Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics

B. M. Connors[1,2,3], D. C. Braun[3], R.M. Peterman[1], A. B. Cooper[1], J. D. Reynolds[3], L. M. Dill[3], G. T. Ruggerone[4], & M. Krkošek[2,5]

[1] School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
[2] Salmon Coast Field Station, Simoom Sound, BC, V0P 1SO, Canada
[3] Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
[4] Natural Resources Consultants, Seattle, WA, 98199, USA
[5] Department of Zoology, University of Otago, Dunedin, 9016, New Zealand

Abstract

Climate, competition, and disease are well-recognized drivers of population dynamics. These stressors can be intertwined by animal migrations, leading to uncertainty about the roles of natural and anthropogenic factors in conservation and resource management. We quantitatively assessed the four leading hypotheses for an enigmatic long-term decline in productivity of Canada's iconic Fraser River sockeye salmon: (1) delayed density-dependence, (2) local oceanographic conditions, (3) pathogen transmission from farmed salmon, and (4) ocean-basin scale competition with pink salmon. Our findings suggest that the long-term decline is primarily explained by competition with pink salmon, which can be amplified by exposure to farmed salmon early in sockeye marine life, and by a compensatory interaction between coastal ocean temperature and farmed-salmon exposure. These correlative relationships suggest oceanic-scale processes, which are beyond the reach of current regulatory agencies, may exacerbate local ecological processes that challenge the coexistence of fisheries and aquaculture-based economies in coastal seas.

Introduction

Multiple interacting stressors such as climate (Kausrud *et al.* 2008), competition (Hansen *et al.* 1999), and disease (Anderson & May 1980) can be important drivers of the dynamics of animal populations (Folke *et al.* 2004; Ives & Carpenter 2007). Migration may entangle these stressors (Altizer *et al.* 2011), giving rise to "ecological surprises" (Paine *et al.* 1998) that cannot be predicted based on the additive effect of each stressor on its own (Darling & Côté 2008). Such multiple stressors can lead to uncertainty and debate about the influence of natural and anthropogenic factors in maintaining biodiversity, conservation, and resource management (Myers *et al.* 1996; Krkosek 2010).

Sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia, Canada, are one of the most socially, economically, and ecologically important fish stocks in the North Pacific. The productivity (adults produced per spawner) of many Fraser populations has declined since 1990 (Peterman *et al.* 2010; Figure 1), culminating in only 1.5-million adult sockeye returning to all Fraser tributaries in 2009, the lowest in over 50 years. This decline has put immense pressure on aboriginal and commercial fishing communities that depend on these
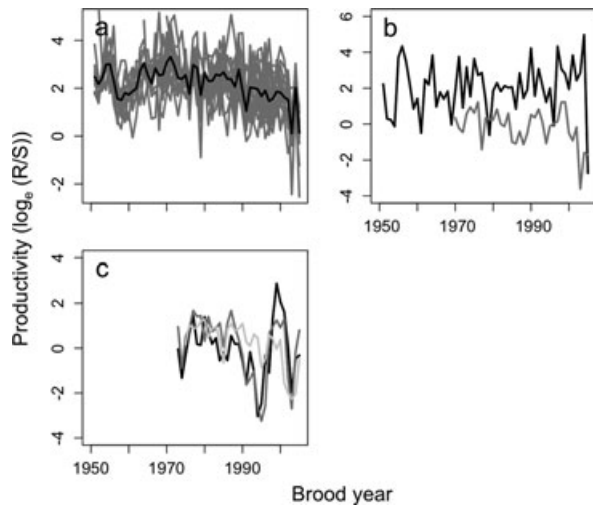
Figure 1 Productivity (log$_e$[adult recruits (R) per spawner (S)]) of Fraser River sockeye salmon populations that migrate up the east coast of Vancouver Island (A) (individual Fraser populations in grey, mean in black), the west coast of Vancouver Island (B) (Harrison in black, Lake Washington in grey), and the central coast of British Columbia (C) (Owikeno Lake in black, Long Lake in grey, Atnarko Lake in light grey), by brood year (year of spawning). Harrison sockeye, which are from the Fraser River, are plotted separately to highlight their anomalous trend in productivity relative to other Fraser populations. For sockeye salmon, adult recruits are the number of adults that return to the coast, as estimated before the onset of fishing. See SI Figure S1 for location of populations and migration routes.

