (Shiomoto et al. 1997, Batten et al. 2018) that can depress the availability of prey resources for numerous species including salmon (Ruggerone et al. 2003, Ruggerone and Nielsen 2004, Kaga et al. 2013) and seabirds (Toge et al. 2011, Springer et al. 2018). High pink salmon abundance can also depress Pacific herring (*Clupea pallasii*) stocks through competition or predation (Deriso et al. 2008, Pearson et al. 2012), though this is not always the case (Boldt et al. 2019). Density-dependent interactions between pink and Chinook salmon (*O. tshawytscha*) have also been previously hypothesized to occur during the first ocean year of the salmon in the Salish Sea (Ruggerone and Goetz 2004, Ruggerone et al. 2019; Claiborne et al., *in press*), a rich and diverse but highly impacted inland sea in Washington State and British Columbia.

In the central and southern parts of the Salish Sea, almost all pink salmon (>99% of all recorded abundance data; Washington Department of Fish and Wildlife's [WDFW] Salmon Conservation Reporting Engine [SCoRE] database; <https://fortress.wa.gov/dfw/score/score/species/pink.jsp?species=Pink>) spawn in odd-numbered years and juveniles emigrate in even-numbered years. Juvenile Chinook and pink salmon are both found there between April through July of even years (Duffy et al. 2005; B. Berejikian, NOAA Fisheries, *unpublished data*). During this time, both species are opportunistic and generalized consumers but feed on different prey (Kaczynski et al. 1973, Bollens et al. 2010, Duffy et al. 2010, Osgood et al. 2016). Because pink salmon arrive to marine waters first, often in very large numbers in even-numbered years, they may indirectly alter the prey composition that is later available to Chinook salmon. A positive relationship between growth during the first summer at sea and subsequent adult survival has been observed for Puget Sound Chinook salmon (Duffy and Beauchamp 2011), suggesting the importance of local, bottom-up factors in the Sound (Claiborne et al., *in press*). Additionally, predators of juvenile fishes in the Salish Sea, including other fishes, birds, and mammals, may cue more on Chinook salmon when greater numbers of pink salmon are in the system (*sensu* Wells et al. 2017), an example of an indirect interaction known as apparent competition (Holt and Bonsall 2017).

Chinook salmon are a vital part of the Salish Sea ecosystem, of great cultural importance, and an important component of fisheries (TCW Economics 2008). At present, Salish Sea Chinook salmon are at low abundance (WDFW's SCoRE database; <https://fortress.wa.gov/dfw/score/score/>), return at smaller sizes, and exhibit reduced diversity in life history and return timing compared to historical levels (Ohlberger et al. 2018, Losee et al. 2019, Nelson et al. 2019). In Puget Sound (USA), Chinook salmon are listed under the U.S. Endangered Species Act and multiple stocks in the Strait of Georgia (Canada) receive protection under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Additionally, previous work has identified Salish Sea Chinook salmon as the primary summer prey of endangered southern resident killer

whales (SRKWs; *Orcinus orca*; Hanson et al. 2010, Ford et al. 2016).

Increasing the abundance of adult Chinook salmon in the Salish Sea is currently an ecosystem management priority, and hatchery supplementation is a predominant management strategy (Riddell et al. 2013, Southern Resident Orca Task Force 2018). Chinook salmon have been produced by hatcheries for over 100 yr (Beamish et al. 1997), and increased production has been proposed under the premise that this will result in more adult fish for SRKWs to consume (Southern Resident Orca Task Force 2018, WDFW 2019). While numerous studies have examined factors related to marine survival for Salish Sea Chinook salmon (including Coronado and Hilborn 1998, Sharma et al. 2013), the relationship between the number of hatchery Chinook salmon released into the natural environment and their subsequent marine survival has not been quantitatively evaluated and published in the peer-reviewed literature. Given the potential for density-dependent interactions with conspecifics (Greene and Beechie 2004) and pink salmon (Ruggerone and Goetz 2004) and a less-productive North Pacific Ocean marine environment since the mid- to late 1980s (Wolter and Timlin 1998, Kaeriyama et al. 2009), an understanding of this relationship is needed to inform hatchery management and ecosystem processes (Beamish et al. 1997).

Here, we first present data on juvenile Chinook salmon releases and associated marine recovery rates (a proxy for marine survival rates to that point) of immature, coded-wire-tagged (CWT) Chinook salmon from 33 hatchery stocks in Puget Sound, Strait of Georgia, and Strait of Juan de Fuca between 1983 and 2012. We used Bayesian hierarchical regression to relate hatchery Chinook salmon marine survival rates to juvenile Chinook release numbers along with the presence of juvenile pink salmon in the Salish Sea when the Chinook juveniles were emigrating. Second, we examined relationships between the numbers of hatchery Chinook salmon returning to Puget Sound as mature adults from 25 stocks and the corresponding number of hatchery releases in pink vs. non-pink salmon emigration years between 1980 and 2010. We seek to answer the question: In the past, when more hatchery Chinook salmon have

been released into the central and southern Salish Sea in years when juvenile pink salmon are and are not also emigrating, has there been an associated increase in the number of hatchery Chinook salmon that have survived during their migration in the ocean and returned as adults? We also identify the need for future work examining the mechanisms behind our observations.

METHODS

Study species

Sub-yearling hatchery Chinook salmon are released into Salish Sea marine waters starting in April and peaking in late May to early June at lengths of ~80–100 mm (WDFW 2018a, b; B. Berejikian, NOAA Fisheries, *unpublished data*). Yearling hatchery Chinook also enter marine waters starting in April at larger sizes (~165–185 mm). Chinook salmon that leave the Salish Sea for the Pacific Ocean tend to do so the following spring (i.e., after approximately one year in the Salish Sea; Trudel et al. 2009).

Pink salmon, almost all of which are of wild origin, spawn in the central and southern Salish Sea in odd-numbered years; very few (<1%) spawn there in even years as is evident in commercially landed catch (Losee et al. 2019) and spawning ground surveys (WDFW's SCoRE database). The following spring (starting in February), juvenile pink salmon emigrate from freshwater to marine waters at a length of ~28–35 mm and rear in the Salish Sea until leaving for the Pacific Ocean in July of the same year at a length of ~100 mm (Phillips and Barraclough 1978, Healey 1980, Heard 1991, Romanuk and Levings 2005).

Data

Coded-wire-tagged (CWT) hatchery Chinook salmon juvenile release numbers and marine recovery (survival) rates to age 2 or 3.—We used data from the Pacific Salmon Commission's Chinook Technical Committee's monitored CWT stocks (Table 1), many of which were used in Ruff et al. (2017). These data include estimated survival of Chinook salmon juveniles released from a given hatchery during their first year in the ocean—to age 2 yr for those released as sub-yearlings (at 2–

Table 1. List of Salish Sea Chinook salmon coded-wire-tagged hatchery stocks included in this study and their associated region, their release strategy (sub-yearling, SY; yearling, Y), the range of juvenile release years, and the total number of years in which juveniles were released (*n*) during that time period.

Region	Stock	Release strategy	Release year range	Release years (<i>n</i>)
Strait of Juan de Fuca (JUAN)	Dungeness (DUN)	SY	1997–2003	7
	Elwha (ELW)	SY	1986–1995	9
	Hoko (HOK)	SY	1986–2012	26
Hood Canal (HOOD)	George Adams (GAD)	SY	1986–2012	27
	Nooksack (NSF)	SY	1987–1997	10
Northern Washington (NOWA)	Nooksack Spring (NKS)	Y	1990–2012	21
	Samish (SAM)	SY	1986–2012	27
Northern Puget Sounds (NPS)	Skykomish (SKY)	SY	2001–2012	12
	Stillaguamish (STL)	SY	1987–2012	23
	Snohomish Yearling (SNY)	Y	1989–2012	11
	Skagit Spring (SKS)	Y	1986–2012	23
	Skagit Fall (SKF)	SY	2000–2009	10
	Skagit Spring Fingerling (SSF)	SY	1986–2012	20
	Skagit Summ (SFF)	SY	1995–2012	18
	Tulalip Summer (TUL)	SY	1986–2012	11
	Middle Puget Sound (MPS)	Green (GRN)	SY	1986–2012
Grovers Creek (GRO)		SY	1986–2012	27
Issaquah Creek (ISS)		SY	1986–1988	3
Puyallup (PUY)		SY	1998–2012	9
White River Yearling (WRY)		Y	2004–2012	9
South Puget Sound (SPS)	Garrison (GAR)	SY	1988–2012	13
	Nisqually (NIS)	SY	1986–2012	27
	South Puget Sound (SPS)	SY	1986–2012	27
Fraser River (FRA)	South Puget Sound Yearling (SPY)	Y	1988–2012	21
	Harrison (HAR)	SY	1983–2012	28
	Nicola (NIC)	Y	1987–2012	26
	Shuswap (SHU)	SY	1985–2012	28
	Chilliwack (CHI)	SY	1983–2012	30
	East Vancouver Island (VAN)	Quinsam (QUI)	SY	1983–2012
Puntledge (PPS)		SY	1983–2012	29
Big Qualicum (BQR)		SY	1983–2012	30
Cowichan (COW)		SY	1986–2012	25
Nanaimo (NAN)		SY	1983–2005	17

3 months) or age 3 yr for those released as yearlings (at 13–14 months). Much of the natural, density-dependent mortality of salmon in marine waters occurs early in their marine residence (before age 2 or 3; Parker 1962, 1968, Furnell and Brett 1986, Beamish and Mahnken 2001, Lorenzen and Camp 2019). Survival rates were estimated using a backward cohort reconstruction (Ruff et al. 2017; Eq. 1). Survival to (an immature state at) age 2 or 3 in the ocean does not include fishing mortality, which makes it difficult to estimate total mature adult return abundance to the Salish Sea with these data. However, we utilized these data because Chinook salmon must survive

in the ocean to at least age 2 or 3 to return as adults.

