NRC Research Press
ARTICLE

Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest[1]

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Abstract: Predation risk and competition among conspecifics significantly affect survival of juvenile salmon, but are rarely incorporated into models that predict recruitment in salmon populations. Using densities of harbour seals (*Phoca vitulina*) and numbers of hatchery-released Chinook salmon (*Oncorhynchus tshawytscha*) smolts as covariates in spatially structured Bayesian hierarchical stock–recruitment models, we found significant negative correlations between seal densities and productivity of Chinook salmon for 14 of 20 wild Chinook populations in the Pacific Northwest. Changes in numbers of seals since the 1970s were associated with a 74% decrease (95% CI: –85%, –64%) in maximum sustainable yield in Chinook stocks. In contrast, hatchery releases were significantly correlated with Chinook productivity in only one of 20 populations. Our findings are consistent with recent research on predator diets and bioenergetics modeling that suggest there is a relationship between harbour seal predation on juvenile Chinook and reduced marine survival in parts of the eastern Pacific. Forecasting, assessment, and recovery efforts for salmon populations of high conservation concern should thus consider including biotic factors, particularly predator–prey interactions.

Résumé : Le risque de prédation et la concurrence entre individus d'une même espèce ont une incidence significative sur la survie des saumons juvéniles, mais sont rarement intégrés dans les modèles qui prédisent le recrutement dans les populations de saumons. En utilisant la densité de phoques communs (*Phoca vitulina*) et le nombre de saumoneaux relâchés d'écloseries comme covariables dans des modèles bayésiens hiérarchiques spatialement structurés de recrutement au stock, nous avons constaté la présence de corrélations négatives significatives entre la densité de phoques et la productivité de saumons quinnats (*Oncorhynchus tshawytscha*) pour 14 des 20 populations de saumons quinnats sauvages dans le Pacific Northwest. Des variations des nombres de phoques depuis les années 1970 sont associées à une baisse de 74 % (IC à 95 % : –85 %, –64 %) du rendement équilibré maximal dans les stocks de saumons quinnats. En revanche, le nombre de saumoneaux relâchés d'écloseries n'est significativement corrélé à la productivité des saumons quinnats que dans 1 des 20 populations. Nos constatations concordent avec celles de travaux récents sur les régimes alimentaires de prédateurs et la modélisation bioénergétique qui donnent à penser qu'il existe une relation entre la prédation de saumons quinnats juvéniles par les phoques communs et une survie en mer réduite dans certaines parties de l'est de l'océan Pacifique. La prédiction, l'évaluation et les efforts de rétablissement de populations de saumons dont la conservation est très préoccupante devraient donc intégrer des facteurs biotiques, en particulier les interactions prédateurs–proies. [Traduit par la Rédaction]

Introduction

The abundance of predators and intensity of competition within a spatial arena give rise to risks associated with foraging activities that may ultimately affect the survival rates of juvenile fish (Chapman 1966; Walters and Juanes 1993; Walters and Korman 1999). When food is scarce, due to poor environmental conditions or large numbers of competitors, young fish must spend more time actively foraging, which increases their risk of being preyed upon (Walters and Juanes 1993; Ahrens et al. 2012). Physical and environmental factors often mediate these trade-offs between growth and predation risk (Friedland et al. 1993; Linehan et al. 2001; Lee et al. 2016; Andersson and Reynolds 2017), which may explain why strong, enduring correlations between recruitment and any one factor are rarely observed (Walters and Collie 1988; Bradford et al. 1997).

Many studies have attempted to explain recruitment in Pacific salmon populations via environmental (abiotic) covariates in the marine life-history stages (Beamish and Bouillon 1993; Coronado and Hilborn 1998; Beamish et al. 2000*b*; Sharma et al. 2013). However, fewer stock–recruitment analyses have incorporated biological covariates with mechanistic explanations such as competition, disease, and predation that influence numbers of returning salmon (Beamish et al. 2000*a*; Ruggerone and Goetz 2004; Ruggerone and Connors 2015). Incorporating such biotic factors (e.g., abundance of hatchery-produced smolts, densities of predating harbor seals) may improve predictions as well as provide a means to assess their impact on salmon populations of high con-

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Received 27 October 2017. Accepted 30 May 2018.

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[1] This manuscript is part of a special issue based on results of the Natural Sciences and Engineering Research Council of Canada (NSERC) Canadian Fisheries Research Network, a collaboration among fish harvesters, academics, and government.

A correction was made to the e-First version of this paper on 20 November 2018 prior to the final issue publication. The current online and print versions are identical and both contain the correction.

Can. J. Fish. Aquat. Sci. **76**: 447–462 (2019) dx.doi.org/10.1139/cjfas-2017-0481

servation concern. This could be particularly relevant for Chinook salmon (*Oncorhynchus tshawytscha*) populations for which recruitment data have been compiled for several decades.

Marine survival rates of many Chinook salmon populations in the eastern Pacific have declined considerably since the 1970s, particularly in the inland waters of the Salish Sea (Beamish et al. 1995; Neville et al. 2015; Ruff et al. 2017). Concurrently, harbour seal (*Phoca vitulina*) populations along the west coast of North America have grown rapidly following federal protection from hunting and culling in Canada and the United States (Jeffries et al. 2003; Brown et al. 2005; Olesiuk 2010). In the Strait of Georgia in southern British Columbia, the population of harbour seals has increased from a few thousand animals in the late 1960s to nearly 40 000 in 2008 and appears to have stopped growing (Olesiuk 2010). Further south, in Puget Sound, seal populations have seen similar sevenfold increases in abundance (Jeffries et al. 2003).

The importance of adult salmon to the diet of harbour seals has been recognized for some time (Olesiuk et al. 1990; Howard et al. 2013). Harbour seals have also been known to target out-migrating smolts in some areas of the Strait of Georgia (Olesiuk et al. 1995; Yurk and Trites 2000), but were not thought to cause substantial mortality until recently (Thomas et al. 2017). Some biologists now suspect there may be a causal relationship between harbour seal predation on smolts and the low marine survival rates of some salmon and steelhead (*Oncorhynchus mykiss*) populations (Berejikian et al. 2016; Chasco et al. 2017; Thomas et al. 2017).

In addition to the effects of predation on salmonids, there is a substantial literature on the deleterious effects of hatchery supplementation on wild populations of salmon in the eastern Pacific (Naish et al. 2007). However, the majority of research on the effects of hatcheries has focused on interactions between wild and hatchery populations in fresh water and the genetic consequences of hatchery supplementation (e.g., decreased fitness, reductions in effective population size, and weakened portfolio effects; Waples 1991; Baskett and Waples 2013; Satterthwaite and Carlson 2015). Few studies have considered interactions between wild and hatchery populations in the marine environment (Ruggerone et al. 2003, 2010; Zhivotovsky et al. 2012) or attempted to quantify the potential impacts of hatchery fish on wild stocks of conservation concern shortly after ocean entry (Levin et al. 2001), the life-history stage that likely determines brood year recruitment for Chinook and coho salmon (*Oncorhynchus kisutch*) (Beamish et al. 2010*b*, 2012; Neville et al. 2015).

Concern has been expressed in the past about potentially "overloading" the marine environment with hatchery fish (Healey 1980*a*) and the counterproductive density-dependent impacts of large hatchery releases to overall management goals (i.e., increased yield) that could pose risks to wild populations (Peterman 1978). Potential mechanisms for negative interactions between hatchery and wild populations in the early marine stages include increased competition when foraging (Walters and Juanes 1993) or a change in the functional response that results in increased predation rates (Peterman and Gatto 1978). After nearly four decades of annual releases in the tens of millions of Chinook smolts, many of the ecological trade-offs associated with hatchery supplementation remain unclear (Naish et al. 2007), and some have questioned whether the marginal gain from hatchery releases is worth the removal of the wild fish that would sustain hatchery production (Levin et al. 2001; Beamish et al. 2012).

We sought to assess the potential impacts that harbour seal predation and hatchery releases have on wild Chinook salmon productivity and how these vary spatially among Chinook populations in British Columbia and Washington State. We did so using Bayesian hierarchical models applied to 20 individual salmon populations from the Salish Sea and Washington coast and used the best-performing model to identify potential spatial patterns and infer the strength of the relationships between productivity and the covariates. We then used the model to simulate Chinook productivity over a range of combinations of seal densities and hatchery abundances to assess whether predation by seals and competition with hatchery-released fish may negatively affect the sustainable harvest of Chinook salmon.

Methods

Chinook salmon life cycle

Wild Chinook salmon originating from watersheds in the Salish Sea and Washington coast spend 0–1 years in fresh water before migrating to the ocean to rear for 1–5 years, typically between the months of February and June. Juveniles that migrate to the sea after a brief freshwater residency (<1 year) are known as "ocean-type" or "subyearling" fish, while populations with extended freshwater residency (at least 1 year) are termed "stream-type" or "yearling" fish (Healey 1991). Fish exhibiting an ocean-type life history typically return to spawn in natal streams between August and October and are known as "fall" Chinook. Mature stream-type Chinook enter natal streams as early as April. Ocean-type Chinook far outnumber stream-type Chinook in both wild and hatchery populations in the Salish Sea and Washington coast. Chinook salmon are semelparous and die within weeks of spawning.

Salmon data

We used data published by the Pacific Salmon Commission (PSC), an international body mandated to implement the Pacific Salmon Treaty between the United States and Canada (www.psc.org). The PSC analyzes technical information from both countries and provides recommendations pertaining to fisheries management, run forecasting, and enhancement operations. Specifically, we used time series of wild Chinook escapements, brood year exploitation rates, and terminal catches (PSC 2015*a*, 2015*b*, 2016) (Table 1). Wild Chinook from the Salish Sea and coastal stocks are captured in a large marine mixed-stock fishery that targets both wild and hatchery fish. However, due to the high conservation concern surrounding some wild stocks, hatchery fish are marked by adipose fin clips, which allow them to be distinguished quickly from wild fish. Hatchery fish are often implanted with coded-wire tags, which (when recovered in the fishery) allow estimation of exploitation rates on a stock-by-stock basis. Often, these exploitation rates are used as a proxy for harvest rates of wild stocks (PSC 2015*a*, 2015*b*). In this analysis, we only included wild stocks where the exploitation rates were believed to be comparable between wild and hatchery populations originating from the same river. Upon returning to their natal streams, wild fish are counted on their spawning grounds using a variety of methods (also described in PSC 2015*a*, 2015*b*, 2016). These methods include aerial surveys, mark–recapture studies, snorkel surveys, etc. Hatchery-origin fish are collected at the hatchery, although fish are known to stray to wild populations (Naish et al. 2007).

Some data sets — specifically, the escapements of nonindicator stocks — were augmented by the Salmon Escapement Database (NuSEDS) managed by Fisheries and Oceans Canada (DFO) (DFO 2016) and the StreamNet database managed by the Pacific States Marine Fisheries Commission (PSMFC; www.streamnet.org).