Figure 2 Temporal trends in hypothesized drivers of declining productivity of Fraser River sockeye salmon populations. (A) The total number of spawning Fraser River sockeye salmon from populations included in the analysis, as an index of within-population delayed density dependence. (B) Average coastal sea surface temperature (*SST*) anomaly (from 1950 to 2010 average) in January through May for sockeye populations whose juveniles migrate up the east coast of Vancouver Island (ECVI), those that migrate up the west coast of Vancouver Island (WCVI), and those from the central coast of BC (CC); time series are offset by 2 °C to aid in visual comparison. (C) Production of farmed salmon, as an index of potential pathogen transmission, along early marine migration routes of juvenile sockeye that migrate up ECVI or WCVI. (D) Anomaly (from 1950 to 2009 average) of the sum of adult Russian, Alaskan, and Canadian pink-salmon abundances in the North Pacific Ocean (by return year). See SI sections B–E for sources of data.

fish for food, social, and ceremonial purposes, as well as their livelihoods. The cause(s) of this decline have remained enigmatic, prompting a 2.5-year $25-million judicial inquiry by the Government of Canada beginning in the fall of 2009, known as the Cohen Commission. Returns of adult sockeye to the Fraser in 2010 were some of the most abundant in the last 50 years, further complicating the search for an explanation for the long-term decline.

Many explanations have been proposed for the decline in Fraser sockeye productivity; an independent expert panel identified four key hypotheses, which are expanded upon later (Peterman *et al.* 2010; Figure 2 and Supporting Information (SI) sections A–E): (1) delayed density-dependent processes in fresh water arising from high spawner abundance, (2) coastal oceanographic conditions, (3) pathogens (including transmission from farmed salmon), and (4) interspecific competition with pink salmon (*Oncorhynchus gorbuscha*) in the open ocean. Delayed density-dependent processes, which result from high spawner abundance in one brood year reducing the productivity of subsequent brood years in a given population, have long been hypothesized to maintain the cyclic dominance characteristic (i.e., large changes in abundance during each 4-year period) of many Fraser
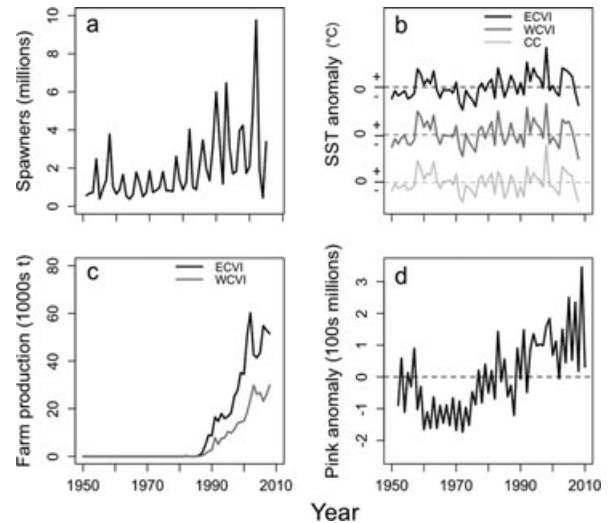
sockeye populations (e.g., Larkin 1971; Myers *et al.* 1997; Martell *et al.* 2008). Management actions that successfully increased the abundance of spawners of Fraser River sockeye (Figure 2A) have therefore led to concerns that delayed density-dependent processes in fresh water, including competition for food and buildup of predator populations (e.g., rainbow trout), may have contributed to depressed productivity of subsequent sockeye generations.

Climate has a well-known influence on salmon productivity (e.g., Mantua *et al.* 1997; Mueter *et al.* 2002a). Coastal sea surface temperature (SST; Figure 2B), a proxy for the biological conditions encountered by salmon soon after entering the ocean, is negatively associated with the productivity of British Columbia sockeye salmon and is a better predictor of productivity than large-scale climate anomalies like the Pacific Decadal Oscillation (Mueter *et al.* 2002a, b; Mueter *et al.* 2005). Increasing marine temperatures may therefore have contributed to declines in sockeye productivity.

A genomic signature, consistent with a response to a virus, is correlated with survival of adults returning to the spawning grounds for some Fraser sockeye populations, but the identity and source of the pathogen is unknown (Miller *et al.* 2010). Disease outbreaks on salmon farms in British Columbia have occurred since the late 1980s (e.g., Kent *et al.* 1990; St-Hilaire *et al.* 2002; Saksida 2006), pathogen transmission from farmed to wild salmon has been demonstrated in other regions of BC and the world (Costello 2009), and reductions in survival and abundance of wild salmonids has been associated with nearby increases in production of farmed salmon in both North American and Europe (Ford & Myers 2008).

Competition in oceanic feeding grounds may have intensified for Fraser sockeye populations, leading to reduced productivity, because of the more than twofold increase in total abundance of some salmon species in the North Pacific since the 1950s (Ruggerone *et al.* 2010). This increase has been primarily driven by pink salmon, which are competitively dominant over other salmon species, leading to altered diet composition, reduced total prey consumption and growth, delayed maturation, and reduced survival of sockeye (Ruggerone & Nielsen 2004).

Here, we report the results of the first quantitative examination of the combined support for these hypotheses for the decline of one of the largest salmon complexes in the world. This study also provides more general lessons about the complexity of interactions between natural and anthropogenic factors influencing population dynamics, with implications for conservation and management.