For the Ruff et al. (2017) analysis, stocks were selected for inclusion based on the accuracy of their survival data (as noted by regional experts) and the length of their time series (minimum 20 yr). In our analysis, we used only data from fish released into Puget Sound, Strait of Georgia, or Strait of Juan de Fuca. We included additional stocks with shorter time series than were included in the Ruff et al. (2017) analysis due to our use of a random-effects model. This resulted in a list of 33 stocks with release numbers and marine survival rates to age 2 or 3 over ocean

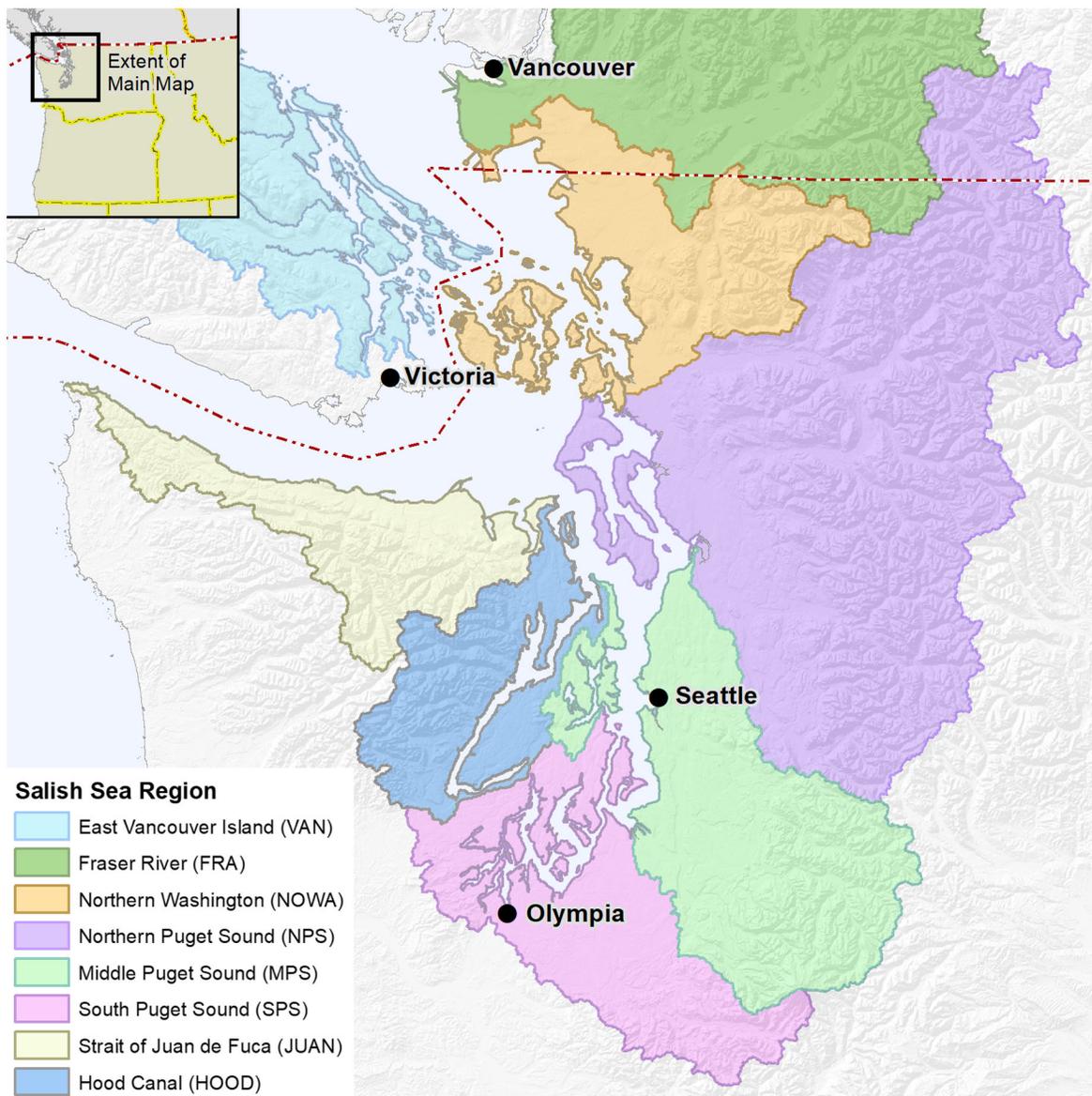


Fig. 1. Map of the eight central and southern Salish Sea regions from which hatchery Chinook salmon were assessed. The red dashed line indicates the border between the United States and Canada.

entry years (OEY) 1983–2012 (Table 1, Fig. 1). This starting point follows the large 1982–1983 El Niño event (Wolter and Timlin 1998), and Strait of Georgia hatchery Chinook salmon marine survival rates in particular appear to have stabilized to some degree in the mid-1980s (Ruff et al. 2017).

The stocks we utilized include both sub-yearling and yearling juvenile release strategies, the

two juvenile life-history types observed in the Salish Sea. Sub-yearling release groups greatly outnumber yearling release groups; typically <10% of juvenile Chinook released into the Salish Sea are yearlings (Nelson et al. 2019).

Stocks were grouped into eight regions, based on the locations from which they were released, in order to account for environmental differences among geographically distinct areas

(Ebbesmeyer et al. 1988, Moore et al. 2008) and be consistent with other studies that used similar groupings (Ruff et al. 2017). Regions included Hood Canal (HOOD), Strait of Juan de Fuca (JUAN), northern Washington (NOWA), northern Puget Sound (NPS; also known as Whidbey Basin), middle Puget Sound (MPS), southern Puget Sound (SPS), east Vancouver Island (VAN), and Fraser River (FRA; Fig. 1).

Hatchery Chinook salmon release numbers and run reconstruction of adults returning to Puget Sound.—The number and mark status of juvenile hatchery salmonids released on the west coast of North America have been aggregated online by species and hatchery in the Regional Mark Information System (RMIS) database (<https://www.rmipc.org/>). All sub-yearling Chinook salmon released into the central and southern parts of the Salish Sea between 1980 and 2010 were queried in the RMIS database. We organized them into regions based on their release location (Fig. 1). The resulting dataset included >1.5 billion Chinook salmon released from >150 hatcheries at >1200 locations.

We also used, as an index of abundance, estimates of the numbers of adult hatchery Chinook salmon returning to the entrance of the Strait of Juan de Fuca (i.e., total run size; before any fish were caught in the Salish Sea) that were compiled from WDFW Run Reconstruction Reports (J. Haymes, WDFW, *unpublished data*) and WDFW databases (SCoRE) from brood years 1980 to 2010. These adult run reconstruction index estimates are comprised of two parts—escapement to Puget Sound hatcheries or spawning grounds (fish not harvested) and stock-specific estimates of harvest by commercial, freshwater sport, and tribal ceremonial and subsistence fisheries in American, but not Canadian, waters of the Salish Sea.

Chinook salmon escapement numbers to hatcheries and spawning grounds in Puget Sound were calculated using a variety of methods depending on the fishes' river of origin. The numbers of hatchery-origin adults returning to hatcheries are available in post-season hatchery escapement reports (<https://wdfw.wa.gov/hatcheries/escapement/>) and WDFW's SCoRE database. River surveys, trap counts, and remote counting methods were assessed to estimate the numbers of hatchery fish on the spawning grounds and

expand those numbers to account for areas not surveyed.

Numbers of hatchery Chinook salmon harvested by commercial, sport, ceremonial, and subsistence fisheries in Puget Sound marine and fresh waters have been estimated annually. For commercial catch, Washington State and Treaty Indian Tribes use a system that reports catch on fish tickets. Information includes landing location, landing date, total landed weight, and total number of fish landed. For sport catch, Washington State relies on a system of self-reporting in the form of Catch Record Cards (CRCs; <https://wdfw.wa.gov/licenses/fishing/catch-record-card>). CRC reports include the date, total number of fish captured by species, mark status, and catch location of harvested fish. Reported catches of hatchery- and natural-origin Chinook salmon were then expanded to account for unreported catch and other fishing-related mortality (E. Kraig, WDFW, *unpublished data*). WDFW allocates annual mixed-stock estimates of Chinook salmon caught by Washington fishers in Puget Sound to specific stocks using proportional escapement-based catch allocation. These estimates do not include sport catch in marine waters of Puget Sound. For freshwater sport, commercial, and ceremonial/subsistence fisheries, catch is allocated to the river or hatchery where catch occurred unless empirical data suggest a proportion of catch is comprised of stocks from other rivers.

Estimated total numbers of adult Chinook salmon returning to Puget Sound were assigned to a year of ocean emigration based on age composition estimates for marked and unmarked Chinook sampled from commercial and sport fisheries in terminal areas of each of the six U.S. regions (Fig. 1). These data are based on scales sampled from >2 million Chinook salmon between 1985 and 2014 (Appendix S1: Table S1). For years 1980–1984, we applied the average age composition from 1985 to 1989.

