

Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean

Gregory T. Ruggerone and Brendan M. Connors

Abstract: Sockeye salmon (*Oncorhynchus nerka*) populations from Southeast Alaska through British Columbia to Washington State have experienced similar declines in productivity over the past two decades, leading to economic and ecosystem concerns. Because the declines have spanned a wide geographic area, the primary mechanisms driving them likely operate at a large, multiregional scale at sea. However, identification of such mechanisms has remained elusive. Using hierarchical models of stock–recruitment dynamics, we tested the hypothesis that competition between pink (*Oncorhynchus gorbuscha*) and sockeye salmon for prey has led to reduced growth and productivity and delayed maturation of up to 36 sockeye populations spanning the region during the past 55 years. Our findings indicate the abundance of North Pacific pink salmon in the second year of sockeye life at sea is a key factor contributing to the decline of sockeye salmon productivity, including sockeye in the Fraser River where an increase from 200 to 400 million pink salmon is predicted to reduce sockeye recruitment by 39%. Additionally, length-at-age of Fraser River sockeye salmon declined with greater sockeye and pink salmon abundance, and age at maturity increased with greater pink salmon abundance. Our analyses provide evidence that interspecific competition for prey can affect growth, age, and survival of sockeye salmon at sea.

Résumé : Les populations de saumons rouges (*Oncorhynchus nerka*) du sud-est de l'Alaska à la Colombie-Britannique, jusqu'à l'État de Washington ont connu des baisses semblables de productivité au cours des deux dernières décennies, suscitant des inquiétudes d'ordre économique et écosystémique. Étant donné la vaste étendue géographique de ces baisses, les principaux mécanismes à l'origine de celles-ci s'opèrent vraisemblablement en mer, à une échelle multirégionale. La nature de ces mécanismes demeure toutefois difficile à cerner. À l'aide de modèles hiérarchiques de la dynamique stock–recrutement, nous avons testé l'hypothèse selon laquelle la concurrence pour les proies entre les saumons roses (*Oncorhynchus gorbuscha*) et rouges a mené à des réductions de la croissance et de la productivité et a retardé la maturation de jusqu'à 36 populations de saumons rouges à l'échelle de la région au cours des 55 dernières années. Nos observations indiquent que l'abondance du saumon rose du Pacifique Nord durant la deuxième année en mer du saumon rouge est un facteur clé de la baisse de productivité des saumons rouges, dont ceux du fleuve Fraser, où il est prédit qu'une augmentation de 200 à 400 millions de saumons roses entraînera une réduction du recrutement de saumons rouges de 39 %. En outre, la longueur selon l'âge des saumons rouges du fleuve Fraser a diminué parallèlement à l'augmentation de l'abondance des saumons rouges et roses, et la maturité selon l'âge a augmenté parallèlement à l'abondance des saumons roses. Nos analyses indiquent que la concurrence interspécifique pour les proies peut avoir une incidence sur la croissance, l'âge et la survie des saumons rouges en mer. [Traduit par la Rédaction]

Introduction

Sockeye salmon (*Oncorhynchus nerka*) is one of the most economically, ecologically, and socially important Pacific salmon species. This is particularly true for Fraser River sockeye salmon, which support major international commercial and First Nations fisheries, spawn in hundreds of unique locations throughout the 220 000 km² Fraser River basin, and are a cultural icon. The Fraser sockeye fishery has been monitored and managed for many decades with the key objectives of meeting spawning objectives and achieving sustainable runs and harvests (Roos 1991). Nevertheless, the abundance of Fraser sockeye salmon has decreased substantially since the late 1980s, leading to considerable concern. In 2009, the run of 1.5 million adult sockeye salmon was the lowest since 1947, and it achieved only 14% of the preseason forecast of 10.5 million salmon (Peterman et al. 2010). This large and unex-

pected decline led to a judicial inquiry and a scientific workshop to uncover factors that might have influenced the long-term decline and the unexpected collapse in 2009 (Peterman et al. 2010), which was followed by an unexpectedly large return in 2010 and higher, though variable, abundances in 2011–2014. Initial scientific analyses indicated the long-term decline in abundance was likely associated with a decline in productivity at sea rather than low parental spawner abundances or other factors in fresh water. Factors in fresh water are known to adversely impact Fraser sockeye salmon (e.g., Hinch et al. 2012), but the observed long-term decline in productivity could not be explained by freshwater processes alone (Peterman et al. 2010; Connors et al. 2012). Recently, a number of investigations have explored early marine factors associated with the unexpectedly small sockeye salmon return in 2009 (Rensel et al. 2010; Miller et al. 2011; Beamish et al. 2012; Thomson et al. 2012; McKinnell et al. 2014).

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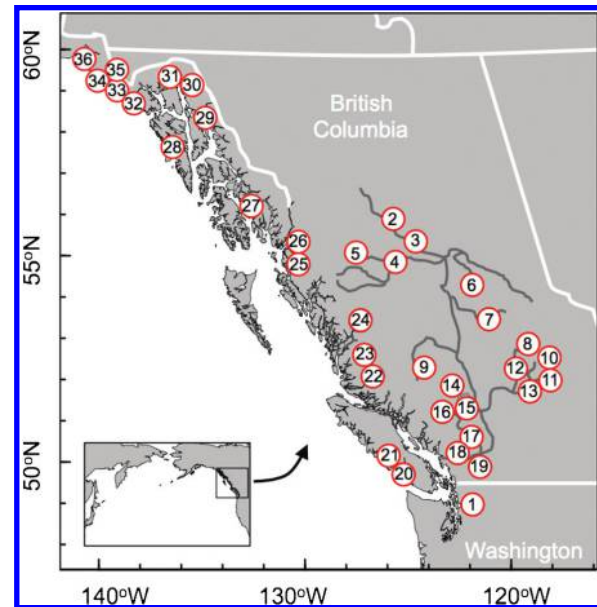
As a means to further identify potential factors influencing Fraser sockeye salmon, Peterman and Dorner (2012) examined the population dynamics of sockeye salmon populations extending from Puget Sound (Washington) through British Columbia (BC) and into western Alaska. They found that the productivity (adult recruits produced per spawner) of sockeye populations from Washington through Southeast Alaska, including the Yakutat region, was positively correlated and exhibited a shared declining trend in recent decades. They recommended that future research on declines in sockeye productivity focus on mechanisms that operate at large multiregional scales, such as marine areas where the sockeye populations overlap.

One potential mechanism that operates at large spatial scales is competition at sea between Fraser sockeye salmon and pink salmon (*Oncorhynchus gorbuscha*) (Peterman et al. 2010). Fraser sockeye salmon and pink salmon from distant regions are broadly distributed and overlap in the North Pacific Ocean (Myers et al. 2007; Beacham et al. 2014). Adult pink salmon returning from the North Pacific Ocean are exceptionally abundant, averaging approximately 4.7 times more adults than sockeye salmon during 1952–2005 (Ruggerone et al. 2010). A review of studies indicated that pink salmon can influence the diet, growth, distribution, age at maturation, and survival of other Pacific salmon (Ruggerone and Nielsen 2004; Atcheson et al. 2012). Sockeye salmon may be especially vulnerable to competition with pink salmon because they share common prey at sea (Percy et al. 1988; Kaeriyama et al. 2000; Bugaev et al. 2001; Davis et al. 2005). For example, growth of sockeye salmon originating from Bristol Bay, Alaska, was inversely related to abundance of Russian pink salmon, and sockeye salmon survival at sea and adult abundance was substantially reduced when they overlapped with pink salmon during odd-numbered years of their second year at sea (i.e., when pink salmon were exceptionally abundant owing to their biennial cycle; Ruggerone et al. 2003, 2005). A number of studies have shown that reduced growth of salmon at sea can lead to lower survival (Moss et al. 2005; Friedland et al. 2009; Farley et al. 2011) and delayed age at maturation (Pyper et al. 1999; Healey et al. 2000; Morita and Fukuwaka 2007; Wells et al. 2007). These studies, and the observation that annual pink salmon abundance has increased over time to approximately 640 million adults in 2009, provide initial evidence that Fraser River sockeye salmon may be influenced by pink salmon.

An examination of broad-scale factors that may have adversely affected the productivity of Fraser and other sockeye populations in BC during the past 50 years concluded that the abundance of pink salmon had the strongest negative relationship with sockeye productivity of the variables examined (Connors et al. 2012). In addition, regional sea-surface temperature appeared to have a moderate effect on sockeye productivity, and exposure to farmed salmon early in marine life (via an unknown mechanism) appeared to exacerbate the influence of competition with pink salmon later in sockeye marine life (Connors et al. 2012). The hypothesis of delayed density dependence in response to high parent spawner abundances was not supported as a common factor responsible for declining productivity across the sockeye populations considered (Connors et al. 2012; Peterman and Dorner 2012). While these analyses provided the most comprehensive examination of correlates of declining productivity in Fraser sockeye to date, they only considered a single line of evidence (lifetime productivity) for a group of populations originating from a smaller portion of the region of shared declines in sockeye productivity (Peterman and Dorner 2012).

Here we use comparisons between odd and even years and hierarchical statistical models of stock–recruitment dynamics to test the hypothesis that competition with pink salmon from across the North Pacific has led to declines in productivity of sockeye populations ranging from Washington State through Southeast Alaska. In addition, we test the hypothesis that pink

Fig. 1. Map with locations of sockeye salmon populations considered in the analyses. See Table 1 for details of the populations corresponding to each number.



salmon abundance influenced length-at-age and age at maturation (years at sea) of Fraser sockeye salmon. These analyses consider the density-dependent effects of sockeye salmon abundance in the North Pacific, as well as the potentially confounding effects of sea-surface temperature and farmed salmon production. We did not test for potential competition between chum (*Oncorhynchus keta*) and sockeye salmon because their diets are often markedly different (Azuma 1995; Davis et al. 2005), and a previous study did not find evidence of competition between chum and sockeye salmon (Rogers and Ruggerone 1993), but we note that stable isotope research suggests trophic overlap of pink, chum, and sockeye salmon (Johnson and Schindler 2009). This examination of multiple lines of evidence provides the most extensive evaluation to date of the hypothesis that competition at sea can influence the population dynamics of Pacific salmon.

Materials and methods

Sockeye salmon data

To test hypotheses related to the influence of competition with pink and sockeye salmon on sockeye salmon productivity, we used time series of the abundance of sockeye salmon spawners and adult recruits (the total number of adults, including those caught in fisheries) from one population in Washington State, 25 populations in BC, and 10 populations in the Southeast Panhandle and Yakutat regions of Alaska (Fig. 1 and Table 1). These 36 sockeye populations span a region of shared declining trends in productivity, suggesting that mechanisms that operate at this large, multiregional spatial scale are (at least partially) responsible for the declines in productivity observed in the Fraser River (Peterman and Dorner 2012). Details of the sockeye productivity time series can be found in Connors et al. (2012) and Peterman and Dorner (2012). Most time series extended back to the 1950s and 1960s, and many of the populations are dominated by salmon spending 1 year in fresh water and 2 years at sea, thereby maturing as 4-year-old salmon (age-1.2). For a subset of Fraser River populations, we analyzed data provided by the Pacific Salmon Commission on the standard length of 4-year-old male and female sockeye on the spawning grounds to test hypotheses related to the influence of competition on sockeye growth (15 populations). Only years with 50 or more individual measurements of each sex per

Table 1. Sockeye salmon populations (stock) considered.

Number	Jurisdiction	Region	Population	Brood years	Male length	Female length	Proportion ocean-age-3
1	Washington	Washington	Lake Washington	36	—	—	—
2	BC	Fraser	Early Stuart	55	35	35	55
3	BC	Fraser	Late Stuart	54	29	29	54
4	BC	Fraser	Stellako	55	—	—	55
5	BC	Fraser	Nadina	30	12	12	30
6	BC	Fraser	Bowron	55	14	14	55
7	BC	Fraser	Quesnel	55	20	20	55
8	BC	Fraser	Raft	55	29	29	55
9	BC	Fraser	Chilko	55	44	44	55
10	BC	Fraser	Seymour	55	39	39	55 ^a
11	BC	Fraser	Late Shuswap	53	22	22	53 ^a
12	BC	Fraser	Fennell	36	14	14	36
13	BC	Fraser	Scotch	22	—	—	22
14	BC	Fraser	Portage	39	21	21	39
15	BC	Fraser	Gates	35	25	25	35
16	BC	Fraser	Birkenhead	55	35	35	55
17	BC	Fraser	Harrison River	55	—	—	39 ^a
18	BC	Fraser	Weaver	37	26	26	37
19	BC	Fraser	Cultus	49	24	24	36 ^a
20	BC	Barkley Sound	Great Central Lake	25	—	—	—
21	BC	Barkley Sound	Sproat Lake	25	—	—	—
22	BC	Central Coast	Long Lake	33	—	—	—
23	BC	Central Coast	Owikeno Lake	33	—	—	—
24	BC	Central Coast	Atnarko	31	—	—	—
25	BC	North Coast	Skeena	35	—	—	—
26	BC	North Coast	Nass	22	—	—	—
27	Alaska	Southeast	McDonald	22	—	—	—
28	Alaska	Southeast	Redoubt	15	—	—	—
29	Alaska	Southeast	Speel	14	—	—	—
30	Alaska	Southeast	Chilkoot	28	—	—	—
31	Alaska	Southeast	Chilkat	24	—	—	—
32	Alaska	Yakutat	Klukshu	30	—	—	—
33	Alaska	Yakutat	East Alsek	26	—	—	—
34	Alaska	Yakutat	Alsek	30	—	—	—
35	Alaska	Yakutat	Italio	26	—	—	—
36	Alaska	Yakutat	Situk	22	—	—	—

Note: Brood years refer to the total number of brood years available from each population for the analysis of productivity. Values in “length” columns are the number of brood years in which there were at least 50 length measurements of 4-year-old male and female sockeye on the spawning grounds. Values in “Proportion ocean-age-3” column are the number of brood years for which we could calculate the proportion of total recruits from a given brood year that spent 3 years at sea.

^aThese populations have, on average, less than 5% of the adult return that spend 3 years at sea and so were excluded from age at maturity analyses because mean age at maturity changed very little from year to year, possibly in response to other factors such as physical constraints imposed by spawning habitat.

population were used in the analyses of growth in relation to pink and sockeye salmon abundance (Table 1). For those Fraser River populations for which we had detailed brood tables (18 populations), we also calculated the proportion of total recruits that spent 3 years at sea to test hypotheses related to the influence of competition on sockeye age at maturity (Table 1). Fraser River populations having less than 5% of the adult return spending 3 years at sea (ocean-age-3), on average, were excluded from this analysis because mean age at maturity changed very little from year to year, possibly in response to other factors such as physical constraints imposed by spawning habitat (Quinn 2005).

Total abundances of sockeye salmon in the North Pacific that may compete with Alaska, BC, and Washington State sockeye salmon were obtained from Ruggerone et al. (2010) for years 1952 to 2005. These data included sockeye salmon returning to Russia, Alaska, BC, and Washington. The dataset was updated using reported runs (catch and escapement) of Russian sockeye salmon during 2006–2010 (www.npafc.org) and a regression of North American sockeye salmon abundance on sockeye catch in Alaska (www.npafc.org) from 1952 to 2005 (North American sockeye abundance in millions = [1.4 × Alaska catch in millions] + 19.8; R² = 0.92; n = 58).