Methods

Data

We compiled data, from 1950 to present, on the abundance of spawners and returning adults for 18 Fraser sockeye populations and 4 other populations (Figure 1) that differ in their exposure to farmed salmon and oceanographic conditions. We also compiled data with which to test the four hypotheses: (1) the abundance of spawners at 1-, 2-, and 3-year lags as a measure of delayed density-dependent processes (Larkin 1971; Collie & Walters 1987), (2) average regional (2° latitude by 2° longitude) SST from January through May in the year of marine entry as a proxy for the physical and biological oceanographic conditions experienced during early marine life (Mueter *et al.* 2005), (3) farmed-salmon production along early marine migration routes as a proxy for potential exposure to pathogens from farmed salmon (Heuch & Mo 2001; Orr 2007), and (4) the abundance of pink salmon in the North Pacific in the second year of

sockeye marine life as an index of competition for food (Ruggerone & Nielsen 2004; Ruggerone *et al.* 2010).

The model

To examine the support for these hypotheses, we built upon the Ricker model (Ricker 1975)

$$log_e \left[\frac{R_{i,t}}{S_{i,t}} \right] = \alpha - b_i S_{i,t} + \varepsilon_{i,t}, \qquad \varepsilon \sim N(0, \sigma^2). \quad (1)$$

where $S_{i,t}$ is spawner abundance for population i in the year of spawning (brood year, t), $R_{i,t}$ is the abundance of adult recruits (i.e., adults that return to the coast, as estimated before the onset of fishing) of all ages resulting from those spawners, α is productivity at low-spawner abundance, b_i is the magnitude of within-population and within-brood-year density dependence, and $\varepsilon_{i,t}$ is residual error.

We added terms for each hypothesis considered, as well as interactions among SST, farmed-salmon production, and pink-salmon abundance because these factors are likely to act in concert and their effects may be synergistic or antagonistic (Peterman *et al.* 2010), for a total of 36 candidate hypotheses. The full model (i.e., all hypotheses considered) was:

$$\begin{aligned} log_e \left[\frac{R_{i,t}}{S_{i,t}} \right] = & \alpha - b_i S_{i,t} - b1_i S_{i,t-1} \\ & - b2_i S_{i,t-2} - b3_i S_{i,t-3} + \delta sst_{i,t+2} \\ & + \gamma farm_{i,t+2} + \varphi pink_{i,t+4} \\ & + \phi(sst_{i,t+2} \bullet farm_{i,t+2}) + \lambda(sst_{i,t+2} \bullet pink_{i,t+4}) \\ & + \psi(farm_{i,t+2} \bullet pink_{i,t+4}) \\ & + \varepsilon_{i,t}, \varepsilon \sim N(0, \sigma^2). \end{aligned} \quad (2)$$

where $b1$, $b2$, and $b3$ are delayed density-dependent effects at lags of 1, 2, and 3 years, δ is the effect of SST in the year of marine entry, γ is the effect of aquaculture production in the year of marine entry, φ is the effect of pink-salmon recruit abundance in the second year of sockeye marine life (except for Harrison River fish, which are in their third year of marine life) and φ, λ, and ψ are the effects of interactions between SST and farmed-salmon production, SST and pink-salmon abundance, and farmed-salmon production and pink-salmon abundance, respectively. SST and aquaculture values for Harrison River sockeye were lagged by 1 year instead of 2 to account for their earlier marine entry.

To account for nonindependence of observations among populations at the scale at which the independent variables were measured (i.e., year and region as identified in Table S1), equation 2 was modified to include

crossed random effects (Baayen *et al.* 2008)

$$log_e \left[\frac{R_{i,t}}{S_{i,t}} \right] = (\alpha + \theta_i + \theta_t + \theta_{t,r})$$
$$- b_i S_{i,t} - b1_i S_{i,t-1} - b2_i S_{i,t-2} - b3_i S_{i,t-3}$$
$$+ \delta sst_{i,t+2} + \gamma farm_{i,t+2}$$
$$+ \phi pink_{i,t+4} + \varphi(sst_{i,t+2} \bullet farm_{i,t+2})$$
$$+ \lambda(sst_{i,t+2} \bullet pink_{i,t+4})$$
$$+ \psi(farm_{i,t+2} \bullet pink_{i,t+4}) + \varepsilon_{i,t},$$

$$\varepsilon \sim N(0, \sigma^2), \theta_i \sim N(0, \sigma_i^2), \theta_t \sim N(0, \sigma_t^2), \theta_{t,r} \sim N(0, \sigma_{t,r}^2),$$

(3)

where θ_i, θ_t, and $\theta_{t,r}$ are intrinsic variation in productivity among populations, common to all populations among years, and among regions and years, respectively.

Data analysis

We fixed the random effects structure a priori (i.e., Equation 3) to account for the nonindependence of observations among populations at the scale at which the independent variables were measured. Models describing the hypotheses were fit to the data using maximum likelihood. To account for model uncertainty, we calculated small-sample Akaike Information Criterion (AIC$_c$) differences from the AIC$_c$ of the top model and all other models and then generated a top model set consisting of models with substantial support (i.e., ΔAIC$_c$ < 4) (Burnham & Anderson 2004) which corresponded to ~80% confidence model set for our baseline analysis. To compare the relative effect sizes of variables, we standardized our data (subtracted the mean and divided by the standard deviation). Parameter estimates from the top model set were reestimated using restricted maximum likelihood (Bolker *et al.* 2008) and averaged across the models in the top model set according to the "zero method" (Burnham & Anderson 2002).

