Optimization of hatchery-origin Chinook and hatchery- and natural-origin coho salmon releases in the Salish Sea through ecosystem-based management: adapting hatchery practices to pink salmon abundance

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Abstract

Understanding how species influence the population dynamics of each other is an essential part of ecosystem-based management. We first analyzed 30 years of data and found that density-dependent survival of hatchery Chinook salmon (*Oncorhynchus tshawytscha*) released into the Salish Sea, on the western side of the US and Canada border, may be associated with the presence of naturally-produced pink salmon (*O. gorbuscha*). Pink salmon are highly abundant as juveniles only in even-numbered years. We 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. 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 hatchery Chinook salmon marine survival 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. This suggests lower, density-dependent survival of juvenile Salish Sea Chinook salmon during even outmigration years. Second, we also evaluated whether wild Chinook salmon productivity was associated with a pink salmon even/odd year signal. We did not find any association. This may be due to emigration periods of hatchery vs. natural-origin Chinook salmon. Finally, we performed a similar analysis for Salish Sea hatchery and wild coho salmon (*O. kisutch*) populations as we did for hatchery Chinook salmon to examine density-dependent survival of these fish. We found a strong negative relationship between coho marine survival and the numbers of hatchery coho salmon released throughout the Salish Sea. However, the presence or absence of pink salmon did not appear to be associated with coho marine survival rates. Our analyses suggest that scientists and managers should further investigate potential mechanisms for density-dependent survival of hatchery Chinook and coho salmon from Salish Sea hatcheries when designing strategies to maximize adult returns.

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, Samhouri et al. 2017, Springer et al. 2018). Species recovery can be informed by understanding the linkages between the components in an ecosystem (Samhouri et al. 2017), such as density-dependent interactions (e.g., Deriso et al. 2008), apparent competition (Holt and Bonsall 2017), and evaluating the success of previously-implemented restoration and recovery actions (e.g., 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 (e.g., Crozier et al. 2008), the abundance of other (non-salmonid) species in the system (e.g., 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 (e.g., 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 (e.g., 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; WDFW's 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; 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). Almost all Salish Sea pink salmon are of wild origin. The spring following spawning, 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).

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 (Washington Department of Fish and Wildlife (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). Natural-origin Chinook salmon have a protracted emigration window into Puget Sound as they enter as fry, subyearlings, and yearling fish (Nelson et al. 2019). Chinook salmon that leave the Salish Sea for the Pacific Ocean tend to do so the following spring (i.e., after ~ one year in the Salish Sea; Trudel et al. 2009). Coho salmon (*O. kisutch*) are, for the most part, released from hatcheries as yearlings into the Salish Sea. All natural-origin coho salmon smolts are one-year old. Thus, for the most part, coho salmon emigrate at different times and at different sizes than most Chinook salmon, which are subyearling releases.

Juvenile Chinook, coho, and pink salmon are all found in the Salish Sea between April through July of even years (Duffy et al. 2005; B. Berejikian, NOAA Fisheries, unpublished data). During this time Chinook and pink salmon 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 before hatchery-origin Chinook salmon (and most natural-origin Chinook), 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 and coho 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 Salmon Conservation Reporting Engine [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 (ESA) 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). Coho salmon in Puget Sound are not listed under the ESA.

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). Increased coho salmon returns are also desired. Chinook and coho salmon have been produced by hatcheries for over 100 years (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, Washington Department of Fish and Wildlife (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 and coho 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.

Third, we perform a similar Bayesian hierarchical regression analysis but this time for to relate hatchery- and natural-origin coho salmon marine survival rates to the abundance of juvenile coho release numbers along with the presence of juvenile pink salmon in the Salish Sea when the coho juveniles were emigrating. Finally, we test whether natural-origin Salish Sea Chinook productivity has been associated with the presence or absence of juvenile pink salmon in the Sea and (potentially interacting with) the abundance of hatchery-origin Chinook released by extending the approach in a previous study (Nelson et al. 2018).

We seek to answer the question: in the past, when more Chinook and coho 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 Chinook and coho 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

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 years for those released as sub-yearlings (at 2-3 months) or age 3 years 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 ages 2 or 3; Parker 1962, 1968, Furnell and Brett 1986, Beamish and Mahnken 2001, Quinn et al. 2005, Lorenzen and Camp 2019). Survival rates were estimated using a backwards cohort reconstruction (Ruff et al. 2017; Equation 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 years). 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 entry years (OEY) 1983-2012 (Table 1 and Figure 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 (e.g., 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; Figure 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.rmpc.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 (Figure 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 1980-2010. 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, 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/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 suggests 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 (Figure 1). These data are based on scales sampled from > 2 million Chinook salmon between 1985 and 2014 (Table A1). For years 1980-1984 we applied the average age composition from 1985-1989.

Coho salmon

We used CWT data from 28 stocks of hathcery- and natural-origin Salish Sea coho salmon (Table 2 and Figure 2) between 1972 and 2015, which were also analyzed and described in detail by Zimmerman et al. (2015).

Natural-origin Chinook salmon

We employed productivity data of 20 wild stocks of Chinook salmon in the Salish Sea and Washington coast (Table 3 and Figure 3) between 1972 and 2008. Detailed information on these stocks and their data are provided in Nelson et al. (2018).

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). No one has examined this relationship for coho salmon yet. 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.

We also sought to examined the relationship between Chinook and coho density-dependent marine survival compared to juvenile chum salmon (*O. keta*) abundance in the Salish Sea. However, while Puget Sound and east coast Vancouver Island annual chum salmon abundance are available from the 1970s to present, data are only available for the Fraser River system from the 1990s to present. Because the Fraser River system produces a large proprtion of the chum salmon emigrating through central and southern Salish Sea, excluding Fraser River system chum abundance data in our analyses was not practical. Thus, we were not able to perform similar analyses on chum salmon abundance as we were for pink salmon presence/absence.

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 $(-log_e(Survival))$ 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 4).

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 4). The eight best-performing models were then compared using an approximation of leave-one-out (LOO) cross-validation from the "loo" package in R (Table A2; 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 competing models, the model with the lowest number of effective parameters is favored (Vehtari 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 2017). 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 samples 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 package'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 estimated survival rates for stocks in each geographical 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-reconstructed index numbers of adult Chinook salmon 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 perform run reconstructions for them) and used simple 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.

Modeling coho salmon marine recovery (survival) rates

To evaluate factors associated with marine survival of coho salmon, we fit hierarchical regression models to survival/mortality rates from CWT data (Table 2). Specifically, we modeled instantaneous mortality rate $(-log_e(Survival))$ from release to ocean age-2 for each stock i in region r in year t ($M_{t,i,o,j}$), as a function of multiple covariates. We explored a total of 30 model formulations, which included combinations of both random- and fixed-effects and several covariates: juvenile coho origin (hatchery vs. wild), release region, the number of annual hatchery releases in each region, seal density, presence of pink salmon in the Salish Sea, and release year. All statistical analysis was performed using the R Programming Environment (R development core team 2017).

Modeling natural-origin Chinook salmon productivity

To evaluate the relationship between natural-origin Chinook salmon productivity and the presence or absence of pink salmon during juvenile emigration years, we used the (best-performing) Bayesian hierarchical model described in Nelson et al. (2018), a Ricker formulation that included regional hatchery abundance and regional harbor seal (*Phoca vitulina*) densities as covariates. We extended the original model to incorporate the presence/absence of pink salmon two forms:

Equation 1: $$\ln\left(\frac{R_{t,i}}{S_{t,i}}\right) = \alpha_i + \beta_i S_{t,i} + q_i Seals_{t+1,i} + h_i Hatch_{t+1,i} + p_i Pinks_t + \varepsilon_{t,i}$$

Equation 2: $$\ln\left(\frac{R_{t,i}}{S_{t,i}}\right) = \alpha_i + \beta_{0_i} S_{t,i} + q_i Seals_{t+1,i} + h_i Hatch_{t+1,i} + p_i Pinks_t + \beta_{1_i}\left(Pinks_t \times Hatch_{t+1,i}\right) + \varepsilon_{t,i}$$

where *R* is the number of recruits resulting from adult spawners (*S*) in brood year (*t*) for stock *i* (*i*=1,…, *N*), α is the productivity parameter for each stock, β is the capacity/density-dependent parameter (Quinn II and Deriso 1999), and ε are the error residuals, which are assumed to be normally distributed and autocorrelated through a lag-1 autoregressive process (see Nelson et al. 2018 for details). Biological covariates included in the model were regional seal density (*q, Seals*), regional hatchery releases (*h, Hatch*), and a binary factor (0, 1) that corresponds to whether or not brood year *t* was a pink/odd year (*p, Pinks*). Additionally, we assumed the regression coefficients associated with the biological covariates (*q, h, p*) were drawn from global/exchangeable distributions:

$$q_i \sim Normal\left(q, \sigma_q\right)$$
$$h_i \sim Normal\left(h, \sigma_h\right)$$
$$p_i \sim Normal\left(p, \sigma_p\right)$$

All statistical analysis was performed using the R Programming Environment (R development core team 2017). Parameters for the above model were estimated in a Bayesian framework using MCMC using WinBUGS software (Spiegelhalter et al. 1996). A more detailed description of the parameter estimation procedure can be found in Nelson et al. (2018).

Results

CWT hatchery Chinook recovery (marine survival) rates

Sub-yearling Salish Sea Chinook salmon marine 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%) (Figure A1). 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 (Figure A1).

The numbers of juvenile Chinook salmon released from hatcheries have varied considerably over time and among regions since the early 1980s (Figure 4). 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 (NOWA) and Vancouver Island (VAN) regions saw the greatest range in total hatchery production of Chinook over the period of this study (Figure 4).

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 4):

Equation 3 $M_{i,r,j,t} = \beta_{0_i} + LifeHist_j + Region_r + \beta_1 Hatch_{t,r} + Pink_t + \beta_2\left(Pink_t \times Hatch_{t,r}\right) + \varepsilon_i$,

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 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 $\varepsilon_i \sim N(0, \sigma_i)$, 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 4). Of note, candidate models that included random effects on independent variables other than the intercept (e.g., *Hatch*, *Pink*, *Pink x 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 effect 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 (Figure A2). 95.3% of the observed data points (653/685) fell within the 95% posterior predictive intervals (Figure A3), 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 5). Only four of 33 stocks (random effects) were different from the mean region effect (Figure A4): 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 (Figure 5 and Table 5). 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 6).

The estimated hatchery release abundance model coefficient (-0.12) suggested strong support (though not statistically "significant") for a positive relationship between survival and hatchery releases in non-pink years (Table 5). Therefore, in these odd emigration years, greater releases of hatchery Chinook salmon were associated with increased marine survival (Figure A5). Finally, the model did not show a significant difference in survival between sub-yearling and yearling Chinook salmon (Table 5).

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 (Figure 6). However, in pink years, increases in Chinook hatchery production were associated with a leveling off or a diminishing numbers 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 (Figure 6).

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 vs. the number of adult Chinook returns was negative in 5 of the 6 regions in Puget Sound (Figure 7). The trend was statistically significant at 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 relationship between hatchery releases and returns was significantly positive (≥ 95% probability of slope parameter being > zero) in either pink or non-pink years (Figure 7).

Coho salmon marine recovery (survival) rates

Model selection criteria (Table 7) showed that the best-performing model was:

Equation 4:
$$\ln\left(M_{t,i,o,j}\right) = \beta_{0_i} + \beta_1 Origin_o + \beta_{2_i} Hatch_{t,j} + \beta_{3_i} Seals_{t,j} + \beta_{4_i} \mathrm{Re}\,gion_j + \beta_{5_i}\left(Seals_{t,j} \times R\mathrm{e}\,gion_j\right) + \beta_{Year_t} + \varepsilon_{t,i}$$

where β_{0_i} is the stock-specific intercept; *Origin* is a binary factor that specifies hatchery- or wild-origin stocks; *Hatch* is the regional (Puget Sound vs. Strait of Georgia) hatchery abundance, which is standardized using a z-score; *Seals* is the regional density of harbor seals (from Nelson et al. 2018), also standardized by z-score, and β_{Year} is a “year effect” to control for common temporal trends in the data that aren’t explained by the aforementioned factors. Details for the Bayesian model-fitting process are identical to the Chinook model described above.

The best-performing model used for this analysis explained ~73% of the total variance in the data (Table 7). Similar to previous studies (Zimmerman et al. 2015), we found that natural origin of the coho salmon (as opposed to hatchery origin) was associated with significantly increased survival rates (i.e., reduced mortality) to ocean age-2 (Figure 8). After controlling for multiple factors, Strait of Georgia stock origin was found to have a positive impact on survival (Figure 8), although not to a statistically “significant” level. Interestingly, while Strait of Georgia stocks had higher than average survival rates compared to Puget Sound, seal density in the Strait of Georgia had a strong negative association with survival rates (Figure 8). The negative association between seal densities in the Strait of Georgia and survival rates of coho salmon persisted, even after controlling for the obvious negative temporal trend that was common in the data between the 1970s and 2010s (Figure 9). It is possible that there is strong confounding between the effects of seal density and temporal trends on coho salmon in the Puget Sound, which may be why the seal effect in the Puget Sound is non-existent. Preliminary univariate analyses between seal density and individual coho salmon stocks in the Puget Sound suggested that this relationship was very different on a stock-by-stock basis. For both regions, abundance of juvenile hatchery coho salmon released was associated with decreasing survival across the entire Salish Sea (Figure 8).