Pink salmon data

We derived indices of the abundance of pink salmon that may compete with sockeye salmon from a dataset of the total number of adult pink salmon from key populations across the North Pacific Ocean from 1952 to 2005. These populations were from Japan, Russia (western Kamchatka, eastern Kamchatka, mainland, and islands), Alaska (Prince William Sound, Kodiak, Alaska Peninsula, and Southeast Alaska), BC (southern and northern BC and the Fraser River), and Washington (Puget Sound) (Ruggerone et al. 2010). These data were updated through 2010 (Japan: North Pacific Anadromous Fish Commission Doc. 1344, www.npafc.org; Russia: North Pacific Anadromous Fish Commission Doc. 1269, www.npafc.org; Prince William Sound: S. Moffitt, Alaska Department of Fish and Game (ADF&G), Cordova, Alaska; Kodiak: ADF&G staff, Kodiak, Alaska; Southeast AK: Piston and Heinel (2011); Fraser: S. Latham, Pacific Salmon Commission). Pink salmon originating in southern BC and Puget Sound from 2006 onwards were estimated from Fraser pink salmon adult recruits by regressing southern BC and Puget Sound pink salmon on Fraser River pink salmon from 1958 to 2005 (southern BC + Puget Sound pink salmon in millions = [1.06 × Fraser pink salmon in millions] + 3.69; R² = 0.86; n = 48).

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Hypotheses

First, since pink salmon tend to be more abundant across the North Pacific in odd-numbered years owing to their 2-year life cycle (Ruggerone et al. 2010), we examined the hypotheses that sockeye productivity and length-at-age were less, and age at maturity later, in odd versus even years. These comparisons between even and odd years were then complemented with more detailed analyses that examined the evidence for four separate hypotheses related to the intensity of interactions between sockeye salmon and abundances of pink and sockeye salmon in the ocean. The first three hypotheses examined the potential influence of competition with pink salmon and conspecifics on sockeye salmon productivity, age at maturity, and growth at sea at two temporal scales (i.e., interactions beginning during first versus second year at sea). The sensitivity of these findings to the spatial scale of pink and sockeye salmon (i.e., North Pacific versus North American populations) and the potentially confounding influences of sea surface temperature (SST) and farm salmon production (Connors et al. 2012) were also examined (see section on Sensitivity analyses). The fourth hypothesis examined the potential role that predation on juvenile sockeye salmon in coastal areas by returning pink salmon plays on sockeye productivity (e.g., Peterman 1982). Below we describe the analyses testing each of these hypotheses in detail.

1. Odd–even year patterns in sockeye characteristics

As an initial examination of the potential effects of pink salmon on sockeye salmon, we plotted sockeye survival (residuals from Ricker stock–recruitment relationship), length of age-1.2 male and female sockeye salmon, and proportion of ocean-age-3 sockeye salmon in adult returns to determine whether there were alternating year patterns consistent with the difference in abundance between even- and odd-year pink salmon. The plots were generated for the entire period of data availability, as well as for the period after the mid-1970s ocean regime shift when abundance of pink salmon in the ocean doubled (Ruggerone et al. 2010). These comparisons between odd and even years provide a first pass examination of the evidence for differences in productivity, growth, and age at maturity between years of lower and higher pink salmon abundance. However, these initial plots do not account for the magnitude of differences in pink salmon abundance between years or other potentially confounding factors (e.g., intraspecific competition). Therefore, we complemented these initial plots with more comprehensive statistical evaluations of the influence of pink salmon as described below.

2. Competition effects on sockeye productivity

We tested whether competition between pink salmon and sockeye salmon in their first and second year at sea leads to reduced sockeye productivity. To formalize this hypothesis, we fit a modified Ricker stock–recruitment relationship (Ricker 1975) to the data as a hierarchical model:

$$(1) \quad \ln\left(\frac{R_{i,t}}{S_{i,t}}\right) = (\mu_\alpha + \alpha_i + \alpha_t) - b_i S_{i,t} + (\mu_j + \delta_{i,j}) E_{j,i,t+x} + \varepsilon_{i,t}$$

where $R_{i,t}$ is the total number of adult sockeye recruits to population i produced by spawners ($S_{i,t}$) in brood year t , μ_α is the intrinsic rate of population growth (i.e., productivity at low spawner abundance) common to all populations, and b_i is density dependence in relation to the carrying capacity of population i . E is one or more of j time series of independent variables experienced in year x of the sockeye salmon life cycle that represent how pink and sockeye salmon might compete with sockeye salmon during each year of sockeye residence in the ocean (see below), μ_j is the overall effect of variable E on productivity, and $\delta_{i,j}$ is the random population-specific effect. The terms α_i , α_t , and $\delta_{i,j}$ are assumed to be popula-

tion- (i) or year- (t) specific deviations from the mean response μ_α and μ_j , where $\alpha_i \sim N(0, \sigma_{\alpha_i}^2)$, $\alpha_t \sim N(0, \sigma_{\alpha_t}^2)$, and $\delta_{i,j} \sim N(0, \sigma_{\delta_{i,j}}^2)$ (Pinheiro and Bates 2000; Mueter et al. 2002a), and $\varepsilon_{i,t}$ is residual error with mean of zero and variance that is estimated (i.e., $\sim N(0, \sigma_\varepsilon^2)$). These terms are often referred to as random effects and in our case the location-dependent random effect (α_i) captures natural variation among populations in productivity. The time-dependent random effect (α_t) captures variation in productivity among years common to all populations and accounts for the nonindependence of observations within years in relation to indices of ocean basin-scale competitors that are the same for all populations within a year. The location-dependent random effects on the slope of the relationships ($\delta_{i,j}$) captures intrinsic differences in how each population responds to an independent variable as opposed to constraining the model to assume all populations respond in the same way (i.e., magnitude and direction) to a given independent variable.

We considered three possible indices of pink and sockeye salmon competitors (i.e., the E_j values in eq. 1). First, as an index of the number of juvenile pink salmon that may begin competing with sockeye salmon in their first year at sea (McKinnell and Reichardt 2012), we used the abundance of adult pink salmon from the Northeast Pacific (northern BC and Alaska) 3 years after each sockeye brood year for sockeye that spent 1 year in fresh water before migrating to sea. For those sockeye populations that spent more than 1 year in fresh water, we used the number of adult pink salmon in years $t + 3$ and $t + 4$ weighted by the proportions of juvenile sockeye entering the ocean each year, as determined by age-specific abundances of adult sockeye salmon. Second, as an index of the potential number of pink salmon that may begin to compete with sockeye in their second growing season at sea, we used the total abundance of adult pink salmon across the North Pacific 4 years after each sockeye brood year (Ruggerone and Nielsen 2004; Connors et al. 2012). These pink salmon would have likely interacted with the sockeye brood beginning in the late portion of their second year at sea, continuing through winter and into the third growing season. In the third growing season, the sockeye would have either matured and returned to fresh water after 2 years at sea (e.g., age-1.2) or delayed maturation until 3 years at sea (e.g., age-1.3). Third, we used the total abundance of sockeye salmon across the North Pacific as an index of potential conspecific competitors during marine life. Additional independent variables were evaluated in the sensitivity analyses described below.

Considering multiple populations simultaneously can increase the chance of finding true relationships by allowing for common responses to be more easily isolated from random demographic noise and sampling errors (e.g., Myers and Mertz 1998). Two possible alternatives to considering all populations simultaneously are the following: (1) no pooling of data and separate tests of the hypotheses for each individual population or (2) complete pooling of data and a single test on aggregated data across all the populations. No pooling ignores information and can give highly variable inferences, while complete pooling of data can be misleading by ignoring among-population variation (Gelman and Hill 2007). While both approaches can provide useful preliminary analyses, we chose to take an approach that allows for the estimation of a common response and that models among-population variation in the response. This approach offers a balance between the overly noisy individual population estimates in alternative 1 and the overly simplified estimate in alternative 2.

All independent variables were standardized in the analyses by subtracting the mean of the time series from each observed value and dividing by the standard deviation. Prior to fitting the models, with the exception of proportion data (see point 5 below), we removed linear time trends from dependent and independent variables to reduce the potential for spurious correlations due to

similar underlying time trends that may arise because of large-scale, longer-term climatic conditions. We present the findings for both detrended and raw data below, but the details of the raw data analyses are shown in the online supplementary material¹.

We compared models fit by maximum likelihood (ML) with and without pink and sockeye salmon abundance as independent variables at both spatial and temporal scales (i.e., the fixed effects) using small-sample Akaike information criteria (AIC_c; Burnham and Anderson 2002). The random effects were kept the same across all models (Zuur et al. 2009). To account for model uncertainty, we generated multimodel averaged estimates of the influence of pink and sockeye salmon abundance across the hypotheses considered according to the “natural average” method (Burnham and Anderson 2002) based on parameter estimates re-estimated by restricted estimate maximum likelihood (REML). The parameters were re-estimated prior to model averaging because REML standard deviation estimates are typically less biased than corresponding ML estimates (Bolker et al. 2009). To capture uncertainty in parameter estimates across models, we calculated unconditional standard error according to eq. 4.7 in Burnham and Anderson (2002). This model selection approach allowed us to consider the relative support for multiple competing hypotheses instead of focusing on whether a single null hypothesis is accepted or rejected. Specifically, we based our inference about the importance of competition on the sign, magnitude, and uncertainty of the multimodel averaged parameter estimates for the relationships between the response variable (sockeye productivity) and pink abundance in the first and second year of sockeye life at sea and sockeye abundance in the second year at sea. This approach to quantifying the influence of pink and sockeye salmon abundance was repeated for each of the hypotheses described below.

3. Competition effects on sockeye growth at sea

We fit a hierarchical model to test the hypothesis that competition between pink salmon and sockeye salmon in their first and second year at sea results in reduced Fraser sockeye growth in years of high pink and sockeye salmon abundance:

$$(2) \quad L_{4,i,t} = (\mu_{\text{length}} + \theta_i + \theta_t) + (\mu_{k,j} + \delta_{k,j,i})E_{j,i,t+x} + \varepsilon_{\text{length},i,t}$$

where $L_{4,i,t}$ is the mean standardized fork length of 4-year-old male or female sockeye from population i and brood year t , and μ_{length} is the predicted mean standardized fork length across all populations at mean pink and sockeye salmon abundance (the intercept). The shared response of sockeye length to pink or sockeye competitor index E_i is $\mu_{k,j}$, while intrinsic variation in body length among populations (θ_i) and common to all populations among years (θ_t), as well as population-specific variability in responses to pink and sockeye salmon abundance (the $\delta_{k,j,i}$ values), were modeled as random effects as described for eq. 1. We fit these models separately for each sex.

4. Competition effects on sockeye age at maturity

To test the hypothesis that competition between pink salmon and sockeye salmon results in delayed Fraser sockeye maturity and a higher probability of spending an extra year at sea, we fit a hierarchical model similar to eq. 2:

$$(3) \quad \text{logit}\left(\frac{R_{3,i,t}}{\sum_{x=1}^3 R_{x,i,t}}\right) = (\mu_{\text{age}} + \theta_{\text{age},i} + \theta_{\text{age},t}) + (\mu_{l,j} + \delta_{l,j,i})E_{j,i,t+x} + \varepsilon_{\text{age},i,t}$$

where $R_{3,i,t}$ is the number of recruits that spent 3 years at sea, $\sum_{x=1}^3 R_{x,i,t}$ is the total recruits from population i and brood year t (i.e., the sum of sockeye that matured after 1, 2, and 3 years at sea), μ_{age} is the logit-transformed mean proportion of ocean-age-3 recruits at mean pink and sockeye salmon abundance (the intercept), and $\mu_{l,j}$ is the common response to pink or sockeye competitor index E_j . Intrinsic variation in the logit-transformed proportion of age-3 recruits among populations ($\theta_{\text{age},i}$) and common to all populations among years ($\theta_{\text{age},t}$), as well as population-specific variability in responses to pink and sockeye salmon abundance (the $\delta_{l,j,i}$ values), were modeled as random effects as described above in eq. 1. We fit eq. 3 as a generalized linear mixed model with binomial error and a logit link function (Zuur et al. 2009), and to account for overdispersion, we included an observation-level random effect in the model (Warton and Hui 2011). We did not detrend the proportion data for these analyses because detrending the time series of proportions would result in a nonsensical dependent variable (i.e., one that was not bound between 0 and 1).

5. Pink predation and sockeye productivity

To test the hypothesis that predation by returning adult pink salmon on out-migrating juvenile sockeye results in reduced sockeye productivity, we fit a modified version of eq. 1, which included an independent variable providing an index of potential pink salmon predators returning to the coast in the year sockeye smolts migrate to sea. This index was the abundance of pink salmon from southern BC and Washington state (for explaining productivity of sockeye populations 1–24), from northern BC and Southeast Alaska (sockeye populations 25–26), Southeast Alaska (sockeye populations 27–31), and the Yakutat region (sockeye populations 32–36). All pink salmon abundances were lagged by 2 years.

Predicted reduction in sockeye returning to Fraser River as a function of pink salmon abundance

We also estimated the number of sockeye that would be predicted to return to just the Fraser River as a function of pink salmon competitors in the second and third sockeye growing seasons at sea:

$$(4) \quad \sum_{i=1}^{18} R_t = S_t e^{(\mu_{\alpha} + \alpha_i + \alpha_t) - b_i S_t (\mu_j + \delta_{l,j,i}) E_{j,i,t+4}} e^{\text{MSE}/2}$$

where $R_{i,t}$ is the total number of recruits to population i (18 sockeye populations total in the Fraser River) in year t , S is the mean spawner abundance in population i , E_j is a particular value from the range of North Pacific pink salmon abundances observed from 1952 to 2010 (118–643 million fish), MSE is the mean squared error from the model fit applied as a bias correction (Newman 1993), and the remaining terms are the same as those estimated in eq. 1. By estimating the total number of recruits returning to the Fraser River across a range of pink salmon abundances, we could illustrate the predicted change in total adult sockeye salmon recruits, that is, those returning to the Fraser River in a given year to both spawn and be available for commercial, recreational, and First Nation’s fisheries as a result of competition with pink salmon in the second and third sockeye growing seasons at sea. These predictions are at long-term mean North Pacific sockeye abundance in the second sockeye year at sea and North Pacific pink abundance in the first sockeye year at sea.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0134>.

Sensitivity analyses

Our main analyses were based upon detrended datasets as a means to reduce the potential for time trends in the data to confound our interpretation of the results. However, removing low-frequency variation in the data (i.e., the time trends) means that any longer-term, slowly changing true relationships between sockeye salmon and the independent variables we considered may not be detected if they exist. Therefore, we reran the analyses using raw data and examined the results for consistency with the findings based on detrended data.

Our main analyses assume that sockeye salmon from BC, Southeast Alaska, and Washington State interact in the open ocean with pink salmon originating from North America, as well as Russia and Japan. Therefore, we included pink salmon abundance from all these populations as an index of competitors in the second year of sockeye life at sea. Although there is evidence for overlap in the distribution of pink salmon from the Far East and sockeye salmon from southern BC (Takagi et al. 1981; Myers et al. 2007; Beacham et al. 2014), the extent of overlap is uncertain. Therefore, we repeated our analyses with an index of pink and sockeye salmon competitors in the second year of sockeye life at sea that was composed of only salmon originating from North America.