We based our inference about the importance of the hypothesized drivers of sockeye dynamics on three lines of evidence: (1) the relative variable importance (RVI) of each hypothesis, i.e., the sum of the Akaike model weights of all models in the top model set in which the variable for the hypothesis occurred (Burnham & Anderson 2002), (2) the sign, magnitude, and uncertainty in the multimodel averaged parameter estimates representing each hypothesis in standard deviation units, and (3) the extent to which the hypothesized variables explained the decline in average productivity in Fraser sockeye salmon since 1990, as quantified by the root mean square error (RMSE) between mean observed and predicted (as described below) Fraser sockeye productivity.

Table 1 Model selection statistics for analyses of hypotheses for declines in productivity of Fraser River sockeye salmon. Hypotheses shown are those within four small-sample Akaike Information Criterion (AIC$_c$) units of the top model, ordered by ΔAIC$_c$. Terms in the hypotheses are farmed-salmon production in 1,000s of metric tons (*farm*), pink-salmon abundance anomalies in millions (*pink*), and sea surface temperature anomalies (*SST*, in °C). Also shown are the log likelihoods, differences from the best model AIC$_c$ (ΔAIC$_c$), and Akaike model weights renormalized to the top model set (w_i). All hypotheses included within-population and within-brood-year density dependence, and hypotheses with interactions included lower order main effects (e.g., "*SST* × *pink*" signifies a model that includes an interaction between *SST* and *pink* as well as single variables for *SST* and *pink*), as well as random effects for populations, year, and region within year.

#	Hypothesis	Log Lik.	ΔAICc	w_i
1	(*pink* × *farm*) + (*SST* × *farm*)	−1295.14	0.00	0.38
2	*SST* + (*pink* × *farm*)	−1297.04	1.66	0.17
3	(*pink* × *farm*) + (*SST* × *pink*) + (*SST* × *farm*)	−1295.10	2.07	0.13
4	*pink* + (*SST* × *farm*)	−1297.25	2.08	0.13
5	*SST* + *pink*	−1299.59	2.50	0.11
6	(*pink* × *farm*) + (*SST* × *pink*)	−1296.87	3.46	0.08

To predict Fraser sockeye productivity, a hierarchical simulation was implemented to accommodate model and parameter uncertainty. In each of 10,000 iterations, a model was randomly selected from the top model set with a probability equal to its Akaike weight. Then a random set of parameter values was drawn from a multivariate normal sampling distribution for the parameters and their variance–covariance matrix, as estimated when the model was initially fit to the data. Parameter values were then multiplied by the value of the corresponding covariates to predict productivity under the conditions experienced by a given brood year. Population-specific, region-specific, and year-specific deviations in intrinsic productivity (i.e., random effects), as estimated during the initial fitting process, were added to annual population-specific productivity. This was repeated for each population in the Fraser River that is assumed to migrate up the east coast of Vancouver Island (ECVI; populations 1–17 in Table S1). Mean and empirical 95% confidence intervals were calculated based on the sampling distribution generated by the simulation in each year and were compared to mean observed productivity to calculate RMSE.

Variation in the independent variables occurs at distinct short and long temporal scales. Specifically, SST varies at decadal and annual scales, salmon aquaculture production shows a systematic increasing trend, and pink-salmon abundance, although also systematically increasing, also has distinct 2-year cycles (Figure 2D). To examine the relative influence of the different scales at which the independent variables varied, we reran our analyses after removing linear time trends in the

Table 2 Multimodel averaged parameter estimates, unconditional standard errors (SE), and relative variable importance (RVI) of parameters appearing in the top set of hypotheses (Table 1). Productivity ($\log_e$[adult recruits (R) per spawner (S)]) at low spawner abundance is α and variables are farmed-salmon production (*farm*), pink-salmon abundance (*pink*), sea surface temperature (*SST*), and their interactions. All parameters were estimated in standard deviation units (SDU) to permit meaningful comparisons because the independent variables are on different numerical scales. For example, the −0.249 parameter estimate for pink-salmon abundance means that a 1 SDU increase in pink-salmon abundance results in a reduction of 0.249$\log_e$(adult recruits (R) per spawner (S)), or 1.28 recruits/spawner.

	Coefficient (in SDU)	SE (in SDU)	RVI
α	2.090	0.180	—
farm	0.004	0.094	0.89
pink	−0.249	0.077	1.00
SST	−0.135	0.063	1.00
pink × *farm*	−0.113	0.088	0.75
SST × *farm*	0.093	0.088	0.65
SST × *pink*	0.001	0.015	0.20

independent and dependent variables. We also examined the sensitivity of our analyses to different assumptions about sockeye migration routes, exposure to salmon farms, and omission of enhanced pink salmon, Russian pink salmon, and particular sockeye salmon populations (SI section F).