Natural-origin Chinook salmon productivity

The addition of covariates for pink salmon presence/absence did not meaningfully improve the goodness-of-fit from the original model. Specifically, both Equations 1 and 2 had a [Bayesian] R-squared value of 0.68—this is identical to that of the original model (see Nelson et al. 2018 Table 3). Further, the addition of pink salmon presence/absence as a single covariate (Equation 1) did not significantly change the effect sizes of other covariates (e.g., seals) from the original model (Table 3). Pink salmon presence was only a “significant” addition for a single Puget Sound stock (Snohomish; Table 3 and Figure 3), where it was negatively associated with natural mortality (i.e., increased survival).

We also tested the explanatory power of an interaction effect between pink salmon presence and hatchery abundance (Equation 2), similar to the one included for hatchery-origin Chinook (above). The global effect of the interaction between pink salmon presence and hatchery abundance was “significantly” positive at the 90% level, which suggests there is some support for an interaction (Figures 10 and A6), similar to what was found for hatchery-origin Chinook salmon stocks.

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 SRWK recovery (Washington Department of Fish and Wildlife (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 weren't 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 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.

In addition to our findings focused on hatchery-origin Chinook salmon, we expanded to examine density-dependent marine survival of coho salmon and productivity and natural-origin Chinook salmon (Nelson et al. 2018). We identified several issues that may be of importance for both species in future research. For coho salmon, the presence or absence of pink salmon during coho salmon smolt outmigration does not appear to be associated with coho salmon marine survival/mortality to a significant extent. This is because the addition of a pink salmon covariate did not meaningfully improve our statistical model for coho marine survival/mortality. However, we did find a strong negative relationship between coho salmon survival and hatchery abundance throughout the Salish Sea. The hatchery abundance variable with the most explanatory power was one in which annual hatchery releases were aggregated on the region scale (Puget Sound vs. Strait of Georgia), which may suggest density-dependent interactions among conspecifics are strongest on a regional or ecosystem level, as opposed to a local scale.

For wild Chinook salmon productivity, we showed that while pink salmon presence/absence alone does not correlate with this productivity, an interaction between pink salmon and abundance of hatchery conspecifics may exist that has a negative association with wild Chinook productivity. This interaction effect was “significant” at the 90% level, but not at 95%, which is the threshold conventionally used. Thus, we conclude that there is some evidence for an interaction similar to the one found for hatchery Chinook salmon and that future research should focus on systematic, experimental approaches to hatchery management to better understand such an interaction and potential mechanisms of such an interaction.

Our analysis is what we believe to be the first to document a strong correlation between harbor seal density and coho salmon marine survival in the Salish Sea. While the effect of seal density was only “significant” in the Strait of Georgia, it was clear from preliminary univariate analysis on a stock-by-stock basis that some coho salmon populations in the Puget Sound may also have a strong negative association with seal density. Thus, we suggest that more flexible alternative modeling approaches, such as the conditional autoregressive (CAR) models described in Nelson et al. (2018), be considered to account for the local/sub-regional effects of harbor seal density on coho salmon marine survival/mortality.

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) has 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 (e.g., 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 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 Bonsall 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 (for example, 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 et al. 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 years 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, Samhouri 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 grams 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).

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 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.

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Table 1. List of Salish Sea hatchery-origin 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 (n)
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
Northern Washington (NOWA)	Nooksack (NSF)	SY	1987-1997	10
	Nooksack Spring (NKS)	Y	1990-2012	21
	Samish (SAM)	SY	1986-2012	27
Northern Puget Sound (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 Summer (SFF)	SY	1995-2012	18
	Tulalip Summer (TUL)	SY	1986-2012	11
Middle Puget Sound (MPS)	Green (GRN)	SY	1986-2012	27
	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
	South Puget Sound Yearling (SPY)	Y	1988-2012	21
Fraser River (FRA)	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	30
	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

Table 2. List of coho salmon stocks included in this study. Shown are the stock names; geographical region (Puget Sound, Strait of Georgia) and sub-regions; the number of CWT groups for each stock (n); the year range represented in the data (Years), and the stock origin (hatchery [H] vs. wild [W]). This dataset was created and curated by the Salish Sea Marine Survival Project Technical Committee. Note: Stock IDs and sub-regions correspond with the map in Figure 2.

Stock ID	Stock name	Sub-region	Region	n	Years	Origin
1	Baker	NPS	PS	5	1983-1993	H
2	Baker wild	NPS	PS	22	1991-2014	W
3	Big Beef wild	HOOD	PS	39	1977-2015	W
4	Deschutes wild	SPS	PS	26	1977-2014	W
5	Dungeness	JUAN	PS	19	1972-2010	H
6	Elwha	JUAN	PS	17	1979-2014	H
7	Green	MPS	PS	40	1973-2015	H
8	Minter Creek	SPS	PS	22	1972-2014	H
9	Minter wild	SPS	PS	9	1982-2007	W
10	Nooksack	NOWA	PS	34	1976-2014	H
11	Puyallup	MPS	PS	40	1974-2015	H
12	Quilcene	HOOD	PS	30	1979-2014	H
13	Skagit	NPS	PS	21	1995-2015	H
14	Skokomish	HOOD	PS	38	1973-2014	H
15	Skykomish	NPS	PS	32	1983-2015	H
16	Skykomish wild	NPS	PS	9	1978-1986	W
17	Tulalip Bay	NPS	PS	36	1974-2014	H
18	Big Qualicum	GST	SOG	42	1973-2015	H
19	Black wild	GST	SOG	30	1985-2014	W
20	Chilliwack	FRTH	SOG	20	1982-2004	H
21	Inch	FRTH	SOG	32	1984-2015	H
22	Louis	FRTH	SOG	14	1990-2007	H
23	Myrtle wild	GST	SOG	14	2000-2011	W
24	Puntledge	GST	SOG	25	1978-2004	H
25	Quinsam	GST	SOG	40	1976-2015	H
26	Waterloo	GST	SOG	5	2002-2006	W
27	Goldstream	GST	SOG	15	1998-2013	H
28	Salmon wild	GST	SOG	19	1986-2007	W

Table 3. Natural-origin Chinook salmon stocks and selected regression coefficients for the Bayesian hierarchical model (Equation 1) for each stock. Marginal posterior effect sizes for pink salmon, regional harbor seal density, and regional hatchery abundance are shown, along with the 95% credible interval for each parameter. Parameters whose credible intervals do not overlap with zero are shown in bold. Locations of each stock are shown in Figure 3 and correspond with the first column in the table (ID).

Stock	**Pinks**	**Seals**	**Hatchery releases**
Cowichan (BC)	-0.18 (-0.38, 0.04)	**-1.50 (-2.39, -0.61)**	0.09 (-0.20, 0.44)
Puntledge (BC)	-0.01 (-0.22, 0.20)	-0.33 (-1.38, 0.82)	0.02 (-0.32, 0.39)
Nanaimo (BC)	0.04 (-0.16, 0.25)	**-1.20 (-1.78, -0.62)**	-0.11 (-0.40, 0.15)
Quinsam (BC)	0.02 (-0.14, 0.16)	**-1.08 (-2.01, -0.22)**	-0.13 (-0.53, 0.15)
Qualicum (BC)	0.02 (-0.12, 0.15)	-0.60 (-1.22, 0.00)	-0.05 (-0.32, 0.20)
Harrison (BC)	-0.04 (-0.21, 0.13)	**-1.08 (-1.75, -0.40)**	0.10 (-0.20, 0.47)
Shuswap (BC)	0.07 (-0.12, 0.26)	-0.21 (-0.70, 0.16)	0.01 (-0.25, 0.20)
Chilliwack (BC)	-0.07 (-0.33, 0.15)	**-1.30 (-2.56, -0.17)**	-0.11 (-0.59, 0.22)
Skokomish (US)	0.04 (-0.11, 0.18)	**-1.13 (-2.00, -0.25)**	0.16 (-0.02, 0.37)
Skagit (US)	-0.16 (-0.36, 0.04)	-0.78 (-1.76, 0.34)	-0.05 (-0.23, 0.12)
Snohomish (US)	**-0.11 (-0.19, -0.01)**	**-1.66 (-2.58, -0.69)**	0.01 (-0.15, 0.20)
Stilliguamish (US)	0.02 (-0.12, 0.14)	**-1.60 (-2.88, -0.49)**	**0.20 (0.00, 0.43)**
Green (US)	-0.01 (-0.12, 0.11)	**-1.71 (-2.79, -0.69)**	-0.00 (-0.19, 0.21)
Lake Washington (US)	0.05 (-0.09, 0.16)	**-1.86 (-2.76, -0.96)**	-0.12 (-0.33, 0.07)
Nisqually (US)	0.02 (-0.18, 0.23)	-0.70 (-1.91, 0.63)	-0.10 (-0.44, 0.18)
Hoko (US)	0.01 (-0.14, 0.13)	0.03 (-0.66, 0.59)	0.12 (-0.07, 0.31)
Elwha (US)	-0.01 (-0.28, 0.23)	-0.81 (-2.16, 0.43)	0.07 (-0.28, 0.56)
Queets (US)	0.05 (-0.11, 0.22)	**-0.52 (-0.70, -0.33)**	-0.17 (-0.45, 0.09)
Quillayute (US)	0.00 (-0.18, 0.19)	**-0.67 (-0.92, -0.39)**	-0.02 (-0.29, 0.23)
Hoh (US)	0.09 (-0.10, 0.30)	**-0.43 (-0.63, -0.24)**	0.05 (-0.18, 0.30)
Global mean coefficients	-0.01 (-0.09, 0.07)	**-0.95 (-1.39, -0.56)**	0.00 (-0.13, 0.11)

Table 4. Summary of model formulations, selection criteria (Widely Applicable Information Criteria [WAIC]), and fit (Bayes R^2) for all candidate models evaluated for hatchery-origin Chinook salmon. *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 Table A2) is bolded.

Model number	**Formula**	**WAIC (+/-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*$_1$	1934 (42)	0.21
6	*LifeHist + Region + Hatch*$_2$	1937 (42)	0.20
7	*LifeHist + Region + Hatch*$_3$	1937 (42)	0.20
8	*LifeHist + Region + Hatch + Pink*	1934 (42)	0.21
9	*LifeHist + Region + Hatch + Pink + (Pink x Hatch)*	1927 (43)	0.22
10	*Stock + LifeHist + Region + Hatch + Pink + (Pink x Hatch)*	1755 (44)	0.44
11	***Stock* + LifeHist + Region + Hatch + Pink + (Pink x Hatch)***	**1753 (44)**	**0.41**
12	*Stock + LifeHist + Region + Hatch + Pink + (Pink x Hatch) + Year*	1729 (49)	0.50
13	*Stock* + LifeHist + Region + Hatch + Pink + (Pink x Hatch) + Year*	1729 (49)	0.48
14	*Stock + LifeHist + Region + Hatch* + Pink* + (Pink x Hatch)* + Year*	1734 (49)	0.50
15	*Stock* + LifeHist + Region + Hatch* + Pink* + (Pink x Hatch)* + Year*	1734 (49)	0.49
16	*Stock* + LifeHist + Region + Hatch* + Pink* + Year + (Pink x Hatch)* + (Region x Year)*	1784 (40)	0.64
17	*Stock* + LifeHist + Region + Hatch + Pink + (Region x Pink x Hatch)*	1769 (45)	0.43
18	*Stock* + LifeHist + Hatch** + Pink** + (Pink x Hatch)***	1759 (44)	0.41

*Denotes random effect (stock level)

**Denotes random effect (region level)

$_1$ Regional hatchery releases

$_2$ Basin hatchery releases (Puget Sound, Strait of Georgia)

$_3$ All hatchery releases (Salish Sea-wide)

Table 5. Summary of posterior distributions for regression coefficients in the best-performing model for hatchery-origin Chinook salmon (Model 11; see Table 4). 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.

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**

Table 6. Hatchery-origin Chinook salmon best-performing model (Model 11; see Table 4) 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 year.

		% survival (95% CI)	
Region	**Stock**	**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)
	TUL	0.97 (0.60-1.56)	0.86 (0.53-1.39)
MPS	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)
	WRY	1.03 (0.49-2.16)	0.91 (0.44-1.90)
SPS	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)
	SPY	0.54 (0.27-1.04)	0.48 (0.25-0.91)
FRA	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)
	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)
VAN	QUI	0.95 (0.71-1.31)	0.85 (0.63-1.16)
	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)

Table 7. Summary of coho salmon model selection criteria (WAIC), and fit (Bayes R^2) for all candidate models evaluated in this analysis. Model selection criteria and model fit are based on eight MCMC chains, each containing 1000 samples. Included in the summary is the expected log of the predictive density (ELPD) and its standard error (ELPD-SE), and the number of effective parameters (p).