It is well known that climate and oceanographic conditions can influence sockeye salmon growth (Cox and Hinch 1997; Hinch et al. 1995) and productivity (Mueter et al. 2002a, 2002b, 2005). It has also been recently suggested that exposure to farmed salmon early in sockeye marine life may increase the influence of subsequent competition with pink salmon on sockeye productivity (Connors et al. 2012), though we note that this correlative relationship is uncertain and the underlying mechanism(s) unknown. Our initial analyses did not account for these other factors, which could potentially confound the relationships we describe. To evaluate whether the conclusions of our main analyses were sensitive to the inclusion of these other factors, we reran the analyses described above to include terms for SST in the winter preceding juvenile sockeye marine entry (e.g., Mueter et al. 2002a; Connors et al. 2012) and farmed salmon production along juvenile sockeye migration routes (as a proxy for potential pathogen exposure; Connors et al. 2012). These factors were considered in models both individually and together. In addition to these individual factors, the analyses also included interactions between farmed salmon production and pink salmon abundance as previously identified and described (Connors et al. 2012). We fit all models, calculated their AIC_c weights, and then generated multimodel averaged parameter estimates for each factor. The multimodel parameter estimates for the influence of pink salmon and sockeye salmon abundance could then be compared with those from the baseline analyses we conducted to evaluate if the relationships quantified in our baseline analyses were sensitive to the inclusion of other potential influential explanatory factors.

All analyses were performed in R (2012) using the lme4 (for the linear mixed effects modeling) and MuMIn (for multimodel inference) packages. The lme4 package is the only R package that supports crossed random effects (i.e., non-nested time and location dependent random effects) but does not allow for autocorrelated errors. Therefore, we examined the assumption that within-population residuals were not temporally autocorrelated by examining the correlation between residuals within populations from the models in eqs. 1–3 at a 1-year lag. In instances where there was significant lag-1 autocorrelation in residuals (at $\alpha = 0.05$), we reran our analysis after removing those populations to determine how influential their results were to the overall conclusions.

Results

Odd-even year patterns

The annual mean abundance of maturing pink salmon returning to natal watersheds from across the North Pacific increased from approximately 209 million fish during the 1950s and 1970s to approximately 385 million fish after the mid-1970s ocean regime shift. Maturing pink salmon were approximately 38% more abundant in odd- versus even-numbered years during both the entire study period and after the mid-1970s ocean regime shift. In North America, pink salmon abundance increased approximately 2.5-fold after the regime shift (from 65 to 170 million fish), and they were 37% more abundant in odd-numbered years of the recent period. Across all years, pink salmon in North America averaged 18% more fish in odd-numbered years.

Sockeye survival rates (residuals from Ricker stock–recruitment relationship) were markedly lower during odd- versus even-numbered brood years for the entire study period and after the regime shift. During the recent period, sockeye survival rates were approximately 20% lower in odd-year broods than even-year broods, on average. Lower survival from odd-numbered broods was observed, on average, in 20 of the 24 sockeye populations (Fig. 2a).

Length-at-age of returning male and female sockeye salmon was markedly lower in odd- versus even-numbered brood years for the entire period of data and for the period after the regime shift. This pattern was consistent among all sockeye populations for both male and female salmon (Figs. 2c, 2d).

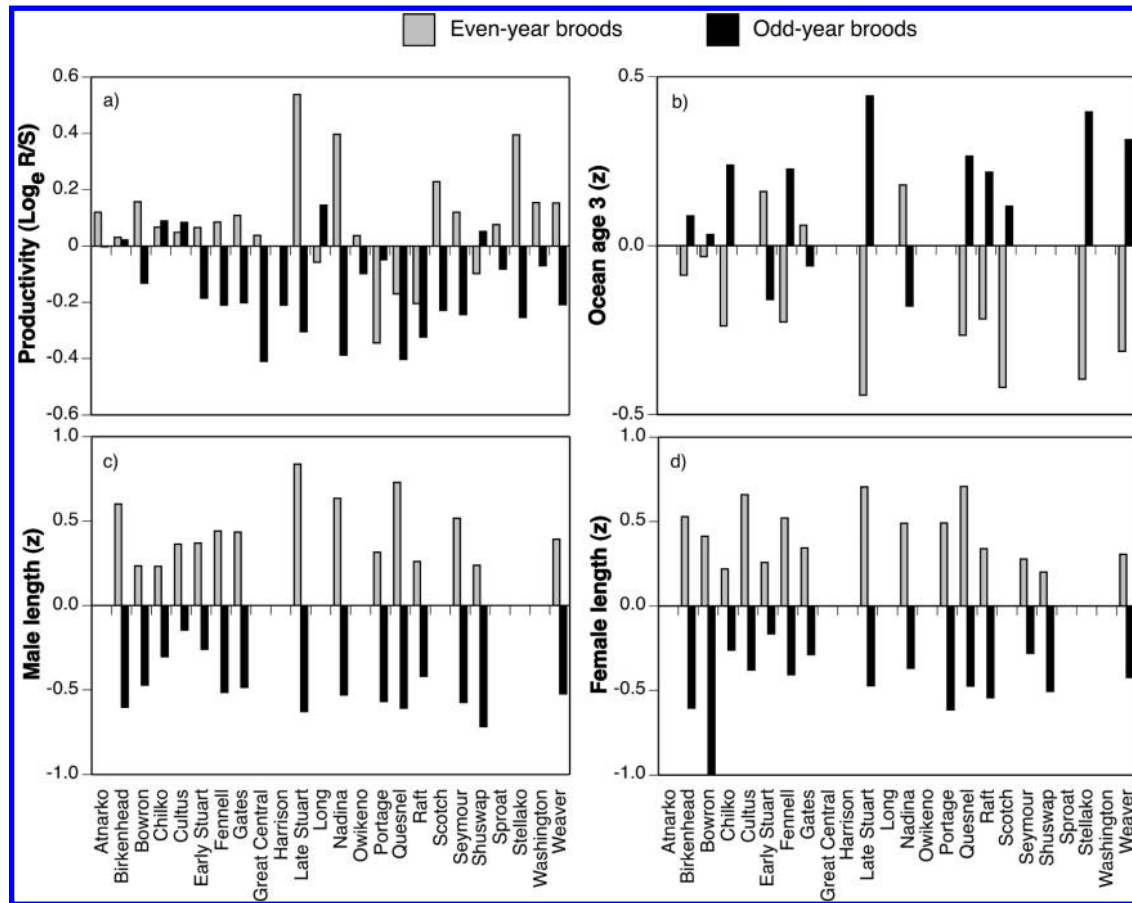
The proportion of sockeye salmon in each population spending 3 years at sea tended to be greater among odd-numbered brood years for the entire study period and after the regime shift, as hypothesized. Delayed maturation was more common in odd- versus even-numbered brood years in 10 of 13 populations (Fig. 2b).

Hypotheses

Sockeye survival rates were typically negatively correlated with the abundance of pink salmon in the North Pacific in the second sockeye growing season at sea (Fig. 3). The hypothesis that competition with pink salmon in the second year of sockeye life at sea leads to reduced productivity had strong data support (i.e., a term for this competition occurred in almost all models that had support as indicated by a relative variable importance close to 1; Table 2 and “Productivity” row in Table 3) and had the strongest predicted negative relationship with sockeye productivity (“Productivity” row in Table 3). There was little data support for inverse relationships between sockeye productivity and pink salmon abundance in the first year, as opposed to second year, of sockeye marine life or the abundance of sockeye in the North Pacific (Tables 2 and 3). These findings suggest that it is competition with pink salmon in the second and later years of marine life, as opposed to conspecific or pink salmon in the first year of marine life, that leads to reduced survival.

For those Fraser River sockeye populations for which we had data, mean male and female length was typically negatively correlated with the abundance of pink salmon in the North Pacific during the second sockeye growing season at sea (Figs. 4 and 5). However, of the hypotheses considered, North Pacific sockeye abundance was predicted to have the strongest negative influence on adult male and female sockeye length, and sockeye abundance appeared in all models that had data support (“Standard fork length” rows in Tables 2 and 3). The abundance of pink salmon across the North Pacific in the second year of sockeye marine life had the second strongest predicted negative influence on adult male and female sockeye length of the hypotheses considered and was more negative for male than female sockeye (Tables 2 and 3). In contrast with the support of the hypothesis that competition with sockeye and pink salmon in the second year of sockeye marine life leads to reduced sockeye growth, there was little support

Fig. 2. Survival (a), proportion of ocean-age-3 (b), and length-at-age of male (c) and female (d) sockeye salmon populations from British Columbia and Washington during odd- versus even-numbered brood years, 1978–2005. Values are normalized (Z) relative to the entire data time series, except survival, which is the mean residual from the recruitment relationship.



for the hypothesis that competition with pink salmon in the first year of sockeye marine life leads to reduced adult male and female sockeye salmon length (Tables 2 and 3). These findings suggest that competition with conspecifics as well as pink salmon in the second and later years of marine life leads to reduced growth at sea and smaller sockeye salmon on the spawning grounds.

The proportion of total sockeye recruits from a given brood year that spent 3 years in the ocean was positively related to the abundance of pink salmon in the North Pacific for most of the sockeye populations we considered (Fig. 6). Of the hypotheses considered, there was strong data support for the hypotheses that North Pacific pink salmon abundance in the first and second year of sockeye ocean life had a positive influence on the proportion of sockeye that delayed maturation and returned at ocean-age-3 (Tables 2 and 3). This effect was weaker for pink salmon abundance in the first, as opposed to second, year of sockeye ocean life, and there was much less support for an effect of North Pacific sockeye abundance (Tables 2 and 3).

The estimated magnitude of the relationships between productivity, length, and age at maturity of sockeye salmon and North Pacific pink salmon abundance based on the hierarchical analyses varied by population (Fig. 7), with Harrison productivity being the most anomalous (Fig. 7a).

We did not find support for the hypothesis that returning adult pink salmon predate upon juvenile sockeye, which would have resulted in reduced productivity in years when sockeye migrated to sea as large numbers of pink salmon returned to spawn. The inclusion of adult pink salmon abundance as an index of potential

predators did not improve model fit relative to the null model without an index of predators (Table 2).

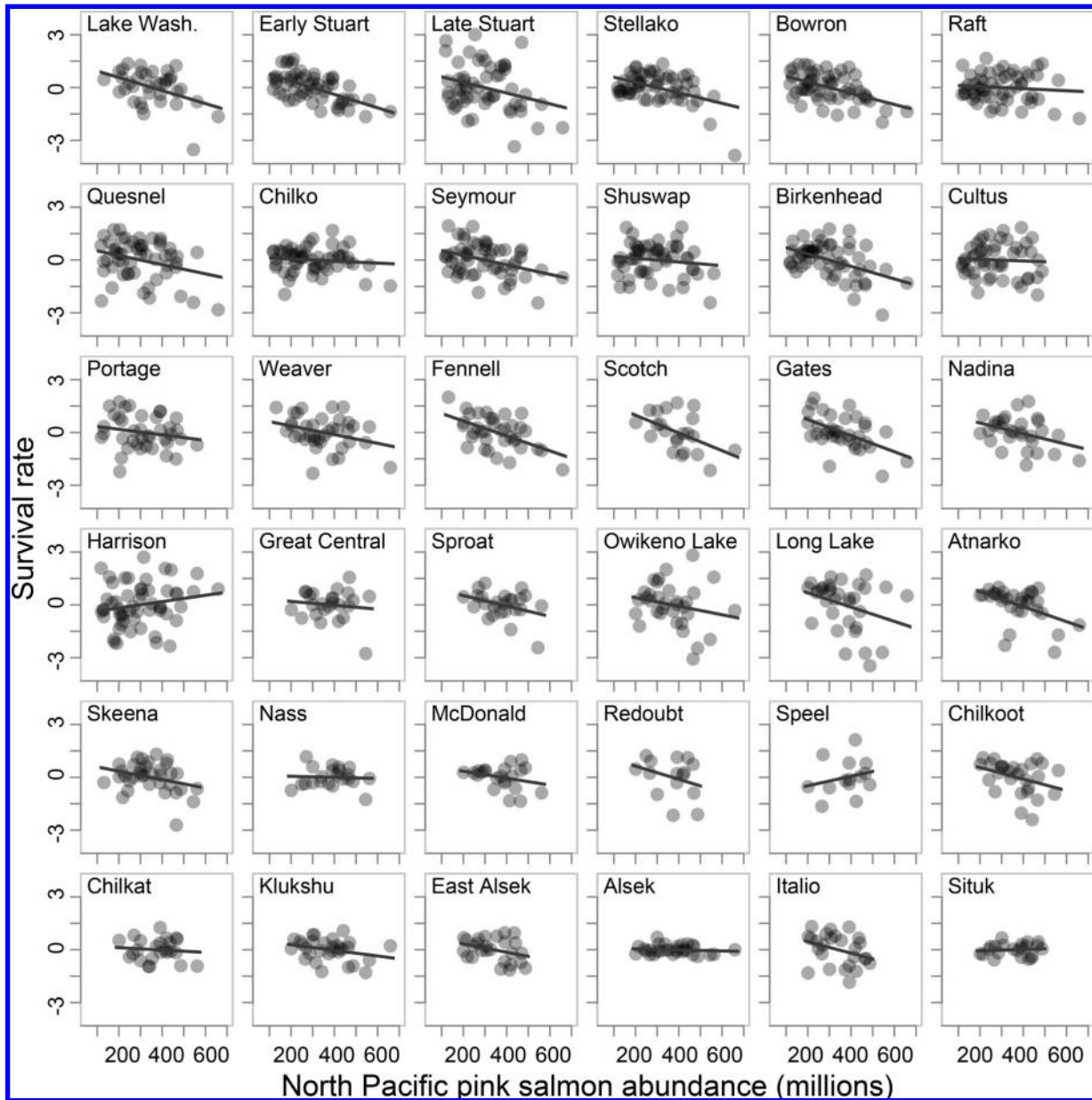
Predicted reduction in sockeye returning to Fraser River as a function of pink salmon abundance

Based on the relationship between North Pacific pink salmon abundance and sockeye productivity quantified in our analyses, across the range of pink salmon abundance observed since the 1950s to present (see eq. 4), competition with pink salmon is predicted to reduce the number of adult sockeye that return to the Fraser River before the onset of fisheries by up to 67% (i.e., from mean recruits of ~16 million sockeye at low pink salmon abundance (150 million pinks) to ~5.3 million sockeye at high pink salmon abundance (600 million pinks); Fig. 8). Following the mid-1970s ocean regime shift, annual pink salmon abundance increased from approximately 200 million to 400 million fish, resulting in a predicted reduction in Fraser River sockeye salmon of ~5.5 million (39%).

Sensitivity analyses

Our finding that pink salmon abundance in the second year of sockeye marine life influenced sockeye productivity was consistent when using either detrended (see above) or raw data (see online Supplementary Tables S1a, S1b¹). Likewise, when using raw data, both North Pacific sockeye and pink salmon abundances during the second year of sockeye marine life had support for their negative relationship with Fraser River sockeye length though the support was weaker for North Pacific pink salmon abundance using the raw data. In contrast with these relatively

Fig. 3. Relationship between sockeye salmon survival rates (residuals of population specific Ricker stock–recruit relationship in log_e space) and North Pacific pink salmon abundance in the second year of sockeye life at sea.



consistent findings, our results involving pink salmon abundance in the first year of sockeye marine life were inconsistent, as shown by the change in the direction of the parameter estimate when using raw versus detrended data, in addition to being weak relationships.