Pink salmon.—The inclusion of pink salmon in our analyses was based on previous findings that the presence of emigrating pink salmon has been associated with hatchery Chinook salmon marine survival in Puget Sound (Ruggerone and Goetz 2004, Claiborne et al., *in press*). Ideally, annual estimates of emigrating fry from major pink-producing basins around the Salish Sea

would be evaluated as a potential explanatory variable in our study. However, such data were currently not available for many Puget Sound basins, so we followed Ruggerone and Goetz (2004) and designated years as pink (even-numbered) or non-pink (odd-numbered) emigration years, depending on whether emigrating juvenile pink salmon from the much more plentiful odd-year spawners were present.

Modeling CWT hatchery Chinook marine recovery (survival) rates

Model specifications and comparison and parameter estimation.—To evaluate factors associated with marine survival of hatchery Chinook salmon, we fit multiple hierarchical regression models to survival rates from CWT data. Specifically, we modeled instantaneous mortality rate ($-\log_e(\text{Survival})$) from release to age 2 or 3 for each stock i in region r in year t ($M_{i,r,t}$) as a

function of multiple covariates. We explored 18 model formulations that included six possible covariates: juvenile Chinook life history (sub-yearling vs. yearling release), release region, the number of hatchery releases per region, presence of pink salmon in the Salish Sea, and release year (Table 2).

Preliminary model selection was completed by comparing widely applicable information criteria (WAIC; Gelman et al. 2013, Vehtari et al. 2017) and Bayesian R^2 values of the candidate models (Gelman et al. 2019; Table 2). The eight best-performing models were then compared using an approximation of leave-one-out (LOO) cross-validation from the loo package in R (Appendix S1: Table S2; Vehtari et al. 2017). Here, the candidate model that maximizes the expected log of the predictive density (ELPD) over all observed data points is considered superior. Should the standard error of the ELPD exceed the absolute value of the difference between ELPDs among

Table 2. Summary of model formulations, selection criteria (widely applicable information criteria [WAIC]), and fit (Bayes R^2) for all candidate models evaluated.

Model number	Formula	WAIC (\pm SE)	Bayes R^2
1	Null	2069 (46)	<0.01
2	LifeHist	2070 (46)	0.03
3	Region	1935 (42)	0.20
4	LifeHist + Region	1936 (42)	0.20
5	LifeHist + Region + Hatch†	1934 (42)	0.21
6	LifeHist + Region + Hatch‡	1937 (42)	0.20
7	LifeHist + Region + Hatch§	1937 (42)	0.20
8	LifeHist + Region + Hatch + Pink	1934 (42)	0.21
9	LifeHist + Region + Hatch + Pink + (Pink \times Hatch)	1927 (43)	0.22
10	Stock + LifeHist + Region + Hatch + Pink + (Pink \times Hatch)	1755 (44)	0.44
11	Stock¶ + LifeHist + Region + Hatch + Pink + (Pink \times Hatch)	1753 (44)	0.41
12	Stock + LifeHist + Region + Hatch + Pink + (Pink \times Hatch) + Year	1729 (49)	0.50
13	Stock¶ + LifeHist + Region + Hatch + Pink + (Pink \times Hatch) + Year	1729 (49)	0.48
14	Stock + LifeHist + Region + Hatch¶ + Pink¶ + (Pink \times Hatch)¶ + Year	1734 (49)	0.50
15	Stock¶ + LifeHist + Region + Hatch¶ + Pink¶ + (Pink \times Hatch)¶ + Year	1734 (49)	0.49
16	Stock¶ + LifeHist + Region + Hatch¶ + Pink¶ + Year + (Pink \times Hatch)¶ + (Region \times Year)	1784 (40)	0.64
17	Stock¶ + LifeHist + Region + Hatch + Pink + (Region \times Pink \times Hatch)	1769 (45)	0.43
18	Stock¶ + LifeHist + Hatch# + Pink # + (Pink \times Hatch)#	1759 (44)	0.41

Notes: LifeHist, juvenile hatchery Chinook salmon life history (sub-yearling vs. yearling release); Hatch, number of hatchery juvenile Chinook salmon released; and Pink, presence of pink salmon during juvenile hatchery Chinook salmon emigration from the Salish Sea. The best-performing model (see Appendix S1: Table S2) is bolded.

† Regional hatchery releases.

‡ Basin hatchery releases (Puget Sound, Strait of Georgia).

§ All hatchery releases (Salish Sea-wide).

¶ Denotes random effect (stock level).

Denotes random effect (region level).

competing models, the model with the lowest number of effective parameters is favored (Veh-tari et al. 2017).

We estimated model parameters in a Bayesian framework using Markov chain Monte Carlo (MCMC) from Stan's (Stan Development Team 2018a) *rstanarm* package (Stan Development Team 2018b) in R (R Development Core Team 2019). To estimate the posterior distributions for each parameter, we generated eight separate MCMC chains of 1000 iterations and discarded the first half of each chain. The remaining sam-ples were used to calculate posterior means, quantiles, and predictive distributions. We assessed model convergence of the MCMC chains by visual inspection of trace plots and evaluation of Gelman-Rubin diagnostic statistics (R-hat) for each parameter (Gelman et al. 2013). Vague, normal priors with means centered on zero were imposed on all model coefficients, and their variances were auto-scaled with the pack-age's default settings.

Predicted numbers of age-2 recruits in the North Pacific Ocean.—We used the posterior predictive distributions (Gelman et al. 2013) from the best-performing model to estimate age-2 Chinook salmon survival in the North Pacific Ocean over the range of observed releases of juvenile hatchery Chinook salmon; the predicted numbers of age-2 Chinook salmon were termed “recruits.” We esti-mated survival rates for stocks in each geograph-ical region in pink and non-pink years and used them to project the numbers of age-2 recruits in the ocean. These projections were only calculated for sub-yearlings (age 2 in the ocean), as >90% of Chinook hatchery releases in the central and southern parts of the Salish Sea have typically been released as this life-history type (Nelson et al. 2019; RMIS database).

Relationship between hatchery Chinook releases and adult returns to Puget Sound for even- vs. odd-year cohorts

We examined the relationship between the numbers of juvenile hatchery Chinook salmon released in pink years (even-numbered, when many pink salmon also emigrate from the central and southern parts of the Salish Sea) vs. non-pink years (odd) and the associated total run-re-constructed index numbers of adult Chinook sal-mon that returned to Puget Sound. We plotted

these cohort-specific values for each of the six regions in Puget Sound (we did not include the two Canadian regions as WDFW does not per-form run reconstructions for them) and used sim-ple linear regression to estimate trends between pink- and non-pink-year emigration cohorts for each region. The regressions used here followed the same Bayesian approach described above.

RESULTS

CWT hatchery Chinook recovery (marine survival) rates

Sub-yearling Salish Sea Chinook salmon mar-ine instantaneous mortality rates to age 2 were typically between 3 and 7 (<2% survival rate) between 1983 and 2012, with the exception of the Fraser River region (FRA) stocks, whose average instantaneous mortality rates were considerably lower (average survival rate of ~5%; Appendix S1: Fig. S1). Yearling Chinook salmon marine mortality rates to age 3, as estimated by the recovery rates of age-3 yearling CWT fish, also varied among regions and over time (Appendix S1: Fig. S1).

The numbers of juvenile Chinook salmon released from hatcheries have varied consider-ably over time and among regions since the early 1980s (Fig. 2). Generally, hatchery production of Chinook salmon appeared to peak in the mid- to late 1980s in most regions, and many have seen a decline or leveling off in production since then. Northern Washington and VAN regions saw the greatest range in total hatchery production of Chinook over the period of this study (Fig. 2).

Model comparison, MCMC model convergence, and posterior predictive checks.—Based on model selection criteria that considered model fit and complexity, the best-performing model was (Model 11; Table 2):

$$M_{i,j,r,t} = \beta_{0_i} + \beta_1 LifeHist_j + \beta_2 Region_r + \beta_3 Hatch_{r,t} + \beta_4 Pink_t + \beta_5 (Pink_t \times Hatch_{r,t}) + \epsilon_i \quad (1)$$

where β_{0_i} is the stock-specific random effect that is assumed to be exchangeable and drawn from a common global distribution; $LifeHist_j$ is a binary factor coded 0 or 1 for sub-yearling and yearling releases, respectively; $Hatch_{r,t}$ is the total number of hatchery releases in region r in year t , which

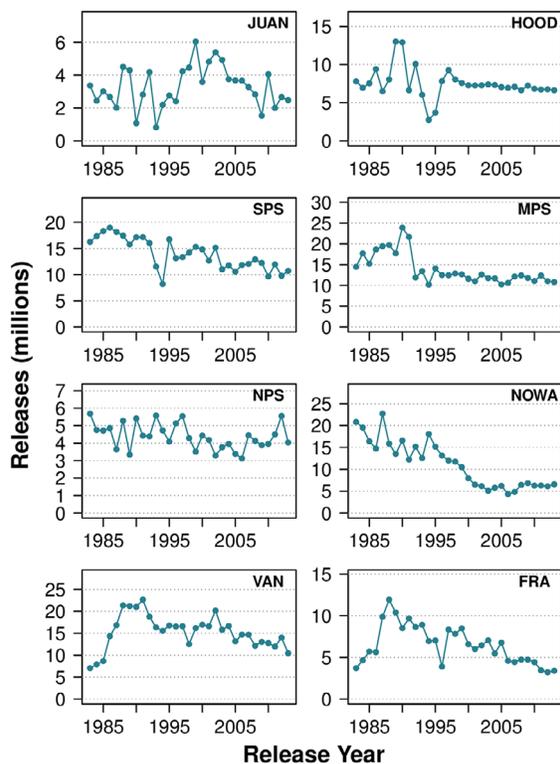


Fig. 2. Annual releases of hatchery yearling and sub-yearling Chinook salmon in the southern Salish Sea, by region, from 1983 to 2012.

were standardized by subtracting the mean and dividing by two standard deviations (Gelman and Hill 2007); and $Pink_t$ is a binary factor for the presence of juvenile pink salmon (0 or 1) in year t . The error terms, which were assumed to be normally distributed $\sim N(0, \sigma_i)$, accounted for all other factors and processes that influenced survival during this time period. This model explained 41% of the variation in the observed survival rates from release to age 2 or 3 (Table 2). Of note, candidate models that included random effects on independent variables other than the intercept (e.g., Hatch, Pink, Pink \times Hatch) provided better fit to the data than Model 11, but the increase in predictive power was not meaningful according to our cross-validation approach. This result could suggest that the effects of pink salmon presence and regional hatchery releases are comparable (i.e., similar in magnitude) over the entire ecosystem.