Collinearity among independent variables was examined using variance inflation factors (VIF; Zuur *et al.* 2009). Correlations ranged from 0.22 to 0.54 (Table S5) and all independent variables had VIF scores <3, which suggests that correlations between the independent variables did not substantially inflate the standard errors of our parameter estimates (Zuur *et al.* 2010). All analyses were performed in *R* (R 2011) using the lme4, MuMIn, mvtnorm, arm, and snowfall packages.

Results

Pink-salmon abundance was estimated to have the strongest negative influence on sockeye productivity of the hypotheses considered and appeared in all models in the top model set (Tables 1 and 2). Accounting for the influence of pink-salmon abundance alone improved our ability to predict the observed decline in Fraser sockeye productivity since 1990 by 33% (percentage change in RMSE for "baseline" dataset in Table S3) relative to a null model of sockeye dynamics (Figure 3A). Accounting for pink-salmon abundance also improved our ability to predict the decline by 23% relative to a model with just the individual effects of SST and farmed-salmon production (compare Figure 3C to B).

SST was also negatively associated with sockeye productivity and appeared in all models in the top model set (Tables 1 and 2). Although our analysis confirms that SST is an important determinant of year-to-year variation in sockeye productivity, SST on its own had little influence on the observed decline in Fraser sockeye productivity since the beginning of the decline. Specifically, relative to a null model of sockeye dynamics, a model that accounted for the influence of SST alone did not reduce RMSE between observed and predicted Fraser sockeye productivity since 1990 (baseline case in Table S3).

Farmed-salmon production appeared in 5 of 6 models in the top model set (Table 1; RVI of 0.89 in Table 2), but the estimated effect of farmed-salmon production at average SST and pink-salmon abundance by itself was essentially zero (i.e., two orders of magnitude smaller than the other main effects; Table 2). As a result, accounting for the influence of farmed-salmon production on its own did not improve our ability to predict the observed decline in Fraser sockeye productivity since 1990 (Table S3).

Though others have found statistical support for across-brood-year delayed density dependence in some of the populations we considered when examined individually (e.g., Martell *et al.* 2008), in the multipopulation approach we have taken, we did not find support for an effect of delayed density dependence on sockeye salmon productivity. Models that included delayed density dependence did not appear in the top set of multipopulation hierarchical models (Table 1).

The combined influence of exposure to farmed salmon during early marine life and competition with pink salmon in the North Pacific later in marine life was greater than the sum of their individual effects (i.e., there was support for a term that estimated a combined synergistic effect in addition to their individual main effects). This farmed-salmon-by-pink-salmon interaction (Table 1) occurred in 4 of 6 models in the top model set (RVI of 0.75) and was negatively associated with sockeye productivity (Table 2). Accounting for this interaction between pink-salmon abundance and farmed-salmon production improved our ability to predict Fraser sockeye productivity since 1990 by 28% relative to a model with just the single effects of SST, farmed-salmon production, and pink-salmon abundance (compare Figure 3D to C).