Spawner–recruit data were compiled for 20 individual stocks ($N = 20$) of fall Chinook salmon from British Columbia and Washington State (Table 1; Fig. 1). Because seal predation rates on salmon smolts may vary according to the body size of their prey (Thomas et al. 2017), we controlled for size-related predation effects by restricting our analysis to populations that exhibit an "ocean-type" life history, where juvenile freshwater residency is less than 1 year (i.e., "subyearlings"). Limiting our analysis to ocean-type Chinook also minimized the possibility of capturing density-dependent effects of hatchery abundance in fresh water, which are believed to be minimal due to the very short residency period. We used a cohort reconstruction approach to calculate the

Table 1. Summary of information used to compile spawner–recruit data for 20 stocks of wild fall Chinook salmon in British Columbia and Washington State.

Stock No.	Stock name	Region	n	Brood years (range)	Sources
1	Cowichan River	SOG	23	1985–2008	1, 2, 3
2	Puntledge River	SOG	33	1975–2008	1, 2, 4, 5
3	Nanaimo River	SOG	19	1979–2004	1, 2, 6
4	Quinsam River	SOG	31	1976–2007	1, 2, 7
5	Big Qualicum River	SOG	36	1973–2008	1, 2, 4, 8
6	Harrison River (Fraser)	SOG	24	1984–2008	1, 2, 4, 8
7	Shuswap River (Fraser)	SOG	25	1984–2008	1, 2, 4, 8
8	Chilliwack River (Fraser)	SOG	28	1981–2008	1, 2, 4, 8
9	Skokomish River	PS	29	1972–2006	1, 2, 9, 10
10	Skagit River	PS	26	1983–2008	1, 2, 10
11	Snohomish River	PS	27	1980–2007	1, 2, 10
12	Stillaguamish River	PS	23	1980–2007	1, 2, 10
13	Green River	PS	31	1975–2007	1, 2, 10
14	Lake Washington	PS	31	1975–2007	1, 2, 10
15	Nisqually River	PS	28	1979–2006	1, 2, 10
16	Hoko River	JDF	20	1986–2006	1, 2, 10
17	Elwha River	JDF	7	1986–1994	1, 2, 10
18	Queets River	WA coast	29	1977–2006	1, 2, 8
19	Quillayute River	WA coast	26	1980–2006	1, 2, 8
20	Hoh River	WA coast	29	1977–2006	1, 2, 8

Note: Sources: 1, PSC (2015*a*, 2015*b*); 2, PSC (2016); 3, Tompkins et al. (2005); 4, NuSEDS Database (via www.npafc.org); 5, Trites et al. 1996; 6, Lam and Carter (2010); 7, Bennett et al. (2010); 8, NMFS (1997); 9, www.streamnet.org; 10, Washington Dept. of Fish and Wildlife and Puget Sound Indian Tribes 2010. Included in the table are population regions: Strait of Georgia (SOG), Puget Sound (PS), Strait of Juan de Fuca (JDF), and Washington coast (WA coast). Also provided are the number (*n*) and range of brood years for each population in the study, in addition to the source of the data.

number of recruits produced in each brood year (the calendar year when parents spawned) from the escapement and catch data (Fleischman et al. 2013). Prefishery recruitment (ocean age-2) for each brood year (R_t) was calculated by adding the total run (N_t) to the number of individuals harvested in ocean and terminal fisheries, which was derived from the stock-specific brood year exploitation rates (U_t) provided by the PSC (PSC 2015*a*, 2015*b*):

$$(1)\qquad R_t = \frac{N_t}{(1 - U_t)}$$

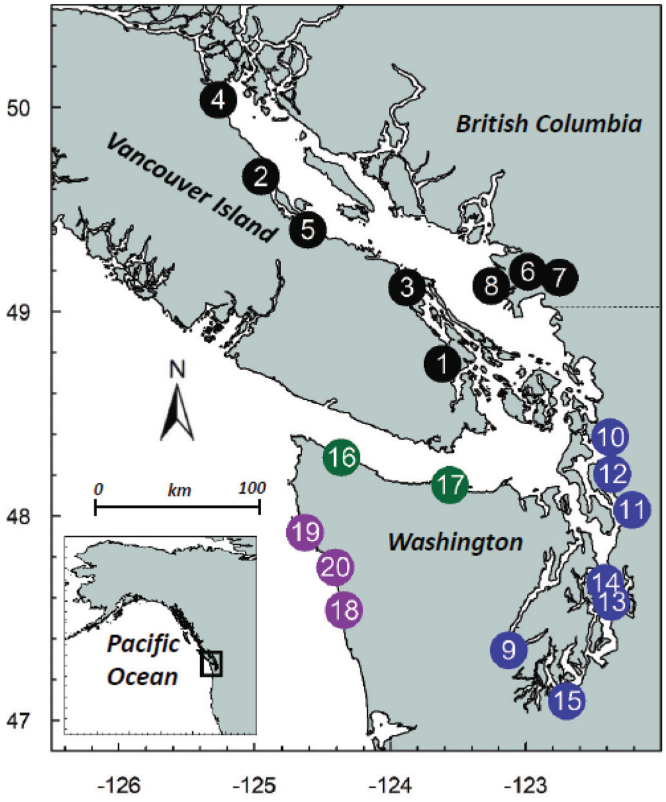
where the total run (N_t) is the sum of spawning adults from the same brood year t across multiple ages (a):

$$(2)\qquad N_t = \sum_{a=2}^{5+} S_{t+a,a}\, p_{t+a,a}$$

and $S_{t+a,a}$ is the number of observed spawners in calendar year $t + a$, and $p_{t+a,a}$ are the proportions of spawners at age a in that calendar year. Because age-at-maturity can be highly variable for Chinook (mature at 2–7 years), age composition from coded-wire tag data gathered on the spawning grounds is necessary to assign escaped fish to brood year. These data were compiled from various resources that were publicly available (see Table 1). For many stocks, age-composition data were not available for every year. In these instances, we used the mean age composition calculated from years where data were available to complete the cohort reconstruction.

Annual hatchery releases of fall Chinook salmon in each region of British Columbia and Washington State (i.e., Strait of Georgia, Puget Sound, Washington coast) were summarized using data from the North Pacific Anadromous Fish Council (NPAFC; http://www.npafc.org/new/science_statistics.html; NPAFC 2016), technical documents published by the PSC (PSC 2016), and the Regional Mark Information System database (http://www.rmpc.org, accessed 25 February 2017; Fig. 2).

Fig. 1. The study area showing locations of the 20 Chinook salmon populations in British Columbia and Washington State included in the analysis. Numbers correspond to the population information and data summaries shown in Table 1. Map data: Schnute et al. (2017); Wessel and Smith (1996). [Colour online.]



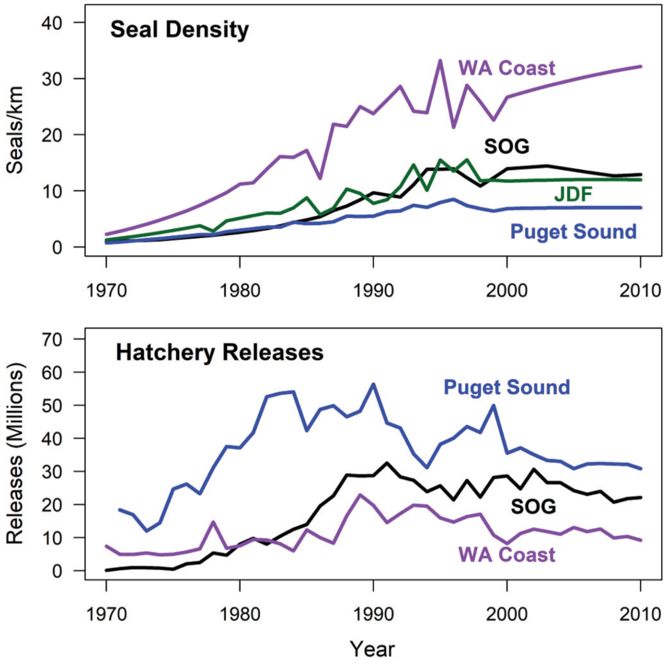
Harbour seal densities

We used published estimates of harbour seal abundances from aerial surveys to estimate predator densities by region (i.e., seals·km^{-1} of shoreline). Regional seal densities were calculated by dividing the total annual abundance in each region by the lengths of shorelines in the corresponding region (Fig. 2; Table 2). A time series of harbour seal abundances in the Strait of Georgia was available from DFO's published aerial survey data (Olesiuk 2010), and estimates of harbour seal abundance in the Puget Sound, Washington coast, and Strait of Juan de Fuca were available from Jeffries et al. (2003). In both British Columbia and Washington, abundance estimates were not available every year — typically every 2–3 years. We thus fit autoregressive state-space models to survey data published by Jeffries et al. (2003) and Olesiuk (2010) to impute abundances for years when surveys were not conducted (see Appendix A).

Modeling approach

The Chinook spawner–recruit data sets were assembled with the seal density and hatchery release data described above, and Bayesian regression models were used to assess how each factor, or combination of factors, may have affected productivity since the 1970s. We evaluated 144 candidate models, using different model structures (nonhierarchical versus hierarchical, nonspatial versus spatial), covariates (seal density, hatchery releases), and assumptions. Our modeling approach used the Ricker stock–recruitment relationship (Ricker 1954) as a base model to account for intrapopulation density-dependent impacts on productivity:

Fig. 2. Time series of harbour seal densities (top panel) and hatchery releases (bottom panel) of fall Chinook salmon in each region between the 1970s through 2010. Geographic regions include Strait of Georgia (SOG), Puget Sound, Strait of Juan de Fuca (JDF), and Washington coast (WA Coast). [Colour online.]



$$R_{i,t} = S_{i,t}\exp(\alpha_i - \beta_i S_{i,t} + \varepsilon_{i,t}) \tag{3}$$

where $R_{i,t}$ is the number of recruits produced from the spawners $S_{i,t}$ in brood year t for stock i ($i = 1, \ldots, N$), α is the productivity parameter, β is the density-dependent parameter (Quinn and Deriso 1999), and ε_t are the error residuals, which are assumed to be normally distributed (Normal(0, σ_i^2)).

We used the Ricker stock–recruitment relationship here because it is conveniently linearized (from eq. 3) to enable evaluation of additional covariates (Hilborn and Walters 1992). Additionally, the Ricker formulation allows for the possibility of reduced productivity at high spawner abundances (Ricker 1954):

$$\ln\left(\frac{R_{i,t}}{S_{i,t}}\right) = \alpha_i - \beta_i S_{i,t} + \varepsilon_{i,t} \tag{4}$$

In the base model, stock-specific parameters (α_i, β_i, and σ_i^2) are estimated separately and without additional covariates. Temporal autocorrelation was accounted for by modeling the error residuals as a first-order autoregressive process, AR(1): $\varepsilon_{i,t} = \rho_i \varepsilon_{i,t-1} + \delta_{i,t}$, where $\delta_{i,t} \sim \text{Normal}(0, \sigma_i^2)$. The AR(1) process was omitted from the model during the first brood year of the time series and in brood years where data from the preceding year was not available.