Our finding that sockeye salmon productivity was negatively related to pink salmon abundance during the second year of sockeye life at sea was sensitive to the use of North Pacific versus North American pink salmon abundances when considering the detrended data (Tables S3a, S3b¹) but not the raw data (Tables S2a, S2b¹). Specifically, there was little support for a negative relationship between detrended North American pink salmon abundance and sockeye productivity, but there was strong support for the negative relationship when raw pink salmon data were used. In addition, there was still support for negative relationships between North American pink salmon abundance and the size of male and female sockeye returning to spawn in the Fraser River at 4 years of age (Tables S2a, S2b and S3a, S3b¹). When considering

just North American salmon abundance, sockeye salmon continued to have the strongest predicted influence on the size of male and female sockeye returning to spawn. Lastly, when considering North American pink salmon abundance, there was still support for the hypothesis that the proportion of ocean-age-3 recruits was positively related pink salmon abundance (Tables S2a, S2b¹).

When the analyses were repeated in a framework that included other potentially influential factors, including oceanographic conditions (e.g., sea surface temperature), potential exposure to pathogens from salmon aquaculture, and a mediating effect of exposure to farmed salmon on the relationship between sockeye productivity and pink salmon abundance during the second year of sockeye life at sea, our findings remained largely the same (Tables S4a, S4b and S5a, S5b¹). Specifically, multimodel averaged predicted effects of pink salmon abundance on sockeye productivity and length-at-age were consistently negative and similar in magnitude to those estimated in analyses without these additional factors (Tables S4a, S4b and S5a, S5b¹). Also, there was still

Table 2. Summary of model selection statistics for analyses of hypotheses related to interactions between pink and sockeye salmon.

Hypothesis	Model	LL	ΔAIC_c	Weight	
1. Productivity	$P_{t+4} + P_{t+3}$	-1594.68	0.00	0.60	
	$P_{t+4} + Sx_{t+4}$	-1595.93	2.50	0.17	
	P_{t+4}	-1597.43	3.34	0.11	
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-1595.35	3.51	0.10	
	Null	-1601.21	8.74	0.01	
	P_{t+3}	-1600.42	9.32	0.01	
	Sx_{t+4}	-1600.82	10.13	0.00	
	$P_{t+3} + Sx_{t+4}$	-1600.43	11.49	0.00	
	2. Standard fork length (males)	$P_{t+4} + Sx_{t+4}$	-396.74	0.00	0.70
		$P_{t+4} + P_{t+3} + Sx_{t+4}$	-396.64	1.99	0.26
Sx_{t+4}		-401.12	6.60	0.03	
$P_{t+3} + Sx_{t+4}$		-400.94	8.40	0.01	
P_{t+4}		-406.66	17.68	0.00	
$P_{t+4} + P_{t+3}$		-406.32	19.17	0.00	
Null		-414.58	31.36	0.00	
P_{t+3}		-414.48	33.32	0.00	
2. Standard fork length (females)		$P_{t+4} + Sx_{t+4}$	-403.59	0.00	0.55
		$P_{t+4} + P_{t+3} + Sx_{t+4}$	-403.24	1.47	0.26
	Sx_{t+4}	-406.17	2.98	0.12	
	$P_{t+3} + Sx_{t+4}$	-405.82	4.45	0.06	
	P_{t+4}	-412.47	15.58	0.00	
	$P_{t+4} + P_{t+3}$	-411.70	16.22	0.00	
	Null	-417.72	23.93	0.00	
	P_{t+3}	-416.83	24.32	0.00	
	3. Proportion ocean-age-3 recruits	P_{t+4}	-103.99	0.00	0.43
		$P_{t+4} + P_{t+3}$	-103.56	1.25	0.23
$P_{t+3} + Sx_{t+4}$		-104.07	2.27	0.14	
$P_{t+4} + P_{t+3} + Sx_{t+4}$		-103.44	3.12	0.09	
P_{t+3}		-105.83	3.69	0.07	
$P_{t+4} + Sx_{t+4}$		-105.66	5.44	0.03	
Null		-108.08	6.08	0.02	
Sx_{t+4}		-108.90	9.82	0.00	
4. Productivity (predation)		Null	-1601.75	0.00	1.00
		$P_{predators}$	-1601.72	12.38	0.00

Note: All models were fit to data with linear time trends removed with the exception of the proportion of ocean-age-3 recruits (see Table S1 for analyses with raw data¹). The dependent variable in each hypothesis is denoted by “Variable” and includes sockeye productivity ($\log_e(\text{recruits}/\text{spawner})$), the mean standardized length of 4-year-old male and female sockeye on the spawning grounds, and the proportion of total recruits from a given brood year that spent 3 years in the ocean. Independent variables in the hypotheses (Model) are North Pacific pink salmon abundance (P_{t+4}) lagged 4 years later from the corresponding sockeye brood year to reflect the abundance of potential pink salmon competitors in the second sockeye growing season at sea, Northeast Pacific pink salmon abundance (P_{t+3}) lagged by 3 years to reflect the abundance of potential pink salmon competitors in the first sockeye growing season at sea, and North Pacific sockeye salmon abundance (Sx_{t+4}) lagged by 4 years to reflect the number of potential conspecific competitors in the second and third sockeye growing seasons at sea. $P_{predators}$ is the abundance of potential pink salmon predators returning to the coast in the year sockeye smolts enter the marine environment. Models for each set of hypotheses are ordered by increasing values of the small-sample Akaike information criterion (AIC_c). Also shown are the log likelihoods (LL), differences in AIC_c from the AIC_c of the top model (ΔAIC_c), and Akaike model weights (w_i). The null model is simply within-population and within-brood-year density dependence.

support for the hypothesis that the proportion of ocean-age-3 recruits was positively related to pink salmon abundance (Tables S4a, S4b and S5a, S5b¹).

Collinearity among the independent variables was weak to moderate for detrended (0.0 to 0.33) and raw variables (0.2 to 0.56; Table S7¹), and all independent variables had variance inflation factors of <2, suggesting that correlations among these independent variables were unlikely to substantially inflate the standard errors of our parameter estimates (Zuur et al. 2009). Overall, there was little evidence of temporal correlation in the population-specific residuals from the best-fit models in both the initial and

Table 3. Multimodel averaged parameter estimates, unconditional standard error (SE), and relative variable importance (RVI) of parameters appearing in the hypotheses in Table 2.

Hypothesis	Variable	Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.153	0.048	0.98
	P_{t+3}	0.049	0.036	0.45
	Sx_{t+4}	0.001	0.022	0.25
2. Standard fork length (males)	P_{t+4}	-0.224	0.073	0.96
	P_{t+3}	-0.033	0.076	0.27
	Sx_{t+4}	-0.347	0.069	1.00
2. Standard fork length (females)	P_{t+4}	-0.181	0.078	0.81
	P_{t+3}	-0.062	0.074	0.33
	Sx_{t+4}	-0.365	0.074	1.00
3. Proportion ocean-age-3 recruits	P_{t+4}	0.552	0.227	0.88
	P_{t+3}	0.298	0.246	0.41
	Sx_{t+4}	0.017	0.303	0.26

Note: All models were fit to data with linear time trends removed. Parameters include the abundance of potential pink salmon competitors beginning in the first (P_{t+3}) and second sockeye growing seasons at sea (P_{t+4}) and well as the number of potential conspecific competitors in the second and third sockeye growing seasons at sea (Sx_{t+4}). Parameter estimates were measured in standard deviation units (SDU) on dependent variables with linear time trends removed.

sensitivity analyses. Rerunning the analyses without those few populations that exhibited significant lag-one correlation in residuals did not affect our conclusions.

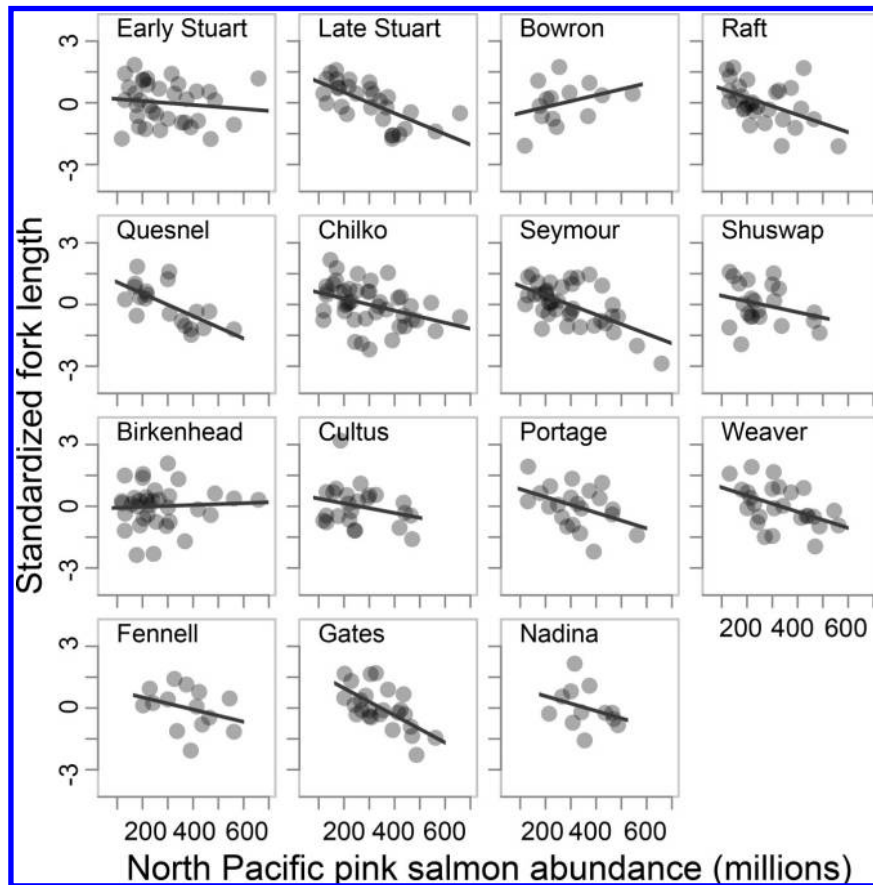
Discussion

The productivity of sockeye salmon populations in BC, Southeast Alaska, and Washington has declined similarly over time and intensified in recent years, suggesting that the primary causal mechanism driving this decline operates at a large, multiregional spatial scale at sea (Peterman and Dorner 2012). We examined the productivity and life history characteristics of up to 36 sockeye populations — including 18 Fraser River populations — spanning this region of similar trends in productivity over the past 55 years to test whether competition between pink and sockeye salmon for resources at sea may have contributed to these declines. We found consistent evidence that productivity of these sockeye salmon populations has declined in response to increasing abundance of pink salmon in the North Pacific Ocean. Furthermore, length-at-age of male and female Fraser River sockeye salmon was inversely correlated with both pink and sockeye salmon abundance, and age-at-maturity of Fraser River sockeye salmon was positively correlated with pink salmon abundance. These findings were consistent for both detrended and raw datasets involving North Pacific pink salmon, indicating that the influence of pink salmon was detected across both short and long time scales. The abundance of pink salmon in the North Pacific alternates from high (odd-numbered years) to relatively low abundance (even-numbered years), and this alternating-year pattern was also observed in sockeye salmon productivity, length-at-age, and age at maturity. Thus, the evidence for competition between pink and sockeye salmon comes from both hierarchical modeling of patterns over time and the natural experiment provided by the 2-year life cycle of pink salmon and its alternating-year abundance. Our analyses predict that an increase in pink salmon abundance from 150 million to 600 million fish (i.e., the observed range) would lead to a ~67% reduction in total abundance of returning Fraser River sockeye salmon (catch and spawning escapement combined) after controlling for other variables in the model such as parental spawning abundance.

Temporal and spatial influence of pink salmon

Sockeye salmon may be influenced by competition with pink salmon throughout their life at sea. Early marine scale growth of two Fraser River sockeye salmon populations (Chilko, Birken-

Fig. 4. Standardized fork length of 4-year-old male sockeye salmon spawners in relation to North Pacific pink salmon abundance in the second year of sockeye life at sea.



head) during their first year at sea tends to be negatively correlated with regional abundances of juvenile pink salmon estimated from adult returns during the following year (McKinnell and Reichardt 2012). In contrast, survival of Babine sockeye salmon at sea is positively correlated with an index of juvenile pink salmon abundance, possibly because juvenile pink salmon may swamp predators of sockeye salmon (Peterman 1982). Our analyses indicated weak and inconsistent support for interactions between pink and sockeye salmon in the first year of marine life. This inconclusive finding may stem, in part, from the opposing effects of competition for prey and predator swamping.

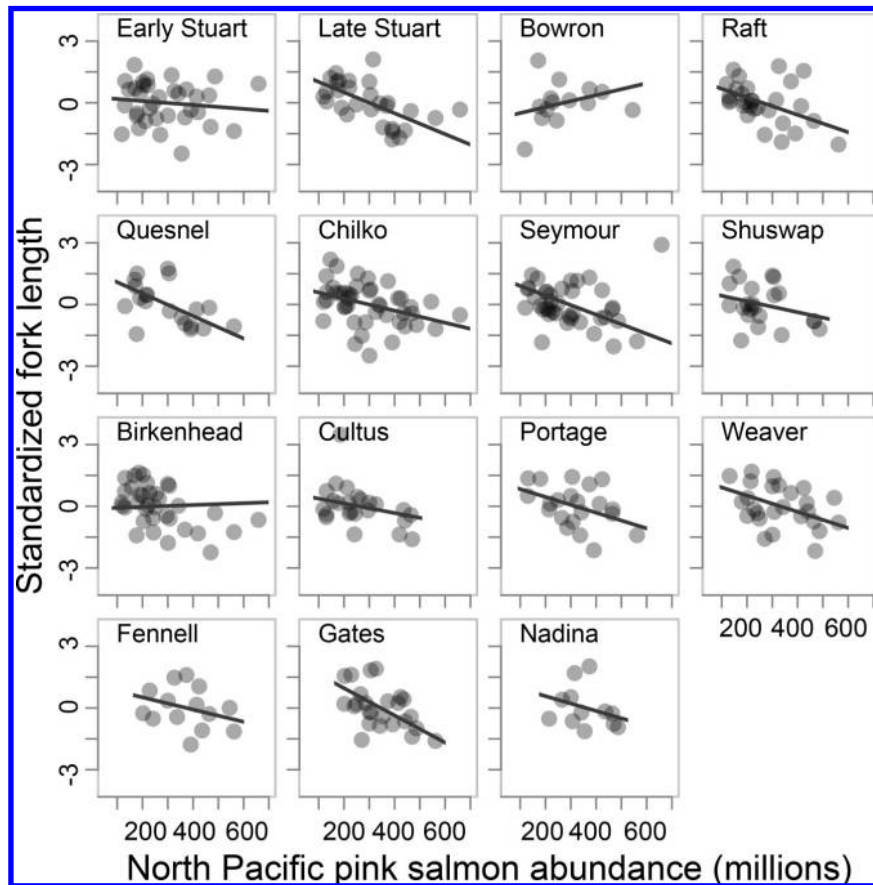
Our analyses provide consistent support for the hypothesis that competition between pink and sockeye salmon begins (or intensifies) during the second year of sockeye marine life. This finding is consistent with the period of interaction between Bristol Bay sockeye salmon and Russian pink salmon (Ruggerone et al. 2003, 2005; Ruggerone and Nielsen 2004). This research in Bristol Bay used scale growth measurements to show that sockeye growth was reduced during their second and third years at sea of odd-numbered years, corresponding with high pink salmon abundance. Scale circuli measurements revealed that sockeye growth reduction in odd-numbered years occurred shortly after peak growth in spring and continued into the fall of their second and third years at sea. Interaction with abundant pink salmon in odd-numbered years led to reduced adult length-at-age and 26%–45% lower smolt to adult survival depending on smolt age. No pink–sockeye salmon interaction was detected during the first year at sea because relatively few pink salmon are present in the southeastern Bering Sea (Ruggerone et al. 2010).