Diagnostic outputs did not indicate any issues with convergence or autocorrelation in the

MCMC chains during the sampling process. Visual inspection of the trace plots showed all MCMC chains were sufficiently well mixed, suggesting the chains had successfully converged. Additionally, the Gelman-Rubin diagnostic statistics for all estimated parameters did not exceed 1.00, and all had effective sample sizes of at least 1400. Posterior predictive checks comparing the posterior predictive distributions to observed data did not suggest any systematic errors associated with the model predictions (Appendix S1: Fig. S2). 95.3% of the observed data points (653/685) fell within the 95% posterior predictive intervals (Appendix S1: Fig. S3), which suggests the model is capable of reproducing the observed data.

Factors associated with Chinook marine survival rates.—Model coefficients were regarded as having significant explanatory power, by conventional (frequentist) interpretation, when the 95% Bayesian credible intervals of their marginal posterior distribution did not overlap with zero. Accordingly, regional effects appeared to be important in explaining marine survival to age 2 or 3 of hatchery Chinook salmon, specifically the Strait of Juan de Fuca (JUAN), middle and northern Puget Sound (MPS and NPS), and Fraser River (FRA; Table 3). Only four of 33 stocks (random effects) were different from the mean region effect (Appendix S1: Fig. S4): South Puget Sound Yearling (SPY) and Issaquah Creek (ISS) had significantly lower mortality rates than other stocks within their region, while Nooksack Spring (NKS) and Big Qualicum River (BQR) were significantly higher.

The interaction between the presence of juvenile pink salmon in the Salish Sea and juvenile hatchery Chinook release numbers was also found to have significant explanatory power in the best-performing model (Fig. 3, Table 3). The coefficient value suggested a significant negative interaction between juvenile pink salmon and hatchery release number. Therefore, in even-numbered years, greater hatchery Chinook salmon releases were associated with decreased marine survival. Predicted mean marine survival rates in these pink years were lower than those in non-pink years (Table 4).

The estimated hatchery release abundance model coefficient (-0.12) suggested strong support (though not statistically significant) for a

Table 3. Summary of posterior distributions for regression coefficients in the best-performing model (Model 11; see Table 2).

Parameter	Mean	SD	2.5% CI	97.5% CI
Intercept (Region 1 [JUAN])	5.46	0.36	4.72	6.18
Region 2 (HOOD)	-0.81	0.73	-2.20	0.67
Region 3 (SPS)	-0.81	0.49	-1.76	0.17
Region 4 (MPS)	-1.19	0.47	-2.09	-0.27
Region 5 (NPS)	-1.07	0.43	-1.91	-0.22
Region 6 (NOWA)	-0.80	0.53	-1.87	0.25
Region 7 (VAN)	-0.79	0.45	-1.66	0.13
Region 8 (FRA)	-1.99	0.49	-2.95	-0.99
Life history	-0.07	0.31	-0.68	0.56
Juvenile hatchery Chinook salmon abundance	-0.12	0.10	-0.31	0.07
Juvenile pink salmon presence	0.12	0.07	-0.01	0.25
Juvenile pink salmon presence x juvenile hatchery Chinook salmon abundance	0.54	0.13	0.28	0.80

Notes: Included are the estimates for the posterior mean, standard deviation, and 95% credible intervals (CIs). Parameter estimates and credible intervals shown in bold do not overlap with zero.

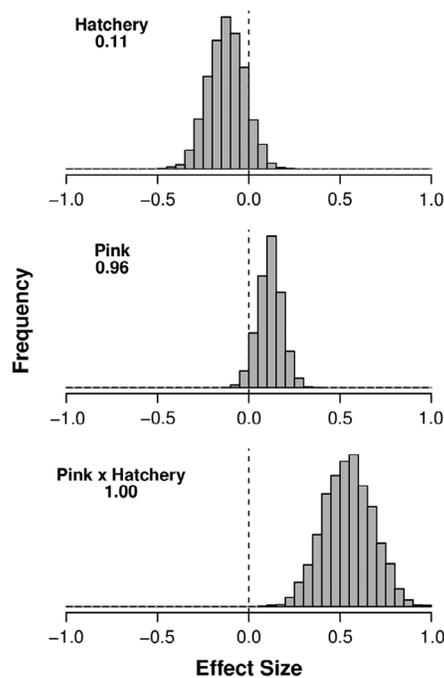


Fig. 3. Marginal posterior distributions of regression coefficients for hatchery releases, pink salmon, and the interaction between pink salmon and hatchery releases. Posterior distributions are based on 4000 Markov chain Monte Carlo samples. The proportion of draws from the posterior distribution that are >0 is shown in the upper-left corner of each histogram.

positive relationship between survival and hatchery releases in non-pink years (Table 3). Therefore, in these odd emigration years, greater releases of hatchery Chinook salmon were

associated with increased marine survival (Appendix S1: Fig. S5). Finally, the model did not show a significant difference in survival between sub-yearling and yearling Chinook salmon (Table 3).

Predicted numbers of age-2 recruits in the North Pacific Ocean.—The relationship between the numbers of sub-yearling hatchery Chinook salmon predicted to survive to age 2 in the North Pacific Ocean (recruits) and the numbers of juveniles released was different for juveniles released in pink and non-pink years. Across regions, in non-pink (odd-numbered) emigration years, increases in hatchery Chinook production were associated with linear increases in age-2 recruits (Fig. 4). However, in pink years, increases in Chinook hatchery production were associated with a leveling off or a diminishing number of recruits, which suggests the presence of density-dependent survival. The uncertainty associated with these estimates is considerable in both pink and non-pink years, and the overlap of the predictive intervals—a measure of uncertainty in the estimated parameters and the observed data—suggests observable differences between pink and non-pink years only when moderate-to-high numbers of hatchery Chinook salmon were released (Fig. 4).

Relationship between hatchery Chinook releases and adult returns to Puget Sound for even- vs. odd-year cohorts

The relationship between hatchery Chinook salmon releases in pink (even-numbered) years

Table 4. Best-performing model (Model 11; see Table 2) posterior mean percent survival rates and 95% credible intervals (CI) for Salish Sea hatchery Chinook salmon by region and stock in pink and non-pink salmon years.

Region	Stock	% Survival (95% CI)	
		Non-pink year (odd-numbered)	Pink year (even-numbered)
JUAN	DUN	0.12 (0.07–0.22)	0.11 (0.06–0.20)
	ELW	0.38 (0.24–0.60)	0.34 (0.21–0.54)
	HOK	1.15 (0.83–1.60)	1.02 (0.74–1.42)
HOOD	GAD	1.00 (0.72–1.41)	0.89 (0.64–1.25)
NOWA	NSF	1.00 (0.51–1.99)	0.89 (0.46–1.78)
	NKS	0.65 (0.41–1.04)	0.58 (0.37–0.94)
	SAM	1.37 (0.99–1.90)	1.22 (0.89–1.68)
NPS	SKY	0.87 (0.55–1.35)	0.77 (0.49–1.21)
	STL	1.51 (1.07–2.10)	1.35 (0.95–1.84)
	SNY	2.39 (1.14–4.99)	2.13 (1.03–4.48)
	SKS	2.07 (1.06–4.08)	1.84 (0.94–3.63)
	SKF	1.44 (0.99–2.06)	1.28 (0.90–1.84)
	SSF	1.05 (0.71–1.54)	0.94 (0.64–1.37)
	SFF	0.63 (0.38–1.03)	0.56 (0.34–0.92)
MPS	TUL	0.97 (0.60–1.56)	0.86 (0.53–1.39)
	GRN	1.22 (0.88–1.70)	1.09 (0.79–1.53)
	GRO	2.17 (1.60–2.93)	1.93 (1.41–2.63)
	ISS	1.33 (0.60–2.85)	1.18 (0.53–2.55)
	PUY	1.53 (0.92–2.58)	1.37 (0.82–2.28)
SPS	WRY	1.03 (0.49–2.16)	0.91 (0.44–1.90)
	GAR	0.68 (0.43–1.05)	0.60 (0.38–0.93)
	NIS	1.34 (0.97–1.83)	1.19 (0.87–1.63)
	SPS	1.79 (1.31–2.45)	1.59 (1.18–2.19)
FRA	SPY	0.54 (0.27–1.04)	0.48 (0.25–0.91)
	HAR	2.07 (1.51–2.80)	1.85 (1.34–2.51)
	NIC	2.13 (1.07–4.07)	1.89 (0.96–3.63)
VAN	SHU	2.70 (1.97–3.65)	2.40 (1.77–3.26)
	CHI	8.62 (6.30–11.78)	7.67 (5.59–10.47)
	QUI	0.95 (0.71–1.31)	0.85 (0.63–1.16)
VAN	PPS	0.54 (0.40–0.72)	0.48 (0.35–0.64)
	BQR	0.63 (0.46–0.87)	0.56 (0.41–0.77)
	COW	1.40 (1.00–1.96)	1.24 (0.89–1.74)
	NAN	1.68 (1.13–2.48)	1.50 (1.01–2.22)