To infer the potential effects of harbour seal predation and hatchery releases on stock productivity, we introduce two covariates to eq. (4):

$$\ln\left(\frac{R_{i,t}}{S_{i,t}}\right) = \alpha_i - \beta_i S_{i,t} + q_i \text{Seal}_{j,t+1} + h_i \text{Hatch}_{k,t+1} + \varepsilon_{i,t} \tag{5}$$

where q_i is the coefficient associated with harbour seal density near stock i, in region j, in year $t+1$ ($\text{Seal}_{j,t+1}$), which is lagged 1 year to coincide with the salmon cohort's first year at sea. The coefficient h_i relates productivity to the number of hatchery conspecifics released in region k ($\text{Hatch}_{k,t+1}$) and is also lagged to correspond to ocean entry timing of smolts from stock i. Prior to fitting the models, we rescaled the values of both independent variables for more efficient computation: (Hatch × 10^{-7}), (Seal × 10^{-1}).

Table 2. Summary of information used to calculate time series of harbour seal densities in each region in British Columbia and Washington State.

Region	Estimated 2008 abundance	Shoreline length (km)	2008 density	Chinook populations (Table 1)
Strait of Georgia	37 552	2965	12.7	1–8
Puget Sound	15 032	2144	7.0	9–15
Juan de Fuca	2 704	225	12.0	16–17
Washington coast*	7 019	224	31.3	18–20

Note: Using 2008 as an example, this includes the annual estimate of abundance and an estimate of shoreline length in each region. The Chinook salmon populations associated with each region are listed in the last column.

*Includes Washington coastal shoreline north of Grays Harbor and south of Neah Bay, which coincides with the "Olympic Peninsula" region delineated in Jeffries et al. (2003).

Hierarchical and spatially correlated prior distributions

We evaluated two types of hierarchical priors on α_i, q_i, and h_i parameters in full and nested versions of eq. 5. The first was a conventional prior that assumed an exchangeable distribution where the stock-specific parameters arise from a common distribution (e.g., $q_i \sim \text{Normal}(\mu_q, \tau_q^2)$). This approach is used frequently in stock–recruitment modeling of salmon populations (Su et al. 2001; Michielsens and McAllister 2004; Liermann et al. 2010) and has the advantage of allowing data-poor stocks to "borrow strength" from those with more informative data. This can lead to more precise estimates of the individual parameters and "shrinkage" of the parameter estimates around a global mean. Noninformative priors were assigned to both the mean (e.g., $\mu_q \sim \text{Normal}(0, 10^5)$) and variance (e.g., $\tau_q^2 \sim \text{IG}(0.01, 0.01)$) hyperparameters for α_i, q_i, and h_i, where IG is an inverse gamma distribution (Su et al. 2001, 2004). We also evaluated models with variance hyperparameters of IG(0.001, 0.001) and found no meaningful differences in parameter estimates.

The second hierarchical prior we evaluated was a spatially correlated Gaussian conditional autoregressive (CAR) prior (Su et al. 2004). Similar formulations of CAR priors are widely used in medical and epidemiological studies, particularly for disease mapping (Carlin and Banerjee 2003; Jin et al. 2005). The spatially correlated prior allows values for individual parameters for those populations in close proximity (e.g., α_i, q_i, and h_i) to cluster, thereby capturing the dynamics that may be unique to a specific region. For instance, it is well documented that variation in migration routes (i.e., different ocean entry points) can result in different survival rates for several species of Pacific salmon (Melnychuk et al. 2010; Welch et al. 2011; Furey et al. 2015; Moore et al. 2015). We hypothesize that encounter rates with predators and conspecifics (competition, disease, etc.) could be a function of where smolts commence their marine migrations.

As an example, the formulation of the CAR prior used on q_i, conditional on the parameters at other locations (q_i given q_j, $j \neq i$), is

$$q_i \mid q_j, j \neq i \sim \text{Normal}\left(\frac{\sum_{j\neq i}\varphi_{i,j} q_j}{\sum_{j\neq i}\varphi_{i,j}}, \frac{\tau_q^2}{\sum_{j\neq i}\varphi_{i,j}}\right); \quad i,j = 1, \ldots, N \tag{6}$$

where $\varphi_{i,j}$ is the influence of q_j on q_i, and τ_q^2 is the variance parameter. When employing a CAR model, a neighborhood structure needs to be specified to facilitate inference about the spatial relatedness among individual parameters (Rodrigues and Assunção 2012). The "neighborhood" for our analysis consisted of a matrix of pairwise distances between populations i and j, which we defined as the approximate over-water distance (in km) between the ocean entry points of each population. More specifically, this is the shortest hydrologic distance (i.e., not crossing over land) between the terminuses of the two individual rivers associated with each population. We assumed an exponential relationship (Su et al. 2004; Ward et al. 2015)

$$\varphi_{i,j} = \exp(-d_{i,j}\omega_q) \tag{7}$$

where $d_{i,j}$ is the interpopulation spatial distance, and ω_q is an estimated parameter that quantifies the degree of spatial relatedness among individual q values. Very small values of ω_q would suggest an exchangeable model where individual parameter values are not dependent on spatial proximity, while large values would suggest parameters that are fully independent from others (also unrelated spatially). Alternatively, moderate values would indicate clustering towards a local average. Similar to Su et al. (2004), we assigned uniform priors to ω_α, ω_q, and ω_h, using a lower bound of 0 and an upper bound of 2. This interval was determined to cover all plausible values of the ω parameters. We assessed sensitivity to the prior for ω using the alternative distributions U(0, 5) and U(0, 10) and concluded there was no discernable difference in model output or performance.

Other prior distributions

For all models, we assigned noninformative prior distributions to the stock-specific parameters β_i and σ_i^2 : $\beta_i \sim \text{Normal}(0, 10^5)$ and $\sigma_i^2 \sim \text{IG}(0.01, 0.01)$ (Su et al. 2004). In models where α_i, q_i, or h_i were fixed effects, we also imposed noninformative priors on the coefficients in the form of a normal distribution with a mean of zero and a large variance: e.g., $\alpha_i \sim \text{Normal}(0, 10^5)$.

Multicollinearity in the independent variables

Harbour seal density and hatchery releases of fall Chinook exhibit similar increasing trends since 1970 in some regions (Fig. 2), so we assessed multicollinearity for combinations of independent variables in all 20 populations (Zar 2009). Variance inflation factors (VIFs) were calculated for each independent variable included in the model: $\text{VIF}_k = (1 - R_k^2)^{-1}$, where R_k^2 is the coefficient of determination for the linear regression where the kth independent variable is a function of the remaining independent variables. The VIF quantifies the increase in variance of a regression coefficient due to collinearity among the independent variables. VIFs of 10 or above are indicative of pathological multicollinearity, which requires re-evaluating the choice of independent variables included in the model (Hair et al. 2010), while a VIF of 1 would indicate no correlation among independent variables. We also calculated correlation coefficients for each combination of parameters associated with the independent variables (spawners (Ricker b), seal densities (q), and hatchery abundance (h)) for the best-performing model. If collinearity exists between independent variables, the level of correlation between their associated parameters may be high.

Estimation of reference points (U_{MSY} and MSY)

One of the most appealing features of the Ricker equation (eqs. 3 and 4) is the availability of precise analytical approximations for biological and management reference points (Hilborn and Walters 1992): a stock's maximum sustainable yield (MSY); the harvest rate that produces MSY (U_{MSY}); the number of spawners required to produce MSY (S_{MSY}); and the size of the spawning stock that yields the most recruit production (S_{MSR}). However, because of the complex age and maturation patterns of Chinook salmon (2–7 years) and the relatively high number of prefishery age-2 recruits (indicated by large values of α in eq. 3; Fleischman et al. 2013), we computed U_{MSY} and MSY using equilibrium yield calculations detailed in Appendix A. For each stock, we computed U_{MSY} and MSY at different combinations of seal densities and hatchery abundances to evaluate the implications of both covariates on levels of sustainable harvest.

Bayesian computation

Bayesian inference was performed using WinBUGS software (Spiegelhalter et al. 1996) via the "R2WinBUGS" package (Sturtz et al. 2005) in the R Programming Environment (R Core Team 2014). For each candidate model, we generated three separate Markov chain Monte Carlo (MCMC) chains of 100 000 iterations per chain and discarded the first half of each (50 000). The remaining samples were used to calculate posterior means, standard deviations, medians, and quantiles for all parameters and quantities of interest. We assessed model convergence by visual inspection of trace plots and evaluation of Gelman–Rubin diagnostic statistics (R-hat) for each model parameter (Gelman et al. 2013).

Model comparison and posterior predictive checking

To compare the within-sample predictive accuracy of candidate models in the analysis, we calculated their deviance information criterion (DIC), which is often used to evaluate Bayesian models with hierarchical structure (Ward 2008; Gelman et al. 2013). A difference of at least two DIC units (ΔDIC) would indicate a significant difference in performance between two competing models (Spiegelhalter et al. 2002). We also used the posterior predictive distributions to evaluate the ability of our best-performing model to replicate the observed data (Gelman et al. 2013). This was achieved by calculating the proportion of data points captured by the 95% posterior predictive intervals and by graphically displaying the observed data alongside the simulated data (i.e., the 95% posterior predictive intervals) to see if any observable patterns or systematic differences existed between the observed and predicted values. Additionally, to assess the goodness of fit of the best-performing model, we calculated its posterior predictive p value (Meng 1994; Gelman et al. 2013). We used the χ^2 discrepancy measure as a test statistic (T) to compare observed and simulated data:

$$\chi^2 : T(y, \theta) = \sum_{i=1}^{n} \frac{[y_i - E(Y_i \mid \theta)]^2}{\text{Var}E(Y_i \mid \theta)} \tag{8}$$

where y_i is the observed (or simulated) data, and $E(Y_i \mid \theta)$ is the expected value, which is a function of the data and the parameters (θ).

Results

Bayesian computation and posterior predictive checking

Convergence diagnostics and predictive checking did not suggest any problems associated with autocorrelation in the MCMC chains, convergence, or model fit (Appendix A).

Multicollinearity in the independent variables

Of the 60 combinations of independent variables (20 populations × 3 variables) used in the candidate models, none exhibited serious levels of multicollinearity (VIF > 10; Table A1). Only one of the variables (seal density, Puntledge River population) had an intermediate VIF of 4.27. The mean VIF (weighted by the sample size of each data set) was 1.89 for seal density, 1.27 for hatchery abundance, and 1.86 for spawner variables across study populations (Table A1). In addition, the correlation coefficients of the parameter combinations for the best model (Model 1) only showed low to moderate levels of correlation (Appendix A, Table A2).