Our analyses support the hypothesis that the combined abundances of both North American and Asian pink salmon influenced

the productivity and life history of Fraser River sockeye salmon, while there was support for hypotheses that included the abundance of only pink salmon from North America when using raw but not detrended data (Tables S2a, S2b and S3a, S3b¹). The lack of support when using detrended data probably reflects the relatively small differences between odd- and even-year abundances of North American pink salmon across all years of the investigation. However, Asian pink salmon are approximately 50% more abundant than pink salmon in North America (Ruggerone et al. 2010), and the limited tagging and genetic data that have been collected demonstrate overlap between Asian pink salmon and sockeye salmon originating from BC (Takagi et al. 1981; Myers et al. 2007; Beacham et al. 2014).

Recent genetic analyses indicate that sockeye salmon originating from BC migrate farther west and overlap to a greater extent with Asian pink salmon than previously indicated by tagging studies (Takagi et al. 1981; Myers et al. 1996). Sockeye salmon from BC have been captured in their first year at sea along the Alaska Peninsula during summer and fall (Tucker et al. 2009), near the Aleutian Islands during winter (Farley et al. 2011), and Fraser River sockeye salmon have been captured in the Bering Sea (Beacham et al. 2014). Juvenile sockeye salmon originating from the Fraser River and adjacent areas dominate the stock composition of sockeye along the Alaska Peninsula during fall, suggesting that these stocks migrate westward as far as 175°E during their first year at sea (Beacham et al. 2014). Asian pink salmon have been reported to migrate eastward to as far as 155°W based on tagging (Takagi et al. 1981), which provides additional evidence to suggest sympatry between BC sockeye and Asian pink salmon. Furthermore, overlap between these species may be greater during odd-numbered years when pink salmon are more broadly distributed

Fig. 5. Standardized fork length of 4-year-old female sockeye salmon spawners in relation to North Pacific pink salmon abundance in the second year of sockeye life at sea.



on the high seas, based on Japanese gillnet surveys across the North Pacific during 1972–1998 (Azumaya and Ishida 2000). We hypothesize that sympatry between Asian pink salmon and North American sockeye salmon is facilitated by the counterclockwise movement of the Alaska Gyre and the westward flow of the Alaska Current along the Alaska Peninsula (Mann and Lazier 2006).

Unique sockeye life history

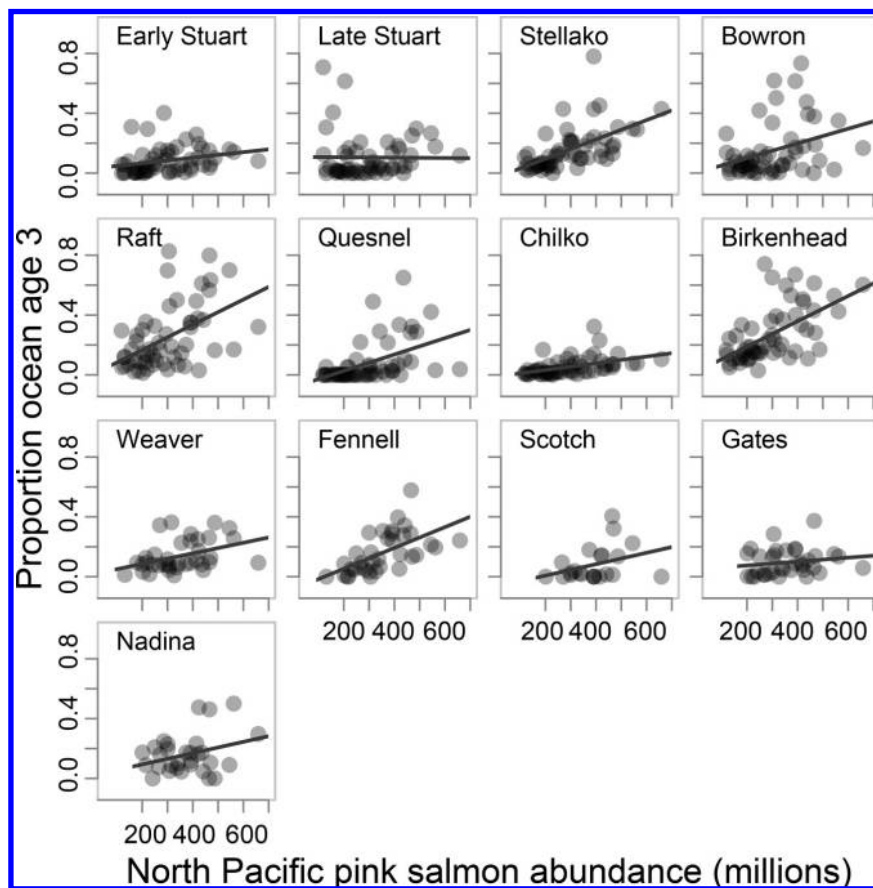
Our hierarchical analyses suggest that the productivity of all but one of 36 sockeye populations considered was inversely related to North Pacific pink salmon abundance. The single outlier, Harrison River sockeye salmon, is noteworthy because these sockeye have a unique life history among the populations we considered and their productivity has trended in the opposite direction of other Fraser River sockeye salmon populations (Tucker et al. 2009; Beamish et al. 2010; Peterman and Dorner 2012). Harrison River sockeye are primarily “ocean-type” salmon that emigrate to sea as subyearlings rather than yearlings that overwinter in lakes, as do most sockeye populations we considered. Harrison River sockeye salmon enter the Strait of Georgia approximately 6–8 weeks after “lake-type” yearling sockeye smolts, initially inhabit inlets rather than offshore areas of the Strait, delay emigration to the ocean until winter, and primarily emigrate through the Strait of Juan de Fuca rather than through Johnstone Strait (Tucker et al. 2009; Beamish et al. 2010; Beacham et al. 2014). These life history characteristics may reduce the extent to which Harrison River sockeye interact with pink salmon in the North Pacific, but odd-year broods may compete with local juvenile pink salmon during the first summer in the Strait of Georgia, leading to reduced productivity and delayed maturation (Beamish et al. 2010).

Oceanographic, prey life history, and predation effects

A variety of factors at sea undoubtedly affect sockeye growth, maturation, and productivity in addition to the species interactions we identify here (e.g., Mueter et al. 2002a, 2002b, 2005; Wells et al. 2007; Healey 2011; McKinnell et al. 2014). These other factors could confound our analyses. However, when we considered the potentially confounding influence of SST and farmed salmon production in the analyses (Connors et al. 2012), our conclusions did not change and species interactions remained the primary factor of influence. Our findings support the hypothesis put forward by Holt and Peterman (2004) that density dependence and its effect on growth and delayed maturation (Healey et al. 2000) may have a greater influence than physical oceanographic features (Cox and Hinch 1997). Irvine and Akenhead (2013) also concluded that the smolt to adult survival of Chilko sockeye salmon (Fraser River population) was more related to indices of total salmon abundance at sea, including Asian salmon, than to oceanographic conditions. Physical oceanographic conditions are important to salmon and they set the baseline for growth and survival, but the dynamic and complex food web and salmon interactions are likely to be equally important though perhaps more elusive to detect and evaluate.

Most salmon mortality at sea is thought to occur during the first year at sea (Ricker 1976; Beamish and Mahnken 2001; Farley et al. 2007). In response to the unexpectedly low return of adult Fraser sockeye salmon in 2009 from the 2007 smolt emigration, investigators reported anomalous oceanographic conditions encountered by sockeye salmon during early marine life. Low sockeye survival was associated with unfavorable winds, high river runoff, and pronounced surface stratification that appeared to cause

Fig. 6. The proportion of all sockeye salmon recruits from a given brood year that matured after 3 years in the ocean in relation to North Pacific pink salmon abundance in the second year of sockeye life at sea.



low prey production and reduced growth (Beamish et al. 2012; Thomson et al. 2012; McKinnell et al. 2014). Other investigators reported disease and toxic algae blooms in the Strait of Georgia as possible factors (Rensel et al. 2010; Miller et al. 2011).

Although mortality during early marine life is unquestionably important to salmon production, recent evidence also indicates that mortality later in marine life may also be important (Bradford 1995). For example, Welch et al. (2011) reported that most mortality of Fraser sockeye salmon occurred after sockeye exited the Salish Sea, based on large acoustically tagged Fraser River sockeye salmon smolts and detection arrays set along the coast and at the mouth of the Fraser River. In western Alaska, adult returns of Chinook (*Oncorhynchus tshawytscha*), chum, and coho (*Oncorhynchus kisutch*) salmon declined abruptly during the 1997–1998 El Niño event, suggesting that El Niño related processes late in marine life (as opposed to early in marine life when El Niño had not yet occurred) contributed to reduced survival and abundance (Aglar 2010). Our investigation, and investigations of Bristol Bay sockeye salmon (Ruggerone et al. 2003), provide additional evidence that significant mortality of salmon may also occur after early marine life. Additional research is needed to improve our understanding of the relative importance of mortality rates early in marine life versus those later in marine life in shaping the dynamics of salmon populations.

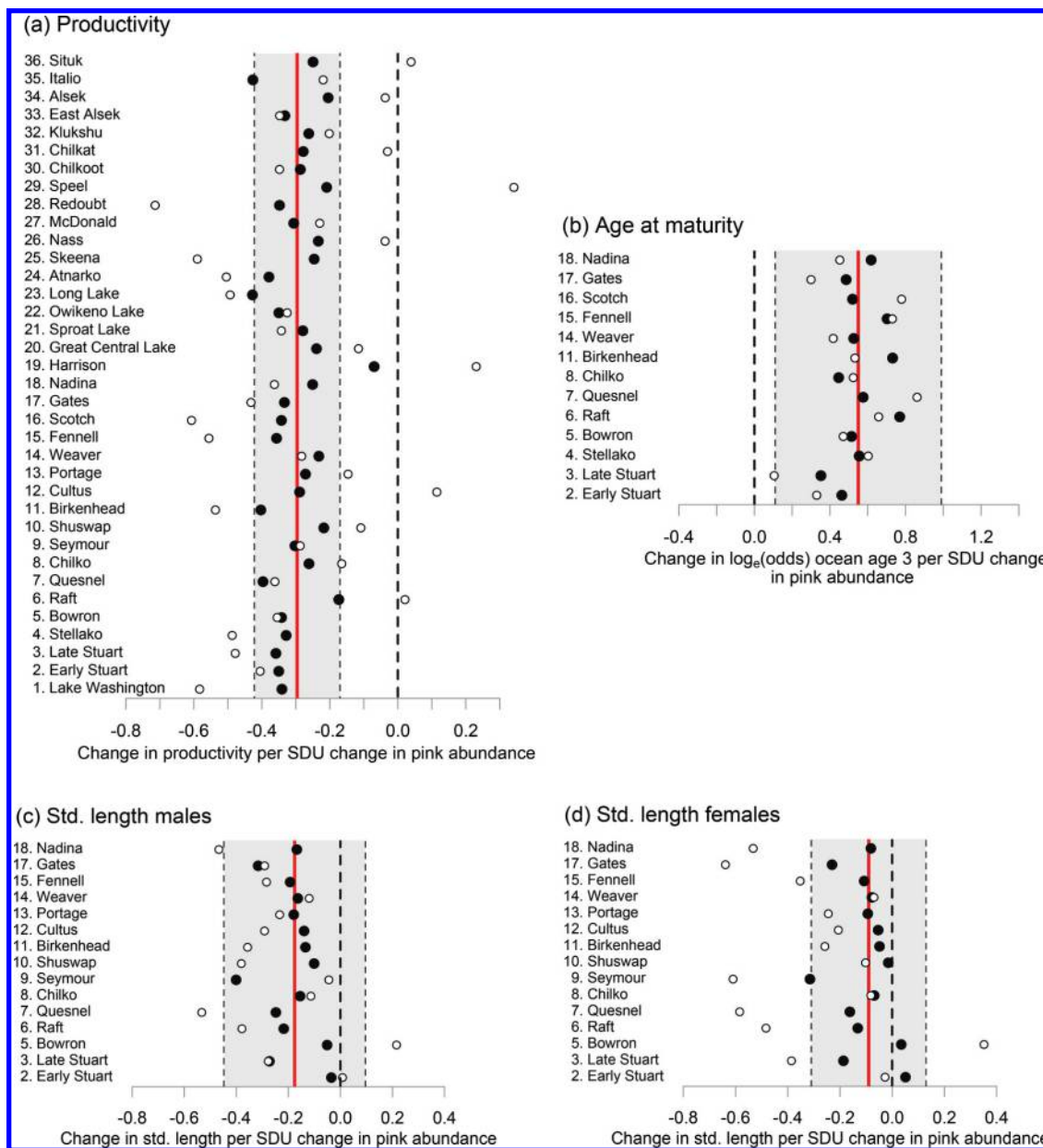
The abundance of both sockeye and pink salmon in Alaska has been relatively high since the mid-1970s (Ruggerone et al. 2010), likely as a result of favorable (warmer) oceanographic conditions during the first year of marine life (Mueter et al. 2002a, 2002b; Stachura et al. 2014), which are correlated with increased early marine growth and survival (Ruggerone et al. 2007). At first glance, this pattern may seem to contradict the hypothesis that competition

between pink and sockeye salmon for prey has led to reduced sockeye growth and productivity. However, while the survival and abundance of Alaska sockeye has been shown to be correlated with increased early marine growth and SST, length-at-age, survival, and abundance of Alaskan sockeye have also been shown to be inversely related to pink salmon abundance later in marine life (Ruggerone et al. 2003, 2007). This suggests that while the survival and abundance of Alaskan sockeye has been strongly positively influenced by favorable oceanographic conditions during early marine life in recent decades, competition for resources with pink salmon may still occur later in marine life. We hypothesize that the balance between these opposing processes may tilt in favor of increased survival and abundance for Alaskan sockeye populations but not those to the south that have, on average, experienced less favorable early marine oceanographic conditions.