Model	**WAIC**	**SE WAIC**	**ELPD**	**SE ELPD**	**p**	**Bayes R^2**
1	502	37	-251	19	2	0.00
2	479	39	-239	19	3	0.04
3	365	43	-183	21	26	0.25
4	455	39	-228	20	9	0.09
5	494	39	-247	20	3	0.01
6	485	40	-242	20	3	0.03
7	458	43	-229	21	3	0.07
8	132	48	-66	24	47	0.48
9	193	39	-96	20	3	0.36
10	504	38	-252	19	3	0.00
11	306	38	-153	19	4	0.25
12	501	38	-250	19	3	0.01
13	240	39	-120	20	6	0.32
14	55	47	-27	23	31	0.52
15	365	42	-182	21	24	0.21
16	455	39	-228	20	9	0.07
17	53	47	-26	23	29	0.50
18	115	45	-58	22	14	0.44
19	-85	41	43	21	48	0.60
20	78	42	-39	21	29	0.48
21	-95	40	47	20	62	0.62
22	37	39	-18	19	48	0.52
23	-20	42	10	21	45	0.56
24	188	38	-94	19	24	0.39
25	-84	40	42	20	30	0.59
26	56	47	-28	23	30	0.50
27	47	46	-24	23	30	0.50
28	-91	40	45	20	40	0.60
29	**-297**	**52**	**148**	**26**	**75**	**0.73**
30	-124	39	62	20	31	0.61

Figures

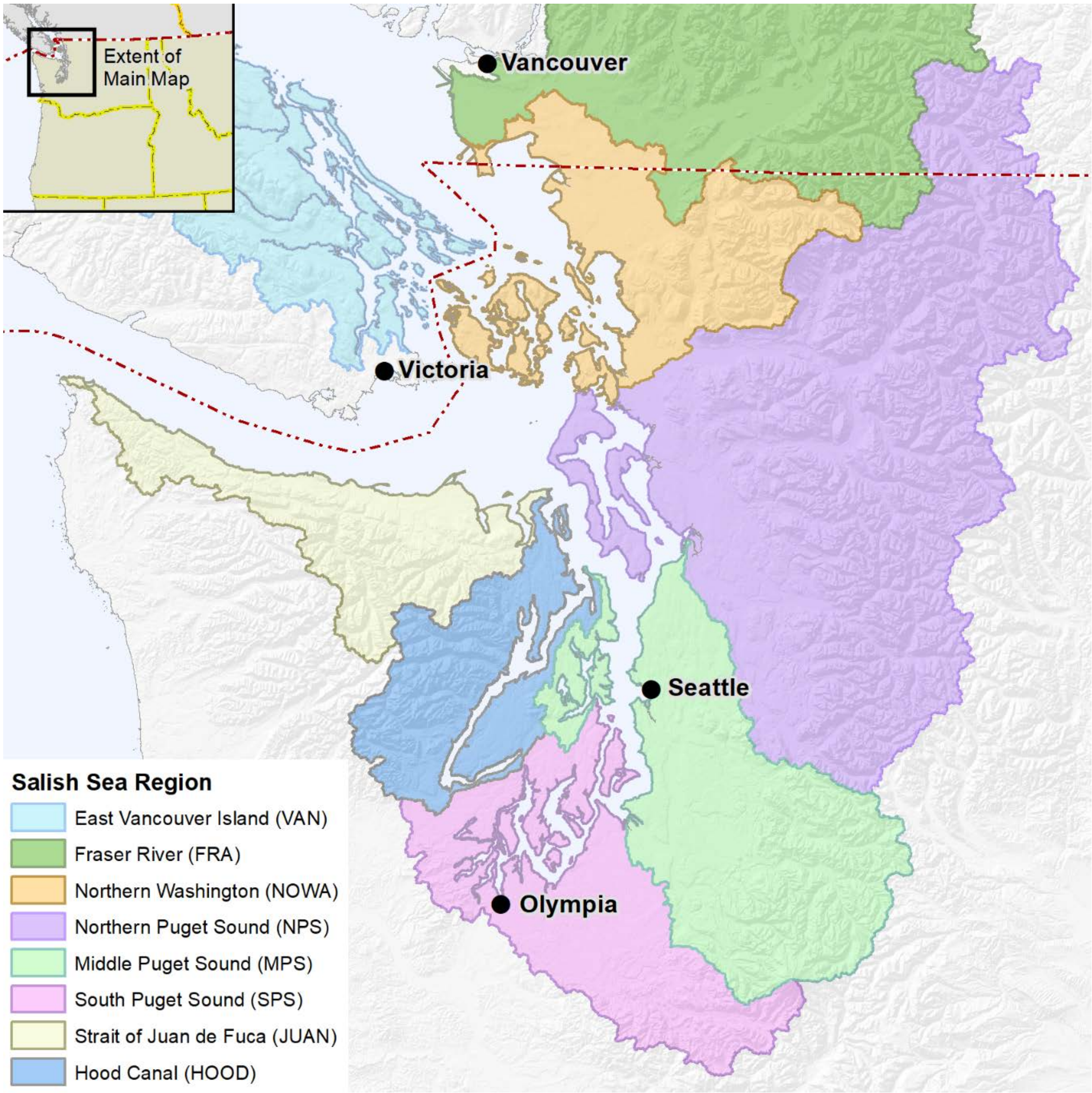


Figure 1. Map of the eight central and southern Salish Sea regions from which hatchery-origin Chinook salmon assessed. The red dashed line indicates the border between the USA and Canada.

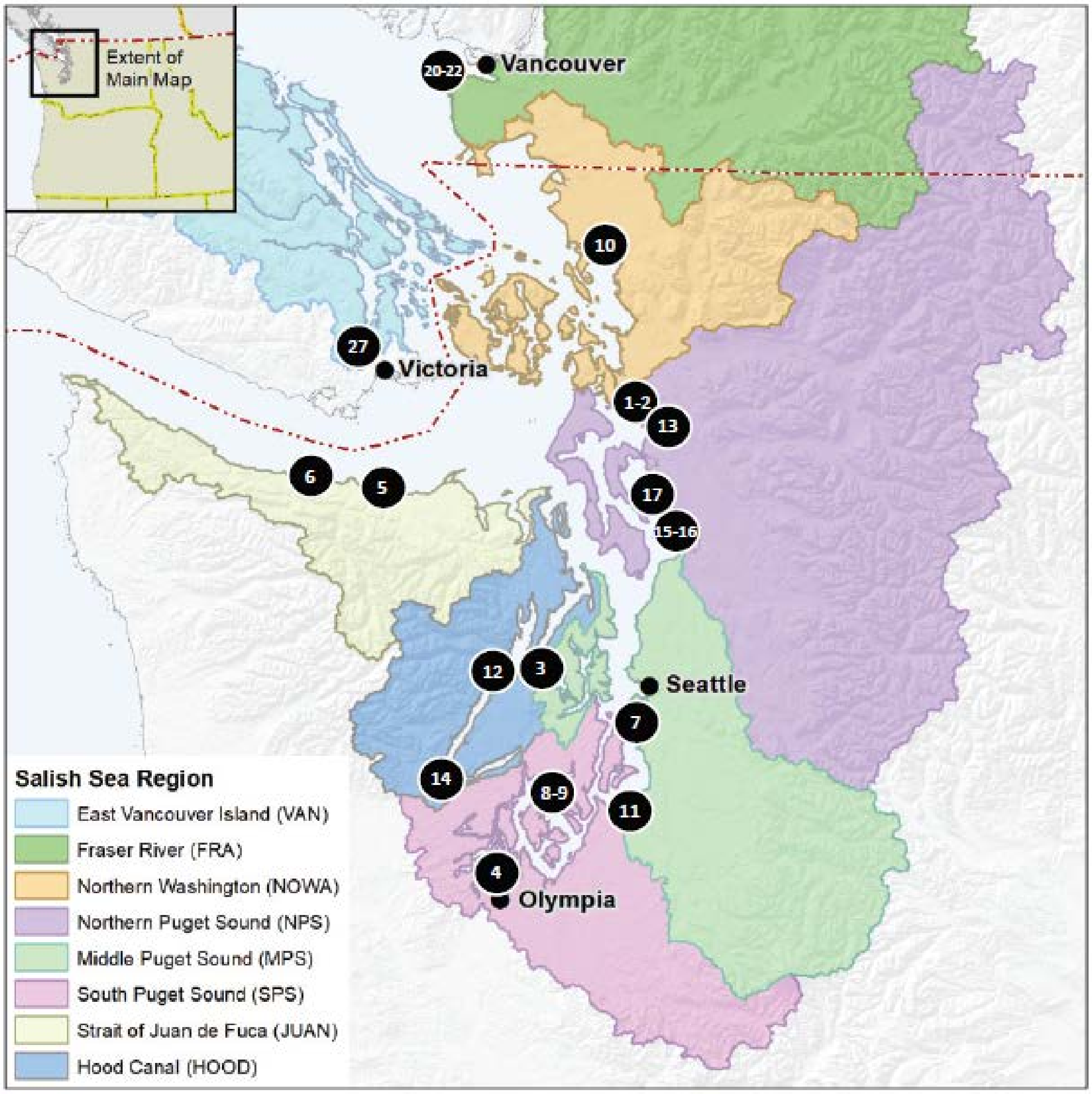


Figure 2. Map of Salish Sea sub-regions, which we used to geographically separate hatchery releases for coho stocks included in this study. In addition to sub-regional groupings shown here, we also aggregated hatchery releases by region (Puget Sound vs. Strait of Georgia); the regional groupings were used in the best-performing model. Numbered circles correspond with the locations of coho salmon stocks listed in Table 2n. Note: several Strait of Georgia stocks are outside the extent of the map.

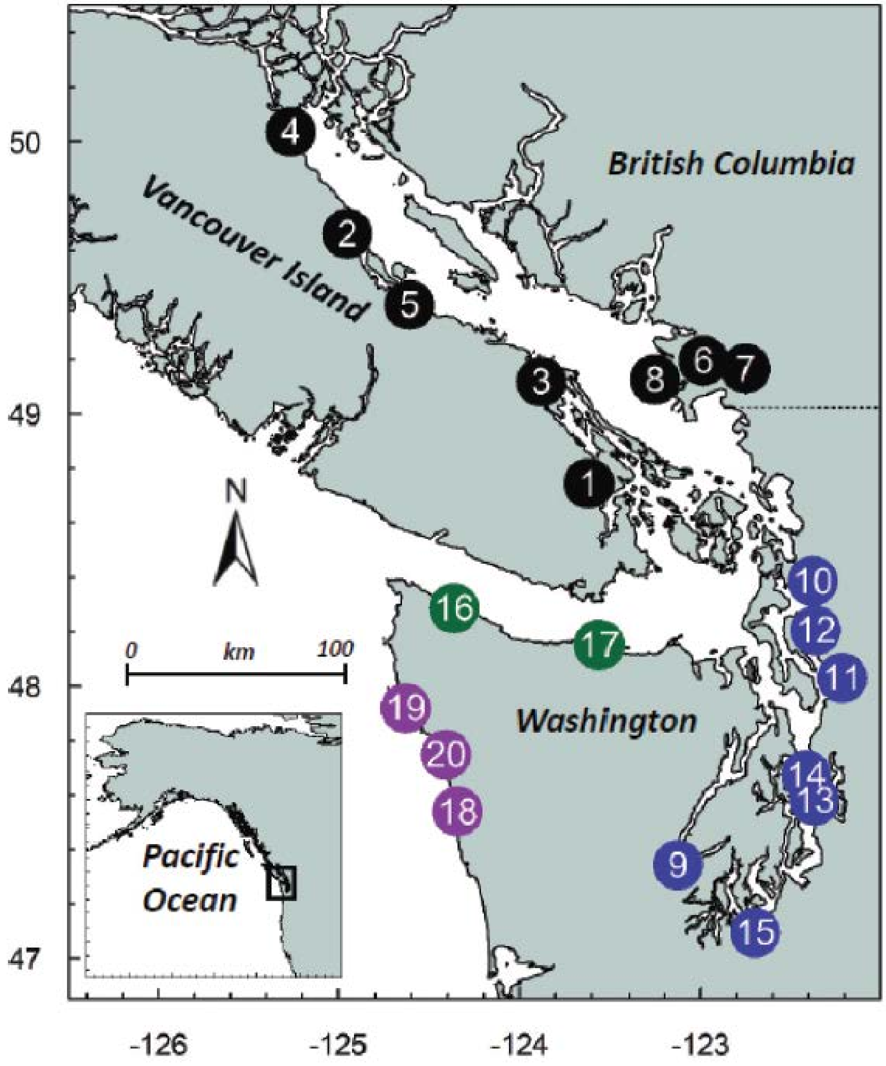


Figure 3. Locations of natural-origin Chinook stocks in Washington State and British Columbia included in this analysis. The numbers on this map correspond with the information in Table 3n, which has been adapted from Nelson et al. (2018).