Model comparison

According to our model selection criteria (described in the previous section), candidate models that assumed a common variance among stocks performed much more poorly than identical

Table 3. Model selection criteria for the top 30 candidate models (Models 1–30), the highest-ranked model not including seal density (Model 37), and the least credible model overall (Model 48).

Model	Model structure	pD	Np	$\overline{D}$	DIC	ΔDIC	R^2
1	α_i + EXH q_i + EXH h_i	100	124	773	773	0	0.68
2	α_i + EXH q_i + CAR h_i	102	124	673	775	2	0.68
3	EXH α_i + q_i + EXH h_i	98	124	678	776	3	0.67
4	α_i + CAR q_i + EXH h_i	99	124	677	776	3	0.67
5	CAR α_i + q_i + EXH h_i	99	124	678	777	4	0.67
6	α_i + EXH q_i + h_i	110	122	668	778	5	0.69
7	α_i + CAR q_i + CAR h_i	101	124	677	778	5	0.68
8	EXH α_i + EXH q_i + h_i	104	124	674	778	5	0.68
9	α_i + q_i + EXH h_i	106	122	673	779	6	0.68
10	CAR α_i + EXH q_i + h_i	104	124	675	779	6	0.68
11	EXH α_i + q_i	91	102	688	779	6	0.67
12	EXH α_i + q_i + CAR h_i	100	124	679	779	6	0.67
13	CAR α_i + q_i + CAR h_i	101	124	679	779	6	0.67
14	α_i + EXH q_i	90	102	689	780	7	0.67
15	CAR α_i + q_i	91	102	689	780	7	0.67
16	α_i + CAR q_i + h_i	107	122	673	780	7	0.68
17	α_i + q_i + CAR h_i	108	122	673	781	8	0.68
18	EXH α_i + EXH q_i + EXH h_i	91	126	691	782	9	0.67
19	EXH α_i + q_i + h_i	110	122	672	782	9	0.68
20	CAR α_i + q_i + h_i	111	122	672	783	10	0.68
21	EXH α_i + CAR q_i + h_i	100	124	683	783	10	0.67
22	CAR α_i + CAR q_i + h_i	101	124	683	784	11	0.67
23	α_i + q_i	97	100	687	784	11	0.67
24	α_i + CAR q_i	90	102	695	785	12	0.67
25	α_i + q_i + h_i	118	120	667	785	12	0.68
26	CAR α_i + EXH q_i + EXH h_i	91	126	696	787	14	0.66
27	EXH α_i + EXH q_i + CAR h_i	93	126	694	787	14	0.67
28	EXH α_i + EXH q_i	83	104	707	790	17	0.67
29	EXH α_i + CAR q_i + EXH h_i	85	126	705	790	18	0.66
30	CAR α_i + CAR q_i + EXH h_i	86	126	706	792	19	0.66
37	α_i + EXH h_i	89	102	799	888	115	0.64
48	α_i (basic Ricker)	76	80	840	916	143	0.61

Note: Coefficients with spatially structured conditional autoregressive (CAR) priors are denoted CAR; coefficients with exchangeable hierarchical priors are labeled EXH; coefficients with independent estimates for each stock are denoted simply by the parameter symbols α_i, q_i, and h_i. Stock-specific β parameters were estimated individually in all candidate models. Included in the table are the number of effective parameters (pD), the total number of parameters (Np), mean deviance ($\overline{D}$), total DIC, ΔDIC, and the coefficient of determination (R^2).

models with a unique variance for each stock (σ_i^2). Additionally, models that accounted for temporal autocorrelation by assuming error residuals follow an AR(1) outperformed identical models without this assumption. Therefore, in the following sections we only present the results for the 48 models that assumed a stock-specific variance term and temporal autocorrelation in those terms.

Several notable outcomes arise from comparing the 48 candidate models. The most obvious and important result is that the models incorporating regional seal density as a covariate performed far better than those that did not (Table 3; Fig. 3). The top hierarchical (Model 1) and nonhierarchical models (Model 23) outperformed their counterparts that omitted a seal covariate by a wide margin (Table 3 and Fig. 3). The disparity in DIC between the lowest-ranked model that included a seal covariate (Model 36) and the highest-ranked model that omitted the seal covariate (Model 37) is substantial (ΔDIC = 90). The highest ΔDIC between models that included a seal covariate is only DIC 25 units (Fig. 3). The best-performing model is a hierarchical model (Model 1) that estimated stock-specific α_i parameters separately and drew seal-associated coefficients q_i from a common distribution (i.e., they were exchangeable). Both models with a ΔDIC ≤ 2 include a hierarchical prior on q_i without spatial structure (Models 1 and 2).

The second important finding from model comparison was the relatively small improvement in model performance gained by including a covariate for regional annual hatchery abundance (Fig. 3). Of the top 36 models that contained a covariate for seal density (Models 1–36), 27 of them included hatchery covariates (Table 3). The top five models according to DIC (Models 1–5) included hierarchical priors on h_i, but the added complexity was not a meaningful improvement over the next highest rated model (Model 6), which had a ΔDIC ≤ 2. Both of the top-tier models (ΔDIC ≤ 2) included a covariate for hatchery abundance.

Fig. 3. The top 48 candidate models for 20 Chinook salmon stocks ranked according to their deviance information criterion (DIC). The *y* axis reflects the model DIC minus the lowest DIC among all candidate models. Model numbers are on the *x* axis and correspond with model structures shown in Table 2. Models 1–10 contain both seal and hatchery covariates. Models 1–36 contain the seal covariate, while Models 37–48 do not.

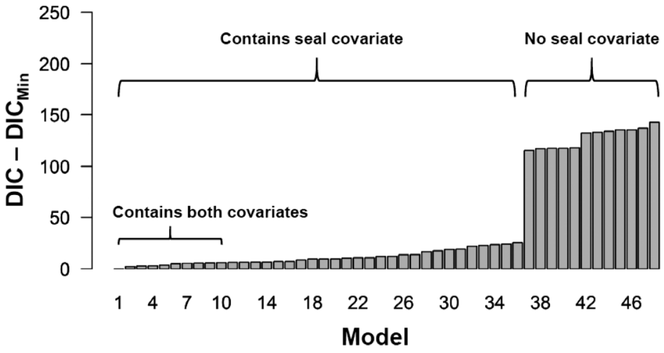
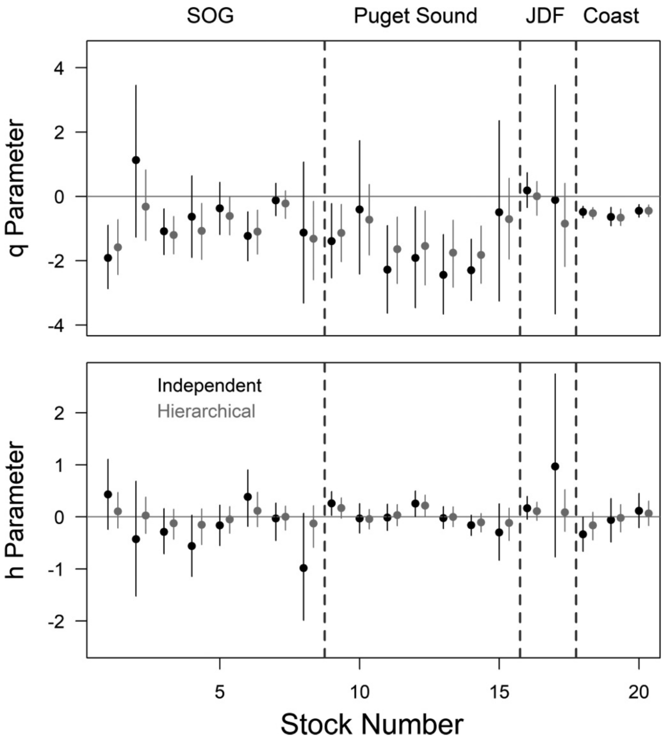


Table 4. Summary of posterior distributions, by Chinook salmon stock, for parameters from the best-performing model (Model 1).

Stock	Stock name	Ricker α	Ricker β ($\times 10^3$)	q	Pr($q < 0$)	h	Pr($h < 0$)
1	Cowichan	3.48 (2.03, 4.80)	−0.10 (−0.17, −0.03)	**−1.59 (−2.43, −0.72)**	100%	0.10 (−0.21, 0.47)	27%
2	Puntledge	2.07 (0.89, 3.27)	−0.21 (−0.35, −0.07)	−0.32 (−1.37, 0.82)	73%	0.03 (−0.32, 0.38)	44%
3	Nanaimo	4.14 (3.15, 5.12)	−0.75 (−1.06, −0.43)	**−1.20 (−1.79, −0.62)**	100%	−0.12 (−0.43, 0.15)	80%
4	Quinsam	3.87 (2.98, 4.78)	−0.33 (−0.47, −0.19)	**−1.08 (−1.96, −0.21)**	99%	−0.15 (−0.53, 0.15)	81%
5	Qualicum	3.02 (2.51, 3.51)	−0.47 (−0.60, −0.35)	**−0.61 (−1.20, −0.01)**	98%	−0.05 (−0.31, 0.20)	65%
6	Harrison	2.78 (1.67, 3.92)	−0.01 (−0.01, −0.01)	**−1.10 (−1.79, −0.42)**	100%	0.12 (−0.19, 0.47)	24%
7	Shuswap	1.69 (1.09, 2.41)	−0.02 (−0.03, −0.01)	−0.23 (−0.69, 0.18)	87%	0.00 (−0.25, 0.21)	47%
8	Chilliwack	4.27 (2.78, 5.75)	−0.04 (−0.06, −0.01)	**−1.32 (−2.59, −0.15)**	99%	−0.13 (−0.59, 0.22)	73%
9	Skokomish	1.74 (0.91, 2.58)	−0.74 (−1.00, −0.47)	**−1.14 (−2.03, −0.25)**	99%	0.17 (−0.02, 0.37)	4%
10	Skagit	2.49 (1.15, 3.87)	−0.09 (−0.11, −0.06)	−0.73 (−1.82, 0.37)	91%	−0.04 (−0.23, 0.14)	66%
11	Snohomish	2.62 (1.31, 3.91)	−0.16 (−0.23, −0.10)	**−1.64 (−2.71, −0.64)**	100%	0.03 (−0.17, 0.24)	36%
12	Stillaguamish	2.22 (0.79, 3.75)	−1.20 (−1.67, −0.84)	**−1.54 (−2.75, −0.45)**	100%	**0.22 (0.01, 0.42)**	2%
13	Green	2.43 (1.41, 3.35)	−0.13 (−0.19, −0.09)	**−1.75 (−2.83, −0.74)**	100%	0.00 (−0.19, 0.19)	53%
14	Lake Washington	3.08 (2.11, 4.02)	−0.98 (−1.31, −0.65)	**−1.82 (−2.70, −0.92)**	100%	−0.11 (−0.29, 0.07)	88%
15	Nisqually	3.10 (1.44, 4.91)	−1.15 (−1.57, −0.73)	−0.71 (−1.95, 0.57)	87%	−0.12 (−0.45, 0.17)	77%
16	Hoko	0.91 (−0.07, 1.99)	−1.24 (−1.62, −0.86)	0.01 (−0.59, 0.47)	45%	0.11 (−0.07, 0.29)	11%
17	Elwha	2.67 (0.12, 5.27)	−1.14 (−1.96, −0.32)	−0.85 (−2.18, 0.41)	91%	0.09 (−0.28, 0.52)	33%
18	Queets	2.91 (2.44, 3.37)	−0.12 (−0.19, −0.06)	**−0.53 (−0.71, −0.35)**	100%	−0.16 (−0.44, 0.09)	89%
19	Quillayute	3.28 (2.58, 3.95)	−0.12 (−0.17, −0.07)	**−0.66 (−0.91, −0.39)**	100%	−0.02 (−0.29, 0.24)	56%
20	Hoh	2.82 (2.34, 3.33)	−0.30 (−0.42, −0.19)	**−0.45 (−0.63, −0.26)**	100%	0.07 (−0.17, 0.31)	29%

Note: Posterior means and 95% credible intervals (in parentheses) are presented for each parameter. Seal density (q) and hatchery release (h) coefficients with posterior credible intervals that do not overlap with zero (i.e., are "significant") are shown in bold. Also shown (columns 6 and 8) are the probabilities that coefficients q_i and h_i have a value less than zero.