The life history of key prey shared by pink and sockeye salmon likely contributes to the strong species interaction shown in this and other studies (Ruggerone et al. 2005). Pink salmon reportedly influence the standing crop of macrozooplankton (Shiomoto et al. 1997; Sugimoto and Tadokoro 1997), which are also consumed by sockeye salmon. Squid (e.g., *Berryteuthis anonychus*) are an exceptionally important prey of both species, and squid abundance in their diets is reduced in odd-numbered years when pink salmon are abundant (Aydin 2000; Kaeriyama et al. 2004; Davis et al. 2005; Aydin et al. 2005). These squid (*B. anonychus*) exhibit a 2-year life cycle and predation by pink salmon may be a key factor controlling squid abundance (Nesis 1997; Jorgensen 2011). Predation by pink salmon on prey with biennial life histories (Tsuda et al. 2004) may enhance the alternating-year pattern of prey abundance, leading to the alternating-year pattern of sockeye salmon growth, productivity, and age at maturation. Furthermore, advection and

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Fig. 7. Multimodel averaged predicted relationships (solid vertical line \pm 2 unconditional standard errors — dashed lines) between North Pacific pink salmon abundance during the second sockeye growing season at sea and (a) sockeye productivity (\log_e (recruits/spawner)), (b) the proportion of total sockeye recruits that matured after 3 years in the ocean, and the standardized length of 4-year-old male (c) and female (d) spawners. A dashed vertical line at “0” highlights the observed relationship relative to no effect. The x axis in each plot is the response of each dependent variable to a one standard deviation unit increase in pink salmon abundance (\sim 120 million pink salmon). For the coefficients in panel (b), the response is the \log_e (odds) of maturing after 3 years instead of 2 years. For example, a \log_e (odds) of 0.5 is equivalent to a 1.65 greater chance of maturing at ocean-age-3. Solid circles corresponding to each individual population are multimodel averaged estimates of population-specific responses to a one standard deviation unit increase in pink salmon abundance based on hierarchical models fit to all populations simultaneously. Open circles are corresponding multimodel averaged parameter estimates based on models fit to each population independently. All parameter estimates are based on models fit to data without linear time trends removed.



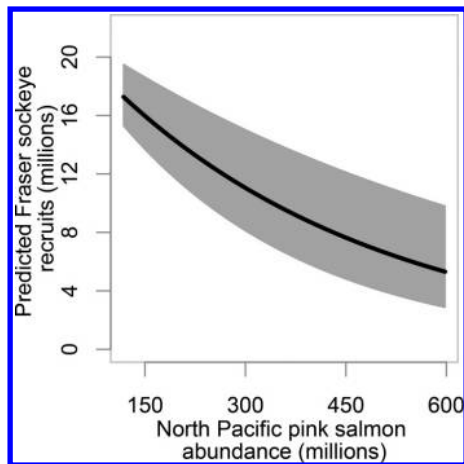
active migration of key prey, such as squid, in the eastward-flowing Subarctic Current (Mann and Lazier 2006) may indirectly enhance the interaction between Asian pink salmon and sockeye salmon in this study.

Predation is often a key factor affecting salmon survival (Quinn 2005), but we found no evidence that predation by returning adult pink salmon influenced sockeye salmon productivity. This finding is consistent with observations of few juvenile salmon consumed by returning adult pink salmon in Southeast Alaska (Sturdevant et al. 2012).

Management implications

Our study has important implications for policy and management of salmon hatcheries because it provides strong evidence that salmon species compete for prey at sea, leading to potentially important effects on salmon productivity and life history characteristics. Approximately 1.4 billion hatchery pink salmon are released into the North Pacific each year, of which 70% are from hatcheries in North America (Ruggerone et al. 2010). A key goal of hatcheries is to maintain and stabilize high levels of salmon harvests. However, even though overall abundance of wild pink

Fig. 8. Predicted Fraser River adult sockeye recruits (black line \pm 2 standard errors) as a function of the abundance of potential North Pacific pink salmon competitors in the second sockeye growing season at sea.



salmon has been exceptionally high during the past 30 years, hatchery operators have proposed substantial increases in hatchery pink salmon in Prince William Sound, Kodiak, Yakutat, Southeast Alaska, and Russia (<http://www.adfg.alaska.gov/index.cfm?adfg=fishingHatcheriesPlanning.enhance>). The greatest production of hatchery pink salmon occurs in Prince William Sound, Alaska, where hatchery pink salmon reportedly reduced the growth of wild pink salmon because of food limitations in near-shore and oceanic areas (Cross et al. 2005), and hatchery pink salmon reduced wild pink salmon abundances from up to 17 million fish per year (Hilborn and Eggers 2000, 2001) to between 0 and 4.6 million fish per year (Wertheimer et al. 2004).

Pink salmon, including those produced in hatcheries, appear to have a strong influence on the North Pacific ecosystem. Seabird diet, body mass, and reproductive success near the Aleutian Islands are reduced in odd-numbered years when pink salmon abundance is exceptionally high (Toge et al. 2011; Springer and van Vliet 2014). In Prince William Sound, recovery of Pacific herring (*Clupea pallasii*) populations during the 20-year period after the Exxon Valdez oil spill may have been inhibited by competition with juvenile hatchery pink salmon for prey (Pearson et al. 2012). Additionally, salmon migrate long distances from their natal rivers, and abundant hatchery fish in Asia may compete with depleted wild populations in Norton Sound, Alaska, more than 2000 km away (Ruggerone et al. 2012). In response to the growing evidence for ecological interactions of salmonids at sea, scientists have argued for international cooperation among nations in the North Pacific to reduce competition among hatchery and wild salmon at sea (Peterman 1984; Holt et al. 2008; Peterman et al. 2012) and among hatchery salmon and other ecosystem components, including seabirds (Springer and van Vliet 2014).

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References

- Agler, B.A. 2010. Historical analysis of Arctic-Yukon-Kuskokwim and Asian chum salmon. In *Protecting the future of salmon: research and discovery report, 2002–2010*. AYK Sustainable Salmon Initiative, Anchorage, Alaska. pp. 33–34.
- Atcheson, M.E., Myers, K.W., Davis, N.D., and Mantua, N.J. 2012. Potential trophodynamic and environmental drivers of steelhead (*Oncorhynchus mykiss*) productivity in the North Pacific Ocean. *Fish. Oceanogr.* **21**: 321–335. doi:10.1111/j.1365-2419.2012.00627.x.
- Aydin, K.Y. 2000. Trophic feedback and carrying capacity of Pacific salmon (*Oncorhynchus* spp.) on the high seas of the Gulf of Alaska. Ph.D. thesis, University of Washington, Seattle, Wash.
- Aydin, K.Y., McFarlane, G.A., King, J.R., Megrey, B.A., and Myers, K.W. 2005. Linking oceanic foodwebs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. *Deep Sea Res. Part II*, **52**: 757–780. doi:10.1016/j.dsr2.2004.12.017.
- Azuma, T. 1995. Biological mechanisms enabling sympatry between salmonids with special reference to sockeye and chum salmon in oceanic waters. *Fish. Res.* **24**: 291–300. doi:10.1016/0165-7836(95)00383-3.
- Azumaya, T., and Ishida, Y. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *N. Pac. Anadr. Fish Comm. Bull. No. 2*: 165–174.
- Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014. Stock-specific migration pathways of juvenile sockeye salmon in British Columbia waters and in the Gulf of Alaska. *Trans. Am. Fish. Soc.* **143**: 1386–1403. doi:10.1080/00028487.2014.935476.
- Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progr. Oceanogr.* **49**: 423–437. doi:10.1016/S0079-6611(01)00034-9.
- Beamish, R.J., Lange, K.L., Neville, C.M., Sweeting, R.M., Beacham, T.D., and Preikshot, D. 2010. Late ocean entry of sea type sockeye salmon from the Harrison River in the Fraser River drainage results in improved productivity [online]. NPAFC Doc. 1283. Available from www.npafc.org.
- Beamish, R.J., Neville, C., Sweeting, R., and Lange, K. 2012. The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser River in 2009. *Mar. Coastal Fish. Dyn. Manage. Ecosy. Sci.* **4**: 403–414. doi:10.1080/19425120.2012.676607.
- Bolker, B., Brooks, M., Clark, C., Geange, S., Poulsen, J., Stevens, M., and White, J. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**: 127–135. doi:10.1016/j.tree.2008.10.008. PMID: 19185386.
- Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. *Can. J. Fish. Aquat. Sci.* **52**(6): 1327–1338. doi:10.1139/f95-129.
- Bugaev, V.F., Welch, D.W., Selifonov, M.M., Grachev, L.E., and Eveson, J.P. 2001. Influence of the marine abundance of pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. *Fish. Oceanogr.* **10**: 26–32. doi:10.1046/j.1365-2419.2001.00150.x.
- Burnham, K.P., and Anderson, D.R. 2002. *Model selection and multimodel inference*. Springer, New York.
- Connors, B.M., Braun, D.C., Peterman, R.M., Cooper, A.B., Reynolds, J.D., Dill, L.M., Ruggerone, G.T., and Krkošek, M. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. *Conserv. Lett.* **5**: 304–312. doi:10.1111/j.1755-263X.2012.00244.x.
- Cox, S.P., and Hinch, S.G. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature. *Can. J. Fish. Aquat. Sci.* **54**(5): 1159–1165. doi:10.1139/f97-009.
- Cross, A.D., Beauchamp, D.A., Armstrong, J.L., Blikshteyn, M., Boldt, J.L., Davis, N.D., Haldorson, L.J., Moss, J.H., Myers, K.W., and Walker, R.V. 2005. Consumption demand of juvenile pink salmon in Prince William Sound and the coastal Gulf of Alaska in relation to prey biomass. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **52**: 347–370. doi:10.1016/j.dsr2.2004.09.021.
- Davis, N.D., Fukuwaka, M., Armstrong, J.L., and Myers, K.W. 2005. Salmon food habits studies in the Bering Sea, 1960 to present. *N. Pac. Anadr. Fish Comm. Tech. Rept.* **6**: 24–28.
- Farley, E.V., Moss, J.H., and Beamish, R.J. 2007. A review of the critical size, critical period hypothesis for juvenile Pacific salmon. *N. Pac. Anadr. Fish Comm. Bull.* **4**: 311–317.
- Farley, E.V., Starovoytov, A., Naydenko, S., Heintz, R., Trudel, M., Guthrie, C.M., Eisner, L., and Guyon, J.R. 2011. Implications of a warming eastern Bering Sea for Bristol Bay sockeye salmon. *ICES J. Mar. Sci.* **68**: 1138–1146. doi:10.1093/icesjms/fsr021.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., O'Maoileidigh, N., and McCarthy, J.L. 2009. The recruitment of Atlantic salmon in Europe. *ICES J. Mar. Sci.* **66**: 289–304.
- Gelman, K., and Hill, J. 2007. *Data analysis using regression and multilevel/hierarchical modeling*. Cambridge University Press, New York.
- Healey, M. 2011. The cumulative impacts of climate change on Fraser River sockeye salmon (*Oncorhynchus nerka*) and implications for management. *Can. J. Fish. Aquat. Sci.* **68**(4): 718–737. doi:10.1139/f2011-010.
- Healey, M.C., Henderson, M.A., and Burgetz, I. 2000. Precocial maturation of