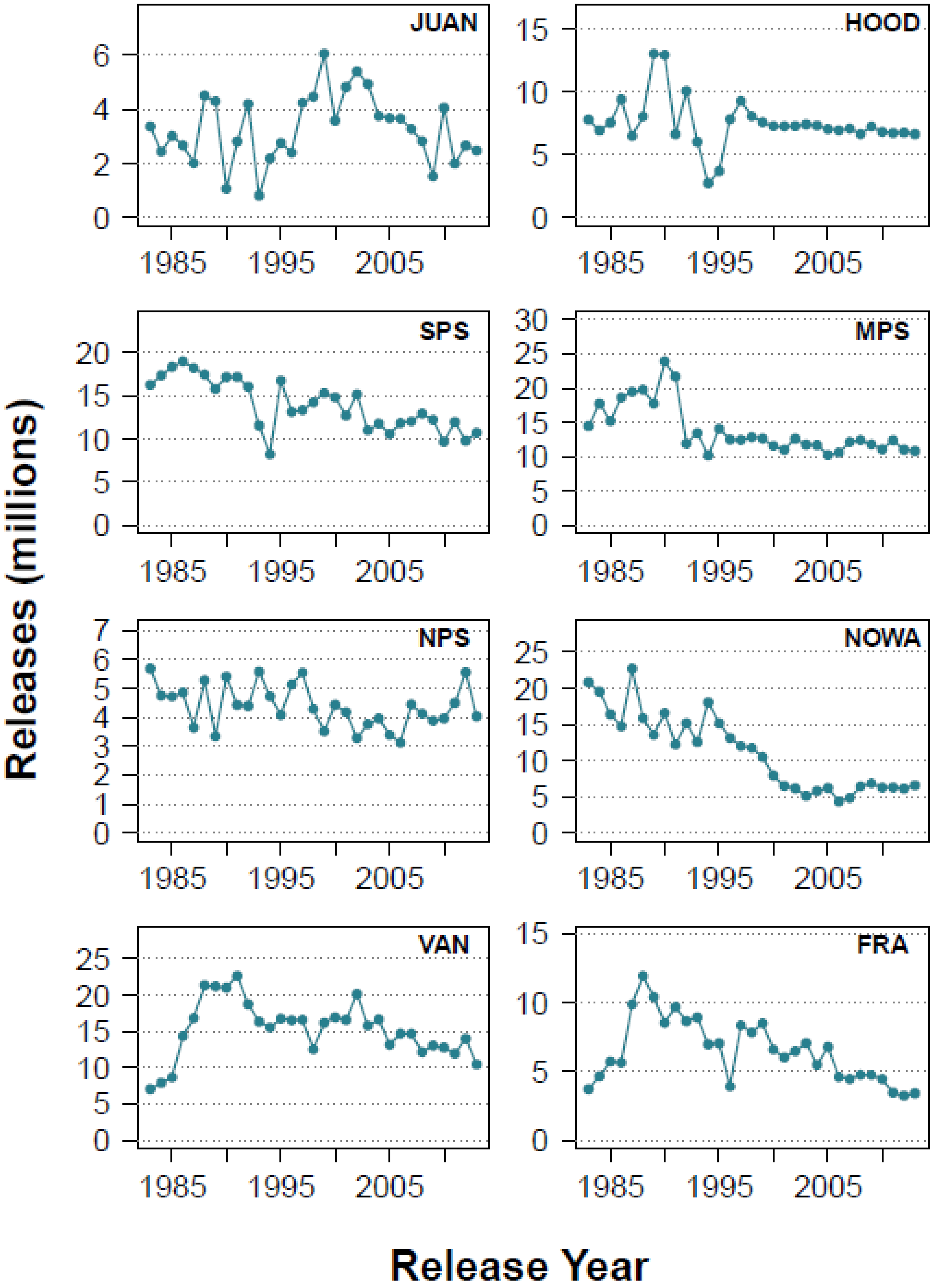


Figure 4. Annual releases of hatchery-origin yearling and subyearling Chinook salmon in the southern Salish Sea, by region, from 1983-2012.

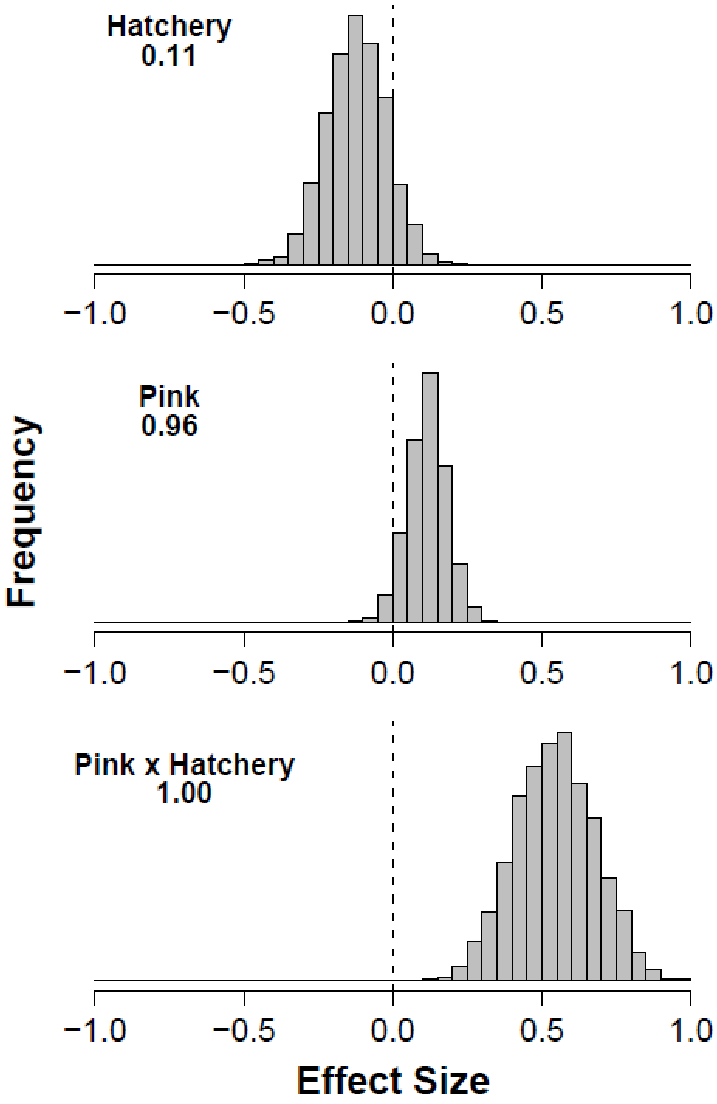


Figure 5. Marginal posterior distributions of regression coefficients for hatchery-origin Chinook salmon releases, pink salmon, and the interaction between pink salmon and hatchery-origin Chinook releases. Posterior distributions are based on 4000 MCMC samples. The proportion of draws from the posterior distribution that are > zero is shown in the upper-left corner of each histogram.

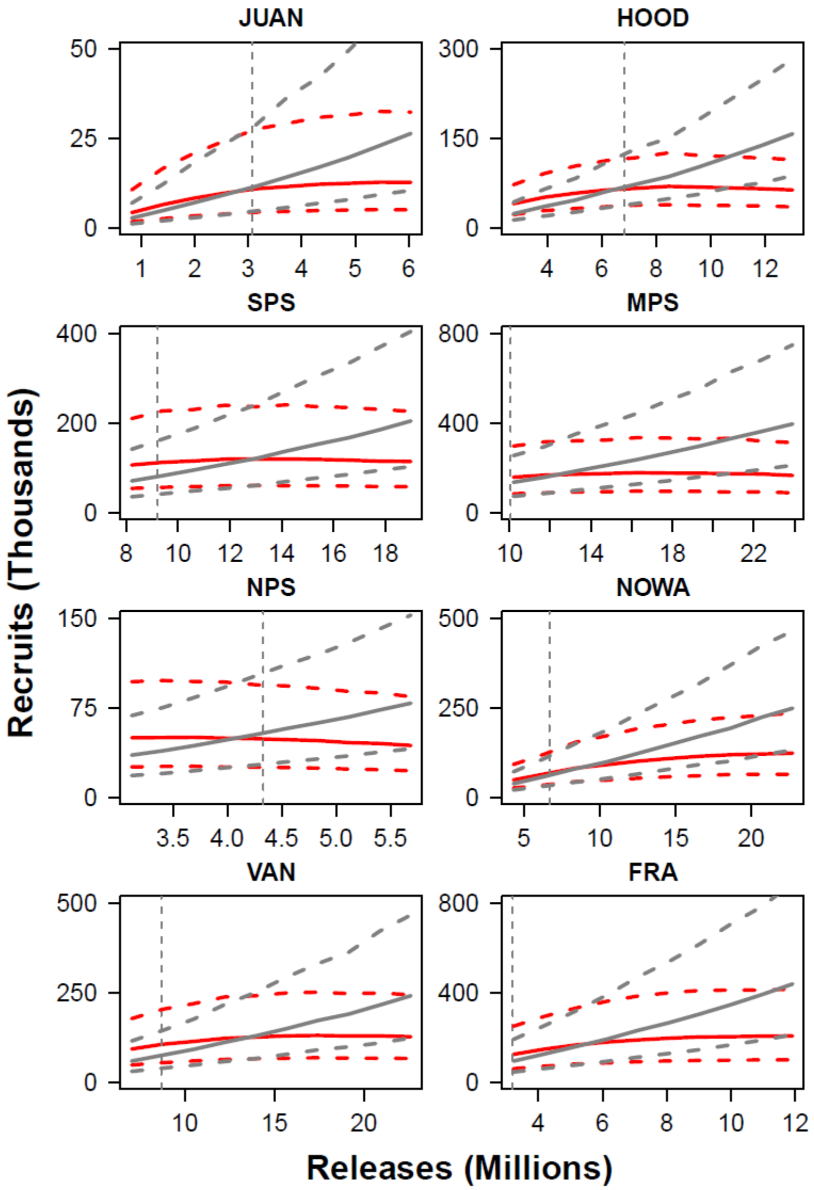


Figure 6. Projected hatchery sub-yearling Chinook salmon recruits (age 2) in the ocean (y-axis) vs. the total number of juveniles released in each region (x-axis). Release number minimums and maximums on the x-axes reflect the observed range of total hatchery Chinook released in each region (Figure A5). Grey 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 5 years in each region.

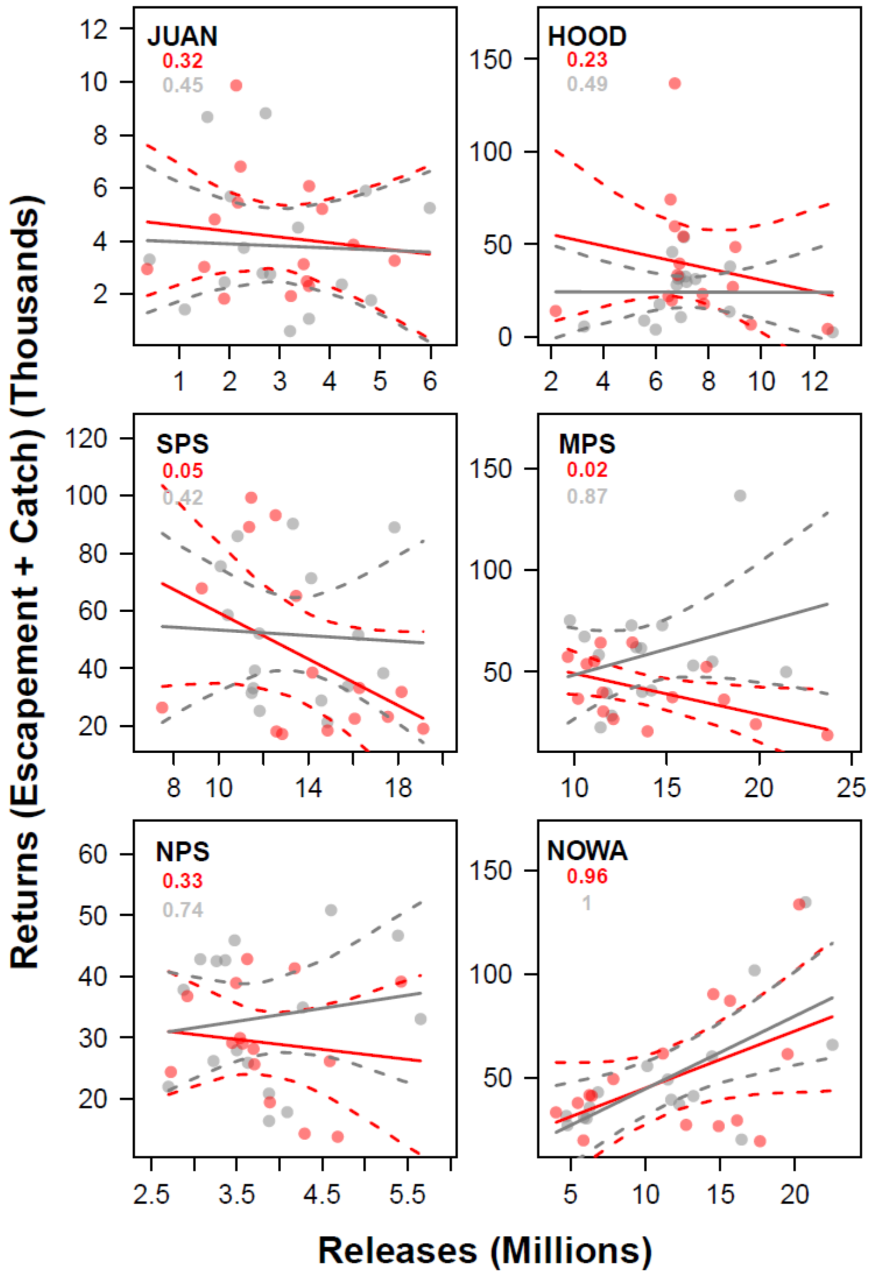


Figure 7. Run reconstruction of the total numbers of adult hatchery-origin Chinook salmon from each region returning to Puget Sound (y-axis) vs. the number of juveniles released that produced those adults (x-axis). The grey line is the regression trend line of data from non-pink years (odd emigration 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 grey numbers are the probability of each slope being > zero.