Notes: DUN, Dungeness; ELW, Elwha; HOK, Hoko; GAD, George Adams; NSF, Nooksack; NKS, Nooksack Spring; SAM, Samish; SKY, Skykomish; STL, Stillaguamish; SKF, Skagit Fall; SNY, Snohomish Yearling; SKS, Skagit Spring; SKF, Skagit Fall; SSF, Skagit Spring Fingerling; SFF, Skagit Summer; TUL, Tulalip Summer; GRN, Green; GRO, Grovers Creek; ISS, Issaquah Creek; PUY, Puyallup; WRY, White River Yearling; GAR, Garrison; NIS, Nisqually; SPS, South Puget Sound; SPY, South Puget Sound Yearling; HAR, Harrison; NIC, Nicola; SHU, Shuswap; CHI, Chilliwack; QUI, Quinsam; PPS, Puntledge; BQR, Big Qualicum; COW, Cowichan; NAN, Nanaimo.

vs. the number of adult Chinook returns was negative in five of the six regions in Puget Sound (Fig. 5). The trend was statistically significant at

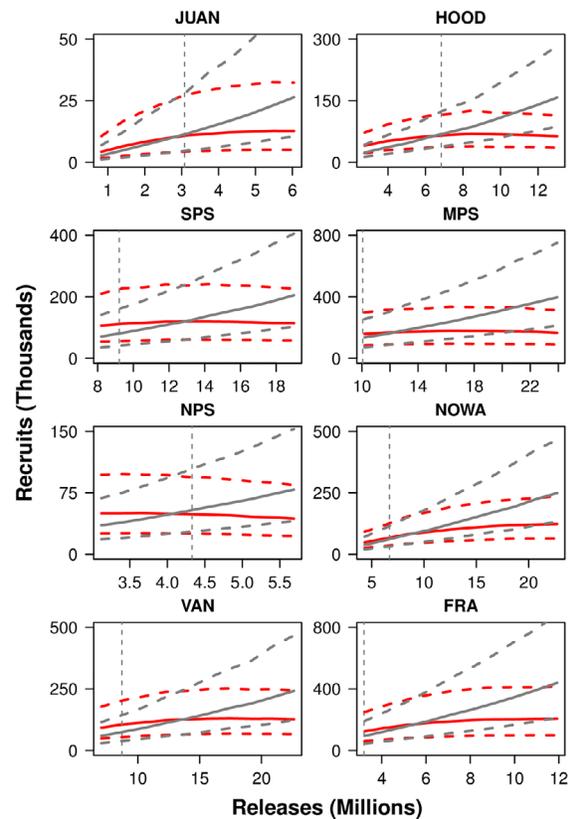


Fig. 4. Projected sub-yearling Chinook salmon recruits (age 2) in the ocean (*y*-axis) vs. the total number of juveniles released in each region (*x*-axis). Release number minimums and maximums on the *x*-axes reflect the observed range of total hatchery Chinook released in each region (Appendix S1: Fig. S5). Gray lines show projected values in non-pink (odd-numbered) years, while red lines show values in pink years. Dashed lines for each depict 95% posterior predictive intervals. The vertical dashed lines show the average annual number of releases for the most recent five years in each region.

the 0.05 level for two regions (SPS and MPS). On the other hand, this relationship was significantly positive for NOWA. For non-pink-year (odd-numbered) emigrants, the slope of the regression line was positive for three regions (MPS, NPS, and NOWA [significantly so for this region]) and negative for the three others. In five regions, the linear trend in pink years was more negative than it was in non-pink years, though not statistically significantly so at the 95% level. Notably, there was only one region (NOWA) where the

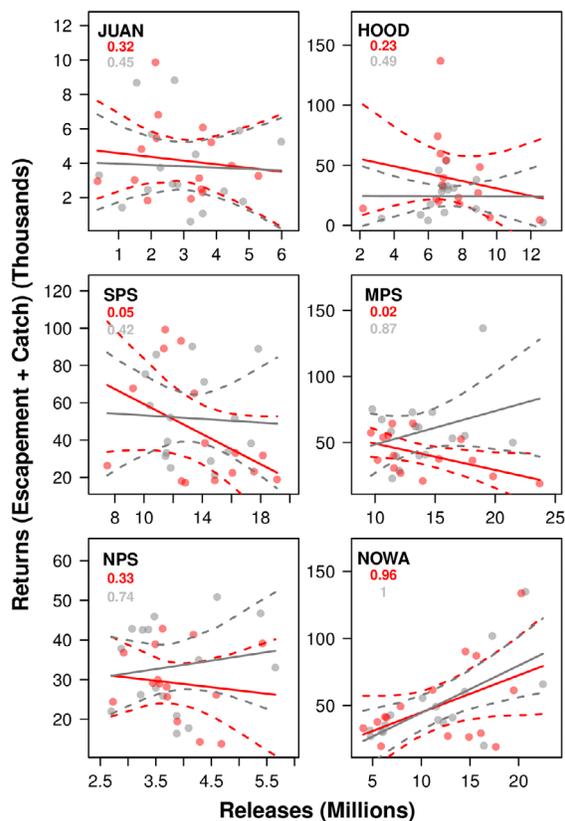


Fig. 5. Run reconstruction of the total numbers of adult hatchery Chinook salmon from each region returning to Puget Sound (y -axis) vs. the number of juveniles released that produced those adults (x -axis). The gray line is the regression trend line of data from non-pink years (odd emigration years), while the red line is the best-performing regression line of pink-year data (even years). Dashed lines depict 95% credible intervals for each series. The red and gray numbers are the probability of each slope being $>$ zero.

relationship between hatchery releases and returns was significantly positive ($\geq 95\%$ probability of slope parameter being $>$ zero) in either pink or non-pink years (Fig. 5).

DISCUSSION

Our results show that since the early 1980s, in even-numbered years when pink salmon juveniles emigrated into marine waters, higher levels of hatchery supplementation of Chinook salmon in the Salish Sea have been associated with stable or decreased marine survival to age 2 or 3 in

most regions. Our findings suggest that the presence of emigrating juvenile pink salmon may somehow alter the relationship between the abundance of juvenile Chinook hatchery released and their marine survival. Therefore, hatchery Chinook salmon may have experienced density-dependent survival in years when there were higher total numbers of Chinook and pink salmon in the Salish Sea. Opposite patterns were found in odd-numbered years (when few pink salmon juveniles were present in the central and southern parts of the Salish Sea): A positive relationship was found between the numbers of hatchery Chinook released and the numbers of these fish that survived in the ocean.

It is important to note that there was considerable uncertainty in the estimates of age-2 hatchery Chinook salmon recruits in the ocean in pink vs. non-pink years at lower and moderate levels of hatchery releases. It was only at the higher release numbers in the various regions that strong differences in the numbers of recruits are apparent. In the most recent five years, Chinook hatchery release numbers have been in the low-to-moderate ranges relative to historical releases. Proposed increases in hatchery releases associated with SRKW recovery (WDFW 2019) could achieve hatchery Chinook salmon abundance values that have not been seen since the late 1980s and early 1990s in some regions. It is not reasonable to directly extrapolate future hatchery Chinook salmon release numbers onto our historical results. However, our work does highlight the importance of further evaluations and studies to implement hatchery release strategies that maximize adult returns.

Despite considerable inter-annual variability in the hatchery Chinook marine survival rates, the addition of a year effect or the interaction between release year and release region did not meaningfully improve model performance (relative to the increase in model complexity). While these spatiotemporal effects were not included in our best-performing model, they likely do explain much of the variation in the year-to-year Chinook salmon early marine survival (Satterthwaite et al. 2014). Future work could evaluate the association between the abundance of hatchery Chinook salmon juveniles released, pink salmon presence, and hatchery Chinook marine survival rates during different time periods in

the past. Additionally, the effects of certain covariates like pink salmon presence and hatchery release abundance values on individual stocks may differ from the global or mean effect inferred from the best-performing model.

When we compared the abundance of hatchery Chinook salmon juveniles released into Puget Sound in pink (even-numbered) years to the reconstructed adult run size of each emigration cohort, five of the six regions showed moderate-to-strong support for a negative relationship. This result also supports the potential for density-dependent survival of hatchery Chinook salmon in the Salish Sea in some years; on average, when higher numbers of hatchery Chinook juveniles emigrate with juvenile pink salmon, fewer of them survive their ocean migration and return as adults to Puget Sound. In contrast, this pattern was not consistently observed for non-pink-year juvenile Chinook salmon emigrants.

It is noteworthy that we have typically not observed a strong positive relationship between the numbers of juvenile Chinook released from hatcheries and the number of adults that returned over the time period assessed—only the northern Washington region (NOWA) had a strong positive relationship between hatchery Chinook releases and returns. This was similar to what Beamish et al. (1992) showed for coho and Chinook salmon released from Strait of Georgia hatcheries between the early 1970s and mid-1980s. Fishing in the North Pacific Ocean and other sources of marine mortality are likely variable over the study period and likely affect the adult returns to Puget Sound, influencing the observed patterns. However, it is unlikely that there would consistently have been more fishing or greater natural mortality on even-emigration-year cohorts, especially given the overlapping age cohorts of Chinook salmon when they were subjected to fishing mortality in the ocean.