- male sockeye salmon in the Fraser River, British Columbia, and its relationship to growth and year-class strength. *Can. J. Fish. Aquat. Sci.* **57**(11): 2248–2257. doi:10.1139/f00-202.
- Hilborn, R., and Eggers, D. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Trans. Am. Fish. Soc.* **129**: 333–350. doi:10.1577/1548-8659(2000)129<0333:AROTHP>2.0.CO;2.
- Hilborn, R., and Eggers, D. 2001. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska: response to comment. *Trans. Am. Fish. Soc.* **130**: 720–724. doi:10.1577/1548-8659(2001)130<0720:AROTHP>2.0.CO;2.
- Hinch, S.G., Healey, M.C., Diewert, R.E., Henderson, M.A., Thomson, K.A., Hourston, R., and Juanes, F. 1995. Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon. *Can. J. Fish. Aquat. Sci.* **52**(12): 2651–2659. doi:10.1139/f95-854.
- Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and Patterson, D.A. 2012. Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. *J. Fish Biol.* **81**: 576–599. doi:10.1111/j.1095-8649.2012.03360.x. PMID:22803725.
- Holt, C.A., and Peterman, R.M. 2004. Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. *Can. J. Fish. Aquat. Sci.* **61**(12): 2455–2470. doi:10.1139/f04-193.
- Holt, C.A., Rutherford, M.B., and Peterman, R.M. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. *Mar. Pol.* **32**: 607–617. doi:10.1016/j.marpol.2007.11.001.
- Irvine, J.R., and Akenhead, S.A. 2013. Understanding smolt survival trends in sockeye salmon. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **5**: 303–328. doi:10.1080/19425120.2013.831002.
- Johnson, S.P., and Schindler, D.E. 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecol. Res.* **24**: 855–863. doi:10.1007/s11284-008-0559-0.
- Jorgensen, E.M. 2011. Ecology of cephalopod early life history in the Gulf of Alaska and Bering Sea. Ph.D. thesis, University of Washington, Seattle, Wash.
- Kaeriyama, M., Nakamura, M., Yamaguchi, M., Ueda, H., Anma, G., Takagi, S., Aydin, K.Y., Walker, R.V., and Myers, K.W. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. *N. Pac. Anadr. Fish Comm. Bull.* **2**: 55–63.
- Kaeriyama, M., Nakamura, M., Edpalina, R.R., Bower, J.R., Yamaguchi, H., Walker, R.V., and Myers, K.W. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* **13**: 197–207. doi:10.1111/j.1365-2419.2004.00286.x.
- Mann, K.H., and Lazier, J.R.N. 2006. Dynamics of marine ecosystems, biological-physical interactions in the oceans. 3rd ed. Blackwell Publishing, Mass.
- McKinnell, S., and Reichardt, M. 2012. Early marine growth of juvenile Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to juvenile pink (*Oncorhynchus gorbuscha*) and sockeye salmon abundance. *Can. J. Fish. Aquat. Sci.* **69**(9): 1499–1512. doi:10.1139/f2012-078.
- McKinnell, S., Curchitser, E., Groot, K., Kaeriyama, M., and Trudel, M. 2014. Oceanic and atmospheric extremes motivate a new hypothesis for variable marine survival of Fraser River sockeye salmon. *Fish. Oceanogr.* **23**: 322–341. doi:10.1111/fog.12063.
- Miller, K.M., Li, S., Kaukinen, K.H., Ginther, N., Hammill, E., Curtis, J.M.R., Patterson, D.A., Sierocinski, T., Donnison, L., Pavlidis, P., Hinch, S.G., Hruska, K.A., Cooke, S.J., English, K.K., and Farrell, A.P. 2011. Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science*, **331**: 214–217. doi:10.1126/science.1196901. PMID:21233388.
- Morita, K., and Fukuwaka, M. 2007. Why age and size at maturity have changed in Pacific salmon. *Mar. Ecol. Progr. Ser.* **335**: 289–294. doi:10.3354/meps335289.
- Moss, J.H., Beauchamp, D.A., Cross, A.D., Myers, K.W., Farley, E.V., Murphy, J.M., and Helle, J.H. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Trans. Am. Fish. Soc.* **134**: 1313–1322. doi:10.1577/T05-054.1.
- Mueter, F.J., Peterman, R.M., and Pypser, B.J. 2002a. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* **59**(3): 456–463. doi:10.1139/f02-020.
- Mueter, F.J., Ware, D.M., and Peterman, R.M. 2002b. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. *Fish. Oceanogr.* **11**: 205–218. doi:10.1046/j.1365-2419.2002.00192.x.
- Mueter, F.J., Pypser, B.J., and Peterman, R.M. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Trans. Am. Fish. Soc.* **134**: 105–119. doi:10.1577/T-04-033.1.
- Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S., and Dahlberg, M.L. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. *N. Pac. Anadr. Fish Comm. Doc.* **192**. FRI-UW-9614. Fisheries Research Institute, University of Washington, Seattle, Wash.
- Myers, K.W., Klovach, N.V., Gritsenko, O.F., Urawa, S., and Royer, T.C. 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. *N. Pac. Anadr. Fish Comm. Bull.* **4**: 159–177.
- Myers, R., and Mertz, G. 1998. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. *Fish. Res.* **37**: 51–60. doi:10.1016/S0165-7836(98)00126-X.
- Nesis, K.N. 1997. Gonatid squids in the subarctic North Pacific: ecology, biogeography, niche diversity and role in the ecosystem. *Adv. Mar. Ecol.* **32**: 243–324. doi:10.1016/S0065-2881(08)60018-8.
- Newman, M.C. 1993. Regression analysis of log-transformed data: Statistical bias and its correction. *Environ. Toxicol. Chem.* **12**: 1129–1133. doi:10.1002/etc.5620120618.
- Pearcy, W.G., Brodeur, R.D., Shenker, J., Smoker, W., and Endo, Y. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches, and oceanographic conditions in the Gulf of Alaska, 1980–1985. *Bull. Ocean. Res. Inst.* **26**: 29–78.
- Pearson, W.H., Deriso, R.B., Elston, R.A., Hook, S.E., Parker, K.R., and Anderson, J.W. 2012. Hypotheses concerning the decline and poor recovery of Pacific herring in Prince William Sound, Alaska. *Rev. Fish Biol. Fish.* **22**: 95–135. doi:10.1007/s11160-011-9225-7.
- Peterman, R.M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. *Can. J. Fish. Aquat. Sci.* **39**(6): 904–913. doi:10.1139/f82-121.
- Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **41**(12): 1825–1829. doi:10.1139/f84-223.
- Peterman, R.M., and Dorner, B. 2012. A widespread decrease in productivity of sockeye salmon populations in western North America. *Can. J. Fish. Aquat. Sci.* **69**(8): 1255–1260. doi:10.1139/f2012-063.
- Peterman, R.M., Marmorek, D., Beckman, B., Bradford, M., Mantua, N., Riddell, B.E., Scheuerell, M., Staley, M., Wieckowski, K., Winton, J.R., and Wood, C.C. 2010. Synthesis of evidence from a workshop on the decline of Fraser River sockeye. 15–17 June 2010 [online]. A report to the Pacific Salmon Commission, Vancouver, B.C. Available from <http://www.psc.org> [accessed 1 November 2012].
- Peterman, R.M., Holt, C.A., and Rutherford, M.R. 2012. The need for international cooperation to reduce competition among salmon for a common pool of prey resources in the North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Tech. Rep.* **8**: 99–101.
- Pinheiro, J., and Bates, D. 2000. Mixed effects models in S and S-Plus. Springer, New York.
- Piston, A.W., and Heintz, S.C. 2011. Chum salmon stock status and escapement goals in Southeast Alaska [online]. Alaska Department of Fish and Game, Special Publication No. 11–21, Anchorage. Available from www.adfg.alaska.gov/FedAidpdfs/SP11-21.pdf [accessed 1 June 2013].
- Pypser, B.J., Peterman, R.M., Lapointe, M.F., and Walters, C.J. 1999. Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **56**(6): 1046–1057. doi:10.1139/f99-038.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.
- Rensel, J.E., Haigh, N., and Tynan, T.J. 2010. Fraser River sockeye salmon marine survival decline and harmful blooms of *Heterosigma akashiwo*. *Harmful Algae*, **10**: 98–115. doi:10.1016/j.hal.2010.07.005.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish population. *Bull. Fish. Res. Board Can.* **191**: 1–382.
- Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in saltwater, and non-catch mortality caused by fishing. *J. Fish. Res. Board Can.* **33**(7): 1483–1524. doi:10.1139/f76-191.
- Rogers, D.E., and Ruggerone, G.T. 1993. Factors affecting the marine growth of Bristol Bay sockeye salmon. *Fish. Res.* **18**: 89–103. doi:10.1016/0165-7836(93)90042-6.
- Roos, J.F. 1991. Restoring Fraser River salmon: a history of the International Pacific Salmon Fisheries Commission, 1937–1985. The Pacific Salmon Commission, Vancouver, B.C., Canada.
- Ruggerone, G.T., and Nielsen, J.L. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Rev. Fish Biol. Fish.* **14**: 371–390. doi:10.1007/s11160-004-6927-0.
- Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L., and Rogers, D.E. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish. Oceanogr.* **12**: 209–219.
- Ruggerone, G.T., Farley, E., Nielsen, J., and Hagen, P. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fish. Bull.* **103**: 355–370.
- Ruggerone, G.T., Nielsen, J.L., and Bumgarner, J. 2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. *Deep Sea Res. II Top. Stud. Oceanogr.* **54**: 2776–2793. doi:10.1016/j.dsr2.2007.08.016.
- Ruggerone, G.T., Peterman, R.M., Dorner, B., and Myers, K.W. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **2**: 306–328. doi:10.1577/C09-054.1.
- Ruggerone, G.T., Agler, B.A., and Nielsen, J.L. 2012. Evidence for competition at

- sea between Norton Sound chum salmon and Asian hatchery chum salmon. *Environ. Biol. Fish.* **94**: 149–163. doi:10.1007/s10641-011-9856-5.
- Shiomoto, A., Tadokoro, K., Nagasawa, K., and Ishida, Y. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Mar. Ecol. Progr. Ser.* **150**: 75–85. doi:10.3354/meps150075.
- Springer, A.M., and van Vliet, G.B. 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proc. Natl. Acad. Sci. U.S.A.* **111**: 1880–1888. doi:10.1073/pnas.1319089111.
- Stachura, M.M., Mantua, N.J., and Scheuerell, M.D. 2014. Oceanographic influences on patterns in North Pacific salmon Abundance. *Can. J. Fish. Aquat. Sci.* **71**(2): 226–235. doi:10.1139/cjfas-2013-0367.
- Sturdevant, M.V., Orsi, J.A., and Fergusson, E.A. 2012. Diets and trophic linkages of epipelagic fish predators in coastal Southeast Alaska during a period of warm and cold climate years, 1997–2011. *Mar. Coastal Fish. Dyn. Manage. Ecosyst. Sci.* **4**: 526–545.
- Sugimoto, T., and Tadokoro, K. 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* **6**: 74–93. doi:10.1046/j.1365-2419.1997.00031.x.
- Takagi, K., Aro, K.V., Hartt, A.C., and Dell, M.B. 1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull. No.* 40.
- Thomson, R.E., Beamish, R.J., Beacham, T.D., Trudel, M., Whitfield, P.H., and Hourston, R.H. 2012. Anomalous ocean conditions may explain the recent extreme variability in Fraser River sockeye salmon production. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **4**: 415–437. doi:10.1080/19425120.2012.675985.
- Toge, K., Yamashita, R., Kazama, K., Fukuwaka, M., Yamamura, O., and Watanuki, Y. 2011. The relationship between pink salmon biomass and the body condition of short-tailed shearwaters in the Bering Sea: can fish compete with seabirds? *Proc. R. Soc. B Biol. Sci.* **278**: 2584–2590. doi:10.1098/rspb.2010.2345.
- Tsuda, A., Saito, H., and Kasai, H. 2004. Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Copepoda: Calanoida) in the western subarctic Pacific Ocean. *Fish. Oceanogr.* **13**: 10–20. doi:10.1111/j.1365-2419.2004.00315.x.
- Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E., Wallace, C., Teel, D.J., Crawford, W., Farley, E.V., Jr., and Beacham, T.D. 2009. Seasonal stock-specific migrations of juvenile sockeye salmon along the west coast of North America: implications for growth. *Trans. Am. Fish. Soc.* **138**: 1458–1480. doi:10.1577/T08-211.1.
- Warton, D.I., and Hui, F.K. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, **92**: 3–10. doi:10.1890/10-0340.1. PMID:21560670.
- Welch, D.W., Melnychuk, M.C., Payne, J.C., Rechisky, E.L., Porter, A.D., Jackson, G.D., Ward, B.R., Vincent, S.P., Wood, C.C., and Semmens, J. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc. Natl. Acad. Sci.* **108**: 8708–8713. doi:10.1073/pnas.1014044108. PMID:21558442.
- Wells, B.K., Grimes, C.B., and Waldvogel, J.B. 2007. Quantifying the effects of wind, upwelling, curl, turbulence, sea surface temperature and sea level height on growth and maturation of a California Chinook salmon (*Oncorhynchus tshawytscha*) population. *Fish. Oceanogr.* **16**: 363–382. doi:10.1111/j.1365-2419.2007.00437.x.
- Wertheimer, A.C., Heard, W.R., Maselko, J.M., and Smoker, W.W. 2004. Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter? *Rev. Fish Biol. Fish.* **14**: 321–334. doi:10.1007/s11160-004-2942-4.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York.

Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean

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Supplementary tables

These supplementary tables provide model selection summaries and parameter estimates for models fit to the raw data without time trends removed (S1a, b), models that only considered North American pink and sockeye abundance (raw data: S2a, b; de-trended data: S3a, b) and models that included additional hypotheses (raw data: 4a, b; de-trended data: S5a, b). A correlation matrix of all independent variables used in the main and sensitivity analyses is shown in Table S6.

Table S1a. Summary of model selection statistics for analyses of hypotheses related to interactions between pink and sockeye salmon using data **without linear time trends removed**. The dependent variable in each hypothesis is denoted by “Variable” and includes sockeye productivity ($\log_e[\text{recruits/spawner}]$), the average standardized length of four-year old male and female sockeye on the spawning grounds and the proportion of total recruits from a given brood year that spent three years in the ocean. Terms in the hypotheses (Model) are **North Pacific** pink salmon abundance (P_{t+4}) lagged by four years from the corresponding sockeye brood year to reflect the abundance of potential pink salmon competitors in the second sockeye growing season at sea, Northeast Pacific pink salmon abundance (P_{t+3}) lagged by 3 years to reflect the abundance of potential pink salmon competitors in the first sockeye growing season at sea and **North Pacific** sockeye salmon abundance (Sx_{t+4}) lagged by 4 years to reflect the number of potential conspecific competitors in the second and third sockeye growing season at sea. $P_{predators}$ is the abundance of potential pink salmon predators returning to the coast in the year sockeye smolts enter the marine environment. Each set of hypotheses is ordered by small-sample Akaike Information Criterion (AIC_c). Also shown are the log likelihoods (LL), differences in AIC_c from the AIC_c of the top model (ΔAIC_c), and Akaike model weights (w_i).

Hypothesis	Model	LL	Δ AICc	Weight
1. Productivity	P_{t+4}	-1704.67	0.00	0.51
	$P_{t+4} + P_{t+3}$	-1704.43	1.68	0.22
	$P_{t+4} + Sx_{t+4}$	-1704.59	2.00	0.19
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-1704.38	3.74	0.08
	Sx_{t+4}	-1710.72	12.10	0.00
	$P_{t+3} + Sx_{t+4}$	-1710.50	13.81	0.00
	P_{t+3}	-1712.95	16.56	0.00
	null	-1714.07	16.64	0.00
2. Std. fork length (males)	Sx_{t+4}	-434.61	0.00	0.38
	$P_{t+4} + Sx_{t+4}$	-433.94	0.82	0.25
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-433.23	1.57	0.17
	$P_{t+3} + Sx_{t+4}$	-434.32	1.59	0.17
	P_{t+4}	-438.03	6.84	0.01
	$P_{t+4} + P_{t+3}$	-438.02	8.99	0.00
	P_{t+3}	-441.44	13.66	0.00
	null	-442.94	14.51	0.00
2. Std. fork length (females)	Sx_{t+4}	-426.03	0.00	0.52
	$P_{t+4} + Sx_{t+4}$	-425.91	1.93	0.20
	$P_{t+3} + Sx_{t+4}$	-425.93	1.97	0.19
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-425.71	3.70	0.08
	P_{t+4}	-430.72	9.38	0.01
	$P_{t+4} + P_{t+3}$	-430.39	10.88	0.00
	P_{t+3}	-431.90	11.73	0.00
	null	-434.24	14.28	0.00
3. Proportion ocean-age-3 recruits	P_{t+4}	-103.99	0.00	0.43
	$P_{t+4} + P_{t+3}$	-103.56	1.25	0.23
	$P_{t+3} + Sx_{t+4}$	-104.07	2.27	0.14
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-103.44	3.12	0.09
	P_{t+3}	-105.83	3.69	0.07
	$P_{t+4} + Sx_{t+4}$	-105.66	5.44	0.03
	null	-108.08	6.08	0.02
	Sx_{t+4}	-108.90	9.82	0.00
4. Productivity (predators)	null	-1715.23	0.00	1
	$P_{predators}$	-1714.33	12.05	0

Table S1b. Multimodel averaged parameter estimates, unconditional standard error (SE) and relative variable importance (RVI) of parameters appearing in the hypotheses in Table S1a. Parameters include the abundance of potential **North Pacific** pink salmon competitors in the first (P_{t+3}) and second and third sockeye growing season at sea (P_{t+4}) and well as the number of **North Pacific** potential conspecific competitors in the second and third sockeye growing season at sea (S_{t+4}). Parameter estimates were measured in standard deviation units (SDU) on dependent variables with **without linear time trends removed**.

Hypothesis		Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.296	0.063	1.00
	P_{t+3}	-0.034	0.079	0.26
	S_{t+4}	-0.019	0.057	0.27
2. Std. fork length (males)	P_{t+4}	-0.176	0.136	0.43
	P_{t+3}	0.107	0.137	0.34
	S_{t+4}	-0.394	0.101	0.99
2. Std. fork length (females)	P_{t+4}	-0.081	0.136	0.29
	P_{t+3}	0.051	0.141	0.27
	S_{t+4}	-0.400	0.097	0.99
3. Proportion ocean-age-3 recruits	P_{t+4}	0.552	0.227	0.88
	P_{t+3}	0.298	0.246	0.41
	S_{t+4}	0.017	0.303	0.26

Table S2a. Same as Table S1a but based on **North American** pink and sockeye salmon abundance and models fit to data **without linear time trends removed**.

Hypothesis	Model	LL	Δ AICc	Weight
1. Productivity	P_{t+4}	-1705.82	0.00	0.52
	$P_{t+4} + Sx_{t+4}$	-1705.65	1.84	0.21
	$P_{t+4} + P_{t+3}$	-1705.78	2.09	0.18
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-1705.64	3.98	0.07
	Sx_{t+4}	-1709.97	8.31	0.01
	$P_{t+3} + Sx_{t+4}$	-1709.75	10.04	0.00
	P_{t+3}	-1712.27	12.92	0.00
	null	-1713.44	13.10	0.00
2. Std. fork length (males)	Sx_{t+4}	-430.50	0.00	0.52
	$P_{t+3} + Sx_{t+4}$	-430.27	1.70	0.22
	$P_{t+4} + Sx_{t+4}$	-430.49	2.15	0.18
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-430.20	3.74	0.08
	P_{t+4}	-436.73	12.46	0.00
	$P_{t+4} + P_{t+3}$	-436.59	14.36	0.00
	P_{t+3}	-438.13	15.27	0.00
	null	-440.03	16.91	0.00
2. Std. fork length (females)	Sx_{t+4}	-426.29	0.00	0.53
	$P_{t+3} + Sx_{t+4}$	-426.19	1.95	0.20
	$P_{t+4} + Sx_{t+4}$	-426.27	2.13	0.18
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-426.10	3.95	0.07
	P_{t+4}	-431.08	9.58	0.00
	$P_{t+4} + P_{t+3}$	-430.92	11.42	0.00
	P_{t+3}	-432.41	12.23	0.00
	null	-434.79	14.85	0.00
3. Proportion ocean-age-3 recruits	P_{t+4}	-107.08	0.00	0.33
	P_{t+3}	-107.36	0.57	0.25
	$P_{t+4} + P_{t+3}$	-106.64	1.23	0.18
	$P_{t+3} + Sx_{t+4}$	-107.48	2.91	0.08
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-106.57	3.20	0.07
	$P_{t+4} + Sx_{t+4}$	-108.01	3.97	0.05
	null	-110.80	5.35	0.02
	Sx_{t+4}	-109.88	5.61	0.02

Table S2b. Same as Table S1b but based on **North American** pink and sockeye salmon abundance and models fit to data **without linear time trends removed**.