Fig. 4. Plots of q_i (seal density coefficient, top panel) and h_i (hatchery releases coefficient, bottom panel) by Chinook salmon stock. The black series shows estimates for the full nonhierarchical model (Model 25), while the grey series is the top-ranked hierarchical model by DIC (Model 1). Circles represent the posterior means and the solid vertical lines show the 95% posterior credible intervals. The black vertical dashed lines separate the stocks by region: Strait of Georgia (SOG); Puget Sound (PS); Strait of Juan de Fuca (JDF), and Washington coast (Coast).



Accounting for spatial correlations among stock-specific covariates did not significantly improve model performance (Table 3). Only one of the top-tier models (Model 2) included spatial structure using the CAR prior (on the h_i coefficient). The most complex candidate models evaluated (number of parameters >124) imposed exchangeable or spatially structured priors on three coefficients (α_i, q_i, h_i) and were outperformed by models that had no hierarchical structure (Model 17; Table 3). However, there was a positive correlation between model complexity and performance and ranking (Table 3). For example, the top models all had at least 100 parameters, while the worst performing model (Model 48), the basic Ricker, had the fewest parameters (60). As intended, hierarchical models facilitated borrowing of information, as suggested by the lower number of effective parameters (pD) compared with the actual number of model parameters (Np) in all cases (Table 3). Conversely, the nonhierarchical models had numbers of effective parameters that were close to or even exceeded the number of actual parameters (e.g., Models 17 and 48; Table 3).

Effect of seal density

The mean seal density coefficient (q) for the best-performing model (Model 1, exchangeable prior on q) was −0.96 (95% CI: −1.39, −0.57) and had a very high probability of being negative (>99%).[2] In addition, the individual posterior means (q_i) were negative for 19 of 20 populations (Table 4), and 14 of those populations had 95% posterior credible intervals that did not overlap with zero (Table 4 and Fig. 4). Regions where there was a high probability (>95%) of a negative q_i included the central Puget Sound (Snohomish, Stillaguamish, Green, and Lake Washington), east Vancouver Island (Cowichan, Nanaimo, Quinsam, Qualicum), and the Washington coast (Queets, Quillayute, Hoh; Table 4). The only populations where the probability of a negative q_i was less than 90% included the Puntledge (73%) and Shuswap (87%) in the Strait of Georgia, the Nisqually (87%) in the Puget Sound, and the Hoko (45%) in the Strait of Juan de Fuca (Table 4).

Effect of hatchery releases

The mean coefficient for hatchery releases (h) for the top-ranked model (DIC) (Model 1, exchangeable prior on h) was 0.00 (95% CI:

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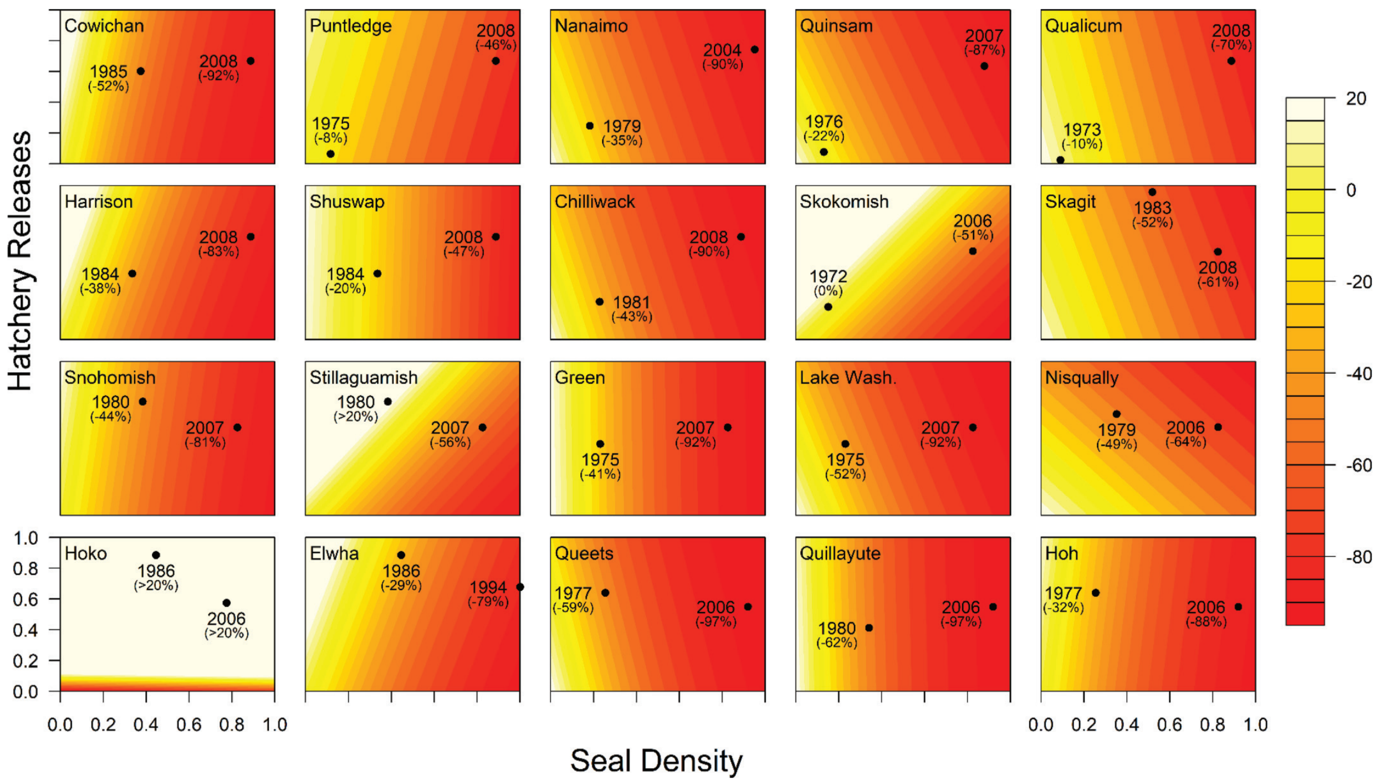
[2] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0481.

Fig. 5. Estimated percent change in maximum sustainable yield (MSY) since 1970 over different combinations of seal densities and hatchery abundance for 20 Chinook salmon stocks. Both variables are standardized by the maximum observed value of each variable between 1970 and 2010. The predicted change in MSY for the first and last years in the data set for each population (see Table 1) are shown using black circles, with the estimated percent change in MSY in parentheses. [Colour online.]



–0.12, 0.12) and had a 48% probability of being negative. Ten of the stock-specific coefficients h_i had posterior means with negative values. However, 19 of the 20 coefficients had posterior credible intervals that overlapped with zero (Table 4). The Stillaguamish River in the central Puget Sound was the only stock whose posterior distribution of h_i did not overlap with zero (Table 4). Several populations in the analysis had a high (but not statistically significant) probability of a negative h_i parameter: Nanaimo (80%), Lake Washington (88%), and Queets (89%) (Table 4).

No spatial patterns were apparent when examining the individual h_i parameters generated by the best-performing model (Model 1; Table 4; Fig. 4). Furthermore, the second-ranked model by DIC (Model 2), which performed virtually the same as the highest-ranked model (ΔDIC = 2), included a CAR prior on h_i with a posterior mean of 0.03 (95% CI: 0.00, 0.09) for ω_h. The mean value implies populations separated by less than approximately 23 km have correlated h_i parameters (assuming a correlation of 0.50, using eq. 7). However, the wide credible intervals associated with this parameter preclude making any strong conclusions regarding the spatial relatedness of hatchery effects.

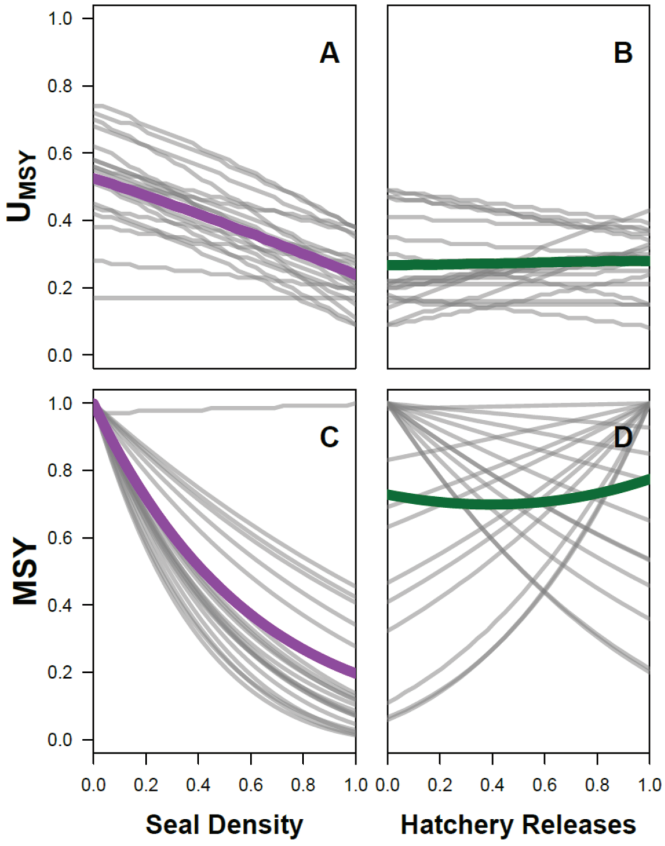
Management reference points

The implications of seal density and hatchery abundance on the U_{MSY} and MSY for each stock (Figs. 5 and 6) were based on projections using the estimated parameters from Model 1. After simulating yield over all observed levels of hatchery abundance, we estimated that changes in seal density between 1970 and mid-2000s resulted in a mean decrease in MSY of –74% (95% CI: –85%, –64%; Table 5). Similarly, the mean decrease in U_{MSY} due to seal effects across all stocks was 44% (95% CI: –52%, –35%). With the exception of the Hoko River population, there was an inverse relationship between seal density and yield (Fig. 5). The most drastic reductions in yield due to seal effects were in the Cowichan River (–94%) and along the Washington coast (Table 5).