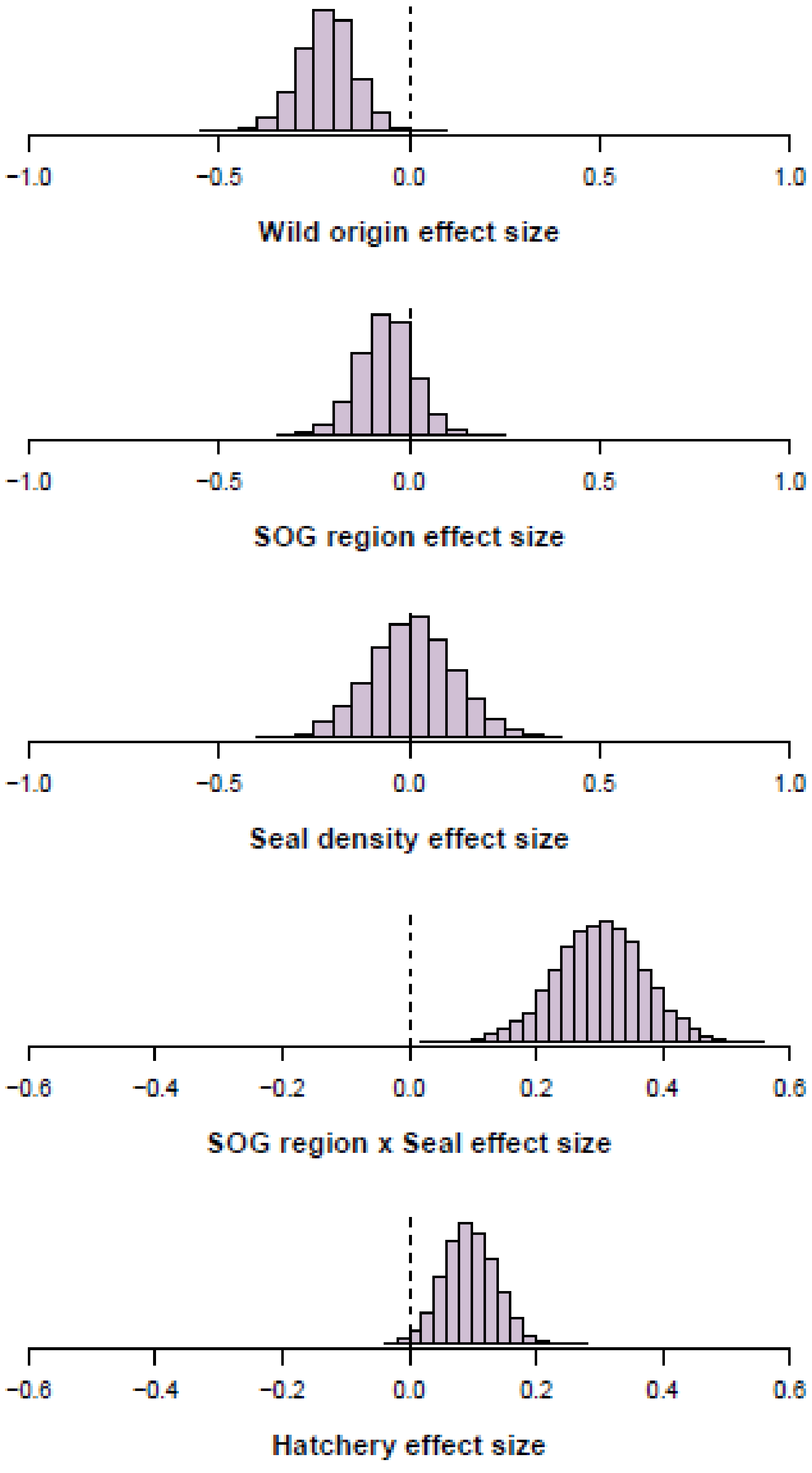


Figure 8. Marginal posterior distributions for effect sizes (relative to mortality) of several covariates in the coho salmon survival/mortality model (Equation 4).

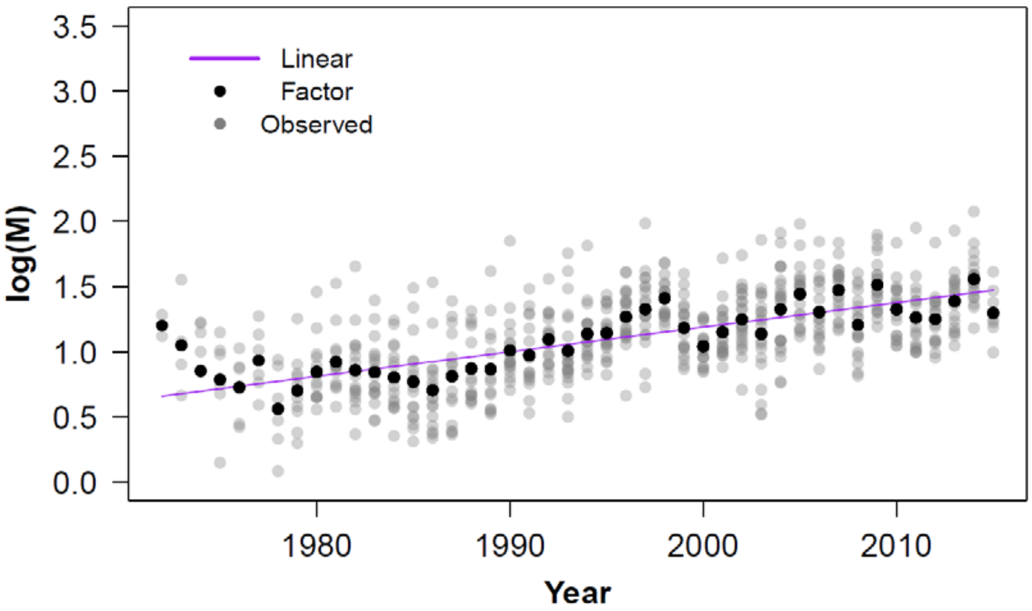


Figure 9. Year effects estimated from the coho salmon survival/mortality model (Equation 4). The gray circles are the observed mortality rates for all stocks in the analysis, while the black circles are the mean year effect that was incorporated as a covariate in the model. The purple line is added to show the significant positive linear trend in time for coho natural mortality rates among stocks included in the dataset, between the mid-1970s and 2010s.

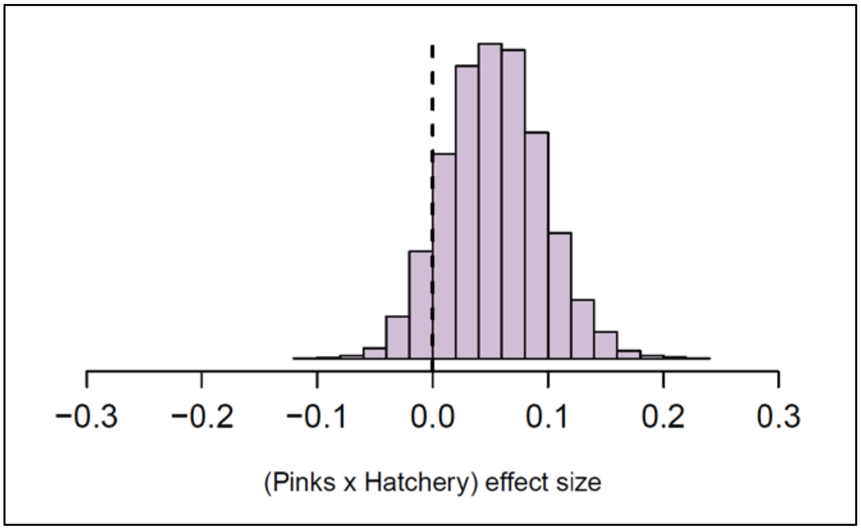


Figure 10. Marginal posterior distribution of the interaction effect between pink year and hatchery-origin Chinook salmon abundance (Pinks x Hatch) on natural-origin Chinook salmon productivity in Equation 2.

Appendix

Table A1. Number of hatchery-origin Chinook salmon sampled (top) and proportional contribution (bottom) from terminal commercial and sport fisheries of ages 3, 4, and 5 in each of the six Puget Sound regions between 1985 and 2010.

	NOWA			MPS			JUAN			NPS			HOOD			SPS		
Return Year	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5	Age 3	Age 4	Age 5
1985	1,145	2,738	31	234	660	1	15	31	17	278	640	32	240	206	1	33	50	7
1986	483	2,519	129	359	701	91	70	48	10	128	727	183	94	345	11	120	226	30
1987	490	1,190	142	704	875	59	21	120	66	174	328	125	221	321	42	273	327	27
1988	1,122	40	2	479	1,483	115	94	686	357	337	305	23	203	-	11	222	435	38
1989	905	919	3	1,540	554	71	72	123	76	249	732	28	220	457	-	1,178	285	26
1990	1,798	668	72	253	1,516	18	43	197	125	231	417	128	242	276	17	700	1,346	14
1991	905	369	14	749	295	320	-	531	219	326	911	58	31	567	66	568	356	220
1992	495	307	13	198	630	72	128	138	241	253	1,016	95	136	134	54	700	609	78
1993	809	334	22	431	180	34	72	262	64	445	517	89	197	272	31	1,289	284	77
1994	573	339	15	448	723	22	42	172	91	439	761	19	206	159	34	688	1,524	7
1995	627	248	15	2,504	948	62	106	230	356	356	539	63	414	360	38	5,742	660	104
1996	260	402	17	2,801	2,295	74	160	555	426	439	666	57	780	497	25	1,113	3,161	2
1997	1,059	194	32	948	1,540	82	75	465	276	352	697	30	139	994	82	678	813	72
1998	488	519	10	452	1,411	75	31	257	376	219	939	58	835	401	239	524	966	112
1999	1,460	261	29	2,730	592	92	49	208	330	584	217	108	1,004	390	14	4,495	473	83
2000	1,430	612	12	1,652	1,491	34	102	257	63	413	1,497	17	242	554	6	991	2,576	11
2001	1,458	1,475	67	2,875	3,259	103	250	326	56	761	1,589	171	997	1,829	188	17,113	1,395	128
2002	29,222	656	70	9,461	5,261	221	88	409	387	676	5,383	784	396	619	113	18,534	19,132	93
2003	19,532	8,015	19	10,750	14,896	778	32	338	349	946	3,387	726	405	682	34	12,568	27,132	2,001
2004	10,869	5,459	236	5,565	34,542	2,530	141	142	529	1,245	5,110	1,068	718	600	28	16,595	31,781	2,744
2005	12,263	6,388	338	14,297	15,108	4,486	88	152	49	1,412	2,356	540	1,948	595	81	27,485	18,238	2,821
2006	22,640	11,716	643	16,842	30,415	1,207	112	684	67	1,499	3,782	816	6,054	1,511	23	48,778	26,386	889
2007	16,545	9,952	543	37,965	28,138	1,984	12	111	137	5,943	5,666	881	4,874	3,461	50	46,865	44,771	821
2008	20,343	8,771	556	13,152	22,193	715	6	25	186	2,829	8,114	206	19,933	2,800	163	47,313	23,954	524
2009	15,064	8,134	370	15,116	15,310	335	146	111	18	1,206	3,227	500	14,760	16,512	60	17,549	36,268	171
2010	23,463	12,183	693	9,933	19,391	1,141	317	58	14	2,988	3,726	857	30,098	9,475	346	45,104	13,679	902
1985	0.29	0.70	0.01	0.26	0.74	0.00	0.24	0.49	0.28	0.29	0.67	0.03	0.54	0.46	0.00	0.37	0.55	0.08
1986	0.15	0.80	0.04	0.31	0.61	0.08	0.55	0.37	0.08	0.12	0.70	0.18	0.21	0.77	0.03	0.32	0.60	0.08
1987	0.27	0.65	0.08	0.43	0.53	0.04	0.10	0.58	0.32	0.28	0.52	0.20	0.38	0.55	0.07	0.44	0.52	0.04
1988	0.96	0.03	0.00	0.23	0.71	0.06	0.08	0.60	0.31	0.51	0.46	0.04	0.95	0.00	0.05	0.32	0.63	0.06
1989	0.50	0.50	0.00	0.71	0.26	0.03	0.27	0.45	0.28	0.25	0.73	0.03	0.32	0.68	0.00	0.79	0.19	0.02
1990	0.71	0.26	0.03	0.14	0.85	0.01	0.12	0.54	0.34	0.30	0.54	0.17	0.45	0.52	0.03	0.34	0.65	0.01
1991	0.70	0.29	0.01	0.55	0.22	0.23	0.00	0.71	0.29	0.25	0.70	0.04	0.05	0.85	0.10	0.50	0.31	0.19
1992	0.61	0.38	0.02	0.22	0.70	0.08	0.25	0.27	0.47	0.19	0.74	0.07	0.42	0.41	0.17	0.50	0.44	0.06
1993	0.69	0.29	0.02	0.67	0.28	0.05	0.18	0.66	0.16	0.42	0.49	0.08	0.39	0.54	0.06	0.78	0.17	0.05
1994	0.62	0.37	0.02	0.38	0.61	0.02	0.14	0.56	0.30	0.36	0.62	0.02	0.52	0.40	0.08	0.31	0.69	0.00
1995	0.70	0.28	0.02	0.71	0.27	0.02	0.15	0.33	0.51	0.37	0.56	0.07	0.51	0.44	0.05	0.88	0.10	0.02
1996	0.38	0.59	0.02	0.54	0.44	0.01	0.14	0.49	0.37	0.38	0.57	0.05	0.60	0.38	0.02	0.26	0.74	0.00
1997	0.82	0.15	0.02	0.37	0.60	0.03	0.09	0.57	0.34	0.33	0.65	0.03	0.11	0.82	0.07	0.43	0.52	0.05
1998	0.48	0.51	0.01	0.23	0.73	0.04	0.05	0.39	0.57	0.18	0.77	0.05	0.57	0.27	0.16	0.33	0.60	0.07
1999	0.83	0.15	0.02	0.80	0.17	0.03	0.08	0.36	0.56	0.64	0.24	0.12	0.71	0.28	0.01	0.89	0.09	0.02
2000	0.70	0.30	0.01	0.52	0.47	0.01	0.24	0.61	0.15	0.21	0.78	0.01	0.30	0.69	0.01	0.28	0.72	0.00
2001	0.49	0.49	0.02	0.46	0.52	0.02	0.40	0.52	0.09	0.30	0.63	0.07	0.33	0.61	0.06	0.92	0.07	0.01
2002	0.98	0.02	0.00	0.63	0.35	0.01	0.10	0.46	0.44	0.10	0.79	0.11	0.35	0.55	0.10	0.49	0.51	0.00
2003	0.71	0.29	0.00	0.41	0.56	0.03	0.04	0.47	0.49	0.19	0.67	0.14	0.36	0.61	0.03	0.30	0.65	0.05
2004	0.66	0.33	0.01	0.13	0.81	0.06	0.17	0.18	0.65	0.17	0.69	0.14	0.53	0.45	0.02	0.32	0.62	0.05
2005	0.65	0.34	0.02	0.42	0.45	0.13	0.30	0.53	0.17	0.33	0.55	0.13	0.74	0.23	0.03	0.57	0.38	0.06
2006	0.65	0.33	0.02	0.35	0.63	0.02	0.13	0.79	0.08	0.25	0.62	0.13	0.80	0.20	0.00	0.64	0.35	0.01
2007	0.61	0.37	0.02	0.56	0.41	0.03	0.05	0.43	0.53	0.48	0.45	0.07	0.58	0.41	0.01	0.51	0.48	0.01
2008	0.69	0.30	0.02	0.36	0.62	0.02	0.03	0.12	0.86	0.25	0.73	0.02	0.87	0.12	0.01	0.66	0.33	0.01
2009	0.64	0.35	0.02	0.49	0.50	0.01	0.53	0.40	0.06	0.24	0.65	0.10	0.47	0.53	0.00	0.33	0.67	0.00
2010	0.65	0.34	0.02	0.33	0.64	0.04	0.82	0.15	0.04	0.39	0.49	0.11	0.75	0.24	0.01	0.76	0.23	0.02

Table A2. Comparison of the top eight candidate models for hatchery-origin Chinook salmon from Table 3 by approximation of leave-one-out cross validation (LOO). For each model, the difference between each model and model with the highest ELPD (ΔELPD^{Best}), the expected log of the predictive density (ELPD) and its standard error (ELPD-SE), and number of effective parameters (p) is given. Given that the ELPD-SE values exceed the absolute value of the difference between competing models' ELPDs, the model with the lowest p is favored here (Vehtari et al. 2017). The best-performing model is bolded.