Conversely, the combined influence of exposure to farmed salmon and SST during early marine life was less than the sum of their individual effects (i.e., there was support for a term that estimated a combined antagonistic effect in addition the their main effects). This farmed-salmon-by-SST interaction (Table 1) occurred in 3 of 6 models in the top model set (RVI of 0.65) and was positively associated with sockeye productivity (Table 2). This interaction improved our ability to predict Fraser sock-
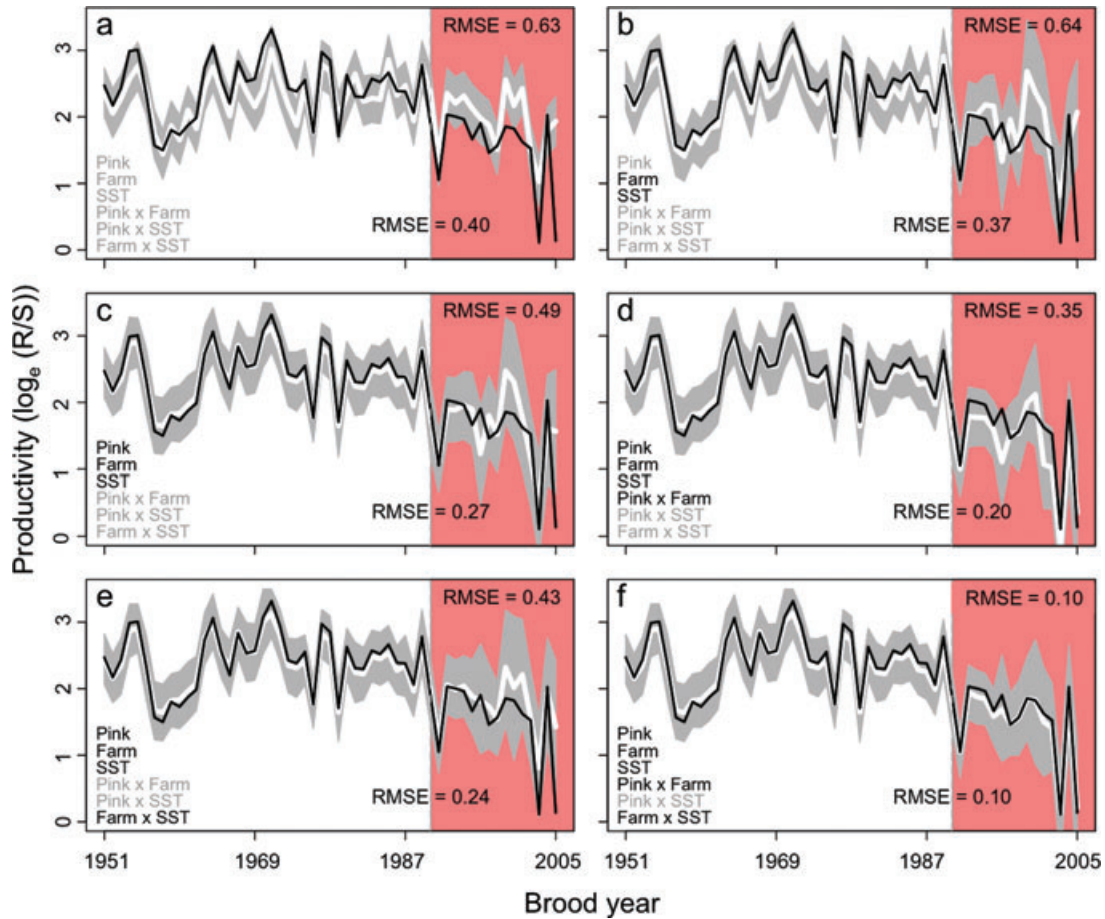
Figure 3 Observed (solid black line) versus predicted (solid white line with 95% confidence intervals in grey) Fraser River sockeye salmon productivity, in units of $\log_e$(adult recruits (*R*) per spawner (*S*)). Each panel (a–f) is based on a given combination of hypothesized drivers of sockeye dynamics, including sea surface temperature (*SST*), farmed-salmon production (*farm*), pink-salmon abundance (*pink*), and their interactions (see Methods for details of simulations to predict productivity). Predicted productivity in each panel is based on the terms that appear in black in legends, as well as within-population and within-brood-year density dependence. The root mean square error (RMSE) between observed and predicted productivity under each scenario is presented for the entire time series (bottom center right in each plot) and for the period since the decline in average Fraser sockeye productivity began in 1990 (red shading, top right in each plot). For the RMSE of all possible variable combinations, as well as for the sensitivity analyses, see SI Table 3. Note the *y*-axis is in $\log_e$ units; for example, the decline in observed $\log_e$(adult recruits (*R*) per spawner (*S*)) from 2.78 in 1989 to 0.14 in 2005 is equivalent to a decline from ∼16.1 recruits per spawner to ∼1.2 recruits per spawner.

eye productivity since 1990 by 12% relative to a model with just the main effects of SST, farmed-salmon production, and pink-salmon abundance (compare Figure 3E to C).

Together, these two interactions (i.e., SST and pink-salmon abundance with farmed-salmon production) improved our ability to predict the decline in Fraser sockeye productivity since 1990 by 84% relative to the null model of sockeye dynamics (compare Figure 3F to A). Although an interaction between pink-salmon abundance and SST appeared in the top set of models, its RVI was less than one-third of the RVI of the other variables, and its predicted effect on productivity was extremely weak (Table 2).

Although the RVI and magnitude of the standardized coefficients did vary under alternate analyses, our main finding (that accounting for the interaction between farmed-salmon production and pink-salmon abundance improved our ability to predict the decline in Fraser sockeye) is robust to assumptions about sockeye migration routes, exposure to salmon farms, and omission of enhanced pink and sockeye salmon populations (SI section F and Tables S2–S4). In contrast, when the contribution of Russian pink salmon to the index of pink salmon competitors was removed (Russian pink salmon are ∼65% of total pink-salmon abundance from 1952 to 2010), accounting for the interaction between pink-salmon abundance and farmed-salmon production

barely improved our ability to predict the decline in Fraser sockeye (SI section F and Tables S2–S4). Whereas long-term variation in SST, pink-salmon abundance and farmed-salmon production were associated with long-term variation in sockeye productivity, only short-term variation in SST and pink-salmon abundance were associated with short-term year-to-year variation in sockeye productivity (SI section G).

Data on individual Fraser sockeye populations that returned in large numbers from the 2006 brood year were unavailable at the time of writing. However, the mean total Fraser sockeye salmon productivity observed from the 2006 brood year ($2.60\log_e$[adult recruits (R) per spawner (S)]), which was available, falls within the 95% CIs of predicted mean productivity based on our formal analyses ($1.83\log_e$[adult recruits (R) per spawner (S)]; 95% CIs: 0.67–2.92; SI section H).