The effect of hatchery releases on U_{MSY} and MSY was not nearly as consistent compared with the effect of seal density (Fig. 6; Table 5). We estimated that changes in hatchery releases between 1970 and mid-2000s resulted in a mean increase in MSY of 9% (95% CI: –6%, 25%; Table 5). High levels of hatchery releases were associated with increased sustainable harvest rates and yields for some populations (Fig. 6). The model suggests that increased hatchery abundance may buffer harvest yield against low to moderate seal densities in the Skokomish and Stillaguamish populations in the Puget Sound (Fig. 5). However, hatchery releases appeared to suppress the potential yield in others (Figs. 5–6). The effect of hatchery releases on U_{MSY} and MSY varied considerably, even among populations within the same geographic region. For example, on east Vancouver Island in the Strait of Georgia, high harvest rates on the Nanaimo, Quinsam, and Qualicum river stocks appear to have coincided with low seal densities and low levels of hatchery production (Fig. 5). Conversely, harvest rates of Chinook from the Cowichan and Puntledge populations appeared to be higher when densities of seals were low and hatchery releases were high.

For the Chinook populations examined here, observed harvest rates dropped by an average of 45% over the range of brood years for which we had data. The Shuswap River was the only population where harvest rate increased (33%). However, our simulations suggest observed harvest rates still exceeded U_{MSY} in recent years for many populations, such as the Cowichan, Puntledge, and Shuswap in the Strait of Georgia; the Skagit and Green in the Puget Sound; and all three populations on the Washington coast (Queets, Quillayute, and Hoh).

Fig. 6. Plots show the harvest rate at maximum sustainable yield (U_{MSY}) and maximum sustainable yield (MSY) over a range of seal densities (A and C) and hatchery releases (B and D). The independent variable on the *x* axis is scaled from zero to the highest observed value (1.0) in the time series, while the other variable remains constant at the most recent value in the time series. MSY on the *y* axis of plots C and D is scaled from zero to the largest value of MSY (1.0) for each stock. The light grey lines represent the individual stocks, and darkest line in each panel shows the mean U_{MSY} and MSY for all 20 stocks of Chinook salmon. [Colour online.]



Trends in wild Chinook salmon productivity

For many of the Chinook populations we considered, our models suggest productivity declined between the late 1970s and early 1980s and the mid-1990s (Fig. 7). Populations in east Vancouver Island (Cowichan, Quinsam, Qualicum), central Puget Sound (Snohomish, Stillaguamish, Green, Lake Washington), and Washington coast (Queets, Quillayute, Hoh) showed the most pronounced drops in productivity, while Fraser River stocks (with the exception of the Chilliwack) were relatively stable. The two Juan de Fuca Chinook stocks did not show any clear temporal patterns in productivity, nor did several stocks from the northern and southern regions on Puget Sound (Skagit, Skokomish, and Nisqually). Stocks that experienced the most pronounced drops in productivity between the 1970s and 1990s appear to be associated with negative q_i values whose posterior distribution did not overlap with zero (i.e., is "significant"; Table 4). Following the declines in productivity that occurred between the 1970s and 1980s, many stocks exhibited somewhat stable trends after 1995. This appears to coincide with seal populations in the Salish Sea reaching carrying capacity (Olesiuk 2010) (Fig. 2). The best examples of this pattern are the Cowichan, Qualicum, and Chilliwack populations from the Strait of Georgia, the Stillaguamish and Green in the Puget Sound, and all three populations on the Washington coast (Fig. 7).

Discussion

We evaluated the relationship between two biotic covariates (seal density and hatchery abundance) and productivity in 20 populations of wild fall Chinook salmon in British Columbia and Washington State and found negative relationships between Chinook productivity and harbour seal density in 19 of the 20 populations, of which 14 were considered "significant". Our model projections showed that increases in the number of harbour seals since 1970 was associated with an average decrease in MSY of 74%. Thus, predator density is associated with reduced productivity and yield in populations in most of the major Chinook-producing rivers in lower British Columbia and Washington State. In contrast, effects of hatchery abundance on wild stock productivity were mixed and weak in most populations, except for one population (Stillaguamish River) in central Puget Sound.

There is a tendency in analyses of fish recruitment to overestimate the strength of correlations and predictive power (Shepherd et al. 1984; Myers 1998). Therefore, evaluating correlative evidence for causality in the absence of manipulative experiments requires consideration of such factors as (*i*) the strength of the correlation; (*ii*) its consistency across multiple populations or units of observation; (*iii*) mechanistic explanations from experiments; and (*iv*) alternative–competing explanations (Hilborn 2016).

Effects of seal predation

The density of harbour seals in the Strait of Georgia, Puget Sound, and along the Washington coast was negatively associated with Chinook productivity in nearly every population in these three regions. Scientists have been cognizant of the concurrent decrease in Chinook abundance and the increase in seal numbers in the Salish Sea for at least two decades. However, the magnitude of decline in marine survival in Chinook has not been consistent among the different populations (PSC 2015*a*, 2015*b*; Ruff et al. 2017).

Our study is the first to assess the relationship between seals and Chinook abundances at the population (sub-basin) scale in the Pacific Northwest. In addition, our approach provides a rigorous statistical framework to quantify the effect of biotic covariates on key management parameters.

Our model predictions are consistent with recent mechanistic evidence for a causal relationship between seal predation and declines in Chinook marine survival since the 1970s. Most notably, new methods for quantifying juvenile salmon in predator diets have found seals targeting juvenile Chinook salmon more than chum (*Oncorhynchus keta*) and pink (*Oncorhynchus gorbuscha*) salmon smolts, despite the latter two species being much higher in abundance (Thomas et al. 2017). These studies show that the overall contribution to the seal diet is small during the spring and summer (typically <5%), but potentially results in the loss of tens of millions of Chinook smolts each year because of the large number of seals in the Strait of Georgia. Bioenergetics modeling further suggests that predation on Chinook smolts by seals in the Puget Sound has probably increased sevenfold following enactment of the Marine Mammal Protection Act and that as many as one in four hatchery smolts are eaten by harbour seals in recent years (Chasco et al. 2017).

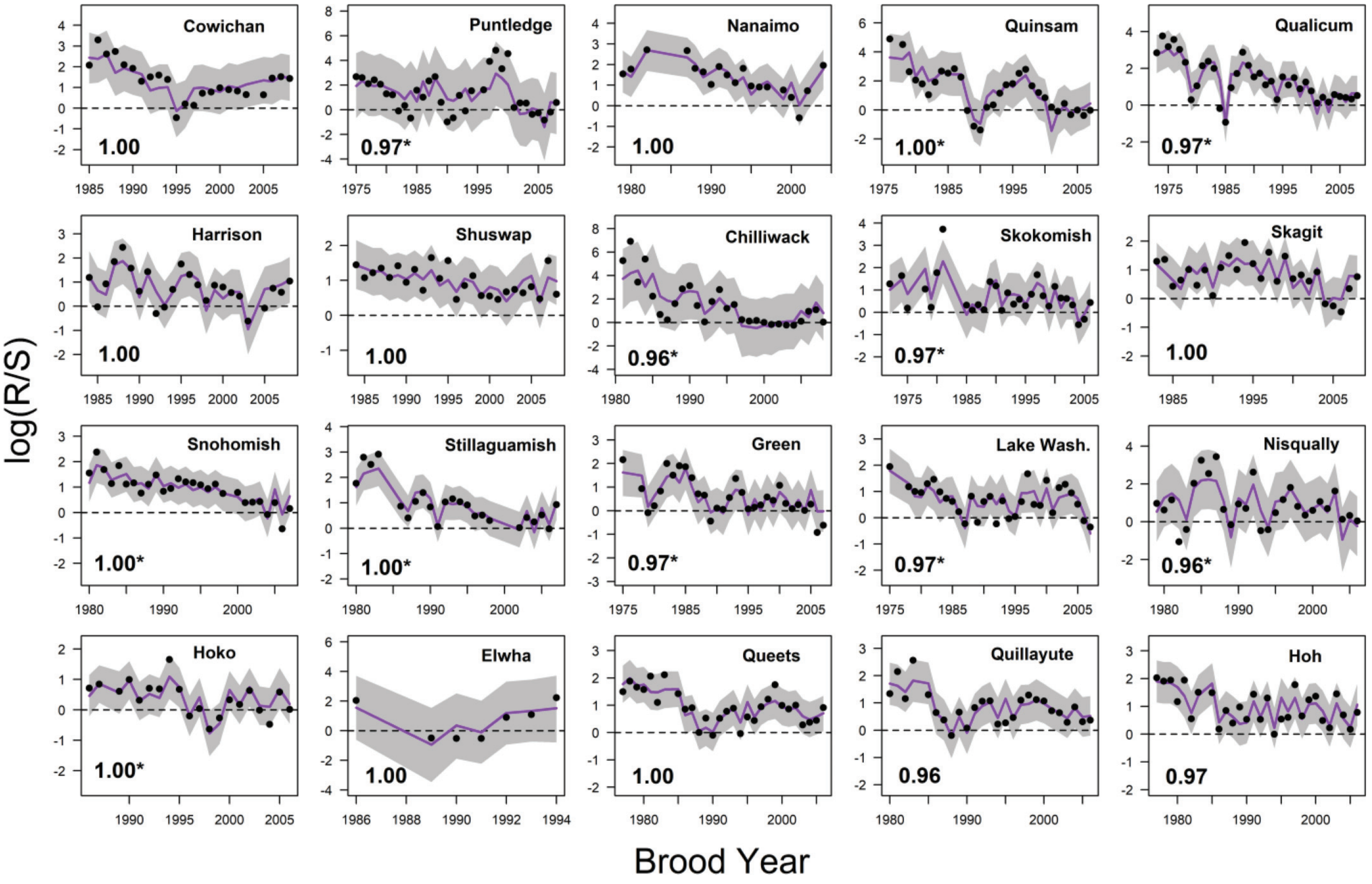
While much of the recent research involving seal predation in the eastern Pacific has focused on the Salish Sea, including a major transboundary research effort (Riddell et al. 2009), our results suggest that seal predation on Chinook from coastal stocks may also be of concern. The three coastal populations assessed showed very high probabilities of a significant negative relationship between seal densities and productivity (Fig. 5; Table 4). Additionally, populations along the Washington coast also appear to have experienced declines in productivity since the 1970s, although they appear to have stabilized at higher levels compared with those in the Strait of Georgia and Puget Sound (Fig. 3). It is

Table 5. Percent change in maximum sustainable yield (MSY) and harvest rate at MSY (U_{MSY}) between 1970 and the last year in the time series due to changes in each variable (seal density and hatchery abundance) for all 20 populations of Chinook salmon.