Model	**ΔELPD^{Best}**	**ELPD**	**ELPD-SE**	**p**
9	-97.9	-963.4	21.4	14.3
10	-12.2	-877.7	21.1	38.7
11	**-11.4**	**-876.9**	**21.9**	**36.6**
12	0.0	-865.5	24.7	66.8
13	-0.2	-865.7	24.6	65.8
14	-2.8	-868.3	24.5	74.6
15	-3.4	-868.9	24.4	81.4
16	-63.6	-929.1	21.6	242.1

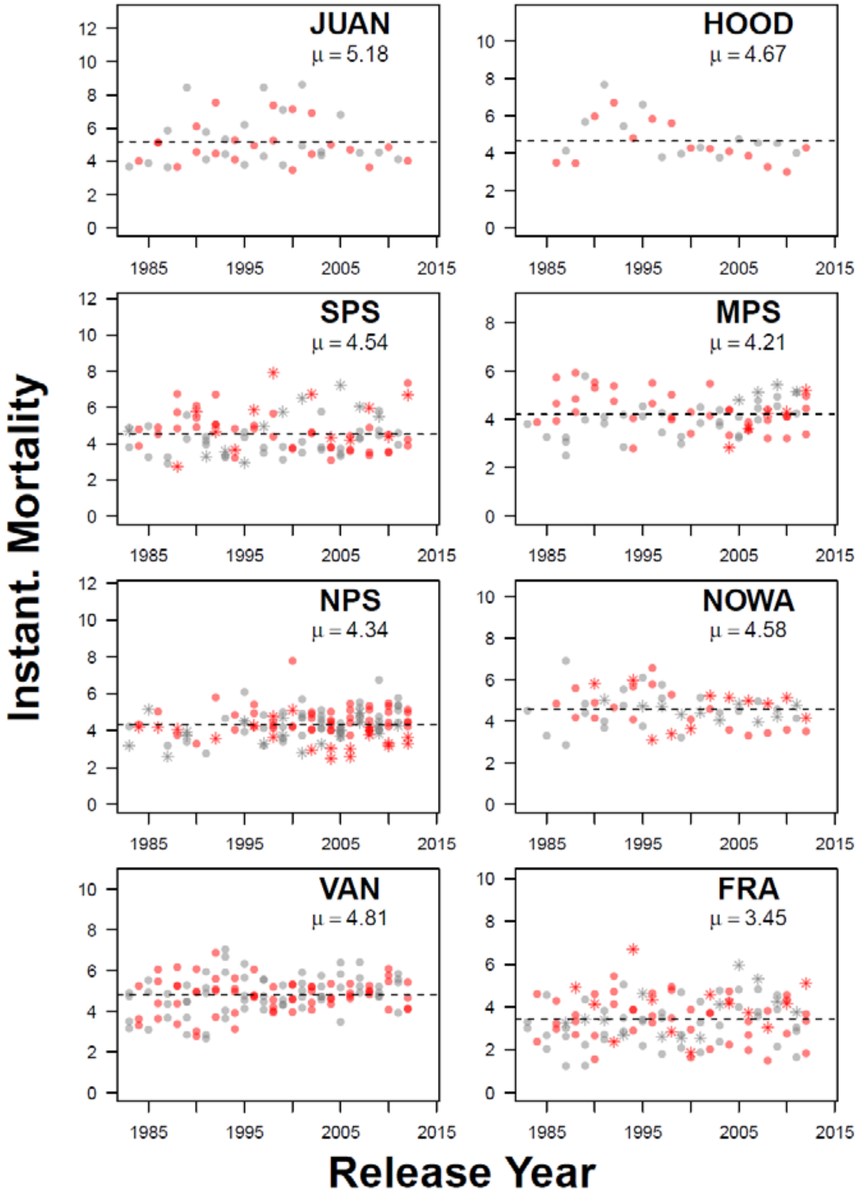


Figure A1. Time series of hatchery-origin Chinook salmon marine instantaneous mortality rate (to age 2 or 3) in eight regions of the Salish Sea between 1983 and 2012 derived from coded-wire tag (CWT) data. Red symbols are juvenile releases that occurred in even years, when juvenile pink salmon were present; grey symbols are odd years. Circles are releases of sub-yearling Chinook salmon juveniles, while stars represent yearling juveniles. No difference in mortality rate was detected between sub-yearlings and yearlings. Mean instantaneous mortality rates for each time series (μ) are shown by dashed horizontal lines.

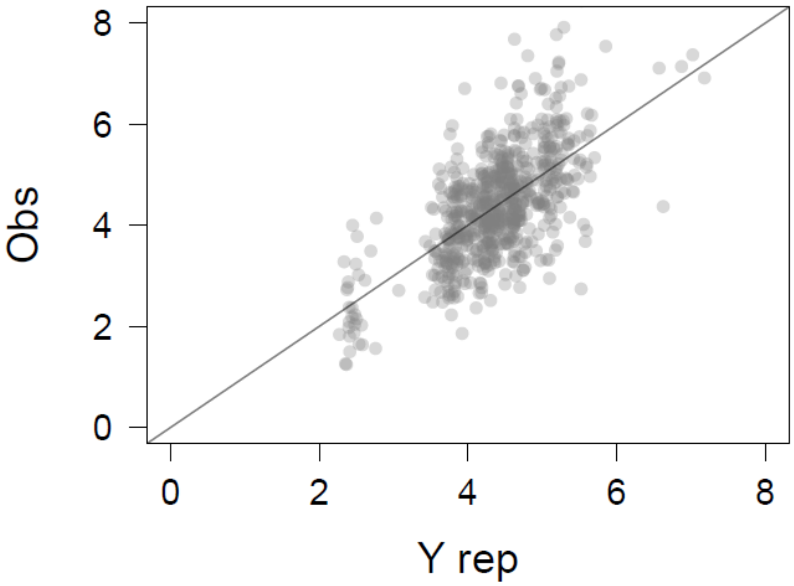
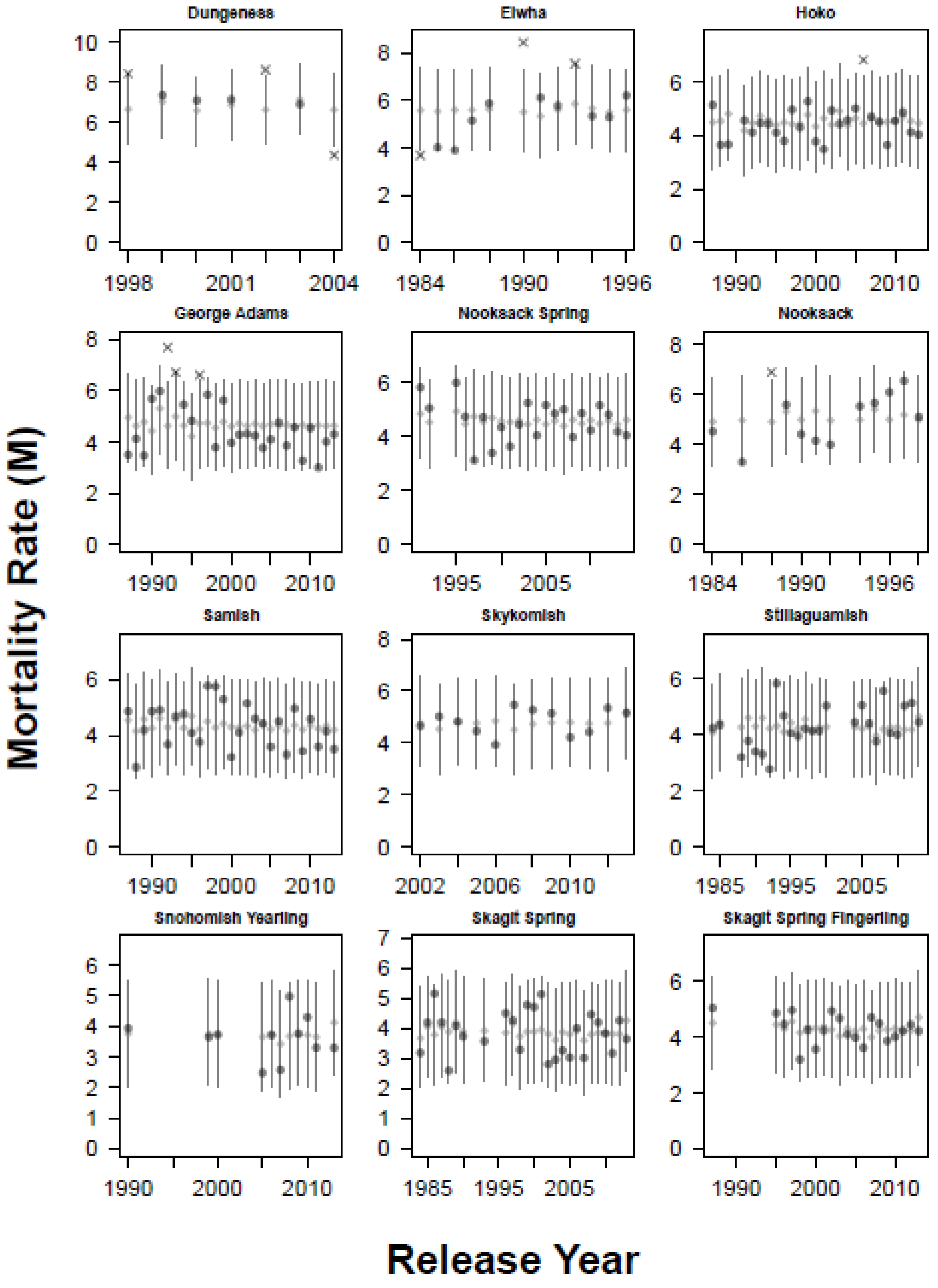
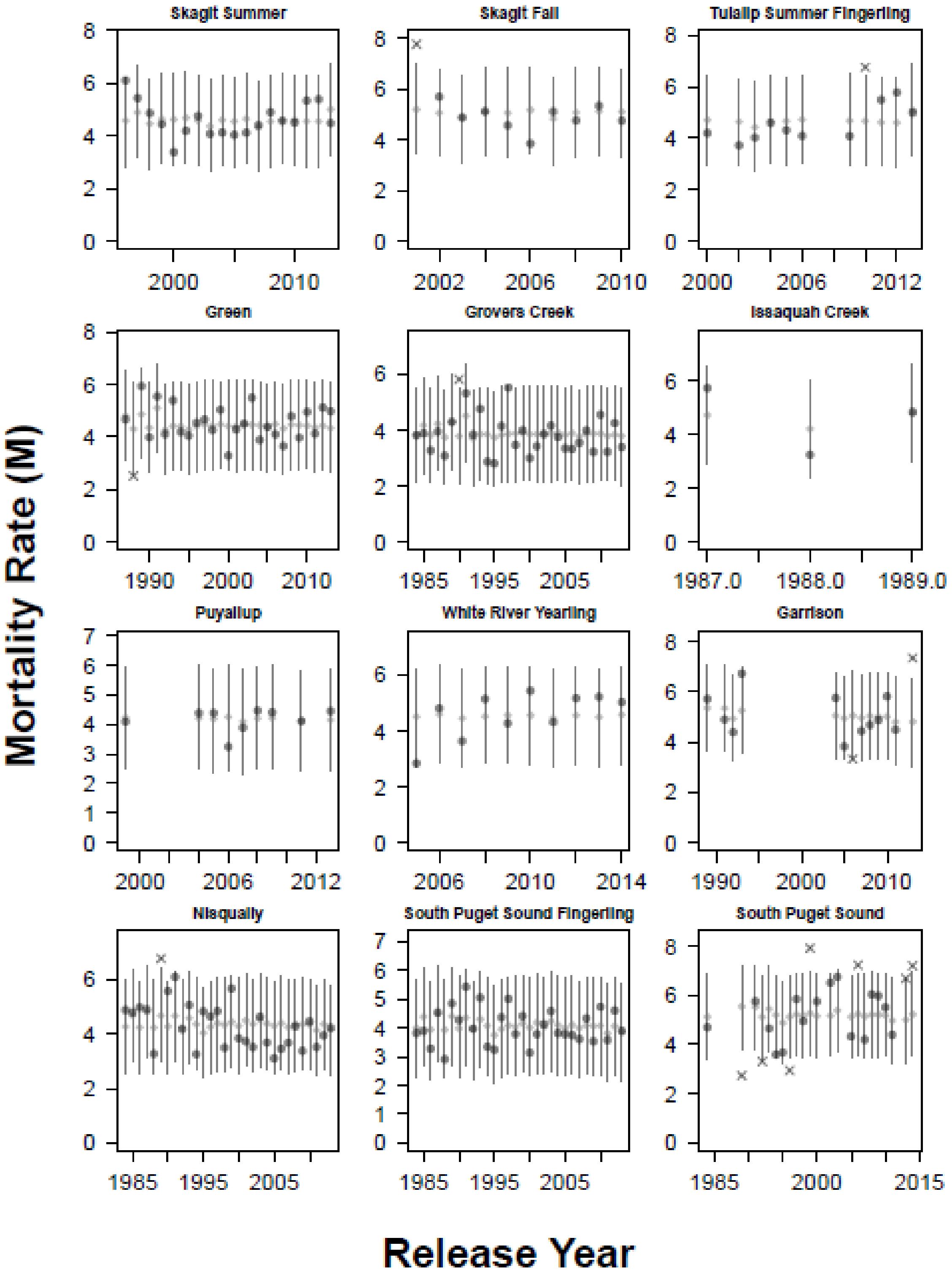