Previous work has suggested that Puget Sound Chinook salmon growth and survival during their first year in the ocean (i.e., when they are within the Salish Sea) have been impacted by the presence of high pink salmon abundance (Ruggerone and Goetz 2004, Claiborne et al., *in press*). While studies have also documented density-dependent interactions between Pacific salmon and pink salmon in the North Pacific Ocean, evidence for density-

dependent interactions occurring beyond their first year of ocean residence is lacking for Chinook salmon compared to other species such as sockeye salmon (Ruggerone and Nielsen 2004, Ruggerone et al. 2005). Additionally, Salish Sea hatchery Chinook salmon marine survival trends were found to be significantly different than those for northern and southern coastal hatchery Chinook salmon (Ruff et al. 2017), emphasizing the need to examine factors influencing survival within the Salish Sea (Andersen et al. 2017). All told, greater understanding of potential density-dependent interactions focused within in the Salish Sea in the past may help inform Chinook salmon hatchery production and encourage future work evaluating potential mechanisms behind the findings.

Several potential mechanisms could explain the decreased Chinook salmon survival observed in years when juvenile pink salmon emigrate. Evaluation of these mechanisms may shed light on the spatial and temporal scales of the interactions between Chinook and pink salmon in the Salish Sea.

First, juvenile Chinook salmon in the Salish Sea may experience indirect competition from juvenile pink salmon in even-numbered years, when large numbers of pink salmon enter the Salish Sea earlier than Chinook salmon and alter the preyscape within shared habitats. Pink salmon are known to feed more heavily on zooplankton (especially epibenthic harpacticoid copepods and calanoid copepods) than Chinook salmon, who consume mostly insects and gammarid amphipods in the nearshore environments, then focus initially on decapods (crab larvae in particular) as they move offshore, and then become progressively more piscivorous by late summer or early fall (Kaczynski et al. 1973, Duffy et al. 2010, Osgood et al. 2016). A trophic cascade may occur between the copepods preyed upon in some years by pink salmon that would otherwise be consumed by young-of-year (age-0) Pacific herring, insects, amphipods, and decapods, which support Chinook salmon (Boldt et al. 2019). Chinook salmon marine survival is especially related to their feeding in offshore habitats of the Salish Sea in June–July (Duffy and Beauchamp 2011), and changes in the prey base at lower trophic levels have been directly linked to Chinook salmon survival in the coastal ocean

(Losee et al. 2014). Further studies on zooplankton abundance and predation in the Salish Sea throughout the spring and summer months would be needed to better evaluate this hypothesized mechanism.

Pink salmon diets are similar to those of forage fishes like young-of-year Pacific herring (Osgood et al. 2016, Boldt et al. 2019), which are very abundant in the offshore environment of the Salish Sea (Therriault et al. 2009, Siple and Francis 2016). Young-of-year herring are key prey for juvenile Chinook salmon in the Salish Sea in the summer and fall (Duffy et al. 2010). A recent study showed that young-of-year herring abundance was positively associated with juvenile pink (competitors of herring) and Chinook (predators of herring) salmon abundance between 1992 and 2016 (Boldt et al. 2019), indicating that environmental conditions favorable for young-of-year herring (and potentially numerous other fish species) also benefited their competitors and predators. Thus, competition and predation should be considered across the entire Salish Sea epipelagic community.

This competition-related mechanism is also pertinent to a recent study by Claiborne et al. (*in press*). They examined the relationship between Puget Sound Chinook salmon first-year marine growth and survival between 1976 and 2008 and found that when juvenile Chinook salmon emigration cohorts experienced above-average growth, lower numbers of juvenile pink salmon were documented emigrating through the Salish Sea.

Second, apparent competition (Holt and Bon-sall 2017) may be occurring wherein predation on juvenile Chinook may be increased when higher numbers of pink salmon were present. Predator responses from marine mammal (e.g., harbor seals; Thomas et al. 2016), avian (e.g., Caspian terns [*Sterna caspia*], double-crested cormorants [*Phalacrocorax auritus*], and glaucous-winged and western gulls [*Larus glaucescens* and *L. occidentalis*]) (Collis et al. 2002), and fish (e.g., spiny dogfish [*Squalus acanthias*]) (Beamish 1992) species may be possible. Cannibalism by age 1–3 resident Puget Sound Chinook salmon on juvenile Chinook salmon has also been documented as a potentially significant source of mortality on these fish (Beauchamp and Duffy 2011). Further

research on Chinook salmon predators is needed to shed light on this mechanism.

An additional possible mechanism behind Chinook salmon density-dependent survival is related to higher total densities of salmon in the Salish Sea. Rhodes et al. (2011) studied bacterial kidney disease (BKD) in recently emigrated juvenile Chinook salmon in Puget Sound during one outmigration year and found that increased juvenile Chinook salmon density was an important factor associated with higher BKD infection prevalence and intensity across the Sound. The authors did not examine how the abundance of pink salmon was related to hatchery Chinook salmon BKD infection, which is an area of further study that would support an ecosystem-based strategy to understanding Chinook salmon marine survival.

Regional differences were seen in the relationships between the numbers of hatchery Chinook salmon released into the Salish Sea, their marine survival, and the presence of emigrating juvenile pink salmon. This may be due to hatchery Chinook salmon from different regions using coastal areas for different periods of time and varying environmental and habitat conditions within the Salish Sea, including differences in prey composition, predator abundance, and other factors (Jeffries et al. 2003, Rice et al. 2011, Khangaonkar et al. 2012).

Our work builds upon a study by Ruggerone and Goetz (2004) that examined marine growth and survival of hatchery juvenile Chinook salmon emigrating with and without pink salmon in even- vs. odd-numbered years, respectively, from Salish Sea rivers between 1972 and 1997. Our study differs from that of Ruggerone and Goetz (2004) as we modeled marine survival/mortality rates specifically considering the abundance of hatchery Chinook salmon juveniles released; our goal was not to replicate Ruggerone and Goetz's analysis with an additional 15 yr of data—though that is a study worthy of future analysis. Together, these studies and ours suggest the need for hatchery practices to consider ecosystem-based interactions to benefit Chinook salmon abundance and species recovery in the Salish Sea (Pikitch et al. 2004, Marshall et al. 2016, Samhoury et al. 2017, Levin et al. 2018).

The Salish Sea ecosystem has changed over the last half-century (Preikshot et al. 2013), and

exploring how the various changes have been associated with Chinook marine survival is an important undertaking. Such exploration is currently being facilitated by the Salish Sea Marine Survival Project (<https://marinesurvivalproject.com/>) and so is not a part of our current analyses. With regard to changing hatchery practices over time, records show that large numbers (~10–30% of total releases) of hatchery Chinook fry releases (<2–3 g body weight), in addition to the sub-yearlings and yearlings, were released into the Salish Sea until 2000 (RMIS database). The modest predictive power of a year effect in our candidate models of Salish Sea hatchery Chinook salmon marine survival and the fact that fry releases did not differ between even- and odd-numbered outmigration years (RMIS database) suggest that these changing hatchery practices are likely not strongly related to the relationships of hatchery Chinook salmon release numbers and juvenile pink salmon presence on hatchery Chinook marine survival.

While we show here that pink salmon abundance is associated with lower survival of Salish Sea hatchery Chinook salmon, it is important to note that pink salmon are an essential part of the Salish Sea ecosystem. Given that they are often the most numerous salmonid in the Salish Sea, especially in recent decades (Losee et al. 2019), they provide essential marine-derived nutrients and food resources to many freshwater systems (Ward and Slaney 1988, Cederholm et al. 1999, Marston 2017, Bailey et al. 2018). Pink salmon rely minimally on freshwater habitats compared to other salmonids (Quinn 2005), which may serve them especially well in the future given the potential impacts of climate change on freshwater ecosystems (Ward et al. 2015).

Though this is an analysis of marine survival of hatchery-origin Chinook salmon, the implications of our results for natural-origin populations deserve further analysis. Unlike natural-origin fish, hatchery-released Chinook salmon are managed for rapid downstream migration to the ocean, compressing their temporal patterns of residence. In contrast, natural-origin fish, by virtue of their extended and variable freshwater and estuary residency during downstream migration (Healey 1991), have a protracted temporal distribution (Rice et al. 2011, Nelson et al. 2019). Due to their compressed timing of release

(resulting in many hungry mouths in the same time and place), hatchery-origin juvenile Chinook salmon might be expected to experience higher feeding competition with pink salmon already resident in the Salish Sea. In fact, while this and other studies (Ruggerone and Goetz 2004, Claiborne et al., *in press*) documented odd vs. even year differences in hatchery Chinook salmon marine survival, Greene et al. (2005) were unable to detect a similar signal in life-cycle productivity of the largest population of natural-origin Chinook salmon in Puget Sound. Nevertheless, if the presence of juvenile pink salmon combined with the abundance of juvenile hatchery Chinook salmon is related to the marine survival of hatchery-origin Chinook, as shown herein, juvenile natural-origin Chinook salmon may also experience impacts in years when pink salmon emigrate and large numbers of hatchery Chinook are released. However, a recent study on wild Chinook populations in the Salish Sea and Washington coast found that hatchery Chinook salmon release abundance was significantly correlated (in this case positively) with wild Chinook productivity in only one of 20 populations (Nelson et al. 2018). The presence of emigrating juvenile pink salmon (i.e., even- vs. odd-numbered year) was not included as a covariate in this analysis, which could be done to expand on the findings of our work here.