Discussion

Our analyses suggest that a multifactorial and nonadditive complex of processes influence the dynamics of Fraser sockeye. Specifically, our findings indicate that (1) ocean-basin scale competition with pink salmon may reduce sockeye productivity, (2) the negative influence of competition with pink salmon increases with increased numbers of farmed salmon that wild sockeye migrate past early in marine life, and (3) the negative influence of warm marine waters on sockeye productivity is reduced with increased numbers of farmed salmon that wild sockeye migrate past. These results suggest that the consequences of exposure to farmed salmon are mediated by the state of the ecosystem (i.e., abundance of competitors or water temperature) such that they are not readily detectable if only examined on their own.

A possible mechanism for the synergistic interaction between salmon-farm exposure and pink-salmon abundance is that juvenile sockeye that are exposed to pathogens early in marine life are less able to compete for resources with pink salmon later in marine life. Alternatively, reduced food availability from competition with pink salmon may lead to disease expression in sockeye that are infected but not diseased. The antagonistic interaction between exposure to farmed salmon and oceanographic conditions during early marine life suggests that the effects of warmer SST and exposure to farmed salmon production on sockeye productivity may be compensatory whereby some sockeye that die because of poor ocean conditions would have died because of disease, and vice versa, but not because of both.

Our analyses are correlative and are not necessarily evidence of causal mechanisms. Other unmeasured factors that occur at the same temporal and spatial scales may confound the relationships we have quantified. Therefore, our findings are an important first step towards understanding the factors that influence variation in sockeye productivity, which provides a foundation upon which further research into underlying mechanisms can be based. The temporal scale at which the relationships we describe were observed highlight that while both short- and long-term variation in SST and pink-salmon abundance are associated with variation in sockeye productivity, it is primarily the long-term (and not short-term) variation in farmed salmon production that is associated with sockeye productivity. This suggests that the long-term changes in the number of farmed salmon (and potential pathogen transmission from them) may be driving the relationship between sockeye productivity and farmed-salmon production. In addition, the sensitivity of the pink by farmed salmon interaction to the inclusion of Russian pink salmon highlights the important role of pink salmon from Russia in the relationships we have quantified.

Current levels and continued expansion of open net pen aquaculture in British Columbia and around the world is a topic of intense debate (Ford & Myers 2008; Costello 2009). At the same time, the number of Pacific salmon in the North Pacific is increasing, in part because of artificial propagation in hatcheries (Ruggerone *et al.* 2010). Our findings (1) argue for large-scale experimental manipulation of farmed-salmon production coupled with increased understanding of the spatial and temporal distribution of pathogens in wild and farmed salmon to more definitively assess the effects of salmon aquaculture on sockeye salmon, (2) identify a need for multinational regulatory processes among conservation and fishery agencies to manage finite salmon resources at an oceanic scale (Peterman 1984; Holt *et al.* 2008), and (3) suggest policies designed to minimize interactions among farmed, hatchery, and wild fish to improve wild salmon productivity.

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References

Altizer, S., Bartel R. & Han B.A. (2011). Animal migration and infectious disease risk. *Science*, **331**, 296-302.

Anderson, R.M. & May R.M. (1980). Infectious disease and population cycels of forest insects. *Science*, **210**, 658-661.

Baayen, R.H., Davidson D.J. & Bates D.M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *J. Mem. Lang.*, **59**, 390-412.

Bolker, B.M., Brooks M.E., Clark C.J., *et al*. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *TREE*, **24**, 127-135.

Burnham, K.P. & Anderson D.R. (2002). *Model selection and multimodel inference*. Springer, New York.

Burnham, K.P. & Anderson D.R. (2004). Multimodel inference—understanding AIC and BIC in model selection. *Socio. Meth. Research*, **33**, 261-304.

Collie, J.S. & Walters C.J. (1987). Alternative recruitment models of Adams river sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish Aquat. Sci.*, **44**, 1551-1561.

Costello, M.J. (2009). How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc. R. Soc. Lond. B* **276**, 3385-3394.

Darling, E.S. & Côté I.M. (2008). Quantifying the evidence for ecological synergies. *Ecol. Lett.* **11**, 1278-1286.

Folke, C., Carpenter S., Walker B., *et al*. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. S.*, **35**, 557-581.

Ford, J.S. & Myers R.A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biol.*, **6**, 411-417.

Hansen, T.F., Stenseth N.C., Henttonen H. & Tast J. (1999). Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. *Proc. Natl. Acad. Sci. USA*, **96**, 986-991.

Heuch, P.A. & Mo T.A. (2001). A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. *Dis. Aquat. Org.*, **45**, 145-152.

Holt, C.A., Rutherford M.B. & 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.

Ives, A.R. & Carpenter S.R. (2007). Stability and diversity of ecosystems. *Science*, **317**, 58-62.

Kausrud, K.L., Mysterud A., Steen H., *et al*. (2008). Linking climate change to lemming cycles. *Nature*, **456**, 93-97.