Hypothesis		Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.264	0.065	0.99
	P_{t+3}	-0.069	0.092	0.25
	Sx_{t+4}	-0.019	0.060	0.29
2. Std. fork length (males)	P_{t+4}	-0.027	0.146	0.26
	P_{t+3}	0.087	0.131	0.30
	Sx_{t+4}	-0.413	0.092	1.00
2. Std. fork length (females)	P_{t+4}	-0.054	0.154	0.25
	P_{t+3}	0.054	0.140	0.27
	Sx_{t+4}	-0.409	0.098	1.00
3. Proportion ocean-age-3 recruits	P_{t+4}	0.481	0.223	0.63
	P_{t+3}	0.353	0.245	0.58
	Sx_{t+4}	0.094	0.284	0.21

Table S3a. Same as Table S1a but based on **North American** pink and sockeye salmon abundance and models fit to data **with linear time trends removed**.

Hypothesis	Model	LL	Δ AICc	Weight
1. Productivity	null	-1600.44	0.00	0.22
	P_{t+3}	-1599.55	0.40	0.18
	P_{t+4}	-1599.61	0.51	0.17
	$P_{t+4} + P_{t+3}$	-1598.59	0.62	0.16
	Sx_{t+4}	-1600.33	1.95	0.08
	$P_{t+3} + Sx_{t+4}$	-1599.45	2.35	0.07
	$P_{t+4} + Sx_{t+4}$	-1599.58	2.60	0.06
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-1598.55	2.72	0.06
2. Std. fork length (males)	$P_{t+4} + Sx_{t+4}$	-401.62	0.00	0.51
	Sx_{t+4}	-403.53	1.67	0.22
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-401.58	2.10	0.18
	$P_{t+3} + Sx_{t+4}$	-403.46	3.67	0.08
	P_{t+4}	-412.51	19.63	0.00
	$P_{t+4} + P_{t+3}$	-412.19	21.14	0.00
	null	-418.22	28.89	0.00
	P_{t+3}	-417.62	29.84	0.00
2. Std. fork length (females)	$P_{t+4} + Sx_{t+4}$	-404.15	0.00	0.57
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-403.88	1.64	0.25
	Sx_{t+4}	-406.77	3.07	0.12
	$P_{t+3} + Sx_{t+4}$	-406.38	4.45	0.06
	P_{t+4}	-413.77	17.07	0.00
	$P_{t+4} + P_{t+3}$	-413.14	17.98	0.00
	P_{t+3}	-419.03	27.59	0.00
	null	-420.15	27.68	0.00

Table S3b. Same as Table S1b but based on **North American** pink and sockeye salmon abundance and models fit to data **with linear time trends removed**.

Hypothesis		Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.063	0.047	0.44
	P_{t+3}	0.050	0.037	0.43
	Sx_{t+4}	-0.001	0.002	0.27
2. Std. fork length (males)	P_{t+4}	-0.145	0.074	0.69
	P_{t+3}	-0.026	0.072	0.26
	Sx_{t+4}	-0.386	0.073	1.00
2. Std. fork length (females)	P_{t+4}	-0.177	0.077	0.82
	P_{t+3}	-0.061	0.075	0.31
	Sx_{t+4}	-0.375	0.078	1.00

Table S4a. Same as Table S1a but with additional hypotheses including sea surface temperature anomalies in the winter preceding sockeye marine entry from the 1950-2010 average (SST, in °C), farmed salmon production in 1000s of metric tons (F), and an interaction between farmed salmon production and **North Pacific** pink salmon abundance (*FxP*). All models were fit to data **without linear time trends removed** and only models within 4 Δ AICc of the top model are shown. Each model is as described in equations 1-3 except for the inclusion of the $\delta_{i,j}$ terms because with their inclusion models routinely failed to converge.

Hypothesis	Model	LL	Δ AICc	Weight
1. Productivity	$SST + F + FxP + P_{t+4}$	-1680.36	0.00	0.44
	$SST + F + FxP + P_{t+4} + Sx_{t+4}$	-1680.11	1.65	0.19
	$SST + F + FxP + P_{t+4} + P_{t+3}$	-1680.28	1.99	0.16
	$SST + F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-1679.97	3.54	0.07
2. Std. fork length (males)	$F + P_{t+4} + Sx_{t+4}$	-437.20	0.00	0.18
	Sx_{t+4}	-439.96	1.31	0.09
	$SST + F + P_{t+4} + Sx_{t+4}$	-436.98	1.67	0.08
	$F + FxP + P_{t+4} + Sx_{t+4}$	-437.14	2.00	0.07
	$P_{t+4} + Sx_{t+4}$	-439.26	2.01	0.07
	$F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-437.16	2.03	0.07
	$F + Sx_{t+4}$	-439.38	2.26	0.06
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-438.48	2.56	0.05
	$P_{t+3} + Sx_{t+4}$	-439.64	2.77	0.05
	$SST + Sx_{t+4}$	-439.68	2.84	0.04
	$SST + P_{t+4} + Sx_{t+4}$	-438.95	3.50	0.03

	$SST + F + FxP + P_{t+4} + Sx_{t+4}$	-436.93	3.71	0.03
	$SST + F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-436.98	3.80	0.03
	$SST + F + Sx_{t+4}$	-439.15	3.89	0.03
2. Std. fork length (females)	$F + P_{t+4} + Sx_{t+4}$	-424.76	0.00	0.15
	$F + Sx_{t+4}$	-425.98	0.33	0.12
	Sx_{t+4}	-427.13	0.53	0.11
	$SST + F + P_{t+4} + Sx_{t+4}$	-424.53	1.66	0.06
	$F + FxP + P_{t+4} + Sx_{t+4}$	-424.58	1.76	0.06
	$F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-424.67	1.94	0.06
	$SST + F + Sx_{t+4}$	-425.74	1.95	0.06
	$SST + Sx_{t+4}$	-426.82	2.00	0.05
	$F + P_{t+3} + Sx_{t+4}$	-425.88	2.24	0.05
	$P_{t+3} + Sx_{t+4}$	-427.01	2.38	0.04
	$P_{t+4} + Sx_{t+4}$	-427.02	2.41	0.04
	$SST + F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-424.30	3.33	0.03
	$SST + F + FxP + P_{t+4} + Sx_{t+4}$	-424.32	3.36	0.03
	$SST + F + P_{t+3} + Sx_{t+4}$	-425.49	3.57	0.02
	$SST + P_{t+4} + Sx_{t+4}$	-426.70	3.88	0.02
	$F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-424.58	3.88	0.02
3. Proportion ocean-age-3 recruits	P_{t+4}	-104.55	0.00	0.38
	$P_{t+4} + P_{t+3}$	-103.85	0.66	0.27
	$F + P_{t+4} + P_{t+3}$	-103.18	1.39	0.19
	$SST + F + P_{t+4} + P_{t+3}$	-103.29	1.61	0.17

Table S4b. Same as Table S1b but with additional parameters for sea surface temperature anomalies from the 1950-2010 average (SST, in °C), farmed salmon production in 1000s of metric tons (F), and an interaction between farmed salmon production and **North Pacific** pink salmon abundance (*FxP*). All models were fit to data **without linear time trends removed**. Note for models pertaining to productivity the SST parameter was estimated separately for populations north and south of the Skeena watershed in Northern BC to allow for opposite responses to SST between the two regions (Mueter et al. 2002).

Hypothesis	Parameter	Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.204	0.053	1.00
	P_{t+3}	-0.021	0.054	0.27
	Sx_{t+4}	0.035	0.046	0.31
	<i>SST (south)</i>	-0.162	0.044	0.99
	<i>SST (north)</i>	0.018	0.073	0.99
	<i>F</i>	-0.076	0.072	0.98
	<i>FxP</i>	-0.123	0.047	0.88
2. Std. fork length (males)	P_{t+4}	-0.263	0.149	0.68
	P_{t+3}	0.062	0.155	0.30
	Sx_{t+4}	-0.348	0.114	0.97
	<i>SST</i>	0.065	0.104	0.30
	<i>F</i>	0.217	0.138	0.62
	<i>FxP</i>	-0.029	0.105	0.14
2. Std. fork length (females)	P_{t+4}	-0.199	0.153	0.52
	P_{t+3}	-0.033	0.168	0.29
	Sx_{t+4}	-0.406	0.115	0.99
	<i>SST</i>	0.080	0.109	0.31
	<i>F</i>	0.228	0.139	0.68
	<i>FxP</i>	0.061	0.110	0.12
3. Proportion ocean-age-3 recruits	P_{t+4}	0.580	0.215	1.00
	P_{t+3}	0.284	0.051	0.62
	Sx_{t+4}	-	-	-
	<i>SST</i>	0.179	0.221	0.17
	<i>F</i>	0.012	0.092	0.36
	<i>FxP</i>	-	-	-

Table S5a. Same as Table S4a but with models fit to data **with linear time trends removed.**

Hypothesis	Model	LL	Δ AICc	Weight
1. Productivity	$SST + P_{t+4} + P_{t+3}$	-1580.20	0.00	0.30
	$SST + P_{t+4} + P_{t+3} + Sx_{t+4}$	-1579.46	0.66	0.21
	$SST + F + P_{t+4} + P_{t+3}$	-1579.88	1.50	0.14
	$SST + F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-1579.10	2.10	0.10
	$SST + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-1579.68	3.27	0.06
	$SST + P_{t+3}$	-1583.17	3.78	0.05
	$SST + F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-1578.86	3.78	0.04
2. Std. fork length (males)	$SST + F + FxP + P_{t+4} + Sx_{t+4}$	-398.57	0.00	0.15
	$F + FxP + P_{t+4} + Sx_{t+4}$	-399.72	0.18	0.14
	$P_{t+4} + Sx_{t+4}$	-401.89	0.29	0.13
	$SST + P_{t+4} + Sx_{t+4}$	-401.35	1.31	0.08
	$SST + F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-398.39	1.79	0.06
	Sx_{t+4}	-403.73	1.89	0.06
	$F + P_{t+4} + Sx_{t+4}$	-401.71	2.04	0.05
	$F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-399.71	2.29	0.05
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-401.85	2.33	0.05
	$SST + F + P_{t+4} + Sx_{t+4}$	-400.86	2.47	0.04
	$SST + Sx_{t+4}$	-403.10	2.72	0.04
	$SST + P_{t+4} + P_{t+3} + Sx_{t+4}$	-401.19	3.12	0.03
	$F + P_{t+4}$	-403.62	3.75	0.02
	$P_{t+3} + Sx_{t+4}$	-403.67	3.85	0.02

2. Std. fork length (females)	$P_{t+4} + Sx_{t+4}$	-404.15	0.00	0.16
	$SST + F + P_{t+4} + Sx_{t+4}$	-402.19	0.30	0.13
	$SST + F + FxP + P_{t+4} + Sx_{t+4}$	-401.29	0.64	0.11
	$SST + P_{t+4} + Sx_{t+4}$	-403.70	1.21	0.08
	$P_{t+4} + P_{t+3} + Sx_{t+4}$	-403.88	1.57	0.07
	$SST + F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-400.73	1.66	0.07
	$F + P_{t+4} + Sx_{t+4}$	-404.05	1.91	0.06
	$F + FxP + P_{t+4} + P_{t+3} + Sx_{t+4}$	-401.97	1.99	0.06
	$SST + P_{t+4} + P_{t+3} + Sx_{t+4}$	-403.19	2.29	0.05
	$SST + P_{t+4} + F + Sx_{t+4}$	-403.40	2.71	0.04
	Sx_{t+4}	-406.77	3.14	0.03
	$F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-403.79	3.51	0.03
	$SST + F + P_{t+4} + P_{t+3} + Sx_{t+4}$	-402.83	3.70	0.02

Table S5b. Same as Table S4b but **with linear time trends removed**. Parameter estimates for sockeye abundance, pink abundance in the first year of marine life and SST are not presented under hypothesis 3 because they were not in the top model set (i.e., within $4 \Delta \text{AICc}$ of the top model).

Hypothesis		Coefficient (in SDU)	SE (in SDU)	RVI
1. Productivity	P_{t+4}	-0.091	0.035	0.91
	P_{t+3}	0.097	0.034	0.95
	Sx_{t+4}	0.042	0.035	0.41
	$SST (south)$	-0.178	0.041	1.00
	$SST (north)$	0.004	0.067	1.00
	F	-0.035	-0.042	0.11
	FxP	-0.029	0.04	0.39
2. Std. fork length (males)	P_{t+4}	-0.132	0.073	0.81
	P_{t+3}	-0.030	0.072	0.28
	Sx_{t+4}	-0.377	0.074	1.00
	SST	0.123	0.092	0.46
	F	-0.028	0.013	0.58
	FxP	0.014	0.020	0.39
2. Std. fork length (females)	P_{t+4}	-0.167	0.077	0.88
	P_{t+3}	-0.067	0.076	0.34
	Sx_{t+4}	-0.364	0.078	1.00
	SST	0.123	0.100	0.43
	F	0.011	0.021	0.56
	FxP	-0.028	0.014	0.37

Table S6. Correlation matrix of all independent variables used in the main and sensitivity analyses of sockeye salmon productivity, length at age, and age at maturity. Correlations below the diagonal are for detrended time series while those above the diagonal are for raw values. Variables include the abundance of adult pink salmon (P_{t+3}) from the Northeast Pacific (Northern BC and Alaska) three years after each sockeye brood year as an index of competitors early in the first year of sockeye marine life, the abundance of adult pink salmon (P_{t+4}) from the North Pacific (BC through Russia) four years after each sockeye brood year as an index of competitors in the second year of sockeye marine life, and the abundance of sockeye salmon (Sx_{t+4}) from the North Pacific (BC through Russia) four years after each sockeye brood year as an index of conspecific competitors in the second and third year of sockeye marine life. Also included are the two additional variables from the sensitivity analyses: sea surface temperature anomaly in the winter preceding juvenile sockeye marine entry (SST), and farmed salmon production along sockeye salmon early marine migration routes (Farm).

	P_{t+3}	P_{t+4}	Sx_{t+4}	SST	Farm
P_{t+3}	-	0.46	0.45	0.38	0.51
P_{t+4}	-0.15	-	0.56	0.24	0.44
Sx_{t+4}	0.12	0.26	-	0.28	0.22
SST	0.33	0.08	0.19	-	0.21
Farm	0.01	0.09	-0.22	-0.08	-