Increasing the abundance of adult Chinook salmon in the Salish Sea, and thus aiding the recovery of SRKWs, will be a complicated and difficult process (Williams et al. 2011, Marshall et al. 2016) that will need to address the range of the 4-Hs of human impacts on salmon (harvest, hydropower, hatcheries, and habitat quantity and quality; Ruckelshaus et al. 2002). Regarding hatcheries, responsive programs that consider the ecosystem into which they release the fish, including the numerous species interactions, are essential to meet conservation and management challenges in a cost-effective manner. The story of density-dependent survival of hatchery Chinook salmon in the Salish Sea is by no means complete, though we have found signs of lower survival when many juvenile hatchery Chinook and pink salmon have been present in the system. The findings of this paper should not simply be applied to future hatchery releases; environmental conditions faced by hatchery Chinook

salmon in the past years will not be the same as those faced in the future. However, by considering potential density-dependent interactions of hatchery Chinook salmon with pink salmon in the Salish Sea and exploring the ecosystem patterns and mechanisms behind these findings, hatchery management practices and research can be further informed to benefit Chinook salmon and SRKW conservation.

ACKNOWLEDGMENTS

This is Publication Number 40 from the Salish Sea Marine Survival Project: an international, collaborative research effort designed to determine the primary factors affecting the survival of juvenile Chinook, coho, and steelhead survival in the combined marine waters of Puget Sound and Strait of Georgia (www.marinesurvivalproject.com). Funding for this project was received from the Pacific Salmon Commission Southern Fund. Thank you to Dale Gombert of WDFW for creating the map in Fig. 1. We received helpful data, insights, reviews, and comments from Jameal Samhoury, Barry Berejikian, Kathryn Sobocinski, Correigh Greene, Eric Ward, and Kristin Marshall of NOAA-NWFSC; Mike Haggarty and Morgan Robinson of NOAA NMFS; Joe Anderson, Todd Sandell, Marisa Litz, Jeff Haymes, and Jon Carey of WDFW; Mike Hawkshaw of DFO-Pacific; Dave Beauchamp of USGS; Galen Johnson and Chris James of NWIFC; and Tom Chance of Lummi Nation.

LITERATURE CITED

- Andersen, K. H., N. S. Jacobsen, T. Jansen, and J. E. Beyer. 2017. When in life does density dependence occur in fish populations? *Fish and Fisheries* 18:656–667.
- Bailey, C. J., D. C. Braun, D. McCubbing, J. D. Reynolds, B. Ward, T. D. Davies, and J. W. Moore. 2018. The roles of extrinsic and intrinsic factors in the freshwater life-history dynamics of a migratory salmonid. *Ecosphere* 9:e02397.
- Batten, S. D., G. T. Ruggerone, and I. Ortiz. 2018. Pink Salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. *Fisheries Oceanography* 27:548–559.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. Mahnken, and C. M. Neville. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *ICES Journal of Marine Science* 54:1200–1215.
- Beamish, R. J., B. L. Thomson, and G. A. McFarlane. 1992. Spiny dogfish predation on chinook and coho salmon and the potential effects on hatchery-produced salmon. *Transactions of the American Fisheries Society* 121:444–455.
- Beauchamp, D. A., and E. J. Duffy. 2011. Stage-specific growth and survival during early marine life of Puget Sound Chinook salmon in the context of temporal-spatial environmental conditions and trophic interactions. Final report to the Pacific Salmon Commission. Washington Cooperative Fish and Wildlife Research Unit, Seattle, Washington, USA.
- Boldt, J. L., M. Thompson, C. N. Rooper, D. E. Hay, J. F. Schweigert, T. J. Quinn II, J. S. Cleary, and C. M. Neville. 2019. Bottom-up and top-down control of small pelagic forage fish: factors affecting age-0 herring in the Strait of Georgia, British Columbia. *Marine Ecology Progress Series* 617–618:53–66.
- Bollens, S. M., R. vanden Hooff, M. Butler, J. R. Cordell, and B. W. Frost. 2010. Feeding ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) in a northeast Pacific fjord: diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources. *Fisheries Bulletin* 108:393–407.
- Casazza, M., et al. 2016. Endangered species management and ecosystem restoration: finding the common ground. *Ecology and Society* 21:19.
- Cederholm, C. J., M. D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contributions on nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24:6–15.
- Claiborne, A. M., L. Campbell, B. Stevick, T. Sandell, J. P. Losee, M. Litz, and J. Anderson. In press. Correspondence between scale growth, feeding conditions, and survival of adult Chinook salmon returning to the southern Salish Sea: implications for forecasting. *Progress in Oceanography*.
- Cline, T. J., J. Ohlberger, and D. E. Schindler. 2019. Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution* 3:935–942.
- Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537–550.
- Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho and fall

- Chinook salmon in the Pacific Northwest. *Bulletin of Marine Science* 62:409–425.
- Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evolutionary Applications* 1:252–270.
- Deriso, R. B., M. N. Maunder, and W. H. Pearson. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. *Ecological Applications* 18:1270–1286.
- Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68:232–240.
- Duffy, E. J., D. A. Beauchamp, and R. M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. *Estuarine, Coastal and Shelf Science* 64:94–107.
- Duffy, E. J., D. A. Beauchamp, R. M. Sweeting, R. J. Beamish, and J. S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. *Transactions of the American Fisheries Society* 139:803–823.
- Ebbesmeyer, C. C., J. Q. Word, and C. A. Barnes. 1988. Puget Sound: a fjord system homogenized with water recycled over sills by tidal mixing. In B. Kjerfve, editor. *Hydrodynamics of estuaries: estuarine case studies*. CRC Press, Boca Raton, Florida, USA.
- Ford, M. J., J. A. Hempelmann, M. B. Hanson, K. L. Ayres, R. W. Baird, C. K. Emmons, J. I. Lundin, G. S. Schorr, S. K. Wasser, and L. K. Park. 2016. Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. *PLOS ONE* 11:e0144956.
- Furnell, D. J., and J. R. Brett. 1986. Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:999–1004.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2013. *Bayesian data analysis*. CRC Press, Boca Raton, Florida, USA.
- Gelman, A., B. Goodrich, J. Gabry, and A. Vehtari. 2019. R-squared for Bayesian regression models. *The American Statistician* 73:307–309.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Greene, C. M., and T. J. Beechie. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Science* 61:590–602.
- Greene, C. M., D. W. Jensen, G. R. Pess, E. A. Steel, and E. M. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. *Transactions of the American Fisheries Society* 134:1562–1581.
- Grossman, G. D., and T. N. Simon. 2019. Density-dependent effects on salmonid populations: a review. *Ecology of Freshwater Fish*. <https://doi.org/10.1111/eff.12523>
- Hanson, M. B., et al. 2010. Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endangered Species Research* 11:69–82.
- Healey, M. C. 1980. The ecology of juvenile chinook salmon in Georgia Strait, British Columbia. Pages 203–229 in W. J. McNeil and D. C. Himsworth, editors. *Salmonid ecosystems of the North Pacific*. Oregon State University Press, Corvallis, Oregon, USA.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 313–394 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, B.C., Canada.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 119–230 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, B.C., Canada.
- Holt, R. D., and M. B. Bonsall. 2017. Apparent competition. *Annual Review of Ecology, Evolution, and Systematics* 48:447–471.
- Jeffries, S., H. Huber, J. Calambokidis, and J. Laake. 2003. Trends and status of harbor seals in Washington State: 1978–1999. *Journal of Wildlife Management* 67:208–219.
- Jones, H. P., P. C. Jones, E. B. Barbier, R. C. Blackburn, J. M. R. Benayas, K. D. Holl, M. McCrackin, P. Meli, D. Montoya, and D. M. Mateos. 2018. Restoration and repair of Earth's damaged ecosystems. *Proceedings of the Royal Society of London B* 285:20172577.
- Kaczynski, V. W., R. J. Feller, J. Clayton, and R. J. Gerke. 1973. Trophic analysis of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) in Puget Sound. *Journal of the Fisheries Research Board of Canada* 30:1003–1008.
- Kaeriyama, M., H. Seo, and H. Kudo. 2009. Trends in run size and carrying capacity of Pacific salmon in the North Pacific Ocean. *North Pacific Anadromous Fish Commission Bulletin* 5:293–302.