Kent, M.L., Groff J.M., Traxler G.S., Zinkl J.G. & Bagshaw J.W. (1990). Plasmacytoid leukemia in seawater reared Chinook salmon *Oncorhynchus tshawytscha*. *Dis. Aquat. Org.*, **8**, 199-209.

Krkosek, M. (2010). Sea lice and salmon in Pacific Canada: ecology and policy. *Front Ecol. Environ.*, **8**, 201-209.

Larkin, P.A. (1971). Simulation studies of Adams river Sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Brd. Canada*, **28**, 1493-1502.

Mantua, N.J., Hare S.R., Zhang Y., Wallace J.M. & Francis R.C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *B. Am. Meteorol. Soc.*, **78**, 1069-1079.

Martell, S.J.D., Walters C.J. & Hilborn R. (2008). Retrospective analysis of harvest management performance for Bristol Bay and Fraser River sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.*, **65**, 409-424.

Miller, K.M., Li S., Kaukinen K.H., *et al*. (2010). Genomic signature predicts migration and spawning failure in wild Canadian salmon. *Science*, **331**, 214-217.

Mueter, F.J., Peterman R.M. & Pyper 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**, 456-463.

Mueter, F.J., Pyper B.J. & 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.

Mueter, F.J., Ware D.M. & Peterman R.M. (2002b). Spatial correlation patterns in coastal environmental variables and survival rates of Pacific salmon in the Northeast Pacific Ocean. *Fish. Oceanogr.*, **11**, 205-218.

Myers, R.A., Bradford M.J., Bridson J.M. & Mertz G. (1997). Estimating delayed density-dependent mortality in sockeye salmon (*Oncorhynchus nerka*): a meta-analytic approach. *Can. J. Fish. Aquat. Sci.*, **54**, 2449-2462.

Myers, R.A., Hutchings J.A. & Barrowman N.J. (1996). Hypotheses for the decline of cod in the North Atlantic. *Mar. Eco-Prog. Series*, **138**, 293-308.

Orr, C. (2007). Estimated sea louse egg production from Marine Harvest Canada farmed Atlantic salmon in the Broughton Archipelago, British Columbia, 2003–2004. *N. Am. J. Fish. Manag.*, **27**, 187-197.

Paine, R.T., Tegner M.J. & Johnson E.A. (1998). Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535-545.

Peterman, R.M. (1984). Effects of Gulf of Alaska sockeye salmon abundance on survival, body size, growth rate, and age at maturity of British Columbia and Bristol Bay. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1302.

Peterman, R.M., Marmorek D., Beckman B., *et al*. (2010). Synthesis of evidence from a workshop on the decline of Fraser River sockeye. A report to the Pacific Salmon Commission, Vancouver, pp. 158.

R (2011). A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ricker, W.E. (1975). Computation and interpretation of biological statistics of fish populations. Fish Res Brd Canada Bull No. 191.

Ruggerone, G.T. & 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.

Ruggerone, G.T., Peterman R.M., Dorner B. & Myers K.W. (2010). Magnitude and trends in abundance of hatchery and wild pink, chum, and sockeye salmon in the North Pacific Ocean. *Mar. Coast. Fish.: Dynam. Manag. Eco. Sci.*, **2**, 306-328.

Saksida, S.M. (2006). Infectious haematopoietic necrosis epidemic (2001 to 2003) in farmed Atlantic salmon *Salmo salar* in British Columbia. *Dis. Aquat. Org.*, **72**, 213-223.

St-Hilaire, S., Ribble C.S., Stephen C., Anderson E., Kurath G. & Kent M.L. (2002). Epidemiological investigation of infectious hematopoietic necrosis virus in salt water net-pen reared Atlantic salmon in British Columbia, Canada. *Aquaculture*, **212**, 49-67.

Zuur, A.F., Ieno E.N. & Elphick J. (2010). A protocol for data exploration to avoid common statistical problems. *Meth. Ecol. Evo.*, **1**, 3-14.

Zuur, A.F., Ieno E.N., Walker N.J., Saveliev A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York.

Supporting Information

Additional Supporting Information may be found in the online version of this article, including Supplementary Methods and References.

Table S1: Sockeye salmon populations used in the analyses.

Table S2: Summary of model selection statistics for analyses of hypotheses for declines in productivity of Fraser River sockeye salmon, ordered by small-sample Akaike Information Criterion (AIC_c).

Table S3: Root mean square error (RMSE) of mean predicted and observed Fraser River sockeye productivity (for populations that migrate along the ECVI) based on combinations of hypothesized drivers of sockeye dynamics (Hypothesis).

Table S4: Multimodel averaged parameter estimates (coefficient), standard errors (SE), and relative variable importance (RVI) for variables appearing in the top set of hypotheses in SI Table 2 ($\Delta AIC_c < 4$).

Table S5: Correlation matrix of independent variables used in analyses of sockeye salmon productivity.

Figure S1: Map of coastal out migration routes of juvenile sockeye salmon.

Figure S2: Autocorrelation in residuals from the fit of the full model, by population.

Supplementary References