			% Change in MSY		% Change in U_{MSY}	
Stock	Stock name	Region	Seal density	Hatchery releases	Seal density	Hatchery releases
1	Cowichan	SOG	–94	44	–61	14
2	Puntledge	SOG	–51	12	–24	4
3	Nanaimo	SOG	–86	–31	–41	–9
4	Quinsam	SOG	–81	–33	–38	–11
5	Qualicum	SOG	–64	–14	–29	–5
6	Harrison	SOG	–88	57	–55	19
7	Shuswap	SOG	–47	1	–22	0
8	Chilliwack	SOG	–86	–29	–40	–9
9	Skokomish	PS	–78	72	–47	26
10	Skagit	PS	–54	–9	–25	–3
11	Snohomish	PS	–84	9	–50	4
12	Stillaguamish	PS	–80	71	–45	23
13	Green	PS	–91	–1	–64	–1
14	Lake Washington	PS	–87	–24	–55	–11
15	Nisqually	PS	–48	–21	–20	–8
16	Hoko	JDF	2	71	1	26
17	Elwha	JDF	–87	33	–52	11
18	Queets	WA coast	–96	–24	–74	–11
19	Quillayute	WA coast	–97	–3	–73	–1
20	Hoh	WA coast	–89	9	–56	3
Mean (95% CI):			–74 (–85, –64)	9 (–6, 25)	–44 (–52, –35)	3 (–2, 9)

Note: Regions include the Strait of Georgia (SOG), Puget Sound (PS), Strait of Juan de Fuca (JDF), and Washington coast (WA coast).

Fig. 7. Log recruits per spawner of Chinook salmon by brood year, fit with Model 1. 95% posterior predictive intervals are depicted by the grey regions, and posterior means are shown with solid lines. The data points (black circles) show the observed productivity calculated from the spawner–recruit data (Table 1). The proportion of the observed data points included in the predictive intervals is shown in the lower left region of each plot. Asterisks denote populations where autocorrelation among error residuals (ρ_i) was significant. [Colour online.]



possible that the relatively pristine freshwater and estuarine habitats of these coastal watersheds have buffered population productivity and abundance against factors causing poor marine survival, which may allow these populations to be harvested at higher rates than those from the Salish Sea (Fig. 7). Despite these modest harvest rates, our analysis suggests MSY for the Washington State's coastal populations has still been drastically reduced since 1970 (Fig. 5). Unfortunately, we were not able to investigate trends along the outer British Columbia coast (west Vancouver Island) due to the paucity of abundance data for harbour seals in this region (Olesiuk 2010).

Spatial patterns in predation

The strength and consistency of the correlations we detected may not be surprising given the clear inverse relationship between seals and salmon (Fig. 2). However, the weak degree of spatial relatedness of seal effects (q_i) among populations is noteworthy. One explanation for the weak spatial relatedness may be that there simply is not enough information in the data to detect a spatial (statistical) effect (Banerjee et al. 2015). Alternatively, it is conceivable that estuary location, which defines the "neighborhood" of our spatially structured candidate models, was unimportant to, or was a poor proxy for, factors that determine the dynamics of seal predation during the first year that salmon are at sea.

The hypothesis that seal predation is highest for juvenile Chinook outside the estuary is consistent with a recent study in the Strait of Georgia (Allegue 2017). Harbour seals did not respond numerically or change their foraging behavior to target hatchery-released Chinook smolts during spring at the mouth of the Big Qualicum River on Vancouver Island. It appears instead that some seals target the Chinook smolts later in midsummer when the fish are bigger (Allegue 2017), which coincides with movement out of the estuaries to nearshore or offshore habitats (Healey 1980*b*; Duffy and Beauchamp 2011; Beamish et al. 2012). This may explain the high proportion of juvenile Chinook found in the summer seal diet at a number of non-estuary sites (Lance et al. 2012; Thomas et al. 2017).

There is evidence that smolts using regions with low predator densities may fare better than others. For example, in the Strait of Georgia, steelhead smolts originating from the same watershed were twice as likely to survive if they passed through Malaspina Strait, compared with those that migrated west of Texada Island (Furey et al. 2015). Similarly, trawl surveys found high abundances of subyearling Chinook from the South Thompson River, a population whose marine survival rates have actually increased over the last two decades (Beamish et al. 2010*a*; Neville et al. 2015), rearing along the British Columbia's inner coastline from Malaspina Strait to Howe Sound (C. Neville, DFO-Pacific, personal communication, 7 June 2017). In terms of seal abundance in this area, aerial surveys have found significantly lower seal numbers along the inner stretch of coastline than in most regions of the Strait of Georgia (Olesiuk 2010). All told, this suggests that predation by seals on multiple stocks mixing in common rearing and foraging areas may be high during the summer months. This could explain why location of saltwater entry and its distance to the open ocean may not be as influential as we initially hypothesized.

The lack of spatial correlation among the coefficients calculated and the findings from other studies suggest that predation effects on Chinook are strongest outside the estuary at an across-basin scale. Interestingly, this does not appear to be the case for other Pacific salmon species of high conservation concern. Recent research suggests that seal predation on steelhead smolts in the Puget Sound occurs very shortly after ocean entry and that early marine survival is lower for those fish that have longer migration routes to the open ocean (Moore et al. 2010; Moore and Berejikian 2017). In the Strait of Georgia, the Big Qualicum River estuary is a foraging "hotspot" for a portion of the local seal population that specializes in targeting out-migrating coho smolts at the river mouth (Allegue 2017). Other evidence similarly suggests that seal predation on coho salmon smolts is highest within the first month of ocean entry (B.W. Nelson, unpublished data). The apparent disparity in peak seal predation mortality on coho and steelhead and Chinook smolts may be a function of prey size. Chinook smolts may be too small compared with coho and steelhead smolts at ocean entry to be worthwhile targeting (Tollit et al. 1997; Allegue 2017; Thomas et al. 2017).

Effects of hatchery releases

There is some evidence that hatchery smolt abundance may negatively impact marine survival of Chinook salmon in the eastern Pacific (Levin et al. 2001), but our analysis does not support this. A few of the Chinook populations analyzed had moderately high probabilities of a strong negative correlation between productivity and hatchery abundance (Table 4), but the only statistically significant relationship we found was positive (Table 4). One possible explanation for a positive relationship between productivity and hatchery abundance could be predator swamping, which has been observed in freshwater habitats (Furey et al. 2016).

Although our best-performing model had an exchangeable hierarchical prior on h (hatchery effect), we could not completely rule out the second-ranked model (ΔDIC = 2), which had a spatially structured CAR prior (Table 3). Parameter estimates for this model imply that the hatchery effects on Chinook populations occurring within 23 km of each other are correlated with productivity. Only stock combinations from the central Puget Sound region fell within this threshold: Green–Lake Washington, Stillaguamish–Skagit, Snohomish–Stillaguamish, and Snohomish–Skagit. However, uncertainty around the degree of spatial relatedness of hatchery effects (ω_h) was high, and no obvious patterns existed in the individual estimates of the hatchery effects. It therefore remains unclear from our analyses how hatchery smolt abundance impacts wild populations and whether those impacts occur at local or regional scales.

Model assumptions

The structure of our model (eq. 5) makes several important assumptions that warrant discussion. Most relevant to our key findings is our assumption that the functional relationship between predator and prey is type I ($q_i \times \text{Seal}_{j,t}$) and not subject to constraints of handling time (Holling 1965). However, this is likely not an issue here, as Peterman and Gatto (1978) found most predators of salmon smolts are not being saturated and operate on the low end of the functional response curve. This likely applies to interactions between harbour seals and salmon smolts, as all species of juvenile salmon rarely make up more than 10% of the diet of harbour seals at any time throughout the year (Thomas et al. 2017).

A second assumption in our model implies that important alternative prey species are relatively constant over the time series in the analysis. Given comparable abundance time series for key alternative prey species including herring (*Clupea pallasii*), hake (*Merluccius productus*), or walleye pollock (*Gadus chalcogrammus*) (Lance et al. 2012; Steingass 2017), it is plausible that a multispecies relationship could be integrated into this model structure (Walters et al. 1986). However, mass-balance ecosystem models or models of intermediate complexity (Plagányi et al. 2014) are probably better suited for multispecies inference.

Conclusions

Our analysis suggests that harbour seal predation could be driving productivity of wild Chinook salmon populations, but the correlative nature of our study and the inherent possibility of detecting spurious relationships demand treating these findings with caution. The same could be said about the ability of our models to capture important fine-scale interactions between wild populations and hatchery smolts, especially if these interactions are linked to predation or mediated by abundances of other prey species. Deliberate, manipulative experiments are necessary to address methodological issues with our modeling approach, but predator control of seals may not be a viable option for political and ethical reasons (Yodzis 2001). However, hatcheries present a clear opportunity to engineer controlled, replicated experiments and would provide a unique environment to explore questions related to functional relationships between seals and smolts.

Combined with the mechanistic evidence found in the recent diet and bioenergetics of harbour seals studies conducted in the Salish Sea, it may be reasonable to conclude that the relationships we detected between Chinook productivity and seal densities are causal. However, in addition to the increase in marine mammal predators, the Salish Sea and adjacent regions have seen other major ecosystem changes in the past four decades. These include increases in certain contaminates, introduction or proliferation of pathogens, habitat degradation, and changing ocean conditions, which all have the potential to impair the health and behavior of Chinook salmon in the early marine stage of life (Noakes et al. 2000; Magnusson and Hilborn 2003; O'Neill and West 2009; Irvine and Fukuwaka 2011). Therefore, it is conceivable that a composite of factors make juvenile Chinook salmon more vulnerable to predation by efficient, opportunistic predators like harbour seals. None of the approaches applied to date have the ability to evaluate the possibility that seals are merely a proximate source of mortality instead of the ultimate source.

The predatory impacts of seals on commercially important salmon populations are not unique to salmonids in the eastern Pacific. In the Baltic Sea, changing environmental conditions and prey availability appear to have exacerbated predation on Atlantic salmon (*Salmo salar*) postsmolts by gray seals (*Halichoerus grypus*), which have also increased in abundance since the 1980s (Mäntyniemi et al. 2012; Friedland et al. 2017). As conflicts continue to arise from concurrent conservation efforts to recover both predator and prey populations, pressure will increase to develop science-based management strategies and policy tools for navigating these challenges (Marshall et al. 2015; Samhouri et al. 2017). In the interim, studies such as ours highlight the importance of including predator–prey interactions in forecasting and assessment methods and the need to seriously consider well-designed experimental manipulations to test hypotheses about predator–prey interactions and their impact on fisheries.