- Kaga, T., S. Sato, T. Azumaya, N. D. Davis, and M. A. Fukuwaka. 2013. Lipid content of chum salmon *Oncorhynchus keta* affected by pink salmon *O. gorbuscha* abundance in the central Bering Sea. *Marine Ecology Progress Series* 478:211–221.
- Khangaonkar, T., B. S. Sackmann, W. Long, T. Mohamedali, and M. Roberts. 2012. Simulation of annual biogeochemical cycles of nutrient balance, phytoplankton bloom(s), and DO in Puget Sound using an unstructured grid model. *Ocean Dynamics* 62:1353–1379.
- Leslie, H. M., and K. L. McLoed. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* 5:540–548.
- Levin, P. S., M. J. Fogarty, S. A. Murawski, and D. Fluharty. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology* 7: e1000014.
- Levin, P. S., et al. 2018. Building effective fishery ecosystem plans. *Marine Policy* 92:48–57.
- Lorenzen, K., and E. V. Camp. 2019. Density-dependence in the life history of fishes: When is a fish recruited? *Fisheries Research* 217:5–10.
- Losee, J. P., A. Dufault, and N. W. Kendall. 2019. Changing salmon: an analysis of body mass, abundance and survival trends across 45 years in Puget Sound. *Fish and Fisheries* 20:934–951.
- Losee, J. P., J. A. Miller, W. T. Peterson, D. J. Teel, and K. C. Jacobson. 2014. Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook salmon. *Canadian Journal of Fisheries and Aquatic Science* 71:1747–1757.
- Malick, M. J., M. B. Rutherford, and S. P. Cox. 2017. Confronting challenges to integrating Pacific salmon into ecosystem-based management policies. *Marine Policy* 85:123–132.
- Marshall, K. N., A. C. Stier, J. F. Samhour, R. P. Kelly, and E. J. Ward. 2016. Conservation challenges of predator recovery. *Conservation Letters* 9:70–78.
- Marston, G. W. 2017. Do freshwater growth opportunities and migration barriers limit recovery of imperiled anadromous *Oncorhynchus mykiss* populations?. University of Washington, Seattle, Washington, USA.
- Moore, S. K., N. J. Mantua, J. P. Kellogg, and J. A. Newton. 2008. Local and large-scale climate forcing of Puget Sound oceanographic properties on seasonal to interdecadal timescales. *Limnology and Oceanography* 53:1746–1758.
- Nelson, B. W., A. O. Shelton, J. H. Anderson, M. J. Ford, and E. J. Ward. 2019. Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea. *Ecosphere* 10:e02922.
- Nelson, B. W., C. J. Walters, A. W. Trites, and M. K. McAllister. 2018. Wild Chinook salmon productivity is negatively related to seal density, and not related to hatchery releases in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Science* 76:447–462.
- Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries* 19:533–546.
- Osgood, G. J., L. A. Kennedy, J. J. Holden, E. Hertz, S. McKinnell, and F. Juanes. 2016. Historical diets of forage fish and juvenile Pacific salmon in the strait of Georgia, 1966–1968. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 8:580–594.
- Parker, R. R. 1962. Estimates of ocean mortality rates for Pacific salmon (*Oncorhynchus*). *Journal of the Fisheries Research Board of Canada* 19:561–588.
- Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. *Journal of the Fisheries Research Board of Canada* 25:757–794.
- Pearson, W. H., R. B. Deriso, R. A. Elston, S. E. Hook, K. R. Parker, and J. W. Anderson. 2012. Hypotheses concerning the decline and poor recovery of Pacific herring in Prince William Sound, Alaska. *Reviews in Fish Biology and Fisheries* 22:95–135.
- Phillips, A. C., and W. E. Barraclough. 1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Technical Report 830. Department of Fisheries and the Environment, Fisheries and Marine Service, Nanaimo, Canada.
- Pikitch, E. K., et al. 2004. Ecosystem-based fisheries management. *Science* 205:346–347.
- Preikshot, D., R. J. Beamish, and C. M. Neville. 2013. A dynamic model describing ecosystem-level changes in the Strait of Georgia from 1960 to 2010. *Progress in Oceanography* 115:28–40.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington, USA.
- R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhodes, L. D., C. A. Rice, C. M. Greene, D. J. Teel, S. L. Nance, P. Moran, C. A. Durkin, and S. B. Gezhagne. 2011. Nearshore ecosystem predictors of a bacterial infection in juvenile Chinook salmon. *Marine Ecology Progress Series* 432:161–172.
- Rice, C. A., C. M. Greene, P. Moran, D. J. Teel, D. R. Kuligowski, R. R. Reisenbichler, E. M. Beamer, J. R. Karr, and K. L. Fresh. 2011. Abundance, stock

- origin, and length of marked and unmarked juvenile Chinook Salmon in the surface waters of greater Puget Sound. *Transactions of the American Fisheries Society* 140:170–189.
- Riddell, B., M. Bradford, R. Carmichael, D. Hankin, R. Peterman, and A. Wertheimer. 2013. Assessment of status and factors for decline of Southern B.C. Chinook Salmon: independent panel's report. Prepared with the assistance of D.R. Marmorek and A.W. Hall, Vancouver, B.C. for Fisheries and Oceans Canada (Vancouver, B.C.) and Fraser River Aboriginal Fisheries Secretariat (Merritt, B.C.), Canada.
- Romanuk, T. N., and C. D. Levings. 2005. Stable isotope analysis of trophic position and terrestrial vs. marine carbon sources for juvenile Pacific salmonids in nearshore marine habitats. *Fisheries Management and Ecology* 12:113–121.
- Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665–706.
- Ruff, C. P., et al. 2017. Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations. *Fisheries Oceanography* 26:625–637.
- Ruggerone, G. T., and B. M. Connors. 2015. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Science* 72:818–833.
- Ruggerone, G. T., E. Farley, J. L. Nielsen, and P. Hagen. 2005. 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. *Fishery Bulletin* 103:355–370.
- Ruggerone, G. T., and F. A. Goetz. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:1756–1770.
- Ruggerone, G. T., and J. R. Irvine. 2018. Numbers and Biomass of Natural- and Hatchery-Origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 10:152–168.
- Ruggerone, G. T., and J. L. Nielsen. 2004. Evidence for competitive dominance of Pink salmon (*Oncorhynchus gorbuscha*) over other Salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries* 14:371–390.
- Ruggerone, G. T., A. M. Springer, L. D. Shaul, and G. B. van Vliet. 2019. Unprecedented biennial pattern of birth and mortality in an endangered apex predator, the southern resident killer whale, in the eastern North Pacific Ocean. *Marine Ecology Progress Series* 608:291–296.
- Ruggerone, G. T., M. Zimmermann, K. W. Myers, J. L. Nielsen, and D. E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaska sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fisheries Oceanography* 12:209–219.
- Samhuri, J. F., A. C. Stier, S. M. Hennessey, M. Novak, B. S. Halpern, and P. S. Levin. 2017. Rapid and direct recoveries of predators and prey through synchronized ecosystem management. *Nature Ecology and Evolution* 1:0068.
- Satterthwaite, W. H., S. M. Carlson, S. D. Allen-Moran, S. Vincenzi, S. J. Bograd, and B. K. Wells. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Marine Ecology Progress Series* 511:237–248.
- Sharma, R., L. A. Vélez-Espino, A. C. Wertheimer, N. Mantua, and R. C. Francis. 2013. Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography* 22:14–31.
- Shiomoto, A., K. Tadokoro, K. Nagasawa, and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Marine Ecology Progress Series* 150:75–85.
- Siple, M. C., and T. B. Francis. 2016. Population diversity in Pacific herring of the Puget Sound, USA. *Oecologia* 180:111–123.
- Southern Resident Orca Task Force. 2018. Draft report and potential recommendations. https://www.governor.wa.gov/sites/default/files/SRKWDraftReport_09-24-18.pdf
- Springer, A. M., G. B. van Vliet, N. Bool, M. Crowley, P. Fullagar, M.-A. Lea, R. Monash, C. Price, C. Vertigan, and E. J. Woehler. 2018. Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem. *Proceedings of the National Academy of Sciences USA* 115:E5038–E5045.
- Stan Development Team. 2018a. RStan: the R interface to Stan. R package version 2.17.13. <http://mc-stan.org>
- Stan Development Team. 2018b. RStanArm: Bayesian applied regression modeling via Stan. R package version 2.17.14. <http://mc-stan.org>
- Tallis, H., P. S. Levin, M. Ruckelshaus, S. E. Lester, K. L. McLoed, D. L. Fluharty, and B. S. Halpern. 2010.

- The many faces of ecosystem-based management: making the process work today in real places. *Marine Policy* 34:340–348.
- TCW Economics. 2008. Economic analysis of the non-treaty commercial and recreational fisheries in Washington State. Prepared for Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Therriault, T. W., D. E. Hay, and J. F. Schweigert. 2009. Biologic overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). *Marine Ornithology* 37:3–8.
- Thomas, A. C., B. W. Nelson, M. M. Lance, B. E. Deagle, and A. W. Trites. 2016. Harbour seals target juvenile salmon of conservation concern. *Canadian Journal of Fisheries and Aquatic Science* 74:907–921.
- Toge, K., R. Yamashita, K. Kazama, M. Fukuwaka, O. Yamamura, and Y. Watanuki. 2011. The relationship between pink salmon biomass and the body condition of short-tailed shearwaters in the Bering Sea: Can fish compete with seabirds? *Proceedings of the Royal Society of London B: Biological Sciences* 278:2584–2590.
- Trudel, M., J. Fisher, J. A. Orsi, J. F. T. Morris, M. E. Thiess, R. M. Sweeting, S. Hinton, E. A. Fergusson, and D. W. Welch. 2009. Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. *Transactions of the American Fisheries Society* 138:1369–1391.
- Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432.
- Ward, E. J., J. H. Anderson, T. J. Beechie, G. R. Pess, and M. J. Ford. 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. *Global Change Biology* 21:2500–2509.
- Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1110–1122.
- Washington Department of Fish and Wildlife (WDFW). 2018a. FishBooks hatchery database. Hatcheries Data Unit, Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Washington Department of Fish and Wildlife (WDFW). 2018b. Hatcheries headquarters database. Hatcheries Data Unit, Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Washington Department of Fish and Wildlife (WDFW). 2019. Proposal to increase hatchery production to benefit Southern Resident Killer Whales. Washington Department of Fish and Wildlife, Olympia, Washington, USA.
- Wells, B. K., et al. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *Journal of Marine Systems* 174:54–63.
- Williams, R., M. Krkošek, E. Ashe, T. A. Branch, S. Clark, P. S. Hammond, E. Hoyt, D. P. Noren, D. Rosen, and A. Winship. 2011. Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PLOS ONE* 6:e26738.
- Wolter, K., and M. S. Timlin. 1998. Measuring the strength of ENSO—how does 1997/98 rank? *Weather* 53:315–324.

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