Figure A2. Posterior predictive means (Y rep; x-axis) of the best-forming model (Model 11; see Table 3) plotted against the observed data points (Obs; y-axis) for hatchery-origin Chinook salmon. 1:1 values are shown by the solid black line. A total of 685 data points were used in the analysis.


Mortality Rate (M)
Release Year
Dungeness
10
8
6
4
2
0
1998
2001
2004
Elwha
8
6
4
2
0
1984
1990
1996
Hoko
6
4
2
0
1990
2000
2010
George Adams
8
6
4
2
0
1990
2000
2010
Nooksack Spring
6
4
2
0
1995
2005
Nooksack
8
6
4
2
0
1984
1990
1996
Samish
6
4
2
0
1990
2000
2010
Skykomish
8
6
4
2
0
2002
2006
2010
Stillaguamish
6
4
2
0
1985
1995
2005
Snohomish Yearling
6
5
4
3
2
1
0
1990
2000
2010
Skagit Spring
7
6
5
4
3
2
1
0
1985
1995
2005
Skagit Spring Fingerling
6
4
2
0
1990
2000
2010


Mortality Rate (M)
Release Year
Skagit Summer
Skagit Fall
Tulalip Summer Fingerling
Green
Grovers Creek
Issaquah Creek
Puyallup
White River Yearling
Garrison
Nisqually
South Puget Sound Fingerling
South Puget Sound
0
2
4
6
8
2000
2010
2002
2006
2010
2000
2006
2012
1990
2000
2010
1985
1995
2005
1987.0
1988.0
1989.0
1
3
5
7
2000
2006
2012
2006
2010
2014
1990
2000
2010
1985
1995
2005
1985
1995
2005
1985
2000
2015

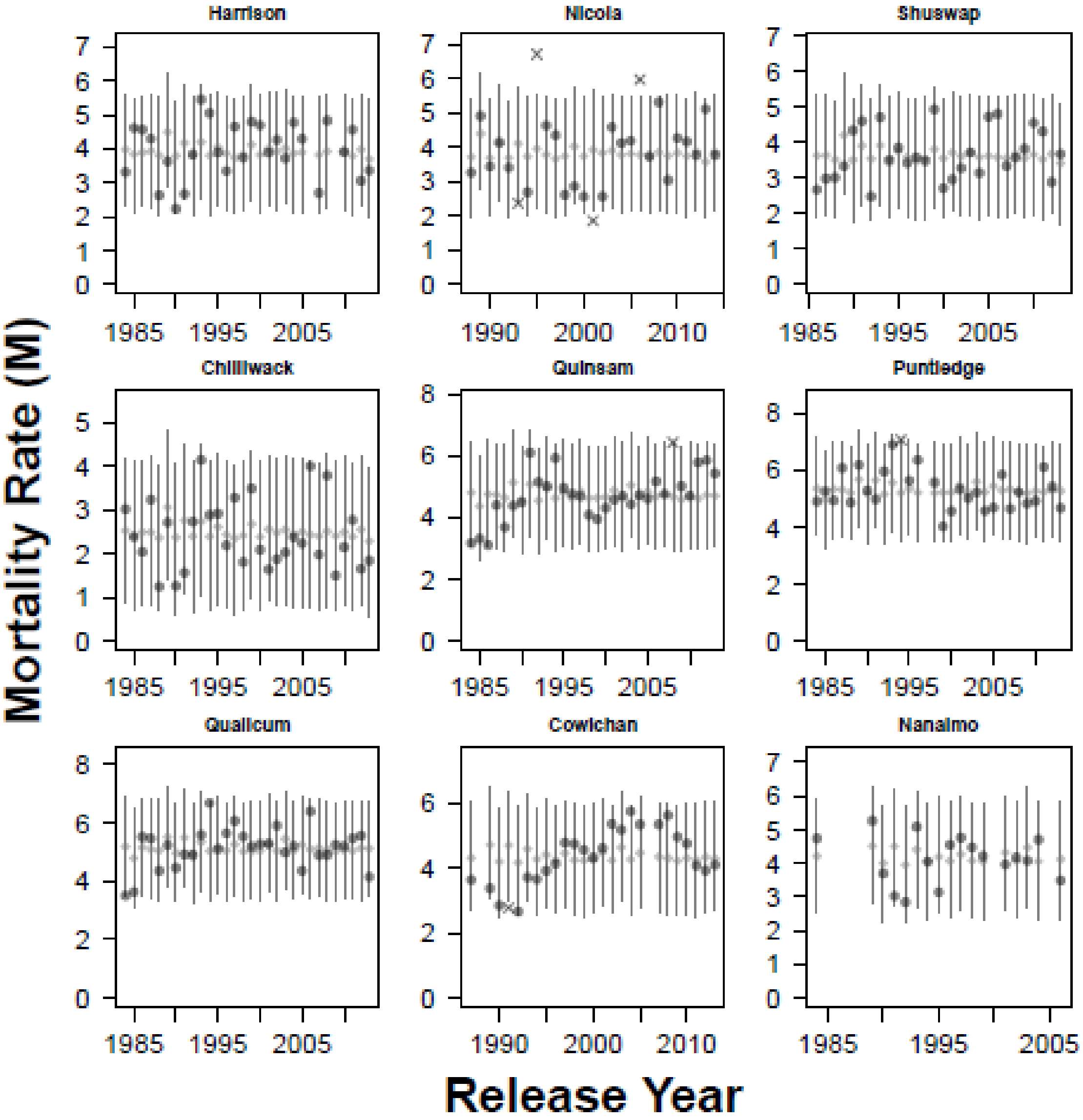


Figure A3. Observed instantaneous mortality rates (M) and posterior predictive distributions from the best-performing model (Model 11; see Table 3) for Salish Sea hatchery-origin Chinook salmon stocks assessed. Light grey vertical lines depict 95% posterior predictive intervals and light grey diamonds show posterior predictive means. Dark grey diamonds show the observed data that fall within the predictive distributions while “x” denotes observations that are outside the predictive distributions.

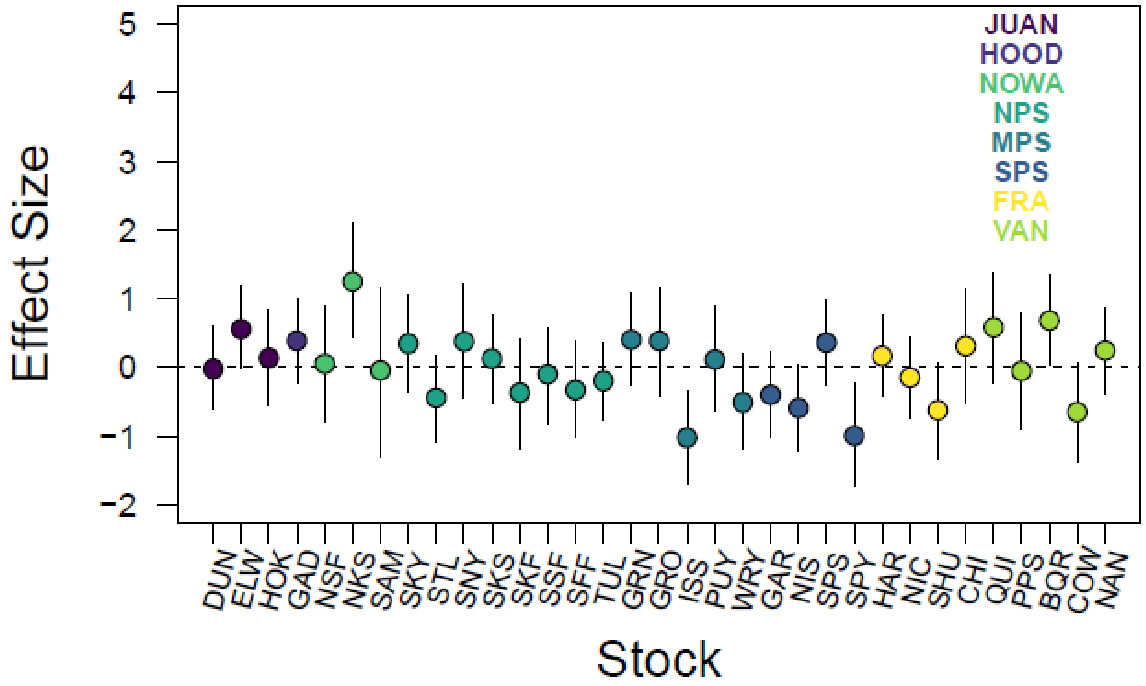
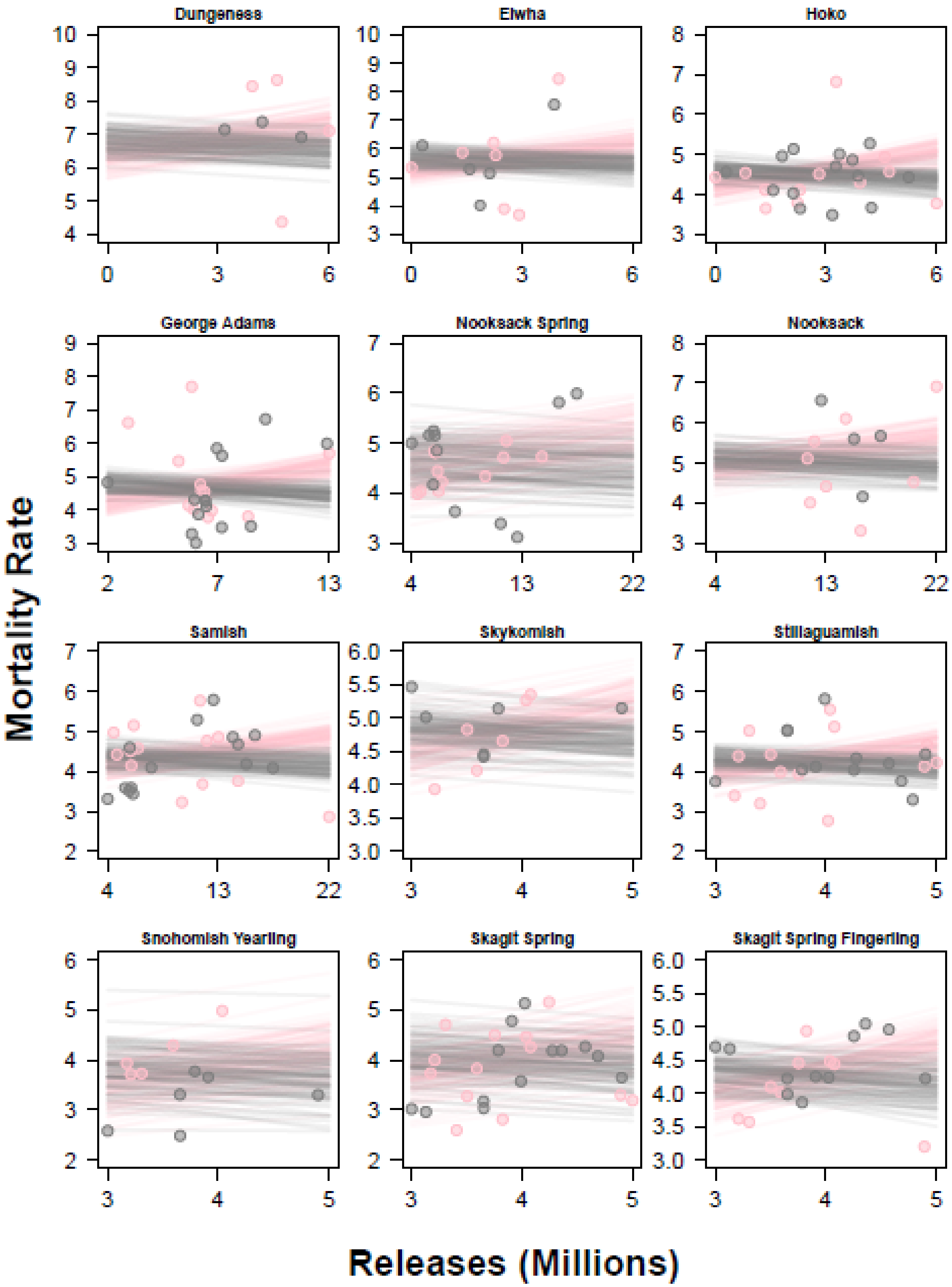
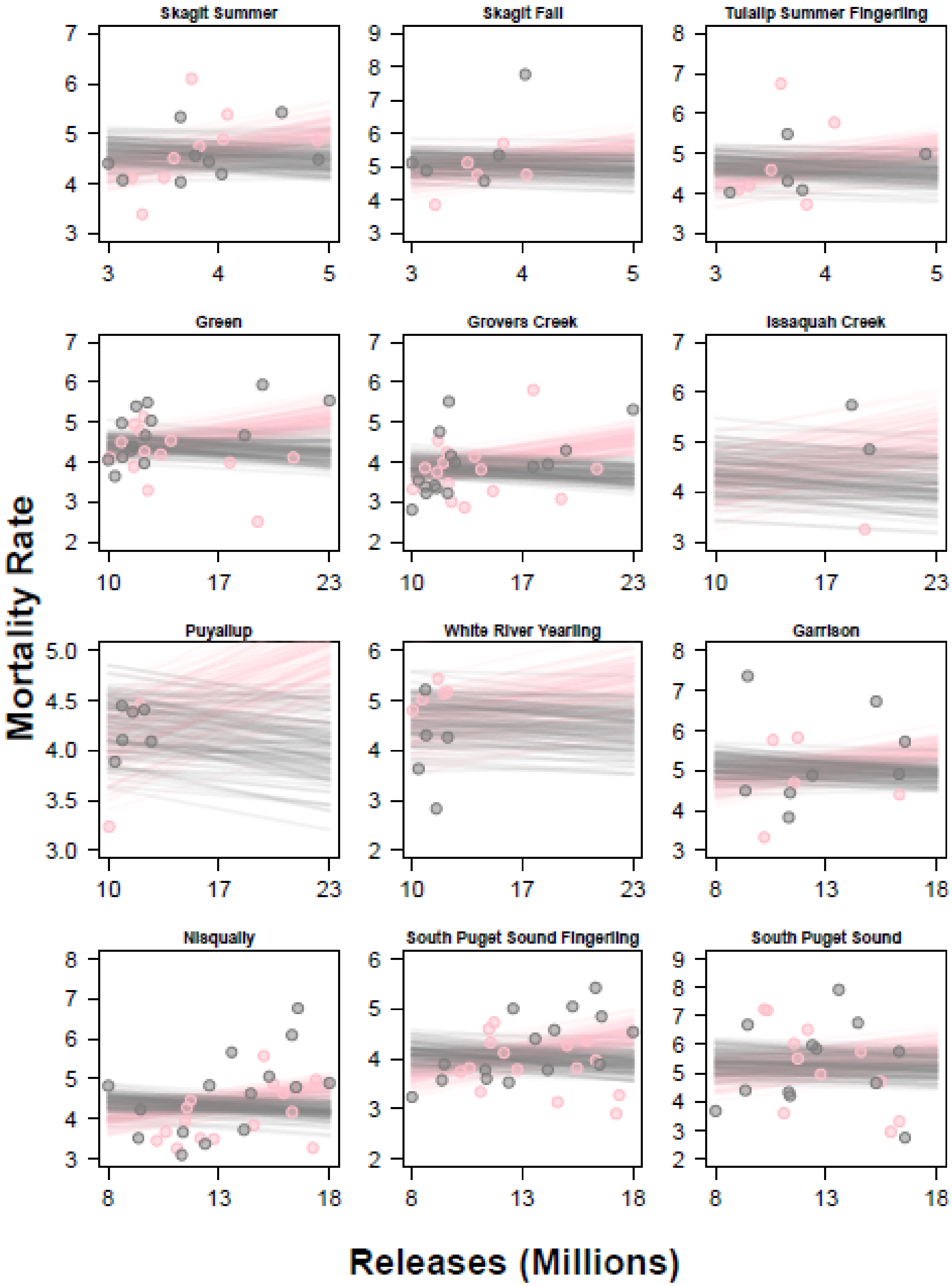