Acknowledgements

B.W. Nelson was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Networks grant to the Canadian Fisheries Research Network (CFRN). C.J. Walters was supported by a grant from the Pacific Salmon Foundation (PSF). We thank Josh Korman and Villy Christensen for providing useful insights and suggestions on early drafts of this manuscript. Mike Hawkshaw was helpful in developing early versions of the models used in this analysis. We also thank Casey Ruff for his advice on procuring data for Chinook populations in Washington State.

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Appendix A

Harbour seal abundance modeling

Aerial survey data from British Columbia and Washington was used to estimate harbour seal abundance for years missing from the time series in published studies (Jeffries et al. 2003; Olesiuk 2010). To impute the abundance of seals in missing years, we employed a univariate state-space model that assumes density dependence and accounts for process and observation error. As the population dynamics of seals on the Washington coast are likely different than those from the Salish Sea, separate models were developed to estimate annual abundances for three regions (Strait of Georgia, Puget Sound, and Washington coast).

Factors mediating population growth in seal populations are likely availability of prey and suitable haulout habitat (Brown et al. 2005). The distribution–availability of seals' primary prey items in the estuarine habitats of the Salish Sea (herring, gadids, and adult salmon; see Lance et al. 2012 and Howard et al. 2013) is likely much different than that around coastal Washington (Steingass 2017). The different correction factors and survey protocols that were applied to aerial survey methods (see below) in each region also justified the use of separate models for each region.

The approach integrates count data from multiple subregions to infer a common regional trend in population dynamics (see Jeffries et al. 2003 and Olesiuk 2010 for descriptions of these subregions). To estimate the regional annual abundance using count data from multiple sites within a region, we assume a single well-mixed population can be represented by the process model (Holmes et al. 2013):

$$x_t = bx_{t-1} + u + w_t \tag{A1}$$

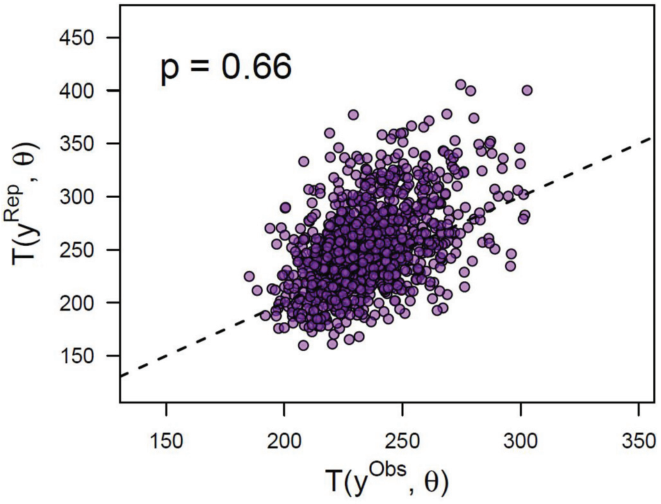
where x_t is natural log of the abundance of seals in year t, b dictates how fast the state reverts to the mean, u is the mean population growth rate, and w_t is the deviation in year t. We assumed the deviations were normally distributed: $w_t \sim \text{Normal}(0, q)$, where q is the process variance.

We assumed the count data from each subregion are observations of a common regional population trend. In other words, these subregions are not isolated from one another, and animals move and intersperse among them. This is supported by studies describing harbour seal movement patterns derived from tag data (Peterson et al. 2012). As such, the observation model is

$$\boldsymbol{y}_t = x_t + \boldsymbol{a} + \boldsymbol{v}_t \tag{A2}$$

where $\boldsymbol{y}_t$ are the abundance time series for the subregions, $\boldsymbol{a}$ is a vector of scalars that capture the bias between the counts and the total population, and $\boldsymbol{v}_t$ is a vector of observation error variances, which we assume are the same in each region because they were performed with the same aerial survey protocols. We assumed the observation error on the natural log of the counts was normally distributed. For the surveys in Washington State, a correction factor of 1.53 (Huber et al. 2001; Chasco et al. 2017) was used to expand abundance estimates, while Strait of Georgia survey data was corrected using site-specific multipliers presented in DFO's published reports (Olesiuk 2010). The model described above was fit to the aerial survey data with maximum likelihood using the MARSS package in R (Holmes et al. 2013).

Fig. A1. The relationship between 1000 simulated (y axis) and realized (x axis) χ^2 discrepancy measures (T), which were used to calculate the posterior predictive p value for Model 1. The dashed line depicts $x = y$. The Bayesian p value of 0.66 suggests Model 1 provides a relatively good fit to the data. [Colour online.]



Estimation of management reference points (U_{MSY} and MSY)

Using equilibrium yield calculations (Walters and Martell 2004), we estimated two reference points for each population of Chinook salmon — the harvest rate that produces maximum sustained yield (U_{MSY}) and maximum sustainable yield (MSY) — over different combinations of independent variables to quantify the impact seal density and hatchery abundance have on yield. For each stock, we started with an initial spawning population, then used the estimated parameters from the best-performing model (Model 1) to simulate cohorts of recruits. We then subjected the cohort to a natural mortality and maturity schedule, as well as a fishery. This process was repeated until the population achieved equilibrium. Yields were calculated across a range of exploitation rates (0.0–1.0, by increments of 0.01) over different combinations of seal densities and hatchery abundances, and the reference points associated with each combination were identified.

This iterative scheme was initialized by generating an estimate of the number of spawners at equilibrium: $S_{\mathrm{Equil},1} = 0.5(\alpha/\beta)$ (e.g., Korman et al. 1995). Then, the following age-structured population model was repeated until S_{Equil} had stabilized:

$$\text{(A3)}\qquad S_{\mathrm{Equil},i+1} = 0.5S_{\mathrm{Equil},i} + 0.5S_i$$

where S_i is the number of spawners generated from $S_{\mathrm{Equil},i}$ at iteration i. The number of age-2 recruits (prefishery) in each iteration was generated from the generalized Ricker equation (eq. 5) with parameter estimates from the best model in the analysis (Model 1):

$$\text{(A4)}\qquad R_{2,i} = S_{\mathrm{Equil},i}\exp(\alpha - \beta S_i + q\mathrm{Seal} + h\mathrm{Hatch})$$

Recruits were then subjected to natural mortality prior to fishing. For each year in iteration i, recruitment at age was calculated by subtracting fish lost to harvest, natural mortality, and maturity:

$$\text{(A5)}\qquad R_{a,i} = \begin{cases} R_{a-1,i}s_a & a = 3 \\ (R_{a-1,i} - C_{a-1,i} - S_{a-1,i})s_a & a > 3 \end{cases}$$

where s_a is the age-specific natural mortality rate. We used the following natural mortality rates at each age: 40% for age-2, 30% for age-3, 20% for age-4, and 10% for age-5 (Sharma et al. 2013; PSC 2015). Catch-at-age is calculated by multiplying the recruits at age a by the harvest rate U:

$$\text{(A6)}\qquad C_{a,i} = U \times R_{a,i}$$

Table A1. Variance inflation factors (VIFs) for each independent variable (seal density, spawners, hatchery (releases)) for each of the 20 stocks of Chinook salmon included in the study.

Stock	Seal density	Spawners	Hatchery	n
1	1.03	1.03	1.00	23
2	4.27	1.44	3.49	33
3	1.81	1.26	2.15	19
4	2.66	1.57	2.92	31
5	3.82	1.25	3.48	36
6	1.10	1.04	1.09	24
7	1.34	1.45	1.15	25
8	2.63	1.93	1.62	28
9	1.06	1.02	1.06	29
10	2.16	1.23	2.22	26
11	1.97	1.29	2.35	27
12	1.89	1.06	1.87	23
13	1.17	1.08	1.15	31
14	1.15	1.07	1.11	31
15	1.50	1.17	1.67	28
16	1.32	1.09	1.38	20
17	1.91	2.79	2.98	7
18	1.23	1.28	1.54	29
19	1.26	1.34	1.56	26
20	1.24	1.07	1.26	29
Min.	1.03	1.02	1.00	7
Max.	4.27	2.79	3.49	36
Mean	1.83	1.32	1.85	26.25
SD	0.91	0.41	0.81	6.19
Weighted mean	1.89	1.27	1.86	—

Note: The stock number in the first column corresponds to population information in Table 1. Summary statistics for each variable's VIF across all populations are included in the bottom rows of the table, and the number of data points (brood years) for each Chinook population data set is shown in the last column (n). The mean VIFs were weighted by the size of the data set (n).

Table A2. Pearson correlation coefficients for thee parameter combinations for 20 stocks of Chinook salmon, using the best-performing model (Model 1).

Stock	q, Ricker β	q, h	h, Ricker β
1	−0.09	−0.01	0.00
2	−0.21	−0.30	−0.07
3	0.00	−0.43	0.31
4	−0.27	−0.35	−0.22
5	−0.11	−0.62	−0.17
6	0.09	−0.13	−0.19
7	−0.57	0.03	−0.28
8	−0.41	−0.12	−0.07
9	−0.04	−0.22	−0.17
10	0.20	0.40	0.18
11	0.06	0.33	0.09
12	0.28	0.37	0.13
13	−0.26	0.16	−0.28
14	0.02	0.03	−0.01
15	−0.03	0.11	0.15
16	0.13	0.08	−0.20
17	0.38	0.04	−0.26
18	−0.05	−0.31	−0.37
19	0.06	−0.30	−0.34
20	−0.14	−0.32	−0.16

Note: The stock number in the first column corresponds to population information in Table 1.

The number of spawners at age a in iteration i is the product of post-fishery recruits and the proportion of fish that mature at a given age (p_a):

$$S_{a,i} = (R_{a,i} - C_{a,i})p_a \tag{A7}$$

We assumed the following maturity schedule: 10% of fish have matured by age-3, 80% by age-4, and 100% by age-5 (PSC 2015). Finally, once the calculation from the above population model stabilized (usually between 20–40 cycles), we calculated the MSY and U_{MSY} for that combination of variables (seal density, hatchery abundance).

MCMC convergence

Visual inspection of trace plots showed all MCMC chains were sufficiently well-mixed, suggesting the chains had successfully converged. Additionally, the Gelman–Rubin diagnostic statistics (R-hat) for all parameters and quantities of interest did not exceed 1.00 in any of the candidate models used in the analysis.

Posterior predictive checking

Figure 7 displays the posterior predictive intervals (95%) for Model 1 and the observed data for each of the 20 Chinook populations included in our analysis. The proportion of data points captured by the posterior predictive interval was 1.00 for 11 of the 20 stocks and no less than 0.96 (Chilliwack, Nisqually, Quillayute) for the others. Of the 525 data points used in the analysis, the posterior predictive intervals of Model 1 captured 516 of them (98.3%). The Bayesian p value for Model 1 was 0.66, which suggests the model is not inconsistent with the observed data (Fig. A1). There were no systematic differences apparent when visually comparing the replicated data (via the predictive distribution) with the observed data.

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