Figure A4. Effect size for each stock of hatchery-origin Chinook salmon included in the analysis. Colored symbols show the mean of the marginal posterior distribution, while vertical lines show the 95% credible intervals for each estimate from the best-performing model (Model 11; see Table 3). Symbol colors correspond with the geographical region of each stock.


Dungeness
Elwha
Hoko
George Adams
Nooksack Spring
Nooksack
Samish
Skykomish
Stillaguamish
Snohomish Yearling
Skagit Spring
Skagit Spring Fingerling
Mortality Rate
Releases (Millions)


Skagit Summer
Skagit Fall
Tulalip Summer Fingerling
Green
Grovers Creek
Issaquah Creek
Puyallup
White River Yearling
Garrison
Nisqually
South Puget Sound Fingerling
South Puget Sound
Mortality Rate
Releases (Millions)
3
4
5
6
7
8
9
10
17
23
13
18
2
3.0
3.5
4.0
4.5
5.0

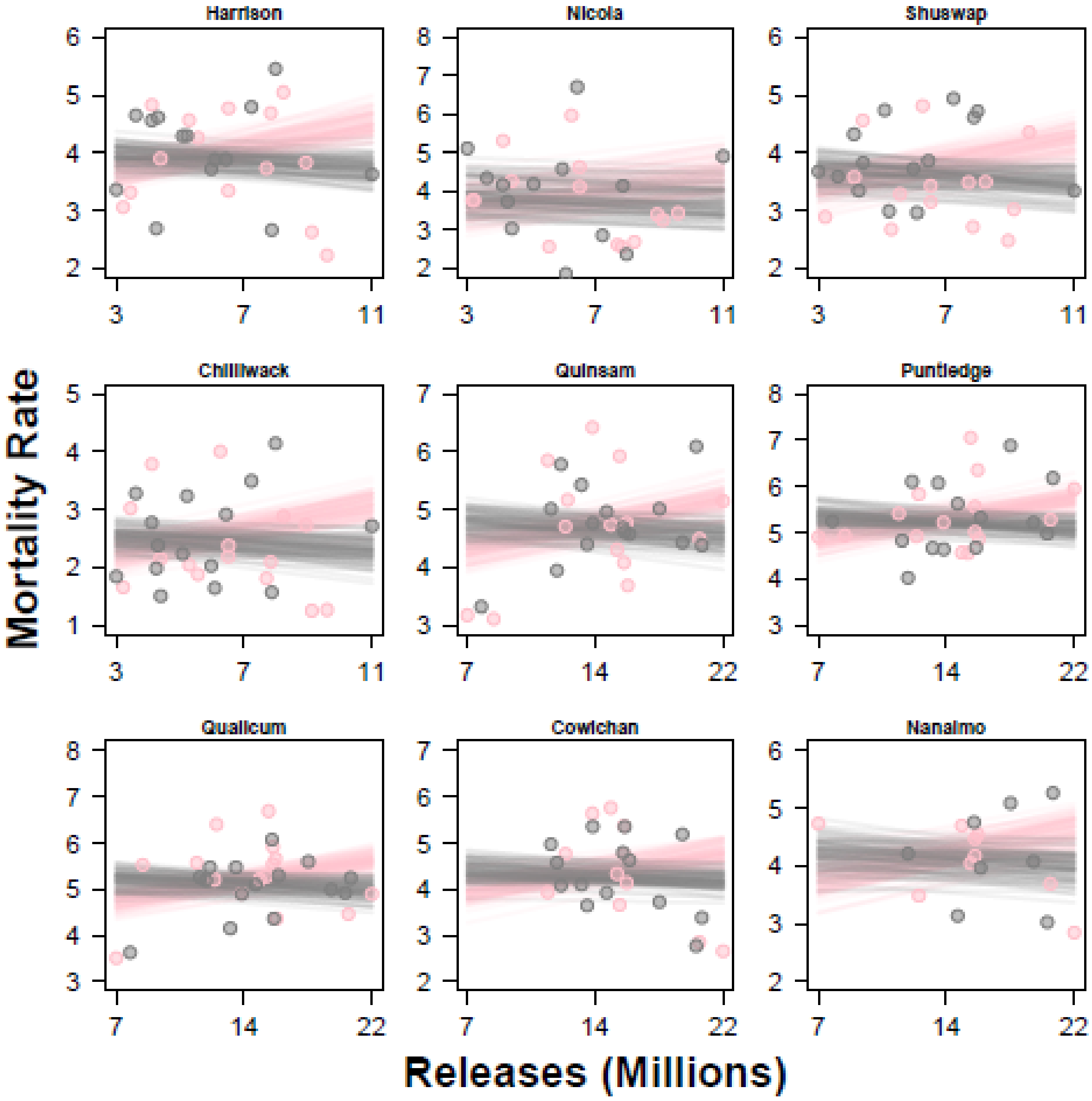


Figure A5. Hatchery-origin Chinook salmon instantaneous mortality rate to age 2 (y-axis) vs. annual regional hatchery releases (x-axis) for each stock assessed. Lines are based on 100 draws from the best-performing model's posterior distributions and show model-predicted survival for pink years (even; pink color) and non-pink years (grey). The ranges of the x-axes correspond to observed release numbers in each stock's region between 1983 and 2012.

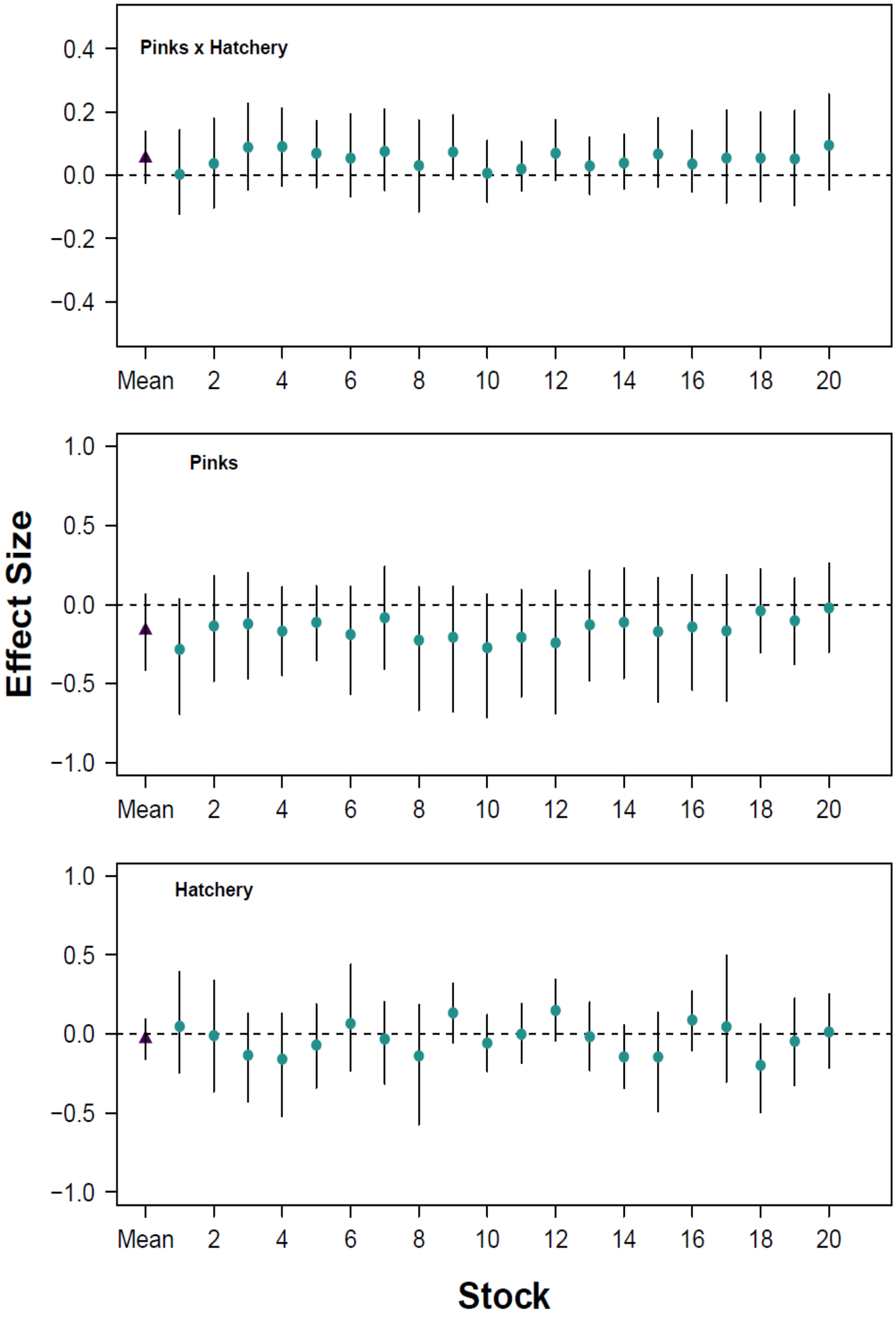


Figure A6. Marginal posterior distributions of natural-origin Chinook model coefficients for Equation 2. Purple triangles depict the global mean estimates for each covariate, while green circles show estimates for each stock grouping. 95% credible intervals are shown with